Fish otoliths from the pre-evaporitic (Early Messinian) sediments of northern Italy: their stratigraphic and palaeobiogeographic significance

Angela Girone · Dirk Nolf · Oreste Cavallo

Abstract The study of otolith assemblages from the pre-evaporitic Messinian deposits allows the reconstruction of a fauna of 79 taxa of which 35 could be identified at the specific level. Three of these are new: *Diaphus rubus, Myctophum coppa*, and *Uranoscopus ciabatta*. The assemblages reflect mainly a neritic environment influenced by the oceanic realm. Analysis of the global present-day geographic distribution of 42 of the recognised Messinian genera indicates that 88% of these are still living in the Mediterranean, 98% in the Atlantic and 78% in the Indo-Pacific realm. These results are in good agreement with the evolutionary trends documented for the Oligocene and Miocene teleost fauna, specifically an increase in percentage of genera inhabiting the modern Mediterranean, a very high percentage of Atlantic and Indo-Pacific genera, and a slight fall of the importance of present-day Indo-Pacific genera from the Rupelian up to the Late Miocene. Analysing the composition of the Early Messinian fauna at the level of nominal species indicates that about 53% of the species represented in the assemblages are still living in the Recent Mediterranean, and that a significant number of these were already present in the Tortonian. It is interesting that these species are mainly neritic. This seems to confirm that the close affinity of the fossil assemblage with the present-day Mediterranean neritic fauna, which was already recorded at the genus level for the Rupelian fauna, persists during the Neogene and continues until the Pleistocene.

Keywords Fishes · Teleostei · Otoliths · Messinian · Appearance · Extinction

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Introduction

During the Late Miocene (Tortonian and Messinian), the Tethyan Ocean was ultimately closed as result of synorogenic collisional tectonism, and its Mesozoic and Cenozoic sedimentary sequences were deformed and uplifted along the emerging Alpine-Himalayan orogenic system. Deepwater, open-sea environments persisted through the Late Miocene in scattered areas in the proto-Mediterranean Basin. During the Messinian, the Mediterranean Basin was affected by palaeoceanographic changes marked in the sedimentary record by both cyclic variations forced by astronomical factors and periodic or abrupt changes related to water mass exchanges with the Atlantic Ocean driven by tectonic/eustatic controls. The main change corresponds to the Salinity Crisis, which was responsible for the deposition of widespread saline deposits over the whole palaeo-Mediterranean area (Hsü et al. 1973; Cita et al. 1978; Rouchy 1982) (Fig. 1). An age between 6 and 5.7 Ma is now commonly accepted for the onset of the evaporite deposition in several basins (Vai et al. 1993; Gauthier et al. 1994; Hilgen et al. 1995; Sprovieri et al. 1996). Evidence exists that although the end of the Messinian Salinity Crisis appears to have been rather abrupt, the onset was gradual. Throughout the Mediterranean, the pre-evaporite sediments display changing lithologies during the Early Messinian,
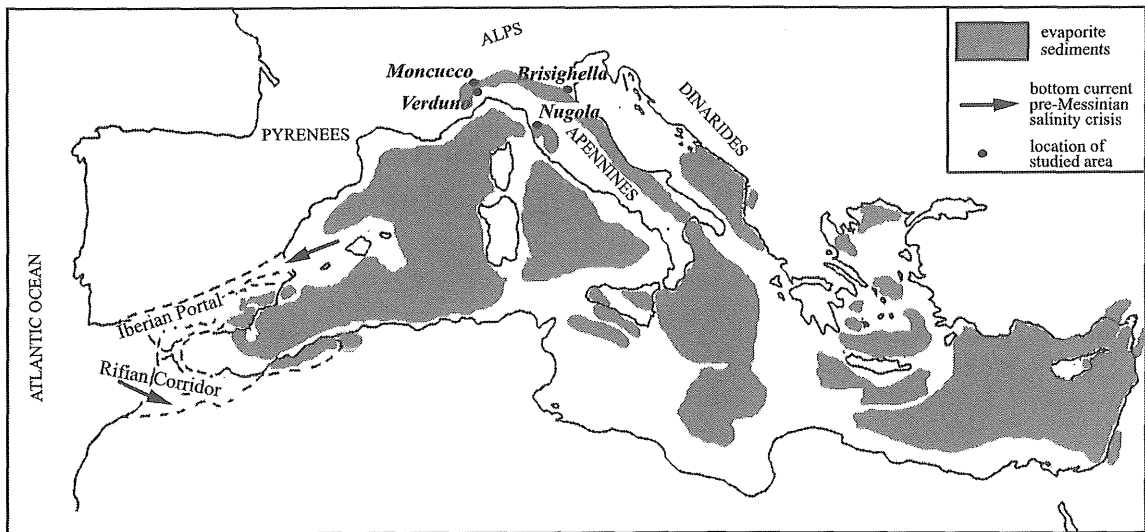
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Fig. 1 Location of the studied area (from Cita and Corselli 1993; modified)

from predominantly marl/sapropel sequences to either diat-omites (e.g. Sicily, Gavdos, northeastern Morocco, Algeria) or euxinic clays (e.g. northern Italy, Tyrrhenian Sea, eastern Mediterranean). Palaeoenvironmental changes related to these lithological transitions are documented by faunal (e.g. Cita 1976; Van der Zwaan 1982; Benson et al. 1991; Sierro et al. 1993; Hodell et al. 1994) and geochemical (stable isotope) parameters (e.g. Vergnaud-Grazzini 1983; Vergnaud-Grazzini et al. 1977; McKenzie et al. 1979; Van der Zwaan and Gudjonsson 1986; Hodell et al. 1994; Kastens 1992). Micropalaeontological studies indicate from the Late Tortonian through Early Messinian, the beginning of deterioration of the Mediterranean water mass circulation, probably related to a warming climate phase (characterised by stratification in the water column) and to the closure of the southern Rifian Corridor representing the corridor for the inflow of Atlantic deep-water during the Tortonian (Benson et al. 1991) (Fig. 1).

The present paper provides an otolith-based reconstruction of the Early Messinian faunas in the Mediterranean realm, based on assemblages from several sections in the Piedmont and Romagna basins (northern Italy) (Fig. 1). Until now, knowledge of the Messinian Mediterranean teleost fauna was based mainly on skeletal material. A synthesis of the data is given by Gaudant (2002). Otolith-based reconstructions of the Miocene fish fauna in the Mediterranean realm deal mainly with Lower Miocene and Tortonian (Upper Miocene) associations from deep-sea sediments in northern Italy (Robba 1970; Nolf and Steurbaut 1983; Nolf and Brzobohaty 2004). Additional data are furnished by neritic assemblages from Lower Miocene deposits of France (Nolf and Cappetta 1980; Reichenbacher and Cappetta 1999) and by Middle Miocene (Langhian) neritic associations from Spain (Hoedemakers and Batllori 2005).

The Early Messinian otolith associations are compared with those from the Tortonian and Pliocene Mediterranean deposits, in order to evaluate the evolution of the fish fauna at the Tortonian-Early Messinian interval and to focus on the principal changes in the composition and diversity of the teleost fauna before and after the Messinian Salinity Crisis in the Mediterranean realm.

Geological context

The studied sections are located in the Tertiary Piedmont Basin (Verduno and Moncucco sections) and inside the thrust belt of the Romagna Apennines (Brisighella sections).

The Tertiary Piedmont Basin is composed of different tectono-sedimentary domains: the Torino Hill and Monferrato (Moncucco section) to the north and the Langhe Basin (Verduno sections), the Alto Monferrato and the Borbera Grue sector to the south. These domains show partially independent tectono-sedimentary evolution and are filled by Eocene to Neogene sediments. The Piedmont Messinian succession outcrops widely in the Langhe area where Sturani (1973, 1978) described a three-fold succession very comparable to coeval Sicilian deposits. However, the Monferrato Messinian outcrops are rather scarce and are represented mainly by evaporitic and post-evaporitic deposits. The classical Piedmont Messinian succession is characterised, from bottom to top, by: (1) lower "pre-evaporitic" deep-water marine sediments, coeval to the Sicilian Tripoli Formation, representing normal and euxinic facies (Sturani 1978) and lithologically referable to the Sant'Agata Fossili Marls (Tortonian-Early Messinian in age); (2) intermediate "evaporitic" shallow-water deposits, referred to the

Gessoso-solfifera Formation, described by Vai and Ricci Lucchi (1977) in the Romagna Basin (see below), starting with calcareous levels indicated as "Calcare di Base" and including gypsum deposits (Sturani 1978); (3) upper "post-evaporitic" brackish deposits of the "Strati a Congerie" correlated to the Mediterranean Lago-Mare facies (Cita et al. 1978). The succession is overlain with open-marine Early Pliocene clays.

In the Brisighella area, the four main formations building the Romagna Apennines are exposed: (1) the upper part of the Marnoso-arenacea Formation (Tortonian-Early Messinian), (2) the Gessoso-solfifera Formation (Messinian), (3) the Colombacci Formation (Late Messinian) and (4) the lower part of the Argille Azzurre Formation, whose base belongs to the MPL1 Zone (Lower Pliocene) (Vai 1989).

As defined by Vai (1989), the Tripoli and Marne tripolacee units of the older literature correspond to part of members 4 and 5 (upper part) of the Marnoso-arenacea Formation. Part of these deposits, characterised by shaly, organic-matter-rich layers, are also named "pre-evaporitic euxinic shales", and Early Messinian in age. The Gessoso-solfifera Formation is the depositional response to the Messinian Salinity Crisis and can be separated in a W Romagna to Emilia selenitic facies (Vena del Gesso Basin) and an E Romagna to N Marche balatino-clayey and sulphur-rich facies (Romagna-Marche Basin) containing reworked clasts of the former (Vai 1989). The Vena del Gesso sequence, included in the Brisighella succession, can be subdivided into five informal members: (1) carbonate cycles, (2) early diagenetic gypsum stromatolites, (3) major evaporitic cycles, (4) VI evaporitic cycle and (5) minor evaporitic cycles. The carbonate cycles, constituted by two to six light grey, yellowish weathering carbonate beds cyclically alternating with grey to dark grey, mainly euxinic shales and pelites, correspond to the "Calcare di Base" of eastern Romagna and Piedmont basins. The first evidence of evaporite precipitation occurs in the uppermost carbonate beds where the base of Gessoso-solfifera Formation is conventionally collocated.

Locality data

Brisighella, Monticino quarry (Fig. 1):

Carta topografica Regione Emilia Romagna 1/25,000, sheet Brisighella (239 SO), $x = 440.800$, $y = 200.750$

In the old Monticino gypsum quarry, which is less than 1 km NW of the town centre of Brisighella, there is a didactic geological park with a well-labelled walkway that was constructed by the Museo Civico di Scienze Naturali di Faenza. This section was visited by us with Gian Paolo Costa and Marco Sami from the Faenza Museum in 2005.

The section offers a complete overview of Messinian sediments, starting in the top of the pre-evaporitic Messinian clays, which are succeeded by huge massive gypsum deposits that are overlain by Lago Mare sediments. Finally, the Messinian is overlain with marine Zanclean clays. The interesting part for otolith studies is the top of the pre-evaporitic clays, just below the massive gypsum beds and underlying "Calcare di Base". This part of the section was measured and additionally sampled in 2007 (Fig. 2). All samples were very rich in otoliths of small mesopelagic fishes, mainly *Diaphus*. The overall weight of the samples is $\pm$ 20 kg for samples a, c, d and e, and about 100 kg for sample b.

The foraminifera of sample b were analysed by Erica Bicchi and indicated the sediment as Messinian N17, *Globorotalia conomiozea* Zone, *Globigerina multiloba* Subzone of D'Onofrio et al. (1975).

Moncucco, gypsum quarry:

Carta d'Italia IGM 1/25,000, sheet Buttigliera d'Asti (56 II SE), $x = 416.400$, $y = 4990.500$

The Moncucco gypsum quarry provides a superb overview of Messinian sediments in the Hills of Torino. The section has been described and figured by Bicchi et al. (2002), Dela Pierre et al. (2002) and Irace (2004) and is reproduced here (Fig. 3). Four sediment samples (SF1, SF2, SF5 and SF8, respectively) each about 3 kg were provided by Erica Bicchi and proved to be extremely rich in small otoliths, mainly of *Diaphus* and *Maurolicus muelleri*. They all come from the Argille di Sant'Agata Fossili between the selenitic gypsum and chaotic complex of Valle Versa. These samples contain abundant very well preserved foraminifera. Among the planktonic ones, *Globigerina multiloba* and *Globorotalia humerosa* indicate that the samples are in the *Globorotalia conomiozea* Zone, *Globorotalia multiloba* Subzone of D'Onofrio et al. (1975) (Early Messinian). In 1984, Nolf and Steurbaut collected a loose block of about 15 kg in the Moncucco quarry. This block, containing thousands of small otoliths and the same planktonic foraminiferal assemblage as samples SF1 to SF8, was also dated as Early Messinian by Erica Bicchi.

Nugola, Strada degli Archi, point 9:

Carta d'Italia IGM 1/25,000, sheet Collesalvetti (284 NO), see also Bossio et al. (1981: p. 72, point 9) and Caputo et al. (2009)

Very recently, when the manuscript of the present paper was almost achieved, a paper on Messinian otoliths from the Strada degli Arch section, about 6 km E of Livorno, about midway between Livorno and Nugola, was published by Caputo et al. (2009). This site had already been sampled for otoliths by Nolf in 1992, but we decided not to include
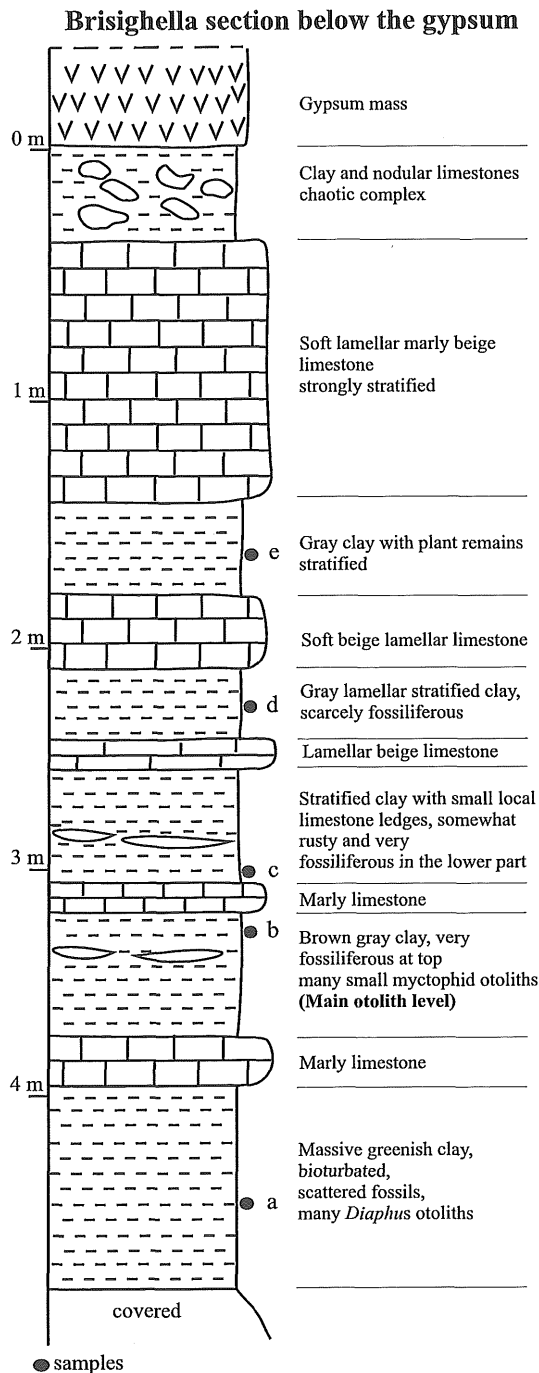
Brisighella section below the gypsum

Fig. 2 Log of the Brisighella section

this material in our study because we thought it might be younger than pre-evaporitic Messinian. As the paper of Caputo et al. provides evidence for a pre-evaporitic Messinian age, based on foraminifera and on the regional geological context, we finally decided that the data from this study had to be evaluated and considered here. Caputo et al. cited and figured 11 taxa:

Atherina aff. *boyeri* (Risso, 1810)
Hemiramphidae ind.

