The Quaternary deep-sea protobranch fauna from the Mediterranean:

composition, depth-related distribution and changes

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ABSTRACT   The Recent bathyal protobranch fauna from the Mediterranean includes 14 species of nuculoids, but not more than 10 species are common and form recurring associations. From 150-200 m to 500-600 m, the nuculoid associations are characterized by *Ennucula aegeensis*, often dominant, and by few species more or less widely distributed on the shelf (*Nucula sulcata, Saccella commutata* and *Yoldiella philippiana*). From 500-600 m down to 1500-2000 m, associations consist mainly of *Ennucula corbuloides, Ledella messanensis, Microgloma tumidula, Yoldiella seguenzae* and *Y. micrometrica*. The deepest species is *Katadesmia cuneata*, occurring from 800-1000 m. The Pleistocene fauna consisted of 37 species at least, ca 20 of which were markedly common. The upper bathyal (150-200 to ca 500 m) associations typically consisted of a dominant shallower ecotype of *L. messanensis* and of several species, most of which with a marked epibathyal range (*Ennucula decipiens, Brevinucula glabra, Deminucula trigona, Yoldiella philippiana, Pseudomalletia isseli, Phaseolus ovatus,* etc.). Within the deeper associations, for which a maximum depth of ca 1000 is inferred, *Bathyspinula excisa, Ledella messanensis* (typical form), *Austrotindaria pusio* and *Katadesmia confusa* were particularly common and associated with other mesobathyal species (*Ennucula corbuloides, E. rotundata, Microgloma tumidula, Thestyleda cuspidata, "Yoldia" minima, Yoldiella seguenzae,* etc.). About half of the species which occurred in the Pleistocene became extinct, with only 14 of them are still living in the Mediterranean. Such a high rate of extinction of bathyal species, most of which are closely related to Recent North Atlantic taxa, is referred to the loss of psychrosphere and the onset of a deep homeothermy (12-13°C) in the Middle-Late Pleistocene. The Recent bathyal nuculoid fauna thus appears to be residual, i.e. consisting of eurytopic species which survived the oceanographic changes. The lack of endemic species is explained by the recentness of the present oceanography. A constant partial isolation of the Mediterranean from the Atlantic during the Plio-Pleistocene did not preclude the deep oceanic circulation, but encouraged the differentiation of the bathyal Mediterranean fauna from the North Atlantic one.

RIASSUNTO   L'attuale fauna batiale a protobranchi del Mediterraneo comprende 14 specie di nuculoidi, delle quali non più di 10 sono comuni e formano associazioni ricorrenti. Fra 150-200 m e 500-600 m, tale fauna è costituita da *Ennucula aegeensis,* spesso dominante, e da poche altre specie con affinità ecologica più o meno forte verso la piattaforma (*Nucula sulcata, Saccella commutata* e *Yoldiella philippiana*). Da 500-600 m fino a 1500-2000 m, le specie prevalenti sono *Ennucula corbuloides, Ledella messanensis, Microgloma tumidula, Yoldiella seguenzae* e *Y. micrometrica*. La specie più profonda è *Katadesmia cuneata*, presente a partire da 800-1000 m. La fauna a nuculoidi del Pleistocene era costituita da almeno 37 specie, circa 20 delle quali erano notevolmente comuni. L'associazione tipica del batiale superiore (da 150-200 a circa 500 m) comprendeva un ecotipo superficiale di *Ledella messanensis*, spesso dominante, e diverse altre specie, in prevalenza a distribuzione tipicamente epibatiale (*Ennucula decipiens, Brevinucula glabra, Deminucula trigona, Y. philippiana, Pseudomalletia isseli, Phaseolus ovatus,* ecc.). Nelle associazioni più profonde, per le quali è stimata una profondità massima di circa 1000 m, erano presenti come specie comuni e/o dominanti *Bathyspinula excisa, Ledella messanensis* (forma tipica), *Austrotindaria pusio* e *Katadesmia confusa,* associate ad altre a distribuzione tipicamente mesobatiale (*Ennucula corbuloides, E. rotundata, Microgloma tumidula, Thestyleda cuspidata, "Yoldia" minima, Yoldiella seguenzae,* ecc.). Circa la metà delle specie presenti durante il Pleistocene è estinta, e solo 14 di tali specie sono ancora viventi in Mediterraneo. Un tasso di estinzione così elevato di specie batiali, molte delle quali avevano strette affinità tassonomiche con specie oggi viventi in Nord Atlantico, è spiegato con la scomparsa della psicrosfera e l'instaurarsi di un regime omotermico profondo (12-13°C) nel Pleistocene mediosuperiore. L'attuale fauna a nuculoidi appare quindi fortemente residuale, cioè formata dalle specie che sono riuscite a sopravvivere alle drastiche variazioni oceanografiche grazie ad un certo grado di euritopia. L'assenza di endemismi è spiegata con la giovane età (poche centinaia di migliaia di anni) delle attuali condizioni oceanografiche. Molte delle specie estinte sembrano essere state endemiche dell'area mediterranea e questo porta a sottolineare il parziale isolamento che il Mediterraneo profondo ha avuto almeno durante il Plio-Pleistocene. Tale isolamento non impediva la circolazione profonda, ma favoriva comunque la differenziazione della fauna mediterranea da quella atlantica.

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INTRODUCTION

Nuculoida and Solemyoida are the two orders traditionally distinguished within the bivalve subclass Protobranchia, one of the most primitive bivalve groups, but new perspectives on early phylogeny and classification of bivalves have been recently proposed (CARTER *et al.*, 2000; COPE, 2000). Although both orders have a long evolutionary history, ranging back to Ordovician, the Nuculoida have had much more success than the Solemyoida. In spite of a certain diversity of form and specialization, nuculoids are one of the most conservative bivalve groups and this is reflected by the difficulties of identification and classification. Their systematic arrangement is thus not well settled yet (e.g. ALLEN & HANNAH, 1986; MAXWELL, 1988; OCKELMANN & WARÉN, 1998).

Nuculoids are dominant within the deep-sea molluscan fauna. Although some species may form dense populations on shelf bottoms, most species live at bathyal and abyssal depths, thus contributing to the typical structural pattern of the deep-sea benthos (ALLEN, 1979; KNUDSEN, 1979; REX, 1981; HICKMAN, 1984; GAGE & TYLER, 1991; ALLEN & SANDERS, 1996b). They have

infaunal habits and feed on detritus by means of palp proboscides (YONGE, 1939; RHOADS, 1963), but with some capacity for gathering food from suspension (STASEK, 1965; DAVENPORT, 1988). TYLER *et al.* (1992) found the intestinal content of three deep-sea nuculoids as mainly composed by diatoms, coccoliths and foraminifers. Digestive efficiency on organically poor sediments must be markedly important for the deep-sea nuculoids as recognised by ALLEN (1992), who outlined a major adaptive trend to elongated hindguts forming multiple loops. While adaptations to different sediment textures are known (e.g. ALLEN, 1954) or expected for the shelf nuculoids, very few data have been reported for the deep-sea species. This is due to the general (but not exclusive; see VIANA *et al.*, 1998) muddy nature of the deep-sea bottoms, but mainly to the lack of works devoted to this subject. The distribution of the deep-sea nuculoids thus seems to be mainly controlled by depth, which means an array of related parameters (temperature, pressure, trophic resources, etc.).

The European deep-sea nuculoid fauna is fairly well known. A series of works devoted to the Atlantic species was carried on by

ALLEN and co-workers between 1973 and 1996 (see ALLEN & SANDERS, 1996b). Other main contributions to the knowledge of the Atlantic and Mediterranean nuculoids have been given by WARÉN (1978, 1989), SALAS (1996) and OCKELMANN & WARÉN (1998). Several works have been devoted to the deep Mediterranean molluscs, mainly focusing on living and dead faunas and including nuculoids (DI GERONIMO & PANETTA, 1973; DI GERONIMO, 1974; DI GERONIMO & LI GIOI, 1981; DI GERONIMO & BELLAGAMBA, 1986; BELLAGAMBA, 1986; JANSSEN, 1989; DI GERONIMO et al., 2001). Also the Pleistocene deep-sea molluscs from the Mediterranean have been recently studied on material from bathyal beds cropping out in Southern Italy (DI GERONIMO, 1979; DI GERONIMO & LA PERNA, 1996, 1997; DI GERONIMO et al., 1997; LA PERNA, 1998 and unpubl.; D'ALESSANDRO et al., 2003).

This amount of data is large enough to provide a "complete" inventory of the deep nuculoid fauna from the Mediterranean Quaternary (Tab. 1), to outline the main patterns of composition and bathymetric distribution of associations, and to point out the changes that occurred during the Quaternary. Although the aim of this paper is not a revision, short taxonomic comments or other notes on most species are given for the sake of completeness. For the same purpose, most species are illustrated.

MATERIAL, METHODS AND TERMINOLOGY

Data on fossil nuculoids are mostly from recent studies on Early-Middle Pleistocene molluscs faunas from Southern Italy (DI GERONIMO & LA PERNA, 1997; DI GERONIMO et al., 1997; D'ALESSANDRO et al., 2003; LA PERNA, unpubl.). Molluscs were studied by means of bulk-samples of 6-100 dm³, which were treated as routinely (disintegration in water, sieving through 0.25 or 0.5 mm mesh screen, residue washing and sorting). Some data are from Würmian (Late Glacial) mollusc faunas dredged from off Western Sardinia (DI GERONIMO & LI GIOI, 1981; DI GERONIMO & BELLAGAMBA, 1986; BELLAGAMBA, 1986; LA PERNA, unpubl.). Data on the Recent nuculoids are mostly from a box-coring Cruise (Eocumm95) on bathyal bottoms in the southern Tyrrhenian Sea (Aeolian Archipelago), whose main results on benthic associations were recently reported by DI GERONIMO et al. (2001). The sole macrofauna occurring in the samples consisted of shelled thanatocoenoses whose age must be referred to the last two-three thousands years, thus they are not strictly "Recent" but Late Holocene in age. It is clear that single box-cored (6.5 dm³) stations do no provide enough material to collect living animals, at least in the deep Mediterranean (most studies on deep-sea fauna are based on epibenthic sled sampling and other qualitative or semi-quantitative towing methods which allow greater amount of surface and subsurface sediment to be sampled: e.g. GAGE & TYLER, 1991; ALLEN & SANDERS, 1996b). It is anyway worth stressing that box-coring and bulk-sampling provide comparable results, with respect to shelled fraction/sediment volume and taphonomic processes (time-averaging in particular).

Two terms are used to distinguish the bathyal horizons, namely epibathyal and mesobathyal, following the zonation model of

the Mediterranean slope developed by PÉRÈS & PICARD (1964) and CARPINE (1970). The epibathyal horizon ranges from the circalittoral/bathyal transition (150-250 m at mid latitudes) to ca 500 m, while the mesobathyal one ranges down to ca 2000 m. CARPINE (1970) distinguished also a deepest horizon ranging down to 3000 m, but the present work does not deal with such great depths. A different model was recently attempted (EMIG, 1997), but the traditional system seems to describe better the past and modern distribution of the bathyal Mediterranean fauna.

In accordance with KIDWELL & BOSENCE (1991), the term association is preferred to the generic assemblage, to stress the palaeoecological significance and implications of the shelled faunas studied in the present work, and their fidelity to the former living communities.

