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Fossil marine fishes and the ‘Lago Mare’ event:

Has the Mediterranean ever transformed into a brackish lake?

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Abstract. According to current hypotheses of Neogene paleoenvironmental evolution of the Mediterranean, during the terminal phase of the Messinian salinity crisis about 5.5 Ma, the entire basin was characterized by the development of non-marine paleobiotopes inhabited by brackish ostracods, mollusks and dinocysts. Such a scenario, commonly known as the ‘Lago Mare’ event, is considered to be the product of the combined effects of humid climate conditions and a remarkably modified drainage pattern with the capture of Paratethyan brackish waters. Some recent studies, however, have suggested that such a scenario represents an oversimplification of the original paleogeographical and paleoenvironmental context. In this paper, we report the ‘Lago Mare’ fish assemblages from seven Italian localities. These fish assemblages are dominated by taxa characterized by a strict marine affinity, thereby suggesting that the Mediterranean was filled by marine waters. Fossil fishes provide unambiguous evidence of the presence of normal marine conditions in the Mediterranean before the Messinian-Zanclean boundary, also demonstrating that a new paleoenvironmental interpretation of the ‘Lago Mare’ event is needed. The fossil record of the ‘Lago Mare’ event and the paleoecological relevance of fish remains for the interpretation of the nature of the Mediterranean water masses are also discussed.

Keywords. Fossil fishes, Messinian salinity crisis, ‘Lago mare’, Mediterranean, paleoenvironment

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1. Introduction

The events related to the Messinian salinity crisis are among the most intriguing and extensively explored of Cenozoic history. The spectacular scenario of a desiccated Mediterranean basin eventually filled by a gigantic catastrophic flood received considerable attention and publicity (see Hsü 1984) and is currently regarded as a well-documented event of Earth history (e.g., Stanley 1989). As a consequence, a remarkable amountof multidisciplinary research has been produced in the last 40 years, stimulating cogent and often conflicting debates extensively discussed in several hundreds of scientific papers (see Roveri et al. 2014).

Extraordinary advancements have been made in our knowledge of Neogene cyclo-, bio-, and magneto-stratigraphy in the Mediterranean region. The refinement of a detailed astronomically tuned time scale has resulted in, among other things in the establishment of the age boundaries for the Messinian stage (Hilgen et al. 2000, Van Couvering et al. 2000), and this has favoured high resolution correlations and paleogeographic reconstructions (see, e.g., Hilgen et al. 1999, Krijgsman 2002, Roveri et al. 2014). More recently, an evolutionary stratigraphic model for the Messinian salinity crisis has been proposed (CIESM 2008), primarily to characterize the various evaporite facies. This model consists of three stages, each defined by peculiar evaporite associations (e.g., Roveri et al. 2009, 2014, Manzi et al. 2012, 2013). Stage 1 (5.97-5.60 Ma) documents the onset of the Messinian salinity crisis and the deposition of primary sulfate evaporites in shallow water marginal basins (Primary Lower Gypsum). During stage 2 (5.60-5.55 Ma), the salinity crisis reached its acme, as evidenced by the massive accumulation of primary halite and clastic gypsum deposits (Resedimented Lower Gypsum). Finally, stage 3 (5.55-5.33 Ma) is characterized by a totally different scenario and is represented by the so-called Upper Evaporites (selenite and cumulate gypsum facies; Upper Gypsum), deposited in shallow water basins in the southern and eastern sectors of the Mediterranean, whereas clastic deposits accumulated in the northern and western Mediterranean sectors. The evaporite-free clastic successions of stage 3 comprise two distinct sequences that originated in response to different climate conditions and precipitation regimes (e.g., Roveri et al. 2008), allowing a subdivision into two sub-stages, 3.1 (5.55-5.42 Ma) and 3.2 (5.42-5.33 Ma). The end of the Messinian salinity crisis appears to be marked by the nearly instantaneous return to fully stable marine conditions in response to the Zanclean deluge (or Zanclean flooding), which was produced by the abrupt collapse of the Gibraltar sill and the development of an enormous rapid (see Garcia-Castellanos et al. 2009) or gigantic waterfall (see McKenzie 1999).

The final phase of the Messinian salinity crisis defined by stage 3 (particularly sub-stage 3.2) approximately corresponds to the so-called ‘Lago Mare’ event. Due to the absence of an efficient biostratigraphic resolution and the highly heterogeneous nature of the sedimentary products, the Mediterranean paleogeographical and paleoenvironmental context during stage 3 is poorly defined (e.g., Roveri and Manzi 2006). In particular, a comprehensive reconstruction of the ‘Lago Mare’ event remains elusive, and its overall setting at the Mediterranean scale has been interpreted based on its peculiar paleontological record, primarily represented by a recurrent assemblage of oligo-mesohaline molluscs and ostracods traditionally considered of Paratethyan affinity (see Orszag-Sperber 2006). Current interpretations postulate that during stage 3 of the Messinian salinity crisis the Mediterranean was characterized by non-marine sedimentation in a series of mysterious interconnected lacustrine-brackish basins. The widespread occurrence of ‘Lago Mare’ deposits appears to be related to the synergistic effect of humid climatic conditions (e.g., Cosentino et al. 2005) and a strongly modified Mediterranean drainage pattern with the capture of the Paratethyan brackish waters through a canyon system located somewhere in the Aegean region (e.g., McCulloch and De Deckker 1989, Orszag-Sperber et al. 2000).

The goal of this paper is to provide a comprehensive overview of the fossil fish remains, mostly otoliths, collected in the ‘Lago Mare’ deposits from seven Italian localities. The data presented and discussed herein provide robust evidence of the presence of normal marine waters during most of stage 3 of the Messinian salinity crisis. The paleontological record of the ‘Lago Mare’ event and the importance of fish remains for the interpretation of the Mediterranean water body during the salinity crisis are discussed.

2. Localities and stratigraphy

In the last decade, extensive exploration of upper Messinian deposits in Italy led to the discovery of at least seven productive localities for fossil fish remains (Fig. 1), Ciabot Cagna, Moncucco Torinese and Verduno in the Tertiary Piedmont Basin, Cava Serredi and Podere Torricella in the Neogene hinterland basins of Tuscany, Capanne di Bronzo in the Marchean Apennine, and, finally, Le Vicenne in the Abruzzo Apennine. Two or more productive fish-bearing layers were recognized in the stratigraphic successions of some of these localities, including Cava Serredi, Moncucco Torinese and Verduno (Carnevale et al. 2006b, 2008a, Colombero et al. 2014, submitted). A minimum quantity of 200 kg of fossiliferous sediments for each productive layer has been sampled and processed for the extraction of fish remains. However, greater amounts of deposits were sampled from some of the productive layers at Cava Serredi and Moncucco Torinese, leading to the sieving of about 3 and 20 tons of sediment, respectively. A brief summary of the stratigraphic features of each of the investigated localities is presented below.

2.1 Tertiary Piedmont Basin

The Tertiary Piedmont Basin is an episutural basin filled with a thick succession of Eocene to Messinian deposits covering the Alps-Apennine junction (Mosca et al. 2010). Moncucco Torinese is located in the Torino Hill, whereas Ciabot Cagna and Verduno pertain to the Langhe domain. In these sectors of the Tertiary Piedmont basin, the Messinian succession is particularly well exposed (e.g., Dela Pierre et al., 2007, 2011, 2015, Natalicchio et al. 2014) and consists of the pre-evaporitic Sant'Agata Fossili marls, followed by the Primary Lower Gypsum unit, which formed during the first stage of the Messinian salinity crisis (between 5.97 and 5.60 Ma; see Roveri et al. 2014). The Valle Versa Chaotic Complex (5.60-5.55 Ma) unconformably overlies the Primary Lower Gypsum unit, and is in turn capped by the fluvio-lacustrine and paralic sediments of the Conglomerati di Cassano Spinola. This latter lithostratigraphic unit primarily consists of clays, silts, sands and gravels comprising both sub-stages 3.1 and 3.2 of the Messinian salinity crisis.

At least four vertebrate-bearing layers pertaining to sub-stage 3.1 (between 5.55 and 5.42 Ma) were recognized at Verduno (Fig. 2), in the so-called Pollenzo section (see Colombero et al. 2014, Dela Pierre et al. 2014). Fish remains (disarticulated bones and otoliths) occur in two of these layers. The vertebrate-bearing layers of Verduno accumulated in a variety of subaqueous paleobiotopes, including a brackish coastal lagoon characterized by thalassogenic waters (Colombero et al. 2014).

The section of Ciabot Cagna is located near the town of Corneliano d'Alba and includes about eight meters of weakly laminated clays referred to the Lago-Mare event based on their paleontological content (Cavallo and Repetto 1988, Cavallo et al. 1993, Caputo 2005, Esu and Popov 2012), particularly the mollusc assemblage (e.g., *Dreissena*, lymnocardiines, *Melanopsis*). According to Cavallo and Repetto (1988), these fossiliferous sediments were deposited in a heterogeneous deltaic-lagoonal paleobiotope.

Six layers containing a diverse assemblage of fish and continental tetrapod remains were recognized in the deposits of sub-stage 3.2 of Moncucco Torinese, stratigraphically constrained between 5.41 and 5.33 Ma (see Alba et al. 2014, Colombero et al. submitted; Fig. 2), thereby being associated to the Lago-Mare event. The fossiliferous deposits of Moncucco Torinese originated in a complex and heterogeneous paralic biotope in which continental vertebrate remains accumulated from a wide spectrum of terrestrial habitats (Colombero et al. submitted).

2.2 Hinterland basins of Tuscany

The Neogene hinterland basin of Tuscany are located on the Tyrrhenian side of the northern Apennines; their origin is related to the tectonic evolution of the Tyrrhenian-Apennine system. Both extensional and compressive tectonic regimes have been proposed to explain the origin of these Neogene sedimentary depressions (e.g., Patacca et al. 1990, Martini and Sagri 1993, Boccaletti and Sani 1998). The sedimentary fills of these basins, also known as ‘neoautochthonous successions’ consist of Tortonian continental deposits covered by Messinian to Pleistocene brackish and marine sediments (see Bossio et al. 1993). The localities discussed herein, Cava Serredi and Podere Torricella, are located on the western side of the Mid-Tuscan Metamorphic ridge, in the Fine and Volterra basins, respectively.

Due to extensive quarrying, a remarkable exposure of Messinian ‘Lago Mare’ deposits occurs at Cava Serredi, one of the classic Italian localities for the study of the Mio-Pliocene boundary (e.g., Bossio et al. 1981). This upper Messinian succession of Cava Serredi consists of two depositional sequences consisting of marls and clays and documenting a variety of paralic depositional environments (see Sarti et al. 1995, Carnevale et al. 2006b). Fish remains have been recovered from ten fossiliferous layers, two of which are exclusively characterized by articulated skeletons (Carnevale et al. 2000, 2006b, 2008a). Based on the general architecture of the succession and the associated ostracod assemblages, the two basal fossiliferous layers possibly pertain to sub-stage 3.1 of the Messinian salinity crisis, whereas the remaining eight can be unquestionably referred to the sub-stage 3.2 (see Sarti 1995, Caputo 2008). Therefore, the age of the fish-bearing horizons can be constrained between 5.45 and 5.33 Ma (see Caputo 2008) (Fig. 2).

Podere Torricella is located in the Spicchiaiola-Pignano area in the south-eastern sector of the Volterra Basin. The 'Lago-Mare' event is recorded in the Volterra Basin by the upper portion of the 'Argille e Gessi del Fiume Era Morta' lithostratigraphic unit (Bossio et al. 1996, 1997). At Podere Torricella, 'Lago-Mare' deposits are well exposed in a small quarry exploited for the extraction of alabastrine gypsum where a fossiliferous layer characterized by abundant molluscs and ostracods associated with exquisitely preserved otoliths occur about 20 m above the uppermost alabastrine layer. Based on stratigraphic and paleontological considerations, the age of the fossiliferous horizon can be constrained between 5.40 and 5.33 Ma (Bossio et al. 1996, 1997, Carnevale et al. 2008a) (Fig. 2).

2.3 Capanne di Bronzo

The locality of Capanne di Bronzo is located in the northern sector of the Montecalvo in Foglia Syncline, Marchean Apennine. The Montecalvo in Foglia Syncline is one of the satellite basins with NW-SE direction running parallel to the chain on the Adriatic side of the Apennines. Upper Messinian deposits are extensively exposed in the core of the Montecalvo in Foglia Syncline, represented by two terrigenous lithostratigraphic units corresponding to the Terreni di Tetto and Colombacci Formation, respectively (Roveri et al. 1998, 2001, Bassetti 2000). The upper Messinian Colombacci Formation records the 'Lago-Mare' event in the Apennine foredeep, and is characterized by a cyclical architecture superimposed to an overall transgressive trend (Bassetti et al. 2004). The Colombacci Formation is well exposed in the Capanne di Bronzo section (Carloni et al. 1974, Borsetti et al. 1975), where a rich fossiliferous horizon occurs about 1 m below the Mio-Pliocene boundary. The fossil assemblage accumulated in a shallow marine environment remarkably influenced by continental outflow (see Bellagamba 1978, Carnevale et al. 2006a) and consists of abundant dreissenids, lymnocardiines, hydrobiids and melanopsids associated with fish otoliths, ostracods (*Cyprideis*, loxoconchids) and benthic foraminiferans (*Ammonia*). According to

Carnevale et al. (2006a), the age of the fossiliferous horizon can be constrained between 5.35 and 5.33 Ma (Fig. 2).

2.4 Le Vicenne

The Le Vicenne basin is located in the Marsica region in the Abruzzo Apennine (e.g., Colacicchi et al. 1967). It is one of the Neogene thrust-top basins developed during the eastward migration of the central Apennine thrust belt (Cipollari et al. 1999). The upper Messinian deposits consist of less than 50 m of conglomerates, sandy marls and fossiliferous clays and siltites. The fossiliferous deposits contain abundant molluscs and ostracods, and relatively uncommon otoliths. According to Cipollari et al. (1999), these deposits are associated with the ‘Lago Mare’ event and originated in a mesohaline coastal lagoon during the second post-evaporitic interval (sub-stage 3.2) of the Messinian salinity crisis (see also Gliozzi 1999) (Fig. 2).

3. Fossil fish remains: diversity and paleoecology

Overall, several thousands of fish specimens were collected from the fossiliferous deposits pertaining to sub-stage 3.2 in six Italian localities, and less abundant material was extracted from the sediments of sub-stage 3.1 at Verduno and from the two basal fossiliferous layers of Cava Serredi. Therefore, limited paleontological information is available for sub-stage 3.1 of the Messinian salinity crisis, whereas the scenario emerging from the ichthyofaunistic data of sub-stage 3.2 is much more heterogeneous and complex. The fossils from this last phase consist in large part of otoliths, but articulated skeletal remains were also collected at Cava Serredi (Carnevale et al. 2000, 2006b, 2008a) (Fig. 3). In fact, not less than 49 taxa belonging to 15 teleostean family-level groups were identified based on material collected from the seven localities documented herein (see Tab. 1). Some of these taxa, particularly some of the gobies (*Gobius* aff. *multipinnatus, Gobius* aff. *niger*, *Gobius* aff. *truncatus, Gobius* sp., "*Gobiidarum*" aff. *weileri*) and lanternfishes (*Diaphus befralai, Diaphus splendidus, Diaphus taaningi*, *Diaphus* sp.), were recognized in two or more localities; however, most of the fish taxa are exclusively known from a single locality (Tab. 1). This scattered distributional pattern seems to suggests that only a limited portion of the original fish diversity has been preserved in the upper Messinian sedimentary record.

Quantitatively, benthic fishes belonging to the Gobiidae and/or Lophiiformes are strikingly abundant in the productive layers of Cava Serredi (see Carnevale et al. 2006b, 2008a), and are also dominant at Le Vicenne. The oceanic lanternfishes of the family Myctophidae are dominant from a quantitative point of view in two localities, Ciabot Cagna and Podere Torricella (see Caputo 2005, Carnevale et al. 2008a), and croackers of the family Sciaenidae are dominant in the localities of Capanne di Bronzo and Moncucco Torinese (Carnevale et al. 2006a, Colombero et al. submitted). Four families - Clupeidae, Gobiidae, Myctophidae and Sciaenidae - comprise 35 taxa, representing more than 70% of the recognized fish diversity. In particular, the families Myctophidae and Gobiidae are represented in nearly all the localities documenting sub-stage 3.2 of the Messinian salinity crisis with 16 and 10 species-level taxa, respectively. Myctophids are highly diverse at Moncucco Torinese, being represented by nine taxa, whereas seven gobiid species-level taxa were reported at Cava Serredi.

In order to properly understand the paleoenvironmental significance of the fish assemblages, each of the identified taxa has been assigned to an ecological guild (Tab. 1). Four guilds have been recognized, in part following the classification proposed by Elliott and Dewailly (1995) and Mathieson et al. (2000). These are diadromous migrants (DM), estuarine residents (ER), marine coastal (MC) and marine oceanic (MO). The guild of diadromous migrants includes those taxa that pass between salt and fresh waters (via brackish biotopes) for feeding and spawning (solely represented by the sprat *Clupeonella* sp.; Fig. 3B). Estuarine residents are those taxa that spend their entire life-cycles in brackish biotopes characterized by thalassogenic waters (croackers, gobies, grey mullets, pupfishes, silversides). Marine coastal taxa include those marine steno- and euryhaline shallow water fish that occupy the inner shelf and appear only irregularly in brackish biotopes (anglerfishes, blennies, croackers, gobies, herrings, mullets, porgies, toadfishes). Finally, the guild of marine oceanic taxa includes the pelagic (primarily mesopelagic) species that inhabit the continental slope or open oceanic waters and only occasionally occur on the continental shelf (cusk-eels, lanternfishes, moras, silvery pouts, silver roughies). Overall, the relative proportion of the represented ecological guilds is rather heterogeneous and exhibits considerable variation between the examined localities, except for the diadromous migrants, which are restricted to Cava Serredi. Estuarine residents and marine coastal taxa are equally abundant at Capanne di Bronzo, Ciabot Cagna and Verduno. Estuarine residents clearly dominate the fish assemblage at Le Vicenne, whereas these are slightly subordinate to marine coastal taxa in the Cava Serredi assemblage. Finally, it is interesting to note that marine oceanic taxa are dominant in the assemblages of Moncucco Torinese and Podere Torricella, representing 71% and 44% of the fish diversity, respectively. Taking into account taxonomic diversity, marine oceanic taxa are clearly dominant, being represented by 38% of the recognized taxa, followed by marine coastal taxa (31%), estuarine residents (29%), and diadromous migrants (2%). Therefore, taxa exhibiting a strict marine affinity represent more than two thirds (69%) of the entire fish diversity (see Fig. 4).

The remarkable diversity of marine taxa, particularly those that are oceanic, is apparently difficult to explain considering that the otolith-bearing deposits originated in a variety of paralic paleobiotopes during stage 3 of the Messinian salinity crisis (Cavallo and Repetto 1988, Cipollari et al. 1999, Carnevale et al. 2006a, 2006b, 2008a, Caputo 2007, Colombero et al. 2014, submitted). Because of their excellent preservation (Fig. 3), with fine and delicate structures clearly recognizable, it is evident that the otoliths belonging to marine taxa are the product of autochthonous embedding, thereby excluding any possibility of reworking from older rocks. The stratigraphic range of the fish taxa recognized in stage 3 deposits spans from the Tortonian or early Messinian to Zanclean (Tab. 2). Overall, the fish assemblage consists of a mix of Late Miocene, Tortonian-Zanclean, and exclusively Zanclean taxa (e.g., Brzobohaty and Nolf 2000, Girone et al. 2010, Lin et al. 2015). In particular, mostof the marine fish taxa (76%) are primarily known from

Zanclean deposits (see Tab. 2), providing additional evidence excluding the possibility of reworking from older rocks.

Marine coastal taxa often represent one of the most diverse groups in paralic biotopes, even if usually represented by a few individuals that scarcely contribute to the standing crop of these settings (e.g., Rebelo 1992, Nordlie 2003, Veiga et al. 2006). As discussed above, most of the marine oceanic fishes recognized in the upper Messinian deposits are mesopelagic. Mesopelagic fishes can be defined as species spending the day at depths between approximately 200 and 1000 meters, and performing diel migrations to reach the upper 200 meters or even the surface during the night (e.g., Gjøsaeter and Kawaguchi 1980). Mesopelagic taxa, particularly lanterfishes of the family Myctophidae, constitute a major part of the biomass in open sea areas (e.g., Ahlstrom 1969, Clarke 1973), representing a significant component in the diet of predatory fishes (tunas, swordfishes, jacks, barracudas, scabbardfishes). The diversity (and abundance) of marine oceanic fishes in paralic settings can be easily explained based on the taphonomic processes that usually resulted in the formation of fossil otolith assemblages. As discussed by Nolf (1985), the predatory activity of large fishes and other vertebrates remarkably contributes to the formation of otolith taphocoenoses. According to Schäfer (1966), the excreta of large predatory fishes foraging in oceanic environments are usually very rich in otoliths, whereas the bones are nearly entirely digested. As a matter of fact, most otoliths enter the sediment through predators (Nolf 2013). Therefore, through the excreta of large predatory fishes, otoliths of mesopelagic taxa are often transported in shallower waters and paralic biotopes, in which predatory fishes periodically occur, attracted by the abundant food and habitat availability (Elliott and Dewailly 1995, Nordlie 2003). Unfortunately, a direct connection with large predatory fishes can be only occasionally established using the fossil record since their otoliths are very thin and delicate and only very occasionally occur in fossil assemblages (Nolf 2013) and the preservation of skeletal remains requires peculiar taphonomic conditions (e.g., Carnevale et al. 2008b).

The migratory activity of predatory fishes and its consequent taphonomic product largely impact on the paleogeographic and physiographic interpretation of the depositional environments. The use of paralic biotopes by means of large predatory fishes moving from oceanic waters is clearly related to the existence of permanently open connections between the open sea and the paralic settings. The presence of a direct connection between the paralic paleobiotopes in which the fossiliferous deposits originated and fully marine waters is also suggested by the co-occurrence of marine coastal taxa and diadromous migrants. Because of their mobility and migratory behaviour, fishes are therefore very useful for large-scale interpretations, providing data about the variety of biotopes contiguous to the depositional environment.

4. Discussion

4.1 Fossil fishes and the 'Lago Mare' conundrum

The fossil record was the primary source of information that supported the emergence of the 'Lago Mare' concept. The benthic assemblages primarily consisting of ostracods and molluscs have been used to postulate a brackish 'Lago Mare' event since the earliest attempts to define the paleoenvironmental context of the Mediterranean at the end of the Messinian (e.g., Ruggieri 1962, Ruggieri and Greco 1965). However, the traditional 'Lago Mare' concept, which hypothesizes a partial refill of a desiccated Mediterranean with fresh- and brackish waters of Paratethyan origin, was developed in the late seventies as a consequence of the extensive geo-paleontological exploration of the Messinian deposits throughout the entire Mediterranean basin (e.g., Cita et al. 1978). The relevance of ostracods and molluscs in the interpretation of the uppermost Messinian paleoenvironments was certainly emphasized by the apparent absence of other kinds of fossils in latest Messinian deposits and their ostensible Paratethyan biogeographic affinity remarkably contributed to the development of the concept. In particular, the ostracod assemblages are regarded as a useful chronostratigraphic tool for the analysis of the deposits of stage 3 of the Messinian salinity crisis (e.g., Cipollari et al. 1999; Grossi et al. 2011), a time interval corresponding to the upper part of the so-called “Non-Distinctive Zone” and “Salinity Crisis interval” of the planktonic foraminifer and calcareous nannofossil biozonations, respectively (e.g., Iaccarino 1985, Raffi et al. 2003). In this context, the absence of marine calcareous plankton communities has been paradigmatically regarded as the actual record of the absence of marine communities and of the existence of non marine conditions in the Mediterranean basin. Moreover, additional paleontological (dinocysts; see Bertini et al. 1995) and geochemical (depleted Sr isotope values; see McCulloch and De Dekker 1989) evidence was used subsequently to consolidate the model. Despite a remarkable number of inconsistencies that emerged in the last three decades, the actual nature of the ‘Lago Mare’ event remains poorly understood and there is still controversy about the environmental dynamics of the Mediterranean basin during the terminal phase of the Messinian salinity crisis.

The integrative analysis of the ecological affinities of the fish taxa unquestionably indicates that the paralic depositional environments in which fossil fish remains accumulated during stage 3 of the Messinian salinity crisis were physically connected with a Mediterranean basin characterized by normal marine conditions. Moreover, the remarkable ecological disparity and taxonomic diversity of the fish assemblages suggest that the Mediterranean marine ecosystems were rather complex during the late Messinian. Finally, the age of the fossiliferous deposits reveal that normal marine waters characterized the Mediterranean for most of sub-stage 3.1 and the entire sub-stage 3.2, thereby implying that the marine refilling of the basin occurred well before the Messinian-Zanclean boundary. In fact, the ecological affinities and taxonomic composition of the ichthyofaunistic assemblage discussed in this study are totally opposite to those expected to be found in ‘Lago Mare’ deposits, which, according to the traditional model should exclusively contain the remains of freshwater and/or brackish fishes.

The picture emerging from the analysis of fossil fish remains is therefore incompatible with the traditional environmental model hypothesized for the ‘Lago Mare’ event, at least as far as concerns the Sr isotope data and the peculiar assemblages of ostracods, molluscs and dinocysts.

Sr^{87}/Sr^{86} values from ‘Lago Mare’ deposits and benthic fossils are usually lower than normal oceanic values estimated from that time interval. However, in the comprehensive evaluation of these isotopic data, it should be taken into account that the contribution of low Sr^{87}/Sr^{86} river waters can be emphasized by the overall physiography of the Mediterranean, especially in the case of severely restricted connections with the Atlantic Ocean. Consequently, the ‘Lago Mare’ low Sr^{87}/Sr^{86} values may be linked to the late Messinian humid climate conditions and the remarkably increased continental runoff (see Flecker et al. 2002, Topper et al. 2011). Moreover, it is interesting to note that the late Messinian Sr^{87}/Sr^{86} values from Paratethyan waters are largely unknown and the presence and possible location of one or more potential Mediterranean-Paratethys gateways are still debated (e.g., Vasiliev et al. 2010, Flecker et al. 2015, Suc et al. 2015).

The presence of marine coastal and oceanic fishes indicates that the brackish ostracods and molluscs traditionally regarded as stratigraphic and paleoenvironmental markers of the ‘Lago Mare’ event likely represent local indicators of marginal paleobiotopes. As discussed above, because of their mobility, marine fishes (or their remains) can occur with typical freshwater orbrackish organisms (and their remains), with relevant implications for the interpretation of the environmental conditions of the areas surrounding those documented by the resident biota. The typical ‘Lago Mare’ ostracods and molluscs primarily occur in deposits accumulated in satellite or marginal basins; during stage 3 of the Messinian salinity crisis these kinds of basins became widespread in the Peri-Mediterranean area, in response to one of the stronger phases of Neogene tectonic deformation, probably related to a major reorganization of the African-Eurasian plate boundary zone (see Meulenkamp and Sissingh 2003). In addition, according to Riding et al. (1998), the remains of ‘Lago Mare’ ostracods and molluscs that occasionally occur in only a few of the deep-sea sites drilled are probably reworked from marginal basins.

The Paratethyan affinity of the ‘Lago Mare’ communities has been traditionally considered as the main evidence of the possible presence of a large brackish lake system comparable to the modern Caspian Sea (e.g., Stoica et al. 2016). The biogeographic affinity of the ‘Lago Mare’ molluscs has been recently reconsidered and nearly all the known taxa actually represent Mediterranean endemics (Esu and Popov 2012, Harzhauser et al. 2015). Dinocysts of Paratethyan affinity likely occurred in the Mediterranean before stage 3 of the Messinian salinity crisis, and certainly preceded the onset of the ‘Lago Mare’ event (e.g., Popescu et al. 2009). As far as the ‘Lago Mare’ ostracods are concerned, the Paratethyan affinity of most of them is undeniable (see, e.g., Gliozzi et al. 2007, Stoica et al. 2016). However, their migration in the Mediterranean possibly preceded stage 3 of the Messinian salinity crisis. For example, typical ‘Lago Mare’ ostracods of Paratethyan affinity (e.g., *Amnicythere propinqua*, *Euxinocythere praebaquana*, *Loxocauda limata*, *Loxoconcha eichwaldi*, *Loxocorniculina djafarovi*, *Zalanyiella venusta*) have been recorded in deposits belonging to stage 1 of the Messinian salinity crisis in Tuscany (Cava Marmolaio; Caponi 2008), where a complex and intricate series of marginal basins and paralic biotopes was present during most of the Late Miocene. As documented by Gliozzi et al. (2007), a diverse contingent of Paratethyan ostracods occurred in the Mediterranean at least since the late Serravallian (see also Ligios et al. 2012). However, only during sub-stage 3.2 was there widespread development of marginal and satellite basins throughout the Peri-Mediterranean, and the humid climate phase (see Griffin 2002) created the conditions for the rapid diffusion and the dramatic demographic explosion of the typical ‘Lago Mare’ ostracod taxa.

Summarizing, the typical ‘Lago Mare’ benthic assemblages, particularly the ostracods, should not be considered alone as valuable indicators of paleoenvironmental conditions at Mediterranean scale for stage 3 of the Messinian salinity crisis and, consequently, they cannot be considered as useful stratigraphic markers. The biostratigraphic ineffectiveness of ‘Lago Mare’ ostracods is evidenced by their diachronous appearance throughout the Mediterranean (see, e.g., Carbonnel 1978), possibly in response to the presence of suitable conditions with the development of marginal or satellite basins.

4.2 Epilogue - Has the Mediterranean ever transformed into a brackish lake?

As extensively discussed above, fossil fish remains provide unambiguous evidence that the re-establishment of normal marine conditions in the Mediterranean occurred before the Messinian-Zanclean boundary, also indicatingthat a new paleoenvironmental interpretation of the ‘Lago Mare’ event is needed. The hypothesis of episodic intra-Messinian marine reflooding has been repeatedly proposed in several studies (e.g., Butler et al. 1995, Bertini et al. 1998, Riding et al. 1998, 1999, Pedley and Maniscalco 1999, Griffin 2002, Aguirre and Sánchez-Almazo 2004, Braga et al. 2006, Mezger 2012, Do Couto et al. 2014, Popescu et al. 2015) and the sedimentary record of the ‘Lago Mare’ event is relatively rich in evidence of at least episodic marine influxes during the late Messinian (e.g., Iaccarino et al. 1999, Rouchy et al. 2001, Crescenti et al. 2002, Clauzon et al. 2005, Orszag-Sperber 2006, Zecchin et al. 2013a, b). Nevertheless, the possibility of a reflooding during stage 3 of the Messinian sality crisis has been substantially rejected, as the proposed evidence has been considered inadequate (e.g., Fortuin et al. 2000, Fortuin and Krijgsman 2003). Fish remains clearly indicate that diverse and heterogeneous marine biotic communities were present in the latest Messinian, suggesting that the Mediterranean never transformed into a brackish lake system. Such a scenario is consistent with that proposed by van der Laan et al. (2006) who demonstrated that the ‘Lago Mare’ interval coincided with a major glacio-eustatic sea level rise (se also Miller et al. 2005, Roveri et al. 2008). The results presented herein are also in good agreement with the conclusions of Keogh and Butler (1999) who proposed that the base level of the Mediterranean was within the range of the world’s oceans, even if the water masses probably had a peculiar but internally homogenous Sr isotope composition.

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Figure Captions

Fig. 1. Geographic location of the fossiliferous localities in Italy. 1 = Verduno; 2 = Ciabot Cagna; 3 = Moncucco Torinese; 4 = Cava Serredi; 5 = Podere Torricella; 6 = Capanne di Bronzo; 7 = Le Vicenne.

Fig. 2. Messinian chronostratigraphy with Messinian salinity crisis events in the Mediterranean (modified from Manzi et al. 2013) showing the age distribution of the fossiliferous localities. See text for a detailed explanation. PLG = Primary Lower Gypsum; RLG = Resedimented Lower Gypsum; UG, Upper Gypsum.

Fig. 3. Selected fossil fish remains from the upper Messinian deposits of Italy. A, *Mugil* cf. *cephalus*, Cava Serredi, scale bar 10 mm; B, *Clupeonella* sp., Cava Serredi, scale bar 1 mm; C, *Diaphus befralai*, Cava Serredi, scale bar 1 mm; D, *Diaphus splendidus*, Podere Torricella, scale bar 1 mm; E, *Myctophum fitchi*, Podere Torricella, scale bar 1 mm; F, *Diaphus* aff. *rubus*, Moncucco Torinese, scale bar 1 mm; G, *Gadiculus labiatus*, Podere Torricella, scale bar 1 mm; H, *Physiculus* sp., Moncucco Torinese, scale bar 1 mm; I, *Grammonus* sp., Cava Serredi, scale bar 1 mm; J, Batrachoididae indet., Cava Serredi, scale bar 1 mm; K, Lophiiformes indet., Cava Serredi, scale bar 1 mm; L, *Hoplostethus* cf. *mediterraneus*, Moncucco Torinese, scale bar 1 mm; M, *Atherina* sp., Cava Serredi, scale bar 1 mm; N, *Blennius* sp., Cava Serredi, scale bar 1 mm; O, *Aphia minuta*, Podere Torricella, scale bar 1 mm; P, *Sciaenidarum* sp. nov., Capanne di Bronzo, scale bar 1 mm; Q, *Argyrosomus* sp.,

Moncucco Torinese, scale bar 1 mm; R, “*Trewasciaena*” sp., Moncucco Torinese, scale bar 1 mm.

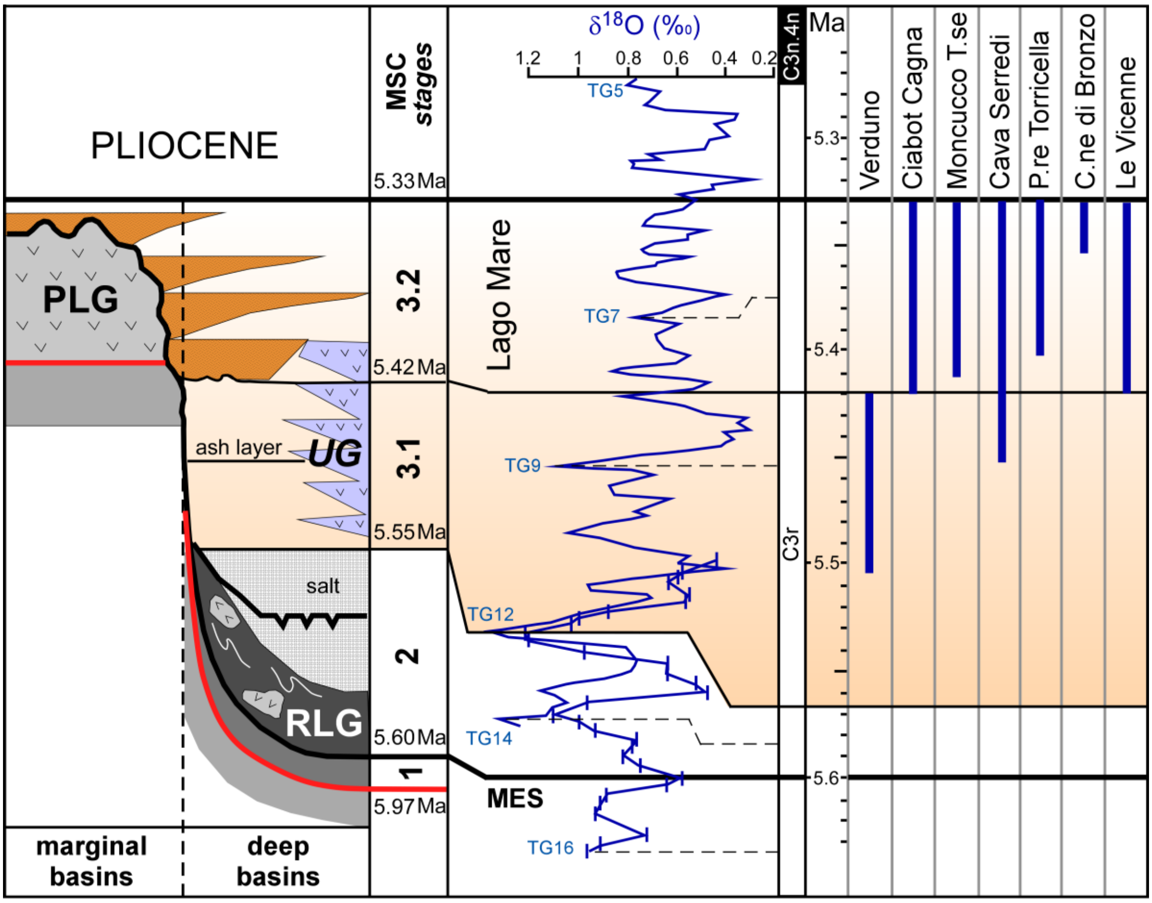
Fig. 4. Schematic paleoenvironmental distribution of the fish ecological guilds recognized in the 'Lago Mare' deposits of Italy.

Table captions

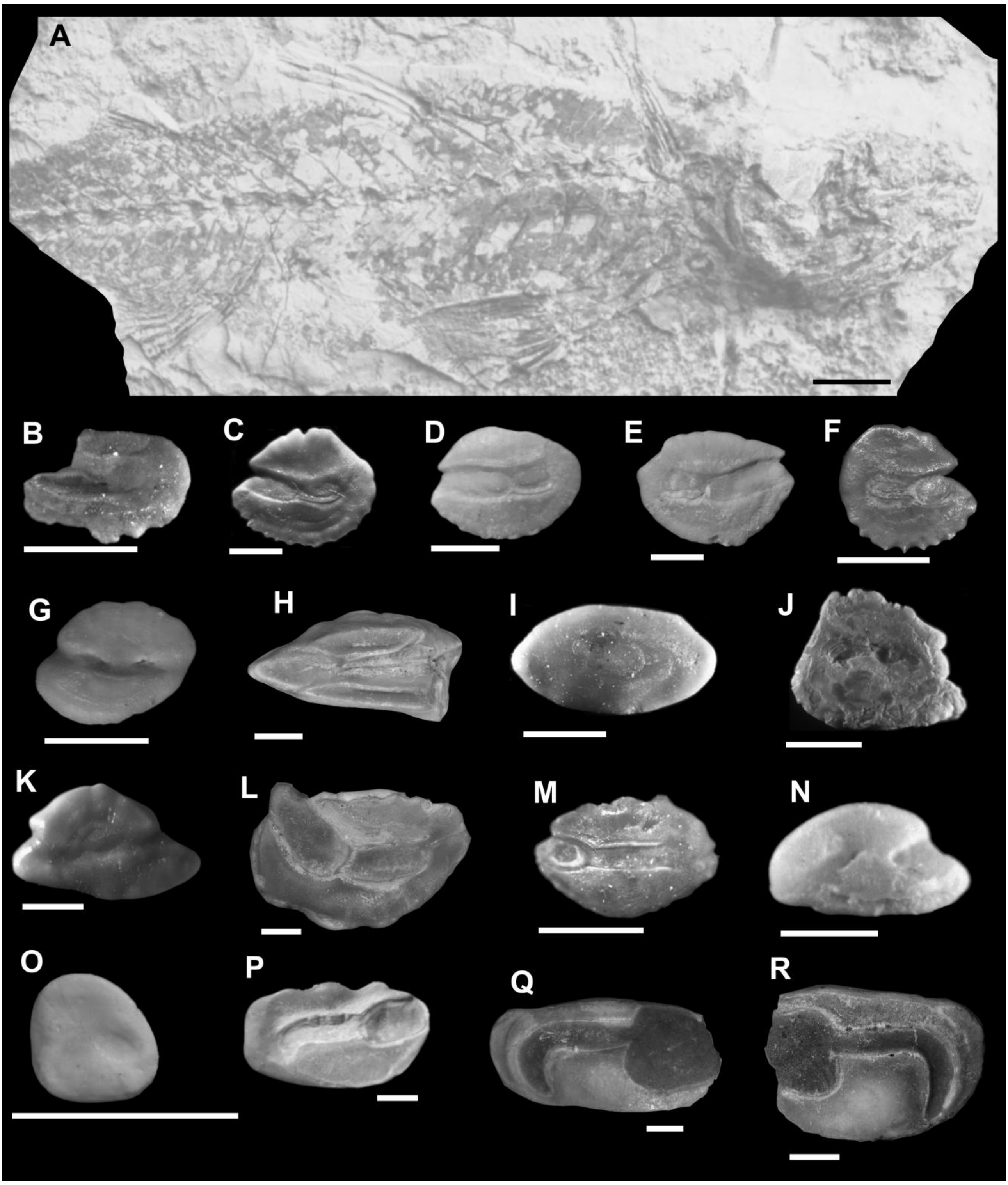
Tab. 1. The Lago Mare fishes of the Mediterranean: list of taxa, ecological guilds and distribution. D = diadromous migrant; E = estuarine; MC = marine coastal; MO = marine oceanic.

Tab. 2. Stratigraphic range of 'Lago Mare' fish taxa in the Mediterranean.

Carnevale et al.
Fig. 1



Carnevale et al., FIG. 2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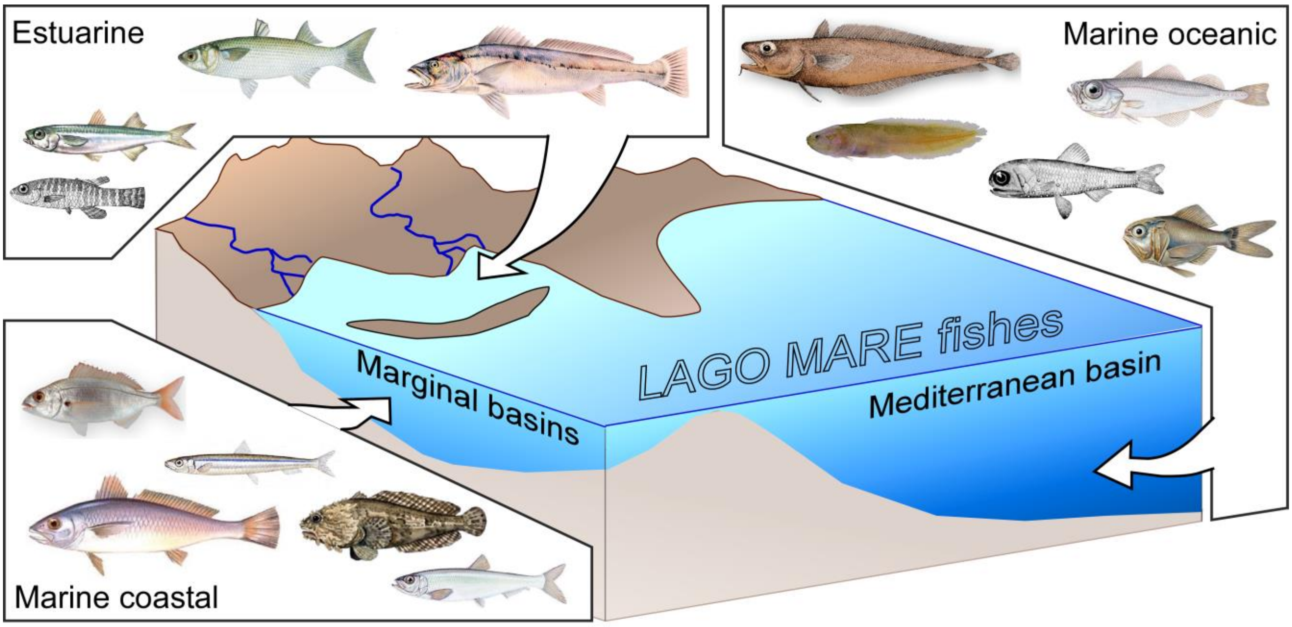

Carnevale et al., FIG. 3

Family	**Taxon**	**Ecology**	Cava Serredi	Capanne di Bronzo	Ciabot Cagna	Verduno	Podere Torricella	Moncucco Torinese	Le Vicenne
Clupeidae	Clupeidae indet.	MC					x		x
	Clupeonella sp.	D	x						
	Spratelloides gracilis	MC	x						
	Sprattus sp.	MC	x						
Myctophidae	*Benthosema fitchi*	MO					x		
	Benthosema aff. suborbitale	MO						x	
	Bolinichthys italicus	MO						x	
	Ceratoscopelus sp.	MO			x				
	Diaphus befralai	MO	x					x	
	Diaphus cavallonis	MO					x		
	Diaphus pedemontanus	MO					x		
	Diaphus aff. *pedemontanus*	MO						x	
	Diaphus aff. *rubus*	MO						x	
	Diaphus splendidus	MO					x	x	
	Diaphus taaningi	MO					x	x	
	Diaphus sp.	MO		x	x				
	Hygophum aff. *derthonensis*	MO						x	
	Hygophum cf. *hygomi*	MO			x				
	Lampadena gracile	MO					x		
	Myctophum coppa	MO						x	
Trachichthyidae	*Hoplostethus* cf. *mediterraneus*	MO						x	
Bythitidae	*Grammonus* sp.	MC	x				x	x	
Batrachoididae	Batrachoididae indet.	MC	x						
Lophiiformes	Lophiiformes indet.	MC	x			x	x		
Gadidae	*Gadiculus labiatus*	MO					x	x	
Moridae	*Physiculus* sp.	MO						x	
Mugilidae	*Liza* sp.	MC	x						
	Mugil cf. *cephalus*	E	x						
	Mugil sp.	E	x						
Atherinidae	*Atherina* sp.	E	x				x		
Cyprinodontidae	*Aphanius crassicaudus*	E	x			x			
Sparidae	*Pagellus* sp.	MC	x						
	Sparidae indet.	MC	x						
Sciaenidae	*Argyrosomus* sp.	MC						x	
	Atractoscion sp.	E	x						
	"Trewasciaena" sp.	E						x	
	Umbrina sp.	MC	x	x					
	Sciaenidarum sp. nov.	E		x				x	
Blenniidae	*Blennius* sp.	MC	x						
Gobiidae	*Aphia minuta*	MC					x		
	Gobius aff. *multipinnatus*	E	x		x		x		
	Gobius aff. *niger*	E	x				x		
	Gobius aff. *paganellus*	E	x						
	Gobius aff. *truncatus*	E		x			x		x
	Gobius sp.	E	x	x	x		x		x
	Lesuerigobius sp.	E						x	x
	Zosterissessor aff. *ophiocephalus*	E	x		x				
	"Gobiidarum" aff. *weileri*	MC	x	x					
	Gobiidae indet.	MC	x	x	x				

Table 1.

TAXON	Tortonian	Messinian			Zanclean
		Pre-MSC	MSC stages 1+2	MSC stage 3	
Spratelloides gracilis	■	■	■	■	■
Benthosema fitchi	■			■	■
Benthosema suborbitale				■	■
Bolinichthys italicus	■	■		■	
Diaphus befralai	■	■		■	
Diaphus cavallonis	■	■		■	■
Diaphus pedemontanus	■	■		■	■
Diaphus rubus		■		■	
Diaphus splendidus	■	■		■	■
Diaphus taaningi	■	■		■	■
Hygophum derthonensis	■			■	
Hygophum hygomii	■	■		■	■
Lampadena gracile				■	■
Myctophum coppa		■		■	
Hoplostethus mediterraneus				■	■
Gadiculus labiatus	■	■		■	■
Mugil cephalus				■	■
Aphanius crassicaudus		■	■	■	
Aphia minuta		■		■	■
Gobius multipinnatus				■	■
Gobius niger				■	■
Gobius paganellus				■	■
Gobius truncatus		■		■	■
Zosterissessor ophiocephalus				■	■
"Gobiidarum" *weileri*				■	■

Table 2.