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The Zanclean marine fish fauna and palaeoenvironmental reconstruction of a coastal marine setting in the eastern Mediterranean

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Abstract

Fossil records of nearshore, shallow marine fish communities are rare. Here, we present the rich and diverse fish fauna of a coastal setting in the eastern part of the Mediterranean during the early Pliocene, which comprises 54 taxa, 77% of which are extant and currently occupy the same shores. We analyse these assemblages to estimate the palaeodepth, the substratum and the climatic and oceanographic conditions prevailing in the region at the time. Furthermore, we review the stratigraphic and geographic distribution of the identified taxa from the Tortonian until today, to establish patterns and trends in the evolution of the Mediterranean coastal fish fauna. Contrary to expectations, the Pliocene coastal fauna is very similar to the Miocene and to the Pleistocene in terms of functional traits as well as taxonomically. Replacements of species seem to have been gradual, through multiple extirpations and reintroductions that led to the final extinction of mostly tropical species from the basin, while subtropical–temperate taxa invaded to take their place.

Keywords Pliocene · Ionian Sea · Otoliths · Teleost · Greece · Biogeography

Introduction

Coastal ecosystems are strongly affected by natural and anthropogenic stressors, especially in the semi-restricted Mediterranean basin. However, the long-term effect of these processes on fish populations is largely unknown due to insufficient data from the geological past. Few studies have explored coastal fish faunas from the Pleistocene and the Pliocene of the Mediterranean (Nolf and Girone 2000, 2006; Girone 2007; Agiadi et al. 2013a, 2018, 2019). In an attempt to improve our knowledge on Pliocene fish, in this study, we investigate the coastal fish fauna established in the eastern Mediterranean during the early Pliocene by identifying fossil fish otolith assemblages in a Zanclean sedimentary sequence cropping out in Agia Triada (southwest Peloponnesus, Greece). We examine the stratigraphic and geographic distribution of the identified fish taxa to draw conclusions on the evolution of the Mediterranean coastal ecosystems. Finally, we use these otolith assemblages, in conjunction with previously published data on the invertebrate fauna from the same area (Koskeridou et al. 2017), to extract information on the palaeoenvironment and its evolution during the studied interval.

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Geological setting

Agia Triada section is located on the southeast coast of Messinia region, southwest Peloponnese (Fig. 1), which

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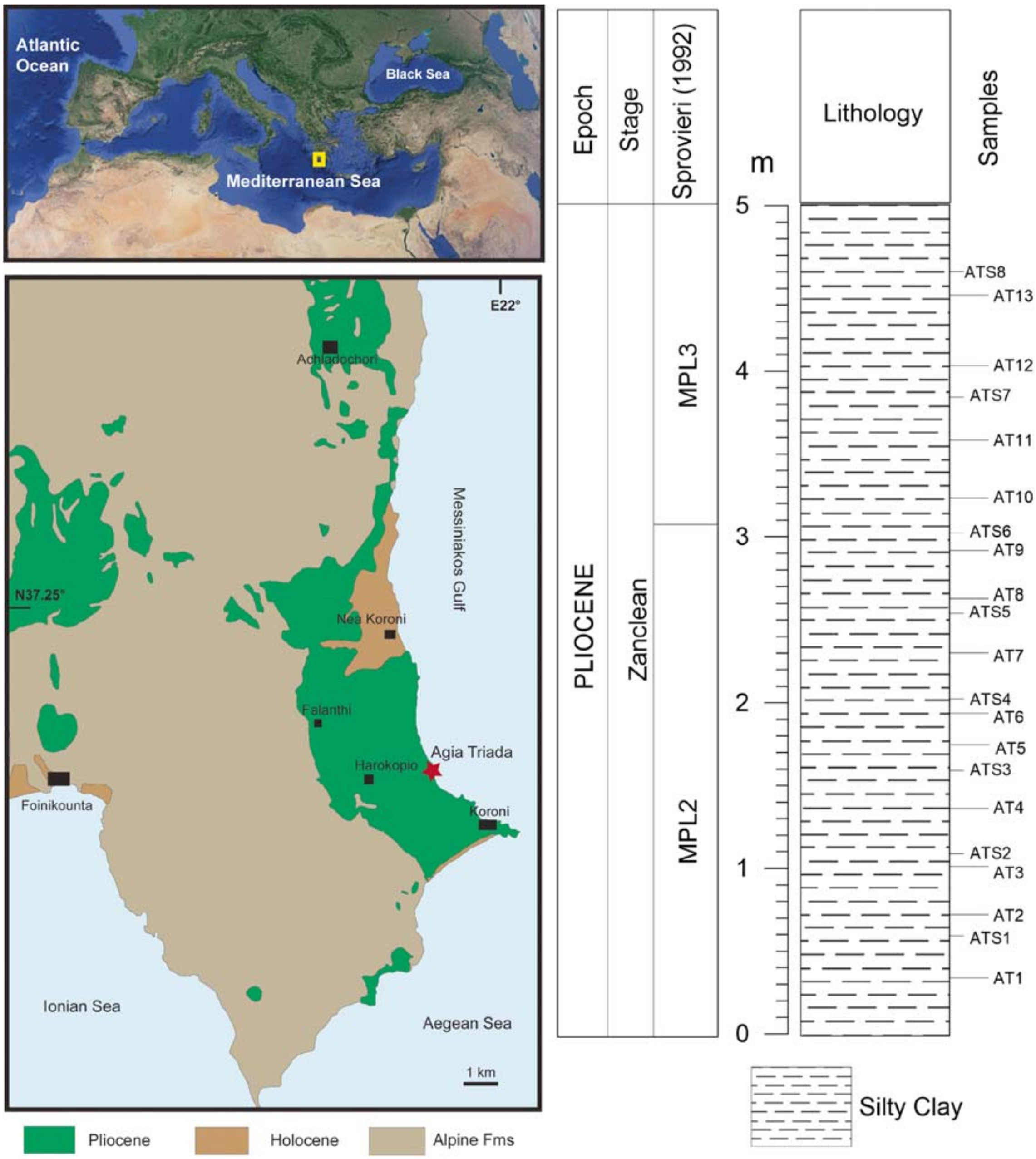

Fig. 1 Map of the study area and stratigraphic column with the position of the sediment samples used for the present analysis (map modified from Fytrolakis 1980)

is a tectonically active region, east of Harokopio village and about 5 km north-west of Koroni city. Marine, lacustrine and continental Neogene and Quaternary sediments in this region are deposited unconformably over the Alpine formations of Pindos, Tripolis, Arna (phyllites–quartzites) and Mani units (Mariolakos et al. 2001). The study area falls within the Falanthi Basin, formed between the Mavrovouni NW–SE–striking marginal fault zone to the west and the Longa-Evangelismo fault zone to the north (Ladas et al. 2004). In particular, Agia Triada section comprises approximately 30 m of blue clays gradually turning into silty clays in the uppermost part (Fig. 1), which were dated in the Zanclean (Koskeridou et al. 2017) within planktonic foraminifer biozones MPL2 and MPL3 (Sprovieri 1992) and Mediterranean mollusc unit MPPMU1 (Monegatti and Raffi 2010) between 5.08 and 3.81 Ma. In particular, the MPL2–ML3 boundary at 4.52 Ma was located in this section just above sample level ATS6 (Koskeridou et al. 2017).

Material and methods

Fish otolith sampling, processing and identification

Twenty 25-kg sediment samples were obtained along the Agia Triada section as shown in Fig. 1. The samples were water-sieved using a 250-μm sieve, and the residues were dried in an oven. The otoliths were handpicked from the residues and identified under the microscope. They were described following the terminology of Nolf (1985) and classification followed the scheme of Nelson et al. (2016). We only present here remarks on taxa identified for the first time in the Zanclean of the eastern Mediterranean, previous ambiguous records in this area or records only based on skeletal parts and not otoliths. At least one characteristic otolith from each taxon was photographed using a scanning electron microscope and is figured here. Otolith identifications were based on direct comparison with the fossil and Recent material available at the University of Athens and the Università degli studi di Bari and a thorough literature review.

Palaeobiogeographical methodology

In light of the presented new record, we revised the stratigraphic and geographic distribution of the identified taxa through comparison with the existing literature. Moreover, we compared in detail the overall structure and composition of this coastal fish association with those from other Pliocene and Pleistocene fossiliferous localities.

Palaeoecological analysis

Since most of the identified taxa are extant, we were able to draw modern ecological information from the literature and through the FishBase database (Froese and Pauly 2018). The data used for the palaeoecological analysis are provided as supplementary data to this article. We grouped the identified taxa based on their lifestyle into pelagic and benthic/benthopelagic taxa. The benthic and benthopelagic taxa were used to estimate the palaeodepth in the studied sedimentary sequence using their present-day bathymetric distribution (Agiadi et al. 2013b) as well as their known distribution is sea-bottom surficial sediments (Lin et al. 2016, 2017b, 2018). Moreover, we were able to infer the depositional setting based on the substratum preferences of the benthic-benthopelagic taxa. Furthermore, we grouped the identified taxa based on the climatic zones they inhabit at present, namely tropical (Tr), subtropical (ST) and temperate (Te). Thus, we could investigate the palaeoclimate in the study area during the Zanclean. Species living in shallow or surface waters were grouped together, assuming their distribution was affected directly by climate, whereas mesopelagic-bathypelagic species living in deep waters were considered to reflect the conditions in the deeper parts of the water column in the eastern Mediterranean basin. Finally, our results were compared with those reached through the analysis of the invertebrate accompanying fauna by Koskeridou et al. (2017).

Results

Systematic palaeontology

Overall, we identified 54 taxa from 23 families and 8 orders (Table 1; Figs. 2, 3, 4 and 5). In the following synonymy lists, only synonyms based on otoliths are listed, as well as first mentions of the species regardless of whether otoliths were described or not. In addition, figure or plate numbers are indicated in the synonyms list only if the figured specimens are otoliths.

Abbreviations: AMPG Athens Museum of Palaeontology and Geology; BMNH British Museum of Natural History; LS Linnean Society of London, London, England, United Kingdom; MNHN Muséum National d' Histoire naturelle, Systématique et Évolution, Laboratoire d' Ichthyologie Générale et Appliquée, Paris, France; MSNG Museo Civico di Storia Naturale di Genova 'Giacomo Doria', Genova, Italy; NMW Naturhistorisches Museum, 1 Zoologische Abteilung, Fische, Vienna, Austria; NRM Naturhistoriska Riksmuseet, Department of Vertebrate Zoology, Ichthyology Section, Stockholm, Sweden; SMF Senckenberg Museum in Frankfurt am Main; SMNS Staatliches Museum für Naturkunde in Stuttgart, Stuttgart, Baden-Württemberg, Germany; ZMB Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Berlin, Germany; ZMUO Universitetets i Oslo, Zoologisk Museum, Oslo, Norway.

Class Actinopterygii Klein, 1885
Order Albuliformes Greenwood, 1977
Family Albulidae Bleeker, 1859
Genus *Pterothrissus* Hilgendorf, 1877
Type species: *Pterothrissus gissu* Hilgendorf, 1877; Recent from Tokyo, Japan.

Pterothrissus compactus Schwarzhans, 1981
Fig. 2a

1981 *Pterothrissus compactus* Schwarzhans, fig. 9–12
1986 *Pterothrissus compactus* Schwarzhans, 1981; Schwarzhans, p. 221
1995 *Pterothrissus compactus* Schwarzhans, 1981; Nolf and Cavallo, pl. 1, fig. 1
2013 *Pterothrissus compactus* Schwarzhans, 1981; Nolf, pl. 15

Table 1 The otolith material from Agia Triada section

Family	Taxon	Samples AT1	AT2	AT3	AT4	AT5	AT6	AT7	AT8	AT9	AT10	AT11	AT12	AT13	ATS1	ATS2	ATS3	ATS5	ATS6	ATS7	ATS8
Albulidae	*Pterothrissus compactus*		1					1							1				1		
Congridae	*Conger conger*							1			1										
	Gnathophis mystax							1													
Clupeidae	*Spratelloides* sp.														1			1			
	indet.							1													
Myctophidae	*Ceratoscopelus maderensis*	1	1								1				1						
	Diaphus rafinesqui		1					2													
	Diaphus splendidus			1																	
	Diaphus sp.		1										1								
	Electrona risso		1																		
	Hygophum hygomii				1							1									
	Notoscopelus resplendens										1	1			1				1		
	indet.									1	2	3			1						
Bregmacerotidae	*Bregmaceros albyi*					1				1			1								
Carapidae	*Carapus acus*						1	1				1									
Ophidiidae	*Ophidion barbatum*		1		1			1			4	1			1						
Bythitidae	*Grammonus bassoli*																		1		
	indet.		1																		
Apogonidae	*Apogon* sp											1									
Gobiidae	*Aphia minuta*	1		8	1		2	1	1		20	8	5		18	1	5	15	3	1	
	Chromogobius zebratus	1	2	1				1		1	2	1									
	Deltentosteus quadrimaculatus							35	1		13	3			2	2			4		
	Gobius bucchichi																		1		
	Gobius cobitis							3			10										
	Gobius cf. *couchi*															1					
	Gobius cf. *geniporus*																	1			
	Gobius cf. *paganellus*							2			10										
	Gobius? sp. 1			4									3		4						
	Gobius? sp. 2			1																	
	Gobius? sp. 3																				1
	Gobius sp.					4		13			44	18	1	1				1			
	Lesueurigobius friesii	8	7	19		5	4		1	5	8		6	1	12	1	9	6	1	2	
	Lesueurigobius sanzi	14	9	18	10	5	3	8	6	10	22	44	15	15	14		21	14		4	1
	Lesueurigobius suerii	6	5	4		2		3					3		17	5		7	2		
	Lesueurigobius sp.	7							2											5	

Table 1 (continued)

	Pomatoschistus marmoratus	1									6	4									
	Thorogobius sp.																			1	
	indet.	60	30	16			5	42	8	4			30	27			2		8		
Blenniidae	*Blennius ocellaris*											1									
Citharidae	indet.						1				1										
Scophthalmidae	*Scophthalmus rhombus*										1										
Bothidae	*Arnoglossus kokeni*		2	2				4		1	4	1	3	1	3	1		2	3	1	
	Arnoglossus laterna	2	2	1				3	3		7							1			
	Arnoglossus cf. *laterna*														1						
	Arnoglossus sp.														1						
Achiridae	*Achirus* sp.														2						
Soleidae	*Buglossidium luteum*										9										
	Microchirus variegatus	2		1	1			2				1	3		1						
	indet.							1			1										
Cynoglossidae	*Cynoglossus obliqueventralis*			1							1										
Acropomatidae	*Verilus mutinensis*					1		1													
Mullidae	indet.										2										
Percidae	indet.										3										
Haemulidae	*Pomadasys incisus*							1													
	indet.							1			1										
Cepolidae	*Cepola macrophthalma*	2																			
Sparidae	*Boops boops*																1				
	Dentex gibbosus			1									1								
	Dentex macrophthalmus										1				1						
	Dentex maroccanus										3			1			1	1			
	Diplodus annularis							1			1										
	Oblada melanura										1										
	Pagellus acarne										1										
	Pagellus bogaraveo							3													
	Pagellus erythrinus			1								2						1			
	Spicara maena					1															
	indet.		4	2	2		1	6	1		10		1				2	2	1		
Indeterminable	indet.	1	1	1		1		22	3		46	6	1					3			
	Total number of specimens	106	69	82	16	20	17	161	26	23	237	97	74	46	82	11	42	56	26	14	2

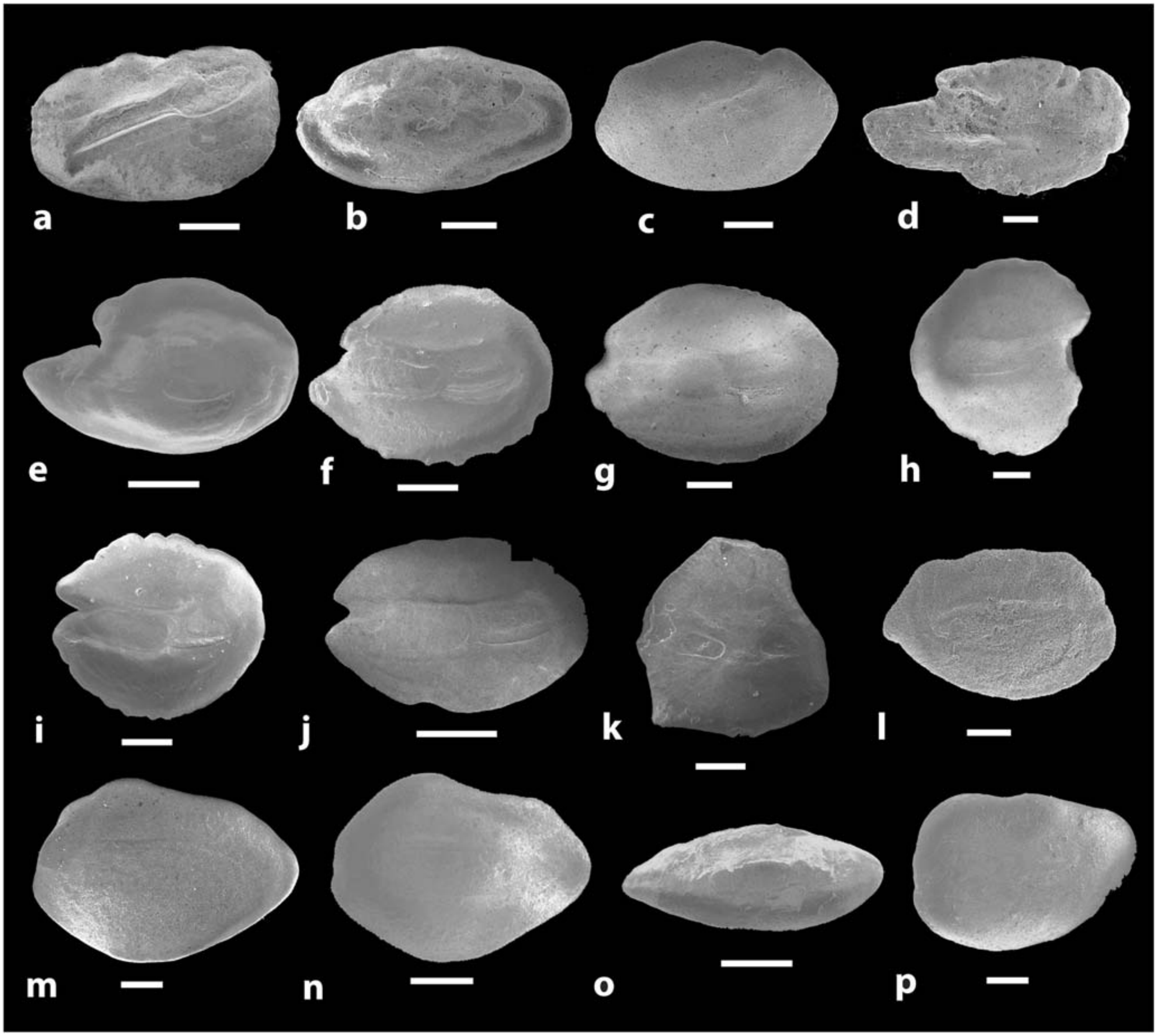

Fig. 2 Fish otoliths from Agia Triada section. **a** *Pterothrissus compactus* (ATS1; L), **b** *Conger conger* (AT10; R), **c** *Gnathophis mystax* (AT7; L), **d** *Spratelloides* sp. (ATS1; R), **e** *Ceratoscopelus maderensis* (AT1; R), **f** *Diaphus rafinesquii* (AT2; R), **g** *Diaphus splendidus* (AT3; R), **h** *Electrona risso* (AT2; L), **i** *Hygophum hygomii* (AT4; R), **j** *Notoscopelus resplendens* (AT10; R), **k** *Bregmaceros albyi* (AT12; R), **l** *Carapus acus* (AT11; L), **m** *Ophidion barbatum* (AT4; L), **n** *Ophidion barbatum* (ATS1; L), **o** *Grammonus bassoli* (ATS6; R), **p** *Apogon* sp. (AT11; R). R right otolith, L left otolith. Scale 1 mm for **a**, **j**; 500 μm for **c**, **e**, **f**, **g**, **h**, **i**, **m**, **n**, **o**, **p**; 200 μm for **a**, **b**, **k**, **l**

Material: One right otolith in sample AT2, one left otolith in sample AT10, one left otolith in sample ATS1, one right otolith in sample ATS6 (AMPG_OT_AT-1–4).

Description: The otoliths of this species are rectangular with curved edges. The sulcus is divided into an oval-shaped ostium that opens dorsally making a curve and not reaching the anterior side, and a thin cauda approximately as long as the ostium, which does not reach the posterior rim. The ventral area is much larger than the dorsal area.

Remarks: Nolf (2013) presented the variability in the morphology of otoliths from fossil and Recent *Pterothrissus* species. In the specimens studied here, the shape is truly rectangular and the sulcus opens dorsally, not anteriorly. These characters differentiate our otoliths from most *Pterothrissus* species. Greater similarity is observed with the otoliths of the Recent species *P. gissu* from the western Pacific and *Nemoossis (Pterothrissus) belloci* from the eastern Atlantic (Nolf 2013). Compared with the *P. gissu*, our otoliths are clearly more rectangular. In addition, the sulcus in *N. belloci* is almost closed and opens only through a small neck toward the dorsal rim. Therefore, we assign our specimens to *P. compactus* based on comparison with the specimens from the Zanclean of southeast France, northern Italy and Portugal

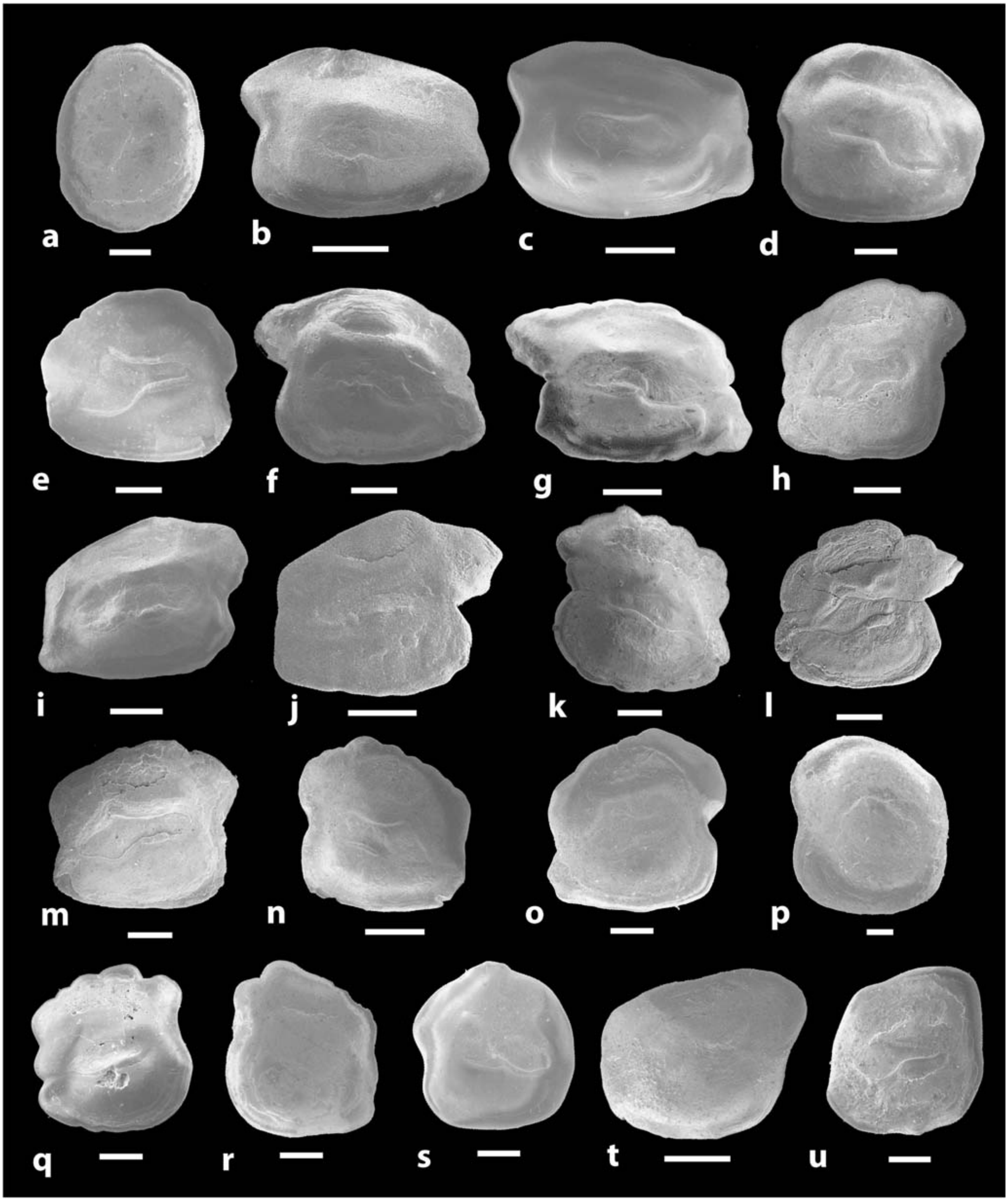

Fig. 3 Fish otoliths from Agia Triada section. **a** *Aphia minuta* (ATS1; R), **b** *Chromogobius zebratus* (AT7; L), **c** *Chromogobius zebratus* (AT1; L), **d** *Deltentosteus quadrimaculatus* (AT10; L), **e** *Deltentosteus quadrimaculatus* (AT7; R), **f** *Gobius bucchichi* (ATS6; L), **g** *Gobius cobitis* (AT10; L), **h** *Gobius* cf. *couchi* (ATS2; R), **i** *Gobius* cf. *geniporus* (ATS5; R), **j** *Gobius* cf. *paganellus* (AT10; R), **k** *Gobius*? sp. 1 (AT3; L), **l** *Gobius*? sp. 1 (AT3; R), **m** *Gobius*? sp. 2 (AT3; R), **n** *Lesueurigobius friesii* (ATS5; L), **o** *Lesueurigobius sanzi* (ATS5; R), **p** *Lesueurigobius suerii* (ATS5; L), **q** *Gobius*? sp. 1 (ATS1; R), **r** *Gobius*? sp. 1 (ATS1; L), **s** *Pomatoschistus marmoratus* (AT10; L), **t** *Thorogobius* sp. (ATS7; R), **u** *Gobius*? sp. 3 (ATS8; R). R right otolith, L left otolith. Scale 1 mm for **b**; 500 μm for **c**, **d**, **e**, **g**, **i**, **j**, **l**, **n**, **o**, **t**; 200 μm for **a**, **f**, **h**, **k**, **m**, **p**, **q**, **r**, **s**, **u**

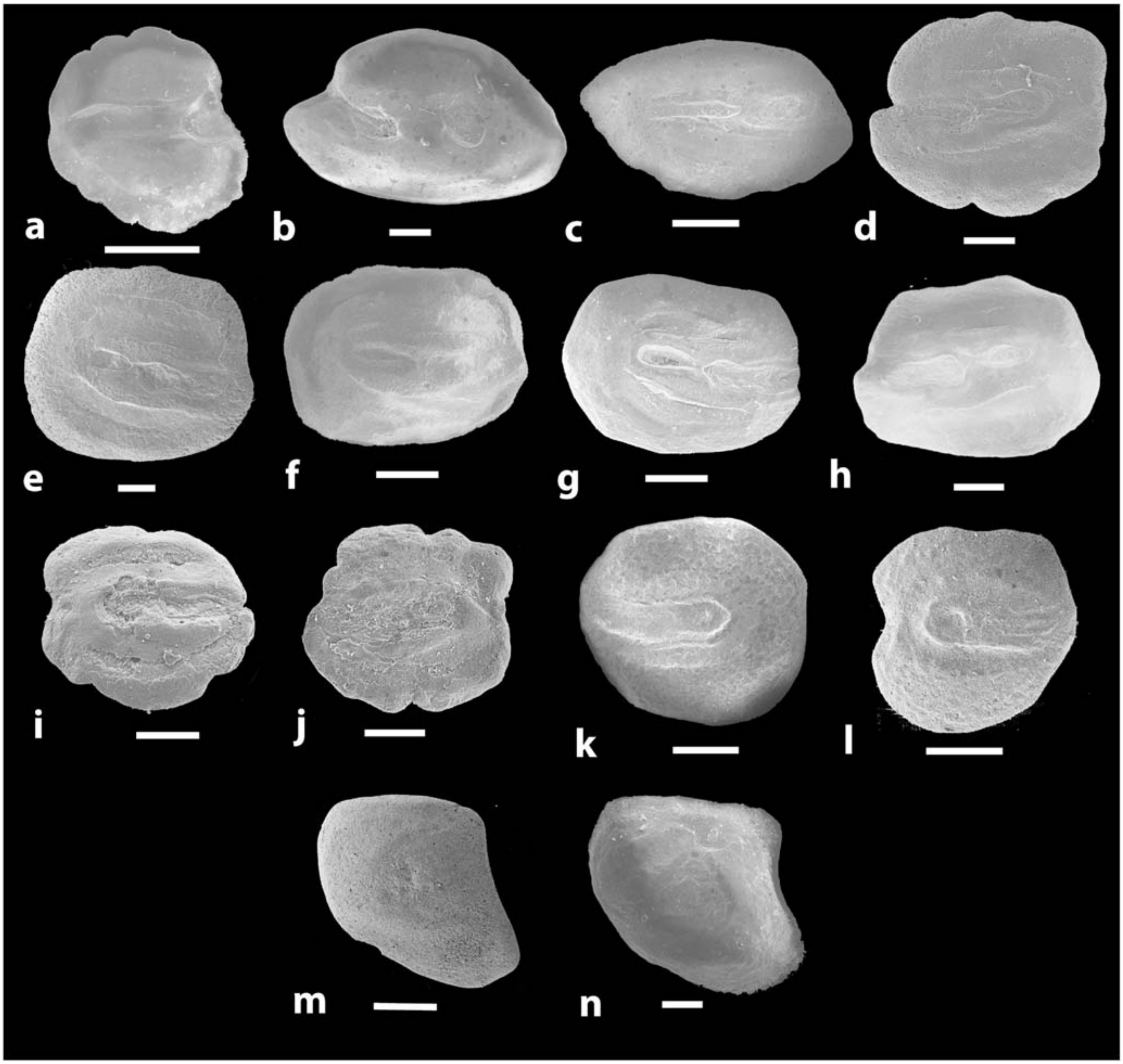

Fig. 4 Fish otoliths from Agia Triada section. **a** Gobiiformes indet. (AT12; L), **b** *Blennius ocellaris* (AT11; R), **c** Citharidae indet. (AT10; L), **d** *Scophthalmus rhombus* (AT10; R), **e** *Arnoglossus kokeni* (AT12; L), **f** *Arnoglossus laterna* (AT1; L), **g** *Arnoglossus laterna* (AT2; L), **h** *Arnoglossus* cf. *laterna* (ATS1; R), **i** *Achirus* sp. (ATS1; R), **j** *Achirus* sp. (ATS1; L), **k** *Buglossidium luteum* (AT10; R), **l** *Microchirus variegatus* (AT12; L), **m** *Cynoglossus obliqueventralis* (AT10; R), **n** *Cynoglossus obliqueventralis* (AT3; R). R right otolith, L left otolith. Scale 500 μm for **a**, **f**, **h**, **k**, **l**, **m**; 200 μm for **c**, **d**, **e**, **g**, **i**, **j**, **n**; 100 μm for **b**

(Schwarzhans 1981, 1986; Nolf and Cavallo 1995; Nolf 2013), which exhibit the same characters.

Order Clupeiformes Bleeker, 1959
Family Clupeidae Cuvier, 1817
Genus *Spratelloides* Bleeker, 1851
Type species: *Spratelloides argyrotaenia* Bleeker, 1851 [=*Clupea argyrotaenia* Bleeker, 1851]; Recent from Makassar, Indonesia.

Spratelloides sp.
Fig. 2d

Material: One right otolith from sample ATS1 and one left otolith from sample ATS5 (AMPG_OT_AT-8–9).
Description: The otoliths of *Spratelloides* are elongated with a very protruding rostrum and a much smaller antirostrum separated by a small excisura. The sulcus is divided into a triangular ostium opening antero-dorsally and an oval cauda.

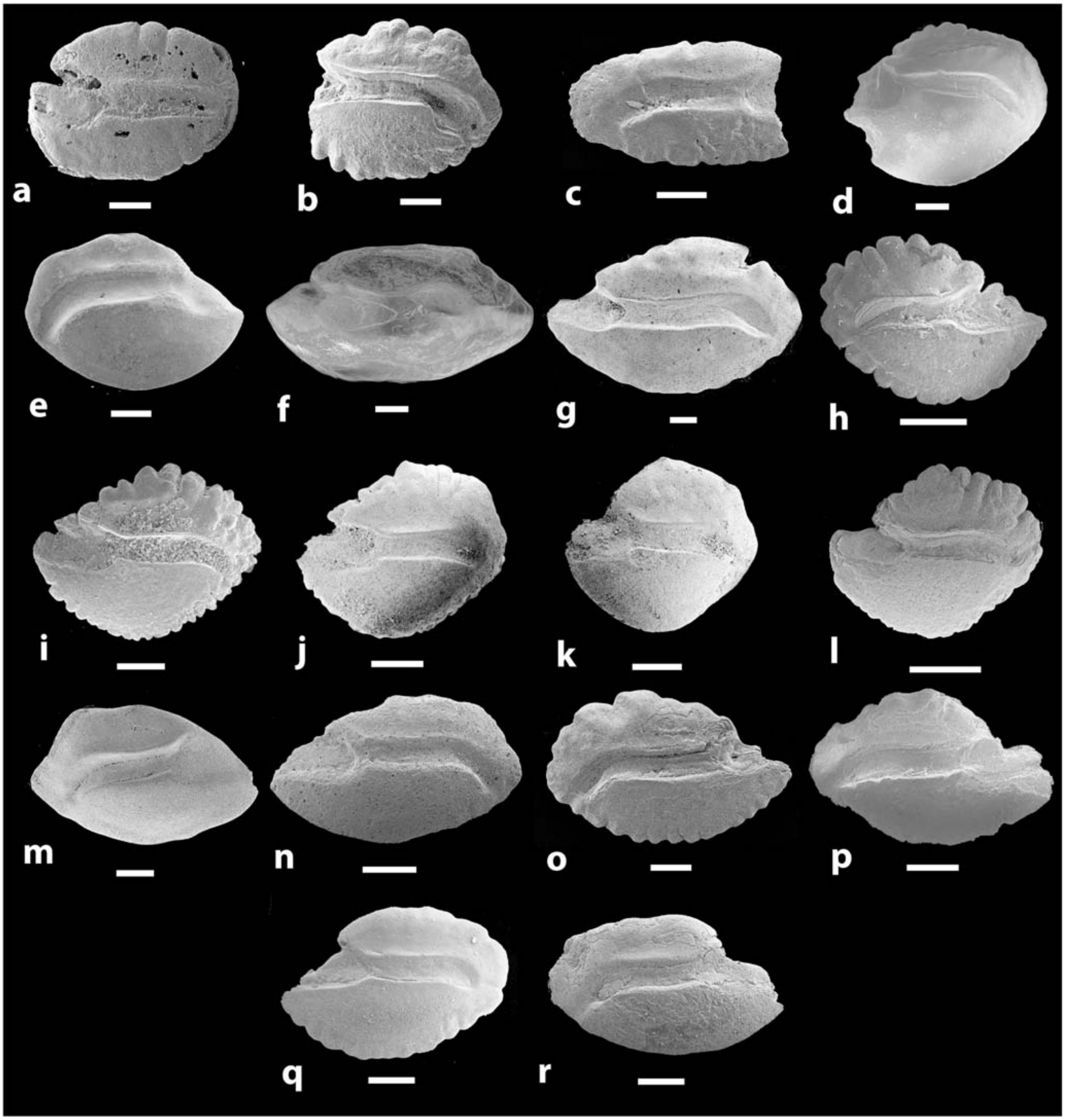

Fig. 5 Fish otoliths from Agia Triada section. **a** *Verilus mutinensis* (AT7; R), **b** Mullidae (AT10; R), **c** Percidae indet. (AT10; L), **d** *Pomadasys incisus* (AT7; R), **e** Haemulidae indet. (AT10; L), **f** *Cepola macrophthalma* (AT1; R), **g** *Boops boops* (ATS3; R), **h** *Dentex gibbosus* (AT12; L), **i** *Dentex macrophthalmus* (ATS1; R), **j** *Dentex maroccanus* (ATS5; R), **k** *Dentex maroccanus* (ATS3; R), **l** *Dentex maroccanus* (AT10; R), **m** *Diplodus annularis* (AT10; L), **n** *Oblada melanura* (AT10; R), **o** *Pagellus acarne* (AT10; L), **p** *Pagellus bogaraveo* (AT7; L), **q** *Pagellus erythrinus* (AT3; R), **r** *Spicara maena* (AT5; L). R right otolith, L left otolith. Scale 1 mm for **d**, **e**, **j**, **k**, **l**, **n**; 500 μm for **a**, **b**, **c**, **f**, **g**, **h**, **i**, **m**, **o**, **p**, **q**, **r**; 100 μm for **e**

The cristae superior and inferior are strong and delineate the sulcus, which is rather deep. The crista superior forms an angleat the point between the ostium and the cauda. The dorsal and posterior rims are round, whereas the ventral rim shows an indentation.

Remarks: Skeletons of *Spratelloides* are often found in the Neogene sediments of the Mediterranean region (e.g. Gaudant 2002). However, otoliths are not as common. The specimens examined here show great similarity to the Recent species *Spratelloides delicatulus* (Nolf 2013) found also as fossil from the Pliocene of southeast France (Nolf and Cappetta 1988) in terms of the shape of the rim and the morphology of the sulcus and very importantly the ventral indentation. The otoliths of *S. gracilis* from the present Pacific Ocean (Rivaton and Bourret 1999) show a wider and more uniform sulcus since they lack the clear indentation of the crista superior. Indeed, we would tend to assign these specimens to *S. delicatulus.* However, we only retain the genus identification due to the small number of specimens found and the lack of comparative material from other species.

Order Ophidiiformes Berg, 1937
Family Bythitidae Gill, 1861
Genus *Grammonus* Gill in Goode and Bean, 1896
Type species: *Grammonus ater* (Risso, 1810) [= *Oligopus ater* Risso, 1810]; Recent from Gulf of Saint-Hospice, Nice, France, northwestern Mediterranean Sea.
Grammonus bassolii (Nolf, 1980)
Fig. 2o

1980 *Oligopus bassolii* Nolf, p. 121, pl. 19, figs. 1–5
2015 *Grammonus bassoli* (Risso, 1810); Lin et al., fig. 4 (14, 15)
2017 *Grammonus bassoli* (Risso, 1810); Agiadi et al., fig. 5 (1)

Material: One right otolith in sample ATS6 (AMPG_OT_AT-50).
Description: The otoliths of this species are very elongated with pointed ends. The sulcus is central, oval and high.
Remarks: The specimen figured here resembles closely those from the Tortonian–Messinian of Crete (Agiadi et al. 2017) and Northern Italy (Lin et al. 2015) in terms of the sulcus and the overall shape. The otoliths of *G. bassolii* are more elongate and more strongly angular in both the posterior and anterior ends than those of *G. ater* from the late Zanclean of Crete (Agiadi et al. 2013a) and the Gelasian of Rhodes (Agiadi et al. 2019).

Order Gobiiformes Günther, 1880
Family Gobiidae Cuvier, 1816
Genus *Chromogobius* de Buen, 1930
Type species: *Chromogobius quadrivittatus* (Steindachner, 1863) [= *Gobius quadrivittatus* Steindachner, 1863]; type by original designation; Recent from Morocco.

Chromogobius zebratus (Kolombatović, 1891)
Fig. 3b, c

1891 *Gobius depressus* Kolombatović
1971 *Chromogobius zebratus* (Kolombatović, 1891); Miller
2013 *Chromogobius zebratus* (Kolombatović, 1891); Nolf, pl. 316
2018 *Chromogobius zebratus* (Kolombatović, 1891); Lombarte et al., fig. 4c
2019 *Chromogobius zebratus* (Kolombatović, 1891); Agiadi et al., fig. 4B

Material: One left otolith from sample AT1, two left otoliths from sample AT2, one right otolith from sample AT3, one right and one left otolith from sample AT7, one right otolith from sample AT9, two right otoliths from sample AT10, one right otolith from sample AT11 (AMPG_OT_AT-143–151).
Description: These specimens are elongated rectangular with a central and deep sulcus, separated into an ostium and a smaller cauda. The postero-dorsal angle is stronger than the antero-ventral angle. There is a deepening in the dorsal area and a curved fissure in the ventral area.
Remarks: Nolf and Girone (2006) reported *Callogobius* sp. from the Zanclean deposits of northern Italy. However, the figured specimens in that study strongly resemble those of *C. zebratus* (Nolf 2013; Lombarte et al. 2018). It is possible, therefore, that these specimens from northern Italy are also *C. zebratus.*

Genus *Gobius* Linnaeus, 1758
Type species: *Gobius niger* Linnaeus, 1758; Recent from eastern Atlantic Ocean.

Gobius bucchichi Steindachner, 1870
Fig. 3f

1870 *Gobius bucchichi* Steindachner
2018 *Gobius bucchichi* Steindachner, 1870; Lombarte et al., fig. 3B

Material: One left otolith in sample ATS6 (AMPG_OT_AT-213).
Description: This otolith is rectangular rhomboidal. The protrusion of the postero-dorsal angle is inclined toward the outer face. The dorsal rim is almost flat with a small convexity around the middle, whereas the ventral margin is flat. The anterior rim shows a small notch in the middle, and the antero-ventral angle is only slightly pointed. The sulcus is inclined and oval.

Gobius cobitis Pallas, 1814
Fig. 3g

1814 *Gobius cobitis* Pallas
2018 *Gobius cobitis* Pallas, 1814; Lombarte et al., fig. 3D

Material: Two left and one right otolith from sample AT7, four left and six right otoliths from sample AT10 (AMPG_OT_AT-214–226).
Description: The otoliths of this species are rectangular and longer than high, with clear postero-dorsal and antero-ventral projections. The sulcus is centred and slightly deep. The cauda and the ostium are round to oval and characterised by the presence of colliculi. The ventral margin is flat, whereas the dorsal margin is slightly oblique with a small convexity.
Remarks: The otoliths of this species somewhat resemble *Gobius paganellus*, in that they are longer than high, with a

strong postero-dorsal projection (Lombarte et al. 2018). However, contrary to that species, they show also a prominent antero-ventral projection.

Gobius cf. *couchi* Miller and El-Tawil, 1974
Fig. 3h

cf. 1974 *Gobius couchi* Miller and El-Tawil
cf. 2018 *Gobius couchi* Miller and El-Tawil, 1974; Lombarte et al., fig. 3C

Material: One right otolith from sample ATS2 (AMPG_OT_AT-227).
Description: This specimen is square and rather high. The dorsal margin is rounded, strongly convex in the middle. The ventral margin is flat. The anterior margin has a very shallow notch just above the antero-ventral projection, which is observable barely. The postero-dorsal projection is strong but curved. The sulcus is central and inclined but wider than that of *Gobius bucchichi.*
Remarks: The characteristic of this species that clearly distinguishes it from the other *Gobius* is the dorsal margin convexity and the square shape. Nevertheless, the anterior rim in our specimen is straighter, and the postero-dorsal expansion is more inclined with respect to *G. couchi* figured by Lombarte et al. (2018). In addition, our specimen seems to be higher (maximum height is 650 μm in Fig. 3h).

Gobius cf. *geniporus* Valenciennes in Cuvier and Valenciennes 1837
Fig. 3i

cf. 1837 *Gobius geniporus* Valenciennes
cf. 2018 *Gobius geniporus* Valenciennes, 1837; Lombarte et al., fig. 3H

Material: Two right otoliths from sample ATS5 (AMPG_OT_AT-228).
Description: The otoliths of this species are rhomboidal in shape and longer than they are high. The sulcus is large and located slightly next to the centre. The ostium is round to elliptic, and the cauda is elongated oval-shaped. The dorsal margin is round and shows a postero-dorsal rounded projection. The ventral margin is flat with rounded edges.
Remarks: Regarding the postero-dorsal part and the rather elongate shape, they resemble the specimens of *Gobius paganellus* also identified in the same sample. However, the postero-dorsal projection is blunt, rather than strong and pointed, and most importantly, the sulcus is larger (1020-μm length in Fig. 3i) than in *G. paganellus* (Lombarte et al. 2018).

Gobius? sp. 1
Fig. 3k, l, q, r

Material: Two left and two right otoliths from sample AT3, two right and two left otoliths from sample ATS1 and two left and one right otolith from sample AT12 (AMPG_OT_AT-241–251).
Description: These otoliths are square, with a convex dorsal margin decorated by small lobes. The anterior margin shows two lobes separated by a deep indentation. The sulcus is small, inclined and oval, without colliculi. There is a strong ventral fissure.
Remarks: These specimens do not resemble any of the Recent *Gobius* species, because they are square with no inclination toward the posterior side, as is commonly observed in *Gobius* spp. Our specimens could have been attributed to a *Lesueurigobius* species instead, but they also show a postero-dorsal protrusion that is not present in *Lesueurigobius* spp. (Nolf 2013). In addition, the protrusion observed is on the anterior rim, whereas *G. cobitis* and *G. paganellus* have antero-dorsal protrusions. The same is true also for the specimens figured by Nolf and Martinell (1980) as "*genus* Gobidarum" sp. III, which however are more similar to our specimens in terms of overall shape and the size and form of the sulcus.

Gobius? sp. 2
Fig. 3m

Material: One right otolith in sample AT3 (AMPG_OT_AT-252).
Description: This otolith is rectangular, with a convex dorsal margin and a pointed postero-dorsal angle. The anterior rim is incised. The sulcus is large, deep and delineated. The posterior part of the sulcus is rounded, and the anterior part is square with one angle around the middle of the dorsal side and another around the middle of the ventral side.
Remarks: The form of the sulcus distinguishes this otolith from all the other *Gobius* species.

Gobius? sp. 3
Fig. 3u

2013a "*Gobiidarum*" sp. 1 Agiadi et al., p. 465, fig. 8(20)

Material: One right otolith in ATS8 (AMPG_OT_AT-253).
Description: The most important characteristic is the square shape with distinct angles. The inner face is concave. The sulcus comprises an oval ostium and a cauda with a small colliculum.
Remarks: This species has been previously identified in the late Zanclean of Voutes section (Heraklion prefecture, Crete; Agiadi et al. 2013a). These are small square otoliths with strongly angular posterior and anterior rims. The sulcus in these specimens resembles that of *Aphia minuta* (Lombarte et al. 2018). However, the square and angular shape does not resemble any of the Recent Mediterranean gobiid species

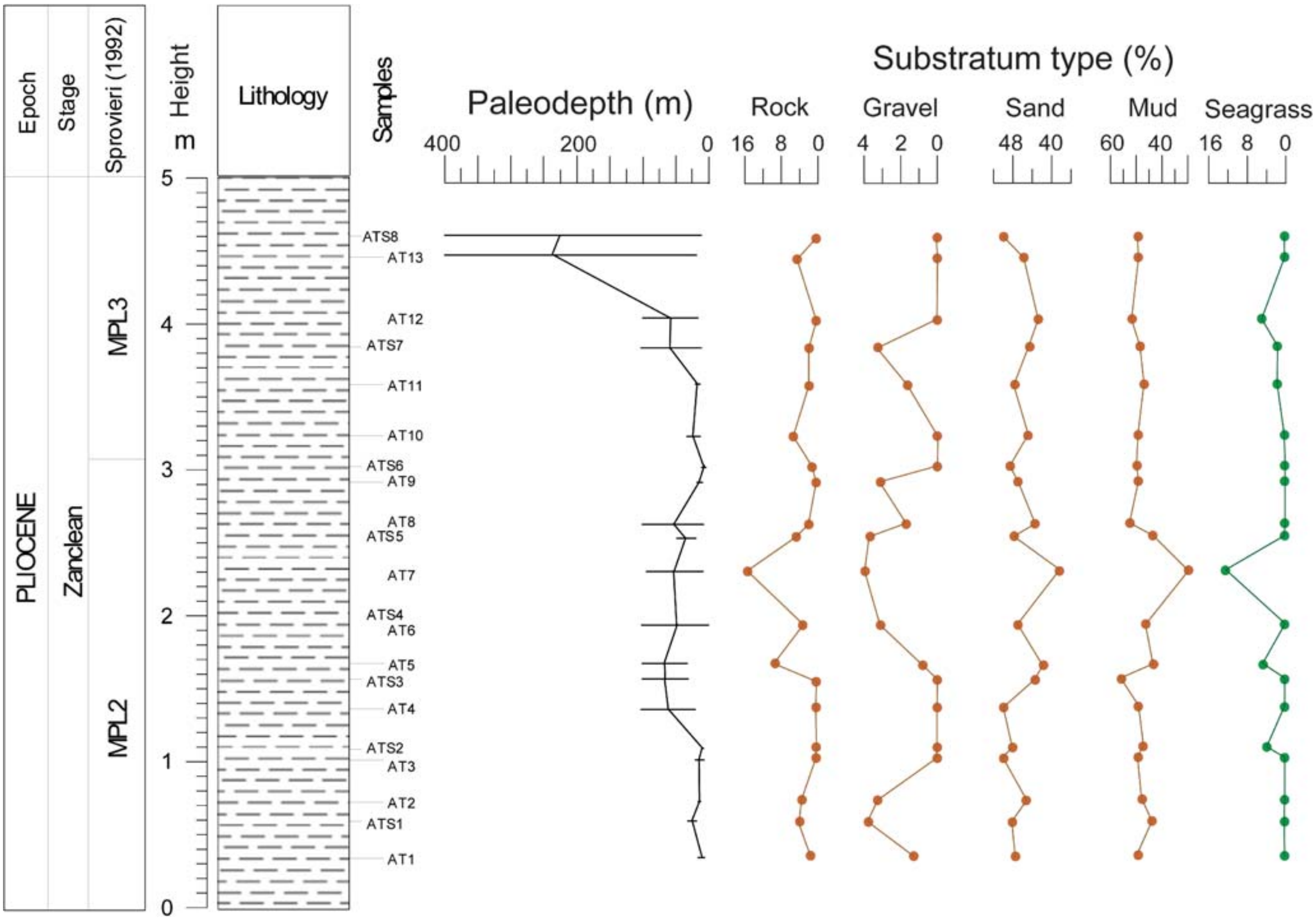

Fig. 6 Palaeobathymetric curve for the Agia Triada section based on the otolith assemblages and relative contribution to the fauna of each group of benthic and benthopelagic fish taxa split based on their substratum preferences, into rock, gravel, sand, mud and seagrass meadows

figured or described by Lombarte et al. (2018).

Genus *Thorogobius* Miller, 1969
Type species: *Thorogobius ephippiatus* (Lowe, 1839) [= *Gobius ephippiatus* Lowe 1839]. Type by original designation.

Thorogobius sp.
Fig. 3t

Material: One right otolith in ATS7 (AMPG_OT_AT-743).
Description: The shape is rhomboidal, longer than high and with a clear round poster-dorsal projection and a flat ventral rim. The sulcus is small and central, and there is a rounded ventral line.
Remarks: This otolith is very similar to the specimens of *G. guerini* figured by Nolf and Martinell (1980). Unlike *G. paganellus* figured by Lombarte et al. (2018), the antero-dorsal protrusion extends mostly toward the dorsal side. We attribute this specimen to *Thorogobius* sp. due to its great similarity to the specimen figured and described by Schwarzhans (2013a), although the antero-dorsal protrusion in the specimens of *T. macrolepis* figured by Lombarte et al. (2018) and *T. angolensis* figured by Schwarzhans (2013b) does not extend as much toward to the dorsal side.

Order Blenniiformes Rafinesque, 1810
Family Blenniidae Rafinesque, 1815
Genus *Blennius* Linnaeus, 1758

Type species: *Blennius ocellaris* Linnaeus, 1758. Type by subsequent designation; location unknown.

Blennius ocellaris Linnaeus, 1758
Fig. 4b

1758 *Blennius ocellaris* Linnaeus
2013 *Blennius ocellaris* Linnaeus, 1758; Nolf, pl. 312

Material: One right otolith from sample AT11 (AMPG_OT_AT-977).
Description: The otoliths of this species are oval elongated, with a clear rostrum and rounded margins. They are longer than higher, with a flat long ventral rim and a rounded short dorsal rim. The sulcus is long, and it is clearly divided into an open ostium and a round cauda.

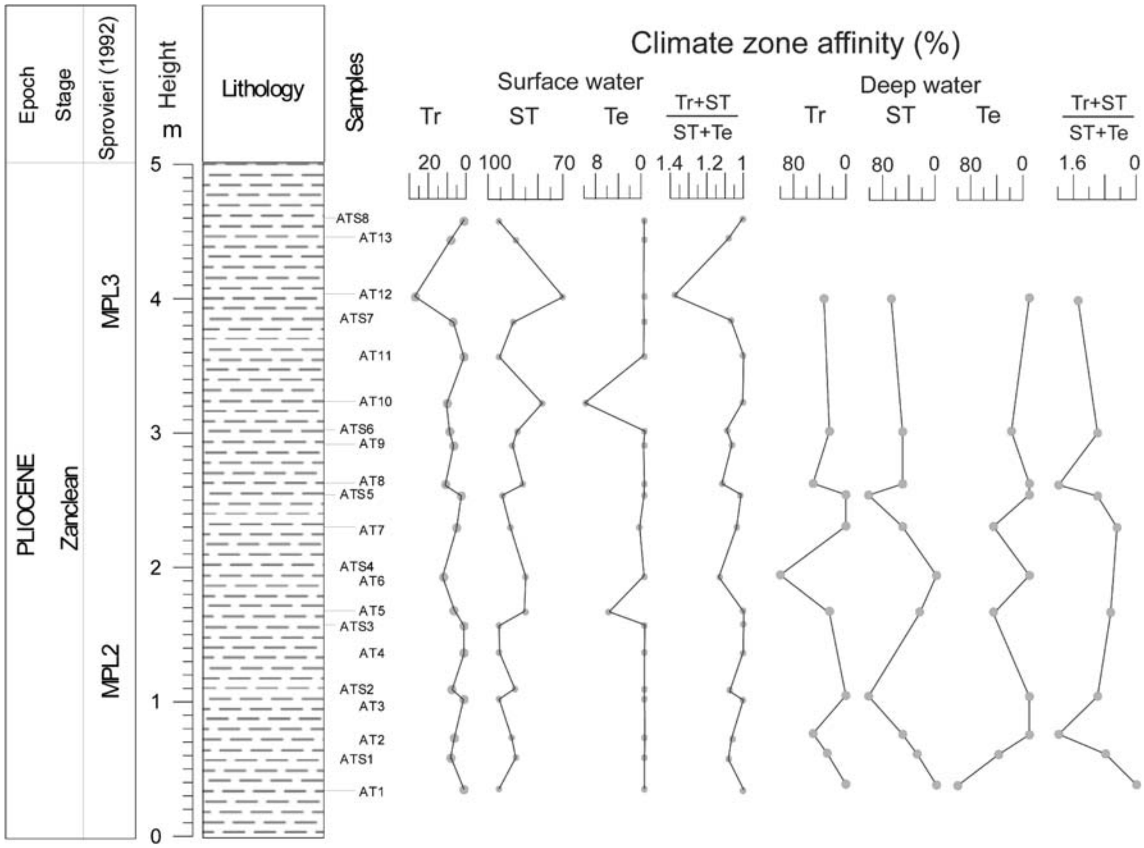

Fig. 7 Climatic affinity groups' contributions to the shallow/surface-water and deep-water fish assemblages. Tr tropical, ST subtropical, Te temperate

Order Pleuronectiformes Bleeker, 1859
Family Scophthalmidae Chabanaud, 1933
Genus *Scophthalmus* Rafinesque, 1810

Type species: *Scophthalmus rhombus* (Linnaeus, 1758) [= *Pleuronectes rhombus* Linnaeus, 1758]. Type by subsequent designation; Recent from Sicily, Italy, Mediterranean Sea.

Scophthalmus rhombus (Linnaeus, 1758)
Fig. 4d

1758 *Pleuronectes rhombus* Linnaeus
1917 *Scophthalmus rhombus* (Linnaeus, 1758); Jordan
2008 *Scophthalmus rhombus* (Linnaeus, 1758); Tuset et al., p. 178, fig. 89(A)

Material: One right otoliths in sample AT10 (AMPG_OT_AT-983).
Description: Elliptic otoliths with dentate margins, especially the ventral margin. The sulcus is separated into a tubular and straight ostium and a round and short cauda; the ostium is much longer than the cauda (270 and 210 µm in length, respectively). This specimen is rectangular with flat posterior rim and curved dorsal and ventral rims. The sulcus is a deep thick line bound by strong cristae. The rostrum is barely visible with a small excisura.

Family Achiridae Rafinesque, 1810
Genus *Achirus* Lacepède, 1802

Type species: *Achirus achirus* (Linnaeus, 1758) [= *Pleuronectes achirus* Linnaeus, 1758]. Location unkown.

Achirus sp.
Fig. 4i, j

Material: One right and one left otolith from sample ATS1 (AMPG_OT_AT-1033–1034).
Description: These otoliths are small, almost square, with convex ventral and anterior margins, almost flat dorsal margin and indented posterior margin. The sulcus is undivided, oval elongated and pointed at the end toward the posterior area. The dorsal margin shows small lobes. There is a very small rounded rostrum, and a very shallow excisura. A ventral line is also present.
Remarks: We could only compare these specimens to those from the Recent west Atlantic species *Achirus lineatus* figured by Nolf (2013). The characteristic shape and lobes around the rims of the otoliths drive us to this identification at the genus

Table 2 Stratigraphic and geographic distribution of the identified fish taxa from the Tortonian until today

Family	Taxon	T	M	Z	P	G	C	MP	UP	H	References
Albulidae	***Pterothrissus compactus***			+							1, 2, 6, 23
Congridae	*Conger conger*	+	+	+	+	+	+	+		+	3–6, 17, 49
	Gnathophis mystax	+		+		+		+		+	3, 6, 17, 49
Clupeidae	*Spratelloides* sp.	+	+	+	+						7–16
Myctophidae	*Ceratoscopelus maderensis*	+	+	+	+	+	+	+		+	1, 3–6, 11, 12, 17–32, 52, 53
	Diaphus rafinesquii	+	+	+	+	+	+	+		+	1, 3, 4, 6, 12, 18, 20, 22, 23, 29–31, 34–36, 49, 50, 52, 53
	Diaphus splendidus	+	+	+	+	+	+	+			1, 4–6, 21–23, 29, 30, 33, 34, 35, 37, 38, 49, 50, 52, 54
	Electrona risso			+	+	+	+	+	+	+	3, 6, 36
	Hygophum hygomii	+	+	+	+	+	+	+	+	+	1, 3, 4–6, 12, 17–23, 25–27, 29–31, 33–35, 49, 50, 52
	Notoscopelus resplendens	+		+	+	+	+				6, 19, 20–23, 25, 33, 49
Bregmacerotidae	***Bregmaceros albyi***	+	+	+	+	+	+	+	+		8, 9, 15, 39, 55–59
Carapidae	*Carapus acus*	+		+	+	+	+	+		+	3, 17, 36, 49
Ophidiidae	*Ophidion barbatum*			+	+	+	+	+		+	3, 4, 6, 17, 36
Bythitidae	***Grammonus bassolii***	+	+	N							49, 50, 52
Gobiidae	*Aphia minuta*		+	+		+	+	+		+	3, 4, 17, 33, 35
	Chromogobius zebratus			N		+	+	+		+	3, 17
	Deltentosteus quadrimaculatus	+	+	+	+	+	+	+		+	3–6, 17, 18, 29, 39, 49, 50, 52
	Gobius bucchichi			N						+	
	Gobius cobitis			N		+				+	17
	Gobius cf. *couchi*			N						+	
	Gobius cf. *geniporus*			N		+				+	17
	Gobius cf. *paganellus*	+		+		+	+	+		+	3, 17, 33, 49, 50
	Lesueurigobius friesii	+	+	+	+	+	+	+		+	3, 4, 6, 17, 22, 29, 38, 39, 49, 50, 52
	Lesueurigobius sanzi		+	+	+	+	+	+		+	3, 6, 17, 21, 33, 35
	Lesueurigobius suerii	+		+	+	+	+	+		+	1, 3–6, 17, 33, 39, 49, 50
	Pomatoschistus marmoratus			N						+	
	Thorogobius sp.			N						+	
	***Gobius*? sp. 3**			+							33
Blenniidae	*Blennius ocellaris*	+		N		+	+	+		+	3, 4, 36, 52
Scophthalmidae	*Scophthalmus rhombus*			N						+	
Bothidae	***Arnoglossus kokeni***	+		+	+	+	+				1, 3–6, 20, 23, 29, 35, 38, 40, 49, 50
	Arnoglossus laterna		+	+	+	+	+	+		+	8, 11, 13, 17, 24–26, 28, 32, 35, 40–44
Achiridae	*Achirus* sp.			N							
Soleidae	*Buglossidium luteum*			+						+	6
	Microchirus variegatus	+		+	+	+	+			+	6, 49, 50
Cynoglossidae	***Cynoglossus obliqueventralis***	+		+							6, 40
Acropomatidae	***Verilus mutinensis***	+	+	+	+	+	+				1, 3, 6, 18, 20–23, 25, 31, 35–38, 45, 49, 50
Haemulidae	*Pomadasys incisus*	+	+	+						+	6, 49, 50
Cepolidae	*Cepola macrophthalma*	+	+	+	+	+	+	+		+	1, 3–6, 17, 20–23, 29, 31, 33, 35, 37, 38, 40, 42, 49, 50
Sparidae	*Boops boops*			+	+	+			+	+	6, 9, 10, 17, 46, 47
	Dentex gibbosus			N						+	
	Dentex macrophthalmus	+	+	+	+	+				+	6, 17, 35, 47–51
	Dentex maroccanus	+	+	+	+	+	+	+	+	+	1, 4–6, 17, 18, 20, 23, 35, 36, 38, 41, 47–50
	Diplodus annularis			+			+			+	3, 6
	Oblada melanura			+			+	+		+	3, 6, 33
	Pagellus acarne	+		+						+	6, 50, 52
	Pagellus bogaraveo			+		+	+	+		+	1, 3, 6, 17, 46
	Pagellus erythrinus			+	+	+	+			+	1, 5, 6, 20, 23, 33, 42
	Spicara maena			+						+	6

Chronostratigraphic stages: *T*: Tortonian, *M*: Messinian, *Z*: Zanclean, *P*: Piacenzian, *G*: Gelasian, *C*: Calabrian, *MP*: Middle Pleistocene, *UP*: Upper Pleistocene, *H*: Holocene. Each "N" indicates a new record. Extinct species appear in bold letters. Present-day distributions are taken from the FishBase Database (Froese and Pauly 2018). References: 1. Nolf and Cavallo (1995), 2. Schwarzhans (1986), 3. Agiadi et al. (2018), 4. Girone and Varola (2001), 5. Nolf and Girone (2000), 6. Nolf and Girone et al. (2006), 7. Carnevale et al. (2006), 8. Landini and Sorbini (1993), 9. Gaudant et al. (1994), 10. Gaudant (2001), 11. Sorbini (1988), 12. Bossio et al. (1986), 13. Bedini and Landini (1986), 14. Gaudant et al. (2010), 15. Gaudant (2004), 16. Gaudant (1993), 17. Agiadi et al. (2019), 18. Agiadi et al. (2011), 19. Brzobohaty and Nolf (1996), 20. Nolf and Martinell (1980), 21. Nolf et al. (1998), 22. Girone (2007), 23. Nolf and Cappetta (1988), 24. Gaudant (2002), 25. Schwarzhans (1979), 26. Landini and Menesini (1986), 27. Sorbini and Landini (2003), 28. Landini and Varola (1983), 29. Girone (2000), 30. Girone (2003), 31. Anfossi and Mosna (1972), 32. Aruta and Greco (1980), 33. Agiadi et al. (2013a), 34. Landini and Menesini (1978), 35. Girone et al. (2010), 36. Girone et al. (2006), 37. Anfossi and Mosna (1976), 38. Anfossi and Mosna (1979), 39. Moissette et al. (2018), 40. Schwarzhans (1999), 41. Landini (1981), 42. Landini et al. (1990), 43. Landini and Sorbini (1992), 44. Sorbini (2000), 45. Anfossi et al. (1982), 46. Aura Tortosa et al. (2002), 47. Sampson (1998), 48. Hoedemakers and Batllori (2004), 49. Lin et al. (2017a), 50. Lin et al. (2015), 51. Nolf and Steurbaut (1983), 52. Agiadi et al. (2017), 53. Karakitsios et al. (2017), 54. Brzobohaty and Nolf (2000), 55. Pedley (1978), 56. Gaudant et al. (2010), 57. Cornée et al. (2019), 58. Gaudant et al. (1997), 59. Gaudant and Courme (2014) level only. However, the figured specimens have clear colliculi inside the sulcus, which we could not observe in our specimens.

Order Perciformes Bleeker, 1859
Family Haemulidae Gill, 1885
Genus *Pomadasys* Lacepède, 1802

Type species: *Pomadasys argentea* (Forsskål, 1775) [= *Sciaena argentea* Forsskål, 1775]. Location unknown.

Pomadasys incisus (Bowdich, 1825)
Fig. 5d

1825 *Anomalodon incisus* Bowdich
1997 *Pomadasys incisus* (Bowdich, 1825); Nolf and Marques Da Silva, pl. 1, fig. 9a
2006 *Pomadasys incisus* (Bowdich, 1825); Nolf and Girone, pl. 1, figs. 6–8
2013 *Pomadasys incisus* (Bowdich, 1825); Nolf, pl. 251

Material: One right otolith in sample AT7 (AMPG_OT_AT-1069–1070).
Description: Almost round shape with large round ostium and long cauda. High and thick otoliths. The single otolith assigned to this species is oval with a large, wide, circular ostium and a long, thin cauda that curves toward the postero-ventral area. The ostium is clearly separated from the cauda by indentations both in the ventral and in the dorsal cristae. The ventral area is very large.

Palaeoecology and palaeobathymetry

We use the present-day distribution of the identified benthic and benthopelagic fish taxa in each sediment sample (data presented in the Supplementary Material) to estimate the palaeobathymetry along the Agia Triada section (Fig. 6). Figure 6 also shows the relative contribution to the assemblage of benthic and benthopelagic taxa, which are grouped according to their substratum preferences (detailed data available in Supplementary Material). The sea bottom is mostly sand and mud for the entire interval covered by our section, with small contributions of rock and gravel occasionally, and rarer appearances of seagrass. Around the middle of the section (sample levels AT5–AT8), the concurrent peaks in the relative contributions of benthic and benthopelagic fish taxa preferring rock, gravel and/or seagrass meadows, under approximately the same palaeodepth, suggest a small change in the palaeoenvironmental setting. However, conditions before and after this interval are about the same with sandy and muddy sea bottom. Nevertheless, rock and gravel increase equally also at sample levels ATS1–AT2 and ATS7, but by smaller values than before.

The relative contribution of each climate affinity group in the neritic/surface water and deep-water assemblages at each sample level is presented in Fig. 7 (detailed data available in Supplementary Material). Overall, the fish assemblages are composed of subtropical and secondarily of tropical taxa. The contribution of tropical taxa increases regularly at sample levels ATS1, ATS2, AT6, AT8 and ATS12; particularly, the relative abundance of tropical taxa increases most strongly at sample level AT12. Temperate (cold-water) taxa in the surface-water assemblage appear only in sample levels AT5, AT7 and AT10, corresponding well to the deep-water assemblage temperate taxa contributions in sample levels AT5, AT7 and ATS6. However, the deep-water assemblage is especially rich in temperate taxa also in sample levels AT1 and ATS1. The deep-water assemblages contain the mesopelagic myctophids and the species *Pterothrissus compactus*. Thus, the observed alterations between temperate and tropical taxa in the deep-water assemblages mostly correspond to recurrent replacements between the mesopelagic species *Ceratoscopelus maderensis*, *Diaphus rafinesquii*, *Electrona risso* (temperate) and *Diaphus splendidus* (tropical). The (Tr + ST)/(ST + Te) ratio is used here to facilitate assessment of these results. Ratio values above one in the shallow/surface-water assemblages, as observed here in all sample levels, should reflect climate warming. On the other hand, the deep-water assemblages present also values below one, suggesting cooling of the intermediate and deeper waters of the eastern Mediterranean at sample levels ATS1, AT1, AT5 and AT7.

Discussion

Palaeobiogeography

Table 2 presents the stratigraphic distribution of the identified taxa within the Mediterranean from the Tortonian until today. Ten species and two genera were identified for the first time in the Zanclean of the Mediterranean: *Grammonus bassolii*, *Chromogobius zebratus*, *Gobius bucchichi*, *Gobius cobitis*, *Gobius* cf. *couchi*, *Gobius* cf. *geniporus*, *Pomatoschistus marmoratus*, *Blennius ocellaris*, *Scophthalmus rhombus*, *Thorogobius* sp., *Achirus* sp. and *Dentex gibbosus*. Among the taxa identified here, only seven are extinct species that have been previously found only in the Mediterranean: *Pterothrissus compactus*, *Bregmaceros albyi*, *Grammonus bassolii*, *Gobius*? sp.3, *Arnoglossus kokeni*, *Cynoglossus obliqueventralis* and *Verilus mutinensis*. Moreover, four of the identified extant taxa are not found today in the Mediterranean: *Spratelloides* sp., *Diaphus splendidus*, *Notoscopelus resplendens* and *Achirus* sp.

Overall, this means that approximately 77% of the identified Zanclean taxa are the same as in the present-day coastal Mediterranean faunas. Notably, only ~44% of the mollusc species identified from the same sediments (Koskeridou et al. 2017) appear in the modern Mediterranean. In the eastern Mediterranean (Agiadi et al. 2019), this percentage reached 100% by the Gelasian. Moreover, a deeper-water fauna identified from Crete and covering a slightly younger interval in the late Zanclean between 3.84 and 3.61 Ma (Agiadi et al. 2013a) showed lower similarity to present-day fish assemblages, with only 57.5% of the identified taxa occupying the present-day Mediterranean. These observations suggest that the modern coastal fish faunas were established earlier in the Mediterranean than deeper water fish faunas and invertebrate faunas.

By comparing Crete record with the one from Peloponnesus that is presented here, we observe that both records include congrids, but different genera and species. In particular, the extra-Mediterranean species *Pseudophichthys splendens* and the extinct Miocene Mediterranean species *Pseudophichthys escavaratierensis* and *Rhynchoconger pantanellii* were found in Voutes section, Crete (Agiadi et al. 2013a), as well as in other Pliocene localities in the western Mediterranean (Schwarzhans 1986; Nolf and Cappetta 1988; Nolf and Girone 2006; Girone 2007). On the other hand, we identified only two extant Mediterranean congrids in the Agia Triada material: *Conger conger* and *Gnathophis mystax*. This is unexpected, considering that Agia Triada section is older than some of the other Pliocene localities are. The only explanation we can offer at this point is that all these species cohabited in the Mediterranean during the Zanclean.

Notable in our assemblages is the record for the first time of several goby species that are known from the present-day Mediterranean coasts. Previously, specific identifications of gobies were often avoided due to the lack of comparative material from Recent fish specimens, leading to several open nomenclature identifications. Fortunately, a recent study provided the missing data from the Recent material (Lombarte et al. 2018). Here, we have used this information to provide improved identifications. In Table 2, *Chromogobius zebratus*, *Gobius bucchichi*, *Gobius cobitis*, *Gobius* cf. *couchi*, *Gobius* cf. *geniporus* and *Thorogobius* sp. are indicated as first records as fossils for the Zanclean of the Mediterranean. This is not surprising, as extant Mediterranean gobies are expected to have evolved around the middle Miocene (Penzo et al. 1998). On the other hand, according to Huyse et al. (2004), *Pomatoschistus marmoratus* evolved around the middle Pliocene, in agreement with our record here.

Palaeoenvironmental reconstruction

The fish assemblages in Agia Triada suggest that the study area was a very shallow, coastal environment during the Zanclean (Fig. 6), in general agreement with previous results by Koskeridou et al. (2017). The invertebrate fauna of Agia Triada section is characterised by abundant bivalves and gastropods, accompanied by benthic forams, echinoids (plates and spines) and rarer barnacles, scaphopods, ostracods and planktonic forams. Bryozoans and decapod crustaceans are always very scarce. Some gravels and charcoal debris also occur. In particular, the molluscan fauna in samples ATS1–ATS8 was composed of soft bottom representatives of the lower infralittoral to upper circalittoral zone (species in dominance: *Turritella tricarinata*, *Sorgenfreispira brachystoma*, *Nassarius semistriatus*, *Tornus excalliferus*, *Ambrogia mytiloides*, *Litigiella glabra*, *Venus nux* and *Pitar rudis*). Indeed, the mollusc assemblages suggest depths between 30 and 50 m (Koskeridou et al. 2017), whereas the palaeobathymetric method based on otoliths, which is applied here, gives depth estimates with smaller range, especially in the lower part of the section. Considering this small difference between the two approaches, we would suggest that the palaeobathymetric method based on otoliths underestimates the palaeodepth in this case of a very shallow marine setting. Therefore, we assume the upper limit of the estimated ranges to be more realistic, which in fact coincides with the estimates based on the mollusc assemblages.

The analysis of the substrate preferences of the identified fish taxa (Fig. 6) indicates that the early Pliocene Agia Triada coast had mostly sand and muddy bottoms with small patches of hard substrates in the surrounding area. Indeed, the majority of mollusc species in Agia Triada section lived stationary within the upper few centimetres of the muddy substrate, suggesting that the sea bottom was characterised by well-oxygenated marine conditions (Koskeridou et al. 2017). Moreover in the lower part of the section (ATS1, ATS3, ATS5), gastropod species preferring rocks or gravels (e.g. *Calyptraea chinensis*, *Anomia ephippium*) were present suggesting the existence of such substrate in the neighbouring area. Species known to live as commensals on echinoderms, sipunculids and porifers such as *L. glabra*, *Kurtiella bidentata*, *Hemilepton nitidum* and species of Pyramidellidae were also present. Furthermore, the fish assemblages indicate that at the middle part of the section (AT5–AT8), the contributions of rock, gravel and seagrasses increased without any change in the palaeobathymetry, although never surpassing those of sand and mud. This may be explained by an increase in river input in the area that would bring more terrigenous material and wash away smaller sediment fractions, while increasing nutrients that support the growth of seagrasses.

The study area fell within the lower part of the subtropical zone, with fish assemblages that include mostly subtropical and tropical taxa. The thermophilic molluscan taxa encountered in Agia Triada (*Ficus geometra*, *Sveltia varicosa*, *Solatia piscatoria*, *Tribia uniangulata*, *Bivetiella cancellata* and *Persististrombus coronatus*; Koskeridou et al. 2017) are consistent with the tropical–subtropical conditions inferred from fish assemblages. Two cooling intervals are suggested by the episodic appearance of temperate taxa at sample levels

AT7 and AT10 (Fig. 7). In particular, the increase of rock- and gravel-dwelling demersal fish abundances at sample level AT7 (Fig. 6) suggests an increase in river input during this cold event. Previously, Koskeridou et al. (2017), based on the planktonic foraminifera assemblages, reported these events in the same section, which were interrupted by a warm period, as suggested by the high sea surface temperature (SST) based on the planktonic palaeoclimatic curve (PPC). The results of the palaeoecological analysis presented here corroborate this conclusion (Fig. 7). Furthermore, we note that the cooling and warming events were expressed in the coastal as well as in the deep-water fauna, although in a lower degree. Finally, the warming trend suggested for the early Pliocene eastern Mediterranean by Kontakiotis et al. (2016) seems to have affected the fish fauna through more intense and long-lasting introductions of warm-water species toward the upper part of the section (Fig. 7).

Conclusions

In the present study of the early Pliocene fish assemblages from Peloponnesus (Greece), we identified 54 taxa from 23 families and 8 orders of fish based on otoliths. Of these, 12 taxa are reported for the first time from the Zanclean of the Mediterranean.

Furthermore, we were able to reconstruct the palaeoenvironmental setting in the study area through the palaeobathymetric and palaeoecological analyses of the identified assemblages. The studied sediments were deposited in a coastal marine setting, with depths between 10 and 100 m for the most part of the section. The substratum was mostly sand and secondarily mud, although coarse sediment and rocks formed significant microhabitats around the middle part of the section. The pelagic and demersal fish associations were composed mostly of subtropical and tropical fish. Two cooling intervals were recognised by the appearance of temperate taxa and the decrease in the tropical species relative abundance.

Coastal marine ecosystems appear to be the first to respond to environmental perturbation in the past, as well as today. The early Pliocene coastal fish fauna of Agia Triada provides insight into the evolution of the coastal fish assemblages in the Mediterranean from the Tortonian until today. Particularly, our focus on the Zanclean fauna allows us to link the Pleistocene and Holocene data to the Miocene oceanic fish faunas prevailing in the Mediterranean even before its very formation. Admittedly, we observe continuity in the record, and several species replacements took place over gradually, through multiple departures and reintroductions in the Mediterranean basin. Overall, the fish fauna of this early Pliocene Mediterranean coast shows great similarities to the Pleistocene one in terms of functional traits of the included species, but also directly in its taxonomic composition.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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