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PALEOBATHYMETRIC INTERPRETATION OF THE FISH OTOLITHS FROM THE LOWER - MIDDLE QUATERNARY DEPOSITS OF KEPHALLONIA AND ZAKYNTHOS ISLANDS (IONIAN SEA, WESTERN GREECE)

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Abstract. Fish otoliths are herein used to estimate the depositional depth of the Early - Middle Pleistocene deposits at SE Zakynthos and SW Kephallonia Islands (Ionian Sea, Western Greece), through comparison with the modern bathymetric distributions of the identified fish taxa. These estimates provide a more detailed picture of the depth variations for the Gelasian - Ionian stage interval in the study areas. The Lower Pleistocene marine deposits of the Gerakas Formation (SE Zakynthos Island, Ionian Sea) were deposited at average depths of 400-450 meters, with eustacy playing an important role in the depth variability, between 1.95 - 1.73 Ma. An uplifting episode, followed by subsidence takes place between 1.73 - 1.66 Ma, taking the area to 200-300 meters of depth, and then back to 400-500 meters. However, the area seems uplifted again to 200-400 meters later on in the Calabrian stage (1.25 - 0.97 Ma). Sedimentation of the Akrotiri deposits (NW Kephallonia Island, Ionian Sea), during the same chronostratigraphic interval, took place in a similar setting. At the Early Pleistocene (1.95 - 1.73 Ma) this basin reached depths of 400-450 meters, with uplift and following subsidence taking place between 1.73 - 1.66 Ma. Overall, the application of fish otolith paleobathymetry in the study areas provide a detailed picture of the depth variations for the Early Quaternary interval and refine the currently hypothesized pattern of tectonic movements.

Riassunto. Gli otoliti di pesce sono utilizzati in questo articolo per stimare la profondità di deposizione dei sedimenti di età pleistocenica, inferiore e media, nelle aree SE di Zante e SO di Cefalonia (Isole Ioniche, Grecia occidentale), mediante confronto con la attuale distribuzione batimetria delle specie identificate. Queste stime forniscono un quadro più dettagliatp delle variazioni di profondità nell'area in studio durante l'intervallo Gelasiano-Ioniano. I depositi marini del Pleistocene ineferiore della Formazione Gerakas (SE ell'isola di Zante) sono stati accumulati ad una profondità media di 400-450 metri, con variazioni della profondità controllate significativamente dall'eustatismo tra 1.95 - 1.73 Ma. Un episodio di sollevamento, seguito da subsidenza avvenne tra 1.73 - 1.66 Ma, portando l'area dapprima a 200-300 metri profondità e poi nuovamente a 400-500 metri. Tuttavia l'area sembra esser stata sollevata nuovamente a 200-400 metri più tardi nel Calabriano (1.25 - 0.97 Ma). La sedimentazione nella successione di Akrotiri (NO dell'isola di Cefalonia) durante lo stesso intervallo di tempo avvenne in una situazione confrontabile. Nel Pleistocene inferiore (1.95 - 1.73 Ma) il bacino raggiunse una profondità di 400-450 metri, seguita da elevamento e nuovamente subsidenza tra 1.73 - 1.66 Ma. Nell'insieme, l'applicazione della paleobatimetria basata sugli otoliti di pesce fornisce un quadro dettagliato delle variazioni di profondità durante il Quaternario e migliora il quadro interpretativo corrente sull'insieme dei movimenti tettonici.

Introduction

Fish otoliths are a unique tool in the investigation of the teleostean fish paleofaunas, due to their taxon - specific morphology, high frequency with which they are found in sediments of varying environments, and their generally good preservation (Nolf 1985). They are known to constitute very valuable paleoecological and paleobathymetrical indicators (Nolf & Brzhobohaty 1994; Girone 2000, 2005) and they also provide important paleobiologic and paleoclimatic information, yielding a level of detail and accuracy rarely matched (Campana 1999).

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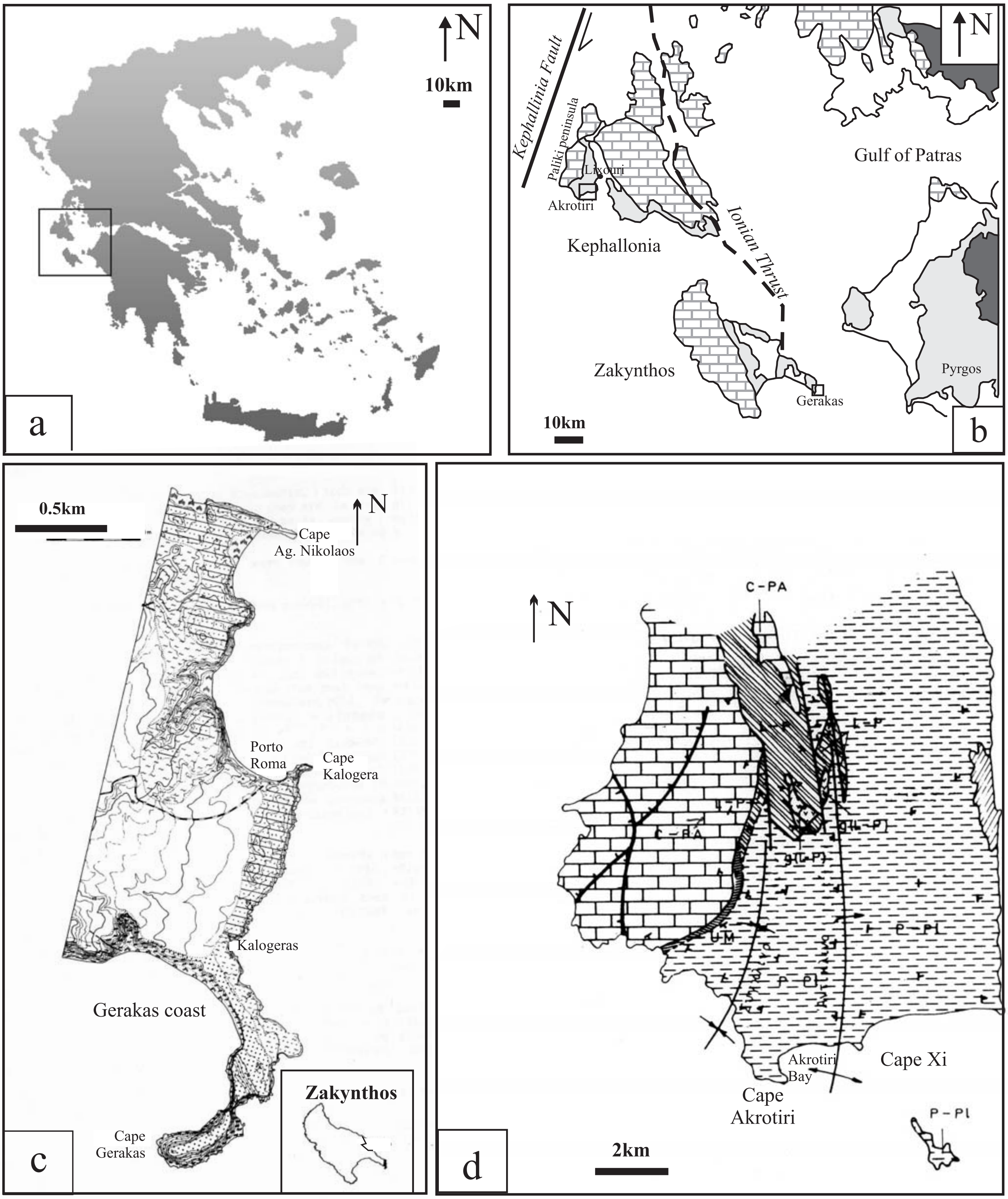


Fig. 1 - Study areas' location. (a) Geographic map of the Greek peninsula showing the location of the study areas in Western Greece, (b) Geologic map of Zakynthos and Kephallonia Islands (Bornovas & Rontogianni-Tsiabaou 1983; Underhill 1989), highlighting the Akrotiri and Gerakas areas, (c) Detailed geologic map of SE Zakynthos island (Dermitzakis et al. 1979), (d) Detailed geologic map of SW Kephallonia island (Nikolaou 1986).

In the present study, two outcrop sections in the Ionian Islands of Kephallonia and Zakynthos have been sampled for fish otolith content, in order to estimate the depositional depth, during the Early - Middle Quaternary time interval. These estimates are crucial in order to determine the timing and origin of tectonic movements in this very active area, located on the north-western boundary of the Hellenic Trench.

Geological context

The islands of Kephallonia and Zakynthos are located in the Eastern part of the Ionian Sea, off shore of Western continental Greece (Fig. 1 a,b). They constitute part of the External Hellenides. The Pre-Apulian zone formations comprise the largest part of Kephallonia and the Western part of Zakynthos, while in the Eastern part of both islands crop out the Ionian zone sediments (Aubouin 1959; Dermitzakis 1978; Nikolaou 1986; Underhill 1989). These authors have extended their studies both to the Neogene and Quaternary formations of these areas, following the until recently prevailing chronostratigraphic scheme. This scheme has recently changed, placing the Gelasian stage/age within the Pleistocene Series/Epoch, reaffirming to the Quaternary a full System/Period status (Gibbard et al. 2009). In order to conform to this official position of the International Commission on Stratigraphy, the following chronostratigraphic data are presented accordingly.