Aphanius crassicaudus (Agassiz, 1839)
Polynemidae ind.
Aphya minuta (Risso, 1810)
Gobius aff. *guerini* (Chaine and Duvergier, 1931)
Gobius aff. *multipinnatus* (von Meyer, 1852)
Gobius aff. *niger* (Linnaeus, 1758)
Gobius sp.
Lesueurigobius aff. *vicinalis* (Koken, 1891)
? *Mesogobius* sp.

Four of those were not recorded from our samples in Piemonte and Emila Romagna: *Atherina* aff. *boyeri*, Hemiramphidae ind., *Aphanius crassicaudus* and *Aphya minuta*. For the genera *Gobius* and *Lesueurigobius*, we prefer to adopt a less rigorous interpretation than Caputo et al., and not to identify them at species level, because in those genera, species identifications on the basis of the otoliths are very delicate, if not impossible in some cases. *Gobius guerini* was described from the Zanclean of Catalania, *Gobius multipinnatus* from the Ottnangian (Burdigalian) of Bavaria, Germany, *Gobius niger* is a Recent species, and *Lesueurigobius vicinalis* was described from the Badenian (Langhian) of Austria (the figure pl. 1, Fig. 6 of Caputo et al. 2009 suggests the same taxon named here *Lesueurigobius* sp. 3). Although the iconography of Caputo et al. (2009) suggests some similarity to the otoliths of those taxa, we judge it as improbable that such a heterogeneous assemblage of species should occur together at the Nugola site. Polynemids and *Mesogobius* were also recorded from our samples from Piemonte.

This leaves us with five additional taxa that we included in our lists and tables, to make our overview of the otolith based Messinian fish fauna as complete as possible:

Atherina aff. *boyeri* (Risso, 1810)
Hemiramphidae ind.
Aphanius crassicaudus (Agassiz, 1839)
Polynemidae ind.
Aphya minuta (Risso, 1810)
Gobius sp.

For the iconography of the concerned species, we refer to Caputo et al. (2009). It also has to be mentioned that *Aphanius crassicaudus* was originally described from a skeleton from the gypsiferous marls of Marche. A similar skeleton with otoliths in situ was discovered by Gaudant et al. (1988). In Tuscani, *Aphanius crassicaudus* is known from the pre-evaporitic deposits (Nugola) till the post-evaporitic deposits (Cava Serradi, near Gabbro).

Verduno, Metalgranda:

Carta d'Italia IGM 1/25,000, sheet Bra (68 II SE), $x = 415.100$, $y = 4948.000$
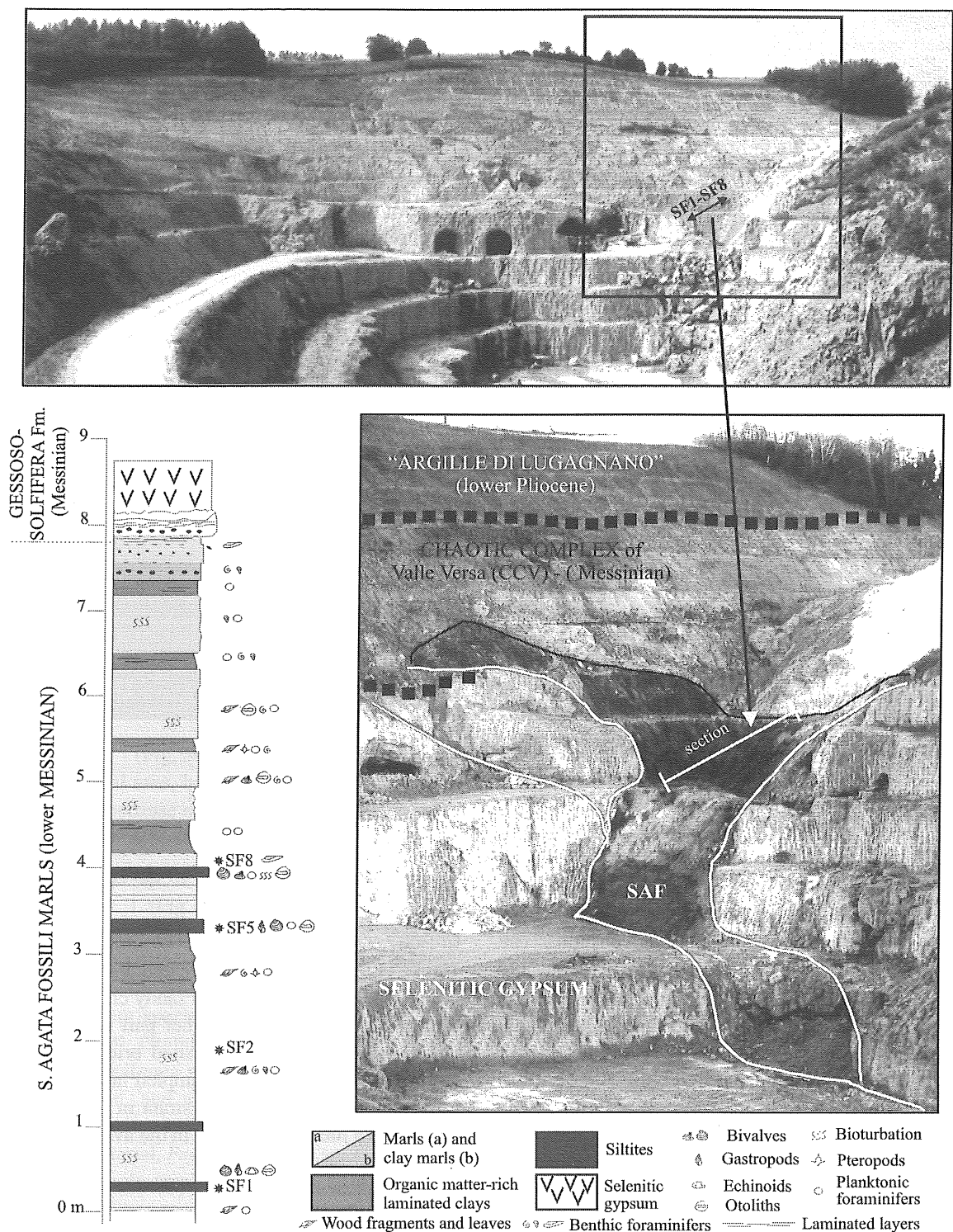
Fig. 3 Panorama of Moncucco quarry (year 2005) and studied section

The section consists of an escarpment on the western side of the private access road to a storage place of the Metalgranda Enterprise. Today, most of the section is hidden by a concrete wall (Fig. 4), and only the sampling site of O. Cavallo (2007) is still accessible. Unfortunately, this site has also started to become overgrown. The sampled bed is a grey silty clay with molluscs and some small pebbles overlain by a 10 to 20-cm-thick calcareous sandstone bank. Above this bank is about 7 m of silty clay, stratified with more sandy layers containing almost no macrofossils. The top of this somewhat overgrown upper series is visible some 40 m to the south.

Fig. 4 Panorama of Verduno Metalgranda (year 2008) and location of the samples analysed in the present paper

The Metalgranda section was extensively sampled for otoliths and molluscs (several hundred kilograms of sediment) by O. Cavallo in 2004 and 2007 and produced a heterogeneous association of neritic and oceanic fishes, which were apparently washed together in a turbidite. The 2004 sampling site was located about 4–5 m below the 2007 site.

E. Martini examined nannoplankton from a small section located some metres lower and sampled by D. Nolf in 2005. Martini defines the association as rather poor in species but relatively well-preserved containing some reworked Upper Cretaceous and Palaeogene species. The autochthonous assemblage is dominated by *Sphenolithus abies* and *Helicosphaera carteri*. *Discolithina* species and *Braarudosphaera bigelowi*, indicators for nearshore and more protected environments, are common. Ceratoliths, including *Aumarolithus primus*, are represented. *Discoaster quinqueramus*, a species that would also be expected in such an association, was not to be found. However, the Nannoplankton Zone NN11b of the Messinian could still be determined. The sample sent to Martini also came from about 5 m below the 2007 sampling point shown in Fig. 4.

Verduno, Hospital, (sampled by O. Cavallo)

Carta d'Italia IGM 1/25,000, sheet Bra (68 II SE), $x = 415.600$, $y = 4974.400$

In 2007, O. Cavallo collected otoliths by washing some 100 kg of sediments from laminated argillaceous strata near base of the exposure and from sandy clay sediments from a slumping structure in the higher part of the section. This large construction pit was visited briefly by Cavallo and Nolf in June 2007, and the sampled layers were observed. The chaotic condition of the strata in the construction pit prohibited a measured section in the available time.

Verduno, Tanaro, left bank:

Carta d'Italia IGM 1/25,000, sheet Bra (68 II SE), $x = 415.325$, $y = 4948.900$

Messinian sandy clays with molluscs and otoliths, very similar to those observed at the Verduno, Metalgranda site, are exposed in the left bank of the Tanaro, and were sampled for otoliths by O. Cavallo. These sediments were overlain with chaotically placed gypsum blocks that were well exposed more upstream in the banks of the Tanaro.

Systematic palaeontology

A list of all otolith-based taxa represented in the samples from the studied area is given in Table 1. The classification adopted is that proposed by Nelson (2006). Additional comments are given for problematic taxa. In cases where specific identity could not be unequivocally decided, the abbreviation aff. (affinis) was inserted between the name of the genus and the name of the group species. The notations a1a, b1a..., a1b, b1b..., a1c, b1c....etc. in the figures are used to indicate respectively ventral, inner (=mesial) and lateral views. For general information about otoliths (morphological nomenclature, composition, diagnostic value, ontogenetic changes, etc.), the reader is referred to Nolf (1985). Concerning collective (or open) generic nomenclature, the current procedure used is that applied in numerous papers on otolith taxonomy. For species of uncertain generic position (i.e. whose systematic position can be identified only at familial, subordinal, or ordinal level) the word "genus", followed by the name of the family or higher category in plural genitive, followed by the species name is used; e.g. "genus Heterenchelyidarum" *circularis*. See also Nolf (1985) for further explanation.

Remarks on taxa requiring comments

(1) Congridae ind. (Fig. 5b)—One thick otolith, recrystallised in the ventral area, has been tentatively referred to the congrid family because of its sulcus morphology, without further generic or specific identification.

(2) *Pseudophichthys* sp. 1 and sp. 2 The otoliths of *Pseudophichthys* sp. 1 (Fig. 5c) are elongated; the dorsal rim is strongly curved towards the anterior portion and delimits a dorsal area that is narrower in the anterior part. The sulcus is generally wide. These features distinguish them from the Recent species *Pseudophichthys splendens* (Lea, 1913) (Fig. 5d). Otoliths of *P. splendens* are higher and they have a dorsal area with an equally wide posterior and anterior portion, and a narrow and weakly incised sulcus.

In the studied material, *Pseudophichthys* sp. 2 (Fig. 5f) is represented by a single small specimen, which was separated from the other two recognised species because of its sub-quadrangular shape, delimited by a linear and sub-vertical posterior rim, a straight dorsal rim and a poorly curved ventral rim.

(3)? *Lestidium* sp. (Fig. 5k)   The paralepidid otoliths collected in the Messinian of Verduno resemble most closely to those of the Recent *Lestidium atlanticum* Borodin, 1928 (see Figs. 5k, 6c) and apparently belong to the same genus. Because there is some confusion about both the generic

nomenclature and otolith morphology of paralepidids, we figure here (Fig. 6) some of the most relevant Recent Atlantic species under their modern generic nomenclature (Quéro et al. 2003).

Confusion about the otoliths of Recent paralepidids is caused by the paper of Rivaton and Bourret (1999) where these authors figured several otoliths on pl. 126, Figs. 1–9 under the names *Lestidium atlanticum, Lestidium* sp. A and *Lestidium* sp. B. The figured otoliths do not fit with the Recent *Lestidium atlanticum* otolith dissected in the MCZ collection at Harvard and figured here (Fig. 6c). The otoliths figured by Rivaton and Bourret might well belong to the genus *Arctozenus*; compare to the *Arctozenus rissoi* otoliths figured here (Fig. 6a). Also the *Macroparalepis affine, M. danae,* and *M.* sp. A otoliths, figured on pl. 126 (Figs. 10–16) of Rivaton and Bourret (1999), strongly differ from the *Macroparalepis nigra* (Fig. 6d) and the *M. affinis* (Fig. 6e) otoliths that we dissected from fishes identified by G. Maul in the Funchal Museum in Madeira. The "*Paralepis*" *atlantica* otoliths figured by Rivaton and Bourret (pl. 126, Figs. 17–18) seem to agree fairly well with the *Magnisudis atlantica* otoliths in our collection (Fig. 6g) and with those figured by Smale et al. (1995), pl. 16, Fig. E1, as *Paralepis atlantica*).

(4) *Bolinichthys italicus* (Anfossi and Mosna, 1971) (Fig. 5e)   This species is characterised by very small otoliths that were originally thought to represent a small *Diaphus* species. Brzobohaty and Nolf (2000) highlighted the similarity between these small fossil otoliths and those of the Recent *Bolinichthys supralateralis* (Parr, 1928), a tropical to subtropical Atlantic species. The fossil otoliths differ from the Recent ones by their more quadrangular outline, their less curved ventral rim, which bears spines, and by their more developed and acuminate rostrum. The species is known from Late Tortonian and Messinian deposits of Italy but never in great abundance.

(5) *Diaphus pedemontanus* (Robba, 1970)   Robba (1970) described this species from the Tortonian of the Rio Mazzapiedi-Castellania. The holotype is a very large specimen about 6.9 mm in length. From the same type locality, Brzobohaty and Nolf (2000) described a specimen of about 7.3 mm in length. In very large specimens, the sulcus is deeply incised, the antirostrum is strongly developed and prominent, and there is a backwards expansion in the lower part of the posterior rim. Brzobohaty and Nolf (2000, pl. 4, Figs. 2–6) figured a reasonable growth series of *D. pedemontanus* from the Zanclean of southeast France. A growth series was also figured by Nolf and Steurbaut (1983, pl. 1, Figs. 26–37) from the Tortonian of Montegibbio and Rio Mazzapiedi-Castellania. These growth series show strong ontogenetic changes and a considerable intraspecific variability. In smaller specimens,

Table 1 List of otolith-based fish taxa from the pre-evaporitic Messinian of northern Italy

	Iconography	Brisighella			Verduno					Moncucco					Nugola
		a	b	c	Hospital slumping	Hospital laminated strata	Metalgranda sample Nolf	Metalgranda sample Cavallo 2007	Left bank of Tanaro River	SF 1	SF 2	SF 5	SF 7	SF 8	Caputo et al. 2009
Congridae															
Congridae ind. (1)	Fig. 5b							1							
Paraconger sp.	Fig. 5a							1							
Pseudophichthys splendens (Lea, 1913)	Fig. 5d		4		1				2						
Pseudophichthys sp. 1 (2)	Fig. 5c		3		3			10							
Pseudophichthys sp. 2 (2)	Fig. 5f							1							
Clupeidae															
Sardina pilchardus (Walbaum, 1792)	Fig. 5h								2						
Argentinidae															
Argentina sphyraena Linnaeus, 1758	Fig. 5i								2				1		
Sternoptychidae															
Maurolicus muelleri (Gmelin, 1789)	Fig. 5j				18	200	1	224	104	97	1	22	129	1	
Paralepididae															
? **Lestidium** sp. (3)	Fig. 5k				2			23	9						
Myctophidae															
Bolinichthys *italicus* Anfossi & Mosna, 1971 (4)	Fig. 5e								12	64	150	89		135	
Diaphus befralai Brzobohaty & Nolf, 2000	Fig. 7d						1	24					1		
Diaphus cavallonis Brzobohaty & Nolf, 2000	Fig. 7a				6	8		5	8				14		
Diaphus pedemontanus (Robba, 1970) (5)	Fig. 7b		10		7	4		23	7	5	5	3	63	1	
Diaphus rafinesquii (Cocco, 1838)						1		2	1			3			
Diaphus rubus n. sp.	Fig. 8a		23		3	2	3	42	159	53	42	48	4	27	
Diaphus aff. **splendidus** (Brauer, 1904)	Fig. 7c						4	9							
Diaphus **taaningi** Norman, 1930					6			5	7	2	2				
Diaphus sp. 1	Fig. 7e							4			1				
Diaphus sp. 2	Fig. 7h							2							
Hygophum hygomi (Lütken, 1892)			12		39		5	135	39	55	6	24	39	9	
Myctophum coppa n. sp.	Fig. 11a		70		40	18	22	263	90	85	18	32	84	17	
Lampadena sp. (6)	Fig. 5g								2				1		
Lobianchia aff. *dofleini* (Zugmayer, 1911)						2	5		3						
Notoscopelus sp.								1							

Table 1 continued

	Iconography	Brisighella			Verduno					Moncucco					Nugola
		a	b	c	Hospital slumping	Hospital laminated strata	Metalgranda sample Nolf	Metalgranda sample Cavallo 2007	Left bank of Tanaro River	SF 1	SF 2	SF 5	SF 7	SF 8	Caputo et al. 2009
Bregmacerotidae															
Bregmaceros sp.	Fig. 8e	24						3	25	21	2	8		18	
Moridae															
Physiculus aff. *huloti* Poll, 1953	Fig. 7f		1		15	3	1	31	12				5		
Merlucciidae															
Merluccius sp.	Fig. 8b												1		
Phycidae															
Phycis musicki Cohen & Lavenberg, 1984			2		4	1	2	10	1				1		
Gadidae															
Gadiculus argenteus (Guichenot, 1850)									1			1			
Gadiculus labiatus (Schubert, 1905)			150	13	13	73	4	72	67	70	22	47	205	20	
Ophidiidae															
Hoplobrotula sp.	Fig. 8d				1		2	11	1						1
"genus Neobythitinarum" sp.	Fig. 7g								1						
Bythitidae															
Bythitidae ind. 1 (7)	Fig. 8g	1	1					2		1					
Bythitidae ind. 2 (7)	Fig. 8f										1				
Bythitidae ind. 3 (7)	Fig. 8h								1						
Lophiidae															
Lophius piscatorius Linnaeus, 1758	Fig. 8i							3							
Lophius sp.					1										
Mugilidae															
Mugilidae ind.								1							
Atherinidae															
Atherina aff. *boyeri* Risso, 1810															N
Atherina sp.	Fig. 8l							1	1						
Hemiramphidae															
Hemiramphidae ind.															N
Belonidae															
Belone sp.	Fig. 8k							1							
Cyprinodontidae															
Aphanius crassicaudus (Agassiz, 1839)															

Table 1 continued

	Iconography	Brisighella			Verduno					Moncucco					Nugola
		a	b	c	Hospital slumping	Hospital laminated strata	Metalgranda sample Nolf	Metalgranda sample Cavallo 2007	Left bank of Tanaro River	SF 1	SF 2	SF 5	SF 7	SF 8	Caputo et al. 2009
Diretmidae															
Diretmus sp.							1								
Holocentridae															
Myripristidae ind.								2							
Triglidae															
Lepidotrigla sp. (8)	Fig. 8j												1		
Triglidae ind.					1			2							
Acropomatidae															
Parascombrops mutinensis (Bassoli, 1906)	Fig. 9e						1			6					
Parascombrops aff. microlepis Norman, 1935 (9)	Fig. 9a							2							
Apogonidae															
Apogon sp.						1		2							
Haemulidae															
Pomadasys aff. incisus (Bowdich, 1825)	Fig. 9b							4							
Sparidae															
Dentex aff. macrophthalmus (Bloch, 1791)	Fig. 9d						1								
Dentex aff. maroccanus Valenciennes, 1830	Fig. 9c				1			1	1						
Diplodus vulgaris (E. Geoffrey Saint-Hilaire, 1817)	Fig. 9f							6							
Spondyliosoma cantharus (Linnaeus, 1758)	Fig. 9i							5							
Polynemidae															
Polynemidae ind.					1			1							N
Sciaenidae															
Sciaenidae ind.							1								
Cepolidae															
Cepola rubescens (Linnaeus, 1766)					4		1	5							
Trachinidae															
Trachinus draco Linnaeus, 1758	Fig. 9g							1							
Uranoscopidae															
Uranoscopus ciabatta n. sp.	Fig. 12b							2							

Table 1 continued

	Iconography	Brisighella			Verduno					Moncucco					Nugola
		a	b	c	Hospital slumping	Hospital laminated strata	Metalgranda sample Nolf	Metalgranda sample Cavallo 2007	Left bank of Tanaro River	SF 1	SF 2	SF 5	SF 7	SF 8	Caputo et al. 2009
Gobiidae (10)															
Aphya minuta (Risso, 1810)															N
Deltentosteus sp.					2			2	1						
Gobius sp.															N
Lesueurigobius sanzoi (De Buen, 1918)	Fig. 10a							5	2						
Lesueurigobius sp. 1	Fig. 10b				3			6	4						
Lesueurigobius sp. 2	Fig. 10c				1			44	5						
Lesueurigobius sp. 3	Fig. 10e				4		3	3	2						N
"genus Gobiidarum" sp. 1	Fig. 10j				5		5	34	7				23		
"genus Gobiidarum" sp. 2	Fig. 10f				1		2	11	4						
"genus Gobiidarum" sp. 3	Fig. 9k							4	1						
"genus Gobiidarum" sp. 4	Fig. 10g				2			8	2	3					
"genus Gobiidarum" sp. 5	Fig. 10i							1							
"genus Gobiidarum" sp. 6	Fig. 10h				2			1	5						
? Mesogobius sp.	Fig. 10d		3		1			12	3						
Trichiuridae															
Lepidopus caudatus (Euphrasen, 1788)	Fig. 9o				1	1		2	1				1	2	
Caproidae															
Capros sp. (11)	Fig. 9j					1									
Bothidae															
Arnoglossus sp.	Fig. 9m	1			1			2					1		
Buglossidium sp.	Fig. 9n							3					1		
"genus Soleidarum" sp. (12)	Fig. 9h				1		1								

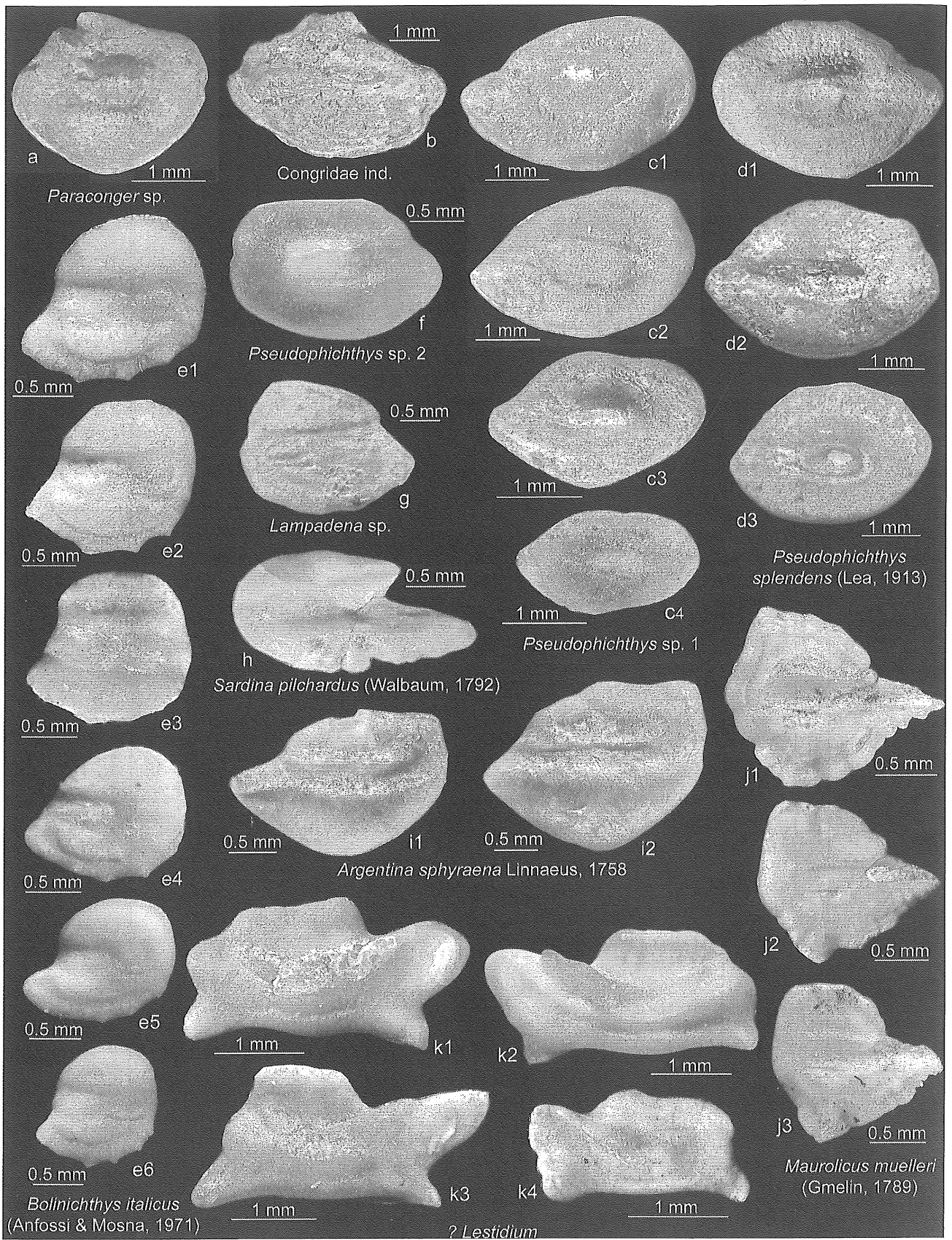*Taxa in bold* represent taxa that disappeared from the modern Mediterranean basin

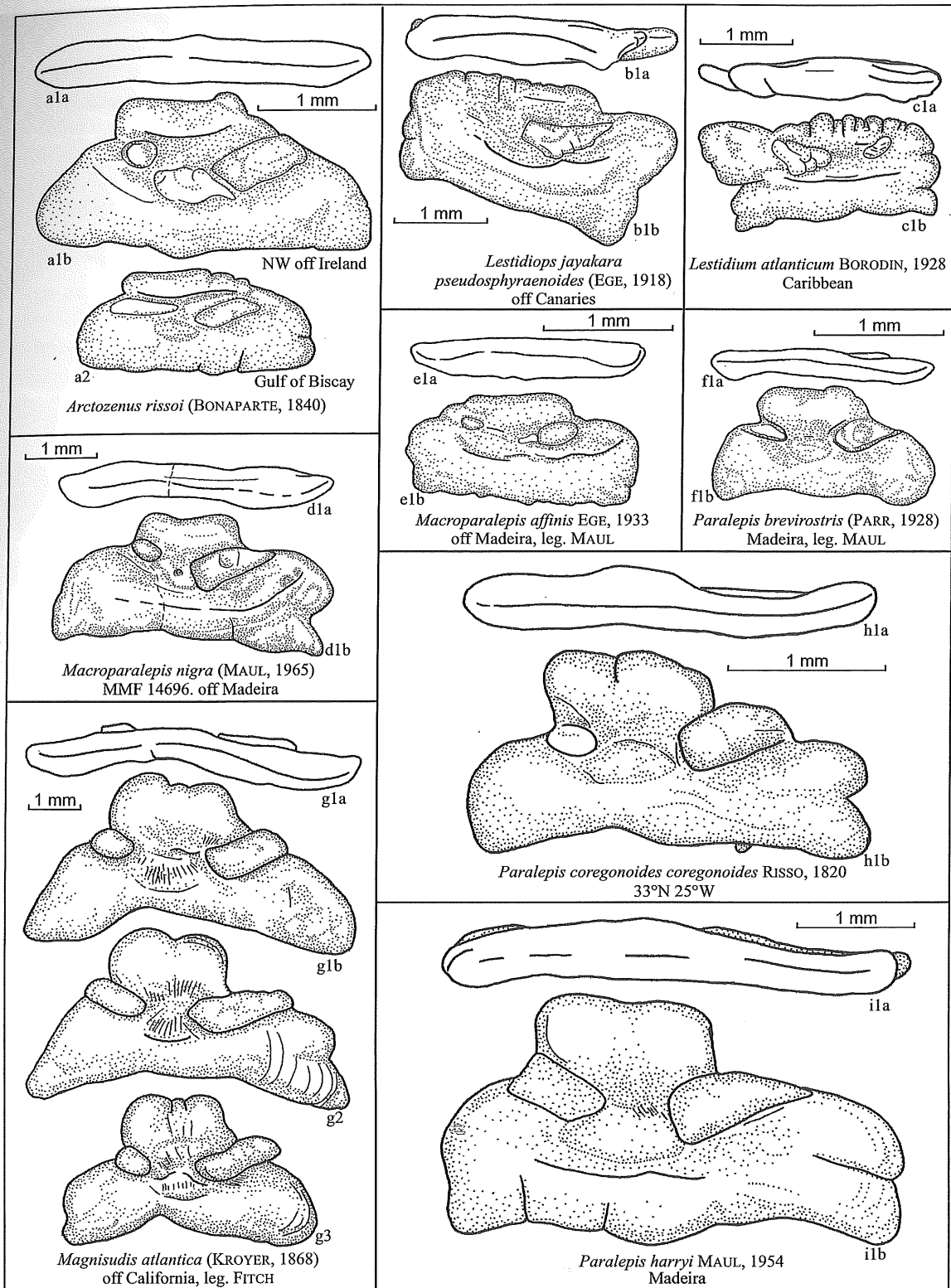**Fig. 5** Early Messinian otoliths from northern Italy (see Appendix 1 for further information)

Fig. 6 Otoliths of the most relevant Recent Atlantic species under their modern generic nomenclature (Quéro et al. 2003)

the prominent antirostrum and backwards expansion are more weakly accentuated. Moreover, Zanclean specimens show a more undulated ventral rim than Tortonian otoliths.

The Messinian otoliths, which tend to be small in size, are referable to *D. pedemontanus* (Fig. 7b) because of their well-incised sulcus, a small backwards expansion of the
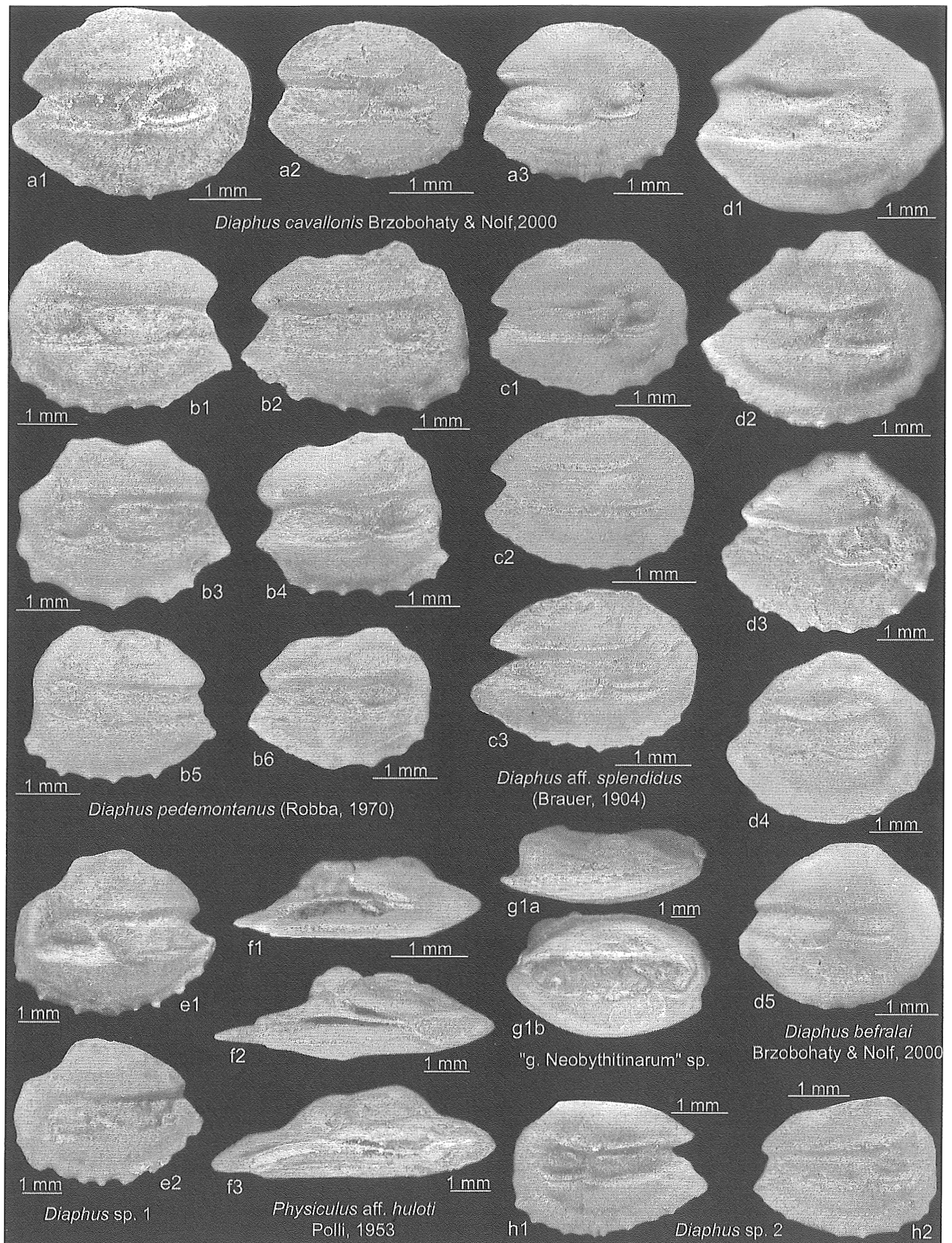
Fig. 7 Early Messinian otoliths from northern Italy (see Appendix 1 for further information)

lower part of their posterior rim that is more or less visible in all specimens and the prominent antirostrum. They compare generally well to the smaller specimens figured by Nolf and Steurbaut (1983) from the Tortonian, but several specimens show a more undulated ventral rim similarly to the Zanclean specimens.

D. pedemontanus is a rather problematic species, because of the strong ontogenetic changes and considerable variability of their otoliths. Comparison with Recent *Diaphus* species such as *D. adenomus*, which obtains large size and develops very large otoliths, with strong ontogenetic and intraspecific variability, suggests that *D. pedemontanus* had a similar habitat. Some Diaphus species which grow to a very large size, change their life habitat from mesopelagic to benthic, during their growth (Brzobohaty and Nolf 2000).

(6) *Lampadena* sp. Otoliths of *Lampadena* are very rare in the studied localities. One larger specimen (Fig. 5g) shows more salient features that allows comparison with the Recent *L. speculigera* Goode and Bean, 1896 and the Middle Miocene *L. speculigeroides* Brzobohaty and Nolf 1996 from the Badenian of the Paratethys. The Messinian otolith has a less prominent backwards expansion in the upper part of the posterior rim, which is a salient feature in otoliths of the Recent *L. speculigera*. The Messinian otolith shows more resemblance to the Middle Miocene species, and in particular seems to be very close to the smaller specimen figured by Brzobohaty and Nolf (1996, pl. 4, Fig. 14). However, *L. speculigeroides* has a more rounded and regularly curved ventral rim and a less prominent postero-ventral angle with respect to the Messinian specimen.

(7) Bythitidae ind. 1—ind. 2—ind. 3 Bythitid otoliths are rare in the studied localities, and are mostly represented by rather poorly preserved small specimens. However, among the larger specimens, three types of bythitid otoliths can be tentatively distinguished, but we are not sure that they could represent three different species because many bithitid taxa show considerable intraspecific variability. The main feature used to distinguish these three types has been the convexity of inner face which is high in Bythitidae ind. 1 (Fig. 8g) and nearly absent in Bythitidae ind. 2 (Fig. 8f) and Bythitidae ind. 3 (Fig. 8h). The general shape is about oval for all three types, but Bythitidae ind. 1 and Bythitidae ind. 2 are more elongated and have a more angular outline. Moreover, the sulcus is shorter and wider in Bythitidae ind. 3 than in Bythitidae ind. 1 and Bythitidae ind. 2. The last has a narrower sulcus located more closely to the ventral rim than in Bythitidae ind. 1 where the sulcus is approximately median in position. Bythitidae ind. 1 also shows a very characteristic depressed area in the posterior portion, just behind the end of the sulcus.

(8) *Parascombrops* aff. *microlepis* Norman, 1935 Otoliths of *Parascombrops* are not very common in the studied localities. Most of those otoliths belong to *P. mutinensis* (Fig. 9e), reported from many Mediterranean Neogene deposits, from the Upper Burdigalian until the Lower Pleistocene (Nolf and Brzobohaty 2004; Nolf 1988; Girone et al. 2006). Two otoliths can be distinguished by their slender shape and less-incised, narrower sulcus. These specimens do not show a well-marked postero-dorsal angle as in *P. mutinensis*. They are characterised by the lack of a posterodorsal angle and by a dorsal area which is highest in its central part. In *P. mutinensis,* the dorsal area is equally wide over most of its extent. These otoliths show a reasonable similarity with those of the recent *P. microlepis* (Fig. 9a). However, the Recent species is characterised by otoliths with a narrower sulcus and a more acuminate posterior portion than the Messinian specimens.

(9) Gobiidae Gobiid otoliths are very common in nearly all neritic Neogene sediments, often in tremendous quantities. Numerous fossil otolith-based species of gobiids have been described, but many are based on eroded specimens or atypical juveniles. Several such species names have been widely used, and it is not rare to see names of otoliths with types from the Paratethys Basin applied to specimens from the North Sea Basin, Aquitaine or Portugal on the basis of doubtful morphological features. Combined with our rather poor knowledge of Recent gobiid otoliths, this results in a chaotic gobiid otolith palaeontology. It is our opinion that in the present state of knowledge it is preferable to leave in open nomenclature all species which cannot be identified with Recent taxa. Most of the examined assemblages in this study were very rich in gobiid otoliths, mainly juvenile specimens. However, for the larger specimens, it is possible to distinguish different otolith morphologies, probably representing different species. In only one case has it been possible to refer some of our specimens to the Recent *Lesueurigobius sanzoi* (De Buen, 1918) (Fig. 10a) and to refer some to the extant genus *Lesueurigobius* (*Lesueurigobius* sp. 1: Fig. 10b; sp. 2: Fig. 10c; and sp. 3: Fig. 10e). Various other cases of gobiid otoliths with recognisable morphology but not referable to precise Recent genera or species are cited in open nomenclature ("genus Gobiidarum" sp. 1: Fig. 10j; sp. 2: Fig. 10f; sp. 3: Fig. 9k; sp. 4: Fig. 10g; sp. 5: Fig. 10i; sp. 6: Fig. 10h).

(10) *Capros* sp. (Fig. 9j) This single otolith is characterised by its high vertical dimension and poorly developed posterodorsal portion. Rostrum and antirostrum are prominent. The ventral area is expanded forwards. The ventral rim is strongly curved and delimits a posterior ventral portion that is much less expanded than the anterior one. This otolith is compared to those of the Recent *Capros aper* (Linnaeus, 1758) (Fig. 9l). In the fossil, the dorsal area is
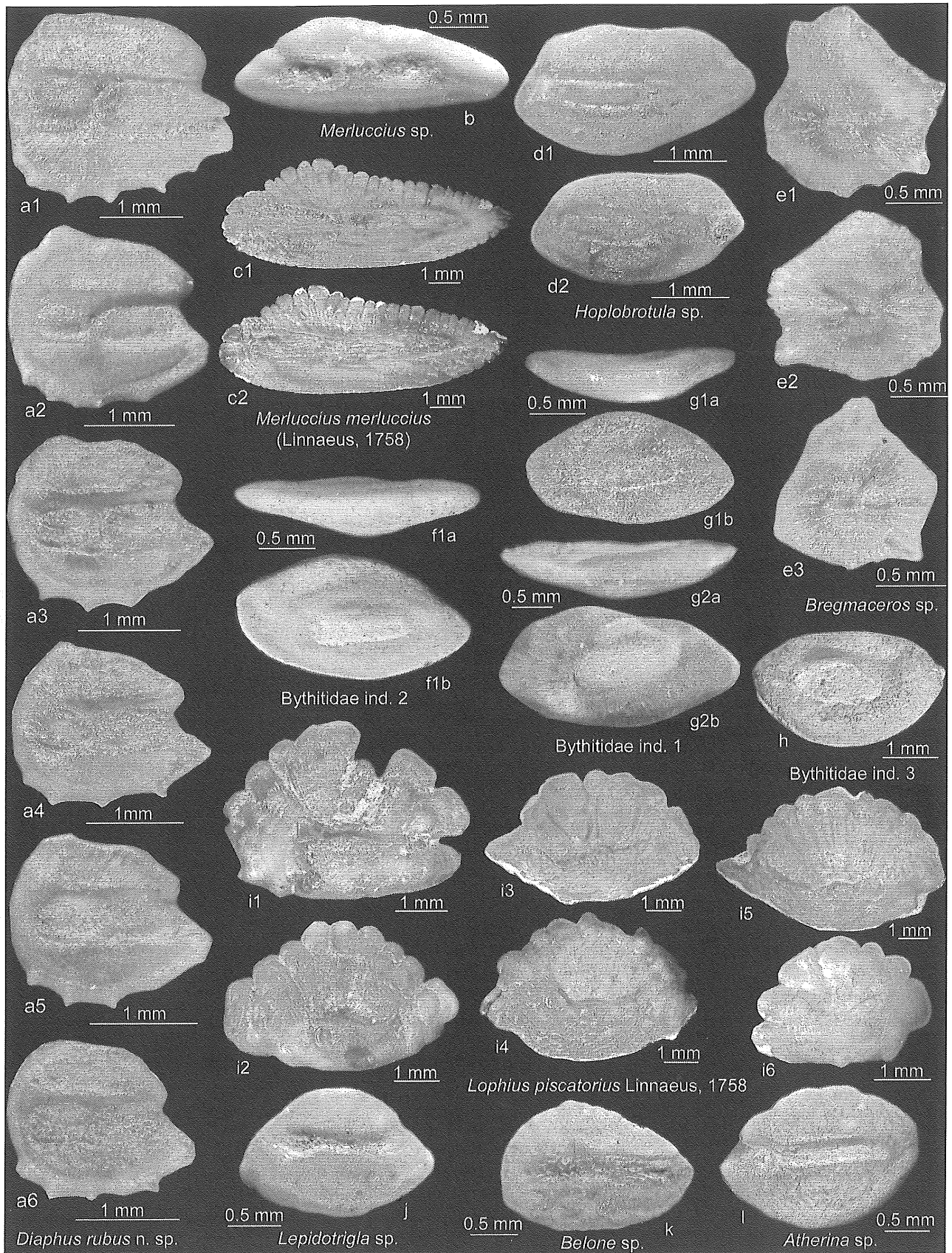
Fig. 8 Early Messinian otoliths from northern Italy (see Appendix 1 for further information)
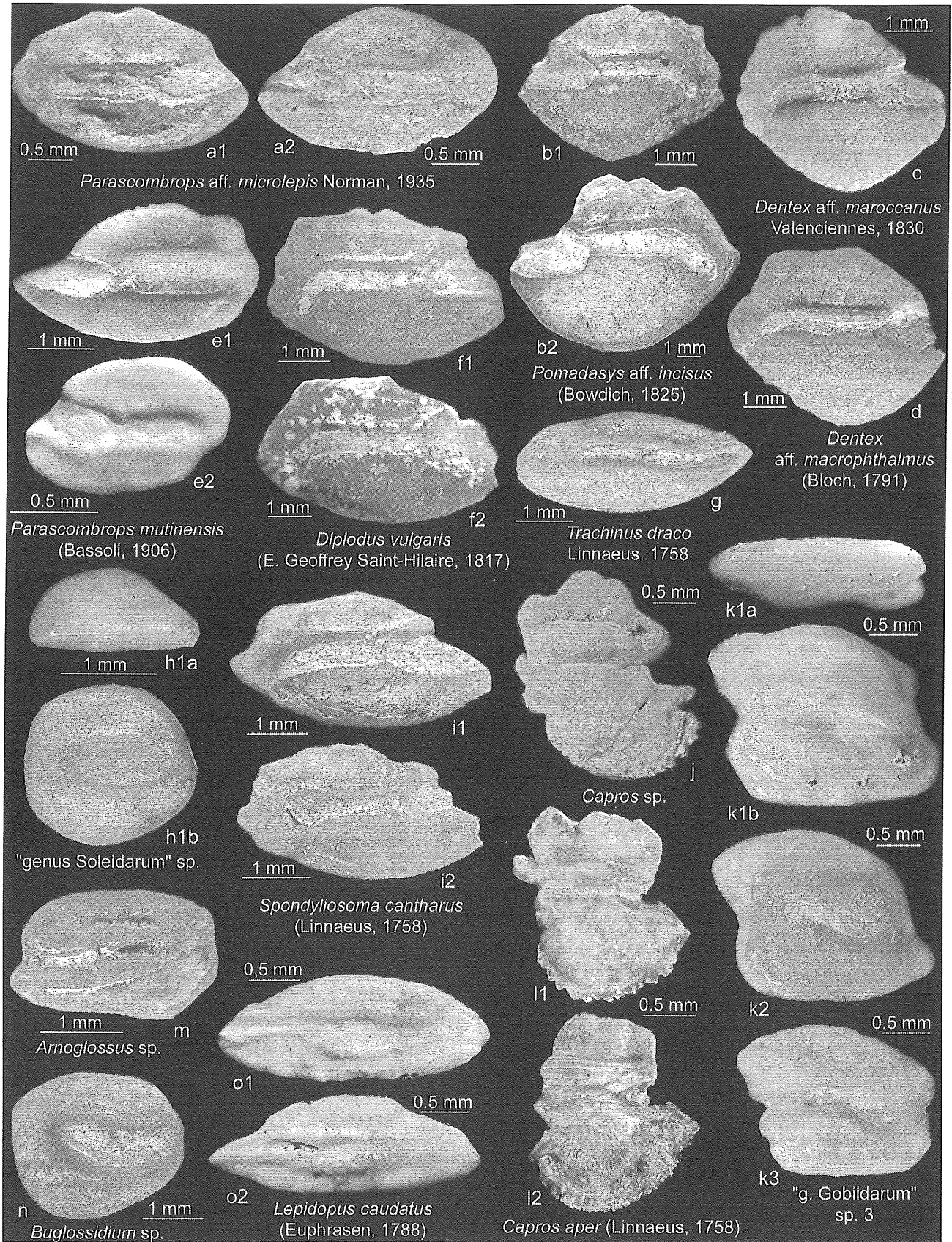
Fig. 9 Early Messinian otoliths from northern Italy (see Appendix 1 for further information)
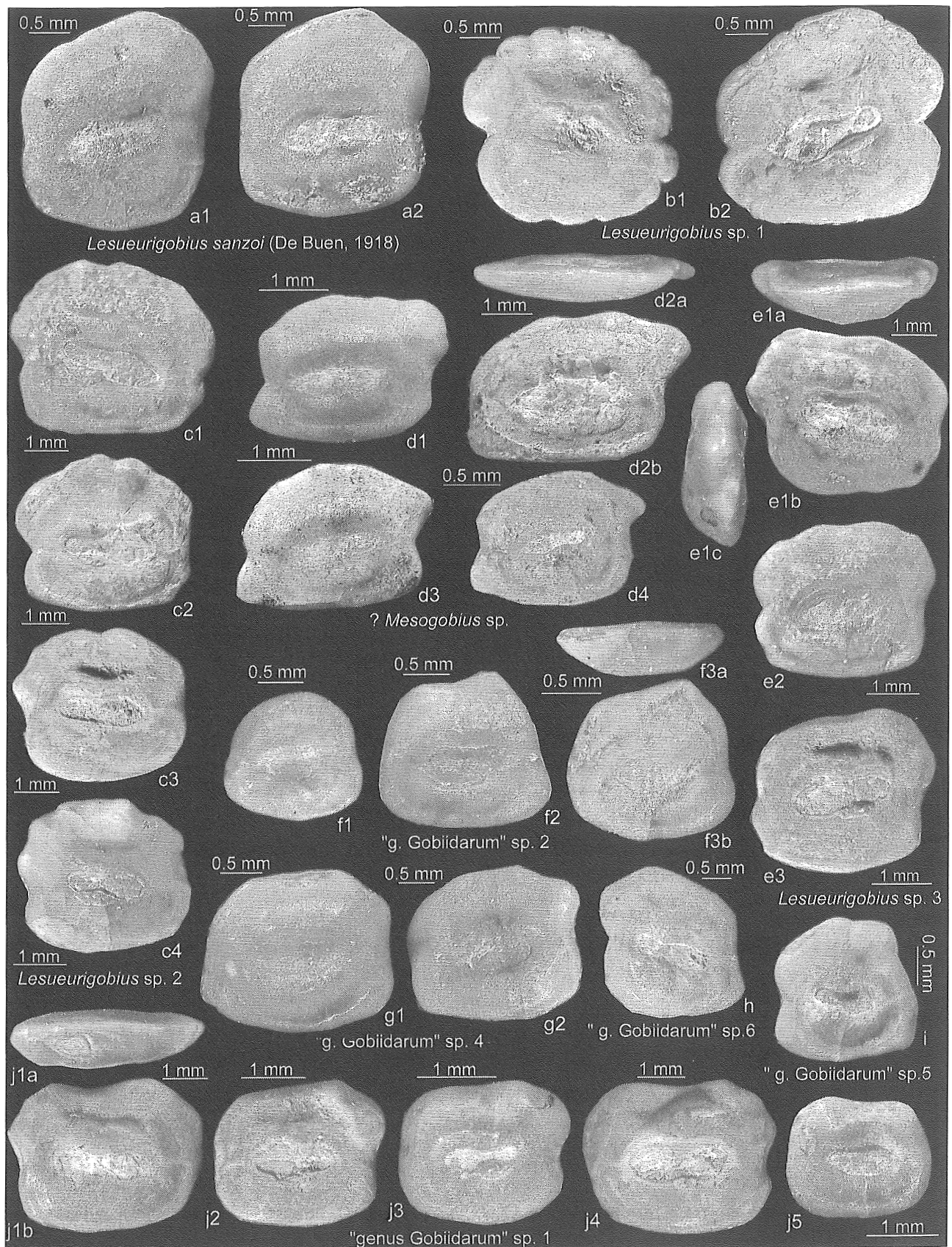
Fig. 10 Early Messinian otoliths from northern Italy (see Appendix 1 for further information)

narrow and delimited by almost straight vertical anterior and posterior rims. The central part of the dorsal rim is nearly horizontal and goes over in the anterior and posterior portions of the rim with a smooth angle.

In the fossil record, *Capros* otoliths are not common. Only one otolith-based species, *Capros parvus* (Menzel, 1986), has been reported from the Middle Miocene of Germany. Two skeleton-based Messinian fossils are known: *Proantigonia radobojana* Gorjanovic-Kramberger, 1882 (= *Proantigonia steindachneri* Gorjanovic-Kramberger, 1882) from the Sarmatian of Croatia and from the pre-evaporitic deposits of Oran (Algeria) and the still extant *C. aper* from pre-evaporitic deposits of north Italy (Gabbro) and Oran (Algeria). Skeletons of the latter are also known from Piacenzian deposits of the Mediterranean Basin (Gaudant 2002).

(11) "genus Soleidarum" sp. (Fig. 9h) A small, very thick otolith with nearly round outline. The dorsal and ventral rims are regularly curved, the posterior rim is almost straight. The sulcus is rather shallow, short and wide, located in median position, and close to the anterior end of the inner face, without reaching the anterior rim. The ostium and cauda are not clearly differentiated and the collicula are fused. The inner face is very flat. The outer face is strongly convex and smooth. Its main thickness is located towards the posterior portion. The general features of this otolith suggest possible relationships to *Bathysolea* and to include it in the soleid family. *Bathysolea* is characterised by thick otoliths, with a nearly round outline and a rather shallow sulcus with poorly differentiated ostial and caudal portions. However, *Bathysolea* has a rather narrow sulcus and an apparent circumsulcal depression. The Messinian specimen has a wider sulcus, does not shows a circumsulcal depression on the inner face and is characterised by a more strongly convex outer face than *Bathysolea* otoliths.

Description of new species

Diaphus rubus nov. sp. (Fig. 8a)

Type material: Holotype: a left otolith (Fig. 8a1), 41 paratypes of which five are figured (Fig. 8a2–6).

Type locality: Verduno Metalgranda, sample Cavallo 2007.

Etymology: *rubus, i* (substantive) = bramble: refers to the strong spines on the ventral rim that resembles the spines of bramble plants.

Description: This species is characterised by relatively high, short, thick otoliths. The dorsal rim is straight and stretches obliquely towards the antirostrum, which makes

the posterior portion of the dorsal area much higher than the anterior portion. The dorsal area shows a narrow depressed area in antero-posterior direction and reaches its maximum height in the posterior portion. The posterodorsal angle is well marked; it is more blunt in larger specimens such as the holotype, but in smaller specimens, it is accentuated by hollow portions of the rims just before and after the angle. The ventral rim, regularly curved, bears three to six coarse spines; usually about four. The ventral area, similar in size to the dorsal area, shows a narrow and well-incised furrow located very close to the ventral rim. The posterior rim is nearly straight in larger specimens (e.g. the holotype), but more curved in smaller specimens. The sulcus is well incised and filled by thick collicula. The crista superior is more strongly marked than the crista inferior.

The outer face is smooth and convex in antero-posterior direction. The maximum convexity is located in the posterior half of the otolith, very close to the posterior rim.

Remarks: These otoliths apparently belong to the same species as the one preserved in a skeleton from the pre-evaporitic Messinian deposits of Roddi, near Alba (Piedmont, Italy) and figured by Gaudant et al. (2008) as *Myctophum* (s.l.) *licatae* (Sauvage, 1870). According to G. Carnevale (University of Pisa), who examined the holotype of *Myctophum licatae*, this holotype is different from the fossil figured by Gaudant et al. (2008), and belongs to the genus *Lampanyctus*. The otoliths of *D. rubus* can be distinguished from those of other *Diaphus* species especially by the strong spines on the ventral margin and by their very sculptured inner face. The last feature resembles otoliths of similar size of *D. pedemontanus,* but these are more elongate and rectangular in shape.

Myctophum coppa nov. sp. (Fig. 11a)

Type material: Holotype: a right otolith (Fig. 11a1), 261 paratypes of which four are figured (Fig. 11a2–5).

Type locality: Verduno Metalgranda, sample Cavallo 2007.

Etymology: *coppa* = glass in bowl form; refers to the rounded, semicircular ventral rim that resembles the typical trappist beer glass.

Description: This species is characterised by moderately thick otoliths with a nearly semicircular ventral rim without ornamentations. It delimits a ventral area which surface is nearly two times as wide as in the dorsal one. The dorsal rim is strongly curved and stretches obliquely towards the antirostrum, delimiting a dorsal area that becomes wider in its posterior portion. The posterodorsal angle is blunt but well marked in juvenile otoliths. In older specimens, the posterodorsal angle becomes somewhat angular. The sulcus is clearly divided into a short and rounded cauda, and an
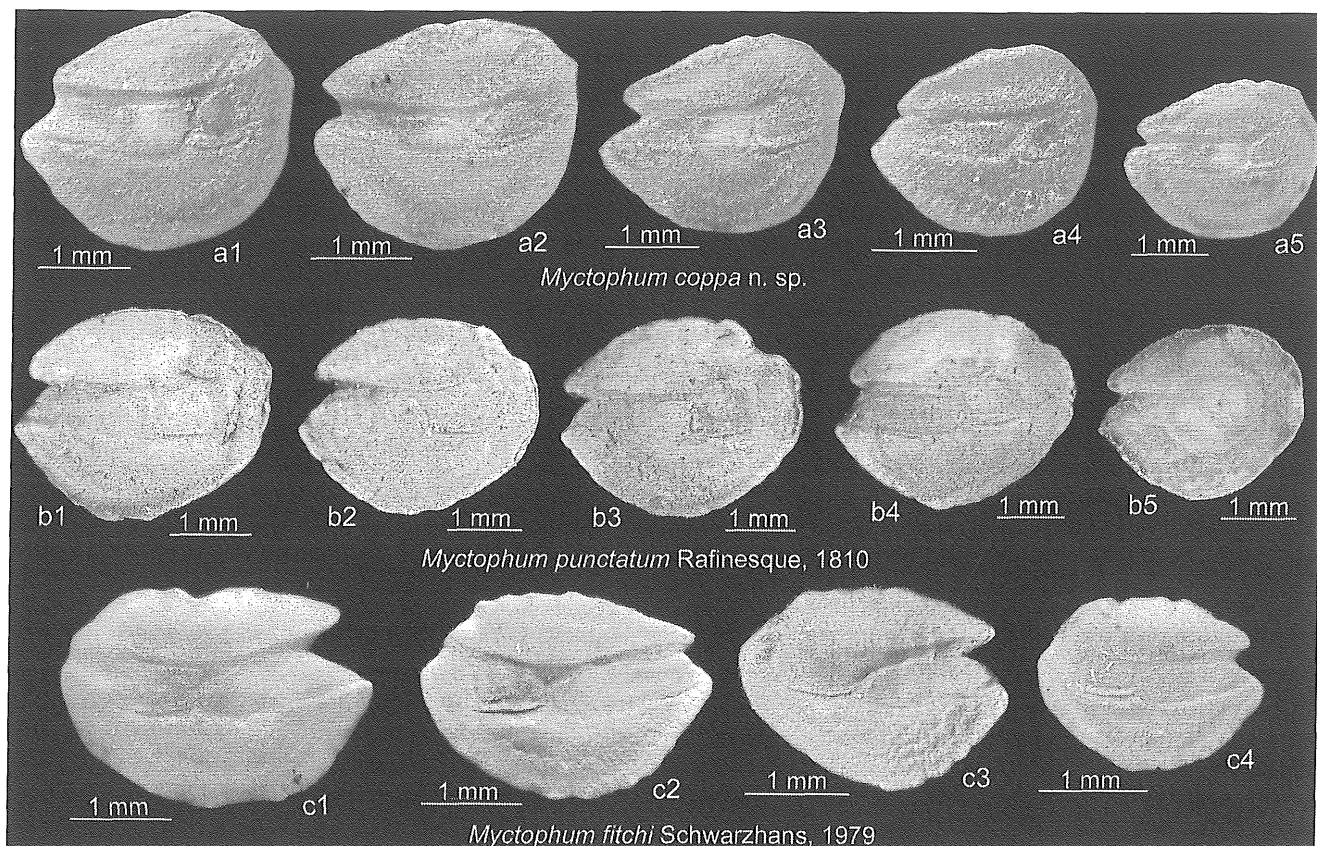
Fig. 11 *Myctophum* otoliths from Early Messinian, Pliocene and present-day Mediterranean species

ostium that is more than twice as long as the cauda. The outer face is blunt and slightly convex.

Remarks: These otoliths apparently belong to the same species as that preserved in a skeleton from the pre-evaporitic Messinian deposits of Roddi, near Alba (Piedmont, Italy) and figured by Gaudant et al. (2008) as *Myctophum* (s.l.) *dorsale* (Sauvage, 1870). According to G. Carnevale (University of Pisa), who examined the holotype of *Myctophum dorsale*, this holotype differs from the fossil figured by Gaudant et al. (2008), and probably belongs to the genus *Ceratoscopelus*.

Otoliths of *M. coppa* are most similar to those of *Myctophum fitchi* (Schwarzhans, 1979) (Fig. 11c), a fossil species reported from Tortonian and Lower to Middle Pliocene deposits of the Mediterranean (Nolf et al. 1998; Nolf and Steurbaut 1983; Schwarzhans 1979), and to those of the Recent *Myctophum punctatum* Rafinesque, 1810 (Fig. 11b) (reported as fossils from the Early Miocene of Venezuela and from the Middle Pliocene to Recent in the Mediterranean realm (Girone 2007; Girone et al. 2006; Nolf and Aguilera 1998). Otoliths of *M. coppa* differ from those of *M. fitchi* by their wider, semicircular ventral area and by their more circular and higher outline. Also, the cauda of *M. coppa* is much shorter. Otoliths of *M. punctatum* show

an anterior and posterior portion of equal height, while in *M. coppa* the anterior portion is much lower than the posterior one.

Uranoscopus ciabatta nov. sp. Fig. 12

Type material: Holotype: a right otolith (Fig. 12b2), 1 paratype (Fig. 12b1).

Type locality: Verduno, Metalgranda, sample Cavallo 2007.

Etymology: ciabatta (Italian) = slipper; also the name of a kind of flat, elongated bread; alludes to the comparable form and shape of the otoliths.

Description: This species is characterised by very thick and robust otoliths, with a salient rostrum and a well-marked excissura. Their shape is highly variable: the length/height proportion is 1.35% in the holotype; 1.93% in the paratype. In the holotype, the posterior rim forms a rounded angle, and the dorsal rim is regularly bent; in the paratype, the posterior rim is truncated, and there is a considerable concavity in the posterior part of the dorsal rim. The holotype is by far the best-preserved specimen. The paratype is affected by some erosion. The outer face is smooth and convex in all directions. The inner face is
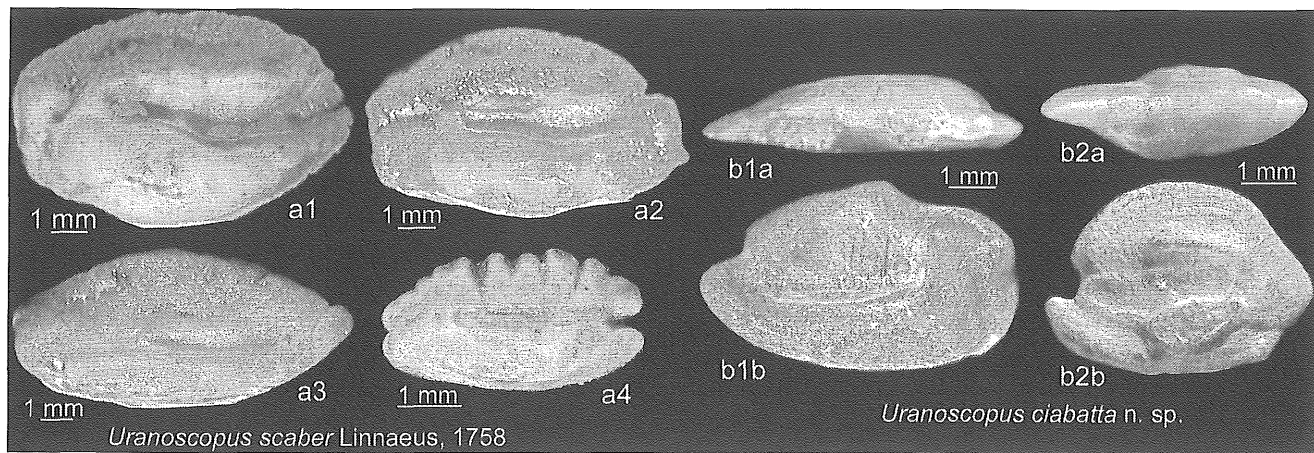
Fig. 12 *Uranoscopus* otoliths from Early Messinian and present-day Mediterranean species

equally convex. This convexity is particularly strong in the paratype. The strongest convexity is located in the ventral portion of the otoliths, while the dorsal area constitutes a rather flat, longitudinal depression. In both specimens, the sulcus is well incised, and a clear crista inferior is observed, but the crista superior tends to become obsolete. In the holotype, the crista inferior is divided in an ostial and caudal portion, but in the paratype the division is not clear.

Affinities: Although the variability observed in the two available specimens is very considerable, we think that *Uranoscopus ciabatta* otoliths characterise an easily recognisable species that is distinguished from the Recent *Uranoscopus scaber* (Fig. 12a) by a strongly salient rostrum, a well-marked obtusely incised excissura and very thick otoliths. Further, one should note that the otoliths of the Recent species are also highly variable.

Composition of the otolith-based fish fauna

The study of otoliths from the Messinian pre-evaporitic deposits in northern Italy permits the reconstruction of a teleost fauna composed of 79 taxa of which 35 could be identified at the specific level.

The **assemblages from the Verduno area** are the most diversified. In these assemblages, benthic and benthopelagic taxa dominate in diversity, but they are not as abundant as some pelagic forms. The benthopelagic assemblages are predominantly a diversified assortment of neritic fishes and some deep neritic—upper slope fishes, among which the gadiform group is the most abundant and diversified. *Gadiculus labiatus* and *Phycis musicki,* together with the still-living eastern Atlantic morid *Physiculus huloti,* are the most common and abundant gadiforms in the association. The benthic portion of the assemblages consists mainly of gobiids, which are very abundant in all associations from

the Verduno area, especially if we take into account the great number of indeterminate specimens (eroded or mainly juvenile otoliths). The assemblages from the Verduno are also characterised by a high diversity of epipelagic and mesopelagic fishes, especially of myctophids. In sample Cavallo 2007 from Verduno, a great number of juvenile specimens of *Diaphus* was found. The Verduno assemblages probably correspond to a deep neritic environment exposed to the pelagic realm, especially considering the occurrence of a significant number of *P.* aff. *huloti* (in the Hospital, slumping, Metalgranda, sample Cavallo 2007 and Tanaro left bank samples). Today, *P. huloti* is found at the outer edge of the shelf, mainly between 271–320 m depth (Cohen 1990) but captured occasionally as shallow as 100 m (Poll 1953). The shallow-neritic component (e.g. some sparids) is represented by very scarce specimens (mainly collected at Metalgranda, sample Cavallo 2007) and several deeper neritic fishes like *Spondyliosoma cantharus* (today the adults can be found as deep as 300 m), *Cepola rubescens, Lepidopus caudatus* and *Parascombrops microlepis.* Moreover, it is important to note that not all gobiids are very shallow-neritic fishes. Some (e.g., *Lesueurigobius*) are also found at greater depths of the shelf.

The **Brisighella assemblages** are quite different. They are dominated by very abundant juvenile *Diaphus* otoliths (more than 90% of the total number of specimens). It is known that the morphology of *Diaphus* otoliths changes markedly during ontogeny and that in most species only adult and large otoliths show clear diagnostic features, while juvenile otoliths cannot be distinguished (Brzobohaty and Nolf 1995, 2000). Therefore, the number of specimens identifiable at the specific level is low in these assemblages and does not reflect the extreme abundance of myctophids in the samples. The high number of juvenile myctophids probably reflects stressed environmental conditions (high salinity or fishes trapped in shallow environments) that did

not allow survival to the adult stage for many of these fishes.

In the **Moncucco assemblages**, the pelagic component is better represented. These assemblages also contain a large number of juvenile *Diaphus* otoliths (most common in Moncucco SF7). Otoliths of benthic neritic and bentho-pelagic fishes are very rare at Moncucco, but deeper ben-thopelagic components like *Gadiculus argenteus*, *Phycis musicki* and *Physiculus* aff. *huloti* are present. The gobiids and more shallow coastal fishes are very rare in the Mon-cucco assemblages with the exception of the Moncucco SF7 sample, which provided 23 gobiid and two flatfish oto-liths. Moncucco and Brisighella could reflect deeper envi-ronments, considering the absence of the benthic and benthopelagic-neritic components. Sturani (1978), who first described the Moncucco section on the basis of molluscan assemblages, refers the Early Messinian pre-evaporitic sed-iments to a bathyal environment (200–500 m). He postu-lated a poorly oxygenated environment with a bottom not favourable for benthic life. More recent studies on forami-niferal assemblages in the same stratigraphic interval but from other exposures in the Piedmont Basin also indicate conditions of anoxia or severe dysoxia at the bottom indi-cated by the absence or rarity of benthic taxa (Violanti et al. 2007). Regarding the fish fauna, it is interesting to note that true benthic taxa (e.g. congrid eels) are completely absent from the Moncucco assemblages.

The small **Nugola assemblage** reflects a very near-shore or even lagoonal environment.

Otolith-based versus skeleton-based Messinian fish faunas

Many skeletal-based Messinian fish species are known, mainly from the vicinity of Oran, Algeria (Arambourg 1927) and from various places in Italy, Spain and various Greek islands.

There are two relatively recent overviews of these early Messinian skeleton assemblages, one by Bianucci and Landini (1993) and one by Gaudant (2002). The data from these two last papers are summarised in Table 2 and compared to the otolith-based data from the present study.

A general summary of the data is given in Table 3.

The first conclusion is without any doubt that the present record is much better documented by skeletal material rather than by otoliths. However, the skeletal-based record is the result of approximately a century of research in deposits that are extraordinary mainly rich in osteological remains, while the present study provides the only published record of Messinian otolith material (except some otoliths known in situ in skeletons). Unfortunately, otolith material preserved in skeletons is usually very badly preserved.

In 1996, D. Nolf examined several Messinian skeletons with otoliths in situ in the collection of the University Museum in Pisa, but abandoned the project because of the poor preservation of the otolith material. In addition, there is considerable doubt if some of the skeletons with otoliths in situ really correspond to the holotypes of the species to which they were attributed. This is exemplified by the two myctophid species that are described as new in this study because we felt it was better to keep the nomenclature of the two fields separate unless there is convincing evidence that the type material of the skeletons and the otoliths really belong to the same species.

Examining the data at the family level, our summary indicates fairly close agreement. It points out that 23 of the 34 otolith-documented families (72%) are also known by osteology. At the generic level, only 13 of the 40 otolith-documented genera (33%) are also known by osteology and at the nominal species level, only three of the 34 species (9%) are represented by skeletons.

Several reasons are hypothesised for these divergences:

- It should be noted that at each taxonomic level, the num-ber of osteology-based records is much higher than the otolith-based records. This creates a significant initial numerical difference. If there are only 32 families with an otolith-based record, then the number in common with those with an osteology-based record can never exceed 32, whatever the abundance of the known skeletons. The percentages were calculated with the otolith-based record as the basis.
- There are major latitudinal differences. Many of the skel-eton-based taxa are known from Algeria only. An analy-sis of Table 2 of Bianucci and Landini (1993) indicates that 42% of their skeleton-based taxa are only known from there, while all otolith-based taxa are from the very northern part of the Messinian Mediterranean Sea. It is well documented that several Recent Mediterranean neri-tic species have a predominantly southern or northern Mediterranean distribution (e.g. the sparids *Dentex macrophthalmus*, *D. maroccanus* and *Pagrus auriga* are predominantly southern Mediterranean, while gobiids like *Aphia minuta*, *Chromigobius*, *Crystallogobius*, *Del-tentosteus quadrimaculatus*, *Gobius auratus*, *Gobius cruentatus*, *Lesueurigobius friesii*, *Leueurigobius suerii*, *Pomatoschistus minutes*, *Pseudaphia*, *Thorogobius ephippiatus* and *Zebrus* are essentially northern Mediter-ranean). It can be postulated that such latitudinal differ-ences also existed during the Messinian.
- Significant ecological and facies differences exist between the assemblages. Articulated or partially artic-ulated skeletons are usually preserved in very unique circumstances related to particular aspects of the sedi-ment. In the case of the Messinian sediments, the fishes

Table 2 List of both skeleton-based and otolith-based teleost taxa from the pre-evaporitic Messinian

Families	Taxa	
	Osteological remains	Otoliths
Muraenidae Sk.	*Muraena sahelensis* Arambourg, 1927	
Congridae: Ot.		*Paraconger* sp.
		Pseudophichthys splendens (Lea, 1913)
		Pseudophichthys sp. 1
		Pseudophichthys sp. 2
Clupeidae	*Sardinella crassa* (Sauvage, 1873)	
	Sardina pilchardus (Walbaum, 1792)	**Sardina pilchardus** (Walbaum, 1792)
	Sardina sp.	
	Alosa elongata Agassiz, 1843	
	Brevoortia sp.	
	Etrumeus boulei Arambourg, 1925	
	Spratelloides gracilis (Temminck & Schlegel, 1846)	
(Argentinidae: Ot.)		*Argentina sphyraena* Linnaeus, 1758
Gonostomatidae Sk.	*Gonostoma albyi* (Sauvage, 1873)	
	Gonostoma sp.	
Sternoptychidae	*Argyropelecus logearti* Arambourg, 1929	
	Maurolicus muelleri (Gmelin, 1788)	
Phosichthyidae Sk.	*Phosichthys larteti* (Sauvage, 1873)	
Synodontidae Sk.	*Synodus avus* Arambourg, 1927	
Paralepididae	*Lestidiops sphekodes* (Sauvage, 1870)	
		? *Lestidium* sp.
	Paralepis albyi (Sauvage, 1870)	
	Paralepis sp.	
	Parascopelus lacertosus (Sauvage, 1870)	
Myctophidae		*Bolinichthys italicus* Anfossi & Mosna, 1971
	Ceratoscopelus miocenicus Bedini et al., 1986	
	Ceratoscopelus? dorsale (Sauvage, 1870)	
		Diaphus befralai Brzob. & Nolf, 2000
		Diaphus cavallonis Brzob. & N., 2000
		Diaphus rafinesquii (Cocco, 1838)
		Diaphus rubus n. sp.
		Diaphus aff. *splendidus* (Brauer, 1904)
		Diaphus taaningi Norman, 1930
		Diaphus sp. 1
		Diaphus sp. 2
	Diaphus (Aethoproa) sp.	
	Diaphus sp.	
	Electrona sp.	
		Hygophum hygomi (Lütken, 1892)
	Lampanyctus? licatae (Sauvage, 1870)	
	Lampanyctus sp.	
	Lobianchia sp.	
	"Myctophum" columnae (Sauvage, 1873)	
	"Myctophum" dainelii d'Erasmo, 1929	
	"Myctophum" larteti (Sauvage, 1870)	
	"Myctophum" probenoiti Arambourg, 1925	

Table 2 continued

Families	Taxa	
	Osteological remains	Otoliths
	"Myctophum" sauvagei (Arambourg, 1925)	
	"Myctophum" vexillifer (Sauvage, 1873)	
	"Myctophum" sp.	
		Myctophum coppa n. sp.
Macrouridae Sk.	*Nezumia* sp.	
	Bathygadus incertus (Sauvage, 1880)	
Bregmacerotidae	*Bregmaceros albyi* (Sauvage, 1870)	
	Bregmaceros sp.	
		Bregmaceros sp.
Moridae	*Gadella* sp.	
		Physiculus aff. *huloti* Poll, 1953
Merluciidae	*Merluccius merluccius* (Linnaeus, 1758)	
	Merluccius sp.	
		Merluccius sp.
Phycidae: Ot.		*Phycis musicki* Cohen & Lavenberg, 1984
Gadidae	*Brosme murdjadjensis* Arambourg, 1927	
	Gadiculus? jonas (de Bosniaki)	
		Gadiculus argenteus (Guichenot, 1850)
		Gadiculus labiatus (Schubert, 1905)
Ophidiidae	*Brotula?* sp.	
		Hoplobrotula sp.
		"genus Neobythitinarum" sp.
Bythitidae : Ot.		Bythitidae ind. 1
		Bythitidae ind. 2
		Bythitidae ind. 3
Batrachoididae Sk.	*Halobatrachus didactylus* (Bloch & Schneider, 1801)	
Lophiidae	*Lophius budegassa* Spinola, 1807	
		Lophius piscatorius Linnaeus, 1758
Mugilidae	*Mugil ornatus* Arambourg, 1927	
	Mugil sp.	
		Mugilidae ind.
Atherinidae		*Atherina* aff. *boyeri* Risso, 1810
		Atherina sp.
	Atherinomorus? etruscus Gaudant, 1995	
Hemiramphidae: Ot		Hemiramphidae ind.
Belonidae	*Belone* sp.	
		Belone sp.
Scomberesocidae Sk.	*Scomberesox licatae* Sauvage, 1880	
Cyprinodontidae	**Aphanius crassicaudus** (Agassiz, 1839)	
Diretmidae: Ot.		*Diretmus* sp.
Holocentridae s.l.	*Microcentrum miletense* (Woodward, 1887)	
		Myripristinae ind.
Zeidae Sk.	*Zeus faber* Linnaeus, 1758	
	Zeus primaevus Cocchi, 1859	
	Zeus sp.	

Table 2 continued

Families	Taxa	
	Osteological remains	Otoliths
Fistulariidae Sk.	*Fistularia licatae* Sauvage, 1880	
	Fistularia sp.	
Centriscidae Sk.	Centriscidae ind.	
Syngnathidae Sk.	*Syngnathus albyi* Sauvage, 1880	
Scorpaenidae Sk.	*Scorpaena jeanelli* Arambourg, 1927	
	Scorpaena boulei Arambourg, 1927	
	Scorpaena sp.	
Triglidae		*Lepidotrigla* sp.
	Trigla macroptera Arambourg, 1927	
	Trigla licatae Sauvage, 1880	
	Trigla sp.	
Acropomatidae: Ot.		*Parascombrops mutinensis* (Bassoli, 1906)
		Parascombrops aff. *microlepis* Norman, 1935
Serranidae Sk.	*Serranus cabrilla* (Linnaeus, 1758)	
	Serranus scriba (Linnaeus, 1758)	
	Epinephelus casottii (Costa, 1853)	
	Epinephelus longispinis Arambourg, 1927	
	Epinephelus progigas Arambourg, 1927	
Priacanthidae Sk.	*Priacanthus* sp.	
Apogonidae	*Apogonoides cottreaui* Arambourg, 1927	
		Apogon sp.
Epigonidae Sk.	*Epigonus* sp.	
Branchiostegidae Sk.	*Latilus mesogeus* Arambourg, 1927	
Carangidae Sk.	*Caranx scillae* Sauvage,1880	
	Caranx albyi (Sauvage, 1880)	
	Trachurus trachurus (Linnaeus, 1758)	
	Trachurus sp.	
	Seriola dalonii Arambourg, 1927	
	Pseudovomer minutus (Sauvage, 1880)	
Haemulidae	*Orthopristis proronchus* Arambourg, 1927	
	Parapristipoma prohumile Arambourg, 1927	
		Pomadasys aff. *incisus* (Bowdich, 1825)
Sparidae	*Boops gortanii* d'Erasmo, 1930	
	Boops roulei Arambourg, 1927	
	Boops sp.	
	Crenidens intermedius Arambourg, 1927	
	Dentex barbarus Arambourg, 1927	
		Dentex aff. *macrophthalmus* (Bloch, 1791)
		Dentex aff. *maroccanus* Valenciennes, 1830
	Diplodus jomnitanus Valenciennes, 1844	
	Diplodus oranensis (Woodward, 1901)	
		Diplodus vulgaris (Geoffrrey St. Hilaire, 1817)
	Diplodus sp.	
	Pagrus leptosomus Arambourg, 1927	
	Pagrus mauritanicus Arambourg, 1927	
	Paracalamus doumergui Arambourg, 1927	

Table 2 continued

Families	Taxa	
	Osteological remains	Otoliths
	Sparus cinctus Agassiz, 1844	
	Sparus neogenicus Arambourg, 1927	
	Sparus? compactus Arambourg, 1927	
		Spondyliosoma cantharus (Linnaeus, 1758)
Polynemidae: Ot.		Polynemidae ind.
Sciaenidae: Ot.		Sciaenidae ind.
Chaetodontidae Sk.	*Chaetodon ficheuri* Arambourg, 1927	
Cepolidae	*Cepola cuneata* Arambourg, 1927	
		Cepola rubescens (Linnaeus, 1766)
Pomacentridae Sk.	*Chromis savornini* Arambourg, 1927	
Labridae Sk.	*Symphodus pellegrini* Arambourg, 1927	
	Symphodus woodwardi Kramberger, 1882	
Leptoscopidae Sk.	*Neopercis mesogea* Arambourg, 1927	
Trachinidae: Ot.		*Trachinus draco* Linnaeus, 1758
Uranoscopidae Ot.		*Uranoscopus ciabatta* n. sp.
Blenniidae Sk.	*Tripterygion pronasus* Arambourg, 1927	
Labrisomidae Sk.	*Labrisomus pronuchipinnis* Arambourg, 1927	
Callionymidae Sk.	*Callionymus pusillus* Delaroche, 1809	
Gobiidae		*Aphya minuta* (Risso, 1810)
		Deltentosteus sp.
	Gobius aidouri Arambourg, 1927	
	Gobius anthonyi Arambourg, 1927	
	Gobius brivesi Arambourg, 1927	
	Gobius ehrmanni Arambourg, 1927	
	Gobius razelaini Arambourg, 1927	
	Gobius xiphurus Arambourg, 1927	
	Gobius sp.	
		Gobius sp.
		Lesueurigobius sanzoi (De Buen, 1918)
		Lesueurigobius sp. 1
		Lesueurigobius sp. 2
		Lesueurigobius sp. 3
		"genus Gobiidarum" sp. 1
		"genus Gobiidarum" sp. 2
		"genus Gobiidarum" sp. 3
		"genus Gobiidarum" sp. 4
		"genus Gobiidarum" sp. 5
		"genus Gobiidarum" sp. 6
		? *Mesogobius* sp.
Gempylidae Sk.	*Hemithyrsites armatus* (Sauvage, 1880)	
Trichiuridae	*Lepidopus albyi* (Sauvage, 1870)	
		Lepidopus caudatus (Euphrasen, 1788)
	Lepidopus proargenteus Arambourg, 1927	
	Lepidopus sp.	
Scombridae Sk.	*Auxis* sp.	
	Euthynnus sp.	

Table 2 continued

Families	Taxa	
	Osteological remains	Otoliths
	Pneumatophorus japonicus (Houttuyn, 1782)	
	Neocybium sp.	
	Orcynus proximus (Sauvage, 1888)	
	Sarda roulei Arambourg, 1927	
	Scomber sp.	
Isiphoridae Sk.	*Xiphiorhynchus courcelli* Arambourg, 1927	
Caproidae	*Capros steindachneri* (Kramberger, 1882)	
	Capros aper (Linnaeus, 1758)	
	Capros sp.	*Capros* sp.
Citharidae Sk.	*Citharichthys oranensis* Arambourg, 1927	
Bothidae	*Arnoglossus abropteryx* Arambourg, 1927	
	Arnoglossus laterna (Walbaum, 1792)	
	Arnoglossus sauvagei (d'Erasmo, 1930)	
	Arnoglossus sp.	
		Arnoglossus sp.
Soleidae	*Achirus mediterraneus* Arambourg, 1927	
		Buglossidium sp.
	Monochirus hispidus Rafinesque, 1814	
	Solea proocellata Arambourg, 1927	
	Solea solea (Linnaeus, 1758)	
		"genus Soleidarum" sp.
Balistidae Sk.	*Balistes procapriscus* Arambourg, 1927	
Diodontidae Sk.	*Chilomycterus acanthodes* (Sauvage, 1870)	
Trigonodontidae Sk.	*Trigonodon juglevi* (Münster, 1846)	

Sk. = Osteology only; Ot. = Otoliths only

Families and taxa in bold are known by both osteology and otoliths

Table 3 Summary data of the comparison between data of Table 2 and data from the present study

Taxa documented by	Skeleton	Otoliths	Skeleton and otoliths
Families	58	34	23
Genera	88	40	13
Nominal species	100	34	3

often died in anoxic or hypersaline waters, and the resulting sediments from these environments are mainly laminated clays and diatomites. The otoliths from Brisighella are also collected in similar deposits, and in this association the mesopelagic myctophids, *Bregmaceros* and small *Gadiculus* dominate, as in the skeletal taphocoenosis. However, the otolith associations from Verduno were collected from a turbiditic sediment of deep neritic origin with significant otoliths from bottom-associated fishes (e.g. the various anguilliform species) which are absent from the laminated sediments. A good example of both skeletal-rich and otolith-bearing sediments is provided by the slightly older Tortonian marls of the Tanaro in Alba. There, an alternation of laminated and compact clay beds can be observed. The skeletons occur only in the laminated clays, and consist mainly of mesopelagic fishes, while the compact clays contain a more diverse fish fauna with several bottom-associated species.

● There are issues of taxonomic reliability. Otoliths were studied on the basis of a very extensive series of Recent comparative material, named according to the most recent revisions of the living fauna, and the taxonomic reliability of the identifications can be considered as quite accurate. Many of the osteological taxa have not really been the subject of thorough nomenclature revision since the original descriptions, often dating back to Arambourg (1927) and even before that. This is especially noted in the myctophids, the "*Myctophum*" citations pinpoint to the less accurate status of the identifications.

The combination of these factors leads to the present situation of quite different faunal reconstructions derived from otolith and skeleton fossil material. As already noted, the study from otoliths found in situ in the skeletons is rather deceiving. Our overview shows that at the specific level only two taxa (*Sardina pilchardus* and *Maurolicus muelleri*) are represented by both kinds of fossils. It is also important to note that these two taxa were from specimens independently identified in the skeleton and otolith material. However, such cases corroborate the reliability of the identifications in both the skeleton and otolith material, but these cases are quite rare, since the two kinds of fossils (skeletal and otolith) usually originate through different sedimentary processes and result in distinct sedimentary facies. Messinian otolith research is also still in its initial stages, and the number of known otolith-based taxa at each taxonomic level is still much lower than the number of skeletal-based ones.

Stratigraphic and palaeobiogeographic affinities of the pre-evaporitic Messinian Mediterranean fish fauna

The present study represents the first otolith-based reconstruction of the pre-evaporitic Messinian Mediterranean teleost fauna. Thirty-five taxa could be identified at the specific level. They indicate a teleost fauna including both neritic and oceanic fishes (Table 4). The fauna has 22 species still extant and 21 of them still live in the present-day Mediterranean. Four are exclusively Atlantic today (*Pseudophichthys splendens, Diaphus taaningi, Physiculus huloti*, and *Parascombrops microlepis*). *Diaphus splendidus* has a worldwide distribution in the Atlantic and Indo-Pacific meso-bathypelagic realm. The extinct *Diaphus rubus, Myctophum coppa, Aphanius crassicaudatus* and *Uranoscopus ciabatta* are the only true Early Messinian species, while the other extinct species were known from the Tortonian or earlier (Table 4).

An interesting observation is that a great part of the Early Messinian fishes that persisted in the modern Mediterranean fauna are typical taxa of the neritic realm. Additional data for the pre-evaporitic Messinian teleost fauna are from the skeletal-based fish fauna which is synthesised by Gaudant (2002). Gaudant's (2002) compilation of data on the skeletal-based marine fish-faunas from the Tortonian, the pre-evaporitic Messinian and the Piacenzian does not point toward major changes between the Tortonian and Messinian faunas, and a persistent Indo-Pacific affinity is found for the Pliocene fauna. Recently, Gaudant et al. (2008) examined the fish fauna based on skeletal remains from the pre-evaporitic deposits outcropping in Roddi, near Alba (Piedmont, Italy) and, again, concluded that the pre-evaporitic fish fauna is very similar to that found in the

nearby Tortonian locality of the Tanaro river, in Alba (Gaudant et al. 2007).

Published data on Tortonian otoliths of the palaeo-Mediterranean Basin are available from the Tortonian stratotype (Rio Mazzapiedi—Castellania, Piedmont) and from Montegibbio (Nolf and Steurbaut 1983; Robba 1970). Additional data are furnished by various new collections from several localities in Piemonte, northern Italy (Nolf, unpublished data). Combining these data, one obtains a list of 82 nominal species for the Tortonian of the palaeo-Mediterranean basin (Table 4). The studied associations are dominated primarily by deep-water fishes, both mesopelagic and benthopelagic from the continental slope (Nolf and Steurbaut 1983). About 61% of the genera represented in the Tortonian fauna are still living in the present-day Mediterranean, 96% in the Recent Atlantic and 76% in the Indo-Pacific realm.

Although informative, this compilation of data provides only a partial view of the changes affecting the Late Cenozoic fauna of the Mediterranean because Table 4 does not consider new occurrences of fish taxa in the successive Plio-Pleistocene stages. Although this is not the appropriate place to provide an updated synthesis of the Plio-Pleistocene Mediterranean otolith-based fish record, we found it useful to include at least a graph, providing numerical data on the extinction and appearance of fossil and Recent Mediterranean fish species as documented by the otoliths (Fig. 13). This graph essentially highlights the disappearance (extinction) of many fossil species at the Messinian/Zanclean boundary and later, at the Zanclean/Piacenzan boundary. At the beginning of the Zanclean, a tremendous occurrence of extant species is observed in the fossil record. During the Zanclean, many of the Recent species are oceanic ones, which today are extra-Mediterranean, while the Recent occurrences in the Gelasian and the Pleistocene are mainly North Atlantic forms from colder waters.

A direct comparison of the data on Early Messinian and Tortonian otolith-reconstructed faunas is biased by the different environmental conditions that prevailed during both periods. There was mainly deep-water during the Tortonian whereas there was neritic or deep neritic-upper bathyal for the Early Messinian. Therefore, direct comparison suggests that many deep-water species did not persist until the Messinian. However, data on the Lower Pliocene (mainly deep-water deposits) otolith assemblages (Nolf and Cappetta 1989; Nolf et al. 1998; Nolf and Girone 2008) shows that about 52% of the deep-water Tortonian species do not cross the Miocene/Pliocene boundary. The Zanclean Mediterranean deep-water fauna, like the Tortonian, was also a circumglobal oceanic fauna but gradually started to increase in species that are more restricted to the Atlantic Ocean (Nolf et al. 1998). As previously mentioned, this Atlantic invasion in the deep-water Mediterranean fish

Table 4 Stratigraphic distribution of the otolith-based nominal species in the Tortonian and pre-evaporite Messinian basin

	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Pleistocene	Recent
Pterothrissus umbonatus (Koken, 1884)	T	–	–	–	–	–	–
Panturichthys subglaber (Schubert, 1906)	T	–	Z	–	–	–	–
Pseudophichthys splendens (Lea, 1913)	T	M	Z	P	–	–	R*
Rhechias aff. *nagymarosyi* N. and B., 1994	T	–	–	–	–	–	–
Rhynchoconger pantanellii (Bassoli, 1906)	T	?	Z	P	G	–	–
Sardina pilchardus (Walbaum, 1792)	–	M	?	?	?	Pl	R
Xenodermichthys kotthausi Brzobohaty, 1986	T	–	–	–	–	–	–
Argentina sphyraena Linnaeus, 1758	–	M	Z	P	?	Pl	R
Maurolicus muelleri (Gmelin, 1789)	T	M	Z	P	G	Pl	R
Valenciennellus aff. *tripunctulatus* (Esmark,1871)	T	?	?	?	?	Pl	R
? Lestidium sp.	–	M	–	–	–	–	–
Scopelarchus analis (Brauer, 1920)	T	?	Z	?	?	Pl	R*
Benthosema fitchi Brzobohaty and Schultz, 1978	T	–	–	–	–	–—	–
Benthosema aff. *glaciale* (Reinhardt, 1837)	T	?	?	P	G	Pl	R
Bolinichthys italicus Anfossi and Mosna, 1971	T	M	–	–	–	–	–
Diaphus befralai Brzobohaty and Nolf, 2000	T	M	–	–	–	–	–
Diaphus cavallonis Brzobohaty and Nolf, 2000	T	M	Z	P	–	–	–
Diaphus aff. *holti* (Taaning, 1918)	T	?	Z	?	?	Pl	R
Diaphus metopoclampoides Steurbaut, 1983	T	–	–	–	–	–	–
Diaphus pedemontanus (Robba, 1970)	T	M	Z	–	–	–	–
Diaphus rafinesquii (Cocco, 1838)	T	M	Z	P	?	Pl	R
Diaphus rubus n. sp.	–	M	–	–	–	–	–
Diaphus aff. *splendidus* (Brauer, 1904)	T	M	Z	P	G	lPl	R*
Diaphus taaningi Norman, 1930	T	M	Z	P	G	Pl	R*
Hygophum derthonense Anfossi and Mosna, 1969	T	–	–	–	–	–	–
Hygophum hygomi (Lütken, 1892)	T	M	Z	P	G	Pl	R
Lampadena dea Fraser–Brunner, 1949	T	?	Z	–	–	–	R*
Lampadena gracile (Schubert, 1912)	T	–	–	–	–	–	–
Lampanyctus latesulcatus Nolf and Steurbaut, 1983	T	–	–	–	–	–	–
Lobianchia aff. *dofleini* (Zugmayer, 1911)	T	M	Z	P	?	Pl	R
Myctophum coppa n. sp.	–	M	–	–	–	–	–
Myctophum fitchi (Schwarzhans, 1979)	T	?	Z	–	–	–	–
Notoscopelus cf. *bolini* Nafpaktitis, 1975	T	?	Z	?	?	?	R
Scopelopsis pliocenicus (Anfossi and Mosna, 1976)	T	?	Z	P	?	Pl	–
Bathygadus novus (Bassoli, 1906)	T	?	Z	–	–	–	–
Gadomus tejkali (Brzobohaty and Schultz, 1978)	T	–	–	–	–	–	–
Trachyrincus scabrus (Risso, 1810)	T	?	Z	P	G	Pl	R
Coelorinchus arthaberi (Schubert, 1905)	T	?	Z	–	–	–	–
Coelorinchus coelorhincus (Risso, 1810)	T	?	Z	?	G	Pl	R
Coelorinchus cristatus (Bassoli, 1906)	T	–	–	–	–	–	–
Coelorinchus maximus (Bassoli, 1906)	T	–	–	–	–	–	–
Coelorinchus robustus (Robba, 1970)	T	–	–	–	–	–	–
Nezumia contorta (Bassoli, 1906)	T	–	–	–	–	–	–
Nezumia ornata (Bassoli, 1906)	T	?	Z	–	–	–	–
Nezumia aff. *sclerorhynchus* (Valenciennes, 1838)	T	?	?	?	G	Pl	R
Laemonema aff. *yarelli* (Lowe, 1841)	T	–	–	–	–	–	R*
Melanonus paralyconus Schwarzhans, 1986	T	?	Z	–	–	–	–
Melanonus triangulus (Robba, 1970)	T	–	–	–	–	–	–

Table 4 continued

	Tortoniano	Messiniano	Pliocene	Piacenzian	Gelasian	Pleistocene	Recent
"g. Melanonidarum" *vanheuckelomae* N. and S. 1983	T	–	–	–	–	–	–
Physiculus aff. **huloti** Poll, 1953	T	M	Z	–	–	–	R*
Merluccius merluccius (Linnaeus, 1758)	T	?	Z	P	?	Pl	R
Phycis musicki Cohen and Lavenberg, 1984	T	M	Z	P	–	–	–
Gadiculus argenteus (Guichenot, 1850)	T	M	Z	P	G	Pl	R
Gadiculus labiatus (Schubert, 1905)	T	M	Z	P	G	lPl	–
Micromesistius planatus (Bassoli, 1906)	T	–	–	–	–	–	–
Hoplobrotula *gibba* (Bassoli, 1906)	T	–	–	–	–	–	–
Bassozetus *otteri* Nolf and Steurbaut (1983)	T	–	–	–	–	–	–
Oligopus bassolii Nolf, 1980	T	–	–	–	–	–	–
"g. aff. *Ogilbia*" aff. *heinzelini* Lanck. and Nolf, 1979	T	?	Z*	–	–	–	–
Lophius piscatorius Linnaeus, 1758	–	M	?	?	?	?	R
Chaunax *lobatus* (Bassoli, 1906)	T	–	–	–	–	–	–
"genus Ogcocephalidarum" *unicus* (Bassoli, 1906)	T	–	–	–	–	–	–
Atherina aff. *boyeri* Risso, 1810	–	M	–	–	–	–	R
Aphanius crassicaudus (Agassiz, 1839)	–	M	–	–	–	–	–
Hoplostethus lawleyi Koken, 1891	T	–	–	–	–	–	–
Hoplostethus praemediterraneus Schubert, 1905	T	–	–	–	–	–	–
Holocentrus weileri Robba, 1970	T	–	–	–	–	–	–
Zenion hololepis Goode and Bean, 1896	T	?	Z	–	–	–	R*
Peristedion cataphractum (Linnaeus, 1758)	T	?	Z	?	?	?	R
Parascombrops *mutinensis* (Bassoli, 1906)	T	M	Z	P	G	lPl	–
Parascombrops aff. *microlepis* Norman, 1935	–	M	–	–	–	–	R*
Epigonus constanciae (Giglioli, 1880)	T	?	Z	?	G	Pl	R
Epigonus denticulatus Dieuzeide, 1950	T	?	?	?	?	?	R
Epigonus italicus (Bassoli, 1906)	T	?	Z	–	–	–	–
"genus Malacanthidarum" *mirabilis* (Bassoli, 1906)	T	–	–	–	–	–	–
Brachydeuterus *speronatus* (Bassoli, 1906)	T	–	–	–	–	–	–
Pomadasys aff. *incisus* (Bowdich, 1825)	T	M	Z	?	?	?	R
"genus Haemulidarum" *lucidus* (Bassoli,1906)	T	–	–	–	–	–	–
Diplodus vulgaris (E. Geoffrey Saint–Hilaire, 1817)	–	M	?	?	?	?	R
Spondyliosoma cantharus (Linnaeus, 1758)	–	M	?	?	?	?	R
Dentex aff. *macrophthalmus* (Bloch, 1791)	T	M	Z	?	?	?	R
Dentex aff. *maroccanus* Valenciennes, 1830	T	M	Z	?	?	Pl	R
Pagellus acarne (Risso, 1826)	T	?	Z	?	?	?	R
"genus Sparidarum" *doderleini* (Bassoli, 1906)	T	–	–	–	–	–	–
Miracorvina meridionalis (Koken, 1891)	T	–	–	–	–	–	–
Cepola rubescens (Linnaeus, 1766)	T	M	Z	P	G	Pl	R
Owstonia *neogenica* Nolf and Cappetta, 1989	T	?	Z	P	–	–	–
Trachinus draco Linnaeus, 1758	T	M	Z	?	?	?	R
Uranoscopus ciabatta n. sp.	–	M	–	–	–	–	–
Lesueurigobius sanzoi (De Buen, 1918)	–	M	Z	?	?	?	R
Prometichthys *prometheus* (Cuvier, 1832)	T	?	Z	–	–	–	R*
Lepidopus caudatus (Euphrasen, 1788)	–	M	Z	?	?	?	R
Antigonia *capros* Lowe, 1843	T	–	–	–	–	–	R*
Citharus linguatulus (Linnaeus, 1758)	T	?	Z	?	?	?	R
Arnoglossus kokeni (Bassoli and Schubert, 1906)	T	?	Z	P	?	Pl	–

Table 4 continued

	Tortoniano	Messiniano	Pliocene	Piacenzian	Gelasian	Pleistocene	Recent
Microchirus aff. *variegatus* Donovan, 1808	T	?	Z	P	?	Pl	R
Solea patens Bassoli, 1906	T	–	–	–	–	–	–

Taxa in bold represent taxa disappeared from the modern Mediterranean basin
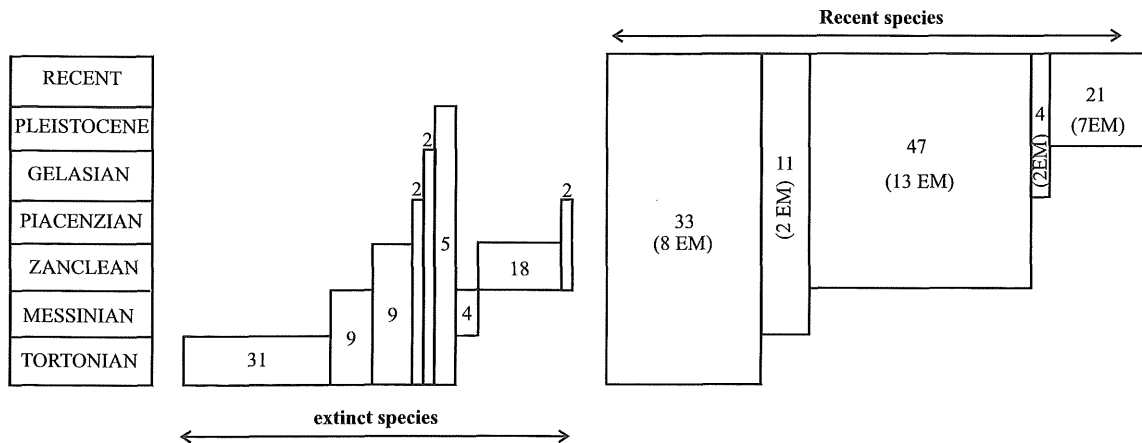
Fig. 13 Extinction of fossil species and appearance of Recent species during the Late Cenozoic (numbers refer to the number of concerned nominal species in each compartment). Based on data from the present study (*EM*) for the Late Miocene, from Nolf et al. (1998) for the Early Pliocene and from Girone et al. (2006) for the Late Pliocene and Pleistocene

fauna is strongly documented from the Late Pliocene until the Late Pleistocene (Girone et al. 2006; Girone 2007).

On the contrary, a great part of the neritic fauna crossed the Miocene/Pliocene boundary, but this seems to be obvious since most of these species are still living in the present-day Mediterranean. The Mediterranean affinity of the neritic fauna, already documented at the generic level for the Rupelian fauna (Nolf and Girone 2008), seems to persist during the entire Neogene and in the Early Messinian, also becomes evident at the specific level.

Analysis of the global present-day geographic distribution of the 42 genera represented in the pre-evaporitic fauna provides a data set composed of 88% of genera with distribution in the Mediterranean, 98% in the Atlantic and 78% in the Indo-Pacific realm. These percentages reflect the well-documented tendency that since the Oligocene there has been a gradual increase in present-day Mediterranean taxa in the palaeo-Mediterranean communities. In the Rupelian, only 35% of the genera are extant in the present-day Mediterranean, 53% of genera are found in Lower Miocene, and 61% of the genera in the Tortonian (compiled from Nolf and Steurbaut 2004; Nolf and Brzobohaty 2004; Girone et al. 2006; Nolf and Girone 2008).

Appendix 1: List of figured material

Institutional abbreviations

IRSNB = Institut Royal des Sciences Naturelles de Belgique.

MMF = Museu Municipal do Funchal, Madeira

Figured material

Arctozenus rissoi (Bonaparte, 1840); Fig. 6a1 Recent, Northwest off Ireland; Fig. 6a2, Recent, Gulf of Biscay (coll. IRSNB)

Argentina sphyraena Linnaeus, 1758; Fig. 5i1-2, Verduno, left bank of the Tanaro River (IRSNB P 8543–P 8544)

Arnoglossus sp.; Fig. 9m, Verduno, Hospital, slumping (IRSNB P 8668)

Atherina sp.; Fig. 8l, Verduno, left bank of the Tanaro River (IRSNB P 8608)

Belone sp.; Fig. 8k, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8609)

Bolinichthys italicus (Anfossi and Mosna, 1971); Fig. 5e1-6, Moncucco SF2 (IRSNB P 8552–P 8557)

Bregmaceros sp.; Fig. 8e1-3, Verduno, left bank of the Tanaro River (IRSNB P 8591–P 8593)

Buglossidium sp.; Fig. 9n, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB 8669)

Bythitidae ind. 1; Fig. 8g1a-b, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8600), Fig. 8g2a-b, Moncucco SF1 (IRSNB P 8601)

Bythitidae ind. 2; Fig. 8f, Moncucco SF2 (IRSNB P 8602)

Bythitidae ind. 3; Fig. 8h, Verduno, left bank of the Tanaro River (IRSNB P 8603)

Capros aper (Linnaeus, 1758); Fig. 9l1-2, Recent, Mediterranean Sea, Girone collection.

Capros sp.; Fig. 9j, Verduno, Hospital, laminated strata (IRSNB P 8667)

Congridae ind.; Fig. 5b, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8533)

Dentex aff. *macrophthalmus* (Bloch, 1791); Fig. 9d, Verduno, Metalgranda sample Nolf (IRSNB P 8620)

Dentex aff. *maroccanus* Valenciennes, 1830; Fig. 9c, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8621)

Diaphus aff. *splendidus* (Brauer, 1904); Fig. 7c1-3, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8578–P 8580)

Diaphus befralai Brzobohaty and Nolf, 2000; Fig. 7d1-5, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8558–P 8562)

Diaphus cavallonis Brzobohaty and Nolf, 2000; Fig. 7a1-3, Verduno, Hospital, laminated strata (IRSNB P 8563–P 8565)

Diaphus pedemontanus (Robba, 1970); Fig. 7b1-6, Verduno Metalgranda, sample Cavallo 2007 (IRSNB P 8566–P 8571)

Diaphus rubus n. sp.; Fig. 8a1, Verduno Metalgranda, sample Cavallo 2007, Fig. 8a1, holotype (IRSNB P 8572), 8a2-6 paratypes (IRSNB P 8573–P 8577)

Diaphus sp. 1; Fig. 7e1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8581–P 8582)

Diaphus sp. 2; Fig. 7h1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8583–P 8584)

Diplodus vulgaris (E. Geoffrey Saint-Hilaire, 1817); Fig. 9f1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8616–P 8617)

"genus Gobiidarum" sp. 1; Fig. 10j1-5, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8636–8640)

"genus Gobiidarum" sp. 2; Fig. 10f1-3, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8653–P 8655)

"genus Gobiidarum" sp. 3; Fig. 9k1-3, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8656–P 8658)

"genus Gobiidarum" sp. 4; Fig. 10g1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8641–P 8642)

"genus Gobiidarum" sp. 5; Fig. 10i, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8659)

"genus Gobiidarum" sp. 6; Fig. 10h, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8660)

"genus Neobythitinarum" sp., Fig. 7g, Verduno, left bank of the Tanaro River (IRSNB P 8604)

"genus Soleidarum" sp.; Fig. 9h, Verduno, Hospital,, slumping (IRSNB 8670)

Hoplobrotula sp.; Fig. 8d1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8598–P 8599)

Lampadena sp.; Fig. 5g, Verduno, left bank of the Tanaro River (IRSNB P 8590)

Lepidopus caudatus (Euphrasen, 1788); Fig. 9o1, Verduno, Hospital, laminated strata (IRSNB P 8665); Fig. 9o2, Moncucco SF5 (IRSNB P 8666)

Lepidotrigla sp.; Fig. 8j, Moncucco SF7 (IRSNB P 8607)

Lestidiops jayakara pseudosphyraenoides (Ege, 1918); Fig. 6b, Recent, off Canaries (coll. IRSNB)

Lestidium atlanticum Borodin, 1928; Fig. 6c, Recent, Caribbean (coll. IRSNB)

? Lestidium sp.; Fig 5k1 and k4, Verduno Metalgranda, sample Cavallo 2007 (IRSNB P 8548–P 8549); Fig. 5k2 and k3, Verduno, left bank of the Tanaro River (IRSNB P 8550–P 8551)

Lesueurigobius sanzoi (De Buen, 1918); Fig. 10a1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8625–P 8626)

Lesueurigobius sp. 1; Fig. 10b1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8627–P 8628)

Lesueurigobius sp. 2; Fig. 10c1-4, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8629–P 8632)

Lesueurigobius sp. 3; Fig. 10e1-3, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8633–P 8635)

Lophius piscatorius Linnaeus, 1758; Fig. 8i1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8505–P 8506); Fig. 8i3-i6, Recent, Gulf of Biscay (Atlantic), (coll. Girone, Univ. Bari)

Macroparelepis affinis Ege, 1933; Fig. e1, Recent, off Madeira (coll. IRSNB)

Macroparalepis nigra (Maul, 1965); Fig. 6d, Recent, off Madeira (MMF 14696)

Magnisudis atlantica (Kroyer, 1868); Fig. 6g1-3, Recent, off California (coll. IRSNB)

Maurolicus muelleri (Gmelin, 1789); Fig.5 j1-3, Verduno Metalgranda, sample Cavallo 2007 (IRSNB P 8545–P 8547)

Merluccius (Linnaeus, 1758); Fig. 8c1-2, Recent, Mediterranean Sea (coll. Girone, Univ. Bari)

Merluccius sp.; Fig. 8b, Moncucco, SF7 (IRSNB P 8597)

? Mesogobius; Fig. 10d1-4, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8661–P 8664)

Myctophum coppa n. sp.; Fig. 11a1-5, Verduno, Metalgranda, sample Cavallo 2007, 11a1, holotype (IRSNB P 8585), 11a2-5, paratypes, (IRSNB P 8586–P 8589)

Myctophum fitchi Schwarzhans, 1979; Fig. 11e1-4, Zanclean, Pliocene, Le Puget sur Argens (France), (fossil coll. Girone, Univ. Bari).

Myctophum punctatum Rafinesque, 1810; Fig. 11b1-5, Recent, Mediterranean Sea (coll. Girone, Univ. Bari)

Paraconger sp.; Fig. 5a, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8532)

Paralepis brevirostris (Parr, 1928); Fig. f1, Recent, Madeira (coll. IRSNB)

Paralepis coregonoides coregonoides Risso, 1820; Fig. 6h, Recent, 33°N25°W (coll. IRSNB)

Paralepis harryi Maul, 1954; Fig. 6i, Recent, Madeira (coll. IRSNB)

Parascombrops aff. *microlepis* Norman, 1935; Fig. 9a1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8612–P 8613)

Parascombrops mutinensis (Bassoli, 1906); Fig. 9e1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8610–P 8611)

Physiculus aff. *huloti* Poll, 1953; Fig. 7f1-3, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8594–P 8596)

Pomadasys aff. *incisus* (Bowdich, 1825); Fig. 9b1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8614–P 8615)

Pseudophichthys sp. 1; Fig. 5c1-4, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8537–P 8540)

Pseudophichthys sp. 2; Fig. 5f, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8541)

Pseudophichthys splendens (Lea, 1913); Fig. 5d1-2, Brisighella, sample B (IRSNB P 8534–P 8535); Fig 5d3, Verduno, Hospital, slumping (IRSNB P 8536)

Sardina pilchardus (Walbaum, 1792); Fig. 5h, Verduno, left bank of the Tanaro River (IRSNB P 8542)

Spondyliosoma cantharus (Linnaeus, 1758); Fig. 9i1-2, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8618–P 8619)

Trachinus draco Linnaeus, 1758; Fig. 9g, Verduno, Metalgranda, sample Cavallo 2007 (IRSNB P 8622)

Uranoscopus ciabatta n. sp.; Fig. 12b1-2, Verduno, Metalgranda, sample Cavallo 2007, Fig. 12b2, holotype, (IRSNB P 8623), Fig. 12b1, paratype, (IRSNB P 8625)

Uranoscopus scaber Linnaeus, 1758; Recent, Fig. 12a1-4, (coll. IRSNB)

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