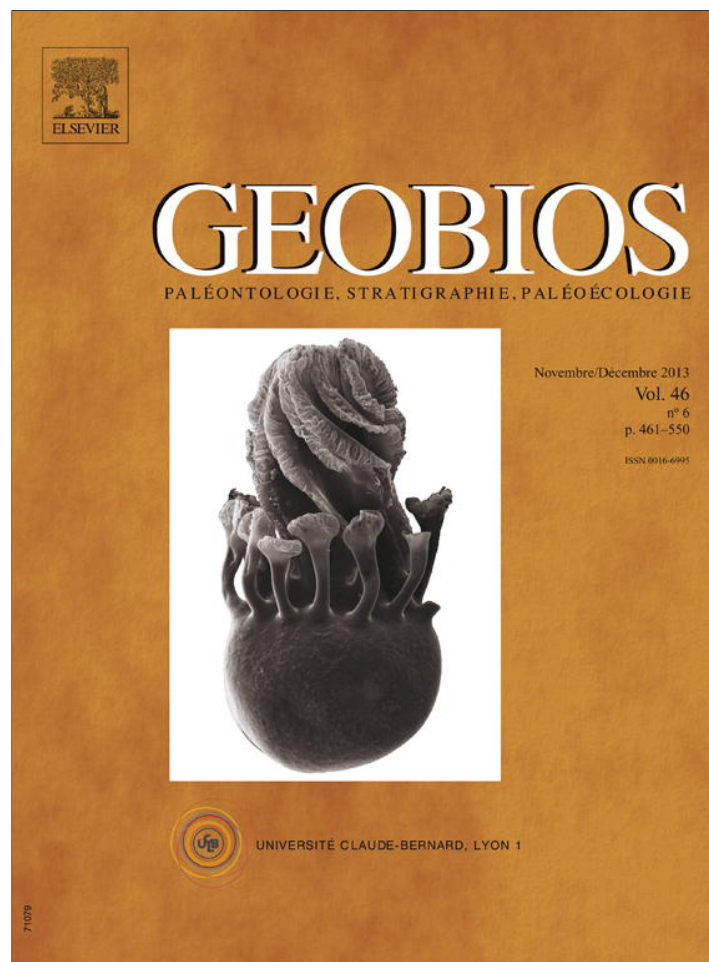


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Original article

Fish otoliths from the Pliocene Heraklion Basin (Crete Island, Eastern Mediterranean)[☆]



Konstantina Agiadi^{a,*}, Efterpi Koskeridou^a, Maria Triantaphyllou^a,
Angela Girone^b, Vasileios Karakitsios^a

^a Department of Historical Geology and Palaeontology, Faculty of Geology and Geoenvironment, National and Kapodistrian University of Athens, Panepistimioupolis 15784, Athens, Greece

^b Facoltà di Scienze, Dipartimento di Geologia e Geofisica, Campus Universitario, Via E. Orabona 4, 70125 Bari, Italy

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ABSTRACT

The Pliocene Eastern Mediterranean fish record is revealed through the study of a 60-m thick stratigraphic sequence near the village Voutes (Heraklion, Crete). Forty-two species belonging to twenty families are identified. Calcareous nannoplankton biostratigraphy places the studied sequence within the biozone MNN16a (latest Zanclean). The stratigraphic distribution of 31 species is modified. Among these, 12 species are reported for the first time in the Eastern Mediterranean Zanclean, while 19 species are first reported outside the Ionian Sea. The Voutes fish fauna presents a diversified benthic and benthopelagic assemblage filling a significant gap in the fossil record.

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1. Introduction

Fish otoliths, the aragonitic incremental structures within the teleostean fish's inner ear, present taxon-specific morphology, which enables fossil fish assemblage reconstruction, since they are highly frequent in sediments of various environmental settings, ranging from lake to deep-sea deposits, and they are generally well preserved (Nolf, 1985). In addition, numerous studies have illustrated their value as palaeoecologic and palaeobathymetric indicators, providing very detailed and accurate palaeobiological and palaeoclimatic information.

The Pliocene Mediterranean fish fauna comprised typical tropical and subtropical taxa, which mostly inhabited the basin following its reconnection to the Atlantic Ocean, after the Messinian Salinity Crisis (Landini and Sorbini, 2005). Pliocene fish remains have been identified through several studies in the Western Mediterranean realm (Nolf and Martinell, 1980; Nolf and Girone, 2006; Girone, 2007). However few studies have been performed in the eastern sub-basin, almost all currently available information coming from fish skeletal remains. New Zanclean otolith-based fish fossil data for the Eastern Mediterranean basin are presented here for the first time, through the systematic study and analysis of the Zanclean fish otolith assemblages of the Voutes section (Heraklion, central Crete).

2. Geological setting

The Crete Island originated during the late Miocene through the N-S and E-W extensional deformation of the south Aegean, resulting in the formation of multiple tectonic blocks and late Miocene to Pleistocene sedimentary basins (Meulenkamp et al., 1988; Van Hinsbergen and Meulenkamp, 2006). The Neogene sediments overlie a pile of alpine nappe substratum, which includes the metamorphic Plattenkalk and Phyllites-Quarzites Units followed by the Tripolis and Pindos-Ethia, as well as other minor units (Zachariasse et al., 2011).

The presently emerged area of the Heraklion Basin is a Pliocene graben structure located at the northern part of the central Crete Island, in the southern segment of the Hellenic Arc, between the mountains Psiloritis and Dicti. The alpine basement formations contain a rich mélange of Triassic to Eocene sedimentary and metamorphic rocks, overlain by Neogene and Quaternary sedimentary deposits, recording a great diversity of environments and ecosystems (Symeonidis and Konstadinidis, 1967). The Pliocene Heraklion Basin occurred in a region marked by a great number of successive paleogeographic Miocene frameworks, in the vicinity of the Messara basin. In the latest Tortonian the activation of the E-W-oriented Agia Varvara fault differentiated the two realms, which evolved separately since that time (Delrieu et al., 1991). The Pliocene deposits of the Heraklion Basin are the most extensive ones in the Island. The marine sediments of the lowermost Pliocene generally overlie the late Messinian deposits (Delrieu et al., 1991;

[☆] Corresponding editor: Gilles Escarguel.

