

Phyletic relationships and ecological implications between *Pagodula vaginata* (De Cristofori & Jan, 1832) and *Pagodula echinata* (Kiener, 1840) (Gastropoda, Muricidae)

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ABSTRACT - Two closely related species, *Pagodula vaginata* (De Cristofori & Jan, 1832) and *Pagodula echinata* (Kiener, 1840), have been recently distinguished (Bouchet & Warén, 1985) on the grounds of larval shell morphology. The former has a multispiral protoconch, indicating a planktotrophic development, whilst the latter has a paucispiral protoconch, referable to a non-planktotrophic development.

Both species occur in the Pleistocene deposits from Southern Italy. At that time, the two species lived in ecologically segregated populations, *Pagodula vaginata* being linked to deep-shelf and upper-slope bottoms, and *Pagodula echinata* to deeper bathyal bottoms. The extinction of *Pagodula vaginata*, in the upper part of the Lower Pleistocene or in the Middle Pleistocene, was probably caused by the Quaternary cooling. *Pagodula echinata* could then spread upward to about 100 m, attaining its present bathymetric range.

The origin of *Pagodula echinata* is referred to *Pagodula vaginata* through a process involving the larval development, known as «loss of planktotrophy». Such a process probably occurred in the Mediterranean during the Middle-Upper Pliocene, within a general development of deep-sea benthos.

RIASSUNTO - [Relazioni filetiche ed implicazioni ecologiche fra *Pagodula vaginata* (De Cristofori & Jan, 1832) e *Pagodula echinata* (Kiener, 1840) (Gastropoda, Muricidae)] - *Pagodula vaginata* (De Cristofori & Jan, 1832) e *Pagodula echinata* (Kiener, 1840), due specie strettamente affini ripetutamente confuse in letteratura, sono state recentemente distinte da Bouchet & Warén (1985) sulla base della morfologia protoconcale. La prima possiede una protoconca multispirale, indicativa di uno sviluppo larvale di tipo planktotrofico, mentre l'altra possiede una protoconca paucispirale, riferibile ad uno sviluppo di tipo non-planktotrofico.

Entrambe le specie sono presenti nei depositi pleistocenici dell'Italia meridionale. Le due specie vivevano allora in popolazioni ecologicamente separate. Mentre *Pagodula vaginata* era distribuita tra la parte più profonda della piattaforma continentale e la parte superiore della scarpata, *Pagodula echinata* era legata a fondali definitivamente batiali. L'estinzione di *Pagodula vaginata*, durante la parte terminale del Pleistocene Inferiore o nel Pleistocene Medio, fu probabilmente causata dal raffreddamento climatico quaternario. *Pagodula echinata* poté allora ampliare la sua distribuzione verso batimetrie più superficiali, raggiungendo l'attuale distribuzione batimetrica che inizia a circa 100 m di profondità.

L'origine di *Pagodula echinata* è riferita direttamente a *Pagodula vaginata*, attraverso un processo evolutivo, riguardante lo sviluppo larvale, noto come «perdita di planktotrofia». È probabile che la comparsa di *Pagodula echinata* sia avvenuta in Mediterraneo durante il Pliocene Medio-Superiore, nell'ambito di un generale processo di sviluppo del benthos profondo.

INTRODUCTION

«*Trophon vaginatus*» (De Cristofori & Jan, 1832) has been frequently reported among the European Neogene molluscan faunas. Specimens from deep Mediterranean and Northeast Atlantic bottoms have been referred to it for a long time, owing to their close resemblance with the fossil shells.

Bouchet & Warén (1985) pointed out a multispiral protoconch in the lectotype of *Murex vaginatus* De Cristofori & Jan, 1832 from the Tabianian stratotype (Lower Pliocene, North Italy), as well as in many shells from Italian Pliocene deposits. These observations allowed them to specifically distinguish the Recent Atlantic-Mediterranean form, often referred to *Trophon vaginatus* (e.g., Bucquoy *et al.*, 1882-1886; Kobelt,

1887; Hidalgo, 1917; Di Geronimo & Panetta, 1973), from the fossil one.

In the light of the relationships between protoconch morphology and larval development, this kind of difference assumes an important biological meaning. Thus, the Pliocene form and the Recent one should be referred to two fully distinct species, namely *Trophon vaginatus* (De Cristofori & Jan, 1832) and *Trophon echinatus* (Kiener, 1840), according to Bouchet & Warén (1985).

Taking into account the protoconch morphology, it has been effectively possible to discriminate the two species from some South Italy Pleistocene malacofaunas. Phyletic and ecologic relationships between the two species are pointed out and discussed in the present paper.

SYSTEMATIC REMARKS

Bouchet & Warén (1985) regarded all the European Trophoninae Cossmann, 1903 as belonging to *Trophon* Montfort, 1810, remarking that radular and shell features do not allow any clear-cut separation, neither among the European species, nor between the Northern and the Southern Atlantic ones. This systematic arrangement is different from that by Radwin & D'Attilio (1976) and Houart (1981), who distinguished some genera among the European species, such as *Trophonopsis* Bucquoy, Dautzenberg & Dolfuss, 1882, *Pagodula* Monterosato, 1884 and *Boreotrophon* Fischer, 1884.

The present species are markedly different from the type-species of *Trophon*, *T. geversianus* (Pallas, 1774) from the Magellanic region, showing a short, inflated and large shell. It is also worth noting that a close relation of this species with *Nucella* Röding, 1798 and *Ocenebra* Gray, 1847 was reported by Kool (1993a), who suspected polyphyly within Trophoninae of authors (see also Kool, 1993b and Houart, 1995).

On the grounds of gross shell morphology, it seems possible, however, to recognize some groups within the European species. These groups might correspond to as many distinct lineages, as suggested by the case of *Pagodula*, and so deserving generic or subgeneric rank.

Monterosato (1884) described *Pagodula* on «*vaginata*», clearly referring to it both the fossil and the living species. The identity of the type-species of *Pagodula* should be therefore regarded as doubtful.

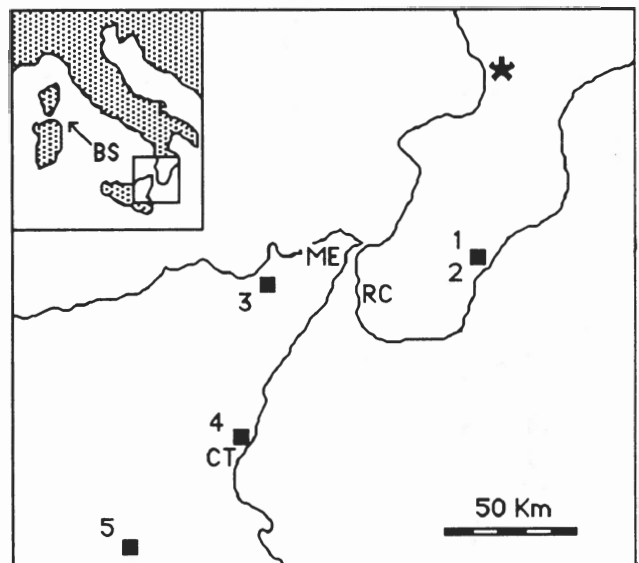
SHELL MORPHOLOGY

It is difficult to find macroscopical meaningful or constant differences between the shells of *Padodula vaginata* and *Pagodula echinata*. A difference could be represented by the maximum size (height), which can exceed 30 mm in *vaginata*, whilst it hardly exceeds 20 mm in *echinata*, at least in Recent specimens. It is also important to stress the morphological variability of both species, shared by other Trophoninae (e.g. see the wide range in *Trophon geversianus* reported by Strebel, 1904). Really, the only character allowing an unambiguous discrimination is represented by the protoconch, which has 2.5 whorls in *Pagodula vaginata* and 1.5 whorls in *Pagodula echinata*.

The protoconch of *echinata* (Pl. 3, figs. 3-6) is crossed by spiral ridges, more or less regularly spread and often interrupted. Its maximum diameter ranges from 640 μm to 730 μm in the fossil

specimens, and from 640 μm to 790 μm in the Recent ones. This variability is probably related to bathymetry. Shells from two stations off Sardinia (Text-fig. 1), whose depths are 472-718 m and 1,293-1,707 m, show mean sizes of about 700 μm (25 measurements) and 790 μm (19 measurements), respectively (Pl. 3, figs. 5, 6).

As remarked by Bouchet & Warén (1985), the shell variability of *Pagodula echinata* is mainly related to bathymetry. While the shallower specimens have a markedly spiny sculpture, the deeper ones usually have a lamellar habitus with less developed spines. The deepest specimens (from 600-1,000 m downward), are almost devoid of spines. Among the examined Mediterranean material (from Tyrrhenian Sea and Sicily Channel), both spiny shells from shallower dredgings, and smoother ones from deeper dredgings, are present. The species described in Atlantic as *Trophon grimaldii* by Dautzenberg & Fischer (1896) and *Trophon cossmanni* by Locard (1897) represent deep ecotypes of *Pagodula echinata* (Bouchet & Warén, 1985). The deepest Atlantic form (*cossmanni*), characterized by a non-spiny lamellar sculpture with thin spiral cords



Text-fig. 1 - Map showing the collecting sites (squares) of the specimens illustrated in the present work. 1) Bovalino Superiore (Lower Pleistocene), 2) Bianco (Lower Pleistocene), 3) Furnari (Lower Pleistocene), 4) Ficarazzi (Lower-Middle Pleistocene), 5) Grammichele (Lower Pleistocene). Stations BS 77/42 (472-718 m) and BS 78/14 (1,293-1,707 m) are indicated by the arrow. The type-locality of *Murex multilamellosum* Philippi, 1844 (Lamato river) is indicated (star). Reggio Calabria (RC), Messina (ME) and Catania (CT) are also indicated.

on last whorl, is probably absent from the Mediterranean, although some deep Mediterranean specimens have a markedly lamellar and non-spiny sculpture.

Shell variability in *Pagodula vaginata* seems to be much more limited. Spines are usually well developed, both in young and in fully grown individuals (Pl. 1, figs. 1-5), both particularly close to the «shallow-water» form of *echinata*. It is worth stressing the close resemblance between the large Pleistocene specimens and the Pliocene topotypic ones, illustrated by Pelosio (1966), as well as the lectotype reported by Pinna (1971) and by Pinna & Spezia (1978).

Protoconch sculpture is rather different from that of *Pagodula echinata*, as the nucleus is crossed by zigzag ridges and only the lowermost part of the following whorls is crossed by spiral ridges (Pl. 3, figs. 1, 2). A more limited size variability has been recorded, as the protoconch ranges from about 600 µm to 700 µm.

NOMENCLATURE REMARKS

For Atlantic and Mediterranean lamellar and moderately spiny specimens of *Pagodula echinata*, the name «*Trophon multilamellosum*» (Philippi, 1844) has often been used (e.g., Kobelt, 1887; Hidalgo, 1917; Sabelli & Spada, 1978). Bouchet & Warén (1985) regarded it as a synonym of «*Trophon vaginatus*», owing to its original use for a fossil specimen. Some remarks about the type-locality of *Murex multilamellosum* could be useful, however, to better define the identity of this species. Philippi (1844) reported it from «Tertiary» deposits along the Lamato river (South Italy) (Text-fig. 1). From the same locality he reported many littoral species, as well as some deep-water species («*Nucula excisa*», «*Nucula cuspidata*», «*Trochus suturalis*», etc.). Along the Lamato river, Gaetani & Saccà (1984) found a scanty outcropping Lower Pliocene marly formation («Trubi»), bearing no macrofaunas, and largely outcropping calcarenitic beds of Pleistocene age, containing shallow-water faunas. However, the presence of fossiliferous outcrops of deep-sea deposits should be expected in the area, as the species described by Philippi from this locality are among the most frequent ones within the Pleistocene bathyal communities (La Perna, 1994; Di Geronimo & La Perna, 1996). It is also worth noting that Philippi compared his species with *Pagodula vaginata* («*M. vaginato simile, sed numero varicum, spina brevi, anfractibus ratione altitudinis large latioribus abunde diversum*»). Some specimens of *Pagodula echinata* coming from

Pleistocene deep-sea deposits of Southern Italy are here illustrated (Pl. 2, figs. 2, 3, 4). These considerations lead us to exclude, almost certainly, the synonymy between *multilamellosum* Philippi and *vaginatus* De Cristofori & Jan, and instead to regard the former as a junior synonym of *echinatus* Kiener, whose type comes from the Sicily Channel.

In turn, «*Trophon multilamellosum*» has been regarded as a synonym of «*Trophon varicosissimus*» (Bonelli in Michelotti, 1841) (e.g. Locard, 1897; Nobre, 1938-1940). This is a poorly known species from the (Middle)-Upper Miocene of Piedmont and Austria. Several authors (Bellardi, 1872; Sacco, 1904; Montanaro, 1935) retained this species distinct from «*vaginatus*»; but the differences pointed out seem rather inconsistent, especially if the shell variability is taken into consideration. Probably, it was a smaller and more lamellar form (a deeper one?) of *Pagodula vaginata*.

Bouchet & Warén (1985) regarded *Murex carinatus* Bivona, 1832 and *Murex calcar* Scacchi, 1836, from the Mediterranean Plio-Pleistocene, as synonyms of *Pagodula vaginata*. Both names are not available, owing to their preoccupied status and there is, however, no certainty about their original use for *Pagodula vaginata*.

ECOLOGICAL OBSERVATIONS

Pagodula vaginata is a frequent species in the Lower Pleistocene marls which largely outcrop in the Hyblean area (Pl. 1, fig. 5; Pl. 3, fig. 2). Their molluscan faunas are well known (Di Geronimo, 1979; Di Geronimo *et al.*, 1982; Amore *et al.*, 1985; La Perna, unpublished). Communities are generally dominated by some «deep-sea» species (in effect, deep-shelf and eurybathic species), such as *Ledella messanensis* (Jeffreys), *Limopsis minuta* (Philippi), *Limopsis pygmaea* (Philippi) and *Kelliella abyssicola* (Forbes). Shallower species occur as well. Some communities show a stronger bathyal character, owing to a scanty presence of *Dentalium agile* Sars, *Entalina tetragona* (Brocchi) and some other bathyal species. These deposits are clearly referable to deep-shelf and upper-slope muddy biotopes, i.e. to the deeper Circalittoral Zone and to the transitional belt with the Bathyal Zone (Di Geronimo *et al.*, 1982). Their age, previously regarded as Calabrian (Di Geronimo, 1979 and references), should be now referred to the Sanernian-Emilian substages, according to the recent classification scheme and nomenclature of Lower Pleistocene (Ruggieri *et al.*, 1984; Rio & Sprovieri, 1986). This is also supported by the «old» character of molluscan faunas, which comprise

some species unknown from younger Pleistocene deposits.

Pagodula vaginata is a frequent species in a definitively bathyal community, from Southern Calabria (Pl. 1, figs. 1-4; Pl. 3, fig. 1), which still show a «shelf affinity», owing to its richness in deep-shelf species. This community comes from the top of a regressive Pleistocene sequence, whose lower part show typically bathyal faunas strongly dominated by the bivalve *Bathyspinula excisa* (see below). Both foraminiferal and macrofaunal assemblages indicate a Lower Pleistocene age not younger than Emilian, which is also supported by the geological data about this area (Ogniben, 1973).

Both bionomic and bathymetric distribution of *Pagodula vaginata* during the Pliocene seems quite similar to that of the Earlier Pleistocene. Pelosio (1966) referred the molluscan fauna from the Tabianian stratotype to a muddy biotope at 150-300 m. However, it should be stressed how such estimate was based on few living species, among which «*Trophonopsis vaginata*» was counted too. Nevertheless, such estimate seems quite correct and close to the values more easily estimated for the Pleistocene communities. On the other hand, *Pagodula vaginata* is not listed among the well-known littoral molluscan faunas from the North Italy Lower Pliocene (Pavia, 1976; Montefameglio *et al.*, 1979), whereas it is present among the Piacenzian molluscan faunas referred to deep-shelf facies (Marasti & Raffi, 1976), similar to that of the Tabianian stratotype.

On the grounds of this data, it is possible to estimate for *Pagodula vaginata* a bathymetric range from about 100 to 300-400 m, at least for the Pliocene to Earlier Pleistocene time span.

The present bathymetric distribution of *Pagodula echinata*, on the grounds of many records (see Di Geronimo & Panetta, 1973 and Bouchet & Warén, 1985), ranges from about 100 m to almost 3,000 m.

Pagodula echinata is one of the most frequent species among the bathyal molluscan faunas from the Mediterranean Lower Pleistocene (Southern Italy area) and it is one of the best represented neogastropods (La Perna, 1994). It is generally represented by moderately spiny and lamellar

specimens (Pl. 2, figs. 2-4). Among the same communities, Trophoninae are also scantily represented by the typically shelf species *Trophonopsis muricatus* (Montagu, 1803) and by another rare deep-sea species, «*Trophon*» *scillae* Seguenza, 1875, recently reported by Palazzi & Villari (1994).

The bathyal communities from the Lower Pleistocene are strikingly different from the Recent ones, as the former are rich in extinct species which have a marked «oceanic» character (La Perna, 1994; Di Geronimo & La Perna, 1996; Di Geronimo *et al.*, in press). The age of these communities ranges from the Lower to the Middle Pleistocene, as indicated by some paleomagnetic records (Aifa *et al.*, 1987). Palaeodepths of 400-600 m are generally estimated (Di Geronimo, 1987; La Perna, 1994), but some communities, in particular those characterized by a high relative abundance in the nuculoid *Bathyspinula excisa*, should be referred at least to 700-800 m, i.e. to upper-mesobathyal bottoms (Di Geronimo & La Perna, 1996).

The bathyal Pliocene molluscan faunas are still poorly known. However, *Pagodula echinata* has been found in an Upper Pliocene bathyal community, from Southern Calabria, whose faunistic composition and palaeoecologic meanings are quite similar to those of the Lower Pleistocene (La Perna, unpublished). In this regard, the species reported as «*Trophonopsis (Pagodula) vaginatus*» by D'Alessandro & De Marco (1993) in typically bathyal communities from the Upper Pliocene of Southern Italy (Basilicata) should probably be regarded as *Pagodula echinata*.

A good example of younger Pleistocene deep-shelf assemblage is represented by the rich molluscan faunas from the geological formation, known as «Sub-Etnean Clays», which outcrops near Catania. The age of this formation is Sicilian or probably younger (Middle Pleistocene) (Geological Map of Mt. Etna, 1979). Their molluscan faunas was extensively studied by Scalia (1900, 1901, 1907, etc.). His collection (Paleontological Museum of Catania University) comprises many specimens of *Pagodula echinata* from clayey outcrops near the coast. They show the typical «shallow-water» form habitus, with long and upward-bending spines (Pl. 2, fig. 1). Only two shells, from more inland and shallower (circal-

EXPLANATION OF PLATE 1

Figs. 1-5 - *Pagodula vaginata* (De Cristofori & Jan, 1832).

1-4) From Bovalino superiore, Lower Pleistocene. Height 19.0, 29.6, 30.3 and 35.5 mm, respectively.
5) From Grammichele, Lower Pleistocene. Height 7.8 mm.



toral) sites, are referable to *Pagodula vaginata*. These observations could effectively suggest the presence of *Pagodula echinata* at deep-shelf depths, comparable with the present ones, as well as the scantiness of *Pagodula vaginata*, during the later Lower Pleistocene.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION

The stratigraphic distribution reported in literature (see Pelosio, 1966 and Malatesta, 1974) for *Pagodula vaginata*, i.e. Middle Miocene to Recent, clearly need to be reviewed. *Pagodula vaginata* survived all through the Lower Pleistocene, becoming extinct during the Sicilian or later (Middle Pleistocene). Likewise, data regarding Miocene probably need to be reviewed, although, the appearance of *Pagodula vaginata* in the Late Miocene is quite an agreeable hypothesis.

Data regarding its geographic distribution fall into two groups (see Glibert, 1952; 1963; Pelosio, 1966; Malatesta, 1974): those regarding the Europe-Mediterranean area, from Miocene to Pleistocene, and those regarding the North Europe Miocene. Probably, such discontinuous data are mainly due to the wide interest towards Neogenic faunas from the Mediterranean area.

Data about the stratigraphic distribution of *Pagodula echinata* might be biased by the poor knowledge of the Plio-Pleistocene deep-sea faunas. As previously remarked, the stratigraphically oldest record of *Pagodula echinata* regards the Upper Pliocene. No species close to *Pagodula echinata*, or hypothetically assimilable to it, is reported among the bathyal molluscan faunas from the Lower Pliocene (Robba, 1981; Tabanelli, 1993, 1994).

Its present geographic distribution comprises the Mediterranean Sea (Western and Eastern basins), and the Northeast Atlantic, from the Azores to the Biscay Gulf and to the Rockall Trough (Northwest Ireland) (Bouchet & Warén, 1985).

DISCUSSION

The close relationships between the morphologic features of larval shell in gastropods and

the type of larval development is a well-known subject (Thorson, 1946; 1950; Robertson, 1974; Shuto, 1974; Jablonski & Lutz, 1980; 1983; Bouchet, 1990; etc.). Following Jablonski & Lutz (1980), the larval development in marine invertebrates is generally classified into two opposed types: a planktotrophic type, comprising free plankton-feeder larvae, and a non-planktotrophic type, comprising yolk-nourished larvae. Non-planktotrophic larvae may lead a short planktonic life, or they may wholly develop on the bottom. Planktotrophic development forms typically multispiral protoconchs (usually with more than 2 whorls) with a small nucleus (related to the small egg size), whilst the non-planktotrophic development forms paucispiral protoconchs (1-1.5 whorls), with a large nucleus (owing to the large yolk-rich eggs).

On the grounds of protoconch features, Bouchet & Warén (1985) suggested a possible planktotrophic development in *Pagodula vaginata* and a non-planktotrophic one in *Pagodula echinata*.

As Scheltema (1978) and Jablonski & Lutz (1983) stressed, the most reliable way to infer the larval development of a species consists in comparing its protoconch morphology with that of a closely related species, whose larval development is known. Observations on the larval development of the North Atlantic species *Boreotrophon truncatus* (Ström, 1768) are reported by Thorson (1946). Its larval development wholly takes place in the egg, from which a crawling stage hatches. Protoconch has 1.5 whorls and it is very similar to that of *Pagodula echinata*, as well as of other Trophoninae species. This kind of development is often termed as «direct» (e.g. Mileikowsky, 1971; 1974), but it would be better defined as «intracapsular» (Bouchet, 1989), to distinguish it from the true direct development, lacking a larval stage (Chia, 1974). Thus, *Pagodula echinata* should be regarded as an holobenthic species, with intracapsular larval development.

In contrast, the protoconch of *Pagodula vaginata* is referable to a planktotrophic development. Besides being of multispiral type, it shows the typical differentiation into protoconch I and II (Pl. 3, figs. 1, 2), i.e. between the egg-linked embryonal stage and the free veliger one. The zigzag pattern on

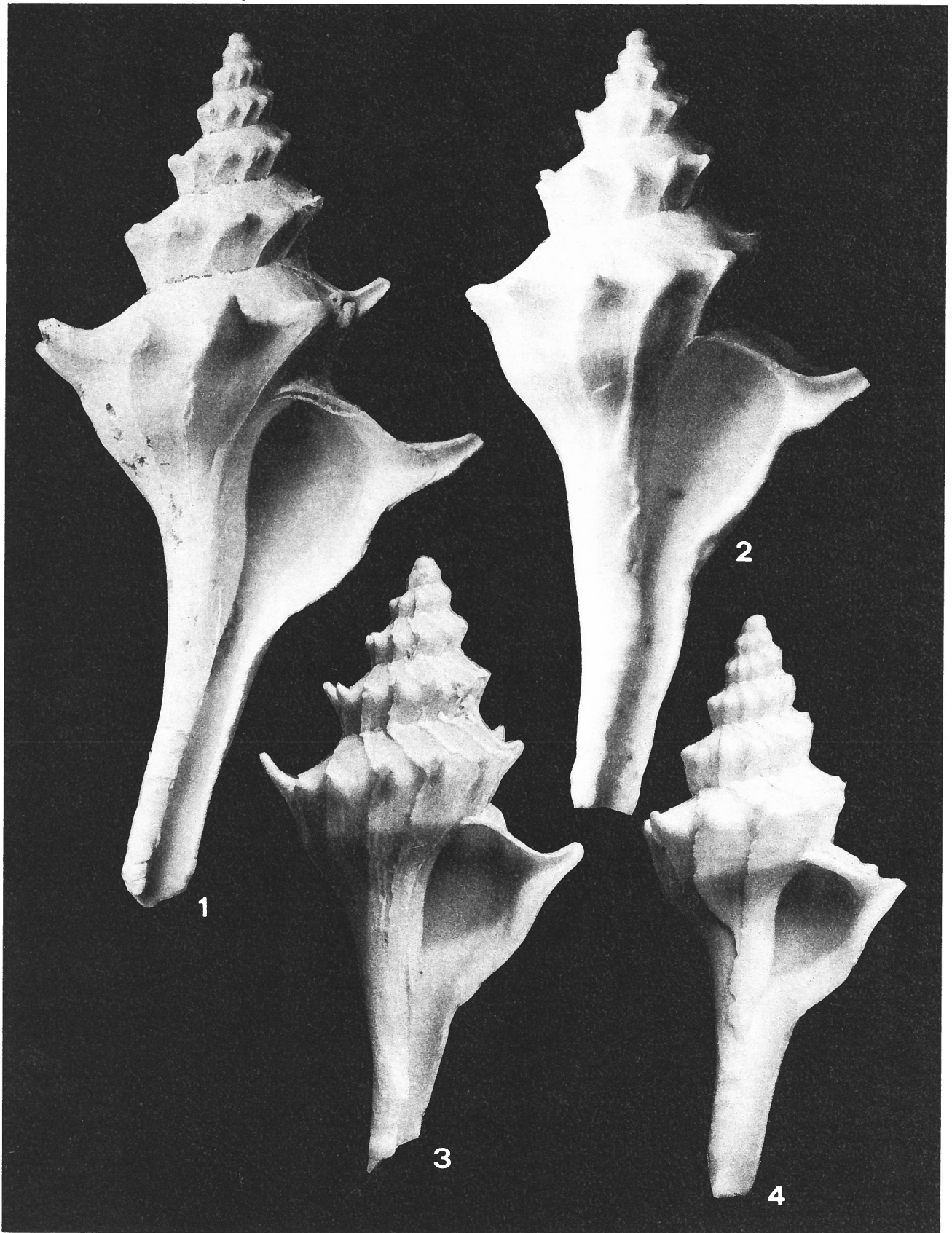
EXPLANATION OF PLATE 2

Figs. 1-4 - *Pagodula echinata* (Kiener, 1840).

1) From Ficarazzi («Sub-Etnean Clays»), Lower-(Middle) Pleistocene. Height 20.0 mm (S. Scalia collection, Paleontological Museum, Catania University).

2) From Bianco, Lower Pleistocene. Height 15.1 mm.

3, 4) From Furnari, Lower Pleistocene. Height 11.5 and 11.7 mm, respectively.



the nucleus is a typical sculptural pattern among planktotrophic larvae. Among the Northeast Atlantic Trophoninae, the only one having a multispiral protoconch, very similar to that of *Pagodula vaginata*, is the bathyal species *Boreothophon dabneyi* (Dautzenberg, 1889) (see Bouchet & Warén, 1985).

The evolutionary process involving the loss of feeding capabilities in larvae («loss of planktotrophy») is regarded as irreversible or highly improbable (Strathmann, 1978; 1985; 1993; Bouchet, 1990). This process seems to have a great importance as a speciation mechanism among marine invertebrates, since a large number of sibling species (subject reviewed by Knowlton, 1993), differing in larval development and often regarded or suspected as poecilogony cases (see reviews by Hoagland & Roberston, 1988 and Bouchet, 1989), are known among gastropods.

Phyletic lines, starting from Miocene species with planktotrophic development and leading to Recent species lacking in planktotrophy, have been reported by Bouchet (1981), for the Eastern Atlantic Terebridae and by Janssen (1993), for the turrid genus *Spirotropis* from the same area. A case of loss of planktotrophy could also involve the living species *Nassarius mutabilis*, as Gili & Martinell (1990) pointed out a paucispiral protoconch in this species, and a multispiral one in the Pliocene form. More recently, Della Bella & Tabanelli (1995), pointed out a multispiral protoconch in the extinct *Vexillum pyramidellus* and a paucispiral one in the living *Vexillum ebenus*, proving the specific separation, debated for a long time, between the fossil and the living form. Gili (1992) reported the case regarding two extremely close species, *Nassarius elatus* (with multispiral protoconch) and *Nassarius martinelli* (with paucispiral protoconch). During the Pliocene, the two species were coexisting in ecologically segregated populations.

Colognola *et al.* (1986) pointed out the coexistence of individuals with paucispiral and multispiral protoconch in Mediterranean populations referred to *Rissoa auriscalpium*. The two «forms» have a different bathymetric distribution, partially overlap-

ping, within the *Posidonia oceanica* grass. Verduin (1985) previously noticed such morphological difference and described the species with paucispiral protoconch as *Rissoa italiensis*.

On the grounds of these data, the phyletic relationships between the sibling species *Pagodula vaginata* and *Pagodula echinata* could appear obvious. Although the stratigraphic distribution of *Pagodula echinata* is not perfectly known, it seems reasonable to refer its origin directly to *Pagodula vaginatus*, through the loss of planktotrophy.

Both *Pagodula vaginata* and *Pagodula echinata* could be regarded as eurythermic species, although with markedly opposite tendencies. In this regard, it is worth noting the Tethysian roots of *Pagodula vaginata*. Even neglecting the Miocene records, it should be stressed that *Pagodula vaginata* lived within Lower Pliocene deep-shelf communities characterized by «warm» taxa. Moreover, it survived during the Lower Pleistocene, in epybathyal communities with a much more marked cold character than the present one. On the other hand, *Pagodula echinata*, should not be regarded as a typically cold-stenothermic taxon, a category which is absent from the deep Mediterranean benthos (Fredj & Laubier, 1985), owing to its wide geographic, latitudinal and bathymetric distribution.

Probably, the eurythermic capacity of *Pagodula vaginata* reached its limits during the upper part of Lower Pleistocene, because of the sharp cooling which allow the discrimination between a «preglacial» Pleistocene and a «glacial» one at 0.8-1.0 m.y. B.P. (Shackleton & Opdyke, 1976; Thunell & Williams, 1983; Ruggieri *et al.*, 1984). The extinction of *Pagodula vaginata* seems to fall, therefore, within the extinction phenomenon which involved the warm taxa, mainly of Tethysian origin, during the Plio-Pleistocene (Marasti & Raffi, 1980; Raffi & Marasti, 1982).

It is reasonable to assume that, when both species were coexisting, their bathymetric range was, on the whole, a continuum, with the upper part occupied by *Pagodula vaginata*, and the deeper one by *Pagodula echinata*. During the Sicilian or later,

EXPLANATION OF PLATE 3

Protoconchs. Scale bars = 250 µm.

Fig. 1 - *Pagodula vaginata* from Bovalino superiore.

Fig. 2 - *Pagodula vaginata* from Grammichele.

Fig. 3 - *Pagodula echinata* from Bianco.

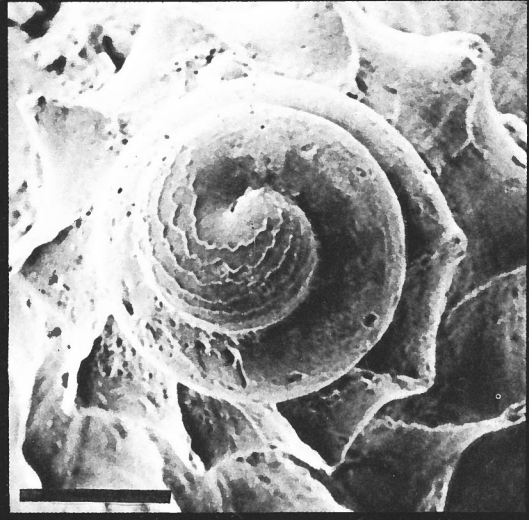
Fig. 4 - *Pagodula echinata* from Furnari.

Fig. 5 - *Pagodula echinata* from station BS 77/42 (472-718 m).

Fig. 6 - *Pagodula echinata* from station BS 78/14 (1,293-1,707 m).



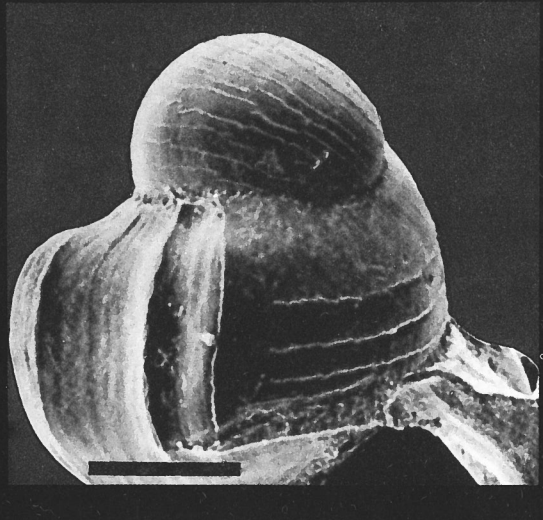
1



2



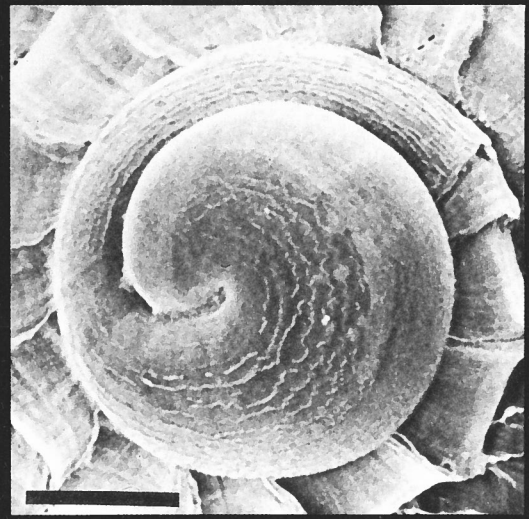
3



4



5



6

Pagodula echinata spread upward, till about 100 m, so holding the bathymetric range previously occupied by *Pagodula vaginata*.

Although planktotrophy is generally regarded as assuring a greater dispersion capability and a wider geographic distribution in comparison with non-planktotrophy, the present distribution of *Pagodula echinata* seems to be equal to that of *Pagodula vaginata*. Probably, it is due to its deep-sea habitat and eurytopy. Longevity in *vaginata* agrees well with its planktonic development, as generally supported (e.g., Shuto, 1974; Hansen, 1980; Gili & Martinell, 1994). In this regard, eurythermy should be regarded as an important factor too.

Although the «fatherland» of *Pagodula echinata* is unknown, we cannot exclude that it was the Mediterranean basin. The appearance of this species might fall within a general development and increasing faunistic diversity of the deep Mediterranean benthos from the Middle-Upper Pliocene to the Lower Pleistocene, which has been recently taken into consideration (Di Geronimo *et al.*, in press; Di Geronimo & La Perna, 1996). Such a process is referred to the Plio-Quaternary cooling trend, as well as to the hydrologic communication with the Ocean, different from the present ones, which allowed the presence of a «psycrosphere» in the Mediterranean (see Benson, 1972). Probably, the benthos impoverishment left by the Messinian crisis also had an important role in favouring the development of the deep Mediterranean benthos.

CONCLUDING REMARKS

There are many arguments to retain the origin of *Pagodula echinata* as directly linked to *Pagodula vaginata*, through a shifting from a planktotrophic larval development to a non-planktotrophic one. This kind of process, as well as its ecological implications, should be thoroughly investigated. From an ecological point of view, a couple of species like the *vaginata-echinata* one, appears almost as a unique «wide» specific entity, in which two opposite reproductive strategies co-occur. The temporal view of paleontology could be very useful to clear up both phyletic and ecologic aspects of such evolutionary lineages.

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