In Kephallonia Island, the study area, Akrotiri (Fig. 1b), is located on the southern part of Paliki Peninsula, south of the city of Lixouri. The Upper Miocene - Pleistocene sediments in the area consist mainly of marls, sands, silts and calcarenites (Georgiadou - Dikaioulia 1967), and the sedimentation during the Late Pliocene takes place in well-formed basins within the Pre-Apulian zone. Underhill (1989) has examined deltaic formations, mainly conglomerates, of Early Pleistocene age, in the western and south-western part of the island, whilst Triantaphyllou (1996) has recognized the Pleistocene deposits in the Paliki Peninsula, based on the presence of the calcareous nannofossil assemblages.

Akrotiri section comprises 100 meters of marls, with thin sand intercalations (Fig. 1c). Three erosional surfaces divide the section, and a bioclastic calcareous bed can be observed in the uppermost part, covered by a beach calcarenite layer. Based on the species abundance of the calcareous nannofossil *Gephyrocapsa*, Triantaphyllou (2001) was able to detect high abundance of gephyrocapsids larger than 4-4.5 μm, at 75 m from the base (Fig. 1c). This occurrence, at the boundary level between the biozones MNN19a / MNN19b (Rio et al. 1990), is related to the Gelasian - Calabrian chronostratigraphic interval. In addition, the low abundance of discoasterids in the lower 20 m of the section, combined with the rare occurrence of the planktonic foraminifer *Globorotalia inflata*, places this part within the MNN18 biozone (Triantaphyllou 2001). The combined calcareous nannofossil and planktonic foraminiferal biostratigraphic study of Akrotiri section by the mentioned author, extends the time frame for these deposits from older than 1.95 Ma (LAD of *D. brouweri* and *D. triradiatus*, according to Lourens et al. 2004) to younger than 1.73 Ma (FAD of normal sized gephyrocapsids, in Lourens et al. 2004).

The study area in Zakynthos Island is located in the south-eastern part of the island, in the Gerakas coast (Fig. 1b). The Neogene deposits of the Central and Southeastern Zakynthos form a monocline, which overlies the Cretaceous - Paleogene limestones, and can be distinguished in a lower, mainly calcareous sequence, and an upper clastic sequence, which is placed in the Pliocene and Pleistocene periods (Dermitzakis 1978). Ionian Thrust movement, during the Pliocene, distinguished the post-orogenic Pleistocene clastic deposits in the north and southeastern Zakynthos from the Cretaceous - Oligocene calcareous and Miocene clastic formations of the Pre-Apulian zone (Sorel 1976; Dermitzakis 1978; Dermitzakis et al. 1979). The Gerakas Formation consists of these Lower - Middle Pleistocene deposits which are well exposed in the southeast and the eastern part of the island of Zakynthos (Tsapralis 1981; Triantaphyllou 1996; Triantaphyllou et al. 1997). According to Zelilidis et al. (1998), the Gerakas Formation was deposited on the western boundary of the rapidly subsiding extensional basin, separating the Ionian Islands from mainland Greece. Due to the formation of an eastern normal fault during the Middle Pleistocene, according to these authors, subsidence ceased at that time and uplift of the area commenced.

Along the coast of Gerakas, the lower part of the formation, in the western side of the section, consists of 30 m of marls with rare lenses and thin horizons of sand and silt, containing few invertebrate macrofossils (Fig. 1c, Tsapralis 1981; Triantaphyllou 1996). The sand horizons increase in density and thickness towards the upper part of the section. Triantaphyllou (1996) and Triantaphyllou et al. (1997) stated that this part of the sequence was most probably deposited in a shallow shelf environment of low energy. The remaining section, which continues to the eastern part of Gerakas coast, consists of 60 m of muds, silty muds and calcarenites, with thin conglomerate intercalations, and appears to have been deposited in relatively stable and calm marine conditions (Triantaphyllou 1996; Triantaphyllou et al. 1997).

The biostratigraphic analysis of the Gerakas section sediments (Triantaphyllou 1996; Triantaphyllou et al. 1997) places the lower part of the section in the calcareous nannofossil MNN18 and MNN19a biozones of Rio et al. (1990). The Gelasian - Calabrian stage boundary horizon is determined by the first occurrence of normal sized gephyrocapsids larger than 4μm, occurring at 36 m from the base of the section and by the paleomagnetic reversal of the Matuyama Chron / top of Olduvai subchron, occurring approximately 5 m below (Papanikolaou 2008). Within the upper part of the section, as observed in Gerakas coast, Triantaphyllou et al. (1997) have recognized the nannofossil biozones MNN19b,c, d, e, and MNN19f of the Early - Middle Pleistocene, which provide a depositional time interval of circa 1.8 - 0.8 Ma to this sequence.

Methodology

In Kephallonia Island, seven samples, weighting approximately 20 kg each, were taken along Akrotiri section (Akrp1-7), one sample at Cape Xi (Xi1) and one also at Cape Akrotiri (Akrakr1). The biostratigraphic analysis places sample Xi1 within biozone MNN19b of Calabrian age (Early Pleistocene). As for sample Akrakr1, it is placed within biozone MNN19f (Middle Pleistocene / Ionian stage) and in particular

List of taxa from Akrotiri Section		**Xi1**	**Akrp1**	**Akrp2**	**Akrp3**	**Akrp4**	**Akrp5**	**Akrp6**	**Akrp7**	**Akrakr 1**
PELAGIC										
NETTASTOMATIDAE	Nettastomatidae ind.						1			
MICROSTOMATIDAE	*Nansenia groenlandica* (Reinhardt, 1840)				1	4	9		1	
ALEPOCEPHALIDAE	*Alepocephalus* sp.								1	
GONOSTOMATIDAE	*Gonostoma* sp.						4			
	Gonostomatidae sp. ind.						1			
STERNOPTYCHIDAE	*Maurolicus muelleri* (Gmelin, 1789)	1	7			3	13		18	
PHOSICHTHYIDAE	*Vinciguerria* cf. *lucetia* (Garman, 1899)						1			
	Vinciguerria poweriae (Cocco, 1838)				1	4	15		1	1
	Vinciguerria sp.						1			
CHLOROPHTHALMIDAE	*Chlorophthalmus* cf. *agassizi*									1
SCOPELARCHIDAE	*Scopelarchus analis* (Brauer, 1902)						2			
MYCTOPHIDAE	*Benthosema glaciale* (Reinhardt, 1837)					4	15	1	7	
	Electrona risso (Cocco, 1829)	1	1						15	
	Hygophum benoiti (Cocco, 1829)	6	1		4	25	15	2	14	
	Hygophum hygomi (Lutken, 1892)	9					1	2		
	Hygophum sp.				1	1				
	Myctophum punctatum Rafinesque, 1810	2			1		6	1	1	
	Ceratoscopelus maderensis (Lowe, 1839)	32	1		4	46	111	67	8	12
	Ceratoscopelus sp.1	4	1			2	4	3		
	Diaphus holti Taning, 1918	2				2	6			3
	Diaphus rafinesquii (Cocco, 1838)	2				2	2			
	Diaphus taaningi Norman, 1930	4				3	11			
	Diaphus sp.1	7			3	12	4	4		
	Diaphus sp.3								1	
	Diaphus sp.	3			2		6	1	3	2
	Lampanyctus sp.					1				
	Lobianchia dofleini (Zugmayer, 1911)					4	4			
	Notoscopelus elongatus (Costa, 1844)		1		2	13	28	2	2	
	*Scopelopsis pliocenicus** (Anfossi & Mosna, 1976)		1				1			
BENTHOPELAGIC										
MYCTOPHIDAE	*Lampanyctus crocodilus* (Risso, 1810)	3				2	5			1
PHYCIDAE	*Gaidropsarus* sp.						4			
GADIDAE	*Gadiculus argenteus* Guichenaut, 1850	1	1				1			
	*Gadiculus labiatus** (Schubert, 1905)	1	3			1		2		
	Gadidae sp. ind.						4		1	
CARANGIDAE	*Trachurus* sp.				1					
SPARIDAE	Sparidae ind.	1								
BENTHIC										
MORIDAE	*Laemonema* sp.						2			
	Moridae sp. ind.						1			
ACROPOMATIDAE	*Parascombrops mutinensis* Bassoli, 1906				1	2	1			
GOBIIDAE	*Deltentosteus quadrimaculatus* Valenciennes, 1837		1	2						
	Lesueurigobius sp.						1			
TRICHIURIDAE	*Aphanopus* aff. *carbo* Lowe, 1839						1			
	Total identified otoliths	79	18	2	21	131	281	85	73	20

Tab. 1 - Fish otolith material from Akrotiri Section (Kephallonia Island).

below the last occurrence of *Gephyrocapsa* sp. 3, which provides a time interval of 0.781 - 0.61Ma. In the Zakynthos Island, seven samples were taken from the lower part of Gerakas section (ST1-7). Additionally, we examined two samples that are located in higher stratigraphic position at the middle part of Gerakas section (Gerp1SE and Gerp3), and are placed by Triantaphyllou (1996) within the nannofossil biozone MNN19e. All the samples were diluted in plain water, and the otoliths were separated from the sediment through 250 µm diameter sieving, and handpicking under a stereoscope.

The fish otoliths were identified (Tab. 1 & 2) based on the morphologic characteristics described by Nolf (1985). The species taxonomic position followed the scheme of Nelson (2006). Selected otoliths from each taxon were photographed using the scanning electron microscope JEOL JSM-6360 of the Department of Historical Geology and Paleontology of the University of Athens.

The depositional depth of the examined sediments in the areas of study was estimated using the method of Nolf & Brzobohaty (1994) for bathyal and deep neritic assemblages, with a significant mesopelagic component. According to this methodology, based on the modern depth ranges of all the taxa in each sample (Tab. 3), the number of possible presences for each 100-meter depth interval is calculated and expressed as a percentage of the total number of taxa involved in the analysis. The depth of deposition for each sediment sample is estimated as the maximum percentage in these plots. In order to enable a more detailed bathymetric analysis, 50-meter depth intervals were used here instead.

The principal requirement, for the application of the above methodology for the depositional depth estimation, is that the systematic position of the fossil taxa included in this analysis is close to that of their modern relatives. Fortunately, the identified assemblages consist in the main part of currently existing taxa.

According to Nolf & Brzobohaty (1994) and Girone (2000, 2005) the night depth ranges of the vertically migratory meso- and bathypelagic species should not be included in the analysis, because that would overesti-

List of taxa from Gerakas section		**ST1**	**ST2**	**ST3**	**ST4**	**ST5**	**ST6**	**ST7**	**Gerp1SE**	**Gerp3**
PELAGIC										
MICROSTOMATIDAE	*Nansenia groenlandica* (Reinhardt, 1840)							1		
STERNOPTYCHIDAE	*Maurolicus muelleri* (Gmelin, 1789)				1			1	1	2
PHOSICHTHYIDAE	*Vinciguerria poweriae* (Cocco, 1838)							4		
STOMIIDAE	*Chauliodus* aff. *sloani* Schneider, 1801							1		
MYCTOPHIDAE	*Benthosema glaciale* ((Reinhardt, 1837)				1	4	1	14	17	
	Electrona risso (Cocco, 1829)			1		2	2	8		
	Hygophum benoiti (Cocco, 1829)		1	3	15	5		68		1
	Hygophum hygomi (Lutken, 1892)				2			3		
	Hygophym sp.				2			4		
	Myctophum punctatum Rafinesque, 1810						3	8	2	
	Myctophum sp.							1		
	Symbolophorus aff. *veranyi* (Moreau, 1888)							1		
	Ceratoscopelus maderensis (Lowe, 1839)	1	3	3	12	7	20	76	3	1
	Ceratoscopelus sp.1					3	10	67		
	Diaphus holti Taning, 1918		2			1	3	2		
	Diaphus rafinesquii (Cocco, 1838)		2		1			2		
	Diaphus taaningi Norman, 1930			7	3	1		7	5	
	Diaphus aff. *taaningi* Norman, 1930									1
	Diaphus sp.1							1		
	Diaphus sp.2								2	
	Diaphus sp.	1	3	5	7	1		5		
	Lobianchia dofleini (Zugmayer,1911)							1		
	Notoscopelus elongatus elongatus (Costa, 1844)							18		
	Notoscopelus sp.				1			1	1	
	*Scopelopsis pliocenicus** (Anfossi & Mosna, 1976)		3							
BREGMACEROTIDAE	*Bregmaceros* sp.			9	1					
BENTHOPELAGIC										
MYCTOPHIDAE	*Lampanyctus crocodilus* (Risso, 1810)	1				2		6	1	1
GADIDAE	*Gadiculus argenteus* Guichenaut, 1850				1					1
	Gadidae sp. ind.							1		
CARANGIDAE	*Trachurus* sp.							1		
BENTHIC										
BYTHITIDAE	*Bellottia* cf. *apoda* Giglioli, 1883		1							
GOBIIDAE	*Deltentosteus* aff. *quadrimaculatus* Valenciennes, 1837								2	2
	Lesueurigobius sp.						1		1	
	Gobiidae sp. ind.								1	
TRICHIURIDAE	*Aphanopus* aff. *carbo* Lowe, 1839							2		
	Total identified otoliths	3	15	28	47	26	40	304	36	9

Tab. 2 - Fish otolith material from Gerakas Section (Zakynthos Island).

Taxon	Life style	Depth (m)	References
Nansenia groenlandica	Bathypelagic	0-1400	Whitehead et al., 1984
Alepocephalus sp.	Benthopelagic	800-1500	D'Onghia et al., 2004
Maurolicus muelleri	Bathypelagic	day: 200-400m, night: 0-100m	Whitehead et al., 1984
Vinciguerria spp.	Meso-bathypelagic	50-1000	Whitehead et al., 1984
Chauliodus aff. *sloani*	Bathypelagic	473-1192	Mytilineou et al., 2005
Chlorophthalmus cf. *agassizi*	Benthopelagic	300-700	Mytilineou et al., 2005
Scoleparchus analis	Mesopelagic	>500	Whitehead et al., 1984
Benthosema glaciale	Meso-bathypelagic	day: 375-1085, night: 12-200 and 600-800	Whitehead et al., 1984; Mytilineou et al., 2005
Ceratoscopelus spp.	Meso-bathypelagic	day: 100-2500, night: 12-300 and 600-800	Whitehead et al., 1984; D'Onghia et al., 2004
Diaphus holti	Meso-bathypelagic	day: 100-780, night: 80-235 and 400-600	Whitehead et al., 1984; D'Onghia et al., 2004
Diaphus rafinesquii	Meso-bathypelagic	day: 400-675, nyctoepipelagic 0-600	Whitehead et al., 1984
Diaphus taaningi	Pelagic	40-475	Hulley, 1990
Electrona risso	Bathypelagic	day: 225-750, night: 150-200 and 400-700	Whitehead et al., 1984
Hygophum benoiti	Mesopelagic	day: 100-1000, night: 12-400 and 700-1000	Whitehead et al., 1984
Hygophum hygomi (juveniles)	Bathypelagic	day: 400-750, night: 0-235	Whitehead et al., 1984
Lampanyctus crocodilus	Benthopelagic	day: 200-1300, night at surface, adults non migratory	Whitehead et al., 1984; D'Onghia et al., 2004
Lobianchia dofleini	Mesopelagic	day: 375-600, night: 25-400	Whitehead et al., 1984
Myctophum punctatum	Mesopelagic	day: 100-150 and 700-1000, night: 0-190 and 700-800	Whitehead et al., 1984
Notoscopelus elongatus	Mesopelagic	day: 375-1000, night: 45-150	Whitehead et al., 1984
Scopelopsis pliocenicus	Meso-bathypelagic	74-400	Girone, 2000
Symbolophorus aff. *veranyi*	Pelagic	0-800	Whitehead et al., 1984
Bregmaceros sp.	Pelagic	0-1260	Castellanos-Galindo et al., 2006
Laemonema sp.	Benthic	200-1200	Whitehead et al., 1986
Gaidropsarus sp.	Benthopelagic	80-600	Whitehead et al., 1986
Gadiculus argenteus	Benthopelagic	200-1000	D'Onghia et al., 1998
Bellotia cf. *apoda*	Benthopelagic	30-700	Mytilineou et al., 2005
Trachurus sp.	Benthopelagic	50-1050	Whitehead et al., 1986
Deltentosteus quadrimaculatus	Benthic	0-333	D'Onghia et al., 2004
Lesueurigobius sp.	Benthic	0-230	Whitehead et al., 1986
Aphanopus aff. *carbo*	Benthic	200-1600	Whitehead et al., 1986

Tab. 3 - Fish taxa modern bathymetric range and life style, for the Mediterranean region and/or the North Atlantic (for the species now absent from the Mediterranean area). The diel migrating taxa have two depth distributions, for their daily and night habitat.

mate the importance of the neritic element in the assemblages. However, it should be noted that these mesopelagic taxa occupy different depth ranges during their ontogenetic growth, and they should be treated accordingly whenever only one age group is present in the assemblage. In the samples from Gerakas and Akrotiri sections, only the juvenile depth ranges were used for the species *Benthosema suborbitale*, since only very small otoliths have been found there.

Remarks on taxa requiring comments

A total of forty taxa were identified in the samples from sections Akrotiri and Gerakas (Fig. 2, 3, Tab. 1, 2).

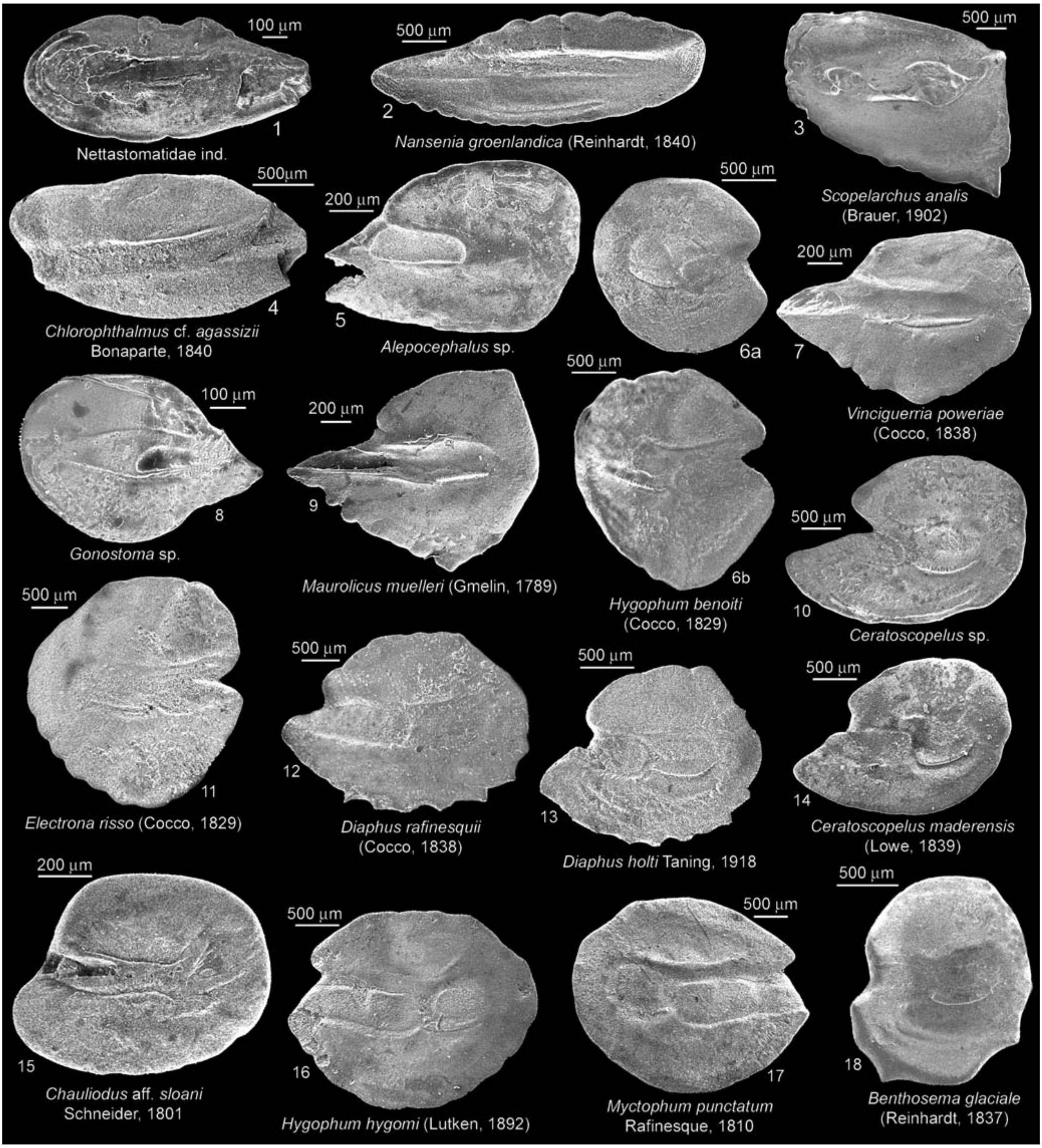


Fig. 2 - Scanning electron microscope photographs of otoliths from Akrotiri and Gerakas sediments. **1**: L, Akrp5, **2**: R, Akrp4, **3:** R, Akrp5, **4**: R, Akrakr1, **5**: R, Akrp7, **6**: **a**, L, Xi1, **b** L, ST7, **7**: R, Akrp5, **8**: L, Akrp5, **9**: R, Akrp7, **10**: R, ST7, **11**: L, Akrp7, **12**: R, Xi1, **13**: R, Akrpakr1, **14**: R, Akrp6, **15**: R, ST7, **16**: R, ST7, **17**: L, Akrp5, **18**: R, Gerp1SE. **L**: left otolith, **R**: right otolith.

The studied material has been stored in the Athens Museum of Paleontology and Geology, repository numbers AMPG_OT_AKR1-710 and AMPG_OT_GER1-508. Additional comments are given only for taxa which are subject to discussion. Many recent fish species were already represented in the Mediterranean Pleistocene, and in several cases, specific identification could not be unequivocally decided. In these situations, the abbreviation *aff. (affinis)* was inserted. The abbreviation *cf. (conformis)* was used whenever the condition of preservation of the otolith did not allow conclusive specific identification. Moreover, several taxa appear in open nomenclature for identification at the species level, due to insufficient knowledge of related recent species or because the fossil material is too limited or too poorly preserved.

Chlorophthalmus cf. *agassizi* (Fig. 2.4)

The otolith from the Middle Pleistocene deposits of Akrotiri (Kephallonia) is very close to extant species *C. agassizi*, which has, however, a slightly narrower dorsal area than the specimen examined here (sample Akrakr1). In the Pliocene and Pleistocene of the Mediterranean realm only the species *Chlorophthalmus costamagnai* has been described so far (Nolf & Cappetta 1989, from Lower Pliocene sediments of Southern France). It appears to have a considerably higher anterior area with respect to the extant Mediterranean *Chlorophthalmus agassizi*, which is characterized by a shorter anterior part and a slightly narrower dorsal area. The Akrotiri material represents the first fossil record of *Chlorophthalmus* cf. *agassizi* in the Mediterranean realm.

Ceratoscopelus spp. (Fig. 2.10 & 2.14)

There are two distinct morphological groups within the genus *Ceratoscopelus* in the samples from both studied areas. The otoliths of the common species *Ceratoscopelus maderensis* (Fig. 2.14) are oval-shaped, with an elongate and protruded rostrum, and a relatively smaller antirostrum. The sulcus is long and wide, separated in a larger ostium and a cauda, which takes approximately half the length of the ostium. The caudal colliculi is round. In comparison the second morphological group, *Ceratoscopelus* sp.1 (Fig. 2.10), exhibits a sharp poster-ventral angle, a larger postero-dorsal area and an almost linear ventral rim, which are quite different from those observed in *Ceratoscopelus maderensis*. Specimens referable to the morphological group of *Ceratoscopelus* sp. have also been found in the sapropelic horizons of Vrica section and in various Plio-Pleistocene sections of Southern Italy (Girone, unpublished data). Accordingly, the available data provides no clear relationship between the occurrence and distribution of this morphological group and the paleoenvironmental parameters; often both morpho-groups are registered within the same sample. Here these groups are treated separately, but we do not exclude the possibility that they can be two subspecies or just morphological variations of *Ceratoscopelus maderensis*, occurring under particular paleoenvironmental conditions.

Notoscopelus elongatus (Fig. 3.3a-b)

All otolith specimens ascribable to *Notoscopelus* sp. are elongate enough to distinguish from those of *Notoscopelus resplendens*, unique *Notoscopelus* species reported so far, within the Lower - Middle Pliocene Mediterranean deposits. The elongate shape refers our specimens to *Notoscopelus elongatus.* According to Brzobohaty & Nolf (1996), the otoliths of the Mediterranean subspecies *Notoscopelus elongatus elongatus* are slightly more elongate than the North Atlantic *Notoscopelus elongatus kroyeri* and exhibit a shorter cauda in the poster-dorsal direction. These features, however, are well visible mostly in the adult specimens. The otoliths from the Early Pleistocene of the Gerakas section can be safely placed in *Notoscopelus elongatus elongatus*, as can some of the specimens from Akrotiri. However, the later locality has yielded several otoliths which are slightly shorter, and could appear to resemble *Notoscopelus elongatus kroyeri*, though not definitely. As a result, no definitive sub-specific separation of the *Notoscopelus* otoliths is suggested for our material, and the entire material is treated here as *Notoscopelus elongatus*.

Parascombrops mutinensis (Fig. 3.11a-d)

In the Mediterranean realm only the fossil species *Parascombrops mutinensis* is known from the Miocene up to the Early Pleistocene. The small specimens from the Akrotiri section resemble the specimens of *Parascombrops (Synagrops) spinosa* figured by Campana (2004) (see Steurbaut 1979 for discussion about the systematic placement of species within the genera *Parascombrops* and *Synagrops*) with respect to their more acuminate shape in the posterior end. However, by observation of a large number of *P. mutinensis* from various localities and time units, the features shared by the Akrotiri otoliths seem to fall within the intra-specific variability of the fossil *P. mutinensis*.

Composition and paleobathymetric analysis

The otolith assemblages from Gerakas and Akrotiri sections are very similar in composition and structure. They are mainly composed of a well diversified and abundant pelagic group and subordinately by a less conspicuous benthopelagic and benthic group.

The pelagic group is rich in myctophids, but the bathypelagic taxa *Chauliodus sloani, Alepocephalus* sp., *Scopelarchus analis* and *Nansenia groenlandica* are also present. The benthopelagic group is composed mostly by gadids, of which *G. argenteus* appears to be more common in the Akrotiri section than in Gerakas, whose benthopelagic assemblages display a lower diversity. *G. argenteus*, at the adult stage, occupies the continental slope, with a maximum abundance between 200 and 400 m, both in the modern Mediterranean and Atlantic, and in the Pleistocene Mediterranean realm (Maurin 1968; Arena & Li Greci 1973; Cohen et al. 1990; Girone 2005, 2007). The Akrotiri assemblages include also eurytopic gadoids such as *Gaidropsarus* and the extinct *Gadiculus labiatus*. *G. labiatus* is a species very common and abundant in various fossil sediments from the Miocene up to the Early Pleistocene. The population structure displayed by the mychtophid *Lampanyctus crocodilus* places this species within the benthopelagic

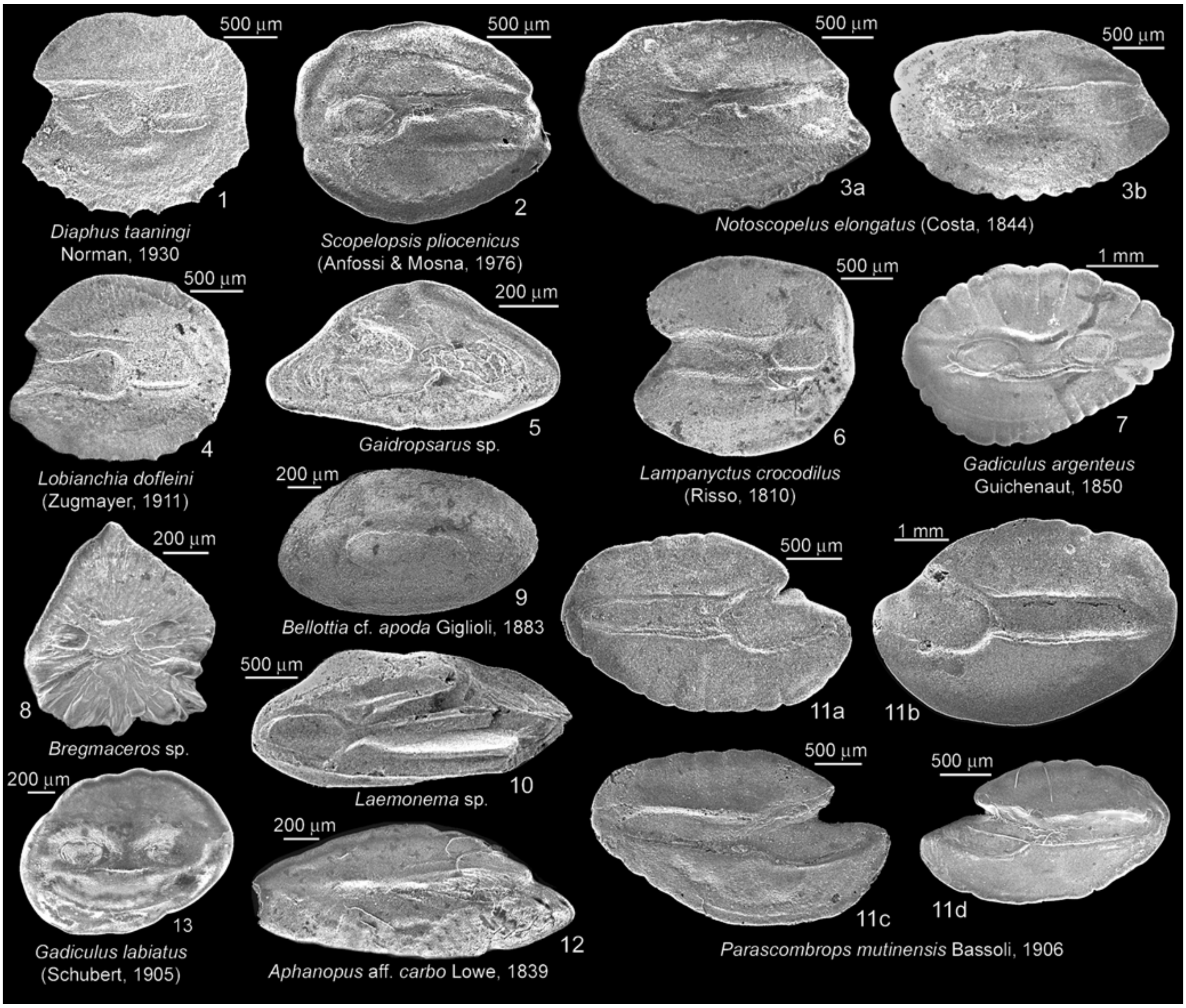


Fig. 3 - Scanning electron microscope photographs of otoliths from Akrotiri and Gerakas sediments (continuing from figure 2). **1**: R, Gerp1SE, 2: **2**: L, Akrp1, **3**: a, L, Akrp5, b, L, ST7, **4**: R, Akrp5, **5**: R, Akrp5, **6**: R, Akrp5, **7**: R, Akrp1, **8**: L, ST3, **9**: ST2, **10**: L, Akrp5, **11**: **a,b**, Otoliths from the Plio-Pleistocene deposits from Paliore river in Southern Italy (Di Geronimo et al. 2003), **c**, L, Akrp3, **d**, R, Akrp5, **12**: L, Akrp5, **13**: R, Akrp1. **L**: left otolith, **R**: right otolith.

group, because of the different life style displayed by these fish during their growth; shifting from mesopelagic during the juvenile stage, to benthopelagic in later stages (Stefanescu & Cartes 1992). In the assemblages from both sections, the populations of *L. crocodilus* are mostly composed by adult and sub-adult specimens (otolith size larger than 2 mm or 1-2 mm), comparable to the structure displayed by other Pleistocene deep bathyal assemblages (Girone 2003, 2005). Moreover, the frequent occurrence of this myctophid at depths exceeding 400 m has also been reported on the sea floor of the recent Mediterranean Sea. In particular, Maurin (1968), Stefanescu et al. (1994) and D'Onghia et al. (1998) highlighted the meaning of *L. crocodilus* in the deep-sea benthopelagic associations on the slope between 400-800 m.

The benthic group is heterogeneous because it includes typical taxa of the slope environment, such as *Bellottia* cf. *apoda*, *Aphanopus* aff. *carbo*, and *Laemonema*, as well as taxa closely associated with shelf environments, such as gobids. These are very rare and are represented by very few specimens, often poorly preserved for any specific identification. The assemblages of Gerps1SE sample show the more diversified gobids component, but they are also characterized by a very low diversity of mycthopids, whilst the bathypelagic taxa are completely absent.

According to the paleobathymetric analysis, the assemblages from the Akrotiri section are all indicative of a slope depositional environment. It is worth noting that all the graphs show higher peaks below the 200 m line (Fig. 4, 5). The Gelasian assemblages of Akrotiri

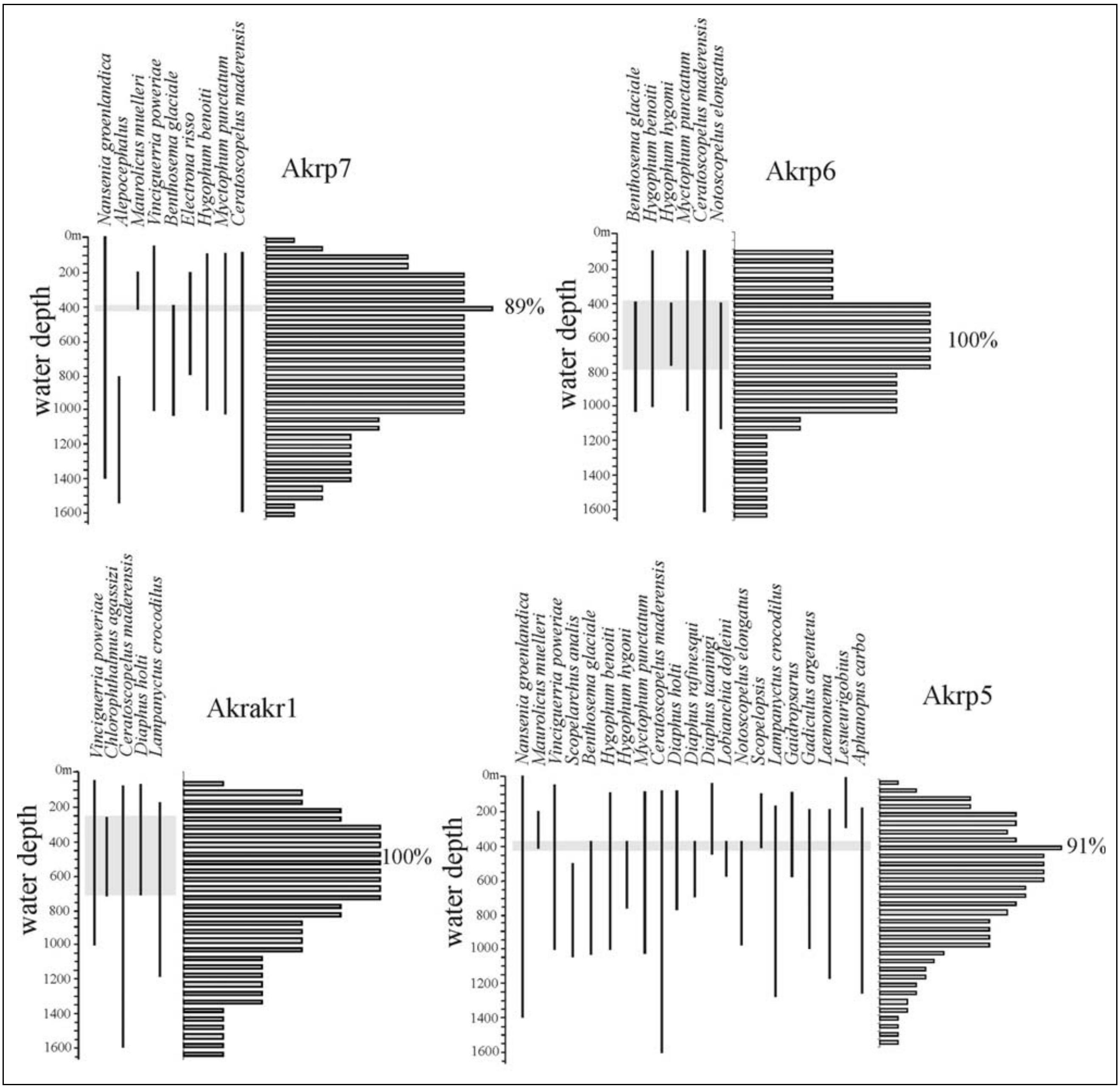
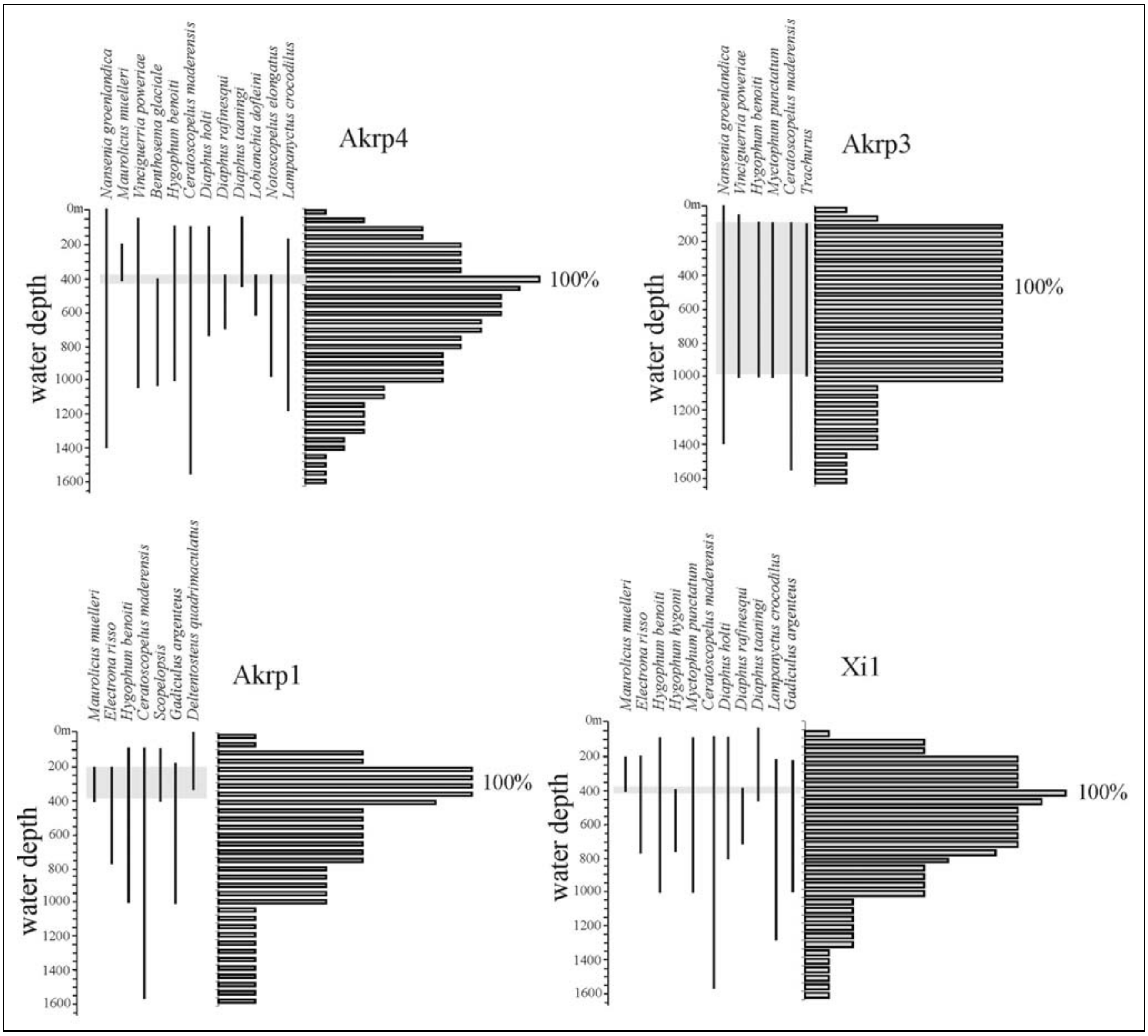


Fig. 4, 5 - The fish otolith paleobathymetric estimation technique applied to the Akrotiri section Lower – Middle Pleistocene deposits. The modern bathymetric range of the taxa present in each sample is shown on the left side of the graphics, whilst on the right side a diagram presents the percentages of possible occurrences of the same taxa for each 50 – meter depth interval. The maximum percentage in each sample corresponds to the estimated depth of deposition based on the fish assemblage.

(Akrp7, 6, 5 and 4) are indicative of deposition ranges below 400 m depth (Fig. 4, 5). Indeed, the samples Akrp 7, 5 and 4 have a very narrow depth range, between 400 and 500 m. On the contrary, sample Akrp6 displays a wider depth range, between 400 and 800 m. The analysis on sample Akrp3 yielded a very wide depth range covering deep-shelf as well as the bathyal setting. The samples of Calabrian age (Akrp1 and Xi1) displayed again a more restricted range, between 200-400 m and 400-500m respectively. On the basis of the composition of benthic and benthopelagic assemblages of these last samples, a shallowing trend can be hypothesized towards the samples Akrp2 and Akrp1, where only the gobiid *Deltentosteus quadrimaculatus* is present. However, the sample Akrp2 was excluded from the analysis, because it yielded only two very small otoliths of the gobiid *Deltentosteus quadrimaculatus*, which is known to inhabit very shallow waters. The depth of deposition for the Middle Pleistocene (Ionian stage) deposits of Akrotiri (Akrakr1) is estimated between 300-700 m, based on the presence of *Chlorophthalmus* cf. *agassizi*.



In Gerakas section, the samples ST1 and ST3 did not provide enough data for a paleobathymetric analysis, and were thus excluded. Also, the absence of significant benthic and benthopelagic assemblages did not permit any paleoecological analysis. Only a single otolith of *Lampanyctus crocodilus* was found in sample ST1. According to the behaviour of this myctophid, the occurrence of sub-adult specimens, as mentioned above, could be indicative of a deep-slope environment but we consider any paleoecological hypothesis for this sample as a speculation.

Other samples from the Gerakas section (ST2, ST4-5 and ST7) are all indicative of a bathymetric range of about 400-500 m, in good agreement with the occurrence of adult specimens of *L. crocodilus* and the bathypelagic fish *Chauliodus sloani* and *Nansenia groenlandica*. The sample ST6 displayed a bimodal graph with a maximum peak between 200-300 m and 400-800 m. According to Nolf & Brzobohaty (1994) graphs exhibiting two maximum peaks are indicative of allochthonous assemblages. In our case, the benthic and benthopelagic assemblages are nearly barren; just one poorly preserved specimen of *Lesueurigobius* is found. At the same time, the pelagic group is composed of epi-mesopelagic taxa, which provide no further palaeoecological indication. The uppermost samples Gerp1SE and Gerp3 (placed within the biozone MNN19e) are indicative of a range between 200-300 m and 200-400 m respectively. The benthic and benthopelagic assemblages from these samples exhibit the co-occurrence of slope benthopelagic taxa, such as *Lampanyctus crocodilus* and *Gadiculus argenteus* and shelf benthic fish, such as gobiids. The latter, in favourable conditions, prefer to inhabit the deeper part of their bathymetric range (Girone 2005). The assemblage of the sample Gerp1SE, with a maximum peak between 200-300 m, is characterised by a higher

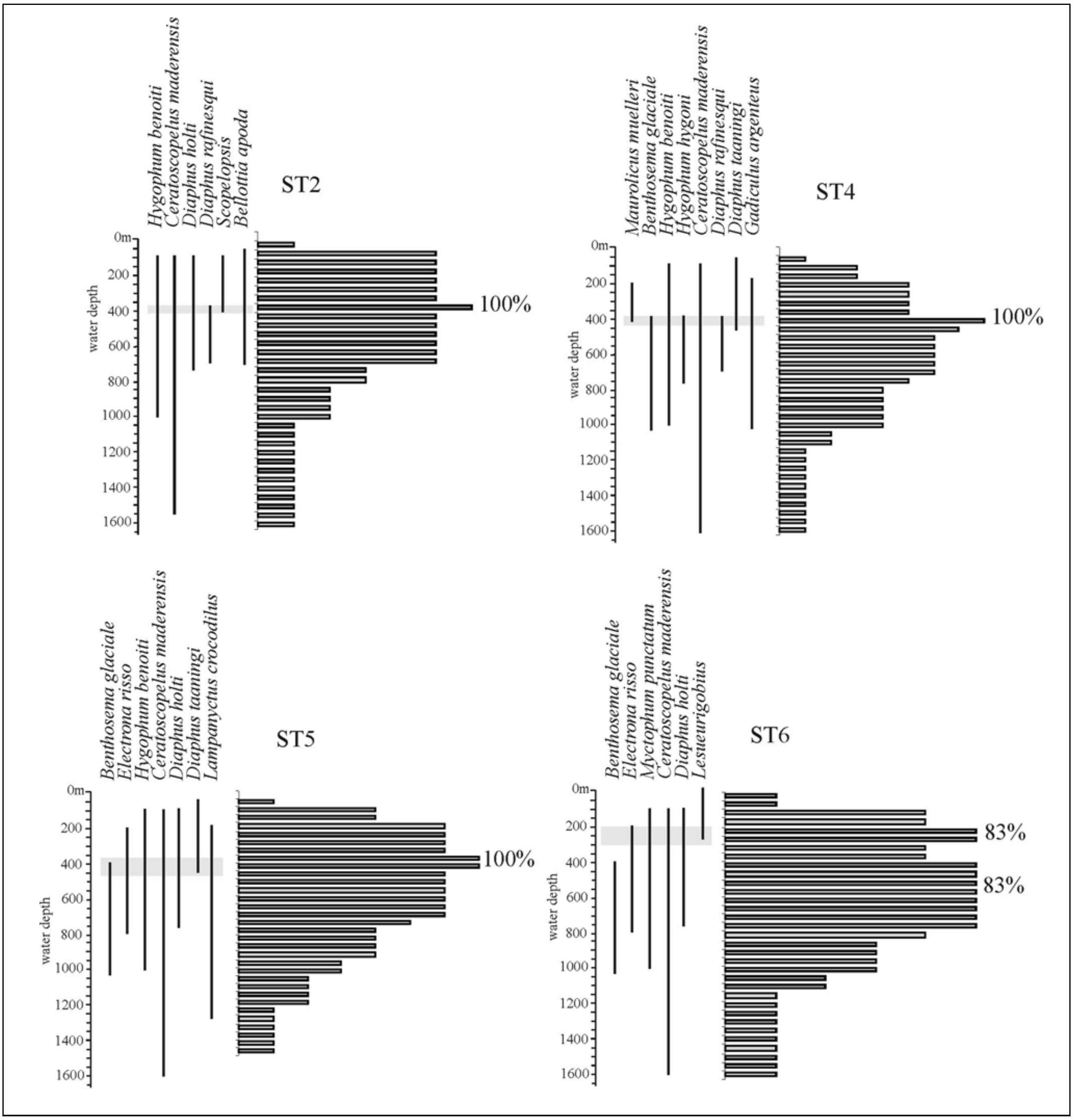
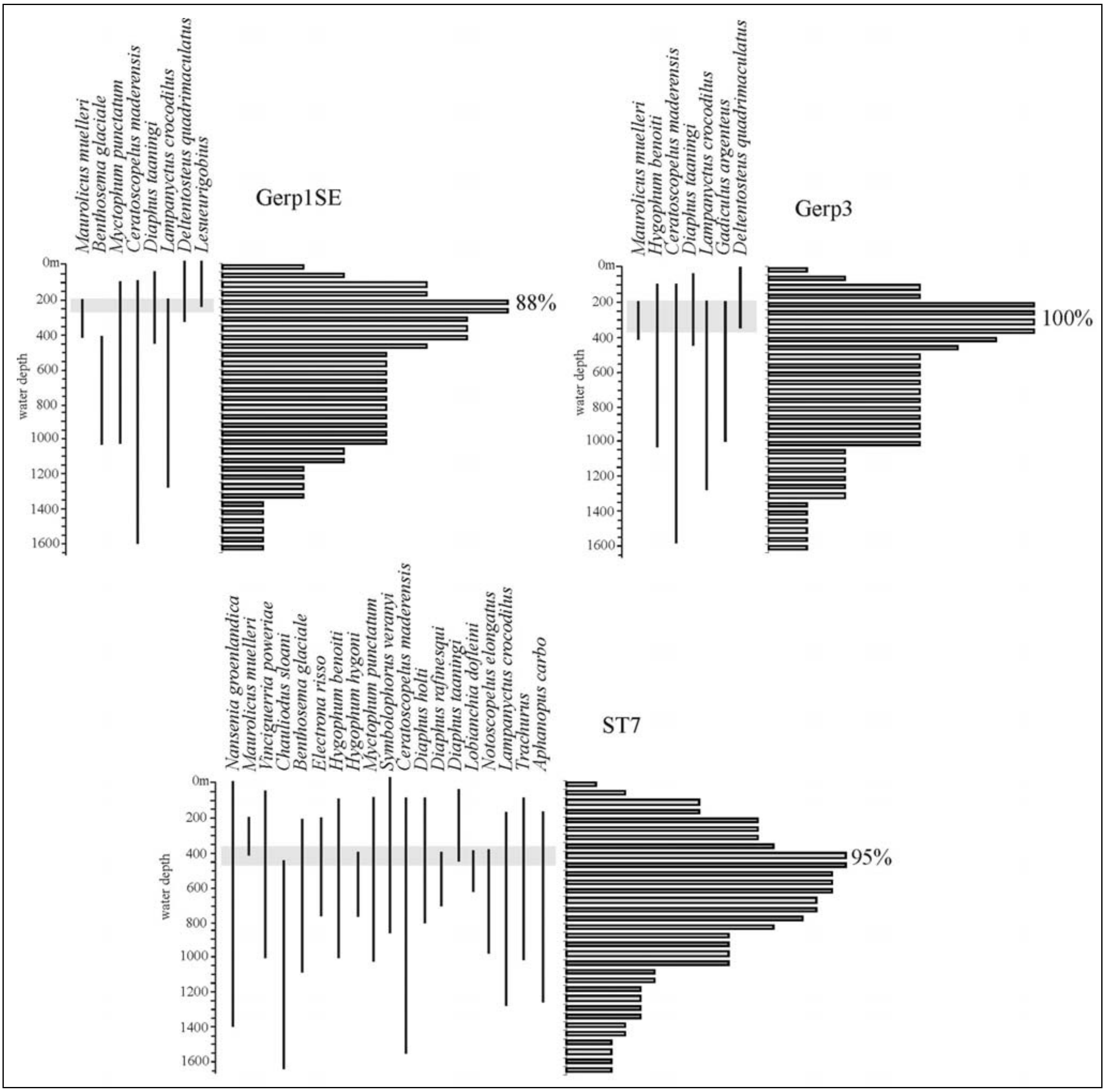


Fig. 6, 7 - The fish otolith paleobathymetric estimation technique applied to the Gerakas section Lower – Middle Pleistocene deposits.

diversity of the benthic group, whilst the benthic taxa are reduced to just one species in Gerp3, which on the contrary has a more diversified benthopelagic assemblage. Based on the above paleobathymetric analysis, the study areas' sediments were most probably deposited in an upper slope transition to deep shelf setting.

Discussion

The estimations of the depositional depth for the sediment samples of Akrotiri and Gerakas sections appear in Figures 4-7. The fish assemblages identified in both areas of study consist mainly of mesopelagic and bathypelagic taxa and can thus be considered as typical of the continental slope environment of depths greater than 200 meters (Nolf & Brzobohaty 1994). The average depth of deposition ranges between 200-600 m for the Akrotiri section, and between 250-450 m for the lower part of Gerakas section. Samples Gerp1SE and Gerp3 gave paleodepth estimations of 200-300 and 200-400 meters respectively. Previous work conducted in these areas by van Hinsbergen et al. (2006) gave a



mean paleodepth of 300-500 meters for the general Lixouri area sediments dated between 2.6 - 1.6 Ma, based on the planktonic foraminifera ratio (% P: 426 m, standard deviation 232 m). The same authors estimated a depositional depth between 500-750 meters (% P: 661 m, standard deviation 108 m) for Gerakas area sediments, dated by them at approximately 1.8 Ma. In addition, Tsapralis (1981) examined the ostracode assemblages in the middle and upper part of Gerakas Formation (sediments corresponding to the nannofossil biozones MNN19c-f; Triantaphyllou 1996; the samples Gerp1SE and Gerp3, in this paper, correspond in part to this stratigraphic interval), and concluded that the deposition of this interval must have taken place in depth less than 300 m, with a further uplifting trend.

The fish otolith paleodepth estimates for the Gerakas section sediments appear in Figure 8. In general, the deposition in Gerakas during the Early Quaternary took place in relatively stable depths of around 400-450 m, influenced mostly by eustatic changes. The present analysis agrees with previous observations, made by Zelilidis et al. (1998) stating that the sedimentation depth in this area, during the Early Pleistocene, was principally controlled by the eustatic sea-level changes. According to the palaeogeographic scheme proposed by these authors, the deepening of the Gerakas area was induced by the general extension and subsidence of the Zakynthos Channel Basin, whilst uplift took place later on in the Middle Pleistocene, due to a normal fault, functioning to the east of Gerakas. On the contrary, the

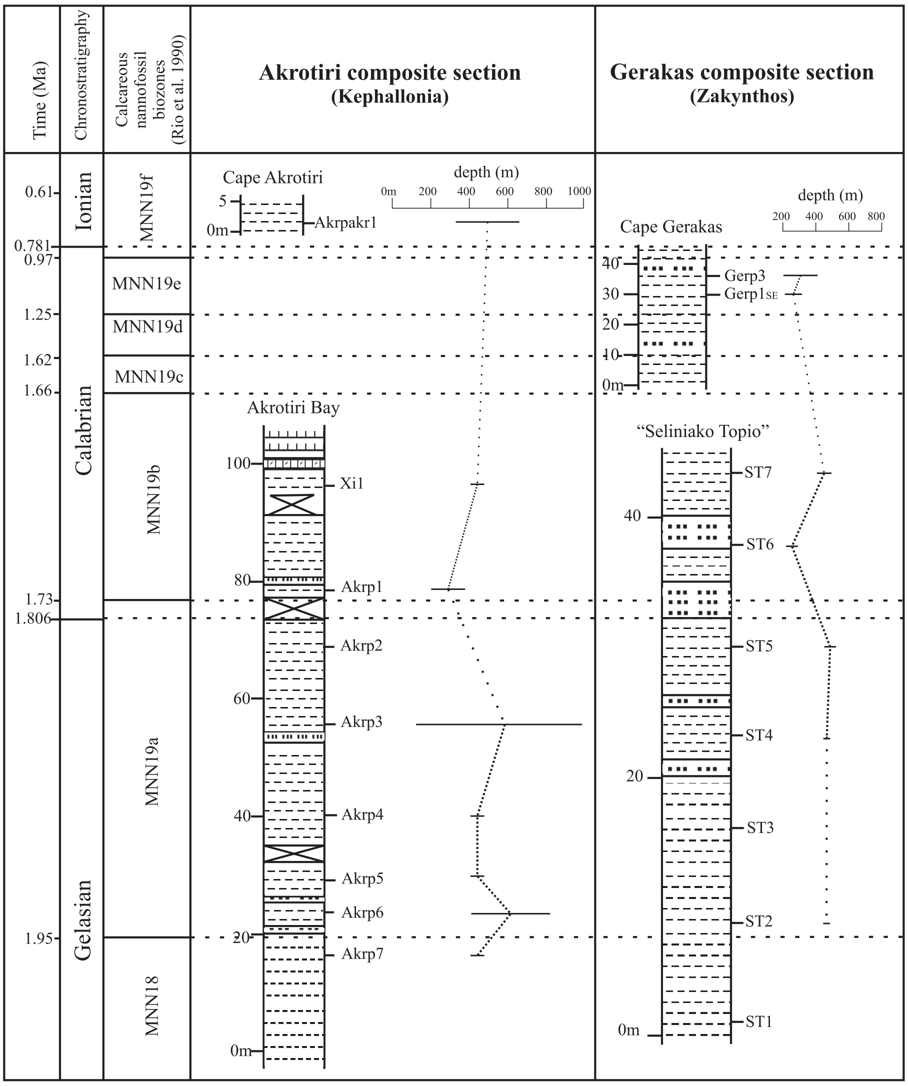


Fig. 8 - The studied sections' lithology, sampling and stratigraphic information. The biostratigraphic data is analyzed in Triantaphyllou (1996, 2001) and Triantaphyllou et al. (1997). Akrotiri and Gerakas sections' Early - Middle Pleistocene paleobathymetry, based on the fish otoliths.

estimated depositional depth for the lower part of Gerakas Formation, in our study, which is stable at 400-450 m in samples ST2, ST4, ST5 and ST7, suggests that subsidence took place prior to the deposition of the basal section sediments, earlier than 1.95Ma. Furthermore, the Middle Pleistocene paleodepths resulted for samples Gerp1SE and Gerp3, in conjunction with those proposed for the middle and upper part of the sequence by Tsapralis (1981) support an uplift episode hypothesis at the beginning of the Middle Pleistocene.

The Akrotiri sections depositional depth estimates are presented in Figure 8. Overall examination of the provided depth estimates reveals a situation similar to that encountered in Gerakas section. The depositional depth in Akrotiri is somewhat stable at 400-450 m during the Gelasian (samples Akrp 4, 5 and 7). Uplift seems to take place at the beginning of the Calabrian, with the depth rising to 200-400 m for sample Akrp1, and again the area subsides later on in the Calabrian, as seen for sample Xi1, with an estimated depth of 400-450 m.

In order to examine the relative role of eustacy and regional tectonics in the relative sea level changes, in the Akrotiri and Gerakas areas during the Gelasian - Ionian interval, the estimated paleodepths were compared to the eustatic sea level changes predicted by Raymo et al. (2006) for the same time. This eustatic curve assimilates a model of ice volume change, consistent with Milankovitch theory and field observations, to predict the sea level / d^{18}O variability for the Early Pleistocene. The predicted sea level, according to these authors, varies between -60 and +5 meters relative to the present, which means that eustatic changes during this time have not exceeded 65 m either way. It can therefore be concluded that the paleobathymetric change in our study should also be attributed to tectonic movements. According to van Hinsbergen et al. (2006), a Pleistocene tectonic phase observed on the Kephallonia Island, affected only the Paliki peninsula. Overall, these authors described two post - Late Miocene tectonic phases encompassing more than 1000 m uplift. The results presented here refine the amplitude and timing of the tectonic movements in the SW Kephallonia for the Early Quaternary.

Conclusions

The current paleodepth estimates based on the fish otolith modern depth distributions provide a detailed picture of the depth variations for the Gelasian - Ionian interval in the study areas (Fig. 8). The average depositional depths in the Gerakas basin, between 1.95 - 1.66 Ma, range between 400-450 meters. This suggests that no significant tectonic movement took place within the time interval encompassed in the studied sediments. The area appears uplifted to 200 - 400 meters later on in the Pleistocene (MNN19e; 1.25 - 0.97 Ma), as has also been estimated from the ostracode assemblages by Tsapralis (1981). The above evidence places the timing of the area's tectonic uplift between 1.66 - 1.25 Ma, a hypothesis which refines the previous palaeogeographic studies performed in this area (Zelilidis et al. 1998).

Regarding the SW Kephallonia Island, a more detailed timing of the Early - Middle Pleistocene tectonic movement is presented here, through the application of fish otolith paleobathymetry. The depositional depth appears stable at 400-450 m until 1.73 Ma (Calabrian stage). At this time a similar situation appears, as in the case of Gerakas area, with uplift and following subsidence taking place between 1.73 - 1.66 Ma.

The complex geographic setting and tectonic evolution of the Eastern Ionian area undoubtedly commands a multiproxy approach for a palaeogeographic study. The application of fish otolith paleobathymetry to the Early Quaternary deposits of SW Kephallinia and SE Zakynthos Islands furthers the knowledge in this field and strengthens the applicability of fish otoliths as paleodepth estimators in deep neritic environments, through comparison of the present results with those provided by foraminifera and ostracoda studies, as well as with the current tectonic models for the recent evolution of Western Greece.

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