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BATHYSPINULA EXCISA (PHILIPPI, 1844) (BIVALVIA, PROTOBRANCHIA): A WITNESS OF THE PLIO-QUATERNARY HISTORY OF THE DEEP MEDITERRANEAN BENTHOS

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Key-words: Bivalvia, Protobranchia, *Bathyspinula*, "*Spinula*", Bathyal benthos, Palaeoecology, Mediterranean Sea, Plio-Pleistocene.

Riassunto. Bathyspinula excisa (Philippi) è un bivalve nuculoide conosciuto nei depositi batiali plio-pleistocenici del Mediterraneo. Comparsa nel Pliocene medio, questa specie raggiunse un notevole successo durante il Pliocene superiore-Pleistocene inferiore, diventando una delle specie batiali più caratteristiche e dominando le più profonde comunità plio-pleistoceniche a molluschi finora note. Sia la comparsa che la diffusione di questa specie corrispondono ad un generale sviluppo e prosperità del benthos profondo del Mediterraneo. Ritenuta in passato come specie atlantica, a causa dell'errata identificazione di una specie strettamente affine vivente in Atlantico, *Bathyspinula excisa* dovrebbe essere considerata come un probabile paleoendemismo profondo del Mediterraneo, appartenente ad un genere oceanico a distribuzione batiale ed abissale. Il caso di *Bathyspinula excisa* non è isolato, poichè molte specie profonde plio-pleistoceniche del Mediterraneo mostrano strette affinità tassonomiche e morfologiche con specie oceaniche. La loro scomparsa dal Mediterraneo, durante il Pleistocene superiore, sembra segnare il passaggio da un ambiente profondo freddo ad uno "caldo" omotermico: cioè, da un Mediterraneo ampiamente connesso all'Oceano, alla sua attuale condizione di "bacino a soglia".

Abstract. Bathyspinula excisa (Philippi) is a nuculoid bivalve known from the Mediterranean Plio-Pleistocene bathyal deposits. It appeared in the Middle Pliocene and reached great success in the Late Pliocene to the Early Pleistocene, dominating the deepest Plio-Pleistocene molluscan communities so far known. Both the appearance and the spreading of this species correspond to a general development and prosperity of the deep Mediterranen benthos. Regarded in past times as an Atlantic species, because of the misidentification of a closely related Atlantic species, *Bathyspinula excisa* should be considered as a probable deep-water Mediterranean palaeoendemism, belonging to a typical oceanic deep-water genus. The case of *Bathyspinula excisa* is not isolated, since many Plio-Pleistocene deep-sea species from the Mediterranean show close taxonomic and morphologic affinities with living deep oceanic species. Their disappearance from the Mediterranean, during the Late Pleistocene, is referred to the change from a cold deep environment, to a "warm" homothermic one: that is from a widely Ocean-connected Mediterranean Sea, to its present "threshold basin" condition.

Introduction.

There are several arguments to state that the deep Mediterranean benthos underwent sharp changes during the Plio-Quaternary. The main points of the Plio-Quaternary evolution of the deep Mediterranean benthos have been recently outlined by Di Geronimo et al. (in press).

Bathyspinula excisa seems to represent very well such an evolution. It is a nuculoid bivalve that was very common among the bathyal communities of muddy bottoms during the Late Pliocene-Early Pleistocene, being one of the most characteristic species. Nevertheless, *Bathyspinula* does today not occur in the Mediterranean. Considering that it is a typically bathyal and abyssal genus, whose distribution is very wide if not really cosmopolitan, its absence from the Mediterranean is even more striking. It is possible to count *Bathyspinula excisa* among a large number of deep-sea species of the Plio-Pleistocene Mediterranean benthos which are characterized by close taxonomic and morphologic affinities towards living oceanic deep-water species.

This paper will be, then, a contribution to the knowledge of this interesting but poorly known species, and an attempt to "reconstruct" its history and meaning within the evolution of the deep Mediterranean benthos.

Historic review.

Philippi (1844, p. 46) described *Nucula excisa* from the "tertiary" outcrops of Southern Calabria (South Italy). He reported the species from several localities (Fig. 1) and gave a good illustration (pl. 15, fig. 4) of a right valve, without any locality indication for it.

Seguenza (1868, 1870, 1875, 1877a, 1877b, 1879) repeatedly reported this species from the "Pliocene" deposits of the Calabria and Messina area. Relying on information from Jeffreys, he regarded this species as presently living in the Atlantic and absent from the Mediterranean (see Seguenza, 1870).

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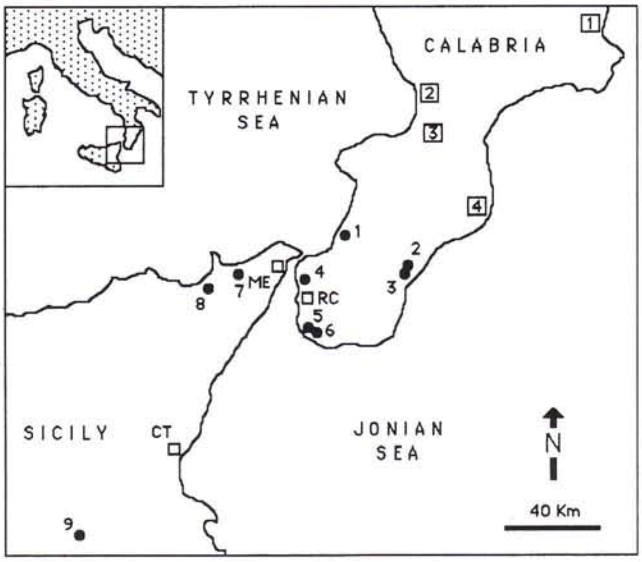

Fig. 1 - Location of the sampled sites (dots): 1 - Palmi (Late Pliocene); 2 - Bovalino Superiore (Early Pleistocene); 3 - Bianco (Early Pleistocene); 4 - Archi (Early Pleistocene); 5 - Lazzàro-Vallone Catrica (Early Pleistocene); 6 - Canale (Early Pleistocene); 7 - Salìce (Early Pleistocene); 8 - Furnari (Early Pleistocene); 9 - Grammichele (Early Pleistocene). Squares indicate the "type-localities" of *Nucula excisa* Philippi, 1844: 1 - Crotone; 2 - Lamato river; 3 - Monterosso Calabro; 4 - Stilo. The main towns in the area are also indicated: RC - Reggio Calabria; ME - Messina; CT - Catania.

