

Original article

Pleistocene fish otoliths from the Mediterranean Basin: a synthesis

Otolithes de poissons pléistocènes du bassin méditerranéen : aperçu synthétique

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Abstract

An overview of upper Pliocene and Pleistocene otolith assemblages is compiled on the basis of both literature data and newly collected material from several sections located mainly in southern Italy. One hundred and five taxa are listed. Additional comments are provided for taxa subject to discussion. The composition and affinities of the Mediterranean Pleistocene otolith associations (consisting mainly of deep sea fishes) is checked against the available data for Pre-Messinian, Pliocene, and Recent Mediterranean fishes. This analysis is based on the recorded nominal species, but some taxa that could be identified at the generic level only are also included when they are relevant from a biogeographic point of view. Some new data on Piacenzian (middle Pliocene) and Gelasian (upper Pliocene) otoliths are also provided because this time interval still constitutes a major gap in the knowledge of the stratigraphic range of Plio-Pleistocene fish taxa. The Pleistocene deepwater fish fauna of the Mediterranean shows a markedly more oceanic character than the present-day one, a tendency that was all ready observed from early Oligocene till Pliocene times. Starting from the late Piacenzian, an increasing number of Atlantic taxa progressively invaded the Mediterranean including several subpolar and temperate forms. This invasion became stronger in the Gelasian. From this period up to the middle and late Pleistocene, the Mediterranean deepwater fish fauna (mesopelagic and benthopelagic) is enriched by taxa which today are typical for the north Atlantic cold deep water. This faunal shift seems to be correlated with the evolution of the Plio-Pleistocene Mediterranean paleoceanographic setting as well as with the global climatic deterioration.

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Résumé

Un aperçu des connaissances sur les otolithes de poissons du Pliocène supérieur et du Pléistocène méditerranéen a été compilé à partir de données bibliographiques et d'abondants nouveaux matériaux, provenant surtout de coupes situées en Italie méridionale. Cent cinq taxa ont été recensés. La composition et les affinités de cette faune (constituée avant tout de poissons d'eau profonde) sont analysées à la lumière des connaissances sur les faunes ichtyologiques prémessiniennes, zancléennes et actuelles de la Méditerranée. La présente analyse est en principe fondée uniquement sur les espèces nominales recensées, mais certains taxa seulement identifiés au niveau générique ont été considérés s'ils s'avéraient importants du point de vue biogéographique. Quelques données inédites sur les otolithes du Pliocène moyen (Plaisancien) et supérieur (Gelasien) sont fournies, car d'importantes lacunes dans nos connaissances des faunes ichtyologiques de cet intervalle subsistent encore. La faune d'eau profonde du Pléistocène méditerranéen montre un cachet nettement plus océanique que la faune y vivant aujourd'hui, une tendance que l'on observe aussi dans ce bassin depuis l'Oligocène inférieur jusqu'au Pliocène. À partir du Plaisancien terminal, un nombre de taxa atlantiques envahit progressivement la Méditerranée, parmi lesquels plusieurs formes subpolaires et tempérées. Cette invasion prend de l'ampleur au Gela-

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sien. Depuis cette période jusqu'au Pléistocène moyen et terminal, la faune d'eau profonde (mésopélagique et benthopélagique) de la méditerranée est enrichie de taxa qui, dans la faune actuelle, sont typiques des eaux froides de l'Atlantique nord. Cette modification faunique semble être induite par l'évolution paléo-océanographique de la Méditerranée plio-pléistocène et par la détérioration climatique globale durant cette période. © 2006 Elsevier Masson SAS. All rights reserved.

Keywords: Otoliths; Paleobiogeography; Paleoceanography; Upper Pliocene; Pleistocene; Southern Italy

Mots clés : Otolithes ; Paléobiogéographie ; Paléo-océanographie ; Pliocène supérieur ; Pléistocène ; Italie méridionale

1. Introduction

In recent years, studies on the Mediterranean Plio-Pleistocene deep-sea faunas mainly focused on invertebrate groups, i.e. ostracods, molluscs, serpulids, corals, and bryozoans (Benson, 1972; Di Geronimo, 1979; Di Geronimo et al., 1996; Di Geronimo and La Perna, 1996, 1997, cum biblio; Corselli, 2001). These works have helped to outline the Plio-Pleistocene evolution of the deep-sea Mediterranean benthos in relationship to global climatic change and the nature of water exchange with the Atlantic.

Studies on the Mediterranean Pliocene and Pleistocene teleost fauna were mainly concerned with the study of complete fish skeletons but rarely with otolith assemblages (i.e. Landini and Varola, 1983; Landini and Menesini, 1978; Gaudant, 2001). Fish otoliths, however, are found in a wide spectrum of marine sedimentary environments and, therefore, are precious tools for investigating the composition, paleobiogeography and paleoecology of extinct teleost faunas (Nolf, 1995; Nolf and Stringer, 1996). Also, faunal reconstructions based on complete fish skeletons only show a restricted scope of the fossil record those fossils being mainly preserved under unusual environmental conditions.

Regarding otolith-based reconstructions of the Pliocene fish faunas in the Mediterranean realm, Nolf et al. (1998) provided an overview of the Zanclean (lower Pliocene) fauna, and more recently, several studies have been focused on the Pleistocene fauna of southern Italy, which mainly consists of deepwater fishes (Girone, 2000a; Girone and Varola, 2001; Girone, 2003). Between those two well documented time units, there is still a marked gap in the data, comprising the middle to late Pliocene (Piacenzian and Gelasian) time-units, a period during which important climatological changes took place in the Mediterranean realm. Pleistocene otolith associations were mainly documented for deepwater environments; data on neritic fishes were restricted to a small fauna from the lower Pleistocene of Tuscany (Nolf and Girone, 2000a) and from some intervals of the Montalbano Jonico section in southern Italy (Girone, 2000b; Girone and Varola, 2001).

In the present work, new data on late Pliocene and Pleistocene otolith assemblages are integrated in the already existing ones to complete the overview of the entire late Pliocene and Pleistocene fauna of the Mediterranean realm. Placing these results in their environmental context and checking the obtained data against those of Pre-Messinian (Nolf and Steurbaut, 1983; Reichenbacher and Cappetta, 1999; Nolf and Steurbaut, 2004; Nolf and Brzobohaty, 2004) and Recent Mediterranean

faunas provide a synthesis of otolith-based teleostean paleobiogeography in the Mediterranean and helps to unravel the causes involved in the evolution of these fish faunas through time. Taxonomic affinity of several taxa in need of revision are evaluated and discussed in the context of an evolving model of the Mediterranean teleostean deepwater fauna.

We also provide some new data on Gelasian and Piacenzian otolith assemblages in order to cover (partially) the gap between the lower Pliocene and Pleistocene associations. This material was mainly collected from classical Plio-Pleistocene southern Italian sites, including the Vrica section, well known as the Global Stratotype Section and Point (GSSP) site for the Plio-Pleistocene boundary. Previous data on the teleostean fauna from this site are provided by Landini and Menesini (1978) who studied the fish skeletons from the sapropel layers. For the middle Pliocene, some data from work in progress by the first two authors of the present paper were included in order to provide a better definition of the stratigraphic distribution of peculiar taxa. Differences between otolith assemblages from the various studied sections were also evaluated with regard to their geographic location and paleoenvironmental setting.

2. Studied materials

The position of the studied sections with regard to the Plio-Pleistocene biostratigraphic scheme is shown in Fig. 1. Aspects of the lithology, biostratigraphy or paleoecology of these sections have been studied in various previous works. A synthesis of the main references and paleoenvironmental setting is provided in Table 1. The studies of otolith assemblages are based mainly on the analyses of bulk samples; further material, especially large specimens and rare species, were picked up by hand at the surface of the outcrops (Table 1). The volume of the processed sediment, homogeneous in each section, was decided on the basis of richness in otoliths in each concerned section (Table 1).

Otolith assemblages from Montalbano Jonico, Archi, Palione River, and Morrone have already been investigated in previous papers (Girone, 2000a, 2000b; Girone and Varola, 2001; Di Geronimo et al., 2003; Girone, 2003). These data are completed here with unpublished material from the early-middle Pleistocene from Vallone Catrica (southern Calabria), Furnari, and Fiumefreddo. The otolith assemblages of these sites are taxonomically and paleoecologically very similar to the coeval ones recovered in the Messina Strait area (i.e. Archi section). Very similar paleoecological conditions have been observed for newly collected otolith assemblages from the

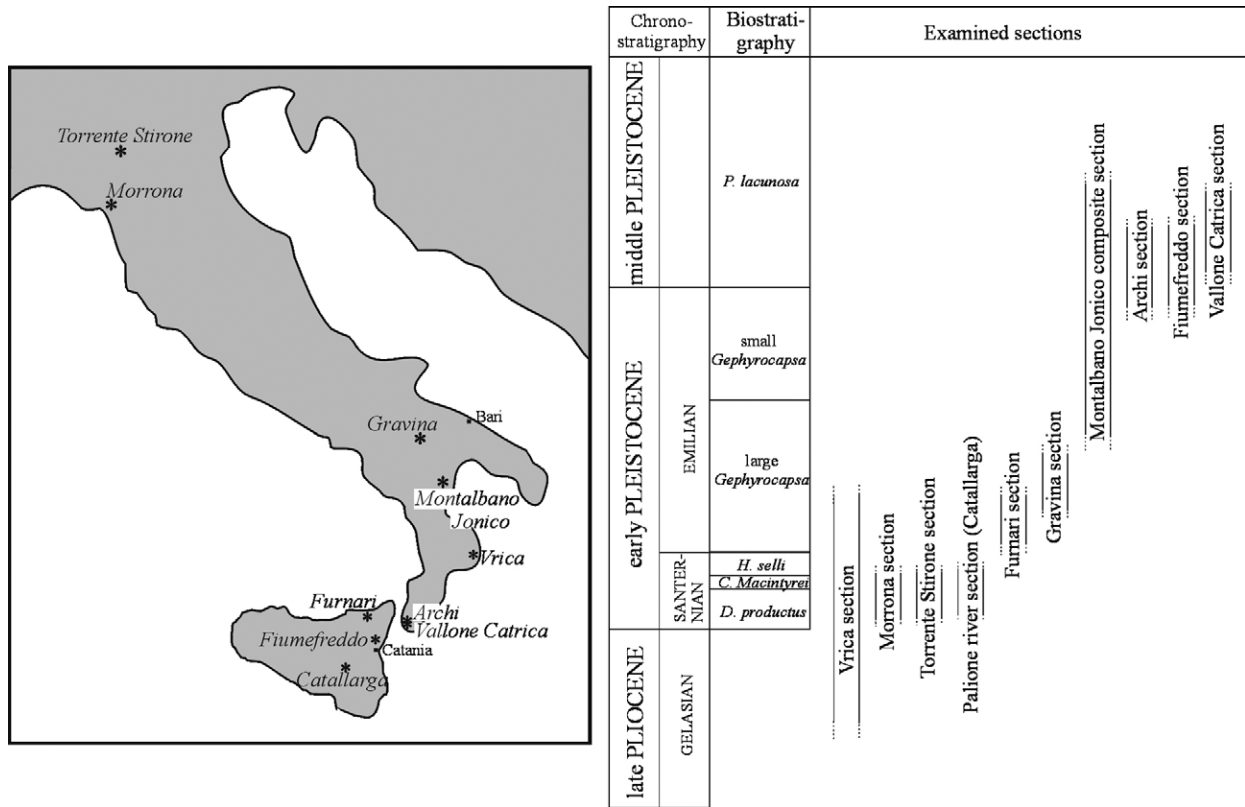


Fig. 1. Geographic and stratigraphic location of the studied sections.
Fig. 1. Localisation géographique et stratigraphique des coupes étudiées.

upper Pliocene–lower Pleistocene Vrica section even if these assemblages contained less abundant material and a lower taxonomic diversity.

3. Systematic paleontology

A list of all otolith-based species from the Mediterranean Pleistocene with their occurrence in the sampled localities is given in Table 2. The classification adopted is the one proposed by Nelson (1994). Otoliths of all species that were not figured previously from the Mediterranean Pleistocene are illustrated. For those already illustrated, a literature reference to the concerned iconography is provided. In some cases, the Recent comparative material on which the generic identification was based is also figured. Additional comments are given only for taxa who are subject to discussion.

Many Recent fish species were already represented in the Mediterranean Pleistocene, and in several cases, specific identity could not be unequivocally decided. In those cases, the abbreviation aff. (*affinis*) was inserted between the name of the genus and the name of the group species. The abbreviation cf. (*conformis*) was used in cases where the condition of preservation of the otolith did not allow conclusive specific identification. Moreover, many taxa appear in open nomenclature for identification at the species level due to insufficient knowledge of related Recent species or because the fossil material is too limited or too poorly preserved to decide.

3.1. Remarks on taxa requiring comments

3.1.1. *Bathylagus* sp. (Fig. 2(7))

The otoliths of this taxon are characterized by a wider and deeper sulcus than *Bathylagus euryops* (Fig. 2(8)) already known in similar assemblages.

3.1.2. *Alepocephalus* sp. (Fig. 2(15))

The family Alepocephalidae includes numerous Recent genera and species. The fossil otoliths reported from lower to middle Pleistocene Archi section by Girone (2003) can be attributed to Alepocephalidae due to their sulcus, but their general morphology does not match exactly to that of any known Recent species. The outline of the fossil otoliths is highly variable, and more than one species may be involved. These fossils are the only alepocephalids known from the Mediterranean Pleistocene.

3.1.3. *Argyropelecus* sp. (Fig. 2(11))

In the lower Pleistocene (large *Gephyrocapsa* biozone) from Montalbano Jonico, Girone (2000a, 2000b) reported the first fossil Mediterranean *Argyropelecus hemigmnus*. Another *Argyropelecus* is cited here from the upper Pliocene Vrica section. These otoliths are very similar those of *A. hemigmnus* but differ from them by a very acuminate central portion of their ventral rim.

Table 1

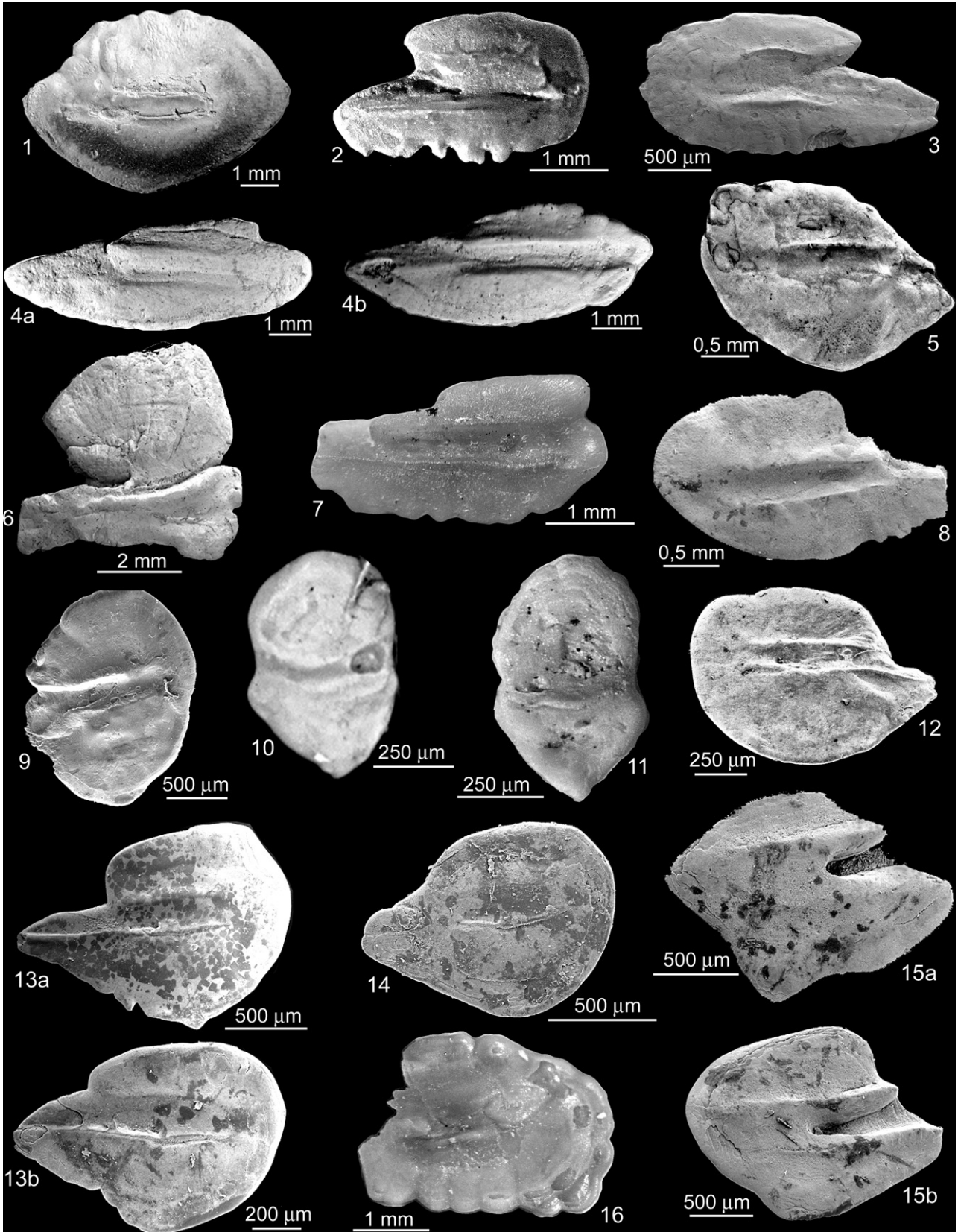
List of the studied sections and samples. For the Vrica section, surface-picked samples were collected by H. Cappetta; bulk samples by A. Girone

Liste des coupes et échantillons étudiés. Dans la coupe de Vrica, des récoltes de surface ont été effectuées par H. Cappetta ; des échantillons pour tamisage ont été prélevés par A. Girone

Locality and stratigraphy	Environmental setting	Coordinates x	(UTM) y	References
UPPER PLIOCENE				
GELASIANO				
VRICA SECTION				
picking above the sapropel "a" and sapropel "c", two bulk samples (30 dm ³) at 0.5 m under and at 1.5 m above the sapropel "d"	deep bathyal (above 500 metres)	684.916	4323.606	Pasini and Colalongo (1994) Landini and Menesini (1978)
LOWER PLEISTOCENE				
SANTERNIANO				
TORRENTE STIRONE SECTION				
1 bulk sample (100 dm ²)	Shallow circalittoral	577.660	4965.971	Monegatti et al. (2001)
VRICA SECTION				
picking above the sapropel "e" 3 bulk samples (30 dm ³) at the 0.5 m under and 1 and 7 m above sapropel "n" 1 bulk sample at sapropel "o"	deep bathyal (above 500 metres)	684.916	4323.606	Pasini and Colalongo (1994) Landini and Menesini (1978)
PALIONE RIVER SECTION				
1 bulk sample (10 dm ³)	Deep shelf- upper slope	469.664	4120.846	Di Geronimo et al. (2003)
MORRONA SECTION				
1 bulk sample (100 dm ³)	Shallow neritic	633.925	4821.500	Bossio et al., (1981) Nolf and Girone (2000a)
LOWER PLEISTOCENE				
Large <i>Gephyrocapsa</i> biozone				
VRICA SECTION				
picking above the sapropel "q"	deep bathyal (above 500 metres)	684.411	4323.853	Pasini and Colalongo (1994) Landini and Menesini (1978)
FURNARI				
1 bulk sample (10 dm ³)	deep bathyal	511.797	4218.724	Di Geronimo and La Perna (1997)
GRAVINA SECTION				
four bulk samples (40 dm ³) indicated 2a–2d in Caldara et al. (1989)	Middle shelf to surface	613.108	4518.960	Caldara et al. (1989)
MONTALBANO JONICO SECTION				
three bulk samples (100 dm ³) QET1–QET3	deep bathyal (about 500–600 metres)	631.600	4463.380	Ciaranfi et al. (2001) Girone (2005)
LOWER PLEISTOCENE				
small <i>Gephyrocapsa</i> biozone				
ARCHI SECTION				
three bulk samples (10 dm ³) (Archi 1–3)	deep bathyal (above 500 metres)	558.301	4222.307	Di Geronimo et al. (1997) Girone (2003)
FIUMEFREDDO SECTION				
8 bulk samples (20 dm ³)	deep bathyal	520.083	4184.049	Di Geronimo and Rosso, pers. comm. Lanzafame et al., 1997
MONTALBANO JONICO SECTION				
8 bulk samples (100 dm ³) (FGQB-CMSQ2)	deep upper slope to break shelf	632.410	4463.430	Ciaranfi et al. (2001) Girone (2005)
MIDDLE PLEISTOCENE				
<i>Pseudoemiliana lacunose</i> biozone				
ARCHI SECTION				
9 bulk samples (10 dm ³) (Archi 4–12)	deep bathyal (above 500 metres)	558.301	4222.307	Di Geronimo et al. (1997) Girone (2003)
FIUMEFREDDO SECTION				
2 bulk samples (20 dm ³)	deep bathyal	520.083	4184.049	Di Geronimo and Rosso, pers. comm. Lanzafame et al., 1997
MONTALBANO JONICO SECTION				
8 bulk samples (100 dm ³) (Vb1-2, Val, II-4, VCT)	Shelf break to inner shelf	631.916- 632.567	4461.415- 4461.736	Ciaranfi et al. (2001) Girone and Varola (2001)
VALLONE CATRICA				
4 bulk samples (20 dm ³)	bathyal	559.881	4202.151	Di Geronimo and La Perna (1997)

Table 2
List of Upper Pliocene and Pleistocene taxa recorded from the Mediterranean upper Pliocene and Pleistocene and their stratigraphic and geographic distribution (in gray the stratigraphic interval studied in more detail)
Liste des taxa recensés dans le Pliocène supérieur et le Pléistocène méditerranéen et leur distribution stratigraphique et géographique (les intervalles stratigraphiques étudiés en détail sont mises en couleur grise)

Mediterranean Pleistocene taxa		Pliocene			Pleistocene				Sections									Iconography						
		Miocene	Zanclean	Piacenzian	Gelasian	Santernian	large Gephyrocapsa biozone	small Gephyrocapsa biozone	Pseud. Lacunosa biozone	Wurmian	Recent	Vrica	Morrone	Gravina	Vallone Cutrera	Montalbano Jonico	Archi		Furnari	Fiume Freddo	Pallone river	Torreone Stirone		
+: fossil record; +*: fossil record only from extra-Mediterranean areas; ++: fossil record on the basis of unpublished data; ?+: questionable fossil record; R: recent species from the Mediterranean; R*: recent species disappeared from Mediterranean of today; taxa in bold (family or genus or species names): living taxa disappeared from the Recent Mediterranean; sk: skeleton-based fossil record in the investigated section																							Girone, 2003 (G.03) Girone & Nolf, 2002 (G&N); Girone & Varola, 2001 (G&V); Nolf & Girone, 2000a (N&G-a); Nolf & Girone, 2000b (N&G-b)	
CONGRIDAE	<i>Conger conger</i> (LINNAEUS, 1758)	+	+		+																		N.&G.-a, pl. 1, fig. 1; G.&V., pl. 1, fig. 4
	<i>Rhynchoconger pantanelli</i> (BASSOLI, 1906)	+	+	+	+																			Fig. 2.1
CLUPEIDAE	<i>Sardina pilchardus</i> (WALBAUM, 1792)			+		+																		Fig. 2.2
	<i>Engraulis cf. encrasicholus</i> (LINNAEUS, 1758)					sk		+																Fig. 2.3
ARGENTINIDAE	<i>Argentina sphyraena</i> (LINNAEUS, 1758)	+	+	+																				Fig. 2.5
	<i>Nansenia groelandica</i> (REINHARDT, 1840)							+	+							Ar	Fu	Ff						Fig. 2.4; G. 03, pl. 1 fig. 1
BATHYLAGIDAE	<i>Bathylagus euryops</i> (GOODE & BEAN, 1896)							+	+							Ar								Fig. 2.8
	<i>Bathylagus</i> sp. (1)							+																Fig. 2.7
ALEPOCEPHALIDAE	<i>Alepocephalus</i> sp. ind. (2)																							Fig. 2.15
	<i>Xenodermichthys</i> sp. ind.																							Fig. 2.6
STERNOPHYCHIDAE	<i>Argyropelecus hemigymnus</i> (COCCO, 1829)					sk	sk	+																Fig. 2.10
	<i>Argyropelecus</i> sp. (3)					+																		Fig. 2.11
	<i>Maurolicus muelleri</i> (GMELIN, 1789)	+	+	+	+	+	+	+	+	+														G.&V., pl. 1, fig. 3
	<i>Polyipnus</i> aff. <i>polli</i> (SCHULTZ, 1961) (4)							+	+															G.&V., pl. 1, fig. 2
	<i>Valenciennellus tripunculatus</i> (ESMARK, 1871)	+						+	+															Fig. 2.9
GONOSTOMATIDAE	<i>Bonapartia pedaliota</i> (GOODE & BEAN, 1896)							+	+															G.&V., pl. 1, fig. 1
	<i>Gonostoma</i> sp. ind.							+	+															
PHOTICHTHYIDAE	<i>Vinciguerria</i> aff. <i>attenuata</i> (COCCO, 1838)					sk		+	+															Fig. 2.14
	<i>Vinciguerria poweriae</i> (COCCO, 1838)	?+	?+	+		sk	+	+	+															Fig. 2.13
CHAULIODONTIDAE	<i>Chauliodus sloani</i> (SCHNEIDER, 1801)					sk		+	+															G.03, pl. 1, fig. 3
CHLOROPHTHALMIDAE	<i>Bathypterois</i> sp. ind.							+	+															G.03, pl. 1, fig. 9
SCOPELARCHIDAE	<i>Scopelarchus analis</i> (BRAUER, 1920)	+	+		+			+																Fig. 2.16
PARALEPIDAE	<i>Paralepis</i> aff. <i>coregonoides</i> RISSO, 1820			+				+	+															Fig. 3.1
MYCTOPHYDAE	<i>Benthoosema glaciale</i> (REINHARDT, 1837)	?+	+	++	+	+	+	+	+															Fig. 3.4
	<i>Benthoosema suborbitale</i> (GILBERT, 1913)			+	+	+	+	+	+															Fig. 3.8
	<i>Ceratosepelus maderensis</i> (LOWE, 1939)			+	+	+	+	+	+															N&G-a, pl. 1, fig. 11; G.&V., pl. 1, fig. 7
	<i>Diaphus holti</i> (TAANING, 1918)			+		+		+	+															Fig. 3.6
	<i>Diaphus rafinesqui</i> (COCCO, 1838)			+		+		+	+															Fig. 3.7
	<i>Diaphus</i> aff. <i>splendidus</i> (BRAUER, 1904)	+	+	+	+	+		+	+															N&G-a, pl. 1, fig. 2
	<i>Diaphus taanangi</i> (NORMAN, 1930)	+	+	+	+	+	+	+	+															Fig. 3.12



3.1.4. *Polyipnus* aff. *polli*

Girone and Varola (2001) reported the extra Mediterranean species *Polyipnus polli* from the middle Pleistocene (*Pseudomilania lacunosa* biozone) deep neritic assemblages of the Montalbano Jonico section. More recently, Girone (2003) assigned several specimens found in coeval deep-sea assemblages from the Archi section to *P.* aff. *polli*. However, due to poor preservation, the precise identification of these specimens is questionable and, consequently, only the record from the Montalbano Jonico section is considered here as fully trustworthy.

3.1.5. *Hygophum benoiti* (Fig. 3(1))

Beside well known *Hygophum hygomii* and *H. benoiti*, Girone and Varola (2001); Girone (2003) reported one more species as *Hygophum* sp. 1. These otoliths show general features of *H. benoiti* but with an angular ventral margin. This identification was based only on comparative Recent material of *H. benoiti* from the Atlantic. Newly collected medium and large specimens of living *H. benoiti* from the Mediterranean (off Messina) revealed differences in the otoliths of Atlantic and Mediterranean populations. The Recent specimens from Messina are characterized by a less rounded ventral rim, which becomes more pointed in larger specimens. Therefore, the specimens previously referred to *Hygophum* sp. 1 can be assimilated with *H. benoiti*.

3.1.6. *Notoscopeus elongatus* (Fig. 4(1, 2))

The Recent *N. elongatus* is considered to be a subpolar-temperate species (Nafpaktitis et al., 1977) and two subspecies are recognized: *N. elongatus kroyerii* (living in the North Atlantic Ocean) and *N. elongatus elongatus* found in the Mediterranean Sea (mainly in the western province). The elongate shape allows to distinguish the otoliths of *N. elongatus* from the higher otoliths of the extra-Mediterranean tropical-subtropical species *N. resplendens* that occurred in the Mediterranean realm from the Miocene to the middle Pliocene. As stated by Brzobohaty and Nolf (1996), otoliths of the two *N. elongatus* subspecies are not easily distinguishable, and only the adult specimens show diagnostic features. Adult otoliths of *N. elongatus elongatus* (Fig. 4(4)) have a longer and narrower shape and a narrower cauda than in the Atlantic subspecies (Fig. 4(3)). The numerous specimens from the upper and lower to middle Pleistocene Mediterranean assemblages show clear *N. elongatus* group features, but the two subspecies are often not really distinguishable. However, in several assemblages from the Vrica section (upper Pliocene interval) and from the Fiumefreddo area (lower to middle Pleistocene), some specimens are characterized by higher and shorter otoliths like in *N. e. kroyerii* (Fig. 4(1)) while others seem closer to *N. elongatus elongatus* (Fig. 4(2)).

3.1.7. *Protomyctophum arcticum* (Fig. 5(5))

Otoliths of this North Atlantic species have been recorded only in dredged samples from Thyrrenian Sea of late Pleistocene (Wurmian). Otoliths of *Protomyctophum* are high bodied, and the outline of their sulcus, especially of the crista superior, is poorly expressed. The otoliths of *P. arcticum* are, in particular, characterized by a regularly curved ventral and posterior rim and a dorsal rim showing a somewhat salient central portion. The crista superior is obsolete. Near the caudal crista inferior, there is a strong collicular crest.

3.1.8. *Scopelopsis pliocenicus* (Fig. 5(13))

The upper Pliocene and Pleistocene specimens are well comparable with the fossil species *S. pliocenicus* reported in the Mediterranean since the Tortonian (Nolf and Steurbaut, 1983). The present-day distribution of the genus *Scopelopsis* is limited to the austral temperate oceans. In the Mediterranean realm, *S. pliocenicus* seems to have survived till the middle Pleistocene.

3.1.9. *Laemonema* sp. *A* (Fig. 3(9))

These otoliths are easily referable to the “*Laemonema*” otolith group sensu Paulin (1989) but do not match with those of any Recent species known to us. Nolf and Steurbaut (1983) reported *L.* aff. *yarelli* Lowe, 1814 from the Tortonian of northern Italy. The Pleistocene species is characterized by extremely thick and short otoliths. We have similar otoliths from Recent sea bottom samples collected on the Porcupine Bank, southwest of Ireland. In this area, only one *Laemonema* species is known, *L. latifrons* Holt and Byrne, 1908. Although we were unable to obtain otoliths of this very rare fish, it is highly probable that this is the right candidate for inclusion of both our *Laemonema* from the Mediterranean Pleistocene and the Porcupine Bank sea bottom. Melendez and Markle (1997) examined the systematics of the *Laemonema* group and emended the subgenus *Guttigadus* to generic rank. According to this revision, *L. latifrons* Holt and Byrne, 1908 is included in the genus *Guttigadus*. However, due to the lack of data on the otoliths of *G. latifrons*, our fossil specimens are referred to the genus *Laemonema* sensu lato.

3.1.10. *Lepidion lepidion* s.l. (Fig. 3(3))

This otolith is very similar to those of the western Mediterranean *L. lepidion* and the North Atlantic *L. eques*. The Recent otoliths of both species do not show any relevant differences. Specific distinction is maintained mainly because the Atlantic and Mediterranean populations are vicariants with a disjunctive areal, but we do not believe that they are truly distinct species. The name *L. lepidion* used here takes precedence.

Fig. 2. 1. *Rhynchoconger pantanelli* (Bassoli, 1906), L, Vrica. 2. *Sardina pilchardus* (Walbaum, 1972), R, Gravina. 3. *Engraulis* cf. *encrasicholus* (Linnaeus, 1758), L, Fiumefreddo. 4a, b. *Nansenia groenlandica* (Reinhardt, 1840), a) L, b) R, Archi. 5. *Argentina sphyraena* (Linnaeus, 1758), L, Montalbano Jonico. 6. *Xenodermichthys* sp., R, Thyrrenian Sea. 7. *Bathylagus* sp., R, Fiumefreddo. 8. *B. euryops* (Goode and Bean, 1896), L, Archi. 9. *Valenciennellus tripunctulatus* (Esmark, 1871), R, Montalbano Jonico. 10. *Argyropelecus hemigymnus* (Cocco, 1829), R, Montalbano Jonico. 11. *Argyropelecus* sp., R, Vrica. 12. *Bonapartia pedaliota* (Goode and Bean, 1896), L, Montalbano Jonico. 13. *Vinciguerria poweriae* (Cocco, 1838), R, Montalbano Jonico. 14. *V.* aff. *attenuata* (Cocco, 1838), R, Archi. 15a, b. *Alepocephalus* sp., L, Archi. 16. *Scopelarchus analis* (Brauer, 1920), R, Fiumefreddo. L: left otolith; R: right otolith.

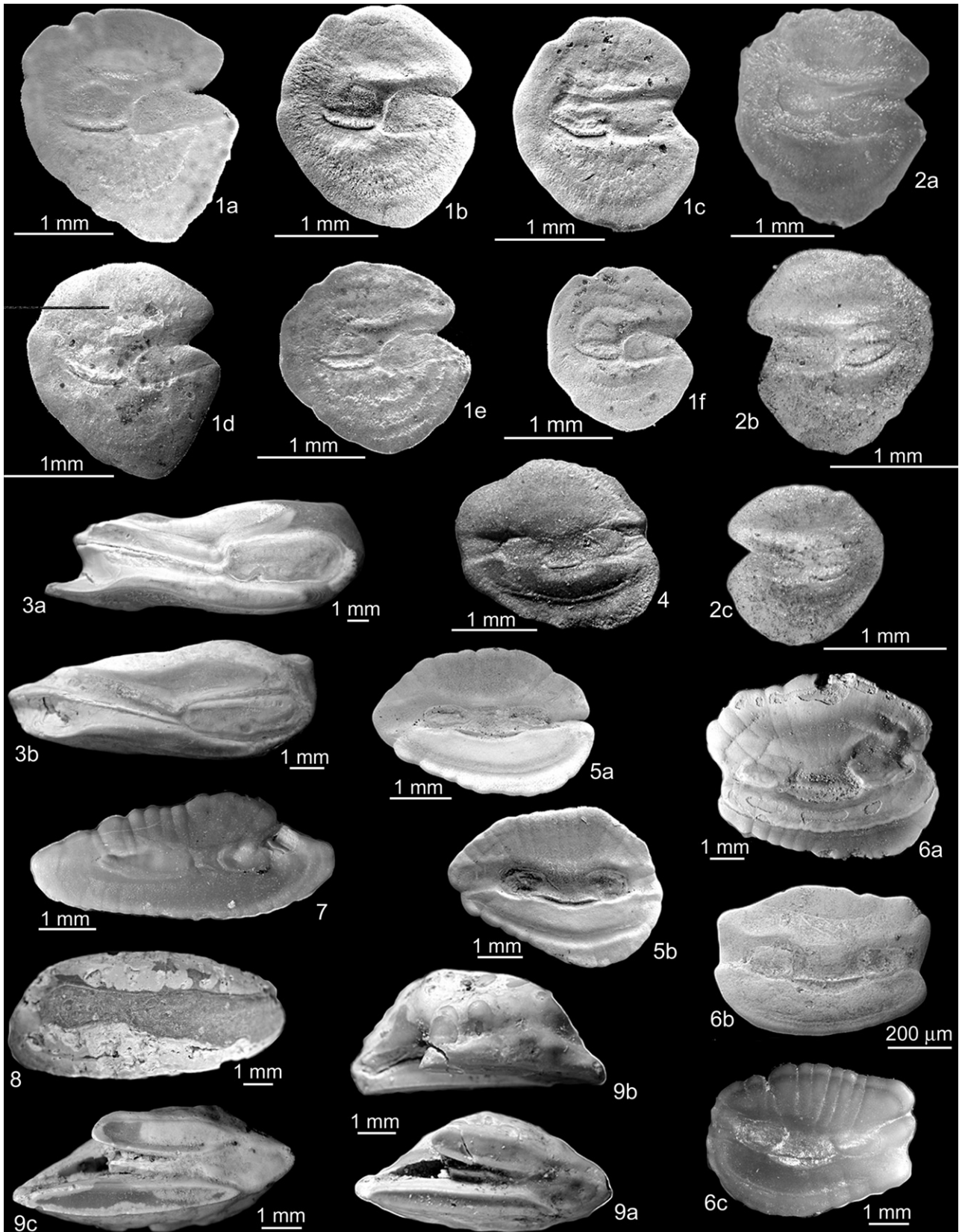


Fig. 3. **1a–f.** *Hygophum benoiti* (Cocco, 1838), L: a-b-e), Montalbano Jonico; c-d-f), Archi. **2a–c.** *H. benoiti* (Cocco, 1838), Recent, Mediterranean Sea: a), R; b), c), L. **3a, b.** *Lepidion lepidion* (Risso, 1810), R, Vallone Catrica. **4.** *Gadiculus labiatus* (Schubert, 1905), L, Vrica. **5a, b.** *G. argenteus* (Guichenot, 1850), L, Montalbano Jonico. **6a–c.** *G. argenteus thori* Schmidt, 1914: a), L, Furnari; b), R, Furnari; c) R, Vallone Catrica. **7.** *Merluccius merluccius* (Linnaeus, 1758), L, Montalbano Jonico. **8.** *Trisopterus luscus* (Linnaeus, 1758), R, Palione River. **9a–c.** *Laemonema* sp. A: a), R, Archi; b) ventral view; c) R, Vallone Catrica. L: left otolith; R: right otolith.

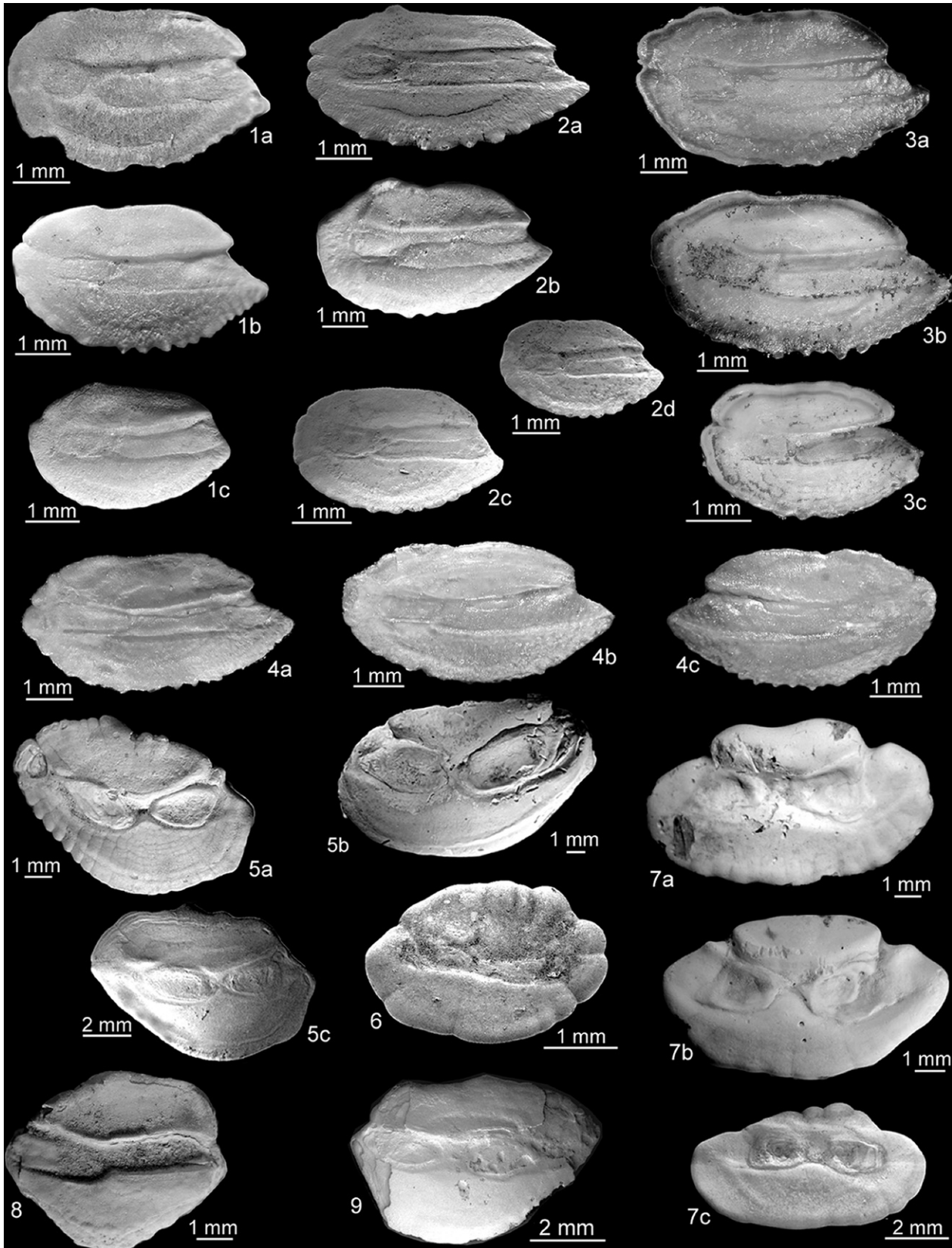
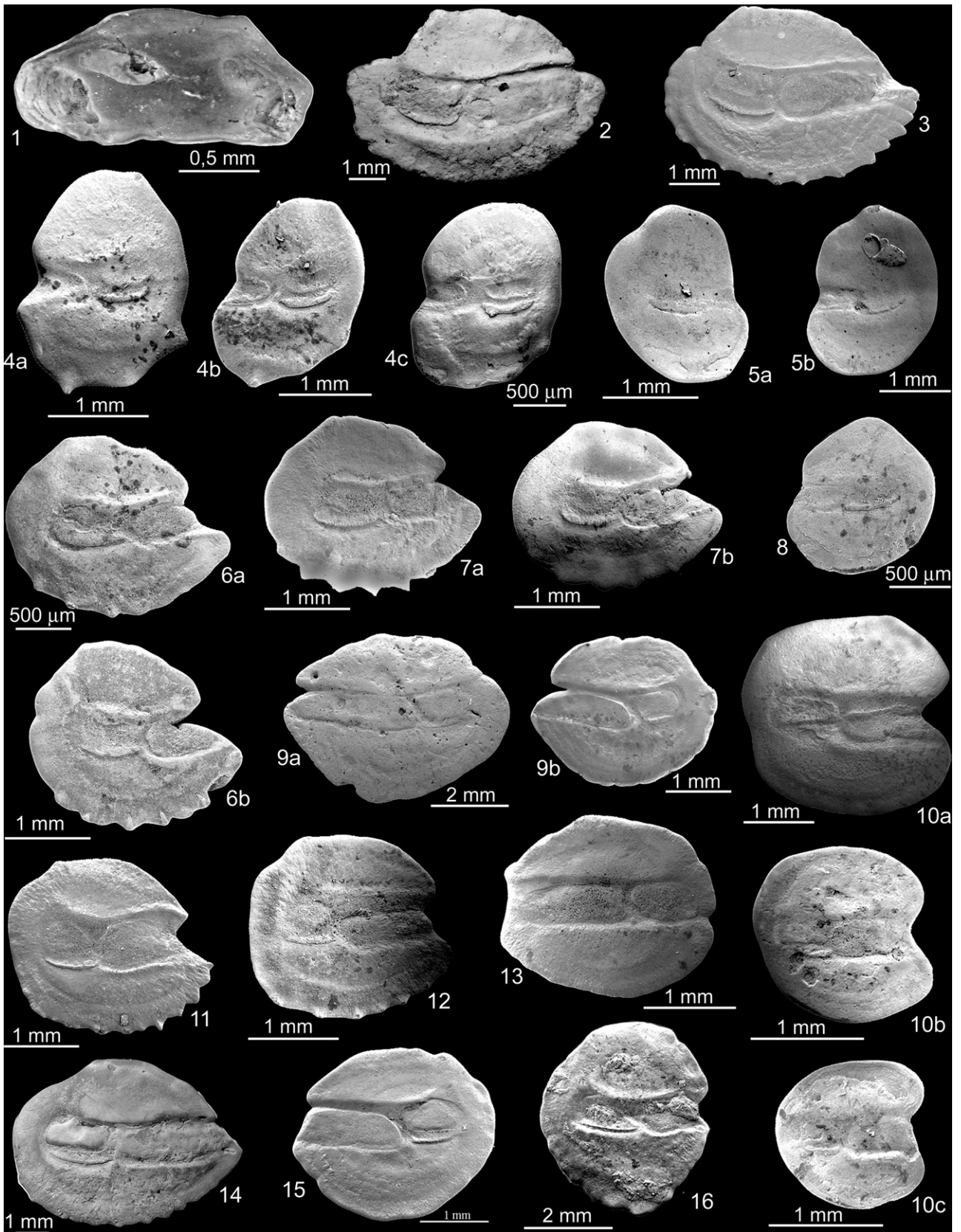


Fig. 4. **1, 2.** *Notoscopeus elongatus* (Costa, 1844), L. **1a–c.** *N. elongatus* aff. *kroyeri*: a–c) Vrica; b, Fiumefreddo. **2a–d.** *N. elongatus elongatus*: a), Montalbano Jonico; b, Vrica; c–d, Archi. **3a–c.** *N. elongatus kroyeri* (Malm, 1861), L, Recent North Atlantic. **4a–c.** *N. elongatus elongatus* (Costa, 1844): a, b, L; c, R, recent Mediterranean Sea. **5a–c.** *Coryphaenoides sicilianus* Schwarzhan, 1986: a), L, Vrica; b), R, Vrica; c, L, Montalbano Jonico. **6.** *C. cf. guentheri* (Vaillant, 1888), L, Archi. **7a–c.** *C. rupestris* (Gunnars, 1765): a, b, R, Valone Catrica; c, Archi. **8.** *Epigonus costanciae* (Giglioli, 1880), R, Vrica. **9.** *Nezumia sclerorhynchus* (Valenciennes, 1838), R, Montalbano Jonico. L: left otolith; R: right otolith.



3.1.11. *Gadiculus argenteus thori* (Fig. 3(6))

G. argenteus is divided into two subspecies, *G. argenteus argenteus* and *G. argenteus thori*. The first one occurs in the western Mediterranean, in the Atlantic around the Strait of Gibraltar, and to the south along the Moroccan coast; the second from the Bay of Biscay to west of the British Isles and along the Scandinavian coast to the North Cape. The otoliths of these species are very well distinguishable in adult fishes. They show a more wide and square shape in *G. argenteus thori* and a more pointed posterior shape in *G. argenteus argenteus*. In the small to medium size otoliths, these features are not so clearly defined, and the identification at subspecies level is more hazardous and consequently, in the analyses they are treated as *G. argenteus* (Fig. 3(5)). The examined Plio-Pleistocene specimens that show the typical *G. argenteus thori* morphology are treated at subspecies level.

3.1.12. *Phycis blennoides* (Fig. 6(1–5))

All upper Pliocene and lower to middle Pleistocene *Phycis* otoliths show quite different features than those of the fossil species *P. musicki* Cohen and Lavenberg, 1884, which is well represented in the Miocene and lower and middle Pliocene Mediterranean assemblages (Nolf and Cappetta, 1988; Nolf et al., 1998, as *P. tenuis*; Girone unpublished data). The otoliths of *P. musicki* are characterized by a blunt anterior part, lack of a developed rostrum, and a distinctly curved ventral margin (Nolf and Cappetta, 1988). Otoliths of the Recent *P. blennoides*, also known as fossils from the lower Miocene of the North Sea Basin (Nolf, 1978), have a well developed, pointed rostrum and a less curved posterior ventral part. Specimens from Mediterranean upper Pliocene till middle Pleistocene deposits have the well developed and pointed rostrum like *P. blennoides*.

3.1.13. *Coryphaenoides rupestris* (Fig. 4(7))

The otoliths of *C. rupestris* are very thick and have a highly variable oval to sub-rectangular outline. The cauda and the ostium are filled by collicula of sub-equal size. Larger specimens have a very narrow, convex dorsal area, but in smaller specimens, the crista superior is not well-defined, the dorsal area is flat and the dorsal rim often shows some lobes. The crista inferior is always present in the smaller specimens but may disappear in larger ones. Most specimens show a well-marked excisura, which is located very near to the antero-dorsal angle.

3.1.14. *Trachyrincus scabrus* (Fig. 6(13))

The specimens reported as *Hymenocephalus italicus* by Di Geronimo et al. (2003) are referable to juvenile *T. scabrus*.

3.1.15. *Bellotia* aff. *apoda* (Fig. 7(11)) and (16) *Grammonus ater* (Fig. 7(9))

Bythitid otoliths are relatively common in the Pleistocene bathyal assemblages, but they mainly belong to juveniles lacking true diagnostic features. The available fossils seem to allow the distinction of two species, *G. ater* and *Bellotia* cf. *apoda*, both still living in the Mediterranean Sea. On the basis of the numerous fossil specimens and the unfortunately scarce comparative Recent material, the following features can be suggested:

- *B. apoda* shows an almost oval and regular curved outline. The inner face is characterized by a slightly concave surface, a short sulcus, and a well-marked crista superior while the inferior crista is obsolete. The crista superior is prolonged anteriorly by a crest-like structure that reaches the anterior margin. The dorsal part of the sulcus is salient with respect to the ventral part and the dorsal area, which is very depressed along the entire length.
- *G. ater* shows a more angular outline especially in the dorsal rim. The sulcus is narrower and longer than in *Bellotia*. The cristae are both poorly developed, and the sulcus is deep and partially filled with colliculum. The dorsal area, which is slightly depressed along the entire length, is wider than the ventral area. The inner surface is slightly convex to flat.

Only a single specimen, from the middle Pleistocene assemblages of Montalbano Jonico, was identified as *G. ater* (Girone and Varola, 2001). The species is unknown in the upper Pliocene and lower Pleistocene but is now recognized by two specimens in middle Pliocene assemblages of northern Italy (Girone unpublished data).

B. aff. apoda is documented by numerous specimens from several deep-sea assemblages of various Pleistocene sections located in southern Italy.

3.1.16. *Scopelogadus* aff. *beanii* (Fig. 7(12))

The main features of these fossils are a well developed and wide excisura and a ventral area that is wider than the dorsal one. These features match with those of the Recent *S. beanii*, although otoliths of Recent specimens show a more obtuse rostrum. The other Recent Atlantic *Scopelogadus*, *S. mizolepis*, may also show a well developed rostrum but is characterized by otoliths that are wider in the dorsal area than in the ventral area and have a less pronounced excisura (see Rivaton and Bourret, 1999: Pl. 141, Figs. 11–20; Smale et al., 1995: Pl. 44, Fig. H1 and Schwarzahns, 1980: Figs. 326–327 for a good series of Recent otoliths). The specimens reported by Anfossi and Mosna (1969) in the Tortonian assemblages from northern

Fig. 5. 1. *Paralepis* aff. *coregonoides* Risso, 1820, R, Fiumefreddo. 2. *Lampadena* aff. *uophaos atlantica* Maul, 1969, L, Vallone Catrica. 3. *L. ionica* Girone and Nolf, 2002, L, Montalbano Jonico. 4a–c. *Benthoosema glaciale* (Reinhardt, 1837): a, b) R, Archi; c) R, Montalbano Jonico. 5a, b. *Protomyctophym arcticum* (Lutken, 1892): a) L, Thyrranean Sea; b) R, Thyrranean Sea. 6a, b. *Diaphus holti* (Taaning, 1918), L, Archi. 7a, b. *Diaphus refinesquii* (Cocco, 1838), L, Montalbano Jonico. 8. *Benthoosema suborbitale* (Gilbert, 1913), R, Montalbano Jonico. 9a, b. *Symbolophorus veranyi* (Moreau, 1888), R, Archi. 10a–c. *Lampanyctus crocodilus* (Risso, 1810), L: a), Montalbano Jonico; b–c), Archi. 11. *Lobianchia dofteini* (Zugmayer, 1911), L, Montalbano Jonico. 12. *Diaphus taaningi* (Norman, 1930), L, Archi. 13. *Scopelopsis pliogenicus* (Anfossi and Mosna, 1976), R, Montalbano Jonico. 14. *Lobianchia* aff. *gemellari* (Cocco, 1838), L, Fiumefreddo. 15. *Myctophum punctatum* (Rafinesque, 1810), R, Archi. 16. *Electrona rissoi* (Cocco, 1829), L, Montalbano Jonico. L: left otolith; R: right otolith.

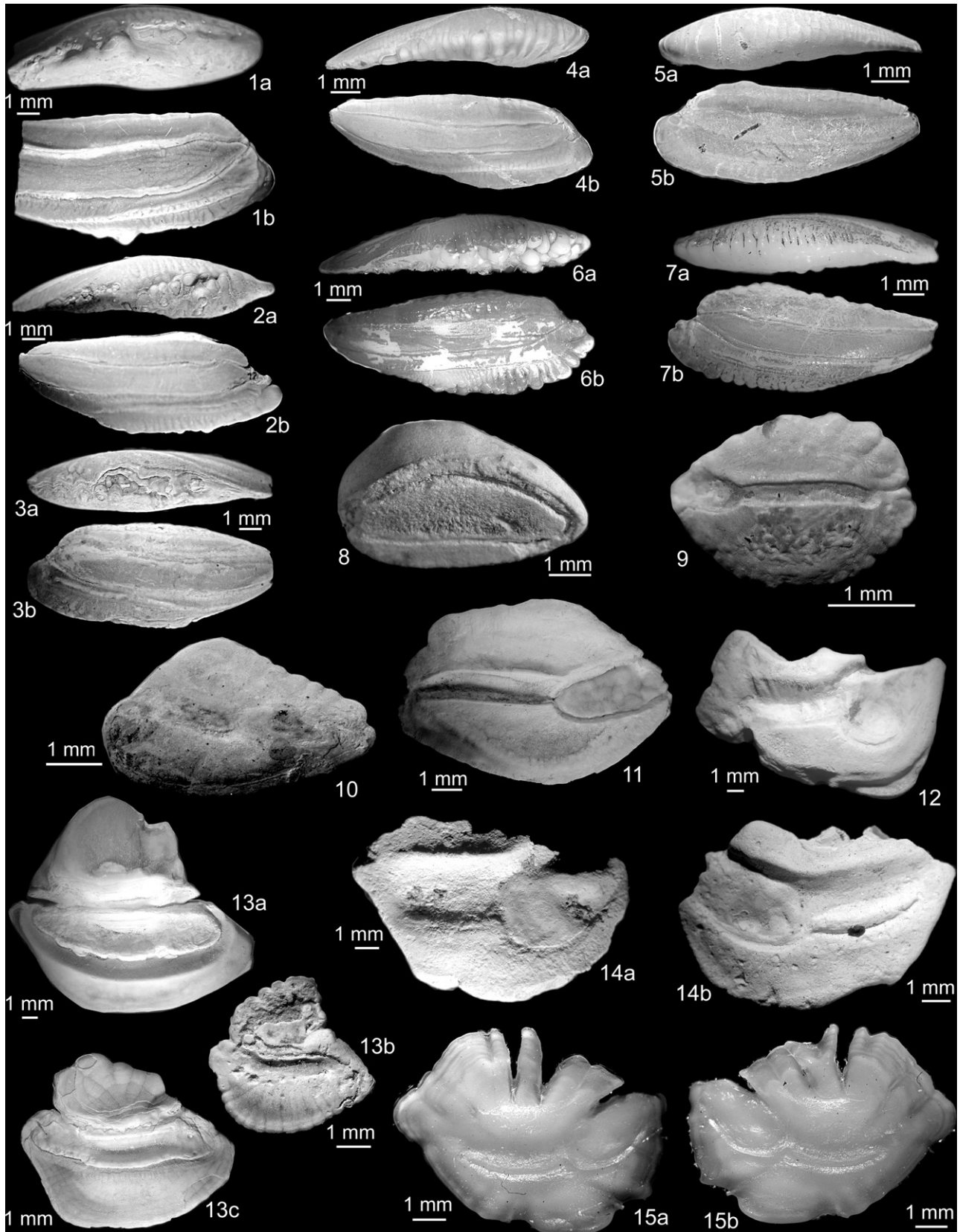


Fig. 6. 1–5. *Phycis blennoides* (Brunnich, 1768): 1a, 5b, ventral view of specimens figured in 1b, 5b. 1–3. Upper Pliocene specimens *P. blennoides*: 1, 2), L, Vrica; 3), R, Vrica. 4, 5. Pleistocene specimens *P. blennoides*: 4), L, Montalbano Jonico; 5) R, Montalbano Jonico. 6, 7. *P. blennoides* (Brunnich, 1768): 6a, 7a, ventral view of the specimens figured in 6b, 7b. 6. L, Mediterranean Sea. 7. R, Mediterranean Sea. 8. *Echiodon praeimberbis* (Weiler, 1971), R, Vrica. 9. *Atherina boyeri* Risso, 1810, R, Torrente Stirone. 10. *Coelorinchus coelorhincus* (Risso, 1810), L, Montalbano Jonico. 11. *Parascombrops mutinensis* (Bassoli, 1906), L, Vrica. 12.

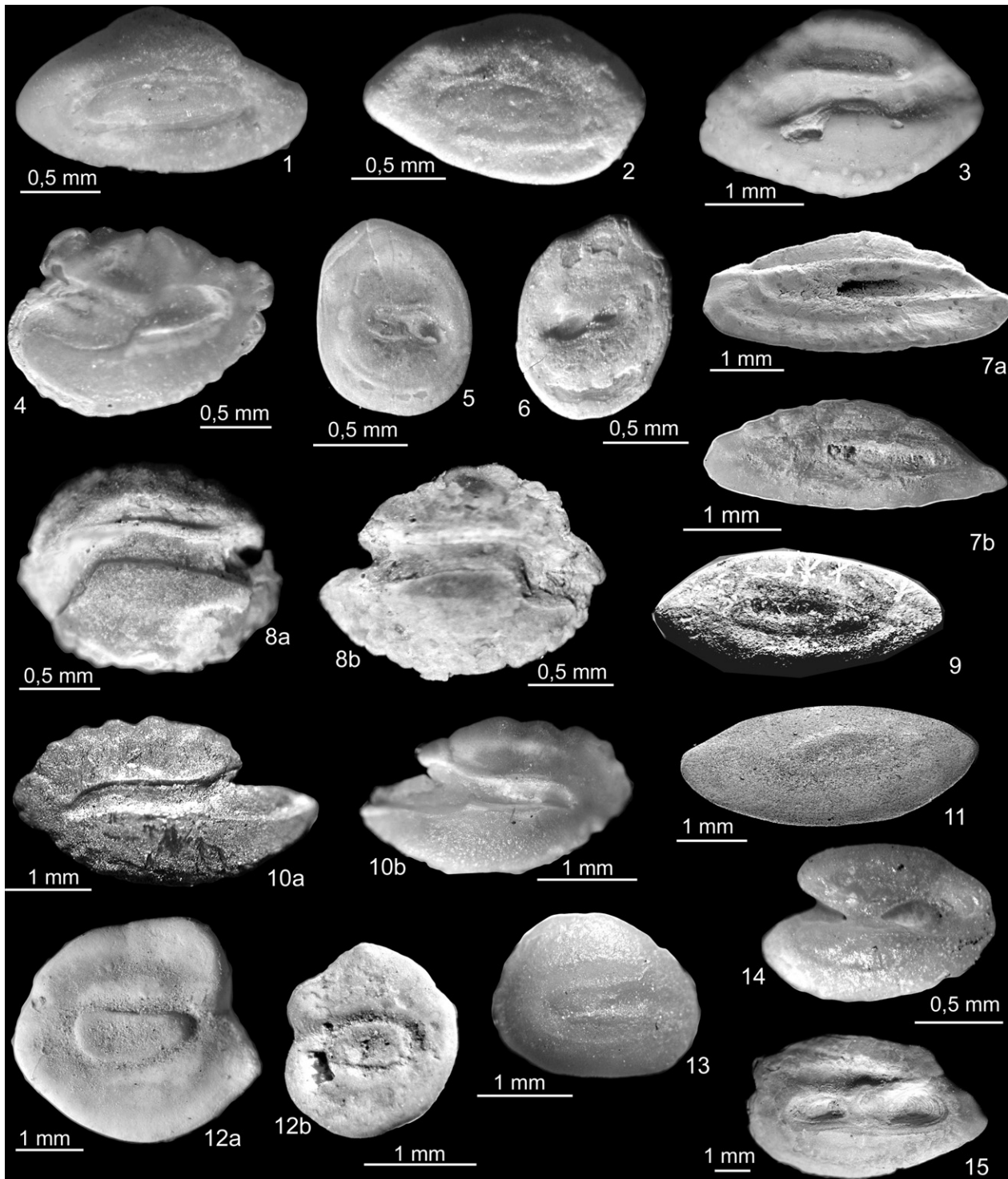


Fig. 7. 1, 2. *Carapus acus* (Brunnich, 1768), Gravina. 3. *Lepidotrigla cavillone* (Lacepede, 1801), L, Montalbano Jonico. 4. *Apogon lozanoi* Bauza, 1957, R, Torrente Stirone. 5, 6. *Aphyia minuta* (Risso, 1826), Gravina. 7. *Aphanopus* aff. *carbo* (Lowe, 1839), L: a, Montalbano Jonico; b, Fiumefreddo. 8a, b. *Mullus barbatus* (Linnaeus, 1758), Gravina: a, L; b, R. 9. *Oligopus ater* (Risso, 1910), R, Montalbano Jonico. 10a, b. *Spicara smaris* (Linnaeus, 1758), Gravina: a, L; b, R. 11. *Bellotia* aff. *apoda* (Giglioli, 1883), Archi. 12a, b. *Scopelogadus* aff. *beanii* (Gunther, 1888): a, L, Vrica; b, R, Fiumefreddo. 13. *Microchirus* cf. *variegatus* (Donovan, 1808), L, Gravina. 14. *Symphodus mediterraneus* (Linnaeus, 1758), R, Gravina. 15. *Platichthys* cf. *flesus* (Linnaeus, 1758), L, Montalbano Jonico. L: left otolith; R: right otolith.

Hoplostethus sp., L, Vrica. 13a–c. *Trachyrincus scabrus* (Rafinesque, 1810), R: a, b, Vrica; c, Palione River. 14a, b. *Hoplostethus* cf. *mediterraneus* Cuvier, 1829: a, L; b, R, Vallone Catrica. 15a, b. *H. mediterraneus* Cuvier, 1829: a, L; b, R, Mediterranean Sea. L: left otolith; R: right otolith.

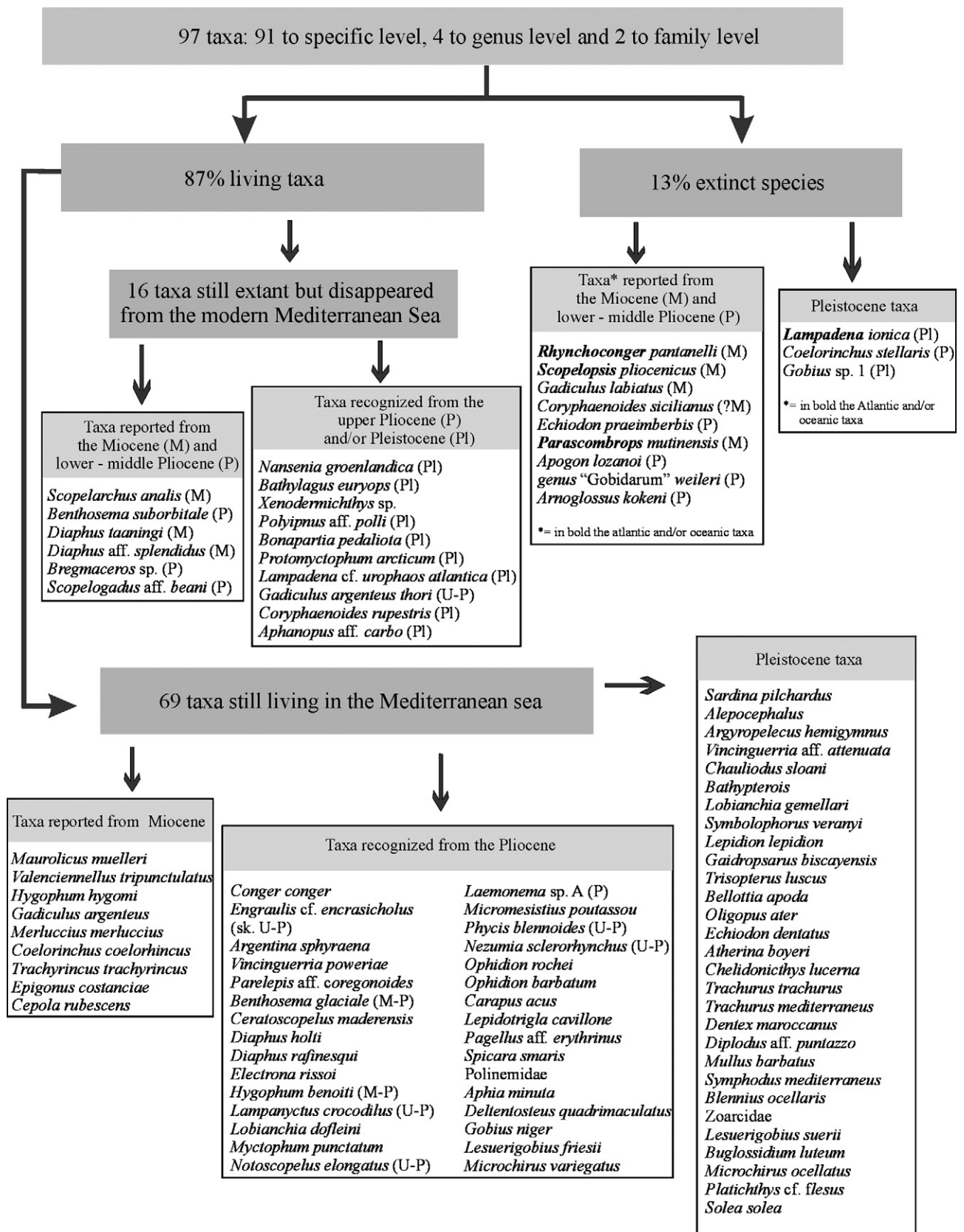


Fig. 8. Composition and affinities of the Pleistocene teleostean fauna in the Mediterranean Sea.
Fig. 8. Composition et affinités de la faune téléostéenne du Pléistocène méditerranéen.

Italy may be attributed to the same species. Numerous otoliths of *S. aff. beanii* are also found in the upper Pliocene and lower Pleistocene of Sicily (Girone unpublished data).

4. Results

An analysis of the composition and affinities of the Mediterranean Pleistocene fauna is provided in Fig. 8. This analysis is based on all the recorded nominal species and some selected taxa that could be identified at generic level only but are relevant from a biogeographic point of view, e.g. *Xenodermichthys* and *Bregmaceros* have no present-day Mediterranean representatives and the *Bathypterois* sp. constitute the only known fossil record of the genus. *Laemonema*, considered for a long time a genus living outside the Mediterranean, is also included in the analysis. Matallanas (1985) described the first specimens of *L. latifrons* from the western Mediterranean at a depth of 550 m and afterwards Quignard and Tomasini (2000) considered this species as a recent neocolonizer of Atlantic origin. The present data show that *Laemonema* may be a taxon of Atlantic origin but was already represented in the Pleistocene Mediterranean fauna.

However other open nomenclature taxa, like *Lepidopus* sp., *Scorpaena* sp., and *Gonostoma* sp., known from both the Atlantic and Mediterranean realm and from various stratigraphic levels of the Neogene, have been discarded from the analysis because they do not provide any relevant information. From this point of view, 97 taxa are considered as relevant for evaluating the biogeographic history and affinities of the Mediterranean upper Pliocene and Pleistocene fauna. This fauna is composed by 87% of living taxa and by 13% of extinct species (Fig. 8).

The Recent taxa include both fishes living in the present-day Mediterranean Sea (81%), but the other 19% of the living group are only known from outside the Mediterranean. The group of Mediterranean species includes (a) species already known since the Miocene, (b) taxa that appeared in the Pliocene and, finally, (c) the taxa recognized only since the Pleistocene. The first group (nine species) is composed mainly of deep-sea benthopelagic species (*Gadiculus argenteus*, *Merluccius merluccius*, *Coelorinchus coelorhincus*, *Trachyrinchus trachyrinchus*, and *Epigonus constanciae*), by one benthic neritic species (*Cepola rubescens*), and three mesopelagic species, *Maurolicus mulleri*, *Valenciennellus tripunctulatus* and *Hygophum hygomii*, with a worldwide distribution (Atlantic, Mediterranean, and Indo-Pacific) (Boehlert et al., 1994; Nafpaktitis et al., 1977).

The group known since the Pliocene (30 taxa) includes benthopelagic species like *Phycis blennoides* and mesopelagic fishes like *Lampanyctus crocodilus* and *Notoscopelus elongatus* that have been recorded in the Mediterranean realm only since the upper Pliocene. The subpolar–temperate species *N. elongatus* seems to enter the Mediterranean Sea during the upper Pliocene and appears to replace the co-generic *N. resplendens*, which is distributed worldwide in the tropical–subtropical extra-Mediterranean realm and very common in the Mediterra-

nean assemblages from the Miocene to the middle Pliocene (Nolf et al., 1998; Brzobohaty and Nolf, 1996; Girone unpublished data). The earliest fossil record of *N. elongatus* is from lower Miocene sediments of Belgium (Brzobohaty and Nolf, 1996) where the distinction between the vicariant subspecies *N. elongatus elongatus* (Mediterranean) and *N. e. kroyerii* (Atlantic) was impossible. As mentioned above, the upper Pliocene and Pleistocene specimens are sometimes closer to the Northern Atlantic subspecies but a sure distinction is questionable.

In the same way, the benthopelagic *Phycis blennoides*, distributed today in the Mediterranean Sea and in the North Atlantic Ocean (from subarctic to about 30°N), seems to enter the Mediterranean Sea during the upper Pliocene, replacing the fossil *P. musicki*. Outside the Mediterranean realm, the Recent species is known from the Miocene sediments of northern Europe (Belgium and northern Germany) (Nolf, 1976; Hoedemakers, 1997) and is reported from the Piacenzian of Portugal (Nolf and Marques da Silva, 1997). In the lower and middle Miocene of Aquitaine, only *P. musicki* is recorded, and the species is apparently confined to warmer temperatures than *P. blennoides*.

Hygophum benoiti and *L. crocodilus* appear in the Mediterranean since the middle Pliocene (Piacenzian) (Girone unpublished data). Even if considered temperate–semisubtropical, these fishes are ranking fairly northwards in the North Atlantic Temperate Region and are also found in the Mauritanian Upwelling. In the Mediterranean Sea, they are considerably less abundant than in the temperate provinces of the open Atlantic (Nafpaktitis et al., 1977).

Since the middle Pliocene, the Mediterranean pelagic realm is enriched by species that seem to have invaded from the subpolar–temperate or temperate Atlantic, e.g. *Benthoema glaciale* and *Myctophum punctatum*. In the North Sea Basin, the earliest occurrence of *B. glaciale* is reported from the lower Pliocene of Belgium (Gaemers and Schwarzahns, 1973; Nolf, 1978).

Apparently, 42% (= 29 taxa) of the fossil record of extant Mediterranean taxa is known only since the Pleistocene. However, this group includes various neritic taxa like *Mullus barbatus*, *Symphodus mediterraneus* and *Blennius ocellaris*, and their Pleistocene appearance may be due to the lack of sampling of shallow neritic Mediterranean Pliocene deposits.

In the group of Recent taxa that disappeared from the modern Mediterranean, there are fishes known from the Miocene and lower and middle Pliocene besides taxa that have been recognized from the upper Pliocene to the Pleistocene (Fig. 8). Among these fishes, there are deep-sea pelagic and benthopelagic taxa reflecting the more oceanic or Atlantic affinities of the Mediterranean deep-sea fauna persisting from the Miocene. Taxa recognized from the upper Pliocene and Pleistocene include species like *Nansenia groenlandica*, *Bathylagus euryops*, *Coryphaenoides rupestris*, and *Gadiculus argenteus thori* which, today, are typical for the North Atlantic cold deep water (Fig. 9). The occurrence of these taxa seems to be linked, alongside global climate changes, to the different paleocean-

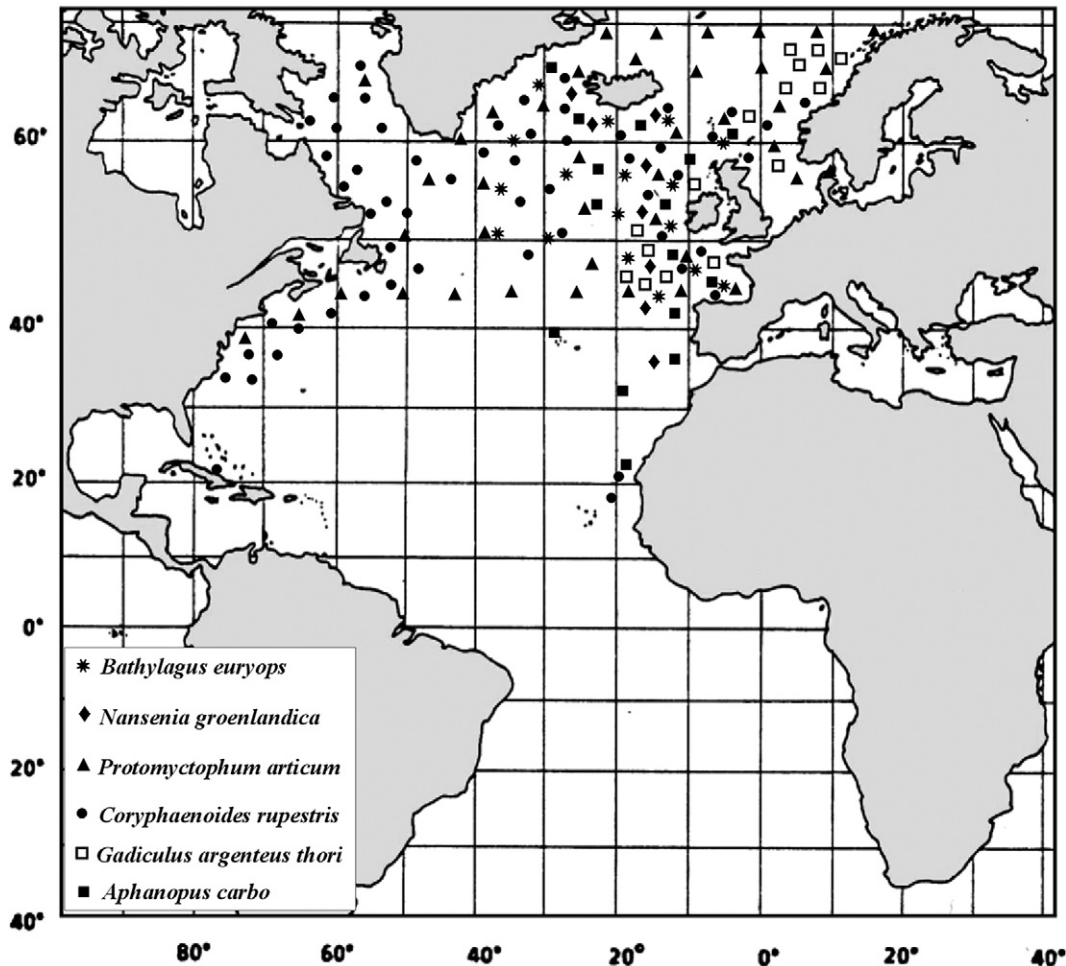


Fig. 9. Modern geographic distribution of extra-Mediterranean species occurring in the early–middle Pleistocene otolith assemblages (data from Nafpaktitis et al., 1977; Whitehead et al., 1989; Cohen et al., 1990).

Fig. 9. Répartition géographique actuelle des espèces extraméditerranéennes représentées dans le Pliocène inférieur et moyen de la Méditerranée (données empruntées essentiellement à Nafpaktitis et al., 1977 ; Whitehead et al., 1989 ; Cohen et al., 1990).

graphic settings in the Plio-Pleistocene Mediterranean with near-bottom temperatures lower than 8–10 °C (Girone, 2003). A comparable temperature range is shared also by *Aphanopus carbo*, which in the Madeira area, type locality, occurs between 700 and 1300 m in waters characterized by low values of dissolved oxygen (ca. 6.0 mg/l), very low salinity gradients (35.6–36.0‰) and a temperature of 8.5–10.5 °C (Morales-Nin and Sena-Carvalho, 1996). Similar ecological and paleoceanographic features are also probable for some extinct species like *Scopelopsis pliogenicus*, *Lampadena ionica* and *Coelorinchus stellaris*, closely related to deep-sea Atlantic or generally oceanic taxa (Nolf and Girone, 2000b; Girone and Nolf, 2002; Girone, 2003).

Following the paleoceanographic model proposed by various authors (e.g. Benson, 1972; Van Harten, 1984; Colalongo et al., 1990; Thunnel et al., 1991; Di Geronimo and La Perna, 1997) for the Plio-Pleistocene Mediterranean basin, the presence of these taxa testify psychrospheric conditions (deep-water masses with temperature lower than 10 °C) different from the present-day homeothermy (temperature of deep-water masses ~13 °C). However, the loss of psychrosphere seems to

be estimated at the end of the small *Gephyrocapsa* Zone (Colalongo et al., 1990). Taxa such as *N. groenlandica*, *B. euryops*, and *C. rupestris* seem to survive the changes from the Pliocene–Early Pleistocene psychrospheric condition to the homeothermy associated with the uplift of the Gibraltar sill, and, in some cases, e.g. *C. rupestris*, they survived till late Pleistocene, as testified by data from box-corer samples referable to the last glacial period (Table 1 and Fig. 1). In the late Pleistocene assemblages *C. rupestris* is associated with subpolar–temperate Atlantic taxa like *P. arcticum*, which is never found in older sediments. The occurrence of these taxa is probably more related to climatic changes and their mode of life. The sea surface waters were subject to major cooling during the Middle–Late Pleistocene caused by global increases in ice volume and decreasing temperatures. In particular, micropaleontological and stable oxygen isotope analyses showed that sea surface temperature (SST) in the western and eastern Mediterranean were on average 4 and 6 °C colder than the present SST, respectively (Thunnel, 1979; Howell et al., 1998; Emeis et al., 2000). Moreover, the benthopelagic *C. rupestris* makes diurnal and seasonal migrations. In the modern geographical distribu-

tion, during the summer months, it moves to deeper water returning to shallower waters in the winter. During the middle to late Pleistocene, probably, *C. rupestris* as well as the mesobathypelagic taxa were able to cross the sill due to colder temperature. According to Corselli (2001), a production of colder deep water could be driven by such decreasing of the temperature of the Mediterranean thermosphere which allowed some deep Atlantic taxa to survive in the Mediterranean basin.

The Pleistocene extra-Mediterranean group includes mainly taxa which modern distribution is restricted to the North Atlantic Ocean, contrasting with the worldwide geographic distribution of the taxa occurring in earlier sediments (Nolf and Brzobohaty, 2004).

5. Concluding remarks

From the compiled data for all Mediterranean upper Pliocene and Pleistocene otolith assemblages, three main features can be highlighted:

- A Pleistocene deepwater fauna that shows a markedly more oceanic aspect than the present-day one, a tendency that is observed in Mediterranean otolith associations from early Oligocene till Pliocene times.
- A gradual replacement from lower Pliocene till lower Pleistocene, of taxa with Indo-Pacific—or, more generally, tropical–subtropical affinities—by temperate taxa. This results in an increasing percentage of taxa still existing in the present-day Mediterranean towards the Pleistocene.
- A mesopelagic and deep bathypelagic fauna with more restricted North Atlantic affinities invading the Mediterranean from the Gelasian till the late Pleistocene.

On the basis of the published data on the Pre-Messinian (mainly Nolf and Steurbaut, 2004; Nolf and Brzobohaty, 2004) and Zanclean fish faunas (Nolf et al., 1998), one can state that the lower Oligocene Mediterranean fauna is a circum-global oceanic one, essentially composed of genera with a Recent Indo-Pacific distribution (90% of the entire fauna). From the lower Miocene up to the Tortonian and during the lower Pliocene (Zanclean), the importance of the present-day Indo-Pacific genera decreases gradually in favor of Atlantic genera.

From the upper Pliocene (Gelasian) on, the Mediterranean otolith-based fossil record shows relevant modifications. The fauna is enriched by taxa (living there today) that seem to have invaded at that time from the subpolar–temperate or temperate Atlantic, e.g. *N. elongatus* and *Phycis blennioides*, and a large group of taxa which distribution is restricted today to the North Atlantic. Although the middle Pliocene (Piacenzian) otolith-based fossil record is less known, the appearance of temperate taxa in the Mediterranean apparently was initiated then (documented from unpublished data from several localities in northern and southern Italy referable to the upper part of the Piacenzian). *M. punctatum*, *B. glaciale*, and *Hygophum* are included in this group. At the same time, typical extra-Mediterranean

tropical–subtropical taxa that were well represented in the Pre-Messinian and Zanclean fauna disappears. Only two extra-Mediterranean species, *Diaphus* aff. *splendidus* and *Benthosema suborbitale* seem to survive till the lower Pleistocene (respectively, till the Santernian and till the large *Gephyrocapsa* biozone). Several extinct taxa, e.g. *Coryphaenoides sicilianus* and *Parascombrops mutinensis*, seem to be in the same case. This pattern may be closely connected to the progressive cooling trend that characterized the climatic history of the Plio-Pleistocene Mediterranean related to global climatic change.

A new invasion of tropical–subtropical taxa from the adjacent Atlantic is registered during the middle Pleistocene (*P. lacunosa* Biozone) in the Montalbano Jonico section, close to interglacial phases (Girone and Varola, 2001). The main feature that characterizes the Mediterranean Upper Pliocene and Pleistocene deep-sea assemblages is the occurrence of taxa which are typical for Recent North Atlantic cold deep water, and which completely disappeared from the Mediterranean at the end of the Pleistocene. The occurrence of these taxa is interpreted here as a response to the Plio-Pleistocene Mediterranean paleoceanographic setting which was quite different from the Recent one, as well as a response to the global climatic deterioration. Colder temperatures during the late Pleistocene favored the migration of North Atlantic mesopelagic and bathypelagic taxa, especially of the ones that were able to make bathymetric excursions in relationship to changing environmental parameters and therefore, could cross the Gibraltar Strait into the Mediterranean when the depth of the threshold changed. From this point of view, it is important to underline that the greater abundance and diversity of these taxa are restricted to Messina Strait area characterized by peculiar oceanographic setting.

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