* Corresponding author.

E-mail address: kagiadi@geol.uoa.gr (K. Agiadi).

Meulenkamp et al., 1979, 1994), and consist of whitish marls and marly limestones of deep-water origin, reflecting the Pliocene flooding which followed the lago-mare episode immediately after the Mediterranean Salinity Crisis.

The studied Voutes section is located southwest of the village Voutes in central Crete, south of Heraklion city. Geologically it is situated in the western section of the Heraklion Basin (Fig. 1). The section sediments may be placed within the Finikia lithostratigraphic group of Benda et al. (1974) and Meulenkamp et al. (1979); they include more than 60 m of marls and sandy marls (Figs. 2–4). On the lower part of the section, strong gravity flows have formed a

series of sand lenses with distinctive sedimentological attributes and characteristic fauna (Fig. 5). The upper part of the section presents three diatomite horizons.

3. Material and methods

Overall, nine sediment samples were taken; 25 kg each, along the Voutes section (Figs. 2 and 3). Sample 1 was taken from the uppermost diatomite horizon, which is bare of other faunal remains. Sample 2 was collected from the uppermost marls, which present a rather rich macro-invertebrate fauna, including

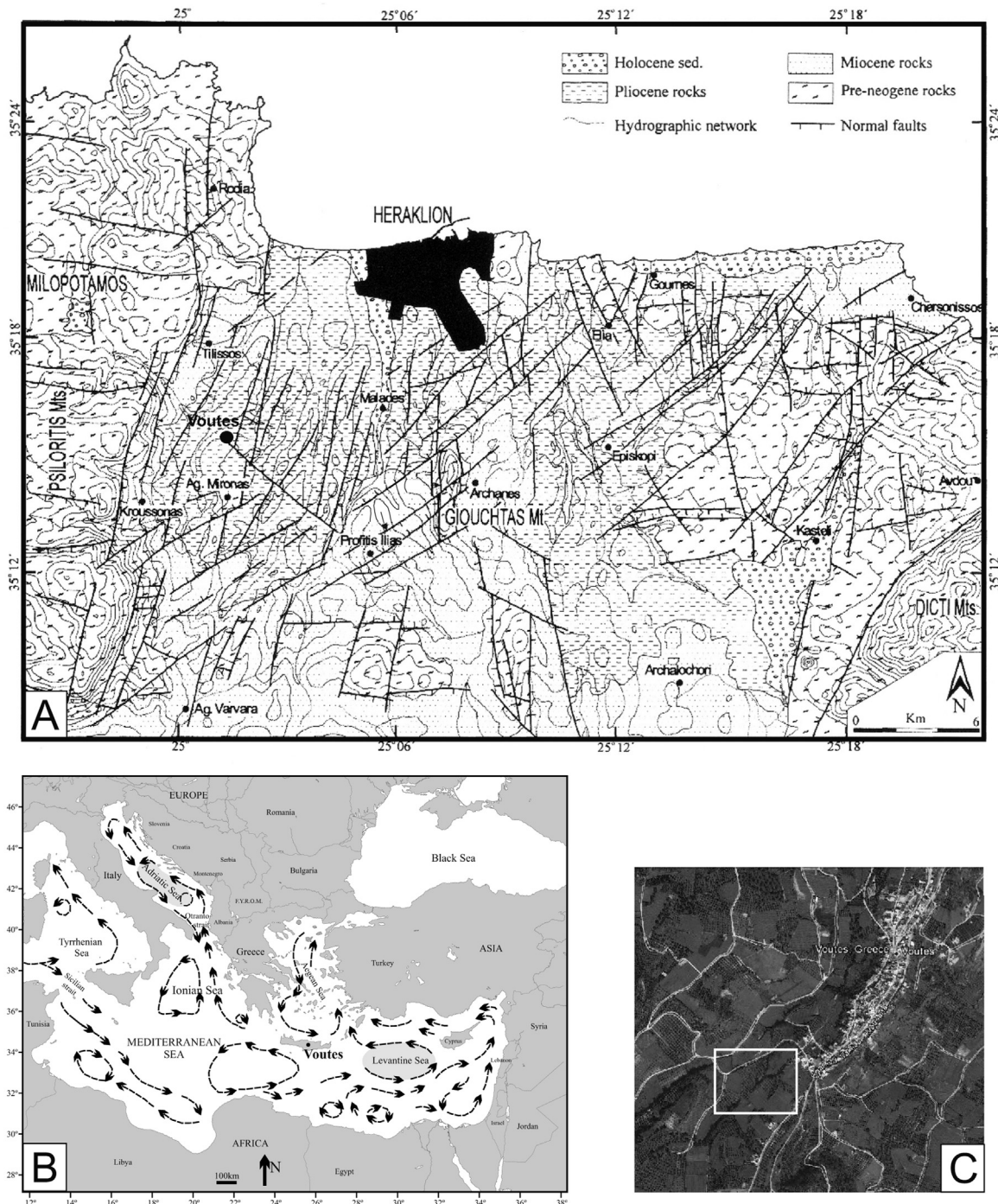


Fig. 1. Location of the study area. **A.** Geological map of the Heraklion area (simplified after Fassoulas, 2001), indicating the Voutes village. **B.** Map of the Eastern Mediterranean including the major circulation patterns. Grey sea areas denote deep-water formation regions. **C.** Photograph of the study area (obtained from Google Earth). The square marks the extent of the Voutes outcrop.