THE RECENT NUCULOID FAUNA

Data from the southern Tyrrhenian thanatocoenoses (250-1550 m) are useful to outline the main depth-related patterns of nuculoid distribution. Fig. 1a,b illustrates a trend of increasing number of species and dominance with depth. Although correlation proves to be weak or not significant at all, such trends match the general depth-related pattern known for the deep-sea nuculoids (ALLEN & SANDERS, 1996b). The maximum number of species (6) was recorded from two stations at 1100-1200 m and most stations deeper than 1000 m provided 3-5 species, while shallower samples provided 1 to 4 species. Between 1000 and 1500 m, nuculoids account for 20-60% of molluscan associations, while this value tends to be lower in the shallower stations.
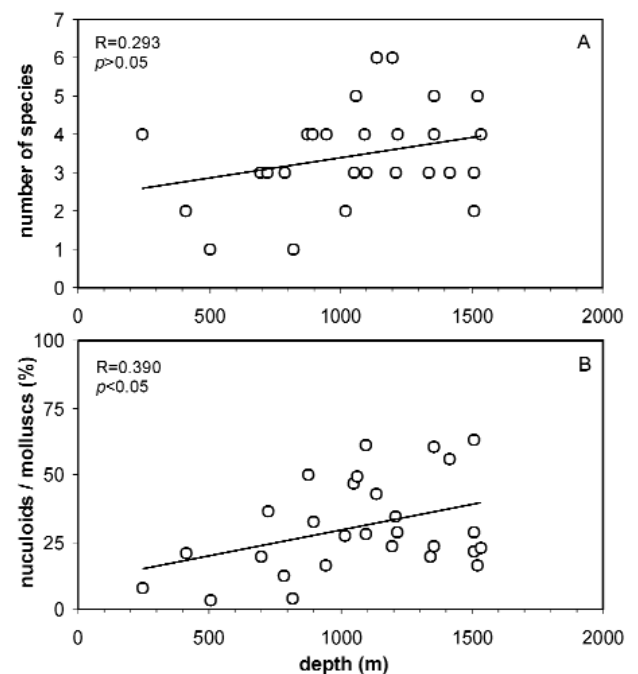

Fig. 1. Bathyal thanatocoenoses from the southern Tyrrhenian Sea. (A) Number of nuculoid species and (B) dominance of nuculoids on mollusc association in each of 28 stations. Data from DI GERONIMO et al. (2001).
Fig. 1. Tanatocenosi batiali provenienti dal Mar Tirreno meridionale. (A) numero di specie di nuculoidi e (B) dominanza dei nuculoidi sulle associazioni a molluschi riportate per ognuna delle 28 stazioni. Dati da DI GERONIMO et al. (2001).

Ennucula aegeensis, known since several decades as a Mediterranean bathyal bivalve ("espèce charactéristique exclusive" of the Bathyal Mud Community, according to PÉRÈS & PICARD, 1964 and CARPINE, 1970), has a mostly epibathyal distribution, from ca 80 m down to ca 500 m (DI GERONIMO & PANETTA, 1973; DI GERONIMO, 1974; SALAS, 1996; DI GERONIMO *et al.*, 2001), although its lower limit is close to 1000 m. Below 500-600 m, *E. aegeensis* is mostly replaced by *E. corbuloides* (Fig. 2a). Two species, *Nucula sulcata* and *Saccella commutata,* are frequently associated with *E. aegeensis.* The former has a wide circalittoral to bathyal distribution (50-1000 m) on muddy bottom, while the latter has a shallower distribution (mostly circalittoral, but ranging down to 300-400 m or more) on muddy-sandy bottoms. Also *Yoldiella philippiana*, ranging from ca 80 m to 500-600 m, is usually found within the epibathyal associations. Its depth range is relatively shallow trough the geographic distribution: usually 100-300 m and shallower (25-200 m) at higher European latitudes (WARÉN, 1989). Below 500-600 m, a closely allied species, *Yoldiella seguenzae*, tends to replace *Y. philippiana* (Fig. 2b). While *N. sulcata* and *S. commutata* cannot be regarded as true deep-sea species, but eurybathic shelf species, *E. aegeensis* and *Y. philippiana* can be regarded as typically epibathyal species. Tab. 3 reports an example of epibathyal (248 m) nuculoid association dominated by *E. aegeensis.*

Below 500-600 m, the nuculoid fauna undergoes remarkable changes in composition. Most stations below this depth provided associations consisting of *Ennucula corbuloides, Ledella messanensis, Yoldiella micrometrica, Y. seguenzae, Microgloma tumidula,* and also including *Katadesmia cuneata* below 800 m. *E. corbuloides*, mostly known from the Tyrrhenian Sea (DI GERONIMO & LI GIOI, 1981; DI GERONIMO & BELLAGAMBA, 1986; DI GERONIMO *et al.*, 2001), is also present in the European North Atlantic (RHIND & ALLEN, 1992; SALAS, 1996, as *E. bushae*: see notes) and in the Eastern Mediterranean (JANSSEN, 1989), from ca 500 m to more than 3000 m. In the southern Tyrrhenian stations it is one of the dominant species, often accounting for more than 50% of nuculoid component (Fig. 2a). *L. messanensis* is also well represented in these stations (Fig. 2d), ranging from ca 600 m and becoming less and less common below 1000 m. Its European depth range is 200-2000 m (WARÉN, 1989), but in the Alboran Sea and the Ibero-Moroccan Gulf it ranges from 450 m (SALAS, 1996). A similar bathymetric distribution is shared by *Y. seguenzae* (BONFITTO & SABELLI, 1995; SALAS, 1996). Two small species, *Microgloma tumidula* and *Yoldiella micrometrica*, are notably common, mostly occurring from ca 700 m (Fig. 2c), with a marked increase in dominance of *Y. micrometrica* with depth. *M. tumidula* has been mostly overlooked until recent times due to its very small size (ca 1 mm). Through its latitudinal distribution (Bay of Biscay south to Canary Islands), it ranges from 200 to more than 2000 m (OCKELMANN & WARÉN, 1998). *Y. micrometrica* (not exceeding 2 mm), mostly reported from the Tyrrhenian Sea (DI GERONIMO & LI GIOI, 1981; DI GERONIMO & BELLAGAMBA, 1986; BELLAGAMBA, 1986; DI GERONIMO *et al.*, 2001), is also present in the Eastern Basin (JANSSEN, 1989). Its occurrence in the Northeast Atlantic (JEFFREYS,1879) need confirmation, as the species has been no
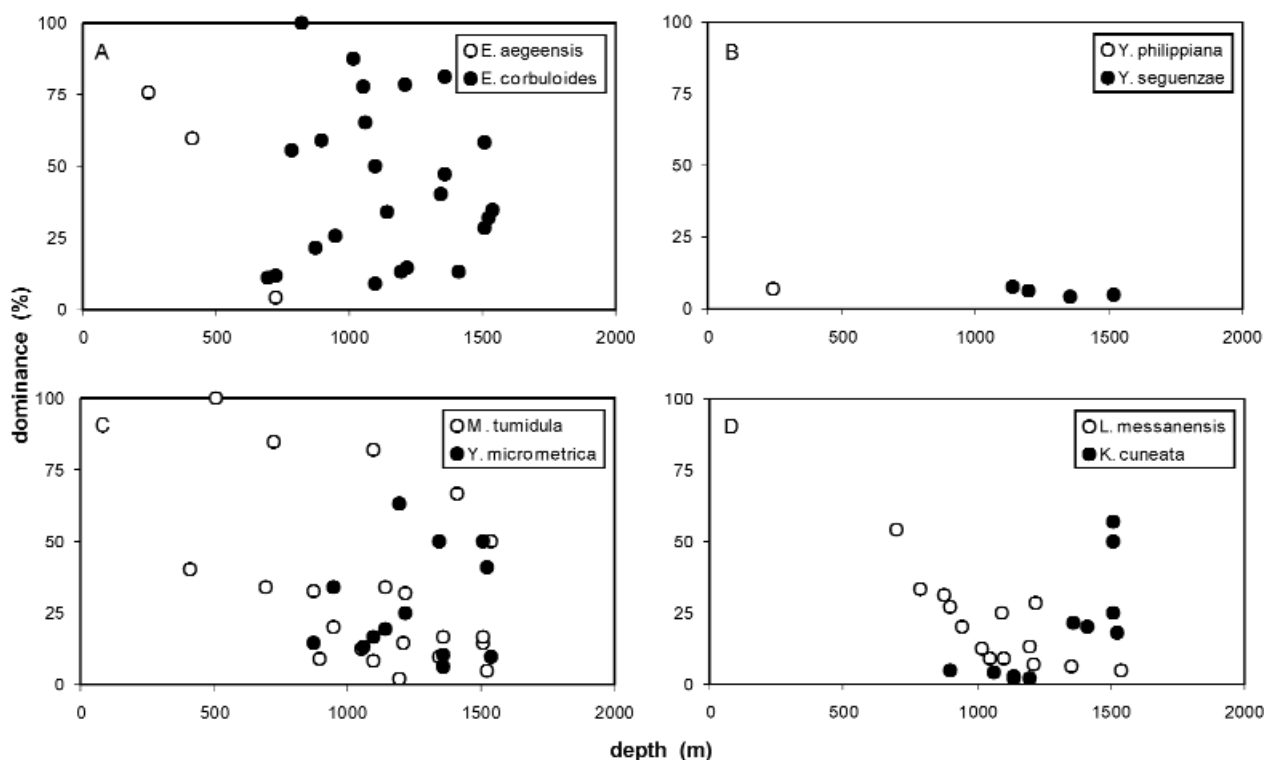

Fig. 2. Bathyal thanatocoenoses from the southern Tyrrhenian Sea. Dominance of the most common species in the nuculoid associations. Each circle denotes a station. Data from DI GERONIMO *et al.*(2001).

Fig. 2. Tanatocenosi batiali del Mar Tirreno meridionale. Valori di dominanza delle specie più comuni nelle associazioni a nuculoidi. Ogni cerchio indica una stazione. Dati da DI GERONIMO *et al.* (2001).

| PROTOBRANCHIA Pelseneer, 1889 | | |
| NUCULOIDA Dall, 1889 | Mediterranean | |
	Pleistocene	Recent
NUCULIDAE Gray J.E., 1824		
Nucula sulcata Bronn, 1831	+	+
Nucula aff. *tumidula* Malm, 1860	+ g	
Ennucula aegeensis (Forbes, 1844)	(+)	+
Ennucula decipiens (Philippi, 1844)	+	+
Ennucula sp.	E	
Ennucula corbuloides (Seguenza, 1877)	+	+
Ennucula rotundata (Seguenza, 1877)	E	
Deminucula trigona (Seguenza, 1877)	E	
Brevinucula glabra (Philippi, 1844)		E
?SAREPTIDAE Stoliczka, 1871		
"*Yoldia*" *minima* Seguenza, 1877	+ g	
NUCULANIDAE Adams H. & A., 1858		
Thestyleda cuspidata (Philippi, 1844)	E	
Propeleda hoernesi (Bellardi, 1875)		E
Saccella commutata (Philippi, 1844)	+	+
Jupiteria erctensis (Brugnone, 1876)		E
Jupiteria gibba (Seguenza, 1877)	E	
Ledella messanensis (Jeffreys, 1870)	+	+
Ledella rectidorsata (Seguenza, 1877)	E	
Yoldiella lucida (Lovén, 1846)	(+) g	
Yoldiella nana (Sars M., 1865)	+	+
Yoldiella philippiana (Nyst, 1845)	+	+
Yoldiella seguenzae Bonfitto & Sabelli, 1995	+	+
Yoldiella micrometrica (Seguenza, 1877)	+	+
Yoldiella sp.	E	
Bathyspinula excisa (Philippi, 1844)		E
Microgloma pusilla (Jeffreys, 1879)	+	+
Microgloma tumidula (Monterosato, 1880)	+	+
Microgloma aff. *yongei* Sanders & Allen, 1973		+
MALLETIIDAE Adams H. & A., 1858		
Pseudomalletia caterinii (Appelius, 1871)	E	
Pseudomalletia obtusa (Sars G.O., 1872)	+	+
Neilo dilatata (Philippi, 1844)	E	
Neilo isseli Bellardi, 1875	E	
Katadesmia confusa (Seguenza, 1877)	E	
Katadesmia cuneata (Jeffreys, 1876)	(+)	+
NEILONELLIDAE Shileyko, 1989		
Austrotindaria latior (Jeffreys, 1876)	g	
Austrotindaria pusio (Philippi, 1844)	E	
Austrotindaria salicensis (Seguenza, 1877)	E	
PHASEOLIDAE Scarlato & Starobogatov, 1971		
Phaseolus ovatus Seguenza, 1877	E	

Tab. 1. Check-list of the bathyal Quaternary nuculoids from the Mediterranean. Symbols: + = occurrence, (+)= inferred occurrence, E= extinct, g= occurrence in the Late Glacial. Systematic arrangement mainly according to OCKELMANN & WARÉN (1998).
Tab. 1. Check-list dei nuculoidi batiali del Quaternario presenti in Mediterraneo. I simboli indicano: + = presenza, (+) = presenza dubbia, E = specie estinta, g = presenza nell'ultima fase glaciale. L'arrangiamento sistematico segue principalmente OCKELMANN & WARÉN (1998).

longer reported from this area. The last species, *K. cuneata*, ranges from ca 800 m becoming more common below 1000 m (Fig. 2d). It seems to have an almost world-wide distribution (KNUDSEN, 1970; SANDERS & ALLEN, 1985) and living specimens have been collected from off Marseille, 1000 m deep (GOFAS, *pers. comm.*). Tab. 2 reports the composition of three mesobathyal associations from 696 m, 1061 m and 1521 m. Three points are worth of being noted: increasing species richness, constant occurrence of *E. corbuloides*, *L. messanensis* and *M. tumidula*, occurrence of *K. cuneata* in the deepest station. Data from the deepest part of the Mediterranean are scant. According to the pattern described above and few literature

records (D'AMICO, 1912; DI GERONIMO & PANETTA, 1973; JANSSEN, 1989), at 2000-3000 m the nuculoid fauna consists mainly of *E. corbuloides*, *Y. micrometrica* and *K. cuneata*.

Some deep-sea nuculoids, mostly known from the Northeast Atlantic, have been recorded from the Mediterranean, where they must be markedly rare or with a limited distribution. Few shells of *Yoldiella nana* were reported by WARÉN (1989) from off southern France and a single valve was found at 786 m in the southern Tyrrhenian (DI GERONIMO *et al.*, 2001). Scant records of valves and specimens of *Microgloma pusilla* were reported by OCKELMANN & WARÉN (1998) from the Tyrrehnian. Also *Pseudomalletia obtusa* has been found in the Tyrrhenian (living?) (D'AMICO, 1912) and as valves in the Jonian (DI GERONIMO & PANETTA, 1973). SALAS (1996) reported *Ennucula decipiens* from epibathyal stations in the Alboran Sea and the Ibero-Moroccan Gulf and few slightly worn valves are from the Sicily Channel (LA PERNA, unpubl.).

Instead other Atlantic species are suspected to be absent from the Recent Mediterranean. Although their shells are found, the bad preservation of this material points to a Late Glacial age. Valves of *Yoldiella lucida*, *Nucula* aff. *tumidula* and "*Yoldia*" *minima* (see notes) may be rather common locally and another species, *Austrotindaria latior* (see notes) is also rarely found. It can be argued that these species shade into the group of "rare" ones, but they cannot be included among the Recent fauna, unless they are found living, or in fresh conditions within associations of clear Holocene age.

THE PLEISTOCENE NUCULOID FAUNA

The Early-Middle Pleistocene deep-sea sediments usually contain rich nuculoid faunas which encompass a rather wide range of composition. As many of these species are extinct, to understand the paleobathymetric meaning of species and associations, a data set consisting of 47 samples x 18 species was processed by means of the Principal Component Analysis (R-mode). On the plane of the first two components, accounting for 55.3 % of the total variance, species were ordered as follows (Fig. 3). Three

| *station* | 37 | 35 | 31 | 15 |
depth	248	696	1061	1521
Nucula sulcata	3.4			
Ennucula aegeensis	75.8			
Ennucula corbuloides		11.4	65.2	31.8
Microgloma tumidula		34.3	13.0	4.5
Saccella commutata	13.8			
Ledella messanensis		54.3	4.3	
Yoldiella micrometrica			13.0	40.9
Yoldiella philippiana	6.9			
Yoldiella seguenzae				4.5
Katadesmia cuneata			4.3	18.2

Tab. 2. Examples of Recent bathyal nuculoid associations from the souhern Tyrrhenian Sea. Data from DI GERONIMO *et al.* (2001) and unpubl.
Tab. 2. Esempi di associazioni batiali attuali a nuculoidi del Mar Tirreno meridionale. Dati da DI GERONIMO *et al.* (2001) e dati non pubblicati.
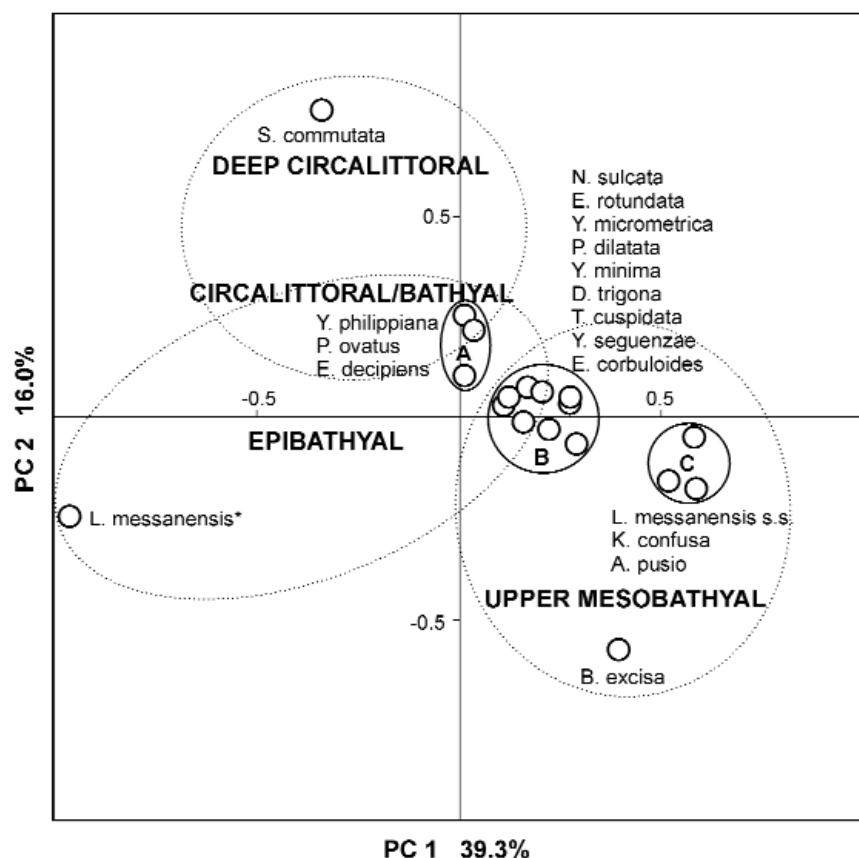
Cluster A, including *Yoldiella philippiana*, *Phaseolus ovatus* and *Ennucula decipiens*, is the nearest to *S. commutata*. Taking into account the Recent distribution of *S. commutata* (mostly circalittoral), of *Y. philippiana* (deep circalittoral to epibathyal) and of *E. decipiens* (epibathyal), this part of the plot appears to be characterised by "shallow" species. Indeed some of the studied nuculoid associations consist of *S. commutata*, *Y. philippiana* and *Nucula sulcata*, clearly indicating (like the whole molluscan fauna) the deepest circalittoral zone to the circalittoral/bathyal transition. This composition, lacking any true deep-sea species, changes towards increasing species richness, the "loss" of *S. commutata* and strong dominance of *L. messanensis** (up to 90%). The nuculoid associations composed mostly by *L. messanensis** and including *Y. philippiana, P. ovatus, E. decipiens* (the last two species usually scarce) and other species, are then indicative of upper bathyal depths, most probably not exceeding 500 m. Cluster B includes some of the species frequently occurring within such epibathyal associations, i.e. *N. sulcata, Deminucula trigona* and *Neilo dilatata*, but other less common species, i.e. *Brevinucula glabra, Jupite-*

Fig. 3. R-Mode PCA analysis on 47 samples x 18 species (covariance matrix). Data on variables (species) were scored as dominance (%) in each nuculoid association (samples). Species are plotted on the first two component plane (55.3% of total variance). Data from Di Geronimo & La Perna (1997), Di Geronimo et al. (1997); D'Alessandro et al. (2003), La Perna (unpubl.). Comments in the text.

Fig. 3. Analisi delle componenti principali (PCA, R-Mode) su 47 campioni per 18 specie (matrice di covarianza). I dati relativi alle variabili (specie) sono espressi come dominanza (%) per ognuna delle associazioni a nuculoidi (campioni). Le specie sono proiettate sul piano delle prime due componenti (55.3% della varianza totale). Dati da Di Geronimo & La Perna (1997), Di Geronimo et al. (1997), D'Alessandro et al. (2003), La Perna (non pubblicati). Commento nel testo.

species, namely *Saccella commutata, Ledella messanensis** (= a shallower ecotype; Fig. 4 and systematic notes) and *Bathyspinula excisa*, are isolated forming the corners of a triangle, while the other species are roughly aligned between *S. commutata* and *B. excisa*, as three clusters (A, B, C).

Tab. 3. Examples of Early-Middle Pleistocene bathyal nuculoid associations from Souhern Italy. Samples A and B from Grammichele, southeastern Sicily (La Perna, unpubl.); sample C from Archi, southern Calabria (Di Geronimo et al., 1997), sample D from Furnari, northeastern Sicily (Di Geronimo & La Perna, 1997). Asterisk indicates unscored species not present in the bulk-sample.

Tab. 3. Esempi di associazioni batiali a nuculoidi del Pleistocene inferiore-medio dell'Italia meridionale. Campioni A e B da Grammichele, Sicilia sud-orientale (La Perna, dati non pubblicati); campione C da Archi, Calabria meridionale (Di Geronimo et al., 1997), campione D da Furnari, Sicilia nord-orientale (Di Geronimo & La Perna, 1997). Gli asterischi indicano le specie non quantificate, non presenti nel campione volumetrico.

| sample	A	B	C	D
Nucula sulcata	7.3	1.6	0.2	5.8
Ennucula decipiens			0.8	0.9
Ennucula curbuloides			1.3	1.2
Ennucula rotundata				0.3
Ennucula sp.				0.1
Deminucula trigona		2.2		
"Yoldia" minima			2.9	0.3
Saccella commutata	30.9	9.0		
Propeleda heornesi		1.0		
Testhyleda cuspidata			1.5	2.0
Ledella messanensis			45.4	4.2
Ledella messanensis*		79.0		
Ledella rectidorsata			1.5	
Yoldiella micrometrica				0.3
Yoldiella philippiana	61.8			
Yoldiella seguenzae			3.3	0.8
Bathyspinula excisa			25.3	73.4
Microgloma tumidula				*
Microgloma pusilla				*
Austrotindaria pusio			13.8	5.2
Pseudomalletia isseli		6.5		
Katadesmia confusa			4.0	4.6
Phaseolus ovatus		0.7		0.9
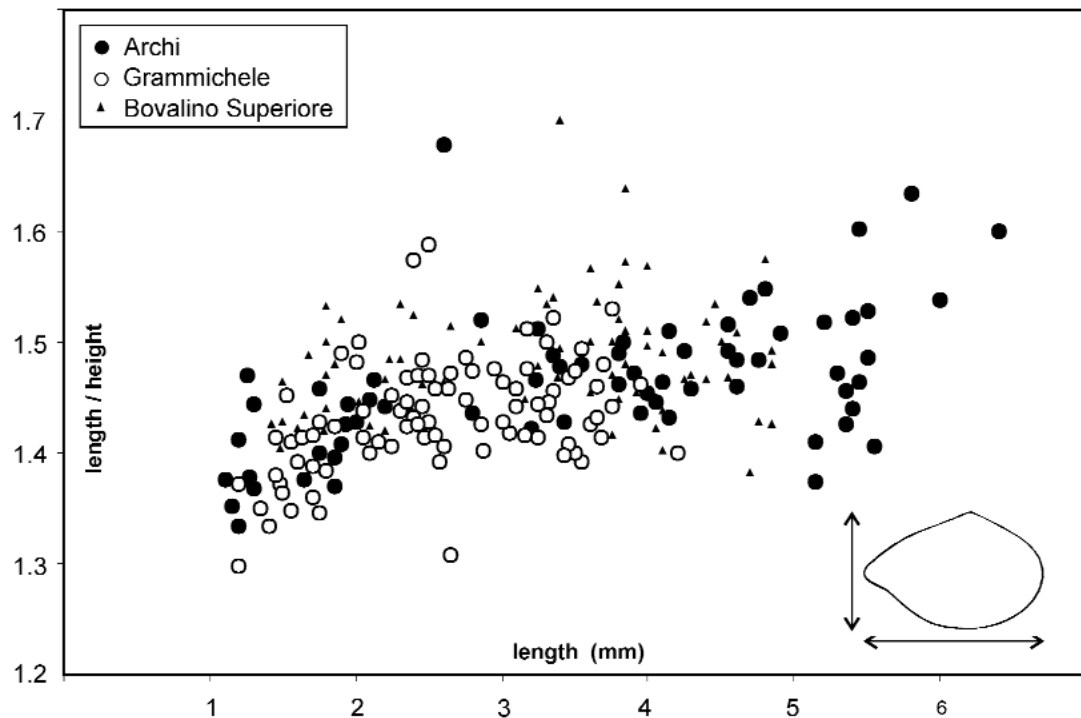
Fig. 4. Morphometric analysis on three Pleistocene populations of *Ledella messanensis*. The examined populations are form Archi, southern Calabria (DI GERONIMO *et al.,* 1997), Grammichele, southeastern Sicily (LA PERNA, unpubl.) and Bovalino Superiore, southern Calabria (LA PERNA, unpubl.). Comments in the text.
Fig. 4. Analisi morfometrica di tre popolazioni pleistoceniche di *Ledella messanensis*. Le popolazioni esaminate provengono da Archi, Calabria meridionale (DI GERONIMO *et al.*, 1997), Grammichele, Sicilia sud-orientale (LA PERNA, unpubl.) e Bovalino Superiore, Calabria meridionael (LA PERNA, dati non pubblicati). Commento nel testo.

ria erctensis, *J. gibba, Propeleda hoernesi, Neilo isseli* and *Pseudomalletia caterinii*, may be present.
One of the compositional changes pointing to deeper associations is the occurrence of some extant species which range mostly from ca 500 m (see above), i.e. *E. corbuloides, Y. seguenzae, Y. micrometrica* and *L. messanensis* s.s. These species, except for the last one, are clustered in B. The associations in which these species occur (*Y. micrometrica* is always rare), often include also *N. sulcata, Ennucula rotundata, "Yoldia" minima, Thestyleda cuspidata* (cluster B) and, more rarely, *Ledella rectidorsata*. However, the most obvious compositional feature is the occurrence of three species, *Katadesmia confusa, Austrotindaria pusio* and *Bathyspinula excisa* (which may be rarely present also within epibathyal associations). These species are placed, together with *L. messanensis* s.s., in the "deepest" part of the plot. Mesobathyal associations, or upper mesobathyal at least, are then characterised by the species clustered in C and by *B. excisa*, together with some of the species clustered in B. DI GERONIMO & LA PERNA (1997) and DI GERONIMO *et al.* (1997) reported several Pleistocene faunas whose composition in nuculoids matches this pattern. The meaning of *B. excisa* and of its high dominance as indicative of "great depths" was stressed by DI GERONIMO & LA PERNA (1996), who remarked the cold deep-sea distribution of the world-wide genus *Bathyspinula*, including only bathyal and abyssal species.
The genus *Microgloma* was present in the Pleistocene with three species (see notes), but only *M. tumidula* was notably common. As most samples were sieved through a 500 mm mesh, quantita-

tive data are not always available for these species.
Tab. 3 reports four Pleistocene nuculoid associations whose composition can be referred to different ecological-bathymetric settings. The first (A), consisting of *Y. philippiana* (dominant), *S. commutata* and *N. sulcata*, can be referred to the deepest circalittoral zone or to the circalittoral/bathyal transition (this may be better defined on the base of the whole mollusc fauna). The following one (B) is more diverse (6 species) and is dominated by the shallower ecotype of *L. messanensis*. Among the other species, *S. commutata, D. trigona* and *N. isseli* are worth of being noted. This fauna represents a typical epibathyal nuculoid association, not exceeding 500 m. Association C is even more diverse (11 species), dominated by *L. messanensis* s.s., *B. excisa* and *A. pusio* (together accounting for 88% of nuculoids) and including also *E. corbuloides* and *Y. seguenzae*. It can be referred to depths greater than 500 m. The last association (D) may be the deepest one: it is highly diverse (16 species), strongly dominated by *B. excisa* (73%), and including *N. sulcata, A. pusio, K. confusa* and *L. messanensis* s.s. as markedly abundant species.
The general meaning of the plot can be then summarized as follows. Species are mainly ordered according to their depth-related dominance. The "alignment" *commutata-excisa* defines the main depth-related pattern (shallow to deep), while the isolated species *S. commutata, L. messanensis** and *B. excisa* characterize, by their strongly contrasting high dominance, distinct ecological/bathymetric settings (deep circalittoral, epibathyal and upper mesobathyal, respectively).
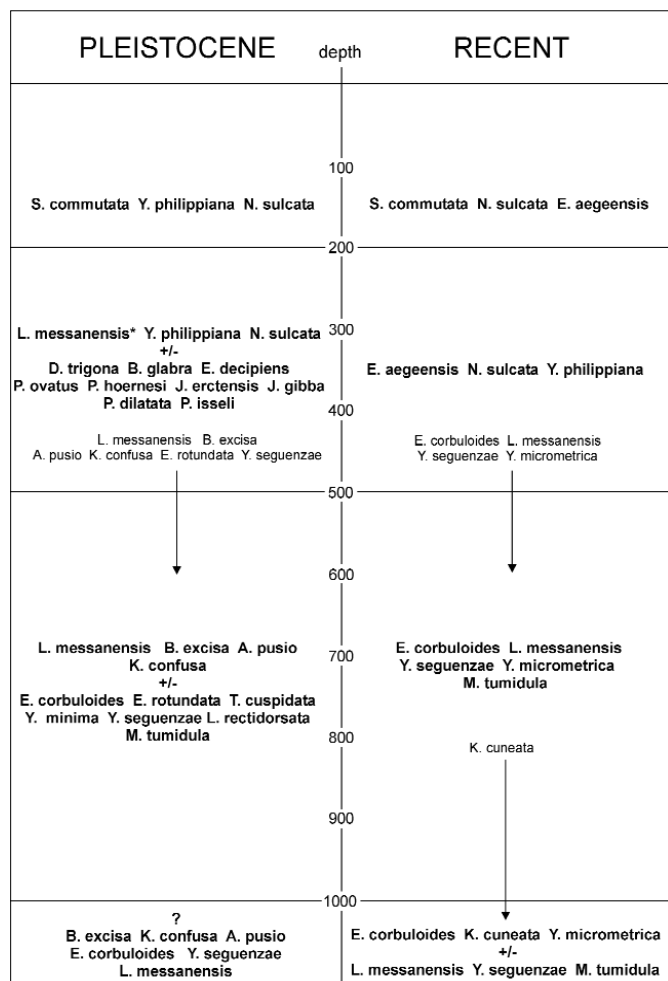Unfortunately, there is no ground to evaluate more precisely

PLEISTOCENE	depth	RECENT
	100	
S. commutata Y. philippiana N. sulcata		S. commutata N. sulcata E. aegeensis
	200	
L. messanensis* Y. philippiana N. sulcata +/- D. trigona B. glabra E. decipiens P. ovatus P. hoernesi J. erctensis J. gibba P. dilatata P. isseli	300 400	E. aegeensis N. sulcata Y. philippiana
L. messanensis B. excisa A. pusio K. confusa E. rotundata Y. seguenzae		E. corbuloides L. messanensis Y. seguenzae Y. micrometrica
	500	
	600	
L. messanensis B. excisa A. pusio K. confusa +/- E. corbuloides E. rotundata T. cuspidata Y. minima Y. seguenzae L. rectidorsata M. tumidula	700 800	E. corbuloides L. messanensis Y. seguenzae Y. micrometrica M. tumidula
		K. cuneata
	900	
? B. excisa K. confusa A. pusio E. corbuloides Y. seguenzae L. messanensis	1000	E. corbuloides K. cuneata Y. micrometrica +/- L. messanensis Y. seguenzae M. tumidula

Fig. 5. Composition and bathymetric distribution of the Pleistocene and Recent nuculoid associations. Bold marks species forming typical associations; arrows indicate species becoming more typical within deeper associations.

Fig. 5. Composizione e distribuzione batimetrica di associazioni a nuculoidi pleistoceniche ed attuali. In grassetto sono indicate le specie che formano associazioni tipiche; le frecce indicano specie più tipicamente presenti in associazioni di maggiore profondità.

depths greater than 500 m, neither basing on nuculoid, nor on molluscs in general or other macrofaunas (DI GERONIMO et al., 1997), but depths greater than "1000 m" are hardly supportable, taking into account the present altitude of the Pleistocene sequences and the vertical tectonic displacements (BARRIER et al., 1985; MONTENAT & BARRIER, 1987).

SYSTEMATIC NOTES

Several Pleistocene bathyal nuculoids were elsewhere commented on and illustrated (DI GERONIMO & LA PERNA, 1996, 1997; DI GERONIMO et al., 1997; LA PERNA, 1998). In the following part further comments on these and other less known species are given.

Nucula aff. tumidula Malm, 1860

Few Pleistocene valves (Pl. 1, Fig. 10) and some others from Late Glacial thanatocoenoses (Pl. 1, Fig. 9) are tentatively referred to the same species, although the Late Glacial valves

have a thinner wall and a little stronger sculpture. This material is very similar to that reported by SALAS (1996) as *Nucula tumidula* Malm, 1860 from the Ibero-Moroccan Gulf. However, the specimens of *N. tumidula* from the Northern Europe (from which the species was described) are more ovate, tumid and inaequilateral. As suggested by WARÉN (pers. comm.), *N. tumidula* might show a clinal variation. The southern end of such a cline may be represented by the form living in the Ibero-Moroccan Gulf and by the closely related fossil Mediterranean form. More study on geographically intermediate populations is needed to understand the meaning of these differences. *Nucula umbonata* Seguenza, 1877, described from Plio-Pleistocene deepwater beds, was thought by JEFFREYS (1879) to be the juvenile form of *N. tumidula.* However, description and illustrations of *N. umbonata* do not match well *N. tumidula*, they are not based on particularly young specimens and SEGUENZA (1877) himself remarked differences between *N. tumidula* and *N. umbonata.*

Ennucula aegeensis (Forbes, 1844), *E. decipiens* (Philippi, 1844), *Enncucula* sp.

Although the problem of naming the smooth-margined nuculids has been recently reduced (DI GERONIMO & LA PERNA, 1997; KILBURN, 1999), it is still open to question. *Ennucula* Iredale, 1931 should be used for species with ovate, moderately thick-walled shells and a more or less oblique chondrophore. Other smooth-margined nuculids are probably worthy of a distinction (see below).

E. aegeensis (Pl. 1, Fig. 3) is widespread all through the Mediterranean, from the Alboran Sea (SALAS, 1996) to the Eastern Basin (JANSSEN, 1989), and is also present in Ibero-Moroccan Gulf (SALAS, 1996). Although it has been recently recognised in the Late Pliocene of North Italy (Romagna) (CEREGATO, pers. comm.), *E. aegeensis* has been not confirmed for the Pleistocene (past records might be misidentifications of *E. decipiens*). Probably, this species was not as much widespread and common as in the present days.

E. decipiens (Pl. 1, Figs. 1, 2) was described from the Pleistocene of Southern Italy and I agree with the interpretation of this species given by SALAS (1996). It can be distinguished from *E. aegeensis* mainly by having more inaequilateral valves, with a strongly posterior umbo and a more oblique chondrofore. The distribution of *E. decipiens* seems to range from the Bay of Biscay south to the Alboran Sea and the Western Mediterranean (SALAS, 1996; WARÉN, pers. comm.).

Ennucula sp. is rare and the examined material is fragmentary. Valves are markedly elongated, somewhat fragile and with an elongated strongly oblique chondrophore. A valve was illustrated by PALAZZI & VILLARI (1994) as *Nuculoma* sp.

Ennucula corbuloides (Seguenza, 1877), *E. rotundata* (Seguenza, 1877)

SALAS (1996) and DI GERONIMO & LA PERNA (1997) left dubitatively *E. corbuloides* distinct from *E. bushae* (Dollfus, 1898), but the impossibility to find conspicuous differences leads to synonymise *E. bushae* with *E. corbuloides.*

The differences between *E. corbuloides* (Pl. 1, Fig. 7) and *E.*

rotundata (Pl. 1, Fig. 8) were remarked by DI GERONIMO & LA PERNA (1997), who also stressed a close similarity between the latter and the Recent North Atlantic *E. granulosa* (Verrill, 1884), which is considered a distinct species (LA PERNA , unpubl. data) *E. corbuloides* ranges from ca 500 m, and also *E. rotundata* is mostly found within Pleistocene mesobathyal associations. A type valve of "*Nucula corbuloides*" was recently illustrated by BERTOLASO & PALAZZI (2000), but it must be referred to *E. rotundata* (which was described as a variety of *Nucula corbuloides*).

The group including *E. corbuloides, E. rotundata, E. granulosa* and also *E. corticata* (Møller, 1842) differs from the other smooth-margined nuculids properly referred to *Ennucula* by having more convex and equilateral shell, thinner wall, vertically projecting chondrophore and dull surface.

Brevinucula glabra (Philippi, 1844)
Brevinucula Thiele, 1934 includes small nuculids with thick-walled triangular valves, smooth inner margin and a small not projecting chondrophore. *B. glabra* (Pl. 1, Figs. 4, 5) was a common Pleistocene epibathyal species. The sole Recent representative of *Brevinucula* in the Northeast Atlantic is *B. verrilli* (Dall, 1886), with higher valves and a much deeper (from 1600-2000 m) distribution (KNUDSEN, 1970; RHIND & ALLEN, 1992).

Deminucula trigona (Seguenza, 1877)
There is no general agreement about the taxonomic validity of *Deminucula* Iredale, 1931 (e.g. BERGMANS, 1978; MAXWELL, 1988), which includes rather small nuculids, with triangular valves, finely crenulated inner margin, small not projecting chondrophore and a sculpture of thin radial striae (which appear to be an inner wall structure feature, rather than a true sculpture). I allocate in this genus the present species (Pl. 1, Fig. 6), as well as the Pliocene bathyal *D. striatissima* (Seguenza, 1877) (both species illustrated by PALAZZI & VILLARI, 1996). *D. trigona* had a mainly epibathyal distribution. No markedly close species is known from the Northeast Atlantic. *Nucula atacellana* Schenk, 1939, referred to *Deminucula* by RHIND & ALLEN (1992), has a true sculpture of concentric and radial ribs and should be not included in this taxon, in spite of its triangular shape. A good representative is the Eastern Pacific *D. profundorum* (Smith, 1885), which was maintained in *Nucula* by COAN *et al.* (2000).

Jupiteria erctensis (Brugnone, 1876), *J. gibba* (Seguenza, 1877)
The meaning and full validity of *Jupiteria* Bellardi, 1875 was recently stressed by LA PERNA (1998). New studies on the genus *Jupiteria* in the Mediterranean Pliocene are in progress (LA PERNA *et al.*). Both *J. erctensis* and *J. gibba* are found within Pleistocene epibathyal associations.

"Yoldia" minima Seguenza, 1877
It is difficult to find a systematic allocation for this species yet (Pl. 3, Figs. 14, 15), as discussed by DI GERONIMO & LA PERNA (1997). It is tentatively allocated in the Sareptidae, which is also a problematic family (OCKELMANN & WARÉN, 1998). A very similar Northeast Pacific species was treated by COAN *et al.* (2000), who referred it to *Pseudoglomus* Dall, 1898 but, as reported by OCKELMANN & WARÉN, (1998), this genus has a quite different ligament. "*Y.*" *minima* was common in the Pleistocene and occurs also in Late Glacial thanatocoenoses. JEFFREYS (1879) reported this species from some deep-sea stations in the Northeast Atlantic (37°-48°N) and a type valve was recently illustrated by BERTOLASO & PALAZZI (2000).

Thestyleda cuspidata (Philippi, 1844), *Propeleda hoernesi* (Bellardi, 1875)
The reason for keeping *Thestyleda* Iredale, 1929 distinct from *Nuculana* Link, 1807 was discussed by DI GERONIMO & LA PERNA (1997). *T. cuspidata* (Pl. 2, Figs. 2, 3) is found within meso-bathyal Pleistocene associations. No notably similar species is known from Europe, but the genus occurs in the Atlantic (three species were reported by ALLEN & SANDERS, 1996a under *Propeleda*).

The allocation of *Leda hoernesi* Bellardi, 1875 (Pl. 2, Fig. 1) in *Propeleda* Iredale, 1924 was also proposed by DI GERONIMO & LA PERNA (1997). As remarked by MAXWELL (1988), *Propeleda* is characterized by elongated, flat, smooth valves with a rather squat straight rostrum. Teeth are chevron shaped, except for the proximal ones which tend to be slightly lamellar, due to the shortness of the lower limb. A good description of a typical *Propeleda* species was given by NIJSSEN-MEYER (1972). The general distribution of this genus is not known, but it seems to be not particularly deep (circalittoral and epibathyal). *P. hoernesi* was not common in the Pleistocene and is found in epibathyal beds. It was present also in the Late Miocene and the Pliocene (ROBBA, 1990).

Ledella messanensis (Jeffreys, 1870)
DI GERONIMO & LA PERNA (1997) remarked the occurrence in the Mediterranean Pleistocene of a morphotype corresponding to *Ledella nicotrae* (Seguenza, 1877). These shells, which differ from the typical form of *L. messanensis* (Pl. 2, Fig. 6) by being smaller, less solid, less rostrate and with a more thinner hinge (Pl. 2, Fig. 7), are always found in epibathyal associations,

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Plate 1
Figs. 1, 2. *Ennucula decipiens* (Philippi, 1844). 1. Sicily Channel, st. CS 71-16, 396-241 m, Late Glacial, 6.6 mm. 2. Bovalino Superiore (S Calabria), Pleistocene, 5.1 mm. **Fig. 3.** *Ennucula aegeensis* (Forbes, 1844). Southern Tyrrhenian, EOCUMM st. 37, 248 m, 3.1 mm. **Figs. 4, 5.** *Brevinucula glabra* (Philippi, 1844). 4. Grammichele (SE Sicily), Pleistocene, 3.2 mm. 5. Bovalino Superiore (S Calabria), Pleistocene, 3.0 mm. **Fig. 6.** *Deminucula trigona* (Seguenza, 1877). Fiumefreddo di Sicilia (NE Sicily), Pleistocene, 3.4 mm. **Fig. 7.** *Ennucula corbuloides* (Seguenza, 1977), EOCUMM st. 14, 2.2 mm. **Fig. 8.** *Ennucula rotundata* (Seguenza, 1877). Vallone Catrica (S Calabria), Pleistocene, 2.3 mm. **Figs. 9, 10.** *Nucula aff. tumidula* Malm, 1860. 9. Off E Sardinia, st. BS 78-2, 1281-330 m, Late Glacial, 4.2 mm. 10. Fiumefreddo di Sicilia (NE Sicily), Pleistocene, 6.7 mm. **Fig. 11.** *Bathyspinula excisa* (Philippi, 1844), Archi (S Calabria), Pleistocene, 6.3 mm. **Figs. 12, 13.** *Austrotindaria pusio* (Philippi, 1844). 12. Archi (S Calabria), Pleistocene, 5.4 mm. 13. Grammichele (SE Sicily), Pleistocene, 3.2 mm (?= *Leda striolata* Brugnone, 1876).
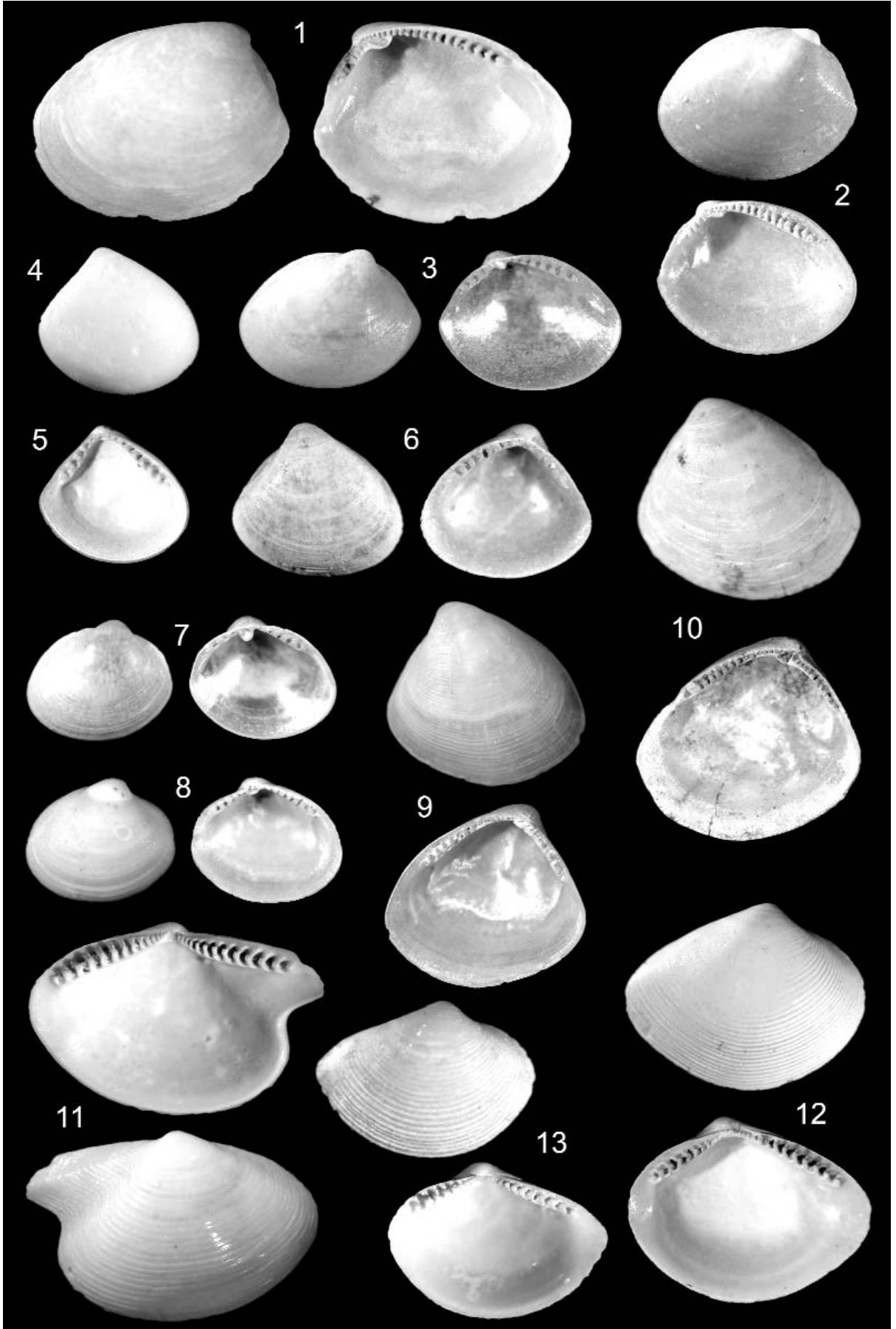
where they are often dominant, while the typical form is found deeper. A morphometric analysis (Fig. 4) on three Pleistocene populations shows a wide overlapping between "*L. nicotrae*", the typical *L. messanensis* and a transitional form. It is also worth noting that the transitional form (Pl. 2, Figs. 8, 9) comes from a deep-epibathyal association. These observations suggest that these populations pertain to a single species. *L. nicotrae* must be then synonymised with *L. messanensis*, of which the former represented a shallower ecotype. Although a certain variability is known amongst the Recent populations of *L. messanensis* (WARÉN, 1978, 1989), "*L. nicotrae*" is only known from the Mediterranean Pleistocene. BERTOLASO & PALAZZI (2000) found type material of *Leda nicotrae* Seguenza which does not match closely the original description and illustrations (replacement or substitution of the original material?). However, the presently studied material leaves no doubt about the identity of *L. nicotrae*.

Ledella rectidorsata (Seguenza, 1877)

This species (Pl. 2, Figs. 10, 11) differs from *L. messanensis* mainly by having less convex valves with a straighter dorsal margin and a fine concentric sculpture. *L. rectidorsata* is markedly similar to *L. folini* Warén, 1978, only known from the Bay of Biscay (WARÉN, 1978). The latter differs mainly by having closely set sharp ridges with intercalating finer lines (a finer sculpture is present in *L. rectidorsata*) and by more pointed anterior and posterior endings. This species is only known from mesobathyal Pleistocene beds, where it can be somewhat abundant and probably related to a conspicuous amount of sandy fraction.

Yoldiella lucida (Lovén, 1846), *Y. nana* (M. Sars, 1865)

Y. lucida (Pl. 3, Fig. 3) is the most common Late Glacial nuculoid found in the Mediterranean. Although yet to be found, the species occurred also in the Early-Middle Pleistocene, as based on the clear illustration given by SEGUENZA (1877) and who also remarked its rareness.

Y. nana (Pl. 3, Figs. 4, 5) is rare in the Mediterranean. It was probably more common during the Pleistocene, when it occurred within deep circalittoral and bathyal faunas. The past Mediterranean records of *Yoldiella frigida* (Torell, 1859), a high-Arctic species, were proved by WARÉN (1989) to be based on misidentifications of *Y. nana*.

Yoldiella philippiana (Nyst, 1845), *Y. seguenzae* Bonfitto & Sabelli, 1995

Even considering *Yoldiella* Verrill & Bush, 1897 in a strict sense, i.e excluding those species which verge towards *Ledella* Verrill & Bush, 1897 (e.g. KILBURN 1994; DI GERONIMO & LA PERNA, 1997; COAN *et al.*, 2000), this genus still remains too heterogeneous. The need to redefine the current usage of

Yoldiella clearly appears by comparing the six species illustrated in the present work (Pl. 3, Fig. 1-8).

Yoldiella micrometrica (Seguenza, 1877), *Yoldiella* sp.

As also noted by SEGUENZA (1877), *Y. micrometrica* was notably rare in the Pleistocene, whereas it is now one of the most common mesobathyal nuculoid. The Pleistocene form (Pl. 3, Fig. 6), which has been never illustrated since its description, seems to match the Recent one (Pl. 3, Fig. 7). A similar rare Pleistocene species (Pl. 3, Fig. 8) seems to be undescribed and is currently under study.

Bathyspinula excisa (Philippi, 1844)

This species (Pl. 1, Fig. 11) was one of the most common bathyal nuculoid in the Mediterranean Pleistocene (DI GERONIMO & LA PERNA, 1996). Doubts about its "real" extinction arise from the record of a single apparently fresh valve in the Ibero-Moroccan Gulf (SALAS, 1996). In the same station (864 m), a single valve tentatively referred to the fossil species *Yoldia bronni* (Bellardi, 1875) was also found (SALAS, 1996; WARÉN, pers. comm). This may imply that also the valve of *B. excisa* is a reworked fossil. However, if *B. excisa* is still living in the adjacent Atlantic, it must be notably rare there. *B. subexcisa* (Dautzenberg & Fischer, 1897), known from the Northeast Atlantic (ALLEN & SANDERS, 1982), has a much deeper distribution (from ca 2000 m) which, together with morphological differences, points to a distinct specific status.

Microgloma tumidula (Monterosato, 1880), *M. pusilla* (Jeffreys, 1879), *M. aff. yongei* Sanders & Allen, 1973

Since the Pleistocene, *M. tumidula* (Pl. 3, Fig. 9) is the most common representative of the micromorphic genus *Microgloma* Sanders & Allen, 1973, whose taxonomy and biology were discussed by OCKELMANN & WARÉN (1998). Rare fossil valves can be referred to *M. pusilla* (Pl. 3, Fig. 11), occurring also in the Recent Mediterranean (OCKELMANN & WARÉN, 1998). Other rare valves might belong to *M. yongei* Sanders & Allen, 1973 (Pl. 3, Fig. 10). However, this identification is puzzling, as *M. yongei* was described from 1900-2700 m depth in the Angola and Cape Verde Basins (SANDERS & ALLEN, 1973), from where no other species is known to occur in Europe (WARÉN, pers. comm.). Moreover, the species reported as *M. pusilla* by SALAS (1996) from the Ibero-Moroccan Gulf seems to be same as the fossil one. I leave open the question, reporting this species tentatively as *M. aff. yongei.* Another Recent species, "*M.*" *guilonardi* (Hoeksema, 1993), needs further studies on taxonomy and distribution. This species has elongated lamellar teeth, similar to those of *Phaseolus* Monterosato, 1875 (see below), and this makes the systematic allocation in *Microgloma* (OCKELMANN & WARÉN, 1998) rather doubtful. Moreover, the Mediterranean

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Plate 2
Fig 1. *Propeleda hoernesi* (Bellardi, 1875), Bovalino Superiore (S Calabria), Pleistocene, 10.1 mm. **Figs. 2, 3.** *Thestyleda cuspidata* (Philippi, 1844), Archi (S Calabria), Pleistocene, 2. 9.7 mm, 3. 9.0 mm. **Fig. 4.** *Jupiteria erctensis* (Brugnone, 1876), Bovalino Superiore (S Calabria), Pleistocene, 6.5 mm. **Fig. 5.** *Jupiteria gibba* (Seguenza, 1877), Bovalino Superiore (S Calabria), 3.7 mm. **Figs. 6-9.** *Ledella messanensis* (Jeffreys, 1870). 6. Archi (S Calabria), Pleistocene, 5.0 mm (=typical form). 7. Grammichele (SE Sicily), Pleistocene, 3.5 mm [=*L. nicotrae* (Seguenza, 1877)]. 8, 9. Bovalino Superiore (S Calabria), Pleistocene, 8. 3.7 mm, 9. 3.9 mm (=intermediate form). **Figs. 10, 11.** *Ledella rectidorsata* (Seguenza, 1877). Lazzaro (S Calabria), Pleistocene, 10. 3.7 mm, 11. 3.4 mm.
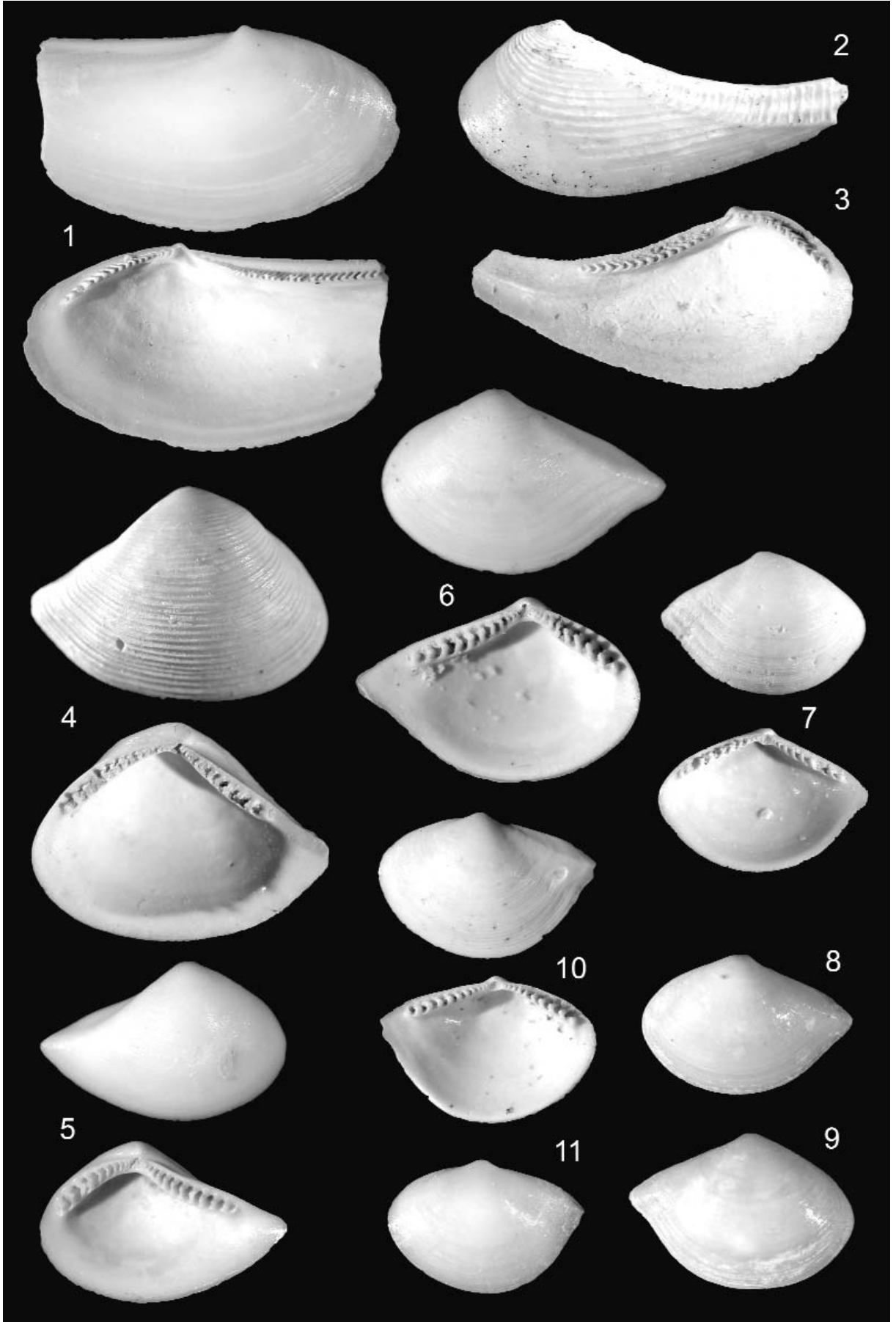
records are from deep waters (CACHIA, 1995; HOEKSEMA, 2000), thus contrasting with the shallow water distribution known in the Northeast Atlantic (HOEKSEMA, 1993, 2000; GOFAS, pers. comm.). The valve reported by HOEKSEMA (2000) from the Tyrrhenian Sea has short, almost chevron-shaped teeth and it may represents a true *Microgloma* species. These observations lead to regard the Mediterranean records of *"M."* guilonardi as based on misidentifications.

Neilo dilatata (Philippi, 1877), *N. isseli* Bellardi, 1875
No North Atlantic species has been recently referred to *Neilo* Adams, 1854, but there is evidence that this genus, probably typical to the Central Pacific (MARSHALL, 1978), was, and is, present in the North Atlantic. The typical features (MARSHALL, 1978) of this malletiid are: shell inflated, solid, with a marked posterior angulation and prominent concentric ribs. The posterior margin may be somewhat sinuous. *N. dilatata* (Pl. 4, Fig. 1) is extinct, and mostly occurring in epibathyal beds. SANDERS & ALLEN (1985) reported a single specimen of *"Malletia dilatata"* from off Cuba in 534 m (and another species from the Guyana Basin which can be also referred to *Neilo*). The shell drawing recalls the Pleistocene species but, since no East Atlantic record is known, a so widely separated distribution seems unlike for a bathyal species. On the other hand, also *N. compta* (Sowerby, 1904) from South Africa (KILBURN, 1994) is markedly similar to *N. dilatata*.
N. isseli (Pl. 4, Fig. 2), traditionally allocated in this genus, has a rather sharp posterior angulation, but the concentric sculpture is lost and the gross shell shape resembles that of *Pseudomalletia* Fischer, 1886. On the other hand, *"Malletia" johnsoni* Clarke, 1961, reported by SALAS (1996) from the Ibero-Moroccan Gulf, appears somewhat intermediate between *Neilo* and *Pseudomalletia*. Such shared features may point to a close relationship between *Neilo* and *Pseudomalletia*, the latter treated by MARSHALL (1978) as a subgenus of the former. *N. isseli* is found within Pleistocene epibathyal beds. It was more common in the Late Miocene and Pliocene (ROBBA, 1981, 1990).

Pseudomalletia obtusa (G.O. Sars, 1878), *Pseudomalletia caterinii* (Appelius, 1871)
P. obtusa seems to occur all through the Northeast Atlantic and the Mediterranean and has a markedly deep range (down to 3000 m, according to KNUDSEN, 1979). Rare Pleistocene valves (Pl. 4, Fig. 3) from mesobathyal beds are referred to this species, of which the fossil *Nucula pellucida* Philippi, 1844 might be a synonym (*nomen oblitum*).
P. caterinii (Pl. 4, Fig. 4) differs from *P. obtusa* by having markedly narrow valves and faint oblique striae, running from the anterior and antero-dorsal margin to ca 2/3 of shell length. There are several cases of oblique sculpture within nuculoids (e.g. *Lembulus* Risso, 1826, *Cnesterium* Dall, 1898, *Adrana* Adams & Adams, 1858, *Scissileda* Kilburn, 1994). Such a feature does not always have real taxonomic weight and this seems the case for *P. caterinii*. This species is rarely found in Pleistocene epibathyal beds, but it was more common during the Late Miocene and Pliocene (ROBBA, 1981, 1990).

Katadesmia cuneata (Jeffreys, 1876), *Katadesmia confusa* (Seguenza, 1877)
As remarked by DI GERONIMO & LA PERNA (1997), a group of deep-sea malletiids, including *K. confusa* (Pl. 4, Fig. 5), differs from the typical form of the genus group, of which *K. cuneata* (Pl. 4, Fig. 6) is a good representative, by having more convex and sharply rostrated valves. Nevertheless, *Katadesmia* Dall, 1908 seems the best position for these species at present. *K. confusa* was a common Pleistocene mesobathyal nuculoid. *K. cuneata* is yet to be found as a fossil (probably due to its markedly deep distribution). Because of its wide distribution, it is unlikely that this species appeared recently, and the present-day depth of the Gibraltar sill (ca 300 m) is too shallow to allow it to cross (nuculoids develop through short-lived non-planktotrophic larvae). Therefore, *K. cuneata* must have been present at least since the Pleistocene.

Austrotindaria pusio (Philippi, 1844), *A. salicensis* (Seguenza, 1877), *A. latior* (Jeffreys, 1876)
Together these species present a puzzle which was discussed by WARÉN (1989), ALLEN & SANDERS (1996a) and DI GERONIMO & LA PERNA (1997). Before summarising the problem, some words of explanation must be made about the systematic position. *Neilonella* Dall, 1881 and *Austrotindaria* Fleming, 1948 have been traditionally synonymised, but MAXWELL (1988) remarked on differences in the ligament. These differences were stressed by DI GERONIMO & LA PERNA (1997), who referred this group of species to *Austrotindaria,* based on their opisthodetic ligament (which is amphidetic in *Neilonella*).
WARÉN (1989) synonymised *Leda latior* Jeffreys, 1876 with *L. striolata* Brugnone, 1876, a Pleistocene species described from Sicily, and with *L. pusio* var. *salicensis* Seguenza, 1877, another fossil species and gave priority to *striolata*. ALLEN & SANDERS (1996a), following WARÉN, synonymised *latior* with *salicensis*, but regarded striolata as a distinct (doubtful?) species. DI GERONIMO & LA PERNA (1997) questioned the synonymy *striolata-latior-salicensis* and 1) illustrated topotypes of *pusio* and *salicensis* which were proved to be distinct species, 2) regarded *striolata* as a species of doubtful identity, 3) maintained the name

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Plate 3
Fig. 1. *Yoldiella philippiana* (Nyst, 1845), Vallone Catrica (S Calabria), Pleistocene, 4.3 mm. **Fig. 2.** *Yoldiella seguenzae* Bonfitto & Sabelli, 1995, Archi (S Calabria), Pleistocene, 3.3 mm. **Fig. 3.** *Yoldiella lucida* (Lovén, 1846), Off E Sardinia, st. BS 78-2, 1281-330 m, Late Glacial, 4.3 mm. **Figs. 4, 5.** *Yoldiella nana* (Sars M., 1865), Villafranca Tirrena (NE Sicily), Pleistocene, 4. 2.7 mm, 5. 2.4 mm. **Figs. 6, 7.** *Yoldiella micrometrica* (Seguenza, 1877). 6. Archi (S Calabria), Pleistocene, 1.7 mm. 7. Southern Tyrrhenian, EOCUMM st. 14, 1139 m, 1.5 mm. **Fig. 8.** *Yoldiella* sp., Vallone Catrica, Pleistocene, 2.0 mm. **Fig. 9.** *Microgloma tumidula* (Monterosato, 1880), Bianco (S Calabria), Pleistocene, 0.77 mm. **Fig. 10.** *Microgloma* aff. *yongei* Sanders & Allen, 1973, Vallone Catrica, Pleistocene, 0.97 mm. **Fig. 11.** *Microgloma pusilla* (Jeffreys, 1879), Furnari (NE Sicily), Pleistocene, 0.97 mm. **Figs. 12, 13.** *Phaseolus ovatus* Seguenza, 1877. Grammichele (SE Sicily), Pleistocene, 12. 1.8 mm, 13. 1.8 mm. **Figs. 14, 15.** *"Yoldia" minima* Seguenza, 1877. 14. Off E Sardinia, st. BS 78-2, 1281-330 m, Late Glacial, 2.8 mm. 15. Vallone Catrica (S Calabria), Pleistocene, 2.4 mm.
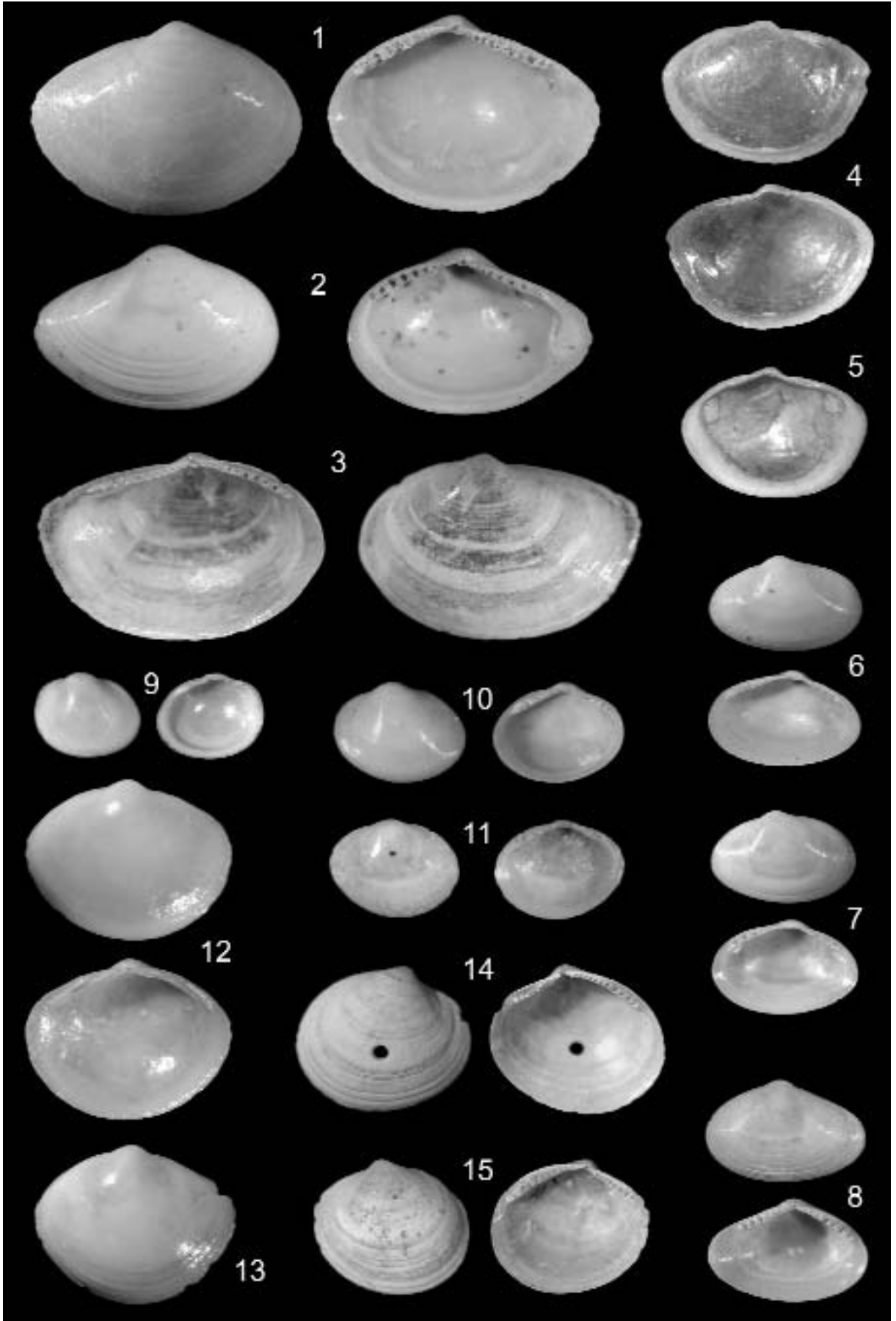
latior for the Recent North Atlantic species. Type material of *Leda pusio* var. *salicensis* was recently found by BERTOLASO & PALAZZI (2000) and the valve they illustrated matches the interpretation of this species given by DI GERONIMO & LA PERNA (1997).

Leda striolata Brugnone, 1876 remains a doubtful species, but since it was described from circalittoral-epibathyal Pleistocene beds in Sicily, it must be one of the presently known nuculoids, unless it is a notably rare species, yet to be found. Valves of *A. pusio* from epibabthyal beds differ from the typical deeper form (Pl. 1, Fig. 12) by being more elongated, posteriorly pointed and with a thinner wall (Pl. 1, Fig. 13). As for *L. nicotrae-messanensis* (see above), there is no way to keep these forms distinct, and I propose this shallower ecotype of *A. pusio* as possible identity of *L. striolata*.

A. pusio was one of the most common Pleistocene nuculoids, mostly occurring within mesobathyal associations, while *A. salicensis* was typical to the Pliocene bathyal faunas (ROBBA, 1981, 1990). A. latior is found in the Mediterranean as rare worn valves of probable Late Glacial age (DI GERONIMO & LA PERNA, 1997).

Phaseolus ovatus Seguenza, 1877

OCKELMANN & WARÉN (1998) stressed the correct usage of the genus *Phaseolus* Monterosato, 1875, which includes nuculoids with thin-walled ovate valves and a few lamellar teeth in the hinge. *Lametila abyssorum* Allen & Sanders, 1973 and *Prelametila clarkei* Allen & Sanders, 1973 from the Western Atlantic (ALLEN & SANDERS, 1973) should be probably placed in *Phaseolus*. The type species, *P. ovatus* (Pl. 3, Figs. 12, 13), was not rare in the Pleistocene, although never abundant, and mostly associated to epibathyal faunas. However, it is worth noting the record of this species by SØRENSEN (1984) from Early-Middle Pleistocene beds in the Isle of Rhodes (Western Mediterranean), where the species was said to be "the most numerous protobranch in all samples", but no other data are available on the nuculoid fauna.

Other deep-sea nuculoids in the Mediterranean Pleistocene?

Some species described by SEGUENZA (1877) from Pliocene or Pleistocene deep-sea beds in the Southern Italy have been not found or definitely recognised yet, such as *Nucula umbonata, Yoldia meridionalis, Malletia bellardii, Neilo messanensis* and *Tindaria solida*. Further studies could be then allow to add other species to the check-list of the Pleistocene deep-sea nuculoid fauna.

