CrossMark

Connectivity controls on the late Miocene eastern Mediterranean fish fauna

Konstantina Agiadi[1] · Assimina Antonarakou[1] · George Kontakiotis[1] ·
Nefeli Kafousia[1] · Pierre Moissette[1,2] · Jean-Jacques Cornée[3] ·
Emmanouil Manoutsoglou[4] · Vasileios Karakitsios[1]

Abstract Environmental change significantly affects the production of fish resources and their dependent societies. The paleontological record offers unique insight into the effects of long-term paleoenvironmental variability on the fish species' distributions and abundances. In the present study, we investigate the late Miocene (7.5–6.5 Ma) fish assemblages of the Potamida section in western Crete (eastern Mediterranean). The determined fish taxa are examined in a paleobiogeographic context, with regard to their geographic and stratigraphic distribution from the early Miocene (~13 Ma) through today. In addition, present-day ecological data are used to reconstruct the paleoenvironmental conditions in the study area. Planktonic foraminifer biostratigraphy significantly improves the earlier dating of the studied sequence. The late Miocene fish fauna of Potamida includes 35 taxa (seven in open nomenclature) from 13 teleost families. The eastern Mediterranean biostratigraphic and geographic distribution of 32 taxa is significantly expanded into the Tortonian, whereas 13 species are recorded for the first time from the Messinian. Four stages are distinguished in the area's paleoenvironmental evolution. (1) The Potamida area was an open marine environment with depths exceeding 150 m between ~7.5–7.45 Ma. (2) Between 7.45–7.36 Ma, the results suggest depths between 300–400 m. (3) The depositional depth increases between 7.36–7.28 Ma to 400–550 m. (4) Later on, approximately between 6.8–6.6 Ma, the depth is again estimated around 100–150 m.

✉ Konstantina Agiadi
kagiadi@geol.uoa.gr

1 Department of Historical Geology and Paleontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Panepistimioupolis, 15784 Athens, Greece

2 Univ Lyon, Université Lyon 1, Ens de Lyon, CNRS, UMR 5276, LGL-TPE, 69622 Villeurbanne, France

3 UMR CNRS 5243, Géosciences Montpellier, Université Montpellier 2, CC 060, Pl. Eugène Bataillon, 34095 Montpellier Cedex 05, France

4 Research Unit of Geology, School of Mineral Resources Engineering, Technical University of Crete, University Campus, 73100 Chania, Greece

Introduction

The Mediterranean fish fauna in the geological past went through a series of transformations, shaped by connectivity and climate change. The Eocene fauna was dominated by typical tropical–subtropical species (Girone and Nolf 2009; Brzobohaty and Nolf 2011), reflecting its connection to both the Atlantic and the Indian Ocean, the latter lost after the middle Miocene (Karami et al. 2011). As the Mediterranean basin was gradually formed, the fish assemblages, especially their pelagic component, had to conform to more confined conditions, losing their oceanic character. This gradual process already manifested itself during the Oligocene (Nolf and Steurbaut 2004; Nolf and Girone 2008). The Tortonian fish fauna comprised a strong deepwater and a rather diverse neritic element (Lin et al. 2015). Starting from the early Messinian (7.251 Ma), however, the gradual restriction of the marine connections to the Atlantic Ocean led to the almost complete desiccation of the Mediterranean

Fig. 1 Map of the modern peri-Mediterranean area showing the location of the Potamida section

basin, an event known as the Messinian Salinity Crisis (5.97–5.33 Ma; MSC; Selli 1954; Hilgen et al. 2007; Drinia et al. 2007; Roveri et al. 2014). Following the end of the MSC and the reestablishment of normal marine conditions throughout the basin, at the beginning of the Pliocene (Garcia-Castellanos et al. 2009), Messinian relict species, as well as tropical–subtropical Atlantic fish species colonized the Mediterranean Sea (Nolf and Martinell 1980; Schwarzhans 1986; Nolf and Girone 2006; Girone 2007; Agiadi et al. 2013). Interestingly, most of the early Messinian fishes that inhabited the basin after the MSC were typical neritic taxa, which are also found in the Mediterranean Sea today. Atlantic deepwater species entered the basin as well, but most of them have departed today (Girone et al. 2006). The early middle Pleistocene teleostean fauna was still more oceanic than the present-day one (Girone et al. 2006). At present, the Mediterranean basin is inhabited by cosmopolitan or Atlantic species, as well as a few endemic neritic benthic-benthopelagic fishes. In fact, the MSC, in combination with the oligotrophy of the basin, may be considered the main reasons for the impoverishment of the present-day Mediterranean deepwater fish fauna (Kidd et al. 1975; D'Onghia et al. 2004). On the other hand, the local water circulation modes and nutrient availability, under a constantly changing Cenozoic climatic regime, undoubtedly determined the neritic fauna's composition and diversity (Agiadi et al. 2011).

There are only a few studies on the western Mediterranean Tortonian (Nolf and Steurbaut 1983; Robba 1970; Gaudant et al. 2007; Lin et al. 2015) and Messinian fish faunas (Carnevale et al. 2006, 2008; Caputo et al. 2009; Girone et al. 2010). References on the Miocene distribution

of fish in the eastern Mediterranean are extremely limited (Gaudant 2004, 2014; Gaudant et al. 1997, 2005, 2006; Schwarzhans 2014; Karakitsios et al. 2016) and most of them focus on skeletal material. In the present study, the fossil fish otoliths found in the late Miocene sediments of Potamida (western Crete) are identified and described. The determined fish taxa are examined in a paleobiogeographic context, with regard to their geographic and stratigraphic distribution from the early Miocene through today. In addition, present-day ecological data are used to reconstruct the paleoenvironmental conditions in the study area.

Geological setting

Crete took form during the late Miocene through the N–S/E–W extensional deformation of the south Aegean, as horsts interrupted by grabens, which constituted the late Miocene-Pleistocene sedimentary basins (Figs. 1 and 2; van Hinsbergen and Meulenkamp 2006). The alpine substratum includes the metamorphic Plattenkalk and Phyllites-Quarzites units overlain by the Tripolis and Pindos-Ethia sedimentary rocks and other minor units (Zachariasse et al. 2011). Meulenkamp et al. (1979) separated the Neogene deposits of Crete into six lithostratigraphic groups: the Prina Group, the Tefelion Group, the Vrysses Group, the Hellenikon Group, the Finikia Group, and the Aghia Galini Group.

The Potamida section, which is the focus of the present study, is located in western Crete, SW of the Chania city, and NE of the homonymous village (Fig. 2). The Potamida sediments are placed within the Tefelion Group, and they were first extensively studied by Drooger et al.
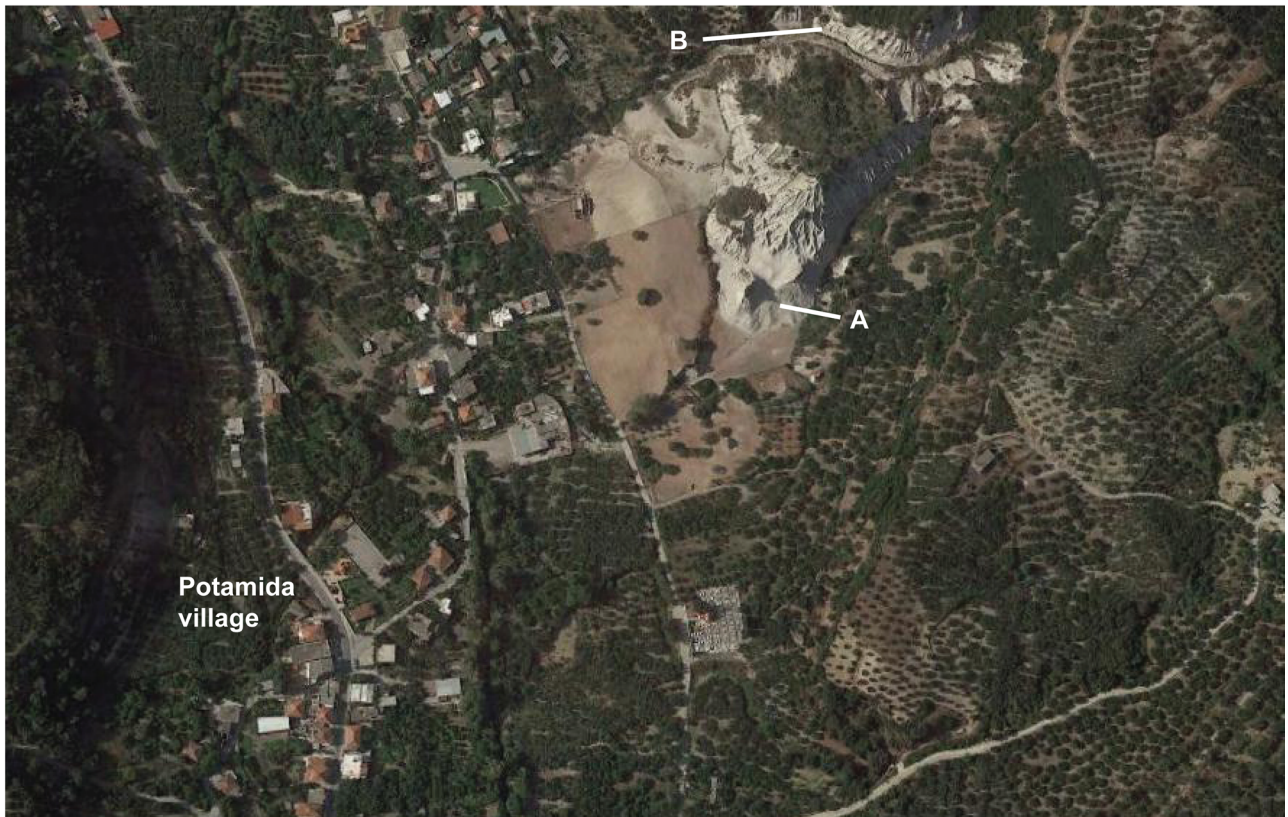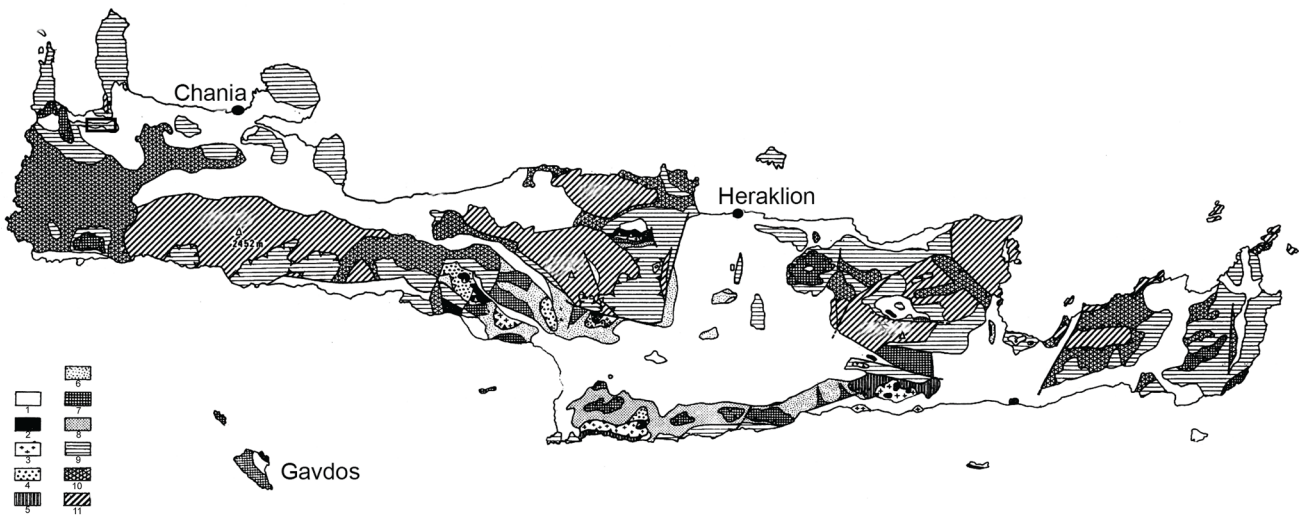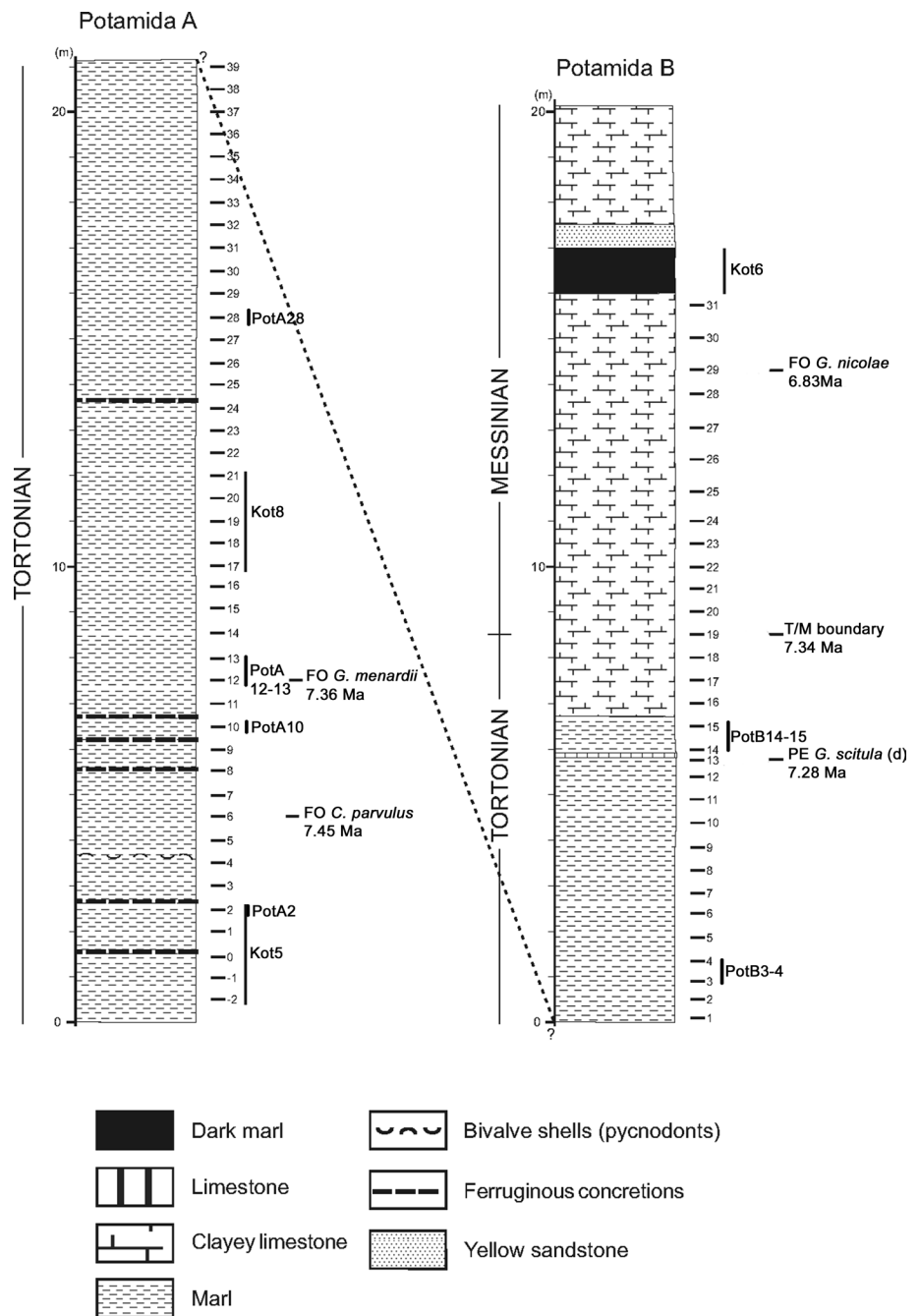
Fig. 2 Geological map of Crete (simplified from Bonneau et al. 1977); *1* Neogene–Quaternary, *2* Ophiolites, *3* Asteroussia nappe, *4* Miamou nappe, *5* Arvi nappe, *6* Pindos-Ethia Eocene flysch, *7* Pindos-Ethia Triassic-Eocene limestones and radiolarites, *8* Tripolis fly-sch, *9* Tripolis Triassic-Eocene limestones, *10* Phyllites-Quartzites unit, *11* Autochthonous Permian-Oligocene. Google earth view of the study locality NE of the village Potamida

(1979). According to these authors, the approximately 45 meters of blue-grey marine marls outcropping in this area were deposited in the Tortonian stage based on the biostratigraphic (planktonic foraminifers and calcareous nannoplankton) and magnetostratigraphic analysis; the upper part of the sequence comprises white-beige marls dated from the Messinian. Furthermore, they identified four high-Fe levels rich in epiphytic benthic foraminifers, which

they attributed to the deposition of distal turbidites. Previous stratigraphic studies identified the first regular occurrence of *Globorotalia conomiozea* in the Potamida section slightly above the Fe III level (Valet and Laj 1981; Langereis et al. 1984). A detailed magnetostratigraphic study in this area was conducted by Valet et al. (1988). Integrating biostratigraphic and magnetostratigraphic data, and through correlation with the insolation La90 curve, the Potamida composite section was placed between 7.35–7.15 Ma (Krijgsman et al. 1994; Postma and Ten Veen 1999).

Materials and methods

In order to determine the fish otolith content in the Potamida sediments, six 25-kg sediment samples were obtained across the studied outcrop (Figs. 2 and 3). In addition, three samples were collected during a different field expedition: Kot5 from the lower part of the section (0–3 m; corresponding to the Potamida A subsection), Kot6 from the upper part of the section just below the sand bed (16–17 m; from the Potamida B subsection), and Kot8 from the

middle part of the section (10–12 m; Potamida A subsection). The sample numbers on Fig. 3 are in direct reference to the biostratigraphy samples (42 samples from Potamida A and 31 samples from Potamida B), as indicated in this figure; this facilitated the respective stratigraphic placement of the otolith samples. Since otolith analysis requires a much greater quantity of sediment (~25 kg per sample), the biostratigraphy samples were inadequate, and it was impossible to obtain the same stratigraphic resolution while sampling this great amount of sediment. Consequently, each sample for the otolith analysis spans a stratigraphic interval encompassing several biostratigraphy sample levels, as indicated in Fig. 3.

The sediment samples were disintegrated, in plain water, and sieved, using a 250-μm mesh sieve. The otoliths were then handpicked from the sediment, under a stereoscope. In addition, several large otoliths were directly collected from the uppermost part of the Potamida A outcrop (PotVar).

The otoliths were identified based on the morphologic characteristics described by Nolf (1985). New morphological observations were made on certain taxa. The species' taxonomic position followed the scheme of Nelson (2006). Several taxa appear in open nomenclature due to insufficient knowledge of related recent species, or because the fossil material is too limited or too poorly preserved to decide. In certain cases specific identification could not be decided based on the available modern and fossil comparative material; thus the abbreviation aff. (*affinis*) was inserted between the name of the genus and the name of the group species. The abbreviation cf. (*conformis*) was used whenever the condition of preservation of the otolith did not allow its conclusive specific identification. Selected otoliths were photographed using the scanning electron microscope JEOL JSM-6360 at the Department of Historical Geology and Paleontology of the University of Athens.

The Potamida composite section was dated through planktonic foraminifer biostratigraphy based on a qualitative analysis of index-species presences, the distribution patterns of five planktonic foraminifer taxa, and the coiling ratio of unkeeled globorotaliids in 70 samples. The biostratigraphic analysis aimed to improve the resolution of the existing framework for the studied section (Langereis et al. 1984; Krijgsman et al. 1994).

The distribution of the identified fish taxa was examined in a Mediterranean basin context, in comparison with the previously published fossil record. Their geographic distribution was investigated with reference to the Paratethys record, the western and eastern Mediterranean sub-basin, and their modern range. The stratigraphic distribution of the identified taxa was revised, from the early Miocene until today.

The paleoenvironmental reconstruction was based on the modern ecological data obtained from the Fishbase database (Froese and Pauly 2015; Table 3 in the Electronic Supplementary Material) for the extant fish taxa. Depth, climate zone distribution, and lifestyle were considered for these extant species. Regarding the extinct species, their ecology was inferred from their modern equivalent species and the accompanying fauna, whenever possible. The paleodepth estimates were based on the distribution of benthopelagic and benthic taxa, also taking into account the composition of the assemblage in general. The identified extant taxa are presently distributed in the tropical, subtropical, and temperate climate zones. The contribution of each group to the total assemblage is examined, to infer the paleoclimatic conditions in the study area.

Results

The fish assemblages

In the present study, we made twenty-eight identifications to the species level and seven to the genus level. Overall, twenty-nine genera were distinguished, belonging to thirteen families: Congidae, Mycrophidae, Macrouridae, Gadidae, Carapidae, Ophidiidae, Bythitidae, Atherinidae, Melamphaidae, Trachichthyidae, Sparidae, Blennidae, and Gobiidae (Table 1; Figs. 4 and 5). Comments on the systematic placement and otolith morphology of selected taxa are available in the Electronic Supplementary Material.

Biostratigraphy

Six planktonic foraminiferal bioevents are recognized and described in stratigraphic order (Fig. 3). *Catapsydrax parvulus* is common to frequent in the lower part of the section; the last occurrence of this taxa is recorded in sample PotA6. The last occurrence of this species was previously dated at 7.45 Ma in the Mediterranean area (Krijgsman et al. 1997). In sample PotA12, the planktonic foraminifer assemblages are characterized by the first occurrence of *Globorotalia menardii* 5 (dextral), indicating an age of 7.36 Ma (Hilgen et al. 1995; Krijgsman et al. 1997). This species occurs in the studied section up to sample PotB18, and it is replaced by the *G. miotumida* group one sample above (PotB19). The replacement of *G. menardii* 5 by the *G. miotumida* group marks the Tortonian/Messinian boundary at 7.24 Ma (Krijgsman et al. 1997, 1999; Sierro et al. 2001; Antonarakou et al. 2004).

The coiling changes of the unkeeled globorotaliids, collectively placed under the *G. scitula* group, provide additional bioevents for the studied section. The *G. scitula* group is dominated by left-coiling assemblages from the base of the section up to sample PotB13. Thereafter, mostly right-coiling specimens are recorded. This level

Table 1 The Potamida otolith material

Family	Species	Samples									
		PotA2	PotA10	PotA12–13	PotA28	PotB3–4	PotB14–15	Kot5	Kot6	Kot8	Pot Var
Congridae	*Pseudophichthys* sp.			1							
	Rhynchoconger pantanellii (Bassoli & Schubert 1906)										5
Myctophidae	*Benthosema suborbitale* (Gilbert 1913)	4		5	3	3	2		7	1	
	Ceratoscopelus maderensis (Lowe 1839)			6		3			1		
	Diaphus aff. *acutirostrum* (Holec 1975)		1		1		1				
	Diaphus befralai (Brzobohaty & Nolf 2000)	1			4	1					
	Diaphus cavallonis (Brzobohaty & Nolf 2000)	2	1	21	6	2	2	1			
	Diaphus rafinesquii (Cocco 1838)	1		3			1				
	Diaphus rubus (Girone et al. 2010)	1	1								
	Diaphus aff. *splendidus* (Brauer 1904)			5							
	Diaphus sp.		4	8	3	5	2	1	21		3
	Hygophum hygomii (Lütken 1892)			3	4				5		1
	Lampadena dea (Fraser-Brunner 1949)			3	4	1		4	3		
	Lampanyctus latesulcatus (Nolf & Steurbaut 1983)	1	1	2	3				4		
	Lobianchia dofleini (Zugmayer 1911)						1		1		
	Myctophum coppa (Girone et al. 2010)			1				1			
	Myctophum fitchi (Schwarzhans 1979)				1	1			1		
	Myctophum punctatum (Rafinesque 1810)		1								
	Myctophum sp.			4	2	1		1			
	Notoscopelus elongatus (Costa 1844)				1			2	3		
	Notoscopelus sp.	1									
	Scopelopsis pliocenicus (Anfossi & Mosna 1976)			2					1		
Macrouridae	*Trachyrincus scabrus* (Rafinesque 1810)										3
	Bathygadus novus (Bassoli 1906)			1							
Gadidae	*Gadiculus labiatus* (Schubert 1905)				1				1		
	indet.			1							
Carapidae	*Echiodon* sp.			1							
Ophidiidae	*Hoplobrotula* sp.										2
	Monomitopus aff. *magnus* (Carter & Cohen 1985)										1
Bythitidae	*Grammonus bassolii* (Nolf 1980)			1			1	2			1
Atherinidae	*Atherina* sp.			1							
Melamphaidae	*Scopelogadus* sp.		1	1	3			2	3		

Table 1 continued

Family	Species	Samples									
		PotA2	PotA10	PotA12–13	PotA28	PotB3–4	PotB14–15	Kot5	Kot6	Kot8	Pot Var
Trachichthyidae	*Hoplostethus* sp.										1
Sparidae	*Pagellus* cf. *acarne* (Risso 1826)			1							
	indet.	1	8			4		3	10		3
Blennidae	*Blennius ocellaris* (Linnaeus 1758)			1							
Gobiidae	*Deltentosteus* aff. *quadrimaculatus* (Valenciennes 1837)								3		
	Deltentosteus sp.			6							
	Lesueurigobius aff. *friesii* (Malm 1874)			9					2		
	Pomatoschistus sp.			7					1		
	"Gobiida" *brioche* (Lin et al. 2015)			2							
	?*Mesogobius* sp.			7					5		

can be correlated to the paracme end of the dextral *G. scitula* group at 7.28 Ma (Hilgen et al. 1995). Dominantly right-coiling representatives of this group are found in low numbers from sample PotB13 up to sample PotB27. They become more abundant above sample PotB29, represented by *G. nicolae*, a dextrally coiled and biconvex form with inflated chambers. The first occurrence of this species was dated at 6.83 Ma (Krijgsman et al. 1997).

Paleobathymetric estimates

The current bathymetric distributions of the extant taxa, combined with the minimum required water depths for the pelagic species (Table 3 in the Electronic Supplementary Material), allow estimating the paleodepth throughout the section. Samples PotA2, PotA10, PotB14–15, and Kot8 include solely mesopelagic species, whose general depth distribution exceeds 50 m. *Lampadena dea* is also present in samples PotA12–13, PotA28, PotB3–4, Kot5, and Kot6, suggesting depths greater than 150 m. The depth estimate for sample PotA28, which was taken from the uppermost part of the Potamida A subsection, is in agreement with the indicated depths from the scattered otolith specimens collected at the bottom of this outcrop; these presumably originated from the uppermost sediments of the Potamida A subsection, recently washed out by the rain. These scattered specimens include *T. scabrus* and *Hoplobrotula* sp., which inhabit depths between 395–1700 and 180–550 m, respectively. Sample PotA12–13 is rich in mesopelagic myctophids, as well as deepwater taxa, such as *Bathygadus novus*. Sample Kot6 contains myctophids, including

L. dea, but also the gobiids *D.* aff. *quadrimaculatus* and *L.* aff. *friesii*; the depositional depth is, therefore, estimated around 100–150 m. Notably, samples PotA12–13 and Kot6 contain both abundant myctophids and gobiids. This may be the result of a local mixing of shallow with deeper water faunas, in a steep slope environment, as previously suggested by Agiadi et al. (2013) and Karakitsios et al. (2016).

The occurrences of *Grammonus bassolii* are very interesting in the studied sediments. The genus *Grammonus* includes 11 extant species, distributed worldwide, which inhabit shallow marine waters, over rocky substratum. Nevertheless, the Indo-Pacific species *Grammonus robustus* Smith and Radcliffe, 1913 is found down to a depth of 345 m (Nielsen et al. 1999). The fossil species *G. bassolii* is found together with myctophids, *L. dea*, *Scopelogadus*, and gobiids in the middle part of the Potamida section. Therefore, it may be assumed that its bathymetric distribution resembled more its modern Indo-Pacific counterpart's, than that of the present-day Mediterranean *Grammonus ater*.

Discussion

Paleobiogeography

The Potamida fish fauna includes a rich mesopelagic and a diverse benthic component; myctophids and gobiids contribute the greatest number of specimens and species in the assemblages (Table 1). Table 2 presents the geographic and stratigraphic distribution of the identified taxa in the Mediterranean and the Paratethys from the Miocene through the present. Thirty-two taxa appear in the Tortonian eastern
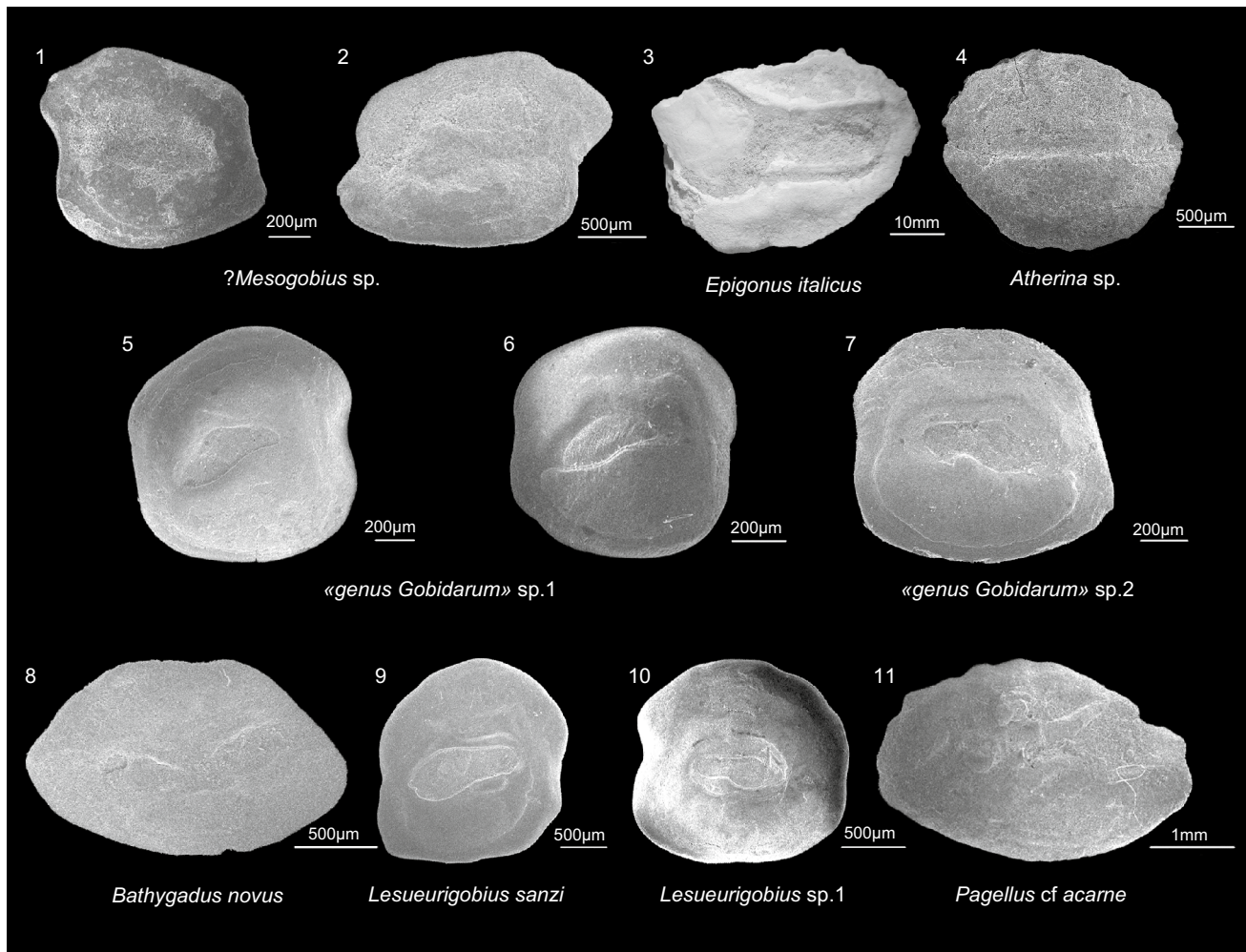
Fig. 4 Fish otoliths from the Potamida area. 1. ?*Mesogobius* sp. PotA12–13, 2. ?*Mesogobius* sp. Kot6, 3. *Hoplostethus* sp. PotVar, 4. *Atherina* sp. PotA12–13, 5–6. *Pomatoschistus* sp. PotA12–13, 7. "Gobiida" *brioche* PotA12–13, 8. *Bathygadus novus* PotA12–13, 9. *Lesueurigobius* aff. *friesii* PotA12–13, 10. *Lesueurigobius* aff. *friesii* Kot6, 11. *Pagellus* cf. *acarne* PotA12–13

Mediterranean for the first time. In addition, the main points to note are:

- Thirteen fish taxa were unprecedented in the Messinian of the eastern Mediterranean, including "Gobiida" *brioche* with a single previous record only from the Tortonian of northern Italy (Lin et al. 2015).
- Overall, the Potamida material includes thirteen extinct taxa. *Myctophum coppa*, *D.* aff. *acutirostrum*, *D. befralai*, *D. rubus*, *L. latesulcatus*, *B. novus*, *G. bassolii*, and "Gobiida" *brioche* are purely Miocene species. *Diaphus cavallonis* is also present during the Pliocene. *Rhynchoconger pantanellii*, *M. fitchi*, *S. pliocenicus*, and *G. labiatus* disappeared in the Pleistocene.
- Extant species *C. maderensis*, *D. rafinesquii*, *H. hygomii*, *L. dofleini*, *M. punctatum*, *T. scabrus*, *P. acarne*, *B. ocellaris*, *D. quadrimaculatus*, and *L. friesii* are reported

from the Tortonian until today in the eastern Mediterranean. *Notoscopelus elongatus* was previously reported mostly in the Pleistocene Mediterranean Sea, apart from one record in the Tortonian of the western sub-basin (Lin et al. 2015).

- Eight extant taxa from those identified in the Potamida sediments are not present today in the Mediterranean Sea. *Pseudophichthys* spp., *Monomitopus* aff. *magnus*, and *L. dea* inhabit the Atlantic Ocean, whereas *Hoplobrotula* spp. are present in the Indian and the western Pacific Ocean. Furthermore, three taxa maintain a circumglobal distribution at present: *D. splendidus*, *Hoplostethus* spp. and *Scopelogadus* spp.
- Today, *Mesogobius* spp. are only present in the Black Sea and the Caspian Sea. Nevertheless, it is possible that it was distributed in the Mediterranean during the Miocene and Pliocene, given the occasional connections between
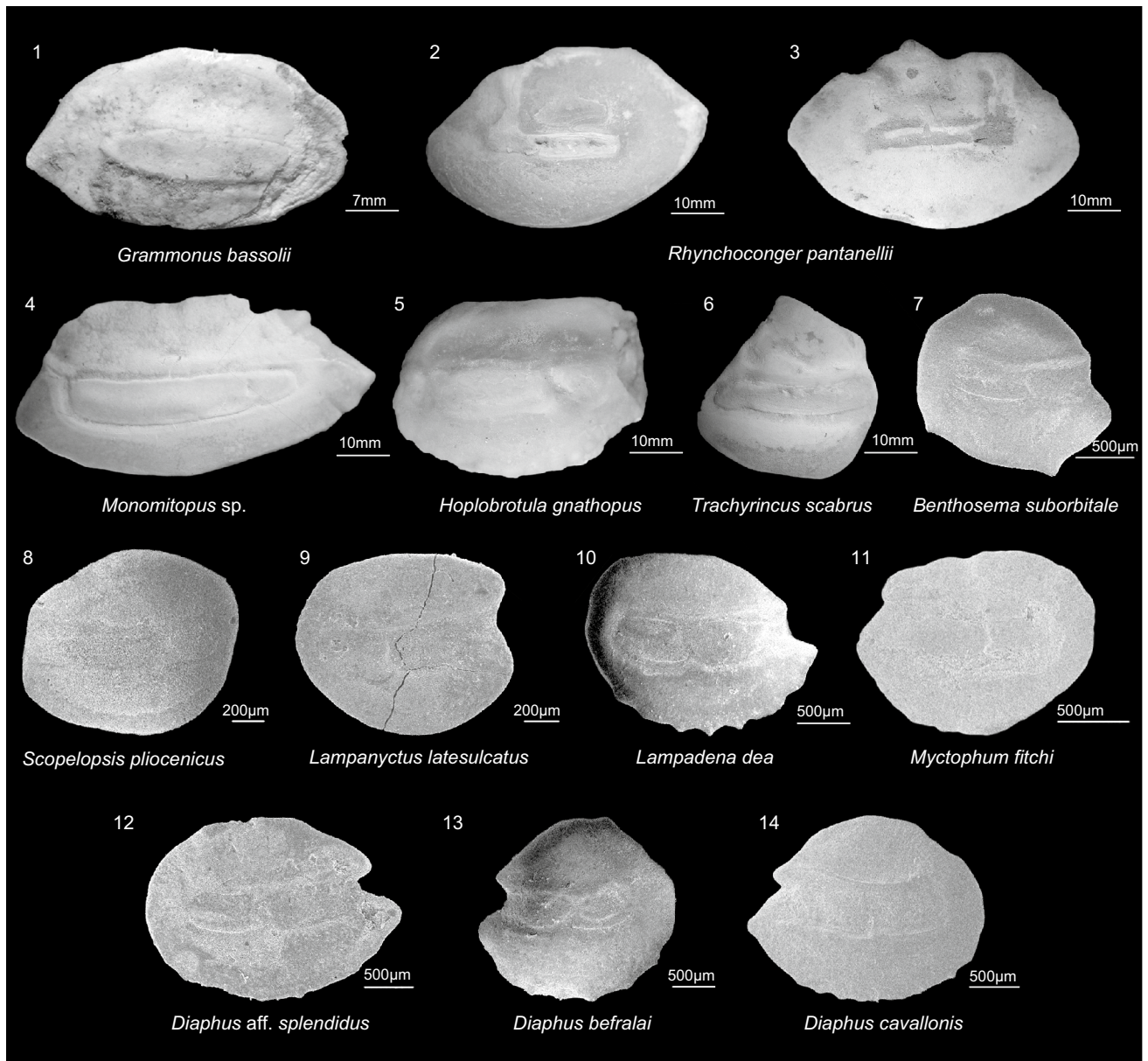
Fig. 5 Fish otoliths from the Potamida area (continuation). 1. *Grammonus bassolii* PotVar, 2–3. *Rhynchoconger pantanellii* PotVar, 4. *Monomitopus* aff. *magnus* PotVar, 5. *Hoplobrotula* sp. PotVar, 6. *Trachyrincus scabrus* PotVar, 7. *Benthosema suborbitale* Kot6, 8. *Scopelopsis pliocenicus* Kot6, 9. *Lampanyctus latesulcatus* PotA12–13, 10. *Lampadena dea* PotA28, 11. *Myctophum fitchi* PotB3–4, 12. *Diaphus* aff. *splendidus* PotA12–13, 13. *Diaphus befralai* PotA28, 14. *Diaphus cavallonis* PotA28

the Mediterranean Sea and the Black Sea and Dacic basin through the Bosporus and the Strymon straits (Popov et al. 2006; Snel et al. 2006; Suc et al. 2015).

Studying otoliths assemblages can be very revealing as to the fish paleofauna of a larger area, in this case, the eastern Mediterranean. Interestingly, the Potamida overall fauna composition strongly resembles that of Vrica section (southern Italy); a rich pelagic-mesopelagic assemblage comprised mostly of myctophids and a diverse benthic-benthopelagic group. The Vrica fauna includes *T. scabrus*, *Scopelogadus* aff. *beani*, *Bathygadus novus*, and gadids, which are also reported in the Potamida sediments. However, the Vrica sediments correspond to a much deeper paleoenvironmental setting; hence, the assemblage does not include the shallow-water benthic gobiids, which are present in Potamida. Such an occurrence was also reported in the southern Aegean Pliocene and Pleistocene (Agiadi 2013; Agiadi et al. 2013) and in the Messinian of western Greece (Karakitsios et al. 2016), where it seemed to be associated

Table 2 Stratigraphic and geographic distribution of the fish taxa identified in the Potamida sediments

Family	Species	PT	Western Mediterranean				Eastern Mediterranean				Recent distribution	
			<S	T	M	Pl	<S	T	M	Pl	Ps–Med	H
Congridae	*Pseudophichthys* sp.			T	M	Z-Pi	Pr-S	**T**	**M**	Z-Pi		A
	Rhynchoconger pantanellii (Bassoli & Schubert 1906)	Mi	L-S	T		Z-Pi	S	T		Z-Pi	G-C	
Myctophidae	*Benthosema suborbitale* (Gilbert 1913)					Z-Pi		**T**	**M**	Z-Pi	G-C	wMd; A; I/P
	Ceratoscopelus maderensis (Lowe 1839)					Z-Pi		**T**	**M**	Z-Pi	G-C-Io	Md; nA
	Diaphus aff. *acutirostrum* (Holec 1975)	Mi						**T**	**M**			
	Diaphus befralai (Brzobohaty & Nolf 2000)		S	T	M			**T**				
	Diaphus cavallonis (Brzobohaty & Nolf 2000)		S	T	M	Z-Pi		T	M	Z-Pi		
	Diaphus rafinesquii (Cocco 1838)		S	T	M	Z-Pi		**T**	M	Z-Pi	G-C-Io	Md; nA
	Diaphus rubus (Girone et al. 2010)				M			**T**	M			
	Diaphus aff. *splendidus* (Brauer 1904)		S	T	M	Z-Pi		**T**	M	Z-Pi	G-C-Io	A; I/P
	Hygophum hygomii (Lütken 1892)	Mi	L-S	T	M	Z-Pi		**T**	**M**	Z-Pi	G-C-Io	Md; A; I/P
	Lampadena dea Fraser-(Brunner 1949)	Mi		T	M	Z		**T**	**M**			seA
	Lampanyctus latesulcatus (Nolf & Steurbaut 1983)			T				**T**	**M**			
	Lobianchia dofleini (Zugmayer 1911)		B-S	T	M	Z-Pi		**T**	**M**	Z-Pi	G-C-Io	Md; A; I/P
	Myctophum coppa (Girone et al. 2010)				M			**T**	**M**			
	Myctophum fitchi (Schwarzhans 1979)			T		Z		**T**	**M**	Z-Pi	G	
	Myctophum punctatum (Rafinesque 1810)			T		Pi		**T**		Pi	G-C-Io	Md; nA
	Notoscopelus elongatus (Costa 1844)			T				**T**	**M**		G-C-Io	wMd

Reference data (see also supplementary material additional references) are obtained from Keupp and Bellas (2002), Muller and Rozenberg (2003), Nolf and Brzobohaty (2004), Girone (2007), Girone and Nolf (2009), Girone et al. (2006, 2010), Brzobohaty et al. (2007), Agiadi et al. (2010, 2013), Agiadi (2013), Bosnakoff (2012), Gaudant (2002; 2014), Schwarzhans (2014), Lin et al. (2015), and Karakitsios et al. (2016). The present-day distribution of the studied taxa is acquired from the Fishbase database (Froese and Pauly 2015)

Bold letters indicate the contribution of the present study

PT Paratethys, *Mi* Miocene, *Pr* Priabonian, *B* Burdigalian, *L* Langhian, *S* Serravallian, *T* Tortonian, *M* Messinian, *Pl* Pliocene, *Z* Zanclean, *Pi* Piacenzian, *Ps* Pleistocene, *G* Gelasian, *C* Calabrian, *Io* Ionian, *H* Holocene, *Md* Mediterranean, *A* Atlantic, *I/P* Indo-Pacific, *w* west, *e* east, *s* south

Paleoenvironmental reconstruction

Considering the present-day ecology of the extant taxa comprising the Potamida assemblages, the study area was placed within the subtropical climatic zone. Most extant taxa are purely subtropical, both deep- and surface-dwellers. Nevertheless, there are thirteen currently extinct taxa also present in these assemblages, whose paleoecologic preferences can only be inferred indirectly (Table 2). *Rhynchoconger pantanellii* is presumably a subtropical–tropical species of the continental slope; it was replaced during the Calabrian by the purely subtropical congrid *Gnathophis mystax*, which occupies the same ecological niche in the Mediterranean until today (Agiadi 2013). In addition, *D.*

cavallonis is a fossil Miocene-Pliocene Mediterranean mesopelagic myctophid with large and robust otoliths suggestive of its warm-water, high-nutrient preferences. Indeed, this species is very abundant in sample PotA12–13, whose assemblage exhibits the greatest diversity. Therefore, these presences suggest that the study area was located well inside the subtropical zone, with warm climatic conditions prevailing throughout the uppermost Tortonian, between 7.5–7.24 Ma.

The present paleobathymetric analysis indicates that the Potamida sediments accumulated in depths below 150 m, although the middle part of the sequence was deposited in greater depths, between 400–550 m. These values are in contrast to the previous estimate of 600–900 m provided by van Hinsbergen and Meulenkamp (2006) based on the general relationship between depth and the planktonic foraminifera fraction. Indeed, this previous estimate seems exaggerated in view of the present data. Although the occurrence of *Bathygadus novus*

and *Scopelogadus* sp. at a level within the lower part of the sequence (PotA12–13) indicate that deepwater environments could be found nearby, the presence and high abundance of gobiids unquestionably point toward much shallower depths in the study area. The mixing of the deep and shallow-water faunas at this level is attributed to the steepness of the underwater topography, which brings the two elements in great proximity (Agiadi 2013; Agiadi et al. 2013).

Four stages are distinguished based on the present paleobathymetric analysis. The Potamida area was an open marine environment with depths exceeding 150 m between ~ 7.5–7.45 Ma. The mixed ichthyofauna identified between 7.45–7.36 Ma suggests steep underwater topography bringing together a shallow-water (100–150 m) and a deepwater component (>150 m), with an overall depth estimate between 300–400 m. Gradual deepening between 7.36–7.28 Ma to depths between 400–550 m is characterized by the presence of *T. scabrus* and *Hoplobrotula* sp.. Unfortunately, in this study, it was not possible to retrieve fish otoliths from the clayey limestones at and above the boundary. Later on, the estimated depth of deposition of the dark marls just below the sand bed, which are dated approximately between 6.8–6.6 Ma, is 100–150 m, based on the concurrent presence of *L. dea*, *D.* aff. *quadrimaculatus*, and *L. friesii*.

Conclusions

A continuous late Tortonian–early Messinian marine sequence is revealed in the Potamida section. The planktonic foraminifer biostratigraphic results indicate that the Potamida composite section encompasses the interval approximately between 7.5 and 6.5 Ma. This estimate differs from the results of previous studies, which suggested an age between 7.35 and 7.15 Ma for the same sediments (Krijgsman et al. 1994, 1995; Hilgen et al. 1995; Postma and Ten Veen 1999). However, those results were based only on a single bioevent, the first regular occurrence of *Globorotalia conomiozea*. Thus, the results presented here offer a substantial improvement in the dating of the Potamida sediments.

Climate changes, in the past as well as in the present, induce large-scale distribution range shifts in marine fish (Perry et al. 2005), which are facilitated by the existence of marine gateways connecting the oceanic environments. The Mediterranean Sea, although it comprises an impoverished marine fish fauna as compared to other warm termperate seas (Schwarzhans 1986; Lin et al. 2016), offered unique conditions for the distribution and interaction of marine fish assemblages, because its changeable connectivity in the geological past enabled species from very disparate ecosystems to come together. Today, several marine fish species invade the Mediterranean Sea in response to climate warming. The Miocene equivalent offers a glimpse into the possible effects of such a phenomenon on the overall fish fauna composition.

Indeed, the late Miocene subtropical fish fauna, revealed through the present study, includes thirty-five taxa from thirteen Teleost families. The eastern Mediterranean biostratigraphic and geographic distribution of thirty-two taxa is significantly expanded into the Tortonian, whereas thirteen species are recorded for the first time in the Messinian, including the recently recognized species "Gobiida" *brioche* from the Tortonian of northern Italy. Overall, twenty-one of these taxa no longer inhabit the Mediterranean Sea; thirteen are extinct, six inhabit the Atlantic Ocean, four may be found in the Indo-Pacific, and one appears in the Black and in the Caspian Sea. Important is the presence of *Hoplobrotula*, because this is the only extant genus from the Potamida fauna currently inhabiting only the Indian and the Pacific Ocean and not the Atlantic Ocean. Many hypotheses were proffered in the past regarding the influence of the eastward sea connections on the Mediterranean fish faunas. The present analysis supports that the Atlantic and the Paratethys had a strong impact on the composition of the fish assemblages in the Mediterranean during the late Miocene, in accordance with the model results presented by Karami et al. (2011).

Modern fish resources and their dependent socio-economic structures are under severe stress under the present environmental changes worldwide. Long-term sustainable fisheries are a major aim of the new Common Fisheries Policy (CFP), which took effect as of January 1, 2014. The present study offers valuable observations on the long-term effects of environmental perturbations on the Mediterranean marine fish assemblages. The eastern Mediterranean during the late Miocene, an analog to the future warm ocean, exhibits a rich and diverse marine fish fauna of worldwide affinities. Conclusively, our study reveals the catalytic role of connective pathways to the distribution of marine fish.

Meulenkamp JE, Dermitzakis M, Georgiadou-Diakeoulia E, Jonkers HA, Boerger H (1979) Field guide to the Neogene of Crete. University of Athens, Athens

Nelson JS (2006) Fishes of the world, 4th edn. John Wiley & Sons Inc, New Jersey

Nielsen JG, Cohen DM, Markle DF, Robins CR (1999) Ophidiiform fishes of the world (Order Ophidiiformes). An annotated and illustrated catalogue of pearlfishes, cusk-eels, brotulas and other ophidiiform fishes known to date. FAO Fish. Synop. 125(18), FAO, Rome

Nolf D (1985) Otolithi piscium. In: Schlutze HP (ed) Handbook of paleoichthyology, vol 10. Gustav Fischer Verlag, Stuttgart and New York

Nolf D, Girone A (2006) Otolithes de poisons du Pliocene inferieur (Zancleen) des environes d' Alba (Piemont) et de la cote Ligure. Riv Piemont St Nat 27:77–114

Nolf D, Girone A (2008) Early Oligocene fish otoliths from the Castellane area (SE France) and an overview of Mediterranean teleost faunas at the Eocene–Oligocene boundary. Neues Jahrb Geol Palaont, Abh 24:139–157

Nolf D, Martinell J (1980) Otolithes de Teleosteens du Pliocene des environs de Figueras (Catalogne). Geol Paleontol 14:209–234

Nolf D, Steurbaut E (1983) Revision des otolithes de teleosteens du Tortonien stratotypique et de Montegibbio (Mioce`ne Supe´rieur d'Italie septentrionale). Meded Werkgr Tert Kwart Geol 20:143–197

Nolf D, Steurbaut E (2004) Otolithes de poissons de l'Oligocene inferieur du bassin Liguro-Piemontais oriental. Ital Riv Piem St Nat 25:21–68

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308:1912–1915

Popov SV, Shcherba IG, Ilyina LB, Nevesskaya LA, Paramonova NP, Khondkarian SO, Magyar I (2006) Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. Palaeogeogr Palaeoclimatol Palaeoecol 238:91–106

Postma G, Ten Veen JH (1999) Astronomically and tectonically linked variations in gamma-ray intensity in Late Miocene hemipelagic successions of the eastern Mediterranean basin. Sedim Geol 128:1–12

Robba E (1970) Otoliti del Tortoniano-tipo (Piemonte). Riv Ital Paleont 76:89–172

Roveri M, Flecker R, Krijgsman W, Lofi J, Lugli S, Manzi V, Sierro FJ, Bertini A, Camerlenghi A, De Lange G, Govers R, Hilgen FJ, Hubscher C, Meijer P, Stoica ThM (2014) The Messinian Salinity Crisis: past and future of a great challenge for marine sciences. Mar Geol 352:25–58

Schwarzhans W (1986) Die Otolithen des Unter-Pliozän von Le Puget, S-Frankreich. Senckenbergiana Lethaea 67:219–273

Schwarzhans W (2014) Otoliths from the middle Miocene (Serravallian) of the Karaman Basin, Turkey. Cainozoic Res 14:35–69

Selli R (1954) II baccino del Metauro. Giorn Geol 24(2):83

Sierro FJ, Hilgen FJ, Krijgsman W, Flores JA (2001) The Abad composite SE Spain: a Messinian reference section for the Mediterranean and the APTS. Palaeogeogr Palaeocl 168:141–169

Snel E, Mărunţeanu M, Meulenkamp JE (2006) Calcareous nannofossil biostratigraphy and magnetostratigraphy of the Upper Miocene and Lower Pliocene of the Northern Aegean (Orphanic Gulf-Strimon Basin areas), Greece. Palaeogeogr Palaeoclimatol Palaeoecol 238:125–150

Suc JP, Popescu S-M, Do Couto D, Clauzon G, Rubino J-L, Melinte-Dobrinescu MC, Quillevere F, Brun J-P, Dumurdzanov N, Zagorchev I, Lesic V, Tomic D, Sokoutis D, Meyer B, Macalet R, Rifelj H (2015) Marine gateway vs. fluvial stream within the Balkans from 6 to 5 Ma. Marine and Petroleum Geology 66(1): 231–245

Valet J-P, Laj C (1981) Paleomagnetic record of two successive Miocene geomagnetic reversals in western Crete. Earth Plan Sci Lett 54:53–63

Valet J-P, Laj C, Langereis CG (1988) Sequential geomagnetic reversals recorded in upper Tortonian marine clays in western Crete (Greece). J Geophys Res 93(B2):1131–1151

Van Hinsbergen DJJ, Meulenkamp JE (2006) Neogene supradetachment basin development on Crete (Greece) during exhumation of the South Aegean core complex. Basin Res 18:103–124

Zachariasse WJ, van Hinsbergen DJJ, Fortuin AR (2011) Formation and fragmentation of a late Miocene supradetachment basin in central Crete: implications for exhumation mechanisms of high-pressure rocks in the Aegean forearc. Basin Res 23:678–701