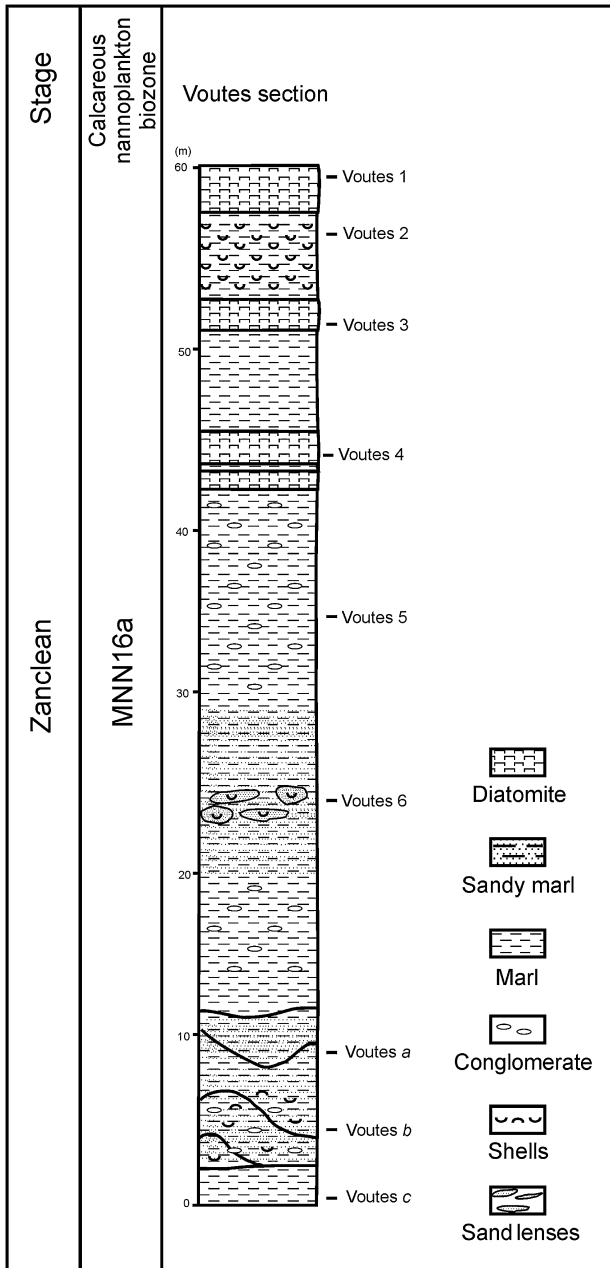


Fig. 2. Stratigraphic column of the Voutes section, indicating sample location. Calcareous nannofossil biozonation following Rio et al. (1990).

nuculoids, pectinids and limids. Samples 3 and 4 were taken from the second and third diatomite horizons, respectively, which present a poor macro-invertebrate fauna of deep-water bivalves. Sample 5 was taken from the blue marls, at the middle part of the section, where pteropods, nuculoids, thin pectinids and *Cadulus* were also identified. Sample 6 comes from marly sands, mostly gravity flows, with pectinids and gastropods. Sample a was collected from sandy marls with *Neopycnodonta navicularis*, pectinids and gastropods. Sample b was taken from one of the sand gravity lenses observed at the lower part of the outcrop (Fig. 5), which also include macrofossils such as naticids, pectinids, venerids, cardiids, turritellids and cerithiids. At the lowermost part of the section, sample c was collected from the marls underneath and around the sand lenses, in which the macroscopic examination showed no evidence of other faunal remains. The microscopic examination of this lowermost bed

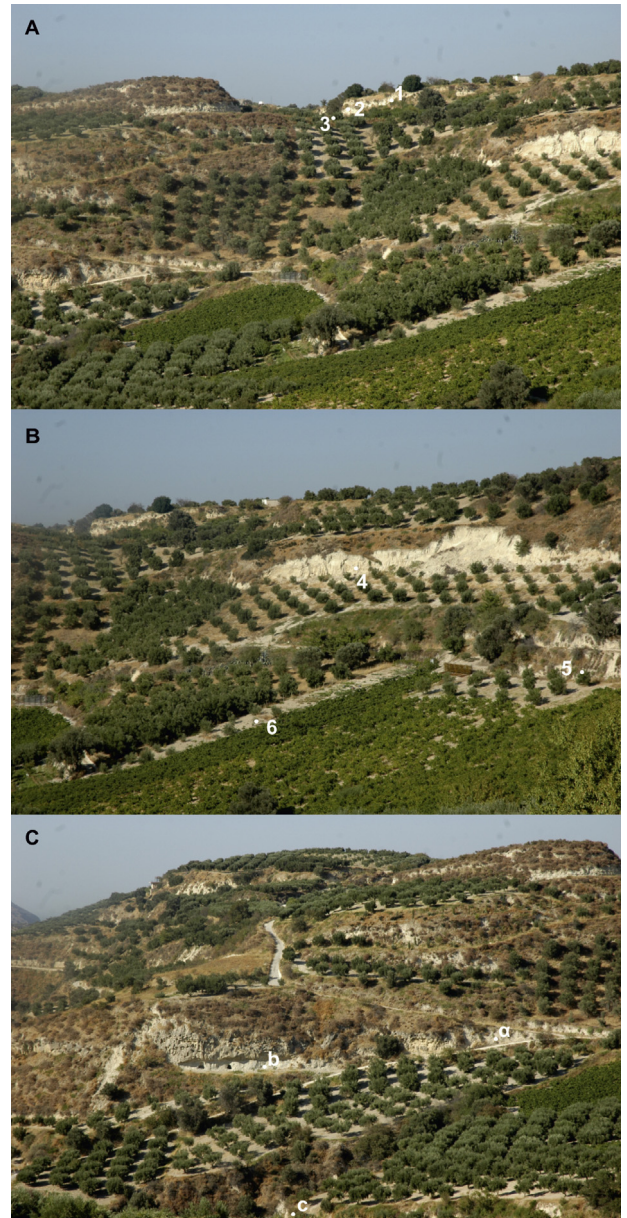


Fig. 3. Photographs of the Voutes section, with sample location. A. Upper part of the section (samples 1–3). B. Intermediate part (samples 4–6). C. Lower part (samples a–c).

revealed the presence of bathyal mollusc elements such as *Kelliella milliaris*, *Limopsis* spp., and *Ledella* sp. The samples were washed and sieved in plain water, using a 250 μm-diameter sieve. The otoliths were then handpicked from the sediment under a stereoscope.