Jeffreys (1876, 1879) reported *Malletia excisa* from 1,215-1,443 fathoms off West Ireland, and from the Azores, at 1,125-1,785 fathoms. He noticed some differences between the fossil specimens and the Atlantic ones, as he wrote (1876): "The transverse striae are rather more numerous and close-set in the recent than in fossil specimens". Although Jeffreys very probably had access to fossil specimens sent him by Seguenza, it is important to stress his anti-Darwinian convinctions, which often led him to compare the living species with the fossil ones, neglecting the possible differences (see Warén, 1980). However, *Malletia excisa* particularly attracted his attention, as he (1879) lingered over the meaning of this Atlantic species, as well as of other deep-sea species, among the fossil faunas from Southern Italy ("the communication between the North Atlantic and the Mediterranean must have been formerly very different from now...").

Smith (1885) also reported from the Azores (1,675 fathoms) *Leda excisa*, noticing that "the sinus in the posterior side is not quite so marked in the two valves from this Station as in Philippi's figure". The same record will be later reported by Dautzenberg (1889), without any other remarks.

Dautzenberg & Fischer (1897) recorded *Leda excisa* from the Azores again (1,846 m), stressing the differences already remarked by Smith ("l'énchancrure est bien moins prononcée chez les exemplaires de l'Atlantique que chez la figure de Philippi"). They referred the Atlantic specimens to a new subspecies: *Leda excisa subexcisa*. The same record will be later reported by Dautzenberg (1927).

Locard (1899) also reported *Malletia excisa* from the Atlantic (Gulf of Biscay, 650-960 m). Although a brief description is given, it is ambiguous and species identity is very doubtful. Surely, it does not refer to Philippi's species, since it does not mention any posterior rostrum and concentric sculpture (i.e. the most obvious features of this species). Moreover, depth data are strikingly shallower than those previously reported for the Atlantic records.

The Atlantic specimens referred by Jeffreys to *Malletia excisa*, were examined by Clarke (1961). He compared them with specimens from the South Atlantic (1,510-2,805 fathoms) and referred them to the same species, i.e. to *Spinula subexcisa* (Dautzenberg & Fischer), noticing that it is "so different from the fossil *excisa* that it certainly deserves specific rank".

Further observations about the relationships between the taxa *excisa* and *subexcisa*, as well as about their systematic position, were made by Allen & Sanders (1982). They examined a large number of specimens from about 2,000 m off Ireland (but none from the late 19th century expeditions) and stated the full specific rank of *Spinula subexcisa*. For the first time, that species was illustrated and extensively described. No research, however, has been carried out about *Spinula excisa*, retained as specifically distinct from the former and unkown among the living species.

The specific rank of *Spinula excisa* was remarked by Warén (1989) too. He regarded the *excisa-subexcisa* case as similar to those represented, within the Atlantic-

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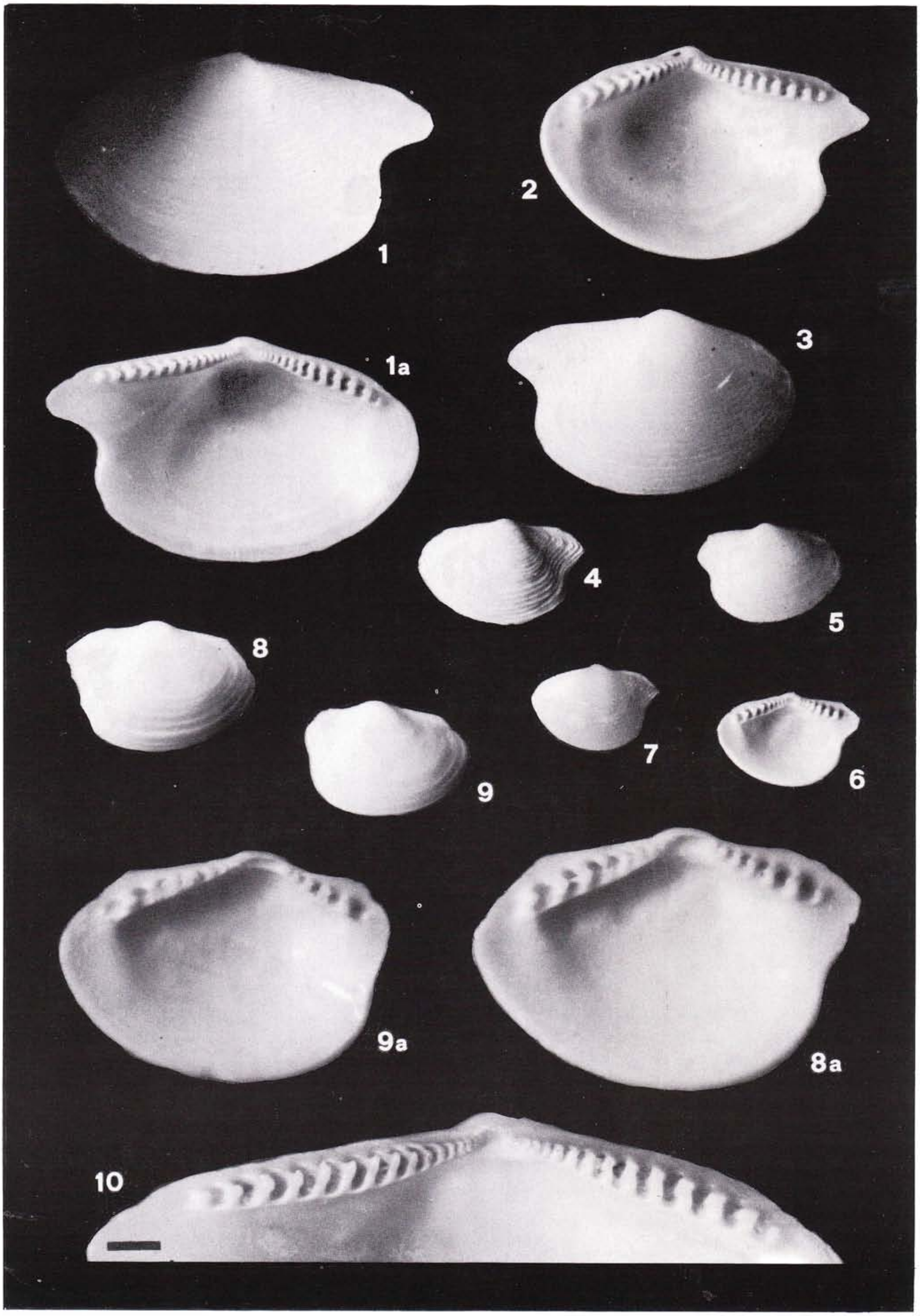
PLATE 1

Bathyspinula (Bathyspinula) excisa (Philippi, 1844).

Fig. 1, 1a - From Bovalino Superiore (Early Pleistocene), 7.2 mm.
Fig. 2 - From Bianco (Early Pleistocene), 6.3 mm.
Fig. 3, 4, 5, 6, 7 - From Furnari (Early Pleistocene), 5.5, 3.2, 2.7, 2.7 and 2.4 mm, respectively.
Fig. 8, 8a, 9, 9a - From Palmi (Late Pliocene), 1.8 and 1.5 mm, respectively. Fig. 8a and 9a are inner enlarged views of fig. 8 and 9.
Fig. 10 - Detail of hinge of specimen in fig. 1, 1a. Scale bar = 500 μm.

Size is expressed as antero-posterior length.


1
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1a
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Mediterranean area, by *Neilonella pusio-striolata* and by *Yoldiella messanensis-acuminata*. The Recent form of each couple, seems to be cronospecifically related to the Plio-Pleistocene one, with which the former has close morphologic affinities.

Morphologic and taxonomic remarks.

Morphology.

Although "*Spinula excisa*" has been recently reported and illustrated (Warén, 1989; Tabanelli, 1993; Palazzi & Villari, 1994), it is still a poorly known species. The only description is the original one and a detailed iconography is still lacking.

Fully adult individuals (Pl. 1, fig. 1-3) have moderately thick and convex valves, subcentral umbo, postero-dorsal margin extending in a prominent rostrum, marked out from ventral margin by a rather deep sinus. Valve surface is rather glossy, crossed by concentric ridges, particularly raised on the posterior side. A microsculpture is also present only on the posterior side (Pl. 2, fig. 1, 1a). It is made up by crowded obliquae striae, becoming parallel to ridges towards the rostrum. Thin, ill-defined and irregular ridges cross radially along the subrostral sinuosity. Rostrum is crossed by a weak keel, extending from umbo to point. Hinge (Pl. 1, fig. 10) is relatively strong, made up by two series of slightly chevron-shaped teeth. Median teeth are well-developed and sharp, whilst the proximal ones are minute and ill-defined. Teeth are up to 28-30 in the largest individuals (9-10 mm in length), the anterior ones being sometimes a little more numerous (1-2) than the posterior ones. Ligament pit is roughly rounded and shallow, slightly creeping under the beak of umbo. Two ligament furrows (nymphae) are externally visible above the hinge: the anterior one extends almost to the middle of tooth series while the posterior one is shorter. Adductor muscle scars are unequal, the anterior one being roughly triangular in shape and 3-4 times larger than the posterior one, which is oval in shape. Pallial line has a well-defined posterior sinus. Larval shell is bean-shaped with a length of 280-350 µm (Pl. 2, fig. 3).

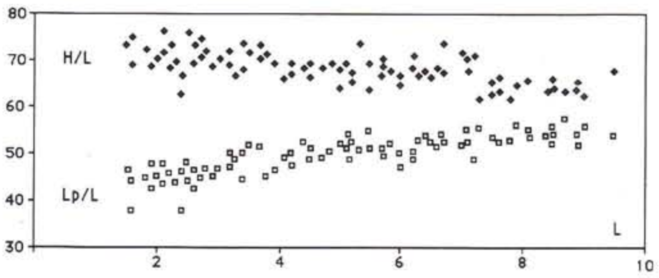

Fig. 2 - Morphologic changes with growth in *Bathyspinula excisa* shown by height to total length (H/L) and posterior length to total length (Lp/L) ratios (per cent) in 100 valves from Upper Pliocene-Lower Pleistocene deposits of the Calabria and Messina area.

Morphologic changes with growth are marked (Fig. 2). In juveniles, smaller than 2-2.5 mm in length (Pl. 1, fig. 8, 9), posterior side is shorter than the anterior one and ventrally expanded; rostrum and sinuosity are only just developed. Concentric sculpture is only present along the postero-ventral margin and sometimes, in even younger individuals, it is quite absent. Ligament pit is long and narrow and only the anterior ligament furrow seems present. During growth, valves become more slender and regularly oval in outline; rostrum becomes prominent and subrostral sinus deeper (Pl. 1, fig. 1-7). Growth of the posterior side (Lp) is linked to the anterior one (La) by an allometric relation, whose pattern is: $Lp=La^{1.266}$. No remarkable morphologic differences have been recorded among populations from different sites. The oldest populations among the examined ones (Late Pliocene) are morphologically equal to the more recent ones (upper part of the Early Pleistocene).

Systematic position.

Originally described (Dall, 1908) as a subgenus of *Leda* (=*Nuculana*), *Spinula* was raised to a genus rank and referred to the family Malletiidae H. & A. Adams, 1858 by Filatova (1958, 1976), who distinguished two subgenera: the typical one, *Spinula* (type-species *Spinula calcar* Dall, 1908) and *Bathyspinula* (type-species *Spinula oceanica* Filatova, 1958). Instead, Allen & Sanders (1982) referred *Spinula* to the family Nuculanidae, *Malletia* being devoid of an inner ligament, and described the new subfamily Spinulinae. They also reported the subgenera *Spinula* and *Bathyspinula*, although they did not treat the subgeneric position of the species. The sy-

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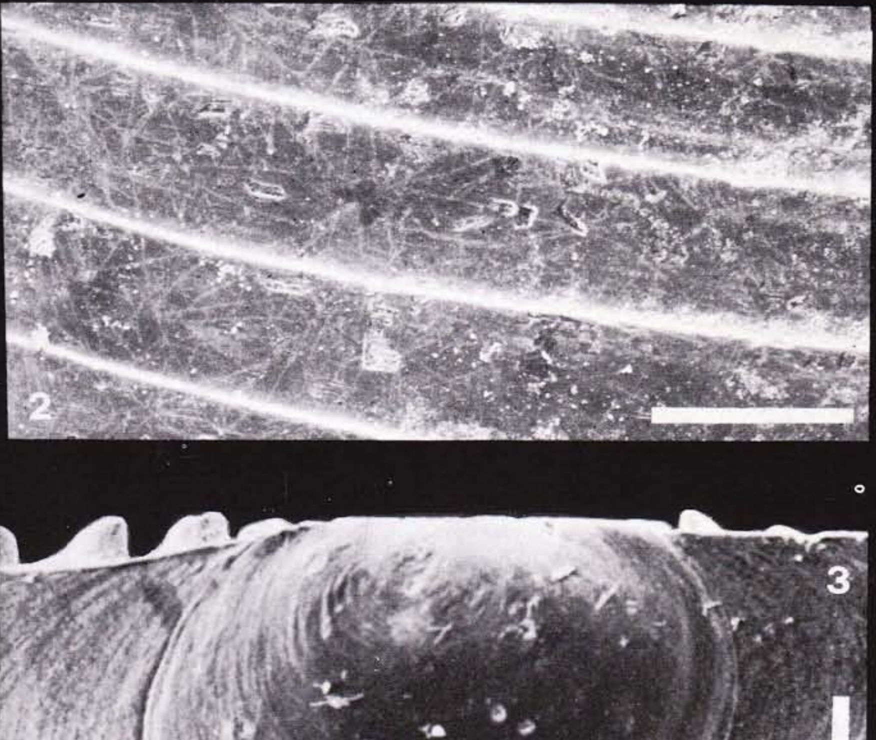
PLATE 2

Bathyspinula (Bathyspinula) excisa (Philippi, 1844).

Fig. 1, 1a	- Details of sculpture on the posterior side (subrostral sinus) in a large specimen from Furnari. Rostrum direction is in correspondence of the upper right corner of fig. 1. Scale bars = 250 µm (fig. 1) and 100 µm (fig. 1a).
Fig. 2	- Detail of sculpture on the anterior end in a large specimen from Furnari. Scale bar = 200 µm.
Fig. 3	- Umbonal view (right-hand side = posterior) of a very young specimen from Palmi. Arrow indicates the metamorphic line between prodissoconch and dissoconch. Scale bar = 200 µm.


1


1a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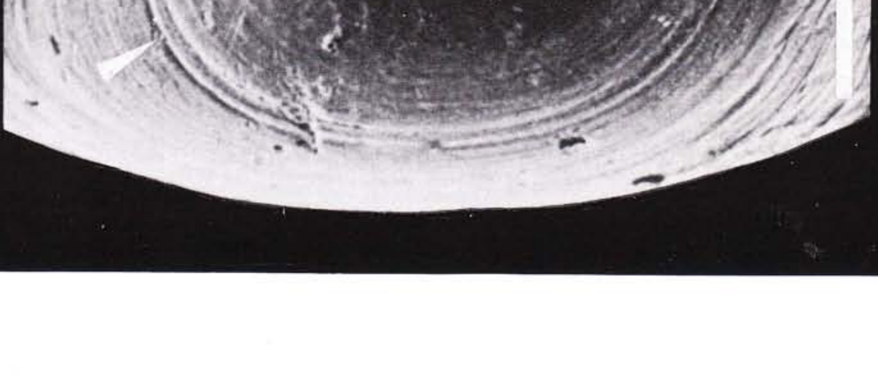
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stematic position of *Spinula* within the Nuculanidae was maintained by Warén (1989), who stressed, with regard to *Spinula excisa*, the presence of a well-developed ligament pit.

Filatova & Schileyko (1984) pointed out the preoccupied status of *Spinula* Dall, 1908 (by *Spinula* Herrich-Schaeffer, 1856). So they replaced it with *Bathyspinula* Filatova, 1958 and proposed *Acutispinula* as a subgeneric rank of *Bathyspinula calcar* (Dall). Filatova & Schileyko (1984) rejected the subfamily Spinulinae and referred *Bathyspinula* to the subfamily Ledellinae Allen & Sanders, 1982, which they raised to a family rank. *Bathyspinula (Acutispinula)* has a rather smooth shell with a slender and sharp rostrum, whereas *Bathyspinula (Bathyspinula)* shows a stronger concentric sculpture and obliquae ridges, in addition to a shorter and blunt rostrum. *Bathyspinula excisa* belongs to *Bathyspinula* s.s., like all the known Atlantic species.

Related species.

The main differences between *Bathyspinula excisa* and *Bathyspinula subexcisa* are those already recorded in past times. The latter has, in fact, a markedly less prominent rostrum and a scarcely incised subrostral sinus. Thus, fully adult individuals of *subexcisa* appear similar in shape to the juvenile ones (2-3 mm) of *excisa*. The maximum shell length recorded for *Bathyspinula subexcisa* are 4.4 mm (Allen & Sanders, 1982), while it is not rare for it to reach 8-9 mm in *Bathyspinula excisa*. According to Allen & Sanders' data, *Bathyspinula subexcisa* does not have a marked rostral keel and its sculpture is thinner and rather crowded (as noticed by Jeffreys); its larval shell is larger, measuring 450 µm. Two other Atlantic species, namely *Bathyspinula scheltemai* and *Bathyspinula hilleri*, are particularly close to *Bathyspinula excisa*. With *excisa* they share the maximum shell size (about 10 mm in length), the shell strength and a well-developed concentric sculpture. Both these species, however, are different from the former in several features (hinge, valve outline, etc.). All these species show growth changes in H:L and Lp:L ratios and in valve outline (see Allen & Sanders, 1982) similar to those recorded for *Bathyspinula excisa*.

Records.

Both the original record and those by Seguenza, who retained this species as typical of the deep-water "Astian" deposits, are today generically referable to the Late Pliocene-Early Pleistocene, as deposits of this age, bearing rich bathyal macrofaunas (Barrier, 1984, 1987; Di Geronimo, 1987; La Perna, 1994), largely outcrop within the Calabria and Messina area. It has been recently reported from this area, among the bathyal molluscan faunas of Early Pleistocene age (Di Geronimo, 1987; Rindone & Vazzana, 1989; Palazzi & Villari, 1994; La Perna, 1994). It is also reported from the Early Pleistocene of the Hyblaean area (Southeastern Sicily) (Di Geronimo, 1979; Di Geronimo et al., 1982; Amore et al., 1985), from the Middle-Late Pliocene of Romagna (Northern Italy) (Padovani & Tampieri, 1970; Taviani, 1975; Marasti & Raffi, 1977; Roveri et al., 1992; Tabanelli, 1993) and from the Late Pliocene of Basilicata (Southern Italy) (Caldara & Garganese, 1990; D'Alessandro & De Marco, 1993). All these records regard deep-sea (bathyal) communities.

Several records of this species are scattered throughout the old paleontological literature about the Italian Plio-Pleistocene faunas, such as those by Monterosato (1872, 1877), Pantanelli (1893), Foresti (1895), Sangiorgi (1928), De Fiore (1937) and Lipparini et al. (1955). Even in these cases, it is possible to recognize *Bathyspinula excisa* as belonging to deep-sea communities, on the grounds of the faunal lists reported.

"*Malletia (Neilo) excisa*" is also reported by Glibert & Van De Poel (1965) among their large inventory of European fossil bivalves, with only the following remarks: "Sicilien - Gerace, Lamato (Calabre, Italie). Messina (Sicile)".

Di Geronimo & Bellagamba (1986) found some valves of this species in a bathyal tanathocoenoses from the Tyrrhenian Sea (773-1,113 m). They regarded such valves, as well as other shells, as coming from older Pleistocene beds involved in dredging activities.

A left valve perfectly referable to *Bathyspinula excisa* is held in the mollusc collection from the BALGIM Expedition (MNHN) (La Perna, pers. obs.). It comes from the Iberian-Maroccan Gulf (St. DR37, 36°18N/07°15W, 860-868 m) and probably belongs to a Pleistocene tanathocoenoses (see below).

There is also a mention of "*Leda excisa*" from the Belgian Tertiary by Nyst (in Dewalque, 1868 fide Glibert, 1945). Already retained as doubtful by its author, this record was later reviewed by Glibert (1945), who illustrated and described the single valve, coming from Upper Miocene ("Anversien") beds. He retained the species quite different from the Philippi's one and he left it undescribed. As noticed by Glibert, it is a young specimen (1.7 mm in length) which is, in effect, somewhat like *Bathyspinula*, since it has a slight posterior sinuosity and a concentric sculpture. However, we can surely exclude it being a specimen of *Bathyspinula excisa*, since it has an entirely different shell outline if compared with the same-sized valves. It is not even a *Bathyspinula*, since it has a "petite fossette ligamentaire triangulaire assez profonde" and, probably, it should be referred to *Yoldiella* Verril & Bush, or to a related genus.

Ecological remarks.

According to Allen & Sanders (1982), *Bathyspinula* may be an active burrowing bivalve, as suggested by some anatomical features (i. e. a large pedal ganglium, an elongated and muscular foot which is anteriorly directed, a long combined inhalant and exhalant siphon, powerful adductor muscles, etc.). It seems to be particularly well-adapted to muddy substrates too. The large byssal gland and the peculiar foot morphology suggest to Allen & Sanders a marked ability to bind and reject the exceeding amount of sediment. Some others features, which are typical in deep-sea bivalves (Allen, 1979; Allen & Sanders, 1982), such as large finely-ridged palps, great volume and length of gut, relatively small gills, are also present in *Bathyspinula*. To these observations some others, regarding shell morphology, could be added. The slender, wedge-shaped morphology and the allometric growth of the posterior side, are easily referable to a well-developed adaptation to an infaunal life habit (see Stanley, 1970). *Bathyspinula* probably attains a relatively deep life position, which could be competitive within the shallow-burrowing communities of detritus-feeders, such as the nuculoid communities.

Nothing is directly known about the larval ecology of *Bathyspinula*. The prodissoconch of *excisa*, whose size is comparable with those of the Atlantic species (375-450 µm), lacks any differentiation into prodissoconch I and II (Pl. 2, fig. 3) and it is very different from a typical planktotrophic larval shell (see Ockelmann, 1965, among others). It should be remarked that nuculoids represent an homogeneous group, as far as the larval development is concerned, since it takes place in a barrel-shaped cyliated test during a brief (3-5 days) planktonic phase (Jablonski & Lutz, 1980, 1983; Webb, 1987 and references).

Bathyspinula has a worldwide bathyal and abyssal distribution. According to the bathymetric ranges of the World and Atlantic species reported by Allen & Sanders (1982), only two species, namely *Bathyspinula subexcisa* and *Bathyspinula filatovae* have an upper bathymetric limit within the Bathyal Zone (1,248 and 1,260 m, respectively). More recently, Filatova & Schileyko (1984) described *Bathyspinula (B.) latirostris* from the Arctic Sea, at 4,300 m. Five species are known from the Atlantic (Allen & Sanders, 1982). Some *Bathyspinula* species are known as rather common among bathyal and abyssal communities. According to Allen & Sanders (1982), the Atlantic species *hilleri* and *scheltemai*, make up a remarkable share (more than 10%) among the nuculoid communities between 2,500 and 5,000 m. *Bathyspinula subexcisa* is also a rather common nuculoid between 1,800 and 2,500 m in the European Atlantic. Two species are particularly widespread in the Pacific Ocean. In the North Pacific abyssal bottoms (3,000-6,000 m), a "*Spinula oceanica* community" (biomass 0.2-1.0 gm^{-2}) and a "*Spinula calcar* community" (biomass 0.1-0.2 gm^{-2}) are known (Filatova, 1969; fide Pérès, 1982).

Recent research about the bathyal molluscan faunas from the Lower Pleistocene deposits (La Perna, 1994) pointed out the typically bathyal character of *Bathyspinula excisa*. Among these bathyal faunas, nuculoids are always well represented, making up, together with scaphopods, nearly the whole of the infauna. Apart from *Bathyspinula excisa*, the most frequent species are: *Nucula sulcata* Bronn, *Nuculoma corbuloides* (Seguenza), *Neilonella pusio* (Philippi), *Propeleda cuspidata* (Philippi), *Yoldiella messanensis* (Seguenza), *Yoldiella philippiana* (Nyst), *Yoldiella* sp., *Sarepta* (?) *minima* (Seguenza).

Within the molluscan communities, *Bathyspinula excisa* reaches, in some cases, up to 20-30% in relative abundance, and up to 80% within the nuculoid communities. These molluscan assemblages, which should be regarded as true *Bathyspinula excisa* communities, are rather scanty in deep-shelf and upper-slope species, such as *Alvania cimicoides* (Forbes) and *Yoldiella messanensis* (Seguenza). On the contrary, some species, such as *Seguenzia formosa* Jeffreys and *Microgloma turnerae* Sanders & Allen, are particularly abundant. The former is known from the North Atlantic bathyal depths (600-3,650 m) (Jeffreys, 1885). The latter is known from the Northeast Atlantic basin, between 950 and 2,350 m (Sanders & Allen, 1973). It has been recently reported (as empty shells) from 650 to 1,500 m in the Southern Tyrrhenian Sea (Di Geronimo et al., 1995). Both the ecological structure and the faunal composition of the *Bathyspinula excisa* communities suggest a rather deep palaeobathymetry, pertaining to the "horizon moyen" as defined by Pérès & Picard (1964) and by Carpine (1970). It is possible to refer such molluscan faunas to 700-800 m, or even more, and to retain them as the deepest Plio-Pleistocene communities so far known.

Although very scantly, this species is also associated with shallower palaeocommunities, generally dominated by *Yoldiella messanensis*, which are referable to upper-slope or epibathyal bottoms. It is therefore possible to estimate the upper bathymetric limit of *Bathyspinula excisa* at about 250-300 m. Even considering difficulties and consequent inaccuracy in estimating palaeobathymetries, *Bathyspinula excisa* shows a markedly "atypical" range, being the shallowest species among the known ones. It is a particularly frequent species among the bathyal faunas from the Late Pliocene too. D'Alessandro & De Marco (1993) recognized a "Protobranchs and Siphonodentaliidae community" among the molluscan faunas from the Late Pliocene of Basilicata. Three species, *Neilo excisus* (=*Bathyspinula excisa*), *Nuculana pusio* (=*Neilonella pusio*) and *Entalina tetragona*, characterize as many facies, all referred to the "horizon moyen" of the Bathyal Zone.

The abundance of *Bathyspinula excisa* and of other nuculoids, among the Mediterranean Plio-Pleistocene bathyal communities, agrees well with the composition of deep-sea benthos, which is well-known as different from the littoral one (Clarke, 1962; Rex, 1981; Hickman, 1984). The Plio-Pleistocene deep-sea nuculoid and scaphopod communities are clearly referable to the "Protobranch Community" (Hickman, 1984), known all over the World Ocean and characterized by a great abundance in nuculoids, with which scaphopods (mainly Siphonodentaliidae) are also associated.

Discussion.

On the grounds of the data so far shown, *Bathyspinula excisa* should be regarded as an extinct species. Considering its relatively shallow range, it seems quite unlikely that the present survival of this species is yet unknown. Otherwise, one should state that its present distribution is extremely limited, in comparison with the Plio-Pleistocene one.

In effect, the case of *Bathyspinula excisa* is not isolated. Among the deep-sea molluscs, as well as among other benthic invertebrates from the Mediterranean Plio-Pleistocene, there are many extinct species which show close taxonomic, morphologic and ecologic affinities with species living in the North Atlantic or in other oceanic areas. Some of these ones, namely *Fissurisepta papillosa* Seguenza, *Neilonella pusio* (Philippi), *Cadulus ovulum* Philippi, are counted among the living Mediterranean molluscs (Sabelli et al., 1990). It has been remarked (La Perna, 1994), however, that their scanty records are based on empty shells. Otherwise, even for these species, one should admit that their present populations are extremely rarefied, since these species were among the most frequent ones within the Plio-Pleistocene bathyal communities. The affinity of some extinct deep-sea Mediterranean molluscs with some species from the World Ocean, have been treated in some detail by Di Geronimo & La Perna (in press) with regard to *Homalopoma emulum* (Seguenza), a turbinid gastropod from the Lower Pleistocene bathyal deposits of Southern Italy. A strikingly similar species, *Homalopoma globuloides* (Dautzenberg & Fischer), is known from bathyal depths in the North Atlantic, whilst no closely similar species is presently living in the Mediterranean. It is noteworthy to mention *Calliotropis marginulatus* (Philippi) too, an extinct species which was common among the bathyal Mediterranean faunas. *Calliotropis* is a worldwide deep-sea genus, presently absent from the Mediterranean. In this connection, other species could be mentioned, such as *Nassarius (Profundinassa) spinulosus* (Philippi), *Propeleda cuspidata* (Philippi), in addition to the already cited *Neilonella pusio* (Philippi), *Cadulus ovulum* (Philippi) and *Fissurisepta papillosa* Seguenza. Rightfully, *Bathyspinula excisa* belongs to this group of species.

Such a kind of affinity is not at all restricted to molluscs, since it has been noticed in several benthic invertebrates: ostracods (Benson, 1972), cnidarians (Zibrowius, 1978, 1987, 1991a, 1991b; Placella, 1978; Zibrowius & Placella, 1981), brachiopods (Gaetani & Saccà, 1984), crinoids (Roux et al., 1988), bryozoans (Rosso & Di Geronimo, in prep.). For each of them, close affinities have been remarked between the deep-sea faunas of the Mediterranean Plio-Pleistocene and the present Atlantic, or in general oceanic ones. The stratigraphical distribution of *Bathyspinula excisa* is fairly well known. It is absent from the bathyal molluscan faunas of the North Italy Early Pliocene studied by Robba (1981) and by Tabanelli (1993, 1994). Data so far known (Padovani & Tampieri, 1970; Tabanelli, 1993; Roveri et al., 1992) suggest its appearance in the Middle Pliocene (Piacenzian). Among the bathyal communities from the Late Pliocene (Caldara & Garganese, 1990; D'Alessandro & De Marco, 1994), the relative abundance of *Bathyspinula excisa* seems equivalent to that recorded in the Early Pleistocene (La Perna, 1993), as biostratigraphically considered (Ruggieri et al., 1984). It is also present and abundant in the marls outcropping near Lazzàro (Reggio Calabria), for which a palaeomagnetic age between 0.9 and 0.47 m.y. B. P. is recorded (Aifa et al., 1987; Barrier, 1987).

As previosuly suggested (Di Geronimo et al., in press), the Mediterranean appearance of *Bathyspinula excisa* during the Pliocene, could be counted among a series of biological events which seem to be strongly affected by the Plio-Quaternary climatic changes. Isotopic records show a marked climatic deterioration since 2.5-3.0 m.y B. P, to which the build-up of the arctic ice-cap is referred (Berggren, 1972; Shackleton & Opdyke, 1976; Thunell & Williams, 1983). Plio-Pleistocene biological events related to cooling are particularly well-known among the Mediterranean littoral molluscs, which were affected by the extinction of a large number of subtropical taxa and by a decreasing taxonomic diversity (Marasti & Raffi, 1980; Raffi & Marasti, 1982). Another well-known event is the appearance, in Mediterranean shelf communities, of Atlantic species ("Boreal Guests") (Raffi, 1986; Malatesta & Zarlenga, 1986, and references).

Data on Early Pliocene bathyal macrobenthos are still too scanty. However, the Early Pliocene molluscan faunas differ considerably from the Late Pliocene ones, which are, in turn, much closer to those from the Early Pleistocene. According to Tabanelli (1993), the deep-sea molluscan faunas from the North Italy Piacenzian, are markedly different and more diversified from the older ones, since new and "Atlantic" species (among which he included "*Spinula excisa*" too) appeared, and deep-sea species (in effect deep-shelf to bathyal species) common in the Early Pliocene became extinct. An increasing faunistic diversity has been recorded also among bathyal ostracod faunas (Colalongo & Pasini, 1988): it is low in the Early Pliocene becoming higher in the Early Pleistocene. Another "event" regarding deep-sea ostracods is represented by the appearance of the Atlantic species *Cytheropteron testudo* Sars (Bonaduce & Sprovieri, 1985) in the Middle Pliocene. Actually, the presence in the Plio-Pleistocene benthos of deep-sea species which are now living in the Atlantic Ocean is a generalized phenomenon, involving a large number of benthic invertebrates.

The deep benthos, then, seems to have reacted differently from the littoral one, under the Pliocene climatic changes. Considering the role of the polar ice in the thermo-halyne circulation and in producing the cold deep waters, it has been suggested (Di Geronimo et al., in press) that the Plio-Pleistocene cooling led to a general renewal and diversification of the deep-sea benthos, with the appearance and success of particularly cold taxa. Even though they have not yet been fully identified, the Plio-Pleistocene events which involved the deep-sea benthos might be comparable, on a largely different scale, to those known for the Eocene-Oligocene age. Then a global cooling (Kennett & Shackleton, 1976) led the old thermospheric ocean to the present "two-layer" (thermosphere-psycrosphere) ocean, producing sharp changes in deep-sea benthos (Benson, 1975, 1984; Hickman, 1984). From this point of view, changes in the deep Mediterranean benthos, might be a "local" aspect of wider and more generalized biological events. Probably, such new environmental conditions, led the deep Mediterranean benthos, drastically impoverished by the Messinian crisis, to a particularly marked evolution and enrichment. In this scenario, some well-adapted species, such as *Bathyspinula excisa*, reached a great population success.

What has been here remarked, presupposes that the Mediterranean Sea was widely connected with the Atlantic Ocean, both faunistically and hydrologically, as suggested by Benson (1972). According to his model, the Pliocene Mediterranean basin was widely connected with the Atlantic, since the Gibraltar threshold was inexistent, or markedly deeper than the present one. Thanks to this, the cold deep waters could spread into the Mediterranean basin, allowing the development of oceanic-like deep faunas. This hypothesis, recently maintained by Roux et al. (1988) and Barrier et al. (1989), is supported by geological data about the Gibraltar area (Bousquet & Philip, 1976; Dillon et al., 1980; Maldonado, 1984). It is known, in fact, that a tensive regime affected the Alboran basin from the Early Pliocene, when a portal opened in the present Strait position. The tensive regime lasted till the upper part of the Early Pleistocene (about 1. m.y. B. P.), when a N-S compression began to involve the area.

It is possible to assume, then, that the Mediterranean attained its present "threshold basin" condition through a progressive uplifiting of the Gibraltar threshold, caused by the Quaternary compression, up to the present depth (280 m). Today, it is a "negative basin" (Lacombe & Tchernia, 1972; Hopkins, 1984), whose peculiar hydrologic features (deep homothermy, high salinity, nutrient depletion, etc.) are well-known. Probably, the disappearance of the rich Mediterranean deep-sea communities took place during the Later Pleistocene, in connection with the establishing of restricted circulation and deep homothermy (Di Geronimo & La Perna, in press; Di Geronimo et al., in press). These conditions "favoured" a markedly eurythermic, eurybathic and generally impoverished deep-sea benthos, lacking in cold stenothermic species (Pérès & Picard, 1964; Fredj & Laubier, 1985). Extinction of the "oceanic-like" species might represent, then, a proof of their general meaning of cold, more or less stenothermic, species. With regard to this, the extinction of the Mediterranean ostracod *Agrenocythere pliocenica* Seguenza, retained a typically psycrospheric species, is noteworthy. Colalongo & Pasini (1988) dated this event in the upper part of the Early Pleistocene ("Small *Gephyrocapsa* Zone") and referred it to the ending of the Mediterranean psycrospheric conditions. It seems, however, that the deep hydrologic conditions "improved" during the Late Pleistocene glacial phases, when the deep Mediterranean communities seem to have flourished again, as shown by the Würmian thanatocoenoses (Di Geronimo & Li Gioi, 1980; Allouc, 1987; Corselli & Bernocchi, 1990, and references).

The extinct species with marked oceanic affinities should be regarded, then, as deep Mediterranean palaeoendemisms (Di Geronimo et al., in press). The rate of deep Mediterranean endemisms, previously regarded as particularly low (Fredj & Laubier, 1985), is presently retained not so scanty and changing throughout the faunal groups (Bellan-Santini et al., 1992). From this point of view, it is possible to state that the Plio-Pleistocene deep-sea benthos were markedly richer in endemic species than at the present time. At present it is not possible, however, to test this asssumption, owing to the lack of data about the Atlantic Plio-Pleistocene deep-sea benthos. The valve of *Bathyspinula excisa*, coming from the Iberian-Maroccan Gulf, could indicate, in effect, a limited spreading of the species beyond Gibraltar. The Pleistocene age of this valve could be supported by the presence, in the same station, of the fossil species "*Yoldia*" *longa* Bellardi (Warén, pers. com.). It is also important to stress the position of that station, falling within an area (Gulf of Cadiz) and a depth (about 860 m) which are involved by the deep Mediterranean outflow (cf. Harmelin & d'Hondt, 1993). It seems, then, that such "Atlantic" populations underwent the same fate as the Mediterranean ones, since they became "isolated" by the threshold and the area became involved by the salt and warm Mediterranean outflowing waters.

Although *Bathyspinula excisa* show closer relations with the Atlantic species *subexcisa*, *hilleri* and *scheltemai*, than with the Pacific *oceanica* and *calcar*, its phyletic relationships remain unclear. No species which could be retained a possible ancestor of *Bathyspinula excisa* is known among the Mediterranean or Atlantic fossil nuculoids. As already suggested with regard to *Homalopoma emulum* (Di Geronimo & La Perna, in press), the appearance of *Bathyspinula excisa* and of other deep-sea species in the Mediterranean seems to be related to allopatric speciations within the Northeastern Atlantic-Mediterranean basin during the Plio-Pleistocene. It is not unlikey, however, that *Bathyspinula subexcisa* is the descendant of *Bathyspinula excisa* (see Warén, 1989). In this case, both species should be regarded as belonging to the same lineage, which is surviving in the Atlantic.

Conclusion.

Geologic phenomena have always had an important role in the faunistic evolution of the Mediterranean. This role seems to have also been fundamental for deep-sea benthos evolution. It is worth noting that, from an oceanographic point of view, the present day Mediterranean is considered as a present example of thermospheric pre-Oligocene Ocean (Hay, 1983). Perhaps, from a merely biologically point of view, this vision is a little extreme but, considering what is so far known, only to a certain extent is it possible to compare the present deep benthos with the Plio-Pleistocene one. And it is impossible to recognize, for them, the same oceanographic meaning.

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