

MARINE LIFE IN THE MEDITERRANEAN DURING THE MESSINIAN SALINITY CRISIS: A PALEOICHTHYOLOGICAL PERSPECTIVE

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Associate Editor: Cristina Lombardo.

To cite this article: Carnevale G. & Schwarzhans W. (2022) - Marine life in the Mediterranean during the Messinian salinity crisis: a paleoichthyological perspective. *Riv. It. Paleontol. Strat.*, 128(2): 283-324.

Keywords: Fossil fish skeletal remains; otoliths; Mediterranean; Lago-Mare; marine; Myctophidae.

Abstract. Almost fifty years after the first definition of the Messinian salinity crisis (MSC), the events that occurred in the Mediterranean during the terminal portion of the Miocene still attract the attention of a large and diverse scientific community. Although fossils are relatively common in the deposits that accumulated during the MSC, their significance for the interpretation of the latest Miocene paleoenvironmental evolution of the Mediterranean has been undervalued. In this paper, we summarize the marine paleoichthyological record of the three stages of the MSC based on both articulated and isolated skeletal remains and otoliths, the latter almost exclusively known from the Lago-Mare phase. We focus on the composition of the marine ichthyofauna of the Mediterranean during the three main stages of the MSC, showing the persistent continuity of marine stenohaline taxa throughout most of the interval between 5.97 and 5.33 Ma. While the record of articulated fish skeletons is unquestionably autochthonous, thereby providing unambiguous evidence of the occurrence of open marine environments in the MSC preceding the Lago-Mare phase, the autochthonous nature of the otolith record has often been questioned. For this reason, the otolith record of marine fishes has been examined in detail from a taxonomic and paleoecological point of view. Three species, *Bellottia verecunda* n. sp., *Bentosema taurinense* n. sp., and *Bostrychus marsilii* n. sp., are described as new and a thorough discussion about the possible origin of the otoliths is provided. Alternative explanations for the occurrence of otoliths of marine fish during the Lago-Mare phase, such as reworking, contamination from overlying Pliocene sediments or import from outside the Mediterranean through aquatic birds are considered unlikely. In our assessment, the occurrence of marine fish otoliths in the Lago-Mare phase can be explained with the presence of normal marine environments in the Mediterranean, at least temporarily. Therefore, we suggest that the paleoichthyological data provided herein should be integrated in the future evolutionary paleoenvironmental reconstructions of the MSC.

INTRODUCTION

The catastrophic scenario of a completely desiccated Mediterranean postulated for the Messinian salinity crisis (MSC) makes this event as one of

the most spectacular of the entire Cenozoic history. During the past five decades, the complex series of events that affected the Mediterranean basin in the late Miocene have been examined from many different perspectives using a variety of approaches, stimulating cogent and controversial debates in the scientific community (see Roveri et al. 2014). The “deep desiccated basin model” proposed by Hsü et

Received: July 13, 2021; accepted: October 14, 2021

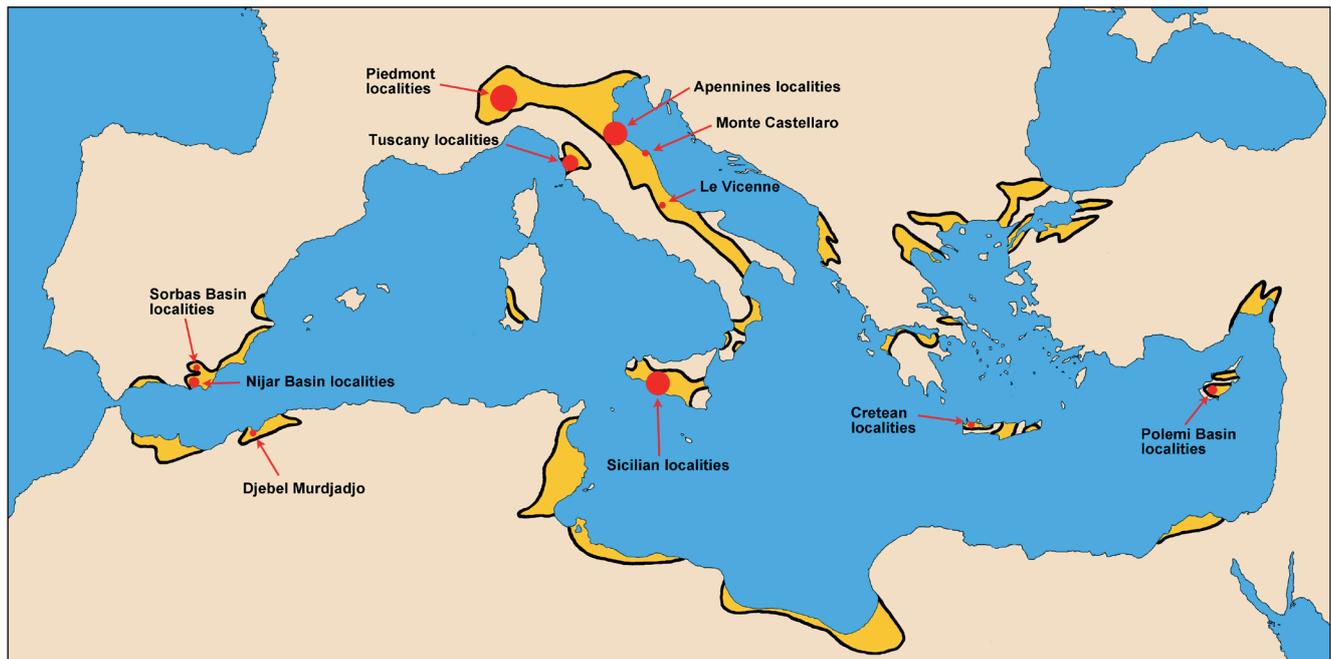


Fig. 1 - Map showing the position of the localities examined for this study. The size of the dots reflects the size of the respective areas with fossil locations. Late Miocene to early Pliocene basins outlines in onshore terrain marked by yellow color and black frame; modified from Schwarzghans et al. (2020).

al. (1973) hypothesized that the base level of the Mediterranean dropped some kilometers below the global sea level, and that the seafloor was eventually occupied by a giant salt desert. According to this model, due to the closure of the Mediterranean-Atlantic gateways, the waterbody of the isolated Mediterranean rapidly reduced its volume through evaporation, becoming hypersaline, completely desiccated and, finally, hyposaline (see Hsü et al. 1977; Rouchy 1982). The accumulation of huge amounts of evaporitic deposits that occurred during the first phase of the salinity crisis was followed by the capture of Eastern Pararethyan non-marine waters that partially refilled the basin leading to the deposition of the fresh- or brackish-water sediments of the Lago-Mare event (e.g., Cita et al. 1978; McCulloch & De Deckker 1989). The adoption of such a scenario necessarily implies an oceanographic apocalypse in the Mediterranean (see Taviani 2002), with the annihilation of its marine eukaryotic biota and the collapse of the marine ecosystem, followed by the establishment of brackish taxa of Paratethyan origin during the Lago-Mare event and the subsequent complete biotic and environmental recovery after the basal Zanclean re-flooding (see Carnevale et al. 2019).

Recent advances in our knowledge of the Miocene astronomical cyclostratigraphy togeth-

er with a profound analysis of the onshore sedimentary record facilitated a more detailed analysis of the events related to the MSC, summarized in a consensus stratigraphic model, which recognizes three main stages, each defined by specific evaporite associations (CIESM 2008; Roveri et al. 2014). The first stage (5.97-5.60 Ma) reflects the onset of the MSC and is characterized by up to 16 cycles of evaporites (Primary Lower Gypsum, PLG) that precipitated at depths shallower than 200 meters in marginal or peripheral basins. The deepwater counterparts of the primary evaporites are dolostones or, more commonly, organic-rich euxinic shales. The second stage (5.60-5.55 Ma) is represented by halite and clastic gypsum deposits (Resedimented Lower Gypsum, RLG), which seem to document the acme of the MSC in a context of considerable tectonic activity at the Mediterranean scale (Roveri et al. 2014). The third stage (5.55-5.33) comprises the Upper Evaporites and the Lago-Mare event, being documented by a broad variety of sedimentary products. Overall, this stage is characterized by an alternation of evaporitic deposits and clastic sediments containing a brackish water biota (ostracods, molluscs, dinocysts) and has been subdivided into two substages, 3.1 (5.55-5.42) and 3.2 (5.42-5.33), of which the latter corresponds to the Lago-Mare phase. The end of the MSC is commonly marked

by a condensed organic-rich layer that document the sudden return to fully marine condition in response to the catastrophic Zanclean flood.

Although this detailed stratigraphic model clarifies several aspects of the progression of this complex event, a comprehensive definition of the paleoenvironmental scenarios remains largely elusive, as well as the nature and extent of the involved sea level changes. The fossil content of the evaporitic and associated deposits has been discussed by Dela Pierre et al. (2015), Carnevale et al. (2019) and Pellegrino et al. (2021) and was shown to be rich and diverse although this has often been underestimated. Conversely, considerable efforts were devoted to the peculiar latest Messinian ostracod and mollusk assemblages of Paratethyan affinity traditionally used to define the environmental context of the Lago-Mare event.

Fossil fish remains are relatively common in Messinian deposits (e.g., Arambourg 1925, 1927; Landini & Sorbini 1992; Gaudant 2002; Carnevale 2004, 2006), especially in those accumulated during the MSC where they are documented by articulated and isolated skeletal remains and otoliths, representing an important source of paleoenvironmental information for the entire interval of the crisis. The goal of this paper, therefore, is to review the marine fishes discovered up to date in the sediments of the MSC. Otoliths of euryhaline marine and brackish water fishes, primarily of the families Gobiidae and Sciaenidae from the Lago-Mare interval have been the subject of previous studies (Bannikov et al. 2018; Schwarzshans et al. 2020). With this paper, our review and assessment of bony fish remains in the sediments of the MSC interval comes to a close.

MATERIAL AND METHODS

The studied material originates from the localities and regions indicated in Fig. 1 and described in the chapter below. The otolith specimens are kept at the Museo di Geologia e Paleontologia, Università degli Studi Torino, Torino (MGPT-PU). Fish skeletal remains housed in several scientific institutions have been studied, including those in the collections of the Museo Regionale di Scienze Naturali, Torino, Italy (MRSN), and the Museo Civico di Scienze Naturali “Malmerendi”, Faenza, Italy (MSF).

Otoliths of extant fishes are cited with the catalogue numbers of the voucher specimens from which they were extracted (as far as possible) and refer to the Australian Museum, Sydney, Australia (AMS); British Museum (Natural History), London, United Kingdom (BMNH); Institut de Ciències del Mar, Consejo Superior de Investigaciones Científicas, Barceloan, Spain (ICM-CSIC); Museum of Comparative Zoology, Cambridge, Massachusetts, USA (MCZ);

Senckenberg Museum, Frankfurt am Main, Germany (SMF); Western Australian Museum, Perth, Australia (WAM); Zoologisches Museum der Universität Hamburg, Germany (ZMH); and Zoological Museum, University of Copenhagen, Denmark (ZMUC).

All the otoliths were studied with a reflected-light microscope. Photographs were taken with a Canon EOS mounted on the phototube of a Wild M400 photomicroscope. The photographs were taken at regular field-of-depth levels for each view with the camera being remotely controlled from a computer. The individual photographs of each view were stacked using Helicon Soft's Helicon Focus software. The continuously focused pictures were digitally processed with Adobe Photoshop to enhance contrast, balance exposition or to retouch small inconsistencies such as sand grains, encrustations or pigmentation spots insofar as doing so was possible without altering the otolith morphology. All the figures show right otoliths. Left otoliths have been mirror-imaged to facilitate better comparison and are annotated in the captions as ‘reversed.’

Abbreviations used in the descriptions of otoliths: OL = otolith length; OL2 (in Gobiiformes) = length of otolith measured from incursions of anterior and posterior otolith rims; OH = otolith height; OT = otolith thickness; OCL = length of ostial colliculum; CCL = length of caudal colliculum; SuL = sulcus length.

LOCALITIES

In their review paper “Messinian fossil fishes of the Mediterranean”, Sorbini & Tirapelle Rancan (1980) mentioned ten Mediterranean localities bearing fossil fish remains from MSC sediments. The vast majority (nine out of ten) of these localities are in Italy and their scarce paleoichthyological content was described throughout the last century (e.g., D’Erasmus 1928, 1929; Sturani 1973). Forty-two years later, the number of MSC fossil fish localities is considerably expanded, and at least 55 assemblages are listed herein primarily from Italy, but also from Greece, Spain, Cyprus, and Algeria, documenting the occurrence of a rather diverse ichthyofaunal assemblage in the Mediterranean during the time interval between 5.97 and 5.33 Ma. While the skeletal material discussed has been already described and/or figured in the past decades and only a few taxonomic adjustments are introduced herein, the status of a number of otoliths is updated, and new taxa are also described. However, the stratigraphic setting of the fish-bearing localities is usually well known and presented with a different degree of detail in the long series of papers in which the fish remains have been described over slightly less than a century. For this reason, a description of the stratigraphic context of the 55 examined localities is not provided herein. Rather, a synoptic scheme showing the age distribution of the fish-bearing strata for each locality is presented

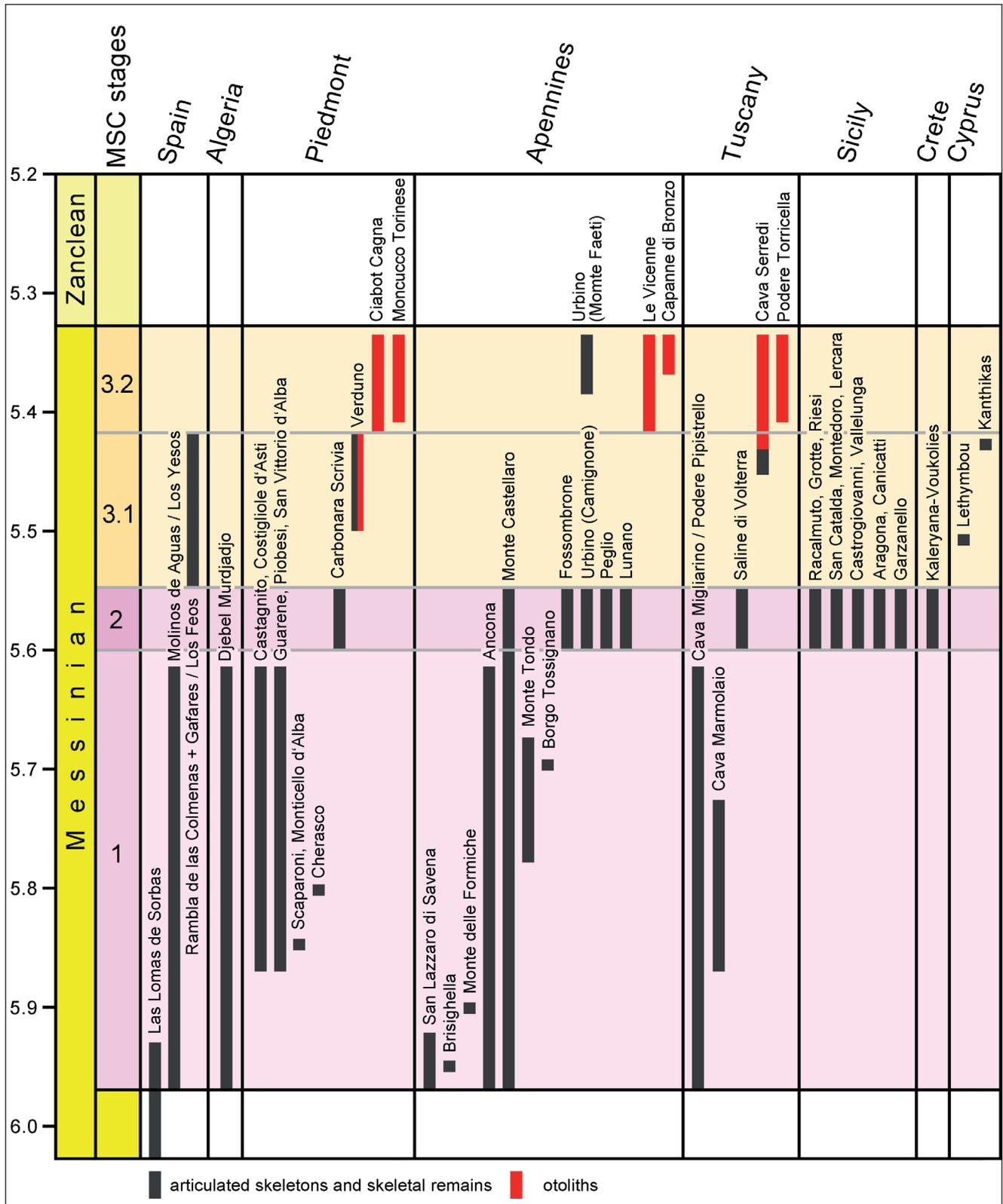


Fig. 2 - Messinian chronostratigraphy showing the age distribution of the productive fish-bearing localities discussed in this study.

in order to evidence the reasonably continuous record throughout the three evolutionary stages of the MSC (Fig. 2).

More than half of the fish-bearing localities (23) pertain to the first stage of the MSC and mostly document the ichthyofaunal assemblages of the

shallow marginal basins of the Piedmont Basin (Castagnito, Cherasco, Costigliole d'Asti, Guarene d'Alba, Monticello d'Alba, Piobesi d'Alba, Santa Vittoria d'Alba, Scaparoni; e.g., Sturani 1973; Gaudant 1981; Cavallo & Gaudant 1987; Fourtani-er et al. 1991; Gaudant & Cavallo 2008), Northern Apennines (Borgo Tossignano, Brisighella-Cava Monticino, Monte delle Formiche, Monte Tondo, Pietralacroce, San Lazzaro di Savena, Senigallia, Sirolo; e.g., Gaudant et al. 1988; Landini & Sorbini 1989; Carnevale et al. 2003; Bedosti et al. 2015), hinterland basins of Tuscany (Cava del Malandrone-Poggio della Maestà, Cava Marmolaio, Cava Migliarino, Podere Pane e Vino; Gaudant 1978, 1981; Landini & Sorbini 1989), Betic Cordillera (Las Lomas de Sorbas, Molino de Aguas; Gaudant & Ott d'Estevou 1985; Néraudeau et al. 2002), and Algeria (Chabet Beida; Gaudant et al. 1997). Precise information about the specific horizon from which the fishes were collected is available solely for certain sites (see Fig. 2), especially those exploited in the last few decades in Piedmont (Cherasco, Monticello d'Alba, Scaparoni) and in the Vena del Gesso Basin in the Northern Apennines (Borgo Tossignano, Brisighella, Monte delle Formiche, Monte Tondo). The Algerian locality of Chabet Beida, in the Djebel Murdjadjo area (Gaudant et al. 1997), has been referred to the first stage of the MSC due to the peculiar stratigraphic position of the fish-bearing diatomites (Mansour & Saint-Martin 1999), which are included in an evaporitic succession and regarded as documenting the onset of the MSC (see, e.g., Cunningham et al. 1997).

Our survey led to the recognition of 19 ichthyofaunal assemblages from the second stage of the MSC, between 5.60 and 5.55 Ma, the vast majority of which are monotypic, solely represented by the cyprinodontid *Aphanius crassicaudus*. The list of localities includes the productive sites (e.g., Aragona, Canicattì, Castrogiovanni, Lercara, Montedoro, Realmonte, Riesi, San Cataldo, Solfara Casino, Solfara di Palagonia, Vallelunga) referred to Racalmuto by D'Erasmo (1928); these localities of the Caltanissetta Basin solely yielding *Aphanius crassicaudus* (see D'Erasmo 1928) pertain to the Resedimented Lower Gypsum Unit, which documents the second stage of the MSC in Sicily (see Manzi et al. 2009; Roveri et al. 2014). With the exception of the sites in the Khania Province, western Crete, where fossil fishes were col-

lected from gypsarenite beds at Kaleryiana and Voukolies (see Freudenthal 1969; Gaudant 1980, 2002), all the other fish localities dating back to the second stage of the MSC are in Italy. In Sicily, fish remains from the second stage of the MSC have been reported also from the pelites interbedded with resedimented evaporites of the Ciminna Basin (Di Stefano & Catalano 1976). A single locality each in Piedmont (Carbonara Scrivia; Gaudant & Mori 1983) and Tuscany (Saline di Volterra; e.g., Capellini 1860, 1874) can be tentatively referred to the second stage of the MSC, while the remaining ones (e.g., Gaudant et al. 1988) are from the outer Adriatic Foredeep deposits of the Apennines, largely exposed in the northern part of the Marche Region (Manzi et al. 2005). Of these, the most significant from a paleoichthyological perspective is that of Monte Castellaro, near Pesaro, central Italy, whose stratigraphic features were briefly summarized by Sorbini (1988) (Fig. 3). As reported by Sorbini (1988), deposits documenting the MSC are well exposed at Monte Castellaro, represented by a variety of sedimentary settings. The section was examined by one of us (GC) in July 2011 in order to better define its lithological features and to locate the fish-bearing layers (Fig. 3). The lower part of the section, referred by Sorbini (1988) to the Marnoso-Arenacea Formation, is characterized by several meters of laminated bituminous shales, locally characterized by abundant skeletal remains of mesopelagic fishes (barracudinas, lanternfishes). The bituminous shales are covered by an alternation of laminated gypsum-rich carbonates and euxinic shales followed by gypsarenites and gypsisiltites (referred to as balatino gypsum by Sorbini 1988) and sandstones alternating with laminated blue-grey marls interrupted by a slump that were assigned by Sorbini (1988) to the Gessoso-Solfifera Formation. The considerably thick upper part of the Messinian section comprises the sediments of the S. Donato and Colombacci (=Cusercoli) formations. During the prospection carried out in 2011, fish remains were found in several parts of the section, confirming the information provided by Sorbini (1988), but a previously unrecognized marine fish assemblage was also discovered in the euxinic shales between the second and third layers of laminated carbonates (Fig. 3). A number of recent stratigraphic studies (e.g., Manzi et al. 2005; Roveri & Manzi 2006) demonstrated that the primary evaporites that accumulated in the marginal basins of the Northern

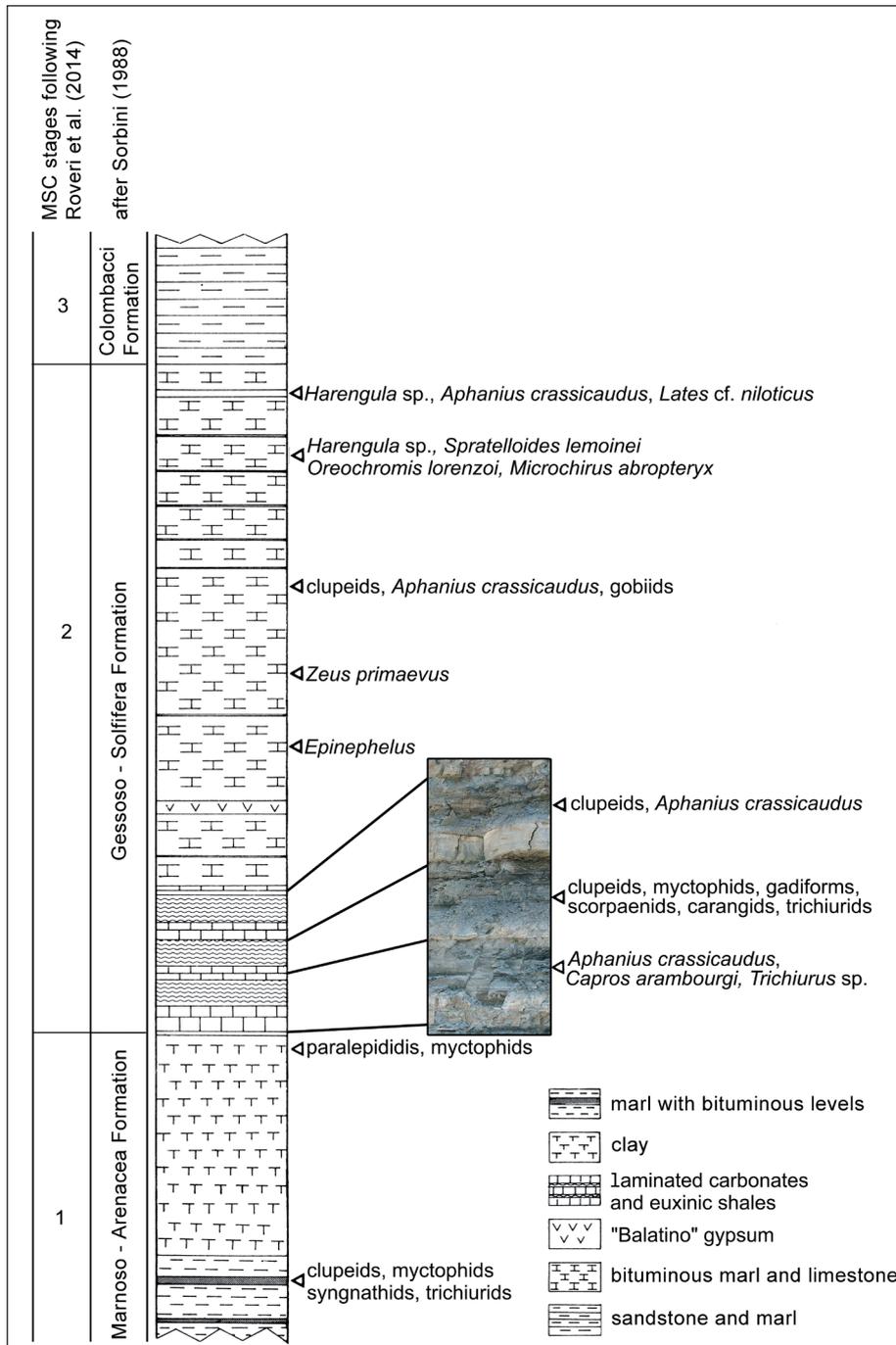


Fig. 3 - Stratigraphic column of the Monte Castellaro section showing the position of the fish-bearing deposits; modified from Sorbini (1988).

Apennines (e.g., Vena del Gesso Basin) during the first stage of the MSC do not occur in the Adriatic Foredeep, where only bituminous shales were deposited before 5.60 Ma (see Roveri et al. 2014). Therefore, following the model proposed by Manzi et al. (2005), the alternation of laminated carbonates and euxinic shales and the overlying alternation of gypsarenites, gypsisiltites, sandstones and blue-grey marls and, consequently, their fossil fish remains should be referred to the second stage of the MSC (Fig. 3). In this context, however, it is likely that the fossiliferous deposits underlying the laminated car-

bonates that Sorbini (1988) referred to the Marnoso-Arenacea Formation, actually represent a deeper lateral equivalent of the primary evaporites, thereby documenting the first stage of the MSC. However, a detailed stratigraphic study of the Monte Castellaro would be desirable in order to properly define the thickness of the different units exposed and the paleoenvironmental significance.

The ichthyofaunal composition of the third stage of the MSC is considerably diverse and documented by seven localities characterized by skeletal remains from Italy, Cyprus, and Spain, plus

		ecology	Senigallia	Ancona (Sirolo)	Ancona (Pietralacroce)	Borgo Tossignano (Cava SPES)	Brisighella (Cava Monticino)	Monte delle Formiche (Monterenzio)	San Lazzaro di Savena	Monte Tondo	Scaparoni	Monticello d'Alba	Cherasco	Castagnito	Guarene d'Alba	Piobesi d'Alba	Santa Vittoria d'Alba	Costigliole d'Asti	Podere Pane e Vino	Cava del Malandrone - Poggio della Maestà	Cava Migliarino	Cava Mammolaio	Chabet Beida	Molinos de Aguas	Las Lomas de Sorbas
Clupeidae	<i>Alosa crassa</i>	M B	•																						
	<i>Clupeonella maccagnoi</i>	M B								•		•													
	<i>Sardina</i> sp.	M																				•			
	<i>Sardina pilchardus</i>	M					•																		
	<i>Spratelloides lemoinei</i>	M									•	•		•	•										
	Clupeidae indet.	M B				•	•																		
Cyprinidae	<i>Paleoleuciscus cf. oeningensis</i>	F											•												
Salmonidae	<i>Salvelinus oliveroi</i>	F											•												
Mugilidae	<i>Mugil</i> sp.	M B											•												
Atherinidae	<i>Atherina cavalloi</i>	M B											•												
	<i>Atherina boyeri</i>	M B				•					•		•												
	<i>Atherinomorus? etruscus</i>	M B																	•				•		
Cyprinodontidae	<i>Aphanius crassicaudus</i>	B F	•	•	•	•			•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
	<i>Cryptolebias senogalliensis</i>	B F	•																						
Scorpaenidae	<i>Scorpaena cf. minima</i>	M											•												
Serranidae	<i>Tavania sturanii</i>	M											•												
Carangidae	<i>Lichia aff. amia</i>	M				•																			
	<i>Trachurus</i> sp.	M				•	•																		
	<i>Trachurus trachurus</i>	M										•													
Callionymidae	<i>Callionymus cf. pusillus</i>	M																					•		
Gobiidae	<i>Gobius aidouri</i>	M																					•		
	<i>Gobius ignotus</i>	M B				•							•						•						
	<i>Gobius meneghini</i>	M	•										•												
	<i>Gobius</i> sp.	M B								•	•											•	•		
	Gobiidae indet.	M B					•																		
Cichlidae	<i>Oreochromis lorenzoi</i>	B F				•																			
Latidae	<i>Lates cf. niloticus</i>	B F					•																		
Scombridae	<i>Sarda</i> sp.	M					•																		
	Thunnini indet.	M				•																			
Trichiuridae	<i>Lepidopus albyi</i>	M									•														
	<i>Lepidopus</i> sp.	M										•		•											
Soleidae	<i>Microchirus abropteryx</i>	M									•	•		•											

Tab. 1 - The MSC stage 1 fishes of the Mediterranean based on skeletal material: list of taxa, ecological affinities, and distribution. Abbreviations: B = brackish, F = freshwater, M = marine.

six otolith-bearing Italian localities, one of which – Cava Serredi – has also provided articulated skeletons (Carnevale et al. 2000, 2006b). While all the otolith-bearing localities pertain to the substage 3.2 (except Verduno) and their stratigraphic features have been repeatedly described in a series of papers (Carnevale et al. 2006a, 2006b, 2008b, 2018, 2019; Colombero et al. 2017; Schwarzshans et al. 2020),

those yielding skeletal remains pertain both to the first (Kanthikas, Lethymbou, Rambla de Las Colmenas, Verduno) and the second (Cava Monticino, Cava Serredi, Monte Faeti) substages of the third stage of the MSC (Fig. 2). The stratigraphic features and fossil content of the Italian localities (Gaudant et al. 1988; Carnevale et al. 2006a, 2008b; Villa et al. 2021), as well as those of Rambla de Las Colmenas

(de la Chapelle & Gaudant 1987) have been extensively discussed, whereas the localities from Cyprus have been described by Rouchy et al. (2001) and Manzi et al. (2016), respectively, but their ichthyofaunal features were only cursorily mentioned. At Kanthikas, fish remains have been observed in the laminated marls below the fifth gypsum bed (between 5.44 and 5.42 Ma) of the Upper Gypsum unit (Rouchy et al. 2001), while at Lethymbou they have been discovered in the marls underlying the second gypsum bed (between 5.52 and 5.50 Ma) of the Upper Gypsum unit (Manzi et al. 2016)

THE MARINE PALEOICHTHOLOGICAL RECORD OF THE MSC

The skeletal record

Articulated skeletal remains of teleost fishes are common fossils in MSC-related deposits, especially in those recording the first two stages. As a matter of fact, one of the paleontological icons of the MSC is a teleost fish, the cyprinodontid *Aphanius crassicaudus* (Agassiz, 1832), which was widespread in the Mediterranean before and throughout the crisis almost always represented by articulated skeletons, often showing pachyostotic condition (Gaudant 1978, 1979; Sorbini & Tirapelle Rancan 1980; Gaudant et al. 1988; Landini & Sorbini 1989; Carnevale et al. 2018, 2019).

Overall, a diverse assemblage of fishes is known based on articulated skeletal remains from the first stage of the MSC (Tab. 1). The vast majority of them have been collected from the euxinic or organic-rich shales that accumulated at different depths in the marginal (or peripheral) basins of the Apennines, Piedmont, Tuscany, Betic Cordillera and Chelif Basin between 5.97 and 5.60 Ma (see Roveri et al. 2014). Many of these marginal basins likely consisted of paralic paleobiotopes with different degree of confinement and filled with thalassogenic waters characterized by a significant continental input (e.g., Lugli et al. 2007, 2010; Carnevale et al. 2008a; Roveri et al. 2014). The fish assemblage is rather heterogeneous from an ecological point of view with a sharp dominance of marine taxa. In particular, more than 80% of the recognized taxa exhibits a clear marine signature, of which slightly less than 50% are fully marine [e.g., *Callionymus* cf. *pusillus* Delaroche, 1809, *Gobius aidouri* Arambourg,

1927, *Gobius meneghini* Cocchi, 1859, *Lepidopus* spp., *Lichia* aff. *amia* (Linnaeus, 1758) (Fig. 4C), *Microchirus abropteryx* (Sauvage, 1870), *Sarda* sp., *Sardina* spp., *Scorpaena* cf. *minima* Kramberger, 1882, *Spratelloides lemoinei* Arambourg, 1927 (Fig. 4B), *Tavania sturani*, Thunnini indet. (Fig. 4F), *Trachurus* spp. (Fig. 4D)] and the remaining part (slightly more than 30%) can be regarded as euryhaline [e.g., *Alosa crassa* Sauvage, 1873, *Atherina* spp., *Atherinomorus? etruscus* (Gaudant, 1978), *Clupeonella maccagnoi* Gaudant, 1987, *Gobius ignotus* Gaudant, 1978, *Mugil* sp.]. The guild of marine euryhaline fishes includes marine taxa able to tolerate varying salinities that make use (more or less extensive) of brackish biotopes during juvenile and/or adult life stages. Only a few of them (e.g., atherinids, *Clupeonella*), despite their clear marine origin, can complete their lifecycle within brackish systems, such as coastal lagoons and estuaries. However, what is especially significant is the occurrence of a number of genuine marine taxa typical of offshore contexts, including many pelagic voracious piscivores such as jacks (e.g., *Lichia*; Fig. 4C), bonitos (*Sarda*; Fig. 4E), tunas or trichiurids (e.g., *Lepidopus*, *Trichiurus*), which can occasionally visit paralic biotopes attracted by the periodic availability of abundant food resources (e.g., Whitfield 1999; Nordlie 2003). While the majority of these fishes

Fig. 4 - Fish skeletal remains from MSC deposits of the Mediterranean basin. A) *Sardinella* sp., MGPT-PU 130414, right lateral view of the skeleton, late Messinian, substage 3.1 of the MSC, Lethymbou, Polemi Basin, Cyprus. B) *Spratelloides lemoinei* Arambourg, 1927, MRSN MC 58, right lateral view of the skeleton, late Messinian, stage 1 of the MSC, Monticello d'Alba. C) *Lichia* aff. *amia* (Linnaeus, 1758), MSF 19, lateral view of the right cleithrum, late Messinian, stage 1 of the MSC, Borgo Tossignano (Rio Sgarba - Cava SPES), Italy. D) *Trachurus* sp., MSF 204, left lateral view of the skeleton, late Messinian, stage 1 of the MSC, Borgo Tossignano (Rio Sgarba - Cava SPES), Italy. E) *Sarda* sp., MSF 5, left lateral view of the skeleton, late Messinian, stage 1 of the MSC, Cava Monticino - Brisighella, Italy. F) Thunnini indet., MGPT-PU 130442, neurocranium in dorsal view, late Messinian, stage 1 of the MSC, Borgo Tossignano (Rio Sgarba - Cava SPES), Italy. G) Clinidae indet., right lateral view of the skeleton, late Messinian, substage 3.1 of the MSC, Lethymbou, Polemi Basin, Cyprus, refigured from Manzi et al. (2016). H) Gobiidae indet., MSF 4, left lateral view of the skeleton, late Messinian, stage 1 of the MSC, Cava Monticino - Brisighella, Italy. Scale bars 10 mm.

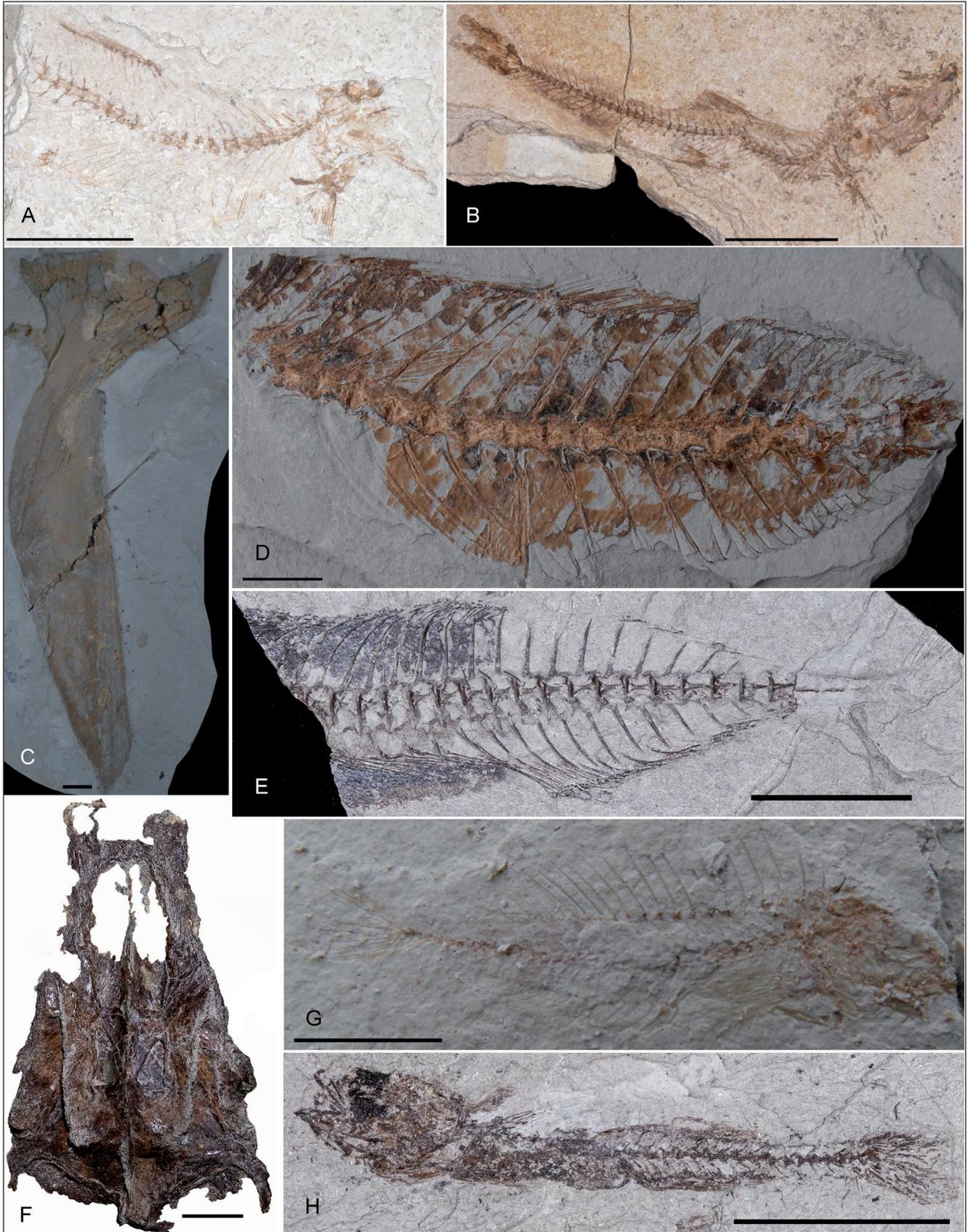


Figure 4

have been described or figured in a series of papers (e.g., Landini & Sorbini 1989; Fourtanier et al. 1991; Carnevale et al. 2008a; Gaudant & Cavallo 2008),

the occurrence of a tuna in the euxinic shales at the base of the 13th evaporitic cycle at Borgo Tossignano has been only cursorily mentioned by Landini &



Fig. 5 - Marine fishes collected in July 2011 from the organic-rich shales between the second and third horizons of laminated carbonates in the Monte Castellaro succession, late Messinian, stage 2 of the MSC. A) right lateral view of a clupeid fish. B) right lateral view of a myctophid lanternfish. C) right lateral view of a trichiurid fish likely belonging to the genus *Lepidopus*. D) right lateral view of a putative large carangid fish. Scale bars 10 mm.

chromis lorenzoi Carnevale, Sorbini & Landini, 2003) origin. The composition of the fish assemblage of Monte Castellaro is especially significant for the interpretation of the chemical nature of the Mediterranean waterbody during the second stage of the MSC. As already reported by Sorbini (1988), at Monte Castellaro fish remains are relatively abundant and occur throughout the succession of organic-rich marls and shales that accumulated during the second stage of the MSC (following the strati-

graphic interpretation by Manzi et al. 2005). Some of the marine stenohaline taxa recovered at Monte Castellaro and documented by Sorbini (1988) are unquestionably indicative of the existence of open marine conditions not far from the depositional environment. In particular, the species of the genera *Capros*, *Trichiurus* and *Zeus*, whose articulated skeletal remains have been found at Monte Castellaro (Sorbini 1988), are benthopelagic and commonly inhabit the shelf areas and slope usually at depths

		ecology	Cava Serredi	Kanthikas (Polemi)	Lethymbou (Polemi)	Cava Monticino	Verduno	Urbino (Monte Faeti)	Rambla de las Colmenas (Nijar)
Clupeidae	Clupeidae indet.	MB		•					
	<i>Spratelloides lemoinei</i>	M	•		•				
Mugilidae	<i>Mugil cf. cephalus</i>	M B	•						
Cyprinodontidae	<i>Aphanius crassicaudus</i>	B F	•			•	•	•	•
Cliniidae	Clinidae indet.	M			•				
Gobiidae	Gobiidae indet.	M B	•						
Cichlidae	?Cichlidae indet.	F				•			
Sciaenidae	?Sciaenidae indet.	M B				•			

Tab. 3 - The MSC stage 3 fishes of the Mediterranean based on skeletal material: list of taxa, ecological affinities, and distribution. Abbreviations: B = brackish, F = freshwater, M = marine.

greater than 50 meters (400 meters in the case of *Zeus* and about 600 meters in the case of *Capros* and *Trichiurus*; see, e.g., May & Maxwell 1986; Nakamura & Parin 1993; Egerton et al. 2017). In addition, during a detailed prospection of the section in July 2011, one of us (GC) collected several articulated skeletal remains belonging to fully marine fishes, including clupeids (Fig. 5A), gadiforms, myctophids (Fig. 5B), trichiurids (Fig. 5C), carangids (Fig. 5D), and juvenile scorpaenids from the organic-rich shales between the second and third horizons of laminated carbonates pertaining to the second stage of the MSC (after Manzi et al. 2005). Therefore, the fossil fishes of Monte Castellaro, although still not completely described in detail, document the presence of a diverse pelagic fish assemblage in the time interval between 5.60 and 5.55 Ma.

The skeletal record of the third stage of the MSC is scattered and rather poor, with rare specimens occasionally reported from a few localities in Cyprus and Italy (Tab. 3). As mentioned above, according to the evolutionary stratigraphic model proposed for the MSC by Roveri et al. (2014), due to the recurred vertical architecture of its characteristic sedimentary sequence, the third stage (5.55-5.33 Ma) of the MSC can be subdivided into two substages 3.1 and 3.2. Skeletal remains of fishes are known for the substage 3.1 (5.55-5.42 Ma) from Verduno, in Piedmont and two localities in the Polemi Basin, in the southern part of Cyprus. The skeletal material from Verduno consists of a number of isolated vertebrae and scales clearly belonging to the cyprinodontid *Aphanius crassicaudus*, associated by a

single otolith of the putative psychrolutid *Enigmacottus socialis* Schwarzahns, Agiadi & Carnevale, 2020 (Colombero et al. 2014; Schwarzahns et al. 2020). On the other hand, the material from Cyprus consists of articulated skeletal remains discovered from two localities, Kanthikas and Lethymbou, but not described in detail. The occurrence of abundant clupeid articulated skeletons from the laminated marls below the fifth gypsum bed (between 5.44 and 5.42 Ma) of the Upper Gypsum unit exposed in the Kanthikas section has been reported by Rouchy et al. (2001). The articulated fish skeletons from the marls underlying the second gypsum bed (between 5.52 and 5.50 Ma) of the Upper Gypsum unit in the Lethymbou section have been documented by Manzi et al. (2016), who erroneously assigned (a taxonomic mistake that persisted in the paper by Andreotto et al. 2021) to *Aphanius crassicaudus* a nicely preserved specimen clearly belonging to the blennioid family Clinidae (Fig. 4G), which was associated to the round herring *Spratelloides lemoinei* and the clupeid *Sardinella* sp. (Fig. 4A). The clinid is especially important because the members of this family of benthic fishes are exclusively marine (see Stepien 1992) being extraordinarily rare in the fossil record (see Bannikov 1998). The specimen from Lethymbou exhibits a number of morphological features (ectopterygoid and endopterygoid separated from each other; dorsal fin continuous with many more spines than segmented rays; segmented dorsal-fin rays unbranched; two anal-fin spines; all pectoral- and caudal-fin rays unbranched; dorsalmost pectoral-fin rays articulating only with the dorsalmost

proximal radial; cycloid scales) that unambiguously support its placement within the marine teleost family Clinidae (see, e.g., George & Springer 1980; Springer 1993). Therefore, the presence of round herrings (and other clupeids) and clinids in the Upper Gypsum unit of the Polemi Basin support the hypothesis that normal marine conditions also occurred in the Mediterranean during the substage 3.1. As far as the substage 3.2 (5.42–5.33 Ma) is concerned, skeletal remains of teleost fishes have been reported from Cava Serredi, Fine Basin, Tuscany (e.g., Carnevale et al. 2006b), Monte Faeti, close to Urbino, Marche (Gaudant et al. 1988) and, as rare isolated bones associated to very abundant tetrapod remains, in the karst fissure fillings of Monticino Quarry, close to Brisighella, Romagna (Villa et al. 2021). The cyprinodontid *Aphanius crassicaudus* is present in all of these localities, being the only known taxon at Monte Faeti. While it is associated with putative cichlids and sciaenids at Monticino Quarry, *Aphanius crassicaudus* is much less common at Cava Serredi, where round herrings (*Spratelloides lemoinei*), mullets (*Mugil* cf. *cephalus*) and gobies (Gobiidae indet.) have been described by Carnevale et al. (2000, 2006b). The presence of the round herring *Spratelloides* is indicative of the occurrence of marine waters also in the substage 3.2. However, as discussed in the following chapter, the relatively rich otolith record known for this substage provides a much more substantial overview of the Mediterranean fish diversity during the terminal portion of the MSC.

The diversity and taxonomic composition of the fish assemblages known based on skeletal material are remarkably different for the three stages of the MSC. While the first stage is documented by a reasonably high number of skeleton-based taxa, the structure and composition of the fish communities during the second and, even more drastically, during the third stage of the MSC cannot be properly interpreted based on the skeletal record alone. However, although not fully adequate for a detailed comparative analysis of the ichthyofaunal dynamics throughout the MSC, the skeletal record provides unquestionable and unambiguous record of the existence of marine taxa necessarily requiring marine conditions to complete their life cycles during all the three stages of the crisis. Intriguingly, the diversity patterns and their paleoecological significance that cannot be interpreted for the third stage

based on skeletal remains, actually can be scrutinized using the rich otolith record of substage 3.2. In any case, an interesting pattern that can be recognized using the skeletal record is the persistent occurrence of at least two taxa – *Aphanius crassicaudus* and *Spratelloides lemoinei* – during all the stages of the MSC. While the paleoenvironmental significance of *Aphanius crassicaudus* has been widely used to support the desiccation scenario hypothesized in the traditional model of the MSC (e.g., Sorbini & Tirapelle Rancan 1980), that of *Spratelloides* has not been previously discussed. Round herring of the genus *Spratelloides* are coastal marine schooling fishes currently found in tropical and subtropical waters of the Indo-Pacific region where they are important as food and bait. Due to their relevance in tuna fisheries, the biology of these fishes has been extensively explored (e.g., Dalzell 1980, 1985, 1987, 1990). All the species of this genus are short-living inhabiting shallow and densely vegetated habitats (e.g., Milton et al. 1991), and their reproduction occurs exclusively in shallow coastal marine environments with deposition of demersal eggs and epibenthic schooling of the larvae (e.g., Leis 1986). The species *Spratelloides lemoinei* was introduced by Arambourg (1927) based on abundant well-preserved material from the pre-evaporitic diatomites of the Chelif Basin, and its presence has been also reported from the Pliocene of Italy (see Sorbini 1988, 1991) and Greece (Gaudant & Symeonidis 1995; Gaudant 2001), in some cases erroneously referred to the extant species *Spratelloides gracilis* (see Sorbini, 1988). This Neogene species has been documented exclusively in the Mediterranean and, more generally, the genus *Spratelloides* has never been recorded along the Atlantic coasts. Therefore, the stratigraphic continuity of its occurrence from the pre-evaporitic Messinian, throughout the MSC and into the Pliocene (see also Gaudant 1989; Sorbini 1991) should be necessarily taken into account in the interpretative analysis of the paleoenvironmental evolution of the Mediterranean.

The otolith record

Otoliths have not been found in sediments of the first two stages of the MSC probably because of the unfavorable conditions for the preservation of aragonitic fossils during this part of the crisis (see Carnevale et al. 2019). However, otoliths have been found regularly in sediments of the

Lago-Mare interval (substage 3.2), but even there they are generally rare, except for a single horizon at Cava Serredi (Fine Basin, Tuscany), and large amounts of sediments have been processed to collect only a relatively small number of otoliths (see Schwarzhans et al. 2020). We are not sure whether this reflects a dilution effect due to relatively high sedimentation rates (see Schwarzhans 2013a) or that fishes were comparatively rare in the Mediterranean during the Lago-Mare event.

In any case, the composition of the fish fauna as recovered from otoliths, is highly diverse and contains clades that would not normally be expected to be found side by side. The most common otoliths in sediments of the MSC are those of the extinct enigmatic putative psychrolutid *Enigmacottus socialis* Schwarzhans, Agiadi & Carnevale, 2020, which however stem with very few exceptions from a single level at Cava Serredi, which probably belongs to the uppermost part of the substage 3.1. The same horizon is also rich in otoliths of the Ponto-Caspian clupeid *Clupeonella*, which otherwise is also rare, although skeletal remains pertaining to this genus are known from the first stage of the MSC (see Tab. 1). Elsewhere, in the sediments of the Lago-Mare interval (substage 3.2) gobiid otoliths are the most common and species-rich except for Moncuco Torinese, where they are very rare. The goby otoliths have been reviewed by Schwarzhans et al. (2020), and most of them were interpreted as related to Paratethyan/Ponto-Caspian clades, some of which were already present in pre-evaporitic Messinian sediments of Strada degli Archi, in Tuscany. The only goby with Atlantic-Mediterranean affinities found in the Lago-Mare interval is *Aphia minuta*, a neotenic species that occurs free swimming, pelagic, not far from the shore (Froese & Pauly 2020). Its occurrence has been explained by Schwarzhans et al. (2020) as connected to its non-demersal life style allowing it to live away from the coastal brackish-water belt. Another group which is rather common in certain localities, particularly at Capanne di Bronzo and Moncuco Torinese are the Sciaenidae. Sciaenids typically inhabit marine waters characterized by considerable fluvial input (Trewavas 1977) and can spend a large part of their life cycles in estuarine environments (e.g., Stringer & Shannon 2019). Many species are euryhaline and amphidromous and hence would be expected in the Mediterranean

during the Lago-Mare event. The sciaenids of the Paratethys and the MSC of the Mediterranean were reviewed by Bannikov et al. (2018). During the Lago-Mare event, Bannikov et al. (2018) recognized species with clear or putative Paratethyan affinities but also species, less common, of Atlantic-Mediterranean origin. Otoliths of other euryhaline fishes are generally rare and include *Aphanius crassicaudus*, which is very rare when compared to the skeletal record, and rare atherinids and mugilids (e.g., Carnevale et al. 2006b).

Stenohaline freshwater fishes, which occur uncommonly but regularly in the skeletal record, are very rare in the otolith record. *Knipowitschia etrusca* Schwarzhans, Agiadi & Carnevale, 2020 was described from Cava Serredi and Le Vicenne and is thought to belong to a clade of extant species of *Knipowitschia* distributed in the freshwater systems of Greece and Turkey. They are hypothesized to have descended from a freshwater habitat into the sheltered prodelta and lagoon environments of these two locations during the Lago-Mare event. Rare and very small lapilli otoliths could not be identified and might represent fishes known otherwise by sagittal otoliths.

Otoliths of stenohaline marine fishes are more common in the Lago-Mare interval and they are subject of the following review. Representatives of demersal and benthic fishes are rare, represented by the Sparidae, Clinidae, and a neritic clade of the ophidiiform family Bythitidae. Open-ocean mesopelagic fishes are the most common in the stenohaline marine guild, primarily represented by the Myctophidae, but also by the Gadidae. Otoliths of bathypelagic fishes are rare (Melamphaidae, Trachichthyidae) as are the demersal fishes commonly inhabiting the slope at intermediate depths (Moridae). Bathydemersal fishes are completely absent, including the Macrouridae.

The following review includes all the previously published records from the Lago-Mare event plus relevant data from other time intervals, as well as a rationale for the review. Fully adequate documentation of the identified taxa is included and descriptions are solely provided for new species or in cases of substantial new information. The latter includes the description of a new eleotrid, a typical amphidromous brackish water fish, that was overlooked in the review of gobioid otolith by Schwarzhans et al. (2020).

SYSTEMATICS

Order **Myctophiformes** Regan, 1911
 Family Myctophidae Gill, 1893
 Genus *Bentbosema* Goode & Bean, 1896

***Bentbosema taurinense* n. sp.**

Fig. 6 K-T

- 1983 *Bentbosema fitchi* Brzobohaty & Schultz, 1978 - Nolf & Steurbaut: pl. 1, fig. 19-22.
 2015 *Bentbosema fitchi* Brzobohaty & Schultz, 1978 - Lin, Girone & Nolf: fig. 2.7-8.
 2017 *Bentbosema fitchi* Brzobohaty & Schultz, 1978 - Lin, Brzobohaty, Nolf & Girone: fig. 4 S, T.
 2017 *Bentbosema* aff. *suborbitale* (Gilbert, 1913) - Colombero et al.: fig. 5.1-2.

Holotype: Fig. 6 P, MGPT-PU 130415, Sant' Agata Fossili, Piedmont, Tortonian.

Paratypes: Three specimens, MGPT-PU 130416, from Sant'Agata Fossili, Piedmont, Tortonian; two specimens, MGPT-PU 130417, from Borelli, Piedmont, pre-evaporitic Messinian; three specimens, MGPT-PU 130306, 130320, 130418, Moncucco Torinese, Piedmont, late Messinian, Lago-Mare phase.

Etymology: After the city of Torino in Piedmont, Italy, in the vicinity of the type localities.

Diagnosis: Relatively large otoliths up to 2.45 mm in length. OL:OH = 1.03-1.11; rostrum length 12-18 % OL; OCL:CCL = 1.25-1.55; distance from tip of antirostrum to highest point of dorsal rim to distance of highest point of dorsal rim to postdorsal tip = 1.7-2.4. Ventral rim very deeply and regularly curved, with two to three, rarely five denticles. Postdorsal rim relatively short, very slight concave.

Description. Relatively large, nearly round otoliths up to almost 2.5 mm length. Rostrum short, only slightly longer than antirostrum (12-18% OL), ventral rim deeply and regularly curved with one denticle below rear part of ostium and a second behind termination of cauda, and zero to three less prominent denticles in between. Dorsal rim anteriorly depressed, nearly straight, ascending to broad, rounded, large dorsal bulge positioned slightly behind middle of dorsal rim; postdorsal portion of rim steeply inclined, relatively short and very slightly concave. Antirostrum and excisura variable, mostly weak. Posterior rim regularly curved, rarely bulged behind tip of cauda.

Inner face nearly flat, slightly bent in horizontal direction. Sulcus long, distinctly suprmedian positioned, shallow, relatively wide, its ostium and cauda of nearly equal length. Ostial colliculum distinctly longer than caudal colliculum and also wider; caudal colliculum slightly reduced anteriorly; OCL:CCL = 1.25-1.55. Caudal pseudocolliculum very long, anteriorly reaching beyond termination of ostial colliculum.

Ventral furrow distinct, positioned relatively far from ventral rim of otolith, very regularly curved. Dorsal field much smaller than voluminous ventral field, with wide, indistinct dorsal depression. Outer face convex, smooth; OH:OT = 3.3-3.7.

Discussion. *Bentbosema taurinense* is a typical representative of the *B. suborbitale* lineage characterized by a compressed shape, a long rostrum, a long concave postdorsal region, a sulcus with nearly equally long ostium and cauda and two distinct and widely spaced denticles along the ventral rim of the otolith. It is a long ranging lineage for which the earliest members are thought to be represented by *B. regulare* (Frost, 1933) from the Otaian and Altonian of New Zealand (Aquitanean to Burdigalian; Schwarzahns 2019). *Bentbosema taurinense* is morphologically intermediate between *B. fitchi* Brzobohaty & Schultz, 1978 (Fig. 6 U-Z) known from the Karpatian and Badenian (late Burdigalian to Langhian) of the Central Paratethys and the extant, cosmopolitan tropical to subtropical *B. suborbitale* (Gilbert, 1913) (Fig. 6 A-F); due to this morphologically intermediate position, this new late Miocene species has been associated with both *B. fitchi* and *B. suborbitale* (see synonymy listing above). It differs from the extant *B. suborbitale* by the more compressed, high-bodied shape (OL:OH = 1.03-1.11 vs 1.13-1.17), regularly curved ventral rim (vs anteriorly pronounced), depressed, nearly straight predorsal rim (vs slightly expanded and rounded), short, steep and only slightly concave postdorsal rim (vs long, less steeply inclined and distinctly concave), as well as for the not anteriorly so much reduced caudal colliculum (OCL:CCL = 1.25-1.55 vs 1.9-2.45). *Bentbosema suborbitale* is a small fish with maximum recorded sizes reaching approximately 40 mm SL (Nafpaktitis et al. 1977; Hulley 1981). Otoliths have been extracted from fishes up to 32 mm SL (Lombarte et al. 2006) and projection indicates otolith sizes to about 2.0 to 2.1 mm length. *Bentbosema taurinense* otoliths reach larger sizes with the maximal measured OL of 2.45 mm. These are all very subtle characters, but combined with each other result in a consistent differentiation.

Otoliths of this lineage from the Zanclean are again intermediate in morphology between *B. taurinense* and *B. suborbitale*, but over all are much closer to the latter than *B. taurinense* and therefore are referred to as *B. aff. suborbitale* (Fig. 6 G-J). These otoliths differ from the extant ones primarily in the higher dorsal bulge and the shorter, steeper, and less strongly

concave postdorsal rim, in which they resemble the late Miocene *B. taurinense*. The proportions of the Zanclean otoliths otherwise are very close to those of the extant specimens and, like the extant species and unlike *B. taurinense*, they usually possess only two widely spaced denticles along their ventral rim.

Bentosema fitchi from the late early and early middle Miocene differs from *B. taurinense* in the even shorter and less developed, nearly straight postdorsal rim, shallower ventral rim, more expanded dorsal rim and relatively long rostrum (>17% OL vs 12-19% OL). The otoliths assigned to this species also have the tendency to show more denticles along their ventral rim, namely three to five, with only a single case solely bearing two denticles (Fig. 6 U).

Bentosema taurinense so far is exclusively known from the Tortonian and Messinian, including the Lago-Mare interval, of the Mediterranean. However, given the wide geographic range of the extant species and, at least, of some of the fossil *Bentosema* species, a much wider distribution has to be expected.

Genus *Ceratospelus* Günther, 1864

Ceratospelus miocenicus Bedini, Francalacci & Landini, 1986

Fig. 7 A-B

1986 *Ceratospelus miocenicus* - Bedini, Francalacci & Landini: pl. 3, fig. 9-10, pl. 5, fig. 1-3.

Material: Five specimens from Podere Torricella, MGPT-PU 130423, and a single specimen from Moncucco Torinese, MGPT-PU 130318.

Discussion. *Ceratospelus miocenicus* was established by Bedini et al. (1986) based on articulated skeletons with otoliths found *in situ* from the pre-evaporitic Messinian of Mondaino. These are the first isolated otoliths recognized for this species, being relatively small in size, measuring slightly more than 1 mm in length and probably belonging to juvenile individuals. Otoliths of *C. miocenicus* differ from those of the extant *C. maderensis* (Lowe, 1839) in having a relatively short rostrum, a feature, however, which is also less prominent in small specimens of the latter species. *Ceratospelus maderensis* is known since the Zanclean in the Mediterranean (Schwarzahns 1978, 1986; Nolf & Cappetta 1988). Otoliths described as *Clupea bonii* Anfossi & Mosna, 1971 from the Tortonian of Piedmont may represent

another species of the genus *Ceratospelus* characterized by the presence of an obtuse mediodorsal angle, a well-developed rostrum, and blunt posterior rim.

Genus *Diaphus* Eigenmann & Eigenmann, 1890

Diaphus cf. barrigonensis Schwarzahns & Aguilera, 2013

Fig. 7 C-E

- ?2000 *Diaphus bolti* Täning, 1918 - Brzobohaty & Nolf: pl. 3, fig. 9.
 2013 *Diaphus barrigonensis* - Schwarzahns & Aguilera: pl. 7, fig. 1-9.
 ?2017 *Diaphus bolti* Täning, 1918 - Lin, Brzobohaty, Nolf & Girone: fig. 5 A.
 2017 *Diaphus* aff. *rubus* Girone, Nolf & Cavallo, 2010 - Colombo et al.: fig. 5.3.
 2018 *Diaphus* aff. *rubus* Girone, Nolf & Cavallo, 2010 - Carnevale et al.: fig. 3 F.
 2019 *Diaphus* aff. *rubus* Girone, Nolf & Cavallo, 2010 - Carnevale et al.: fig. 11i.

Material: A single specimen from Podere Torricella, a single specimen from Moncucco Torinese (MGPT-PU 130293), and a single specimen from Ciabot Cagna.

Discussion. *Diaphus barrigonensis* was originally described from the late Tortonian to Zanclean of the Caribbean where it is particularly common in the early Pliocene sediments of the Cubagua Formation that was deposited in an ancient upwelling system. A few specimens from the Tortonian and Messinian Lago-Mare interval of Italy possibly pertain to this species but differ somewhat in having

Fig. 6 - Otoliths of the genus *Bentosema*. A-F) *Bentosema suborbitalale* (Gilbert, 1913), Recent; A, off Loyalty Islands, SL 31 mm, refigured from Rivaton & Bourret (1999); B-C, central Atlantic, SL 26 and 31 mm, coll. M. Pilar Olivar, refigured from Lombarte et al. (2006) (reversed); D-F, off New South Wales, Australia, coll. Schwarzahns, leg. AMS. G-J) *Bentosema* aff. *suborbitalale* (Gilbert, 1913), SMF P7210-11 and coll. Schwarzahns (G reversed), Zanclean, Le Puget, SE-France. K-T) *Bentosema taurinense* n. sp., P, holotype, MGPT-PU 130415, Tortonian, Sant' Agata Fossili; K-O, paratypes (K-N reversed), MGPT-PU 130418, 130306, 130320, late Messinian, Lago-Mare phase, Moncucco Torinese; Q-R, paratype, MGPT-PU 130417, pre-evaporitic Messinian, Borelli; S-T, paratype (reversed), MGPT-PU 130416, Tortonian, Sant' Agata Fossili. U-Z) *Bentosema fitchi* Brzobohaty & Schultz, 1978, U-V, early Badenian, Bieczyn (RaB-48, coll. Radwan-ska), Poland (reversed), W-Z, early Badenian, Drnovice, Czech Republic, coll. Schwarzahns, leg. Brzobohaty.

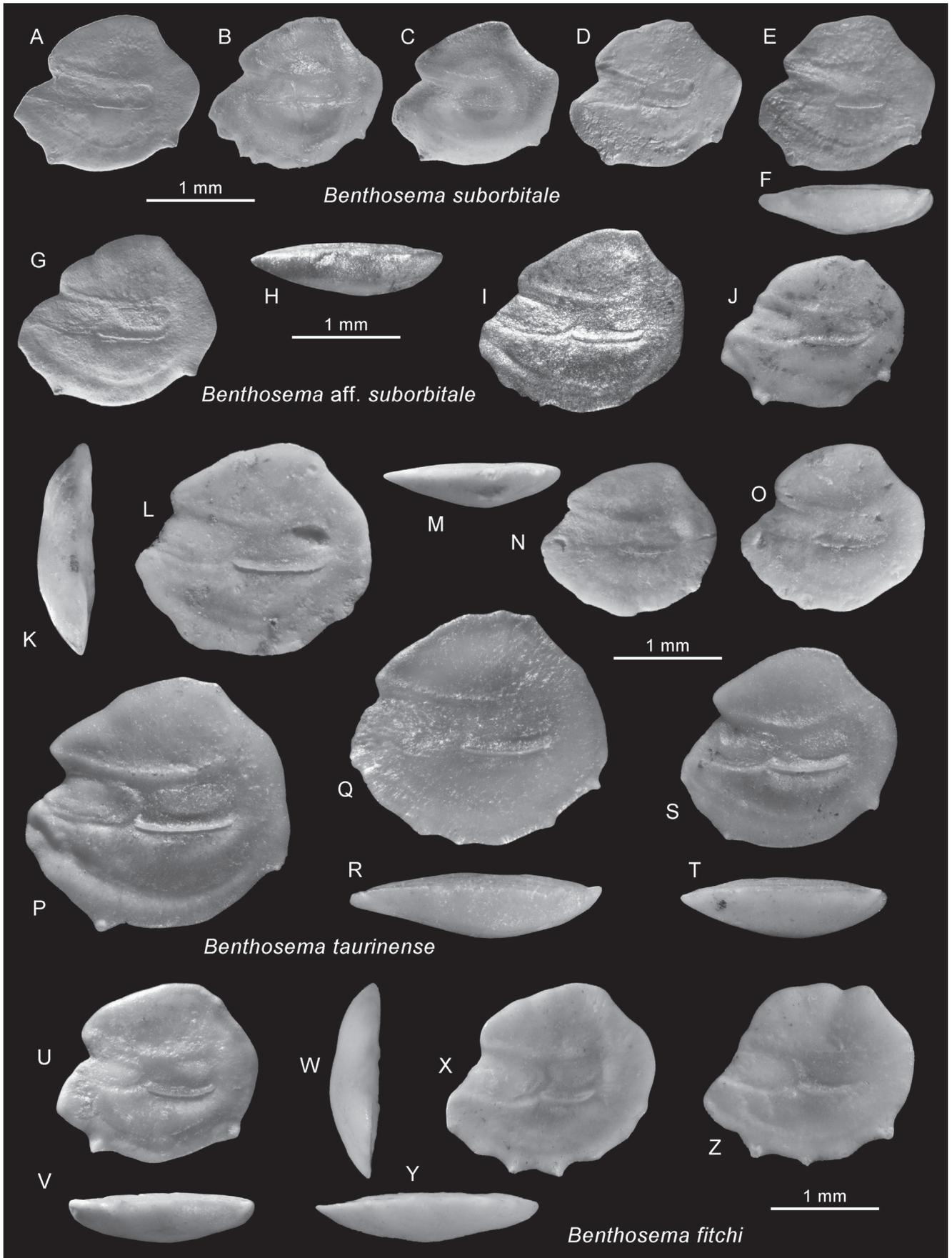


Figure 6

a more posteriorly positioned postdorsal angle and in being slightly thicker. We consider these subtle differences possibly reflecting differences related to the geographic separation of the populations. A similar pattern of slight morphological differences has been observed in the otoliths of the extant pseudo-oceanic species *D. taaningi* Norman, 1930 in its tropical Western and Eastern Atlantic populations (Schwarzahns 2013b).

Diaphus befralai Brzobohaty & Nolf, 2000

Fig. 7 F-H

- 1986 *Aethopora* sp. - Bedini, Francalacci & Landini: pl. 3, fig. 5-6, pl. 4, fig. 6.
 2000 *Diaphus befralai* - Brzobohaty & Nolf: pl. 6, fig. 6-11.
 2006 *Diaphus befralai* Brzobohaty & Nolf, 2000 - Carnevale, Landini & Sarti: fig. 4a.
 2008 *Diaphus* aff. *befralai* Brzobohaty & Nolf, 2000 - Carnevale et al.: fig. 3 C.
 2010 *Diaphus befralai* Brzobohaty & Nolf, 2000 - Girone, Nolf & Cavallo: pl. 7, fig. d1-d5.
 2015 *Diaphus befralai* Brzobohaty & Nolf, 2000 - Lin, Girone & Nolf: fig. 2.11.
 2017 *Diaphus befralai* Brzobohaty & Nolf, 2000 - Lin, Brzobohaty, Nolf & Girone: fig. 5 U.
 2018 *Diaphus befralai* Brzobohaty & Nolf, 2000 - Carnevale et al.: fig. 3 C.
 2019 *Diaphus befralai* Brzobohaty & Nolf, 2000 - Carnevale et al.: fig. 11e.

Material: A single specimen from Cava Serredi (MGPT-PU 130424), and a single specimen from Moncucco Torinese.

Discussion. *Diaphus befralai* is observed in the Serravallian to the (pre-evaporitic) Messinian of the Mediterranean but may actually range into the Zanclean (personal information, van Hinsbergh 2019). Bedini et al. (1986) figured an otolith *in situ*, which pertains to *D. befralai* but, unfortunately, the skeletal remains are inadequately preserved and it is not possible to define the diagnostic morphological features for a proper specific identification of the skeleton.

Diaphus befralai belongs to a large group of species with otolith morphologies that slightly differ from each other, including the extant *D. bolti* Tåning, 1918, *D. hudsoni* Zubrigg & Scott, 1976, *D. kuroshio* Kawaguchi & Nafpaktitis, 1978, *D. rafinesquii* (Cocco, 1838) (see Schwarzahns 2013b for figures) and the fossil *D. crassus* Schwarzahns, 1978 and *D. ecuadorensis* Schwarzahns & Aguilera, 2013. Of these, *D. befralai* closely resembles *D. bolti* and *D. crassus*. It differs from *D. bolti* in the relatively shorter rostrum and ostium and a more rounded dorsal rim.

Although *Diaphus bolti* has been reported since the Serravallian (Brzobohaty & Nolf 2000), the records prior to the Zanclean may require review. *Diaphus befralai* differs from *D. crassus* in having the ostium as wide as the cauda (vs ostium narrower than cauda). *Diaphus crassus* is mostly known from the Zanclean in the Mediterranean (Schwarzahns 1978, 1986) but has also been recorded from the Messinian of tropical America (Schwarzahns & Aguilera 2013). A unique distinguishing character of *D. befralai* is the ventral furrow located far away from the ventral rim of the otolith.

Diaphus cavallonis Brzobohaty & Nolf, 2000

Fig. 7 I

- 2000 *Diaphus cavallonis* - Brzobohaty & Nolf (see there for further synonymies): pl. 5, fig. 7-10, ?11-14.
 2008 *Diaphus* aff. *cavallonis* Brzobohaty & Nolf, 2000 - Carnevale et al.: fig. 6 B.
 2010 *Diaphus cavallonis* Brzobohaty & Nolf, 2000 - Girone, Nolf & Cavallo: pl. 7 fig. a1-a3.
 2013 *Diaphus cavallonis* Brzobohaty & Nolf, 2000 - Schwarzahns & Aguilera: pl. 8, fig. 7-10.
 2015 *Diaphus pedemontanus* (Robba, 1970) - Lin, Girone & Nolf: fig. 2.9-2.10.
 2017 *Diaphus cavallonis* Brzobohaty & Nolf, 2000 - Lin, Brzobohaty, Nolf & Girone: fig. 4 V-W.

Material: 12 specimens from Podere Torricella. MGPT-PU130425.

Fig. 7 - Otoliths of the genera *Ceratoscopelus* and *Diaphus*. A-B) *Ceratoscopelus miocenicus* Bedini, Francalacci & Landini, 1986, MGPT-PU 130423, late Messinian, Lago-Mare phase, Podere Torricella (reversed). C-E) *Diaphus* cf. *barrigonensis* Schwarzahns & Aguilera, 2013, MGPT-PU 130293, late Messinian, Lago-Mare phase, Podere Torricella (reversed). F-H) *Diaphus befralai* Brzobohaty & Nolf, 2000, MGPT-PU 130424, late Messinian, Lago-Mare phase, Cava Serredi. I) *Diaphus cavallonis* Brzobohaty & Nolf, 2000, MGPT-PU 130425, late Messinian, Lago-Mare phase, Podere Torricella. J-P) *Diaphus dirkenolfi* Schwarzahns, 1986, J-L, MGPT-PU 130426, late Messinian, Lago-Mare phase, Podere Torricella (K-L reversed), M-O, Zanclean, Oued Beth at Sidi Mohammed Ech Chleuch near Dar Bel Hamri, Morocco, coll. Schwarzahns; P, Zanclean, Oued Beth ca. 1.5 km south of Dar Bel Hamri, Morocco, coll. Schwarzahns. Q-T) *Diaphus* cf. *draconis* Schwarzahns, 2013, MGPT-PU 130427, late Messinian, Lago-Mare phase, Podere Torricella (R-T reversed). U) *Diaphus pedemontanus* (Robba, 1970), MGPT-PU 130428, late Messinian, Lago-Mare phase, Capanne di Bronzo. V-W) *Diaphus rubus* Girone, Nolf & Cavallo, 2010, MGPT-PU 130429, late Messinian, Lago-Mare phase, Moncucco Torinese.

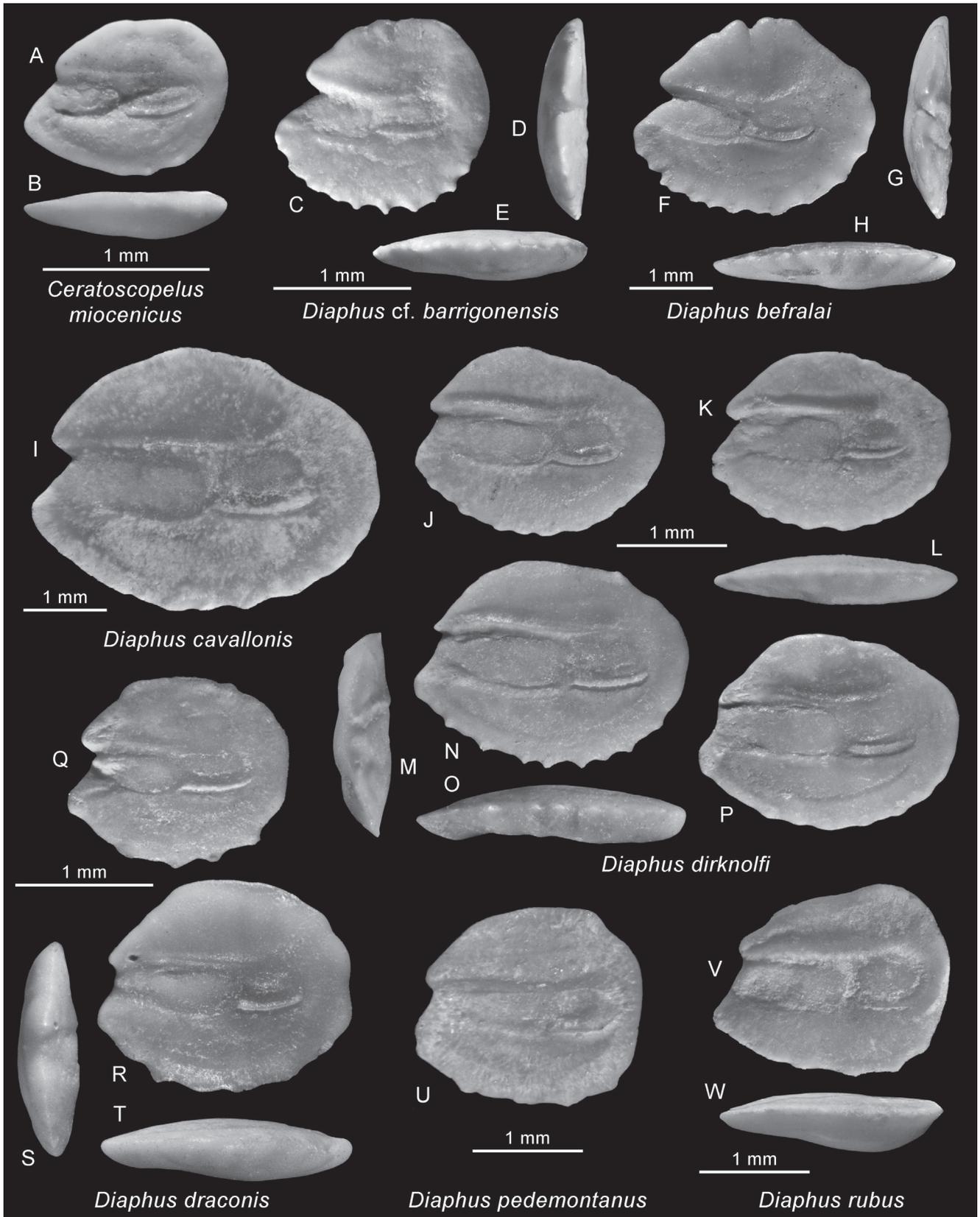


Figure 7

Discussion. *Diaphus cavallonis* is well known and widespread in the Tortonian, Messinian and Zanclean of the Mediterranean and has also been rarely recorded from the Zanclean of tropical America. The Serravallian records should be referred to *D. splendidus* (Brauer, 1904).

***Diaphus dirkenolfi* Schwarzahns, 1986**

Fig. 7 J-P

- 1972 *Myctophum splendidum* (Prochazka, 1893) - Weiler: pl. 1, fig. 3 (non fig. 2).
 ?1980 *Diaphus* sp. 2 - Nolf & Martinell: pl. 3, fig. 13-15.
 1986 *Diaphus dirkenolfi* - Schwarzahns: pl. 3, fig. 34-35.
 2008 *Diaphus* aff. *splendidus* (Brauer, 1904) - Carnevale et al.: fig. 6 A.
 2018 *Diaphus splendidus* (Brauer, 1904) - Carnevale et al.: fig. 3 D.
 2019 *Diaphus splendidus* (Brauer, 1904) - Carnevale et al.: fig. 11f.

Material: Two specimens from Podere Torricella (MGPT-PU 130426), and a single specimen from Moncucco Torinese.

Remarks. Nolf (2013) considered *D. dirkenolfi* as a doubtful species due to the apparent absence of genuine diagnostic features in the figured type specimens. This criticism is probably based on the holotype showing some slight erosion affecting the denticles along the ventral rim. Therefore, we figure herein better preserved specimens from the type locality (right bank of Oued Beth, ca. 1.5 km south of Dar Bel Hamri, near Sidi Slimane, northern Morocco; Fig. 7 P) and the type region (right bank of Oued Beth at Sidi Mohammed Ech Chleuch, ca. 3 km south of Dar Bel Hamri, northern Morocco; Fig. 7 M-O) in addition to well-preserved specimens from the Lago-Mare interval (Fig. 7 J-L) in order to redefine the diagnosis and descriptive analysis of this species.

Diagnosis: Elongate otolith with predorsal rim expanded and postdorsal rim depressed. OL:OH = 1.30-1.35. Ventral rim gently curved, with 6-8 fine denticles. Rostrum slightly longer than antirostrum; excisura feeble. Inner face markedly convex, outer face slightly concave to slightly convex. Ostium slightly wider than cauda and distinctly longer (OCL:CCL = 2.0-2.3).

Description. Moderately large and relatively thin and delicate otoliths with oval outline, measuring up to about 3.7 mm in length. OL:OH 130-1.35; OH:OT = 3.5-4.0. Dorsal rim anteriorly expanded, posteriorly depressed, sometimes with a small denticle above the midlength of the cauda. Ventral rim regularly and gently curved with 6 to 8 fine denticles. Rostrum short, pointed, its length about 10% of OL; excisura small, narrow; anti-

rostrum short, pointed, less than half the length of rostrum. Posterior rim regularly rounded.

Inner face markedly convex, rather smooth, with slightly suprmedian positioned sulcus. Ostium about twice as long as cauda and of about same width; width of ostial colliculum equals width of caudal colliculum and pseudocolliculum combined. OCL:CCL = 2.0-2.3. Dorsal margin of ostium slightly curved. Caudal pseudocolliculum distinct, longer than caudal colliculum. Dorsal depression narrow, long, stretching across most of the dorsal sulcus margin. Ventral furrow distinct and moderately close to ventral rim of otolith. Outer face slightly convex (less than inner face) to slightly concave, smooth.

Discussion. *Diaphus dirkenolfi* belongs to the *Diaphus garmani* otolith morphology group as defined by Schwarzahns (2013b). It closely resembles *D. bataii* Ohe & Araki, 1973, a widespread and long ranging species (late Burdigalian to at least Serravallian, possibly Zanclean) (see Schwarzahns & Aguilera 2013 for synonymies) and the extant *D. dumerilii* (Bleeker, 1856), which is known in the fossil record since at least the latest Miocene. *Diaphus dirkenolfi* differs from *D. bataii* in having a rostrum longer than the antirostrum (vs of the same length), the ostium equally wide to the cauda (vs ostium wider than the cauda) and 6 to 8 denticles on the ventral rim (vs 9 to 12). It differs from *D. dumerilii* by having a longer ostium (OCL:CCL = 2.0-2.3 vs 1.7-2.0) and less denticles along the ventral rim (6-8 vs 9-12). So far, *D. dirkenolfi* is only known from the Zanclean of the Mediterranean and Atlantic Morocco, and now also from the Lago-Mare interval.

***Diaphus* cf. *draconis* Schwarzahns, 2013**

Fig. 7 Q-T

- 2008 *Diaphus* aff. *pedemontanus* (Robba, 1970) - Carnevale et al.: fig. 6 D.
 ?2013c *Diaphus draconis* - Schwarzahns: pl. 4, fig. 8-12.
 ?2017 *Diaphus taaningi* Norman, 1930 - Colombero et al.: fig. 5.4.
 ?2019 *Diaphus draconis* Schwarzahns, 2013 - Schwarzahns: fig. 57.1-3.

Material: Six specimens from Podere Torricella (MGPT-PU 130427), a single specimen from Ciabot Cagna; a single specimen from Moncucco Torinese (MGPT-PU 130253) is also tentatively referred to this taxon.

Discussion. *Diaphus draconis* is a small species with a generalized morphology that makes it diffi-

cult for recognition and separation from juvenile specimens of larger species or other species with small and compressed otoliths such as *D. austriacus* (Koken, 1891) and *D. taaningi* Norman, 1930. It was originally described from the Serravallian to early Tortonian of Gabon and can be distinguished from *D. austriacus* by having 5 to 6 strong denticles on the ventral rim (vs 6 to 8 delicate denticles), and the rostrum longer than the antirostrum. It also appears to be generally thinner than *D. austriacus* (OH:OT = 3.5–3.8 vs 3.0–3.5). *Diaphus draconis* differs from otoliths of *D. taaningi* primarily in being thicker, having a more convex inner face and by showing fewer and more robust denticles along the ventral rim. *Diaphus taaningi* occurred in the Mediterranean since the Zanclean (e.g., Schwarzhans 1986 as *D. cabuzaci*, fig. 32), as well as along the Atlantic coasts of Morocco (unpublished data). Material from the Tortonian of the Mediterranean (e.g., Lin et al. 2015, 2017, the latter as *D. cabuzaci*) is in need of review. *Diaphus draconis* appears to have been a widely distributed species that has recently also been recorded from the Tortonian of New Zealand (Schwarzhans 2019). It seems to range from the Serravallian to the Messinian, although many fossils can only be tentatively assigned to this taxon, including those from Moncucco Torinese figured by Colombero et al. (2017). If the taxonomic identity of the specimens from the Lago-Mare interval will be confirmed, these would represent the youngest occurrence of the species.

Diaphus pedemontanus (Robba, 1970)

Fig. 7 U

- 1970 *Porichthys pedemontanus* - Robba: pl. 16, fig. 8.
 2000 *Diaphus pedemontanus* (Robba, 1970) - Brzobohaty & Nolf (see there for further synonymies): pl. 4, fig. 1, ?2-6.
 2006 *Diaphus* sp. - Carnevale, Caputo & Landini: fig. 3 A.
 2010 *Diaphus pedemontanus* (Robba, 1970) - Girone, Nolf & Cavallo: fig. 7b1-7b6.
 2013 *Diaphus pedemontanus* (Robba, 1970) - Schwarzhans & Aguilera: pl. 9, fig. 1-4.

Material: A single juvenile specimen from Capanne di Bronzo MGPT-PU 130428.

Discussion. *Diaphus pedemontanus* is a typical species of the Tortonian and of the pre-evaporitic Messinian of the Mediterranean area. Brzobohaty & Nolf (2000) also figured specimens from the Zanclean for which the allocation appears to be doubtful and reported them also from the Burdigalian, Langhian and Serravallian. Schwarzhans &

Aguilera (2013) recorded *D. pedemontanus* from the late Tortonian of tropical America. We consider *D. pedemontanus* as a late Miocene species with records from the early and middle Miocene and the early Pliocene requiring additional scrutiny.

Diaphus rubus Girone, Nolf & Cavallo, 2010

Fig. 7 V-W

- ?1986 *Diaphus microsomus* (Sauvage, 1870) - Bedini, Francalacci & Landini: pl. 3, fig. 7-8, pl. 6, fig. 1, 3, 5.
 2008 *Myctophum licatae* (Sauvage, 1870) - Gaudant et al.: fig. 4.
 2010 *Diaphus rubus* - Girone, Nolf & Cavallo: fig. 8a1-8a6.

Material: A single specimen from Moncucco Torinese MGPT-PU 130429.

Discussion. *Diaphus rubus* is a highly diagnostic and easy recognizable *Diaphus* species so far exclusively known from the Messinian of the Mediterranean. It has been found *in situ* by both Bedini et al. (1986) and Gaudant et al. (2008) although the articulated skeletal material from which these otoliths have been retrieved were identified as different species. It is therefore very likely that *D. rubus* will eventually turn out to be synonymous with a previously described skeleton-based species, as this may be the case for many otolith-based myctophid species of the late Miocene of the Mediterranean. However, such an alignment will only become possibly after a careful review of the types of the species formerly described by Sauvage (1870) and a comparison with the specimens that were found with otoliths *in situ*.

Genus *Hygophum* Bolin, 1939

Hygophum dertbonensis Anfossi & Mosna, 1969

Fig. 8 A-B

- 1969 *Hygophus intermedius dertbonensis* - Anfossi & Mosna: pl. 10, fig. 1-2.
 1996 *Hygophum dertbonensis* (Anfossi & Mosna, 1969) - Brzobohaty & Nolf (see there for further synonymies): pl. 3, fig. 20-23.
 2015 *Hygophum dertbonensis* (Anfossi & Mosna, 1969) - Lin, Girone & Nolf: fig. 2.14.
 2015 *Hygophum hygomi* (Lütken, 1892) - Lin, Girone & Nolf: fig. 2.18 (non fig. 2.17).
 2017 *Hygophum dertbonensis* (Anfossi & Mosna, 1969) - Lin, Brzobohaty, Nolf & Girone: fig. 5 R.

Material: Two specimens from Moncucco Torinese, two specimens from Ciabot Cagna. (MGPT-PU 130430)

Discussion. *Hygophum dertbonensis* has not been recorded from the Messinian. Therefore, the specimens documented herein from the Lago-Mare

interval represent the last known occurrence for this taxon.

Genus *Lampanyctus* Bonaparte, 1840

Lampanyctus latesulcatus Nolf & Steurbaut,

1983

Fig. 8 C-E

- 1983 *Lampanyctus latesulcatus* - Nolf & Steurbaut: pl. 2, fig. 34-41.
 ?2013c *Lampanyctus latesulcatus* Nolf & Steurbaut, 1983 - Schwarzahns: pl. 2, fig. 11-12.
 2017 *Lampanyctus latesulcatus* Nolf & Steurbaut, 1983 - Lin, Brzobohaty, Nolf & Girone: fig. 5 S-T.

Material: A single specimen from Moncucco Torinese, MGPT-PU 130245.

Discussion. This species is regularly recorded from the Tortonian of the Mediterranean. A much older record from the Burdigalian of Angola (Schwarzahns, 2013c) is regarded herein as only tentative. The specimen from the Lago-Mare interval represents the youngest record of the species. A similar morphology, although more elongate, is characteristic of the otoliths of *Lepidophanes inflectus* Schwarzahns & Aguilera, 2013, which also exhibit an inflected lower margin of the ostium. This species was originally described from the late Tortonian to Zanclean of tropical America and is now also recognized in the Zanclean of Italy (Fig. 8 F-G), representing yet another case of a fossil myctophid documented from both sides of the Atlantic Ocean.

Genus *Myctophum* Rafinesque, 1810

Myctophum coppa Girone, Nolf & Cavallo, 2010

Fig. 8 H

- 2008 *Myctophum dorsale* (Sauvage, 1870) - Gaudant et al.: fig. 5.
 2010 *Myctophum coppa* - Girone, Nolf & Cavallo: fig. 11a1-11a5.
 2017 *Myctophum coppa* Girone, Nolf & Cavallo, 2010 - Lin, Brzobohaty, Nolf & Girone: fig. 7 B-C.
 2017 *Myctophum punctatum* Rafinesque, 1810 - Lin, Brzobohaty, Nolf & Girone: fig. 7 G, ?7 H.
 2017 *Myctophum coppa* Girone, Nolf & Cavallo, 2010 - Colombero et al.: fig. 5.8.

Material: A single specimen from Moncucco Torinese MGPT-PU 130432.

Discussion. *Myctophum coppa* is a highly diagnostic species from the Tortonian and Messinian of the Mediterranean, including the Lago-Mare interval. It exhibits a relatively compressed shape,

a high, rounded postdorsal region, a depressed predorsal rim, and a small cauda, much shorter than the ostium, which is markedly bent upward. Specimens figured by Lin et al. (2017) and assigned to the extant *M. punctatum* possibly represent a variation of *M. coppa* or *M. arcanum* Schwarzahns & Aguilera, 2013 (see below).

Gaudant et al. (2008) figured an otolith found *in situ* in a specimen identified as *Myctophum dorsale*, which shows all the hallmarks of the isolated otoliths of *M. coppa* and very likely pertains to this species.

Myctophum fitchi (Schwarzahns, 1978)

Fig. 8 I-K

- 1978 *Gymnoscopelus fitchi* - Schwarzahns: fig. 30-31, 129.
 1986 *Myctophum fitchi* (Schwarzahns, 1978) - Schwarzahns: pl.2, fig. 25-27.
 1988 *Myctophum fitchi* (Schwarzahns, 1978) - Nolf & Cappetta (see there for further synonymies): pl. 6, fig. 5-10.
 1998 *Myctophum fitchi* (Schwarzahns, 1978) - Nolf, Mañé & Lopez: pl. 3, fig. 9.
 2008 *Myctophum fitchi* (Schwarzahns, 1978) - Carnevale et al.: fig. 6 F.
 2010 *Myctophum fitchi* (Schwarzahns, 1978) - Girone, Nolf & Cavallo: fig. 11c1-11c4.
 2015 *Myctophum fitchi* (Schwarzahns, 1978) - Lin, Girone & Nolf: fig. 3.3-3.4.
 2017 *Myctophum fitchi* (Schwarzahns, 1978) - Lin, Brzobohaty, Nolf & Girone: fig. 7 D.
 2018 *Myctophum fitchi* (Schwarzahns, 1978) - Carnevale et al.: fig. 3 E.
 2019 *Myctophum fitchi* (Schwarzahns, 1978) - Carnevale et al.: fig. 11g.

Remarks. The synonymy list of this species has been revised, taking into account an error in recording the year of the publication of “Otolithen aus dem Unter-Pliozän von Süd-Sizilien und aus der

Fig. 8 - Otoliths of the genera *Hygophum*, *Lampanyctus*, *Lepidophanes*, *Myctophum*, and *Scopelopsis*. A-B) *Hygophum dertbonensis* Anfossi & Mosna, 1969, MGPT-PU 130430, late Messinian, Lago-Mare phase, Moncucco Torinese. C-E) *Lampanyctus latesulcatus* Nolf & Steurbaut, 1983, MGPT-PU 130245, late Messinian, Lago-Mare phase, Moncucco Torinese. F-G) *Lepidophanes inflectus* Schwarzahns & Aguilera, 2013, Zanclean, Orciano near Pisa, coll. Schwarzahns. H) *Myctophum coppa* Girone, Nolf & Cavallo, 2010, MGPT-PU 130432, late Messinian, Lago-Mare phase, Moncucco Torinese. I-K) *Myctophum fitchi* (Schwarzahns, 1978), MGPT-PU 130433, late Messinian, Lago-Mare phase, Podere Torricella (I reversed). L-O) *Myctophum punctatum* Rafinesque, 1810, Recent, L, MCZ 105476, SL 79 mm; M-O, Walter Herwig cruise, 40°N, 11°W, coll Schwarzahns, leg. Krefft (O reversed). P-S) *Myctophum punctatum* Rafinesque, 1810, MGPT-PU 130434, late Messinian, Lago-Mare phase, Podere Torricella (reversed). T) *Scopelopsis pliocenicus* (Anfossi & Mosna, 1976), MGPT-PU 130435, late Messinian, Lago-Mare phase, Moncucco Torinese.

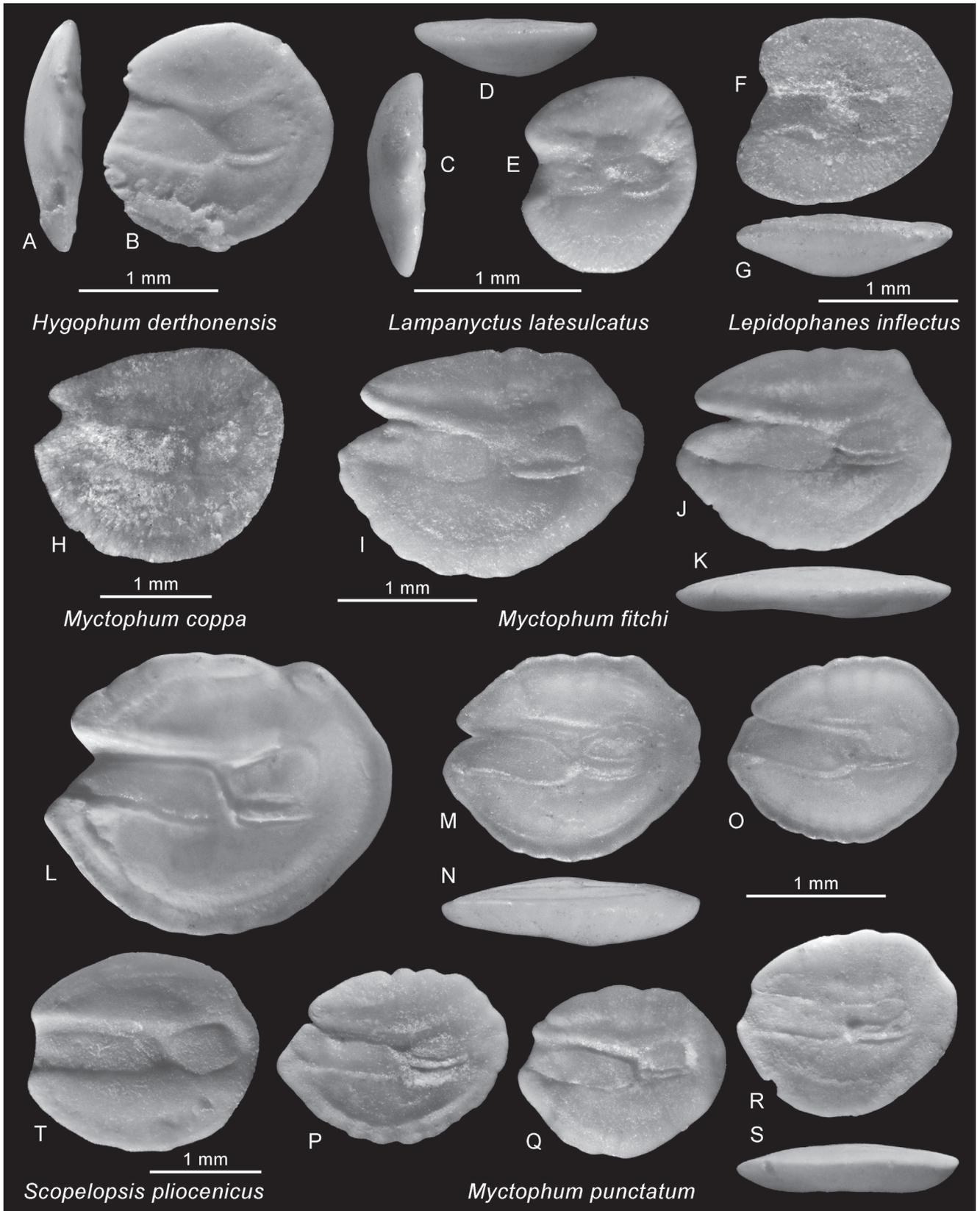


Figure 8

Toscana”, in many cases assigned to 1979, instead of the correct year 1978. The publication appeared in “Berliner Geowissenschaftliche Abhandlungen Reihe A, Band (volume) 8”, which was published in 1978.

Material: Four specimens from Podere Torricella MGPT-PU 130433.

Discussion. *Myctophum fitchi* is a characteristic *Myctophum* species known from the Tortonian to the Zanclean of the Mediterranean. It is characterized by shallow dorsal rim, relatively slender shape (OL:OH = 1.25-1.40), pointed antirostrum and rostrum, and deep excisura. The postdorsal rim behind the postdorsal angle varies from rounded to straight to distinctly concave. *Myctophum fitchi* is replaced in the tropical West Atlantic by *M. degraciai* Schwarzahns & Aguilera, 2013 in the late Miocene and *M. jacksoni* (Aguilera & Rodriguez de Aguilera, 2001) in the early Pliocene, both of which are more elongate and regarded to be related to the extant *M. aurolaternatum* Garman, 1899 known from low latitudes in the Indian and Pacific oceans.

Myctophum punctatum Rafinesque, 1810

Fig. 8 P-S

- 1978 *Myctophum unicum* - Schwarzahns: fig. 9, 125.
 1980 *Myctophum punctatum* Rafinesque, 1810 - Nolf & Martinell: pl. 1, fig. 18-19.
 non 1998 *Myctophum* cf. *punctatum* Rafinesque, 1810 - Nolf & Aguilera: pl. 5, fig. 18-19 (*Myctophum murhani* (Weinfurter, 1952)).
 2007 *Myctophum punctatum* Rafinesque, 1810 - Girone: pl. 2, fig. 5.
 non 2015 *Myctophum punctatum* Rafinesque, 1810 - Lin, Girone & Nolf: fig. 3.2 (*Myctophum arcanum* Schwarzahns & Aguilera, 2013).
 non 2017 *Myctophum punctatum* Rafinesque, 1810 - Lin, Brzobohaty, Nolf & Girone: fig. 7 G-H (*Myctophum* aff. *coppa* Girone, Nolf & Cavallo, 2010).

Material: Eight specimens from Podere Torricella (MGPT-PU 130434), three specimens from Moncucco Torinese (MGPT-PU 130261).

Discussion. The otoliths of the extant *Myctophum punctatum* are less morphologically distinctive compared to the two foregoing species, being characterized by a relatively gently and regularly curved shallow dorsal and deep ventral rim and a ratio OL:OH of 1.20 to 1.25, as well as by a ventrally expanded ostium. It occurs relatively regularly since the early Pliocene (Zanclean) in the Mediterranean, and *M. unicum* Schwarzahns, 1978 from the Zanclean of Orciano, near Pisa is regarded herein as a junior

synonym. Records from the early Miocene of Venezuela (Nolf & Aguilera, 1998 as *M.* cf. *punctatum*) have been referred to *M. murhani* (Weinfurter, 1952) by Schwarzahns & Aguilera (2013). Records from the Tortonian of Italy reported by Lin et al. (2015, 2017) are thought to represent *M. arcanum* Schwarzahns & Aguilera, 2013, which is characterized by a more rounded outline with a short rostrum, albeit similar proportions (OL:OH = 1.15-1.25), or variations of *M. coppa*. We consider the specimens described herein from the Lago-Mare interval as the earliest confirmed record of the species. Extant specimens are figured for comparison (Fig. 8 L-O) and document that the fossil specimens described herein pertained to relatively small individuals.

Genus *Scopelopsis* Brauer, 1906

Scopelopsis pliogenicus (Anfossi & Mosna, 1976)

Fig. 8 T

- ?1929 *Nyctophus (Lamparyctus) edwardsi* (Sauvage, 1873) - d'Erasmus: fig. 12-13.
 1976 *Myctophum pliogenicum* - Anfossi & Mosna: pl. 2, fig. 4-7.
 1978 *Myctophidarum edwardsi* (Sauvage, 1873) - Schwarzahns: fig. 46, 137.
 1983 *Scopelopsis pliogenicus* (Anfossi & Mosna, 1976) - Nolf & Steurbaut: pl. 3, fig. 11-13.
 1986 *Scopelopsis pliogenicus* (Anfossi & Mosna, 1976) - Schwarzahns: pl. 5, fig. 53.
 1998 *Scopelopsis pliogenicus* (Anfossi & Mosna, 1976) - Nolf, Mañé & Lopez: pl. 3, fig. 11-12.
 2006 *Scopelopsis pliogenicus* (Anfossi & Mosna, 1976) - Girone: pl. 2, fig. 3.
 2017 *Scopelopsis pliogenicus* (Anfossi & Mosna, 1976) - Lin, Brzobohaty, Nolf & Girone: fig. 7 A.

Material: Two specimens from Moncucco Torinese (MGPT-PU 130315, 130435).

Discussion. The genus *Scopelopsis* is currently known from a single species inhabiting the Southern Ocean. *Scopelopsis pliogenicus* is the only species known from the northern hemisphere, documented from the Tortonian to the Calabrian (possibly Ionian; Agiadi et al. 2018) of the Mediterranean.

Unidentifiable myctophid otoliths

Remarks. Like in most fossil otolith assemblages, a number of myctophid otoliths cannot be identified to the species level because of their juvenile nature or inadequate preservation, including a single specimen from Cava Serredi, 24 specimens from Podere Torricella, three specimens from Moncucco Torinese, and five specimens from Ciabot Cagna.

Order **Gadiformes** Goodrich, 1909
 Family Moridae Berg, 1940
 Genus *Physiculus* Kaup, 1858

***Physiculus* sp.**

Fig. 9 A-B

- 2017 *Physiculus* sp. - Colombero et al.: fig. 5.10.
 2018 *Physiculus* sp. - Carnevale et al.: fig. 3 H.
 2019 *Physiculus* sp. - Carnevale et al.: fig. 11k.

Material: A single specimen from Moncucco Torinese, MGPT-PU 130436.

Family Gadidae Rafinesque, 1810
 Genus *Paratrisopterus* Fedotov, 1871

***Paratrisopterus labiatus* (Schubert, 1905)**

Fig. 9 C

- 1980 *Gadiculus labiatus* (Schubert, 1905) - Nolf & Martinell: pl. 3, fig. 18.
 1988 *Gadiculus labiatus* (Schubert, 1905) - Nolf & Cappelletta: pl. 11, fig. 18-21.
 1998 *Gadiculus labiatus* (Schubert, 1905) - Nolf, Mañé & Lopez: pl. 3, fig. 13.
 1999 *Gadiculus labiatus* (Schubert, 1905) - Landini & Sorbini: fig. 2.
 2008 *Gadiculus labiatus* (Schubert, 1905) - Carnevale et al.: fig. 6 G.
 2015 *Gadiculus labiatus* (Schubert, 1905) - Lin, Girone & Nolf: fig. 4.3-4.4.
 2017 *Gadiculus labiatus* (Schubert, 1905) - Lin, Brzobohaty, Nolf & Girone: fig. 8 N.
 2017 *Gadiculus labiatus* (Schubert, 1905) - Colombero et al.: fig. 5.9.
 2018 *Gadiculus labiatus* (Schubert, 1905) - Carnevale et al.: fig. 3 G.
 2019 *Gadiculus labiatus* (Schubert, 1905) - Carnevale et al.: fig. 11j.
 2020 *Paratrisopterus labiatus* (Schubert, 1905) - Schwarzhans, Agiadi & Carnevale: fig. 14 U-W.

Material: Three specimens from Podere Torricella, MGPT-PU 130437.

Discussion. *Paratrisopterus labiatus* is a common and long ranging species known from the Langhian of the Paratethys to the Calabrian (Girone 2006; Agiadi et al. 2018) of the Mediterranean. The genus is known for its tendency to evolve endemic lineages in the Oligocene and Miocene of the North Sea Basin (Schwarzhans 1994, 2010) and the middle to late Miocene of the Paratethys (Schwarzhans et al. 2017). In addition to *P. labiatus* in the Lago-Mare interval, the endemic Paratethyan *P. rumanus* (Weiler, 1943) has been found in the pre-evaporitic Messinian of Skyros, Greece (Schwarzhans et al. 2020).

Order **Trachichthyiformes** Bleeker, 1856
 Family Trachichthyidae Bleeker, 1856

Genus *Hoplostethus* Cuvier, 1829

***Hoplostethus* cf. *lawleyi* Koken, 1891**

Fig. 9 D

- 1891 *Hoplostethus lawleyi* - Koken: pl. 9, fig. 2.
 1978 *Hoplostethus pisanus* Koken, 1891 - Schwarzhans: 103, 145.
 non 1978 *Hoplostethus lawleyi* Koken, 1891 - Schwarzhans: fig. 104 (*Hoplostethus pisanus*).
 1983 *Hoplostethus lawleyi* Koken, 1891 - Nolf & Steurbaut (cum syn.): pl. 6, fig. 4-5.
 2017 *Hoplostethus* cf. *mediterraneus* Cuvier, 1829 - Colombero et al.: fig. 5.12.
 2018 *Hoplostethus* cf. *mediterraneus* Cuvier, 1829 - Carnevale et al.: fig. 3 L.
 2019 *Hoplostethus* cf. *mediterraneus* Cuvier, 1829 - Carnevale et al.: fig. 11h.

Material: A single specimen from Moncucco Torinese, MGPT-PU 130438.

Discussion. At least three different *Hoplostethus* species occurred in the Paratethys and the Mediterranean during the Neogene: *H. praemediteraneus* Schubert, 1905 in the Badenian and Tortonian, *H. lawleyi* Koken, 1891 in the Tortonian and Zanclean, and *H. pisanus* Koken, 1891 in the Zanclean. Schwarzhans (1978) confused the two species occurring in the Pliocene and therefore the well preserved specimen of *H. lawleyi* from Orciano near Pisa is figured herein once again (Fig. 9 E-G). *Hoplostethus lawleyi* differs from *H. pisanus* in having a more elongate shape, sharp pre- and postventral angles with spine-like projections, and an anteriorly reduced dorsal rim. *Hoplostethus pisanus* in contrast is much more compressed, with a higher dorsal rim that is not reduced anteriorly (see figures in Nolf et al., 1998). The single specimen from the Lago-Mare interval is somewhat eroded but shows a relatively elongate shape with a backward shifted dorsal rim that resembles that characteristic of *H. lawleyi* and is therefore tentatively referred to that species.

Family Melamphaidae Gill, 1893
 Genus *Scopelogadus* Vaillant, 1888

***Scopelogadus* sp.**

Fig. 9 H-I

Material: A single specimen from Moncucco Torinese, MGPT-PU 130439.

Discussion. There are four extant species of the bathypelagic genus *Scopelogadus*. Otoliths are known for three of them. They all show an ex-

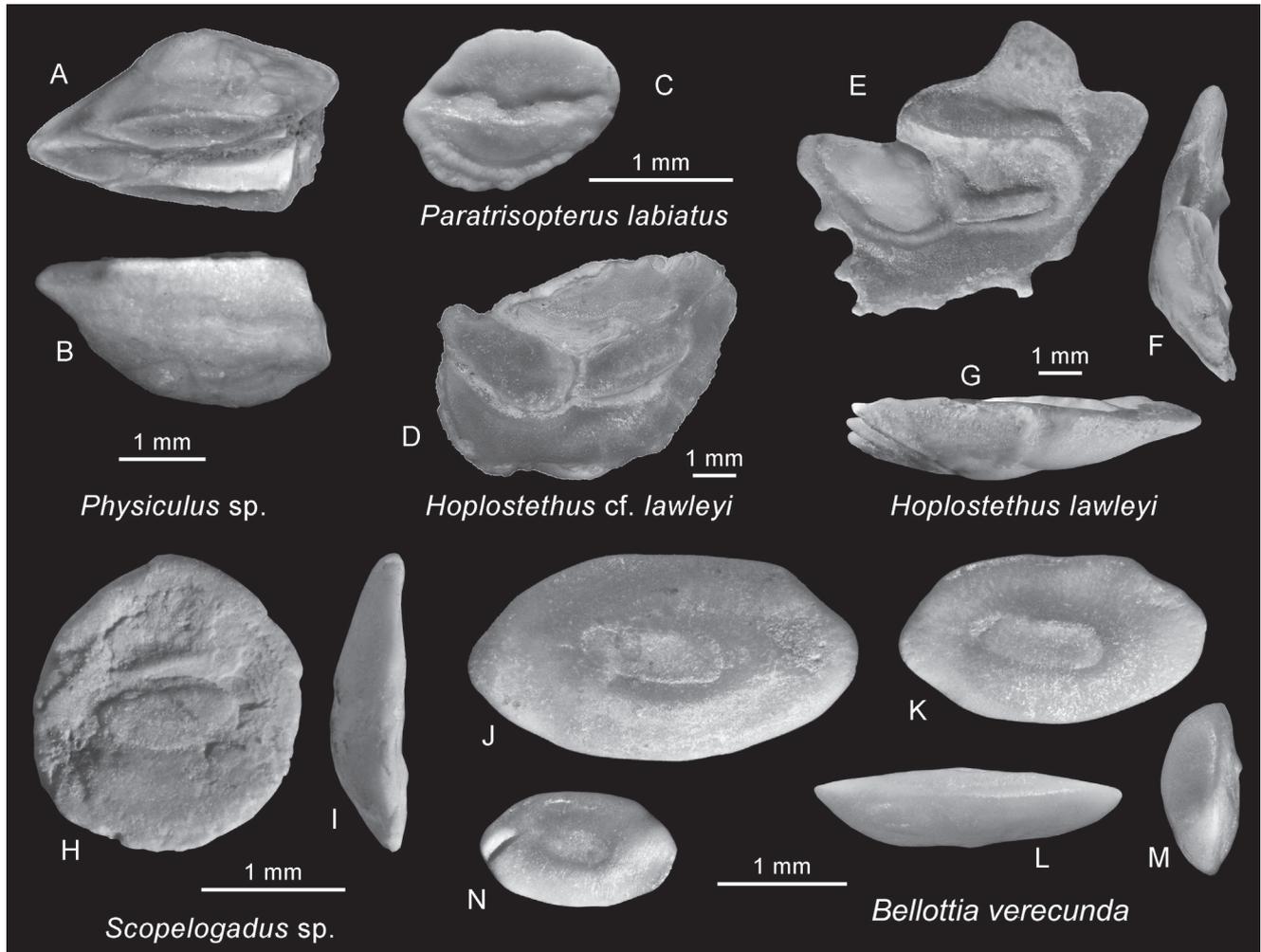


Fig. 9 - Otoliths of the Moridae, Gadidae, Trachichthyidae, Melamphaidae, and Bythitidae. A-B) *Physiculus* sp., MGPT-PU 130436, late Messinian, Lago-Mare phase, Moncucco Torinese (reversed). C) *Paratrisopterus labiatus* (Schubert, 1905), MGPT-PU 130437, late Messinian, Lago-Mare phase, Podere Torricella (reversed). D) *Hoplostethus* cf. *lawleyi* Koken, 1891, MGPT-PU 130438, late Messinian, Lago-Mare phase, Moncucco Torinese. E-G) *Hoplostethus lawleyi* Koken, 1891, Zanclean, Orciano near Pisa, coll. Schwarzahans (reversed). H-I) *Scopelogadus* sp., MGPT-PU 130439, late Messinian, Lago-Mare phase, Moncucco Torinese. J-N) *Bellottia verecunda* n. sp.; J, holotype, MGPT-PU 130419, late Messinian, Lago-Mare phase, Cava Serredi; K-N, paratypes, MGPT-PU 130420, late Messinian, Lago-Mare phase, Podere Torricella (N reversed).

tremely simplified morphology with a nearly round otolith outline, and a simple oval and centrally located sulcus on the flat inner face. Their otolith morphology is so generalized that it appears impossible to reliably distinguish between the species. Consequently, the rare fossil records of *Scopelogadus* otoliths have been left in open nomenclature, for instance in Anfossi & Mosna (1969; pl. 10, fig. 8) from the Tortonian of Piedmont. We have therefore followed the same approach with the unique record from the Lago-Mare interval. It is noteworthy, however, that Deng et al. (2013) have shown that the simplified sulcus pattern of *Scopelogadus* is not reflected by a simplified pattern of the macula acustica as one might expect, but which is nevertheless complex than in other melamphaid genera.

Order **Ophidiiformes** Berg, 1937

Family Bythitidae Gill, 1861

Genus *Bellottia* Giglioli, 1883

***Bellottia verecunda* n. sp.**

Fig. 9 J-N

- 1986 Bythitidarum sp. - Schwarzahans: pl. 6, fig. 69.
- 1988 *Oligopus* sp. - Nolf & Cappetta: pl. 13, fig. 9-10.
- 1994 *Oligopus* sp. - Nolf & Cavallo: pl. 5, fig. 7.
- 1998 *Oligopus* sp. - Nolf, Mañé & Lopez: pl. 5, fig. 9.
- 2006 *Grammonus* sp. - Carnevale, Landini & Sarti: fig. 4b.
- 2008 *Grammonus* sp. - Carnevale et al.: fig. 3 D.
- 2010 Bythitidae indet. 3 - Girone, Nolf & Cavallo: fig. 8.h.
- 2017 Bythitidae indet. - Lin, Brzobohaty, Nolf & Girone: fig. 9 F-G.
- 2017 *Grammonus* sp. - Colombero et al.: fig. 5.11.
- 2018 *Grammonus* sp. - Carnevale et al.: fig. 3 I.

Holotype: Fig. 9 J, MGPT-PU 130419, Cava Serredi, Tuscany, Messinian, Lago-Mare interval, horizon Cs9 (specimen figured by Carnevale et al. 2006b, fig. 4b).

Paratypes: Four specimens: three specimens, MGPT-PU 130420, Podere Torricella, Tuscany, Messinian, Lago-Mare interval; a single specimen, MGPT-PU 130273, Moncuoco Torinese, Piedmont, Messinian, Lago-Mare interval.

Etymology: From *verecundus* (Latin) = modest, humble, referring to the inconspicuous appearance of these otoliths and the fact that the species has not been defined for such a long time.

Diagnosis: Oval otoliths; OL:OH = 1.75-1.85. Inner face nearly flat; outer face convex. Sulcus centrally positioned, rather short, OL:SuL = 2.4-2.9; inclined at 6-8°.

Description. Oval, relatively small otoliths to about 3 mm length (holotype). OL:OH = 1.75-1.85; OH:OT = 1.9-2.2. Anterior and posterior tips rounded, slightly tapering. Dorsal rim gently curved, except for subtle obtuse postdorsal angle followed by straight, inclined section of postdorsal rim; ventral rim regularly and gently curved. All rims smooth.

Inner face nearly flat or slightly convex, but distinctly less than convex outer face. Sulcus short, oval, with single, oval, unstructured sulcus, shallow, positioned at center of inner face, inclined at 6 to 8°; OL:SuL = 2.4-2.9, decreasing with size. Very indistinct dorsal depression and no or very feeble ventral furrow. Outer face convex, smooth.

Discussion. Bythitid otoliths are difficult to allocate at the genus level and to identify at the species level because of their generalized morphological pattern, with an overall ovoid shape and the simplified, oval sulcus characterized by a single undivided colliculum. A number of different otolith morphotypes have been observed in the Tortonian to Zanclean strata of the Mediterranean, but only a few of them have been formally described. Amongst them are *Hepthocara pauper* Schwarzhans, 1978 from the Zanclean, *Grammonus bassolii* Nolf, 1980 from the Tortonian to Zanclean and *Bellottia vonbachtii* (Nolf & Cappetta, 1988) (originally described as “genus Bythitidum” *vonbachtii*) from the Zanclean, and now *Bellottia verecunda* from the Tortonian to Zanclean. In addition, there are at least three further undefined species, one presumably belonging to *Grammonus* (as Bythitidae indet. 1 and 2 in Girone et al. 2010) from the pre-evaporitic Messinian, one probably belonging to *Saccogaster* (as “genus Bythitidum” sp. in Nolf & Cappetta 1988) from the Zanclean, and one which is probably related to *Melodichthys heinzeli* (Lanckneus & Nolf, 1979), the only species with separated ostial and caudal colliculi in this group, described by Lin et al. (2015) from the Tortonian.

Extant otoliths of *Bellottia* (see Nielsen et al. 2009) differ from those of most extant species of *Grammonus* (see Randall & Hughes 2009) in having the inner face relatively flat and certainly distinctly less convex than the outer face (vs inner face more convex than outer face, which is commonly flat or even slightly concave), as well as for a short and inclined sulcus (vs long and not inclined). There are three fossil otolith-based species that may pertain to *Bellottia*: *B. obliqua* (Weiler, 1942) from the early and middle Miocene of the North Sea Basin (see Schwarzhans 2010 for figures; not to be confused with *Saccogaster vanderhochtii* Schwarzhans, 2010 from the same time interval, which has a convex inner face and a nearly flat outer face), and *B. vonbachtii* and *B. verecunda* both from the Zanclean and the latter also from the Tortonian and Messinian of the Mediterranean. *Bellottia verecunda* differs from *B. obliqua* in having more rounded anterior and posterior tips (vs tapering and more pointed) resulting in a slightly more compressed shape (OL:OH = 1.75-1.85 vs 1.80-2.15), and for the lack of the specific ventral furrow seen in *B. obliqua* and its narrow sulcus. *Bellottia verecunda* differs from the time equivalent *B. vonbachtii* in being more elongate (OL:OH = 1.75-1.85 vs 1.60-1.70), thinner (OH:OT = 1.9-2.2 vs <1.9), symmetrically developed anterior and posterior tips (vs pointed anterior and broadly rounded posterior tip), and a more inclined and narrower sulcus (6-8° vs <5°).

Bellottia verecunda appears to be related to the extant *B. apoda* Giglioli, 1883 occurring bathydemersal between 30 and 569 m in the Mediterranean and adjacent eastern Atlantic from which it differs in being more compressed (OL:OH = 1.75-1.85 vs 2.0), and by having a shorter sulcus (OL:SuL = 2.4-2.9 vs 2.2) and lacking a deep dorsal depression. *Bellottia vonbachtii* on the other hand appears to be related to the extant *B. cryptica* Nielsen, Ross & Cohen, 2009 from the Caribbean (see Nielsen et al. 2009 for figures).

Order **Gobiiformes** Thacker, 2009
Family Eleotridae Jordan & Evermann, 1896
Subfamily Butinae Bleeker, 1874
Genus *Bostrychus* Lacépède, 1801

***Bostrychus marsilii* n. sp.**

Fig. 10 A-E

2008 Batrachoididae indet. - Carnevale et al.: fig. 3 E.

2018 Batrachoididae indet. - Carnevale et al.: fig. 3 J.

Holotype: Fig. 10 A-D, MGPT-PU 130421, Cava Serredi, Tuscany, Messinian, Lago-Mare interval, horizon Cs8 (specimen figured by Carnevale et al. 2008b, fig. 3 E).

Paratypes: Two specimens, MGPT-PU 130422, Cava Serredi, Tuscany, Messinian, Lago-Mare interval.

Etymology: Species named after Dr. Stefano Marsili in recognition of his multiple contributions to the interpretation of the structure and diversity of the Neogene Mediterranean ichthyofauna.

Diagnosis: Otolith quadrangular, almost trapezoid in outline with predorsal angle lower than postdorsal angle. OL:OH = 1.25; OH:OT = 3.4-3.6. Preventral projection strong; postdorsal region cut, without projection. Sulcus barbell-shaped, deep, with poorly defined colliculum. OL:SuL = 1.6-1.75; OL2:SuL = 1.3-1.45. Sulcus inclination angle 8-12°. No subcaudal iugum.

Description. Compressed, delicate and thin otoliths up to about 2.6 mm length (holotype). Outline almost trapezoid with the predorsal angle much lower than the postdorsal angle and straight, inclined anterior and posterior rims (70-75° and 65-73° respectively). Preventral projection distinct, long and pointed; no postdorsal projection. All rims irregularly undulating or crenulated except for the relatively smooth ventral one.

Inner face slightly convex with slightly supra-median positioned sulcus. Sulcus barbell-shaped with widened ostium and cauda and contracted collum; widening and contraction particularly strong along ventral sulcus margin. Anterior and posterior tips of sulcus rounded; ostial lobe low and regularly curved. Sulcus long (OL:SuL = 1.6-1.75 and OL2:SuL = 1.3-1.45), inclined at 8 to 12°, deep with poorly defined colliculum and no subcaudal iugum. Dorsal depression wide, relatively shallow; ventral furrow distinct, positioned distinctly far from ventral rim of otolith and not reaching to anterior and posterior tips of sulcus. Outer face flat to slightly convex, indistinctly ornamented.

Discussion. *Bostrychus marsilii* is characterized by a wide and deep sulcus with an indistinct margin of the colliculum, lack of a subcaudal iugum and trapezoid outline of the otolith with a strong preventral projection and a postdorsal rim without projection. It resembles the otoliths of the extant *Bostrychus* species in a number of additional characters, including the ventrally widened cauda, the short ventral furrow positioned far from the ventral rim of the otolith and the relatively long sulcus. Today, *Bostrychus* is known from nine freshwater and brackish water species and some marine

littoral species. Eight species are known from the Indo-West Pacific and one from West Africa (*B. africanus*). Otoliths are known from six species, and three of them are figured herein for comparative purposes: *B. africanus* (Steindachner, 1897) (Fig. 10 I-J), *B. sinensis* Lape re, 1801 (Fig. 10 G), and *B. strigogenys* Nichols, 1937 (Fig. 10 H). They all differ from *B. marsilii* in being more elongate (OL:OH = 1.3-1.4), and by having a vertical to backward inclined posterior rim, sometimes with a small postdorsal projection (vs forward inclined posterior rim and no postdorsal projection) and an angular ostial lobe. Otoliths are known from all the West African eleotrid species, and for the sake of completeness we have also figured herein an otolith of *Batanga lebretonis* (Steindachner, 1870) (Fig. 10 F), which has not previously been figured and which clearly differs from *Bostrychus marsilii* in having a very high-bodied shape. *Bostrychus marsilii* is the first fossil species of the genus and appears to be the last eleotrid in the fossil record of Europe.

Order **Blenniiformes** Bleeker, 1859

Family Clinidae Swainson, 1839

Clinidae indet.

Fig. 10 K-M

2008 *Blennius* sp. - Carnevale et al.: fig. 3 O.

2018 *Blennius* sp. - Carnevale et al.: fig. 3 N.

Material: A single specimen from Cava Serredi, MGPT-PU 130440.

Discussion. The specimen is well preserved and exhibits the typical morphology of the blenniiform otoliths. Blenniiform otoliths are small (slightly less than 1 mm in this case) and their morphological diversity is still poorly understood. The familial allocation of this otolith from Cava Serredi has been inspired by the observation of an articulated clinid skeleton found in coeval rocks from Cyprus (see above). There is a single clinid species known today from the Mediterranean - *Clinitrachus argentatus* (Risso, 1810) - and a fossil clinid with otoliths *in situ* - *Clinitrachoides gratus* (Bannikov, 1989) - reported from the Sarmatian s.s. of the Paratethys (see Lombarte et al. 2006 for figures of the extant species and Bannikov 1989 for the fossil one). Another similar otolith has been referred to as *Blennius* sp. from the Zanclean of Spain by Nolf & Martiniell 1980 (pl. 4, fig. 27).

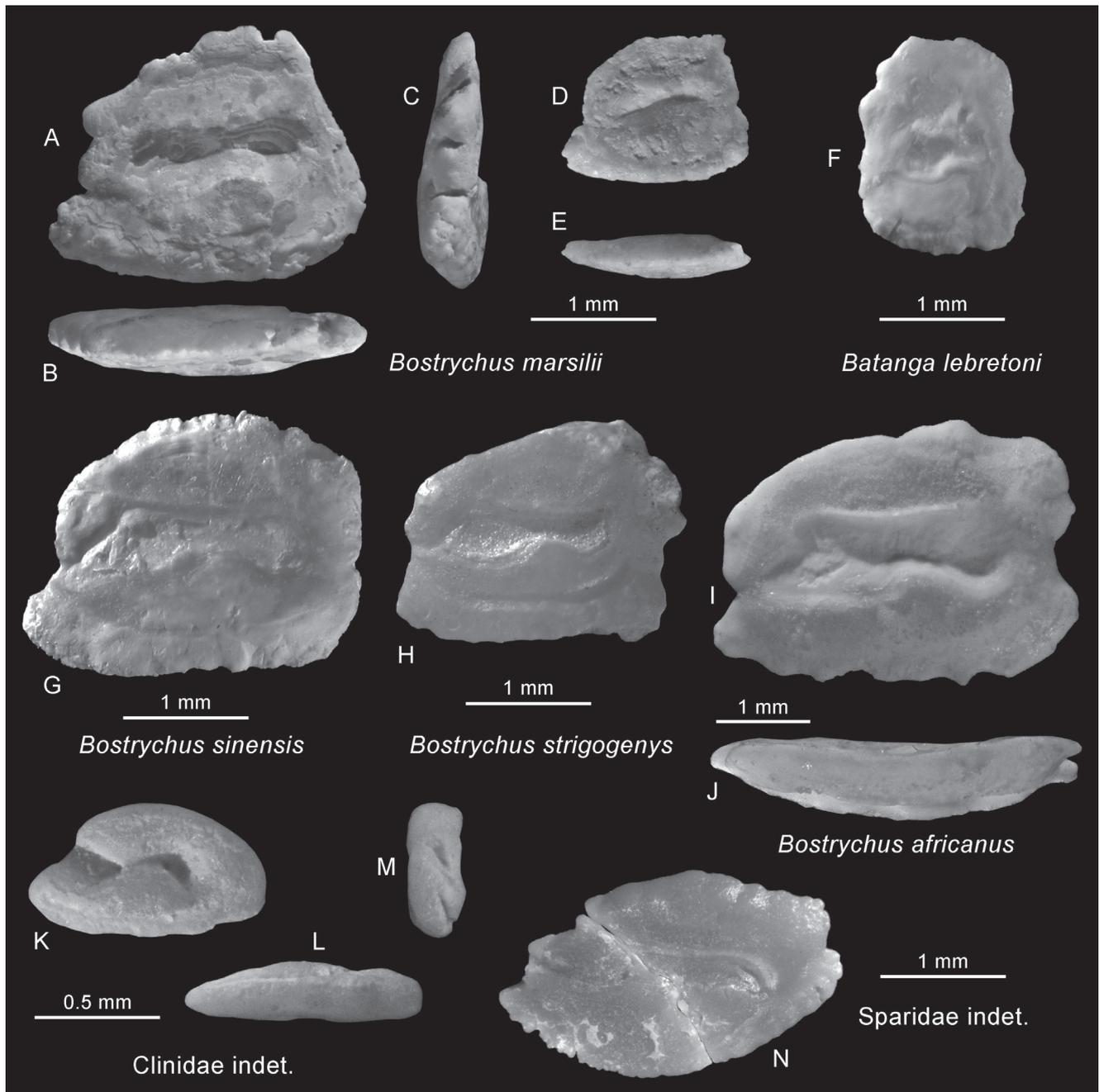


Fig. 10 - Otoliths of the Eleotridae, Clinidae, and Sparidae. A-E) *Bostrychus marsilii* n. sp., late Messinian, Lago-Mare phase, Cava Serredi; A-D, holotype (reversed), MGPT-PU 130421; E, paratype (reversed), MGPT-PU 130422. F) *Batanga lebretonis* (Steindachner, 1870), Recent, BMNH-1908.10.12.9-12, southern Nigeria. G) *Bostrychus sinensis* Lacepède, 1801, Recent, ZMH, China. H) *Bostrychus strigogenys* Nichols, 1937, Recent, WAM 31254-001, 04°26'S, 136°53'E. I-J) *Bostrychus africanus* (Steindachner, 1897), Recent, BMNH-1973.7.18.270 Cameroun, Neme estuary. K-M) Clinidae indet., MGPT-PU 130440, late Messinian, Lago-Mare phase, Cava Serredi (reversed). N) Sparidae indet., MGPT-PU 130441, late Messinian, Lago-Mare phase, Cava Serredi (reversed).

Order **Spariformes** Bleeker, 1876
 Family Sparidae Rafinesque, 1810
 Genus and species indet.

Fig. 10 N

Material: Two specimens from Cava Serredi, MGPT-PU 130441.

Discussion. These poorly preserved otoliths most likely represent an unidentifiable taxon of the family Sparidae. The size of the specimens indicate that they stem from relatively small fishes and the otoliths appear to pertain to immature individuals.

DISCUSSION

On the origin of the marine fishes in the MSC: autochthonous or allochthonous?

In a recent review of the Italian fossil record of the MSC, Carnevale et al. (2019) stated that “a taxonomic and ecologically heterogeneous fish assemblage is known from the first stage of the MSC” based on articulated skeletal remains and concluded that “from an ecological point of view the assemblage is dominated by marine and estuarine taxa”. A variety of marine fish taxa have been reported for the second stage of the MSC, especially from Monte Castellaro (see Sorbini 1988), near Pesaro, central Italy. In his presentation of the Messinian fishes from Monte Castellaro, Sorbini (1988) concluded that the occurrence of fully marine fishes during the first two phases of the MSC “further confirms the existence of normal marine environments during the Messinian event” and that “the debate concerning the total desiccation in the Mediterranean is certainly far from being concluded” (see also Gaudant 1989, 2002). The complete list of marine stenohaline taxa currently known for the three phases of the MSC is included in the present study (Tabs 1-3). In a review of the otoliths of the Gobiidae from the late Miocene and Pliocene of the Mediterranean, Schwarzhans et al. (2020) recognized abundant taxa with Paratethyan affinities in the Lago-Mare interval (MSC phase 3.2), some of which occurred in the Mediterranean already before the MSC. The co-occurrence of otoliths pertaining to fully marine fishes during the MSC phase 3.2 (which are reviewed herein), was interpreted with a broad coastal shallow-water belt with reduced salinity that was occupied by the Paratethyan immigrants, while normal marine fishes, including the mesopelagic lanternfishes, lived offshore. The almost complete lack of bathybenthic elements was interpreted as the results of dysoxic conditions at great depths due to water column stratification.

However, the nature and significance of fish remains of normal marine taxa in the MSC has been interpreted in different ways by other authors. In a recently published discussion about the “controversies and certainties around the terminal phases of the Messinian Salinity Crisis”, Andreetto et al. (2021) argued that the “open marine signature is questionable in the foraminifera, nannofossil, dinocyst, and fish records as well as other biotic groups

such as corals, echinoids and mammals”, which were considered as always reworked, thereby implying that “all marine representatives were reintroduced into the Mediterranean only at the beginning of the Pliocene”. Following this approach, the concept of a “marine model” as proposed by Carnevale et al. (2006a, 2006b, 2008b, 2018) and Grunert et al. (2016) was regarded as unlikely. As far as the fish record is concerned, the occurrence of articulated remains of marine fishes in the first and second phases of the MSC was cursorily mentioned, but most of the discussion was focused on the presumed non-autochthonous origin of the otoliths of marine fishes in the Lago-Mare sediments, particularly of the lanternfishes of the family Myctophidae.

It goes without saying that the presence of articulated skeletal remains of fishes can only be meaningfully explained by autochthonous embedding. This clearly indicates that fully marine fishes lived in the Mediterranean during the first two phases of the MSC. As discussed above, during the third phase, there are only a few articulated skeletons discovered so far. Most of them are from euryhaline estuarine fishes such as *Aphanius crassicaudus* or *Mugil cf. cephalus* but there are also stenohaline marine representatives such as *Spratelloides lemoinei* and a still undescribed member of the exclusively marine blennioid family Clinidae. Admittedly, however, myctophid skeletons have not been formally described from the whole MSC although they are quite common in pre-evaporitic strata (e.g., Arambourg, 1925, 1927; Bedini et al., 1986). Abundant articulated skeletal remains of myctophids, sternoptychids, paralepidids and trichiurids have been described by Sorbini (1988) from Monte Castellaro from sediments that he considered to represent the upper part of the Marnoso-Arenacea Formation predating the MSC, but which according to the stratigraphic model proposed by Manzi et al. (2005) could represent syn-evaporitic euxinic shales. Anyhow, during detailed prospection of the Monte Castellaro section by one of us (GC) in July 2011, myctophid skeletons were also found in levels assigned by Sorbini (1988) to the syn-evaporitic Gessoso-Solfifera Formation (see above for more details) (Fig. 5B).

Conversely to articulated skeletons, there are no otoliths preserved in the sediments of the first two phases of the MSC while many of them have been reported from the Lago-Mare event (MSC

substage 3.2) where there are very few articulated skeletons so far (see above). The Gobiidae are the dominant group represented by otoliths in the Lago-Mare interval, and many of them are of Paratethyan affinities (Schwarzahns et al. 2020). Sciaenids are also locally abundant and, in certain cases, are also indicative of a Paratethyan legacy (Bannikov et al. 2018). However, myctophid and other marine fish otoliths are regularly found as well. Therefore, the main question related to these findings would be whether the myctophid (and other marine fish) otoliths are of autochthonous or allochthonous origin in the Lago-Mare sediments where they were found. In the following section we will discuss the merits and limitations of the various suggested mechanisms for their occurrence in the Lago-Mare sediments. These hypotheses include: 1) autochthonous origin and introduction by piscivore predators who caught them in the open sea and transported their remains into the depositional environment through excreta (Carnevale et al. 2008a, 2018; Grunert et al. 2016); 2) reworking from upper Miocene (or older) deposits (e.g., Caruso et al. 2020, Andreetto et al. 2021); 3) contamination from overlying lower Pliocene deposits (implied as an option in Andreetto et al. 2021); 4) transport by aquatic birds (shown in fig. 11a in Andreetto et al. 2021 without further reference or discussion in respect to the fish fauna).

Autochthonous origin from excreta of marine predators

The underlying assumption of this hypothesis is that the otoliths of oceanic fishes in the Lago-Mare sediments derived from the excreta of piscivorous predators, fishes, cephalopods, or mammals (e.g., squids, tunas, jacks, dolphins, whales) foraging in the open sea that transported bones and otoliths of their preys in shallow water paralic paleobiotopes. The principle mechanism is well-documented and studied in otoliths found in the digestive system and scat of predators and represents a well-established method to identify the diet of predatory fishes (Frost 1924; Clarke et al. 1995; Lin et al. 2020), cetaceans (Fitch & Brownell 1968), seals (Daneri 1996; Yonezaki et al. 2011), bats (Aizpurua et al. 2013), aquatic birds (van Heezik & Seddon 1989; Sabourenkov 1992), turtles (Harrel & Stringer 1997), and squids (Watanabe et al. 2004; Markaida et al. 2008; Pethybridge et al. 2012; Merten et al. 2017). Otoliths are also often found in regurgitation products of aquat-

ic birds (Martini & Reichenbacher 1993; Thompson et al. 1995). Fitch & Brownell (1968) observed a significant dominance of myctophid otoliths in the stomachs of cetaceans. Myctophid otoliths are generally very common in many feeding relicts of a variety of predators (see e.g., Sabourenkov 1992). Otoliths are subject to degradation and ultimately dissolution by the acidic gastric juices in the stomachs of predators before being released (McMahon & Tash 1979; Koelz 1992; Yufera et al. 2012). In the fossil record, however, well-preserved otoliths without substantial evidence of acidic degradation have been found as digestion products of predators in coprolites (Martini 1965; Martini & Reichenbacher 1996; Schwarzahns et al. 2019) and associated with feeding relicts of stomatopod crustaceans (Schwarzahns 2007) or supposed polychaete worms (Schwarzahns et al. 2021). Nevertheless, the exposure to acidic gastric juices may have a taphonomic effect on otolith preservation, thereby representing a potential explanation for the reason why in otoliths of the genus *Diaphus* specimens with eroded ventral denticles prevail in many fossil settings (Brzobohaty & Nolf 2000), or why the delicate and thin otoliths of clupeids are seemingly under-represented in the fossil record when compared to their skeletal record, or why the even thinner and more tiny otoliths of *Cyclothone* have never been found in sediments despite the extreme abundance of these fishes in today's oceans. On the other hand, well-preserved tiny and delicate otoliths of juvenile *Bregmaceros* otoliths are locally abundant (Schwarzahns 2013c) as well as juvenile goby otoliths of less than 0.5 mm length (Schwarzahns 2017). The exposure time to acids in the stomach of the predator and its concentration is pivotal for preservation and recognition of otoliths in the predators releases and appears to vary widely from one species to another and even within the same species and even within a given specimen depending on multiple factors (e.g., da Silva & Neilson 1985; Jobling 1987; Tollit et al. 1997; Radhakrishnan et al. 2010; Yufera et al. 2012). The time of residence of the food in the stomach has been recorded for various fishes (Magnuson 1969) and tunas (e.g., *Katsuwonus pelamis* in Magnuson 1969) were amongst those with the shortest throughput time, which probably enhances otolith preservation. Nolf (1985) and Schwarzahns (2019) suggested that the majority of otoliths found in the fossil record entered the sediments through the excreta of ma-

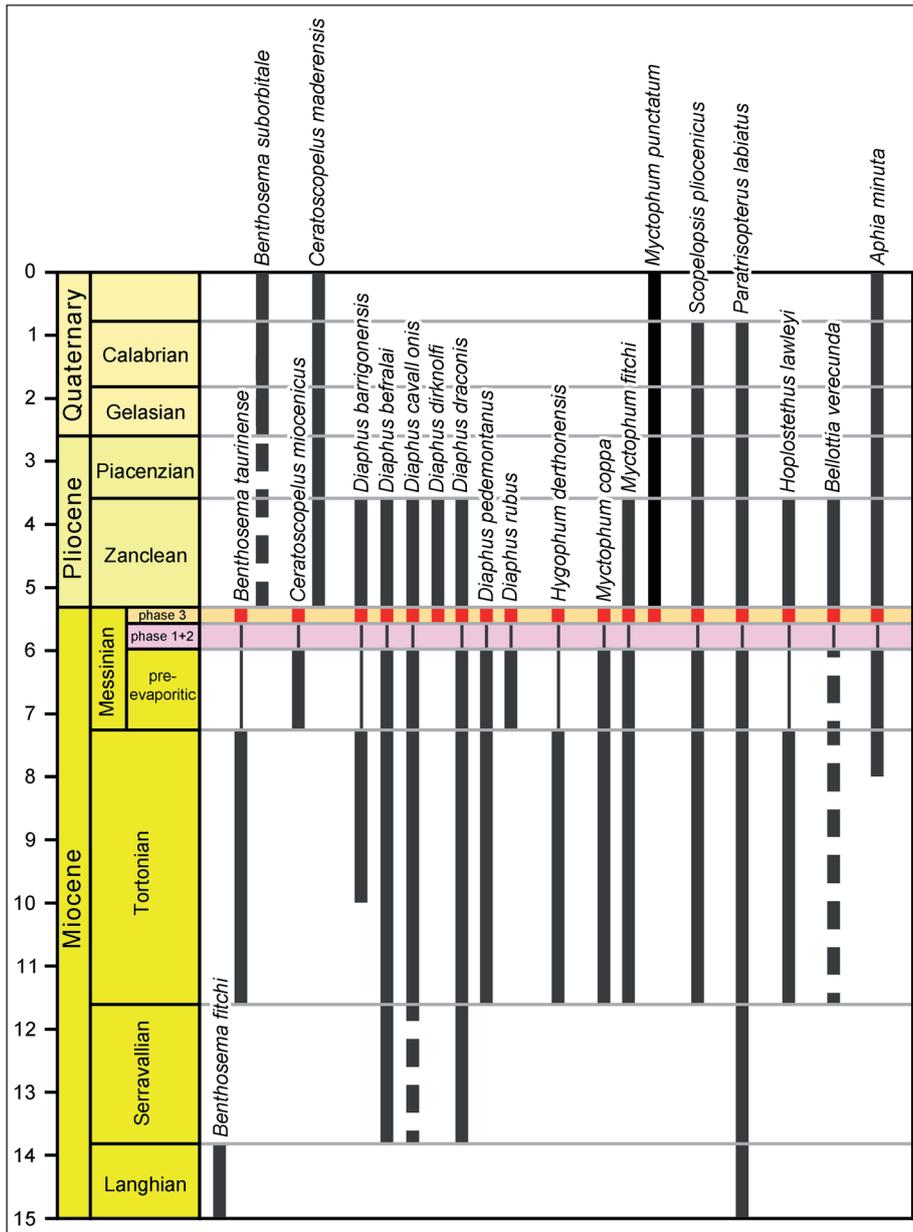


Fig. 11 - Stratigraphic range chart of key marine species in the Lago-Mare interval.

rine predators. Such hypothesis is supported by the predominance of otoliths of small prey fishes with respect to those pertaining to high trophic level predators. However, while the origin of otolith assemblages through the excreta of predatory fishes or marine mammals seems to represent a standard process, the occurrence of mesopelagic otoliths in shallow water sediments necessarily requires regular migration of predators from the open sea into shallow water environments.

Reworking of otoliths from the late Miocene sediments

Reworking from older sediments is a commonly evoked alternative mechanism to justify the

occurrence of otoliths of fully marine fishes (especially the mesopelagic ones) found in the sediments of the Lago-Mare interval (e.g., Caruso et al. 2020; Andreetto et al. 2021). This assumption appears to be in some ways plausible considering that myctophid otoliths are very common in the underlying pelagic Tortonian and pre-evaporitic Messinian sediments (Girone et al. 2010; Lin et al. 2015, 2017). Thanks to the extensive works of Schwarzahns (1986), Nolf & Cappetta (1988), Girone et al. (2010), and Lin et al. (2015, 2017) the stratigraphic range of many mesopelagic and other marine stenohaline fishes in the Mediterranean region is known in great detail as far as concerns the critical time interval from the Tortonian to the Zanclean. The known stratigraphic

distribution of the taxa of marine fishes recognized in the Lago-Mare sediments fits well with their late Miocene-early Pliocene range established for the Mediterranean region (Fig. 11). Most species occur continuously through the late Miocene to the early Pliocene; six species are recorded in the late Miocene but are not known from the early Pliocene and two species (*Diaphus dirkenolfi* and *Myctophum punctatum*) are known from the early Pliocene but have not been found in the Tortonian or pre-evaporitic Messinian. Such a distribution is in conflict with reworking, although it cannot be conclusively excluded that future finds could change the stratigraphic range distributions of species. Overall, reworking of otoliths is not a well-documented phenomenon as in the case of planktonic foraminifers or calcareous nannoplankton. There are reports of otoliths withstanding extended exposure at the sediment surface in condensation settings (Agiadi & Albano 2020), intra-formational re-deposition from shallow to deep environments (Lin et al. 2015; Schwarzhans & Nielsen 2021) or re-deposition in sediment clasts (Schwarzhans 2019), but in none of these cases it is possible to evidence the occurrence of substantial reworking. Otoliths would tend to be eroded quickly during a reworking process, especially the delicate denticles commonly present along the ventral margin of myctophid sagittae. To the best of our knowledge there is no published record of substantial reworking of otoliths like, for example, Cretaceous or Paleogene otoliths found in Miocene sediments, as in the case of planktonic foraminiferans or calcareous nannoplankton (see, e.g., Quilty 2001; Pirkenseer et al. 2010). Conversely, the nearly pristine preservation of delicate morphological structures in several specimens, like the denticles along the ventral margin of myctophid otoliths, would not be expected when reworked. In addition, in all the studied sections, the sediments of the Lago-Mare interval overlay a complete sequence of sediments pertaining to the first two phases of the MSC. Therefore, in order to consider an effective reworking a substantial lateral transport would have to be postulated. Such possibility could be considered as an option for the locality of Moncucco Torinese, which was extensively explored for continental tetrapods, whose remains have been transported into the depositional environment by fluvial discharge (Colombero et al. 2017). While the skeletal remains of mammals or reptiles probably have been accu-

mulated after a more or less prolonged floating of the carcasses, in the case of reworked otoliths, transport along the sediment-water interface would have to be invoked and this would most likely have resulted in the erosion of delicate features. Furthermore, myctophid otoliths are also known from other Lago-Mare sediments, i.e., at Cava Serredi, Capanne di Bronzo, Ciabot Cagna, and Podere Torricella where they are especially abundant. It seems unlikely to us that a reworking mechanism occurred simultaneously during the sedimentation of the Lago-Mare sediments in all these unrelated locations within different and unrelated sedimentary basins and different environments. The $^{87}\text{Sr}/^{86}\text{Sr}$ values obtained from myctophid otoliths from the Lago-Mare interval (Grunert et al. 2016) indicate a near normal marine origin of the fishes. These observations cannot be used for age correlation without calibration with values obtained from myctophid otoliths from the pre-evaporitic Messinian, Tortonian and Zanclean (but see Andretto et al. 2021). Therefore, in our view, there is ample evidence that the reworking hypothesis does not represent a viable option, at least not for the majority of the otoliths of marine fishes found in the Lago-Mare sediments.

Contamination from overlying Zanclean sediments

Andretto et al. (2021) stated (p. 27) that myctophid otoliths were rare and occurred “very close to the base of the Pliocene” hinting at some sort of potential contamination from overlying Zanclean sediments. Indeed, a 30–40 cm thick black muddy layer at the top of the Lago-Mare interval that is intensely burrowed and the burrows filled with sediment of the overlying Zanclean Argille Azzurre Formation has been observed (Trenkwalder et al. 2008, Dela Pierre et al. 2016). This zone has not been sampled for otoliths primarily because it is usually devoid of aragonitic fossils. In our assessment, contamination from overlying Zanclean sediments can be firmly dismissed due to the fact that several myctophid species occurring in the Lago-Mare interval have not been recorded from the well-known Zanclean sediments, as well as by the complete absence of Zanclean deposits overlying the Lago-Mare sediments at Podere Torricella, which is the richest locality in terms of myctophid otoliths. Moreover, myctophid otoliths were found in several levels of the Lago-Mare interval and all

of them have been collected well below the heavily burrowed Mio-Pliocene boundary (see Localities section).

Input from migrating aquatic birds feeding on marine fishes

Passive dispersal via aquatic birds is a well-known dispersal strategy used by freshwater parthenogenetic ostracods as well as by sexually reproducing species with females exhibiting internal brood care (e.g., Whatley 1990, 1992). A similar mechanism has been occasionally discussed in order to explain the arrival and dispersal of Paratethyan ostracods into the Mediterranean during the late Miocene (e.g., Gliozzi et al. 2007). More generally, birds are known to play a prominent role in the biogeographic dispersal of (small) animals and plants (e.g., Figuerola & Green 2002). As far as concerns their potential role in transporting and dispersal of otoliths or other fish remains, this is certainly possible through feces and regurgitates. However, in the case of the Lago-Mare interval an input of otoliths from the Atlantic Ocean via aquatic birds would involve very long distances. The closest East Atlantic location from Moncucco Torinese, for example, would be about 800 km far into the Bay of Biscay. However, Redonian (late Miocene to early Pliocene) otoliths described from the Bretagne (Lanckneus & Nolf 1979) show a completely different faunal composition compared to the marine elements recognized in the Lago-Mare sediments. The nearest extra-Mediterranean fish fauna with a taxonomic composition that would be comparable to that discovered in the Lago Mare interval may be expected to the west of the present Strait of Gibraltar, at least 1500 km away from any of the studied Lago-Mare sections in Italy. Therefore, it is evident that this mechanism does not represent a viable explanation for the occurrence of otoliths of marine stenohaline fishes in the Lago-Mare interval.

In summary, it is clear that there is unambiguous evidence from articulated skeletal remains that marine stenohaline fishes inhabited the Mediterranean during all the three phases of the MSC. Therefore, we consider mandatory that reconstructions of the Mediterranean realms for the MSC interval should consider the existence of normal marine conditions, at least periodically. However, whether such model should also imply the presence of normal

marine open ocean environments largely depends on the interpretation of the occurrence of otoliths of mesopelagic fishes, particularly of the lanternfish family Myctophidae. After a careful scrutiny of the scenarios hypothesized to explain the occurrence of these oceanic fish otoliths, we consider only two of them as potentially viable: 1) entering the sediment through the excreta of pelagic predators that opportunistically forage in offshore marine biotopes or 2) reworking from older, Tortonian or Messinian pre-evaporitic strata known to be rich in myctophid otoliths. As far as concerns the first hypothesis, as discussed above, it is well documented that predatory activities may control the transportation and accumulation of the otoliths in the sediments to a large extent, particularly of the myctophids (Fitch & Brownell 1968; Nolf 1985, 1995). The second scenario is more problematic because of a number of inconsistencies, including the stratigraphic range of certain species that are not known from the Tortonian and pre-evaporitic Messinian, preservation of delicate features that contrasts with the possibility of erosion and re-deposition of the otoliths, widespread occurrence of mesopelagic fish otoliths in different localities of separate paleogeographic and geological contexts and, finally, the almost complete lack of *in situ* reworking due to the presence of underlying MSC sediments in all the studied locations. Moreover, it is important to take into account that very few otoliths of benthopelagic fishes adapted to intermediate depths have been collected and none from deepwater or bathybenthic taxa. In particular, there are no otoliths recorded of the grenadier family Macrouridae, a typical bathybenthic fish clade characterized by thick and highly resistant sagittae, which are also common in the Tortonian and pre-evaporitic Messinian sediments (Lin et al. 2015, 2017). While reworking cannot be excluded in every single case, we consider it extremely unlikely that all of the myctophid otoliths found in the various localities of the Lago-Mare interval have been sourced from a “selective” reworking process, without the involvement of macrourid or other bathybenthic and benthopelagic fishes that were abundant and diverse during the late Miocene and are consistently found associated with myctophid otoliths.

Even though generally rare at all locations during the Lago-Mare interval, myctophid otoliths still vary in abundance from one location to another. Of the six Lago-Mare localities studied for

the otoliths in this review, myctophids have been reported from all the localities except Le Vicenne. The sample size from Le Vicenne was small and produced very few otoliths. It is interpreted to have been positioned in a protected lagoon (Schwarzahns et al. 2020). A single myctophid otolith has been collected at Capanne di Bronzo from a vegetated prodelta environment characterized by a remarkable abundance of a sciaenids of putative Paratethyan affinities (Bannikov et al. 2018) and *Benthophilus gibbosus* (Pana, 1977), a goby also known from the coeval Eastern Paratethys and uncommon at any other studied Lago-Mare location (Schwarzahns et al. 2020). Cava Serredi is one of the richest locations in the MSC in terms of otoliths but has yielded only a single myctophid specimen. This locality is interpreted to represent a sandy prodelta environment in the lowest sampled level, which is the only one studied from the phase 3.1, and from a sheltered prodelta in the phase 3.2 (Schwarzahns et al. 2020). Obviously, Le Vicenne, Capanne di Bronzo and Cava Serredi represent unfavorable localities for investigating myctophid otoliths, chiefly because of the limited access for migrating predators. Ciabot Cagna, Moncucco Torinese and Podere Torricella are all considered to record an open lagoon environment (Carnevale et al. 2008b; Colombero et al. 2017; Schwarzahns et al. 2020) that was likely to be more consistently visited by migratory predators. Podere Torricella is the richest in terms of myctophid otoliths, as documented by the presence of several species. Moncucco Torinese requires some special consideration because it is the only location of the Lago-Mare locations studied for this review which yielded more myctophid than gobiid otoliths. Our explanation for this unexpected outcome is that Moncucco Torinese was positioned in a deep part of an open lagoon, which was dysoxic at the bottom and thus largely prohibitive for demersal fishes. This situation would not hinder organic material of terrestrial origin to have been brought in by periodic fluvial discharge or the occasional visit of pelagic open sea predators.

In our view the most plausible scenario along the most parsimonious line of evidence is to assume the presence of a normal marine offshore environment suitable for mesopelagic fishes during the Lago-Mare interval and dysoxic at certain depths thereby preventing the presence of bathybenthic fishes. In this scenario, myctophid otoliths

and those of other open marine fishes would have been brought in by migrating predators, for instance jacks, tunas or cetaceans, into open lagoonal environments where they released their intestine contents. This hypothesis provides a plausible explanation for the reduced abundance of otoliths compared to normal marine settings. Normal marine demersal fishes are very rare or absent because of dysoxic conditions close to the bottom and in the deep portions of the water column as well as in the deeper parts of lagoons, and in shallow-water environments likely because of the presence of a broad belt of brackish water surrounding the shores.

In summary, the picture emerging from the analysis of the bony fishes skeletal and otolith records of the MSC indicates that marine taxa persisted throughout the entire length of this event. In particular, the skeletal record provides evidence of the presence of a rather diverse assemblage of marine taxa during the first two stages of the MSC, while the otolith record revealed the presence of several normal marine taxa during the third stage, including from mesopelagic fishes. Therefore, we conclude from the rich available set of data that normal marine environments must have existed during the final part of the Miocene epoch.

CONCLUSIONS AND OUTLOOK

The steadily increasing record of articulated skeletons of stenohaline marine teleost fishes in various levels of terminal Messinian sediments is regarded to provide a clear and unambiguous evidence that normal open marine environments must have existed in the Mediterranean during the MSC, at least periodically. The occurrence of myctophid otoliths as well as of those of other stenohaline marine fishes in the Lago-Mare phase is consistent with the presence of normal marine environments in the Mediterranean. We consider alternative explanations not convincing, such as reworking of otoliths, contamination from the overlying Zanclean or import via aquatic birds from outside the Mediterranean. The complete lack of bathybenthic fishes, notably of the family Macrouridae, may be explained by restricted deepwater circulation and dysoxic conditions in the deep basins, including deep lagoons. Nearshore sediments are

dominated by fish remains typical of brackish environments, e.g., cyprinodontids and gobies. The diverse goby assemblage has been recently reviewed (Schwarzahans et al. 2020) and clearly shows consistent Paratethyan affinities.

We realize that the data obtained from analysis of the fish remains discovered in the MSC sediments represent only a small part of the intricate environmental scenario that characterized the Mediterranean during this extraordinary phase of its geological history. However, these data should be necessarily integrated in the production of reliable reconstructions of the Neogene environmental evolution of the *Mare Nostrum*.

Acknowledgements: We wish to thank many colleagues and institutions for their support in respect to extraction of otoliths from extant voucher museum specimens, notably J. Paxton and M. McGrouther (AMS, Sydney), O. Crimmen and J. Maclean (BMNH, London), A. Lombarte (ICM-CSIC, Barcelona), K. Hartel and A. Williston (MCZ, Cambridge, Massachusetts), G. Allen and S. Morrison (WAM, Perth), R. Thiel (ZMH, Hamburg), J. Nielsen and P. Møller (ZMUC, Copenhagen). Ms C. Franz and A. Lord (SMF, Frankfurt/Main) are thanked for their support concerning fossil otoliths from the Senckenberg collection. M. Pavia (MGPT), A. Pistarino (MRSN), M. Sami (MSF), C. Sorbini (Museo di Storia Naturale dell'Università di Pisa, Calci) and R. Zorzin (Museo Civico di Storia Naturale, Verona) are thanked for allowing access to material in their care and logistic support. A number of friends and colleagues contributed to the collection and the preparation of very large amounts of sediment for the extraction of otoliths, including D. Caputo, L. Egisti, P. Giuntelli, M. Ingrassia, S. Marsili, M. Monari, G. Pavia and I. Vujica. L. Pellegrino (Dipartimento di Scienze della Terra, Università degli Studi di Torino, Torino) is thanked for fruitful discussions and advices. Special thanks are also due to R. Brzobohaty (Department of Geological Sciences, Masaryk University, Brno), G. L. Stringer (University of Louisiana at Monroe, Monroe) and an anonymous reviewer for their helpful and valuable suggestions on an earlier draft of this paper. The research of GC was supported by grants (ex-60% 2020 and 2021) from the Università degli Studi di Torino. This is the publication number 361 of the Museo di Geologia e Paleontologia collections at the Università degli Studi di Torino.

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