The fish otoliths were identified based on the morphological characteristics described by Nolf (1985); lapilli were described and identified based on Assis (2005). The species' taxonomic position follows Nelson's (2006) scheme. Many recent fish species were already identified in the Mediterranean Pliocene, but in several cases, specific assignment could not be unequivocally decided, as indicated by the abbreviation "aff." inserted between the name of the genus and the name of the group species. The abbreviation "cf." was used whenever the condition of preservation of the otolith did not allow conclusive specific identification. Moreover, several taxa appear in open nomenclature at the species level due to

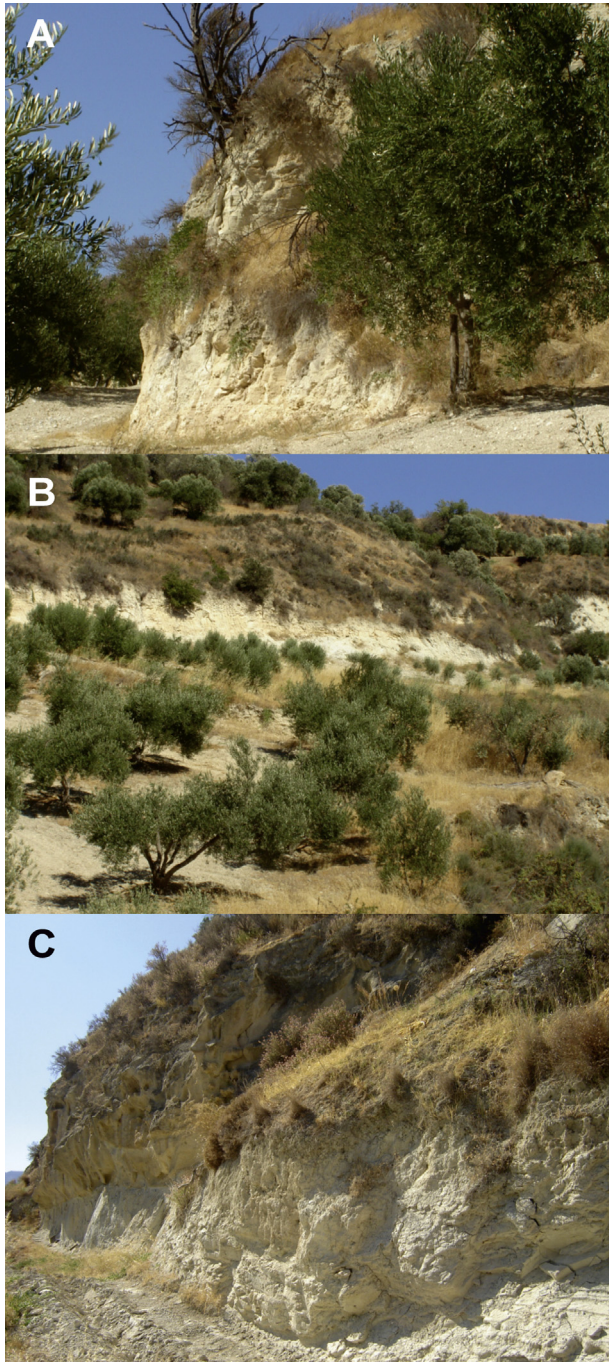


Fig. 4. Photographs of the sampled outcrops, showing different studied intervals. **A.** Upper diatomite horizon. **B.** Middle part of the section. **C.** Lower part of the section, incorporating the sand lenses.

insufficient knowledge of related recent species or because the fossil material is too limited or too poorly preserved to decide.

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 identified material is stored at the Athens Museum of Paleontology and Geology.

The relevant chronostratigraphic framework (Fig. 2) for the evaluation of the results was provided through calcareous nannoplankton biostratigraphy, based on Rio et al.'s (1990) biozonation scheme as incorporated in the magnetobiochronologic framework of Lourens et al. (2004) in Gradstein et al. (2004). Numerical ages of biozone boundaries follow Lourens et al. (2004)

and Raffi et al. (2006). In addition, the relative abundance of *Discoaster* spp. was measured in order to further specify the stratigraphic interval under study.

The palaeobiogeographic distributions of the identified Teleostei were compared to equivalent assemblages across the Mediterranean realm in order to fill gaps in the fossil record as well as to identify ichthyofauna differences and similarities.

4. Systematic palaeontology

Altogether, 42 taxa from 20 families were identified in the Voutes section sediments (Fig. 6). Specific notes on their identifications and systematic placement are made below wherever necessary.

Class ACTINOPTERYGII Klein, 1885
Order ANGUILLIFORMES Berg, 1940
Family CONGRIDAE Kaup, 1856
Genus *Pseudoplichthys* Roule, 1915
Pseudoplichthys spp.
Fig. 7(3)

Remarks: Two specimens are placed within this genus, based on the ostium portion of the sulcus, which is only very shallow and consequently poorly definable, in contrast to other congrids. One specimen is unequivocally comparable to the extant Atlantic *Pseudoplichthys splendens*, also already reported from the Western Mediterranean Pliocene (Nolf and Girone, 2006; Girone, 2007), while the other (Fig. 7(3)) is better placed under the fossil species *Pseudoplichthys escavaratierensis*, also known from the Pliocene of Southern France (Schwarzahns, 1986; Nolf and Cappetta, 1988). These two *Pseudoplichthys* specimens noticeably differ in the placement of the postero-dorsal angle. Moreover, *P. escavaratierensis* has a more rounded posterior margin and a more regularly-curved dorsal margin than *P. splendens*.

Genus *Rhynchoconger* Jordan and Hubbs, 1925
Rhynchoconger pantanellii (Bassoli and Schubert, 1906)
Fig. 7(4)

Remarks: The otoliths placed under this fossil Mediterranean species are well distinguished from *Conger conger* and *Pseudoplichthys* spp. by the closed sulcus, connected to the periphery only through a well-marked and rimed ostial channel almost vertical to the sulcus and the dorsal margin. The Voutes specimens are very similar to the otoliths of the fossil species *Rhynchoconger (Hildebrandia) pantanellii*, also known from the Pliocene sediments of Northern Italy and Southern France (Nolf and Cappetta, 1988; Girone, 2007).