DISCUSSION

The composition of the Pleistocene nuculoid fauna was very different from the Recent one, both at level of species and of supraspecific taxa (Tab. 1). Out of 37 species which occurred in the Pleistocene, 18 are extinct (including the "doubtful" case of

B. excisa), 14 are still living in the Mediterranean and 5 are no longer present (*Nucula* aff. *tumidula, "Yoldia" minima, Yoldiella lucida, Microgloma* aff. *yongei, Austrotindaria latior*). None of the extant species is endemic to the Mediterranean, and none is only known as Recent species. Thus, the deep Mediterranean nuculoid fauna consists only of species already present in the Pleistocene. About 50% of the bathyal nuculoids present during the Early-Middle Pleistocene became extinct and this rate is even higher if the two eurybathic shelf species, *N. sulcata* and *S. commutata*, are excluded from the true bathyal fauna.

There is every reason to refer these dramatic changes in diversity and taxonomic composition, which involved the whole or the greater part of the Mediterranean bathyal macrobenthos, to the loss of psychrosphere and the onset of deep homeothermy (12°-13° C from ca 200 m down to the deepest waters) in the Late Quaternary, as discussed elsewhere (DI GERONIMO & LA PERNA, 1996, 1997; DI GERONIMO et al., 1996, 1997, 2001; CORSELLI, 2001). These oceanographic changes were controlled by the uplifting of the Gibraltar sill, due a compression phase since 1 My (BOUSQUET & PHILIP, 1976; DILLON et al., 1980), which cut the deep Mediterranean from the deep oceanic circulation (BENSON, 1972). The Recent nuculoid fauna, as well as all the bathyal benthos, thus appears to be mostly "residual", i.e. mainly composed of species which endured the changes from psychrospheric to warm homeothermic conditions. It can be hypothesized that the presently living species are the most eurytopic ones, particularly with respect to the present thermohaline conditions.

May the extinct species, or some of them at least, represent a palaeoendemic stock? Unfortunately, nothing is known about their distribution in the North Atlantic Pleistocene, but if these species were also present there, no alternative hypothesis can explain their extinction through the whole area of distribution. As is so far known, most of these extinct species appeared in the Middle-Late Pliocene, that means approximately between 3.0 and 1.7 My. Few of them were more ancient: *Propeleda hoernesi, Neilo isseli* and *Pseudomalletia caterinii* are known since the Late Miocene and *Austrotindaria salicensis* since the Early Pliocene. It is not possible to say much about the age of extinction. The nuculoid fauna described above is known up to the lower part of the Middle Pleistocene (0.8-0.6 My), within the *Pseudoemiliania lacunosa* Zone (DI GERONIMO et al., 1997; D'ALESSANDRO et al., 2003), but extinction had occurred before the Late Glacial (10-15 ky).

As is particularly well known from the bathyal coral communities (e.g. DELIBRIAS & TAVIANI, 1985; ALLOUC, 1987), the Last Glacial represented a "reflourishing" phase for the bathyal Mediterranean benthos. The deep homeothermy was still present but water temperature was lower, some 10-11°C, according to CORSELLI (2001). Some Atlantic species, particularly the species with longer-living free larval stages could enter via Gibraltar and live in the Mediterranean. This is a good hypoth-

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Plate 4
Fig. 1. *Neilo dilatata* (Philippi, 1844), Bovalino Superiore (S Calabria), Pleistocene, 9.7 mm. **Fig. 2.** *Neilo isseli* Bellardi, 1875. Grammichele (SE Sicily), Pleistocene, 6.7 mm. **Fig. 3.** *Pseudomalletia obtusa* (Sars G.O., 1872), Archi (S Calabria), Pleistocene, 10.1 mm. **Fig. 4.** *Pseudomalletia caterinii* (Appelius, 1871), Torre di Ceperano (Romagna), Pliocene, 11.1 mm. **Fig. 5.** *Katadesmia confusa* (Seguenza, 1877), Archi (S Calabria), Pleistocene, 4.6 mm. **Fig. 6.** *Katadesmia cuneata* (Jeffreys, 1876), Southern Tyrrhenian, Eocumm st. 8, 1510 m, 6.3 mm.
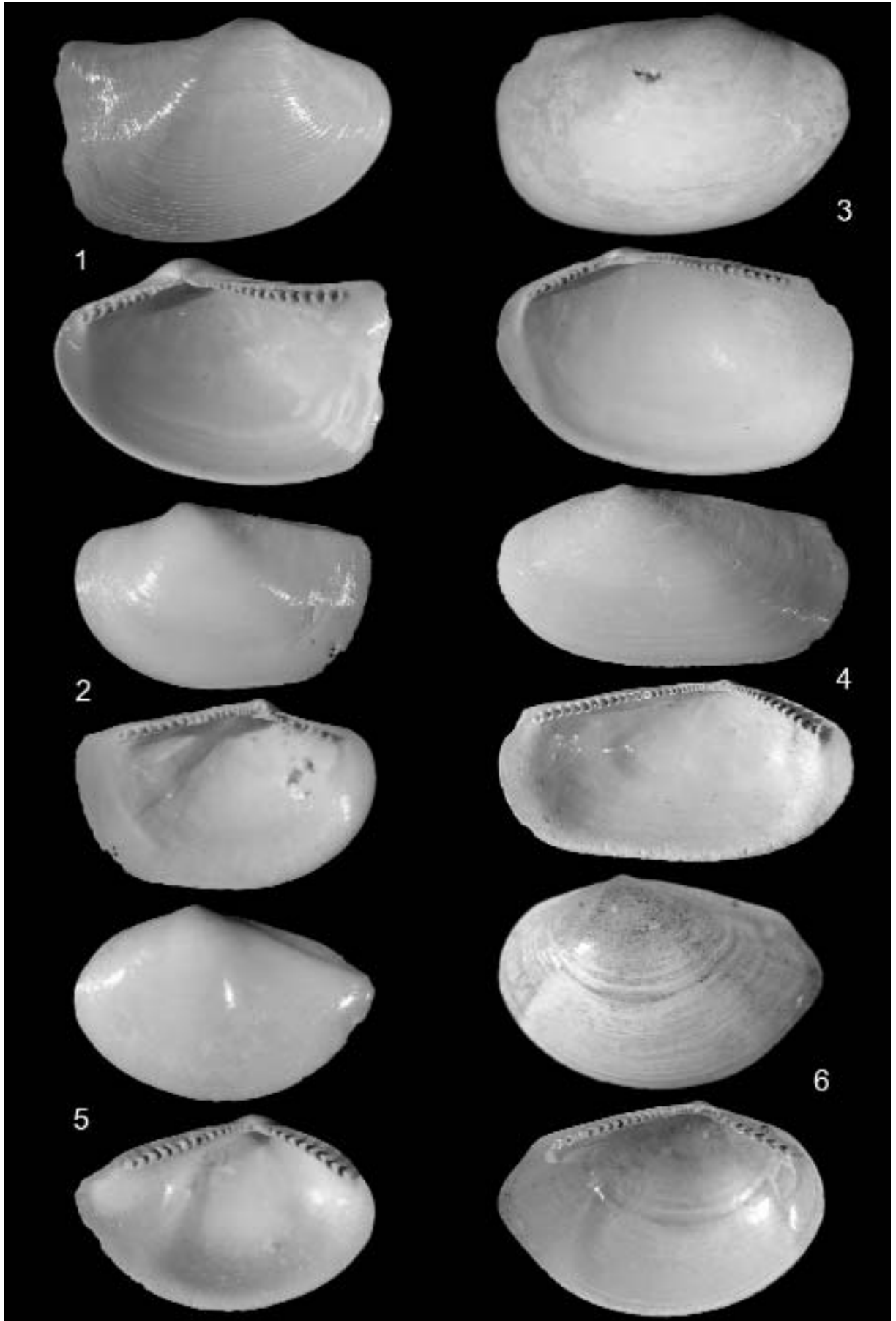
esis for some molluscs (see BOUCHET & FONTES, 1981; BOUCHET & TAVIANI, 1992) but not so good for nuculoids, which lack planktotrophic larval stages (further, the glacio-eustatic lowstand made the Gibraltar sill even shallower than in the present days). Of the four species referred in the present work to the "Last Glacial group" (*Nucula* aff. *tumidula.*, *Yoldiella lucida*, *"Yoldia" minima* and *Austrotindaria latior*), the first three were present also in the Early-Middle Pleistocene (and probably also *A. latior* is yet to be found). During the Last Glacial, these species found improved conditions to develop like (or better, as suggested by *Y. lucida*) during the true psychrosperic phase. They may be now definitively absent from the Mediterranean, or they may occur as small populations in the Western Mediterranean (as suggested by *Ennucula decipiens*).

Changes in the nuculoid fauna composition altered the composition of associations too (Fig. 4). Diversity and most probably also community density were so high to suggest, much more than the Recent Mediterranean fauna, the ecological enigma raised by ALLEN & SANDERS (1996b), i.e. the co-occurrence of many protobranch species which had similar life habits.

Two aspects are worth stressing: 1) the "new" character of the present-day epibathyal nuculoid fauna, 2) the strongly "residual" character of the mesobathyal one. The first consideration arises from the wide occurrence and dominance of *Ennucula aegeensis*, apparently rare in the Pleistocene. Although *E. aegeensis* cannot be assumed to be a good example of deep-sea nuculoid, due to its marked shallow range, its "Mediterranean" character is noteworthy, since its distribution in the Ibero-Moroccan Gulf seems to be mostly controlled by the Mediterranean outflow (SALAS, 1996). *Ennucula corbuloides, Ledella messanensis, Yoldiella micrometrica* and *Katadesmia cuneata* are probably the most common mesobathyal nuculoids. Although they were also present within the Pleistocene associations, the first two species were overwhelmed by a number of species, such as *Bathyspinula excisa, Katadesmia confusa* and *Austrotindaria pusio. Y. micrometrica* was notably rare and *K. cuneata* so rare such as to be so far unrecorded.

Since the Mediterranean is strongly isolated, its deep-sea fauna is expected to bear high degree of endemicity (GAGE & TAYLOR, 1991), but it appears that endemicity of the deep Mediterranean benthos is markedly low (e.g. MENZIES, 1973; FREDJ & LAUBIER, 1985; BOUCHET & TAVIANI, 1992). The nuculoid fauna gives a good example of this. Further, among nuculoids there does not seem to be any occurrence of variation from the Atlantic counterparts, which might allow ongoing differentiation or speciation to be argued. "High" rate of endemicity among some groups (e.g. BELLAN-SANTINI *et al.*, 1992), does not exclude that these endemic species are residual, inherited from the Plio-Pleistocene, and not young species. As speciation in the deep-sea is not regarded as particularly slower than in shallow waters (WILSON & HESSLER, 1987; GAGE & TAYLOR, 1991), the low degree of endemicity of the deep Mediterranean benthos must be explained by the recentness (few hundreds of thousands years) of the present oceanographic conditions. If the extinct species were really palaeoendemics, than the rate of endemicity within the Pleistocene deep Mediterranean fauna was much higher than the Recent one. This may reflect a long history of partial isolation, which was not so strong to bar the deep circulation but encouraged the differentiation of the deep Mediterranean fauna from the North Atlantic one.

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After the preparation of the present work, the identity of *Yoldia micrometrica* Seguenza, 1877 was reconsidered and a neotype proposed for the true Pleistocene *Y. micrometrica* (Pl. 3, Fig. 8, as *Yoldiella* sp.), whereas the Recent species so far known as *Y. micrometrica* was described as new. The occurrence of this last species in the Pleistocene remains doubtful. In the same work, two additional new protobranch species were described from the deep Mediterranean.

More recently, the genus *Jupiteria* was studied by LA PERNA *et al.* (in prep.), with emphasis to the identity of its type species. In the same work, *Ledella nicotrae* (Seguenza, 1877) is proved to occur in the Pliocene and its taxonomic status is reconsidered.

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