Order AULOPIFORMES Rosen, 1973
Family CHLOROPHTHALMIDAE Jordan, 1923
Genus *Chlorophthalmus* Bonaparte, 1840
Chlorophthalmus agassizi Bonaparte, 1840
Fig. 7(2)

Remarks: The unique specimen found in Voutes sediments is the only known Pliocene record of this species. Previously this genus has been referred with the species *Chlorophthalmus costamagnai* Schwarzahns, 1986 from the early Pliocene of Le Puget (Southern France; Nolf and Cappetta, 1988) and Papiol (Spain; Nolf et al., 1998), and with *Chlorophthalmus* cf. *agassizi* from the Middle Pleistocene of Kephallonia (Eastern Ionian Sea; Agiadi et al., 2010). The Voutes specimen exhibits all the morphological characteristics of the modern Mediterranean species *C. agassizi* much better than the Kephallonia specimen. Namely, the Voutes specimen has an elongated shape with almost parallel dorsal and ventral margins, a long linear cauda and a much smaller ostium, which open antero-dorsally. The anterior and posterior dorso-ventral areas are almost equal, in contrast to both *C. costamagnai* and *C. cf. agassizi*.



Fig. 5. Gravity flows at the lower part of the Voutes section.

Order MYCTOPHIFORMES Regan, 1911
 Family MYCTOPHIDAE Gill, 1893
 Genus *Diaphus* Eigenmann and Eigenmann, 1890
Diaphus spp.

Fig. 7(5–7, 11, 12, 14)

Remarks: Overall, six *Diaphus* species are recognized in the Voutes material. *Diaphus* otolith morphology is known to vary greatly with fish age and as such, specific identification can be unequivocally made only with adult specimens of good preservation (Brzobohaty and Nolf, 2000). The otoliths of *Diaphus holti* (Fig. 7(7)) and *D. rafinesquii* (Fig. 7(14)) are both characterized by a strongly denticulate ventral margin, well-developed rostrum and a salient postero-dorsal angle. However *D. rafinesquii* is notably lengthier than *D. holti*; the latter has a greater height/length ratio. In addition, the sulcus of *D. holti* has a nearly rounded caudal colliculum, while it is elongate in *D. rafinesquii*. Six otoliths can be compared with those of the recent Atlantic *Diaphus taaningi* (Fig. 7(11)), characterized by a subquadrangular shape and a wide predorsal angle. This species is represented here only by juvenile and young adult specimens, slightly more elongate than recent material. A similar observation is made in the adult and juvenile specimens of *D. taaningi* from the Early Pleistocene of Montalbano (Western Ionian) and the Early-Middle Pleistocene of Archi (Western Mediterranean; Girone et al., 2006). However, the revision of this taxon proposed by Brzobohaty and Nolf (2000) pointed out that the Pliocene specimens tend to be slightly more elongate than the studied recent material. The same authors also observed such an elongate morphology in specimens from the Early Pliocene of Dar Bel Hamri, Atlantic Morocco. Several specimens present great similarity with the small and medium-sized specimens from Northern Italy (Nolf and Girone, 2006), which were identified as *Diaphus* aff. *adenomus* (Fig. 7(6)).

Order PERCIFORMES Bleeker, 1859
 Family ACROPOMATIDAE Gill, 1893
 Genus *Parascombrops* Alcock, 1889
Parascombrops mutinensis Bassoli, 1906
 Fig. 7(18–21)

Remarks: The three otoliths of this species described here share the same morphological characteristics with all the Pliocene and Pleistocene material described from Western Mediterranean (Nolf

and Martinell, 1980; Nolf and Girone, 2006). *P. mutinensis* specimens from the Early Pleistocene Eastern Ionian basin (Agiadi et al., 2010) had a considerably underdeveloped antero-ventral area. Two specimens in the Voutes material are from adult individuals, and both exhibit a well-developed antero-ventral area. However, the third specimen, belonging to a smaller individual, is undoubtedly smaller in this part, being similar to the Akrotiri specimens (Eastern Ionian). Through direct comparison with the Akrotiri specimen and small and large specimens from Palione river (Di Geronimo et al., 2003), it becomes evident that this difference is within the ontogenetic variability of the species; the antero-dorsal area seems to develop in later stages.

Family GOBIIDAE Cuvier, 1816

Fig. 8(13–20, 24)

Remarks: The members of this family have otoliths with very similar morphological characteristics. The most significant diagnostic characters are the size, shape and placement of the central or off-central sulcus and the overall shape of the otolith. The otoliths of *Aphia minuta* (Fig. 8(19)) are very small, oval-shaped, with a concave inner surface. The sulcus is also small and undivided, while the dorsal margin is irregularly curved. Twelve specimens, even if partially eroded, may be safely identified as *Deltentosteus quadrimaculatus* otoliths. However the Voutes specimens show greater similarity with the otoliths of *D. aff. quadrimaculatus* described from the Early Pleistocene of Northern Italy (Nolf and Girone, 2000, 2006; Girone, 2007), which has a more blunt antero-ventral angle than *D. quadrimaculatus*. The specimen identified here as *Gobius* sp.1 (Fig. 8(13)) strongly resembles *Gobius* sp. from the Pliocene and Pleistocene sediments of Northern Italy (Nolf and Girone, 2000, 2006). In addition, one gobiid specimen exhibits a very characteristic morphology, but cannot be specifically identified, and is referred here to genus “*Gobidarum*” sp.1 (Fig. 8(20)). This is a small square otolith; the posterior and anterior rims are angled outwards. The sulcus is also small and resembles that of *Aphia minuta*, exhibiting a concave inner face.

Order GADIFORMES Goodrich, 1909

Family GADIDAE Rafinesque, 1810

Fig. 8(4)

Family	Genus and Species	Samples								
		c	b	a	6	5	4	3	2	1
PELAGIC TAXA										
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)	–	–	1	–	–	–	1	–	–
Phosichthyidae	<i>Vinciguerria poweriae</i> (Cocco, 1838)	4	–	2	3	2	–	–	–	–
Myctophidae	<i>Ceratospelus maderensis</i> (Lowe, 1839)	9	–	5	18	12	1	5	14	–
	<i>Diaphus</i> aff. <i>adenomus</i> Gilbert, 1905	2	–	–	2	5	–	4	1	–
	<i>Diaphus cavallonis</i> (Brzobohaty and Nolf, 2000)	7	–	15	6	3	1	6	13	–
	<i>Diaphus holti</i> Taaning, 1918	–	–	7	4	13	1	–	1	–
	<i>Diaphus rafinesquii</i> (Cocco, 1838)	2	–	–	–	–	–	–	–	–
	<i>Diaphus</i> aff. <i>splendidus</i> (Brauer, 1904)	–	–	3	7	7	–	1	4	–
	<i>Diaphus taaningi</i> Norman, 1930	–	–	6	–	–	–	–	–	–
	<i>Diaphus</i> sp.	50	8	65	11	8	–	5	42	–
	<i>Hygophum benoitii</i> (Cocco, 1838)	–	–	–	–	–	–	–	1	–
	<i>Hygophum hygomii</i> (Lütken, 1892)	6	–	–	1	3	2	3	3	–
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)	–	–	5	–	–	–	–	–	–
	<i>Myctophum fitchi</i> (Schwarzahns, 1979)	1	–	11	2	–	1	–	4	–
	<i>Notoscopelus resplendens</i> (Richardson, 1845)	2	–	–	5	4	–	–	–	–
	<i>Notoscopelus</i> sp.	–	–	–	–	–	–	2	–	–
	<i>Scopelopsis pliocenicus</i> (Anfossi & Mosna, 1976)	–	–	–	–	2	1	–	–	–
	indet.	6	2	12	5	–	–	1	5	5
	Bregmacerotidae	<i>Bregmaceros</i> sp.	2	19	–	11	23	47	42	7
BENTHIC AND BENTHOPELAGIC TAXA										
Congridae	<i>Pseudoplichthys splendens</i> (Lea, 1913)	–	–	–	1	–	–	–	–	–
	<i>Pseudoplichthys escavaratierensis</i> (Nolf and Cappetta, 1988)	–	–	–	–	–	–	1	–	–
	<i>Rhynchoconger pantanellii</i> (Bassoli, 1906)	–	–	1	3	–	–	–	–	–
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i> Bonaparte, 1840	–	–	–	–	1	–	–	–	–
Moridae	<i>Laemonema</i> sp.	–	–	1	–	–	2	–	–	1
Gadidae	<i>Gadiculus labiatus</i> (Schubert, 1905)	2	–	3	6	4	–	–	9	1
	Indet. lapilli	5	–	–	–	7	–	–	2	1
Bythitidae	<i>Grammonus ater</i> (Risso, 1810)	2	–	–	–	–	–	–	–	–
Carapidae	<i>Echiodon dentatus</i> (Cuvier, 1829)	–	–	1	1	–	–	–	–	–
Atherinidae	<i>Atherina boyeri</i> Risso, 1810	–	–	–	1	–	–	–	–	–
Apogonidae	<i>Apogon</i> sp.	1	–	–	1	–	–	–	–	–
Epigonidae	<i>Epigonus</i> aff. <i>denticulatus</i> Dieuzeide, 1950	2	–	–	–	–	–	–	–	–
	<i>Epigonus</i> sp.	–	–	–	–	–	–	–	1	–
Acropomatidae	<i>Parascombrops mutinensis</i> (Bassoli, 1906)	–	–	–	–	2	–	2	–	–
Sparidae	<i>Oblada melanura</i> (Linnaeus, 1758)	1	–	–	–	–	–	–	–	–
	<i>Pagellus erythrinus</i> (Linnaeus, 1758)	–	–	–	–	1	–	–	–	–
	<i>Pagellus</i> sp.	–	–	–	1	–	–	–	–	–
Indet.	–	1	8	–	–	1	–	–	–	1
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)	–	1	–	1	–	–	–	–	–
Perciformes	Indet.	–	–	2	6	–	–	4	1	1
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)	–	–	2	–	2	–	1	–	–
	<i>Deltentosteus</i> aff. <i>quadriraculatus</i> (Valenciennes, 1837)	–	4	8	–	–	–	–	–	–
	<i>Gobius niger</i> Linnaeus, 1758	–	–	24	–	–	–	–	–	–
	<i>Gobius</i> cf. <i>paganellus</i> Linnaeus, 1758	–	–	1	–	–	–	–	–	–
	<i>Gobius</i> sp.1	–	–	–	1	–	–	–	–	–
	<i>Gobius</i> sp.	–	–	3	–	–	–	–	–	–
	<i>Lesueurigobius friesii</i> (Malm, 1874)	–	8	15	11	1	–	–	–	–
	<i>Lesueurigobius sanzi</i> (de Buen, 1918)	–	–	4	–	–	–	–	–	–
	<i>Lesueurigobius suerii</i> (Risso, 1810)	1	–	2	11	–	–	–	–	–
	<i>Lesueurigobius</i> sp.	–	–	–	–	1	–	1	4	–
	genus « <i>Gobidarum</i> » sp.1	–	–	–	1	–	–	–	–	–
	Indet.	–	2	15	13	1	–	–	–	–
	Indet.	–	–	–	–	–	–	–	1	–
Trichiuridae	<i>Citharus linguatula</i> (Linnaeus, 1758)	–	–	–	1	–	–	–	–	–
Citharidae	<i>Arnoglossus kokeni</i> (Bassoli, 1906)	–	–	1	–	–	–	–	–	–
Bothidae	<i>Arnoglossus</i> sp.	–	–	–	1	–	–	–	–	–
	Indet.	–	–	1	–	–	–	–	–	–
Total number of otoliths		105	45	224	135	102	57	79	113	34

Fig. 6. List of the fish taxa identified in the Voutes section.

Remarks: All the Gadidae identified in the present material undoubtedly belong to the fossil Mediterranean species *G. labiatus*. In addition several lapilli are present in the samples (Fig. 8(4)). These exhibited similar morphological characteristics, so they were grouped together. Through comparison with the descriptions given by Assis (2005), these can safely be placed within Gadidae, with no further identification possible at this time. The specimens were thick, square-shaped with rounded margins. A strong, almost square voluminous protuberance is clearly contained within the otolith margin, when observed from the ventral view.

Order PLEURONECTIFORMES

Fig. 8(21–23)

Remarks: Pliocene and Pleistocene *Arnoglossus* otoliths from the Mediterranean realm have previously been placed under the fossil species *A. kokeni*, which has a linear or convex posterior margin. In extant Mediterranean species *A. laterna* the posterior margin is concave and irregular, occasionally even more slender. The Voutes specimen (Fig. 8(22)) exhibits greater similarity to *A. kokeni* in the sulcus, which is subparallel to the dorsal rim, in contrast to *A. laterna* where it is always parallel.

5. Discussion

5.1. Biostratigraphy

In the Voutes section, the nannoflora assemblage is dominated by discoasterids, which provide important biostratigraphic markers in the Pliocene. Discoasters are relatively well diversified and contain *Discoaster adamanteus*, *D. asymmetricus*, *D. tamalis*, *D. surculus*, and very sporadic *D. pentaradiatus* and *D. brouweri*.

Palcoliths are represented mainly by very abundant *Pseudoemiliania lacunosa*. *Helicosphaera sellii* is also significantly contributing to nannofossil assemblages. *Reticulofenestra pseudoubilicus* (> 7 μm) and sphenolithids are practically absent. The high abundance of both *D. tamalis* (15–35%) and *D. surculus* (15–50%) implies correlation with nannofossil zone MNN16 (Rio et al., 1990). Moreover, the nearly absence of *D. pentaradiatus* supports the recognition of the paracme interval of this species. Therefore the studied interval from the Voutes section is assigned to the biozone MNN16, above the highest occurrence of *R. pseudoubilicus* and

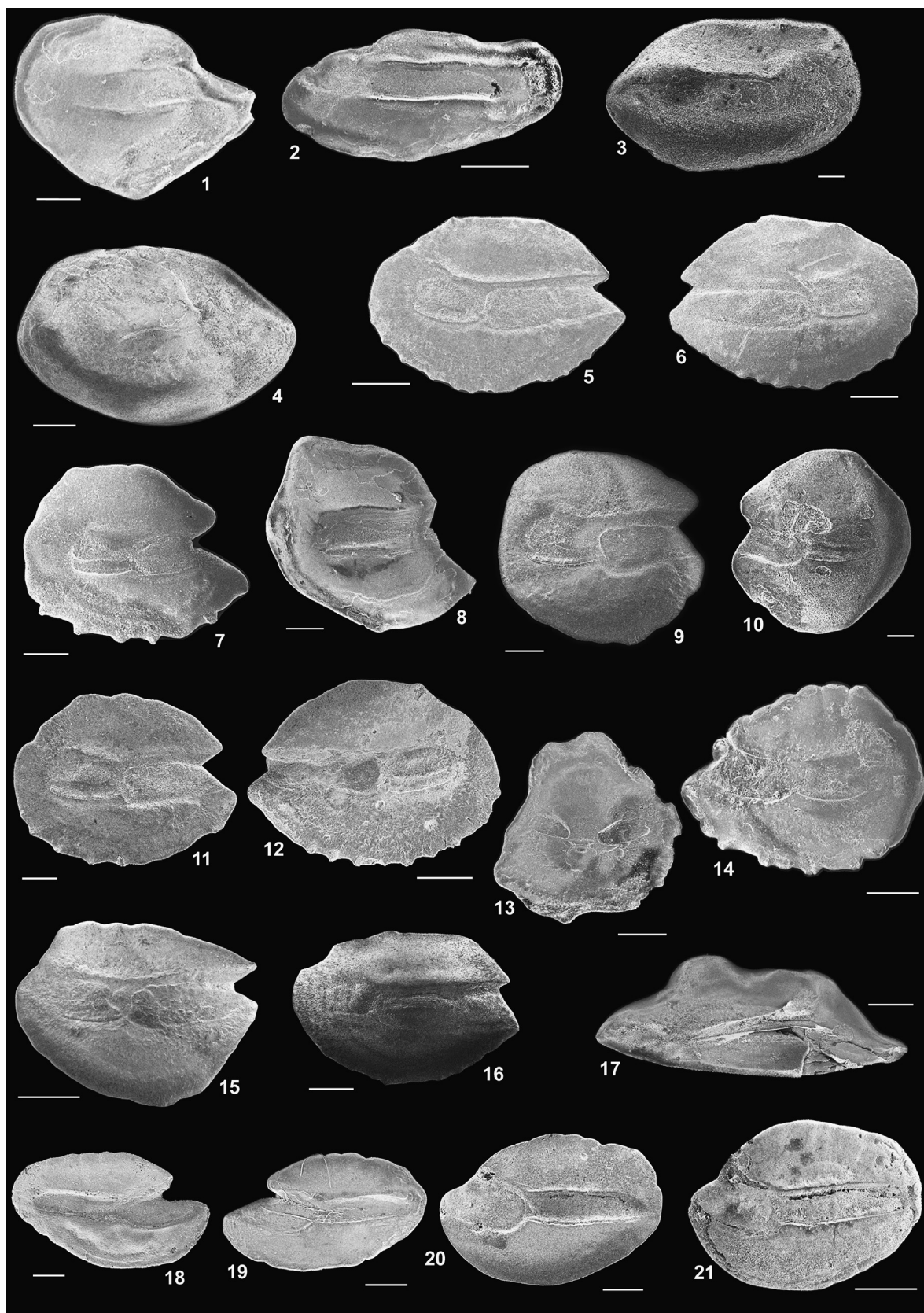


Fig. 7. SEM photographs of the studied otolith material. **1.** *Vinciguerria poweriae* (Cocco, 1838), Voutes 5. **2.** *Chlorophthalmus agassizi* Bonaparte, 1840, Voutes 5. **3.** *Pseudophichthys escavariatierensis* (Nolf and Cappetta, 1988), Voutes 3. **4.** *Rhynchoconger pantanellii* (Bassoli, 1906), Voutes a. **5.** *Diaphus* aff. *splendidus* (Brauer, 1904), Voutes 5. **6.** *Diaphus* aff. *adenomus* Gilbert, 1905, Voutes 2. **7.** *Diaphus holti* Taaning, 1918, Voutes 2. **8.** *Maurollicus muelleri* (Gmelin, 1789), Voutes 3. **9.** *Hygophum hygomii* (Lutken, 1892), Voutes 3. **10.** *Hygophum benoiti* (Cocco, 1838), Voutes 2. **11.** *Diaphus taaningi* Norman, 1930, Voutes a. **12.** *Diaphus cavallonis* (Brzobohaty and Nolf, 2000), Voutes 2. **13.** *Bregmaceros* sp., Voutes 5. **14.** *Diaphus rafinesquii* (Cocco, 1838), Voutes c. **15.** *Myctophum fitchi* (Schwarzahns, 1979), Voutes c. **16.** *Notoscopelus resplendens* (Richardson, 1845), Voutes c. **17.** *Laemonema* sp., Voutes 4. **18–21.** *Parascombrops mutinensis* (Bassoli, 1906); 18–20: eastern Ionian (Agiadi et al., 2010); 21: Voutes 5. Scale bars: 200 μm (1, 3, 8, 10); 500 μm (2, 4, 7, 9, 11, 13, 14, 17–19); 1 mm (5, 6, 12, 15, 16, 20, 21).

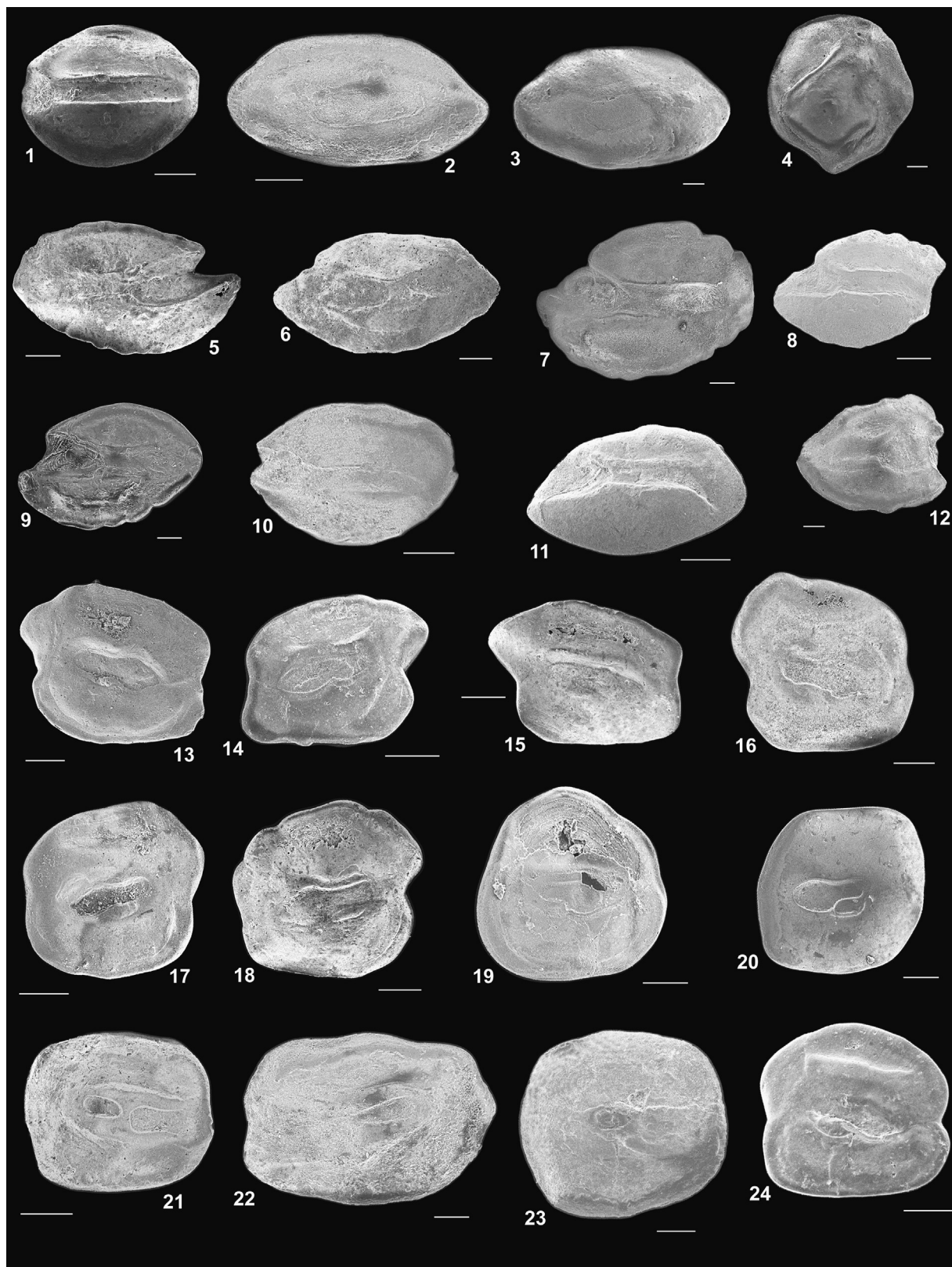


Fig. 8. SEM photographs of the studied otolith material. **1.** *Atherina boyeri* Risso, 1810, Voutes 6. **2, 3.** *Grammonus ater* (Risso, 1810), Voutes c. **4.** Gadidae indet. Lapillus, Voutes 5. **5.** *Epigonus* aff. *denticulatus* Dieuzeide, 1950, Voutes c. **6.** *Cepola macrophthalma* (Linnaeus, 1758), Voutes 6. **7.** *Pagellus erythrinus* (Linnaeus, 1758), Voutes 5. **8.** *Pagellus* sp., Voutes 6. **9.** *Epigonus* sp., Voutes 2. **10.** *Citharus linguatula* (Linnaeus, 1758), Voutes 6. **11.** *Oblada melanura* (Linnaeus, 1758), Voutes c. **12.** *Apogon* sp., Voutes 6. **13.** *Gobius* sp. 1, Voutes 6. **14.** *Gobius* cf. *paganellus* Linnaeus, 1758, Voutes a. **15.** *Gobius niger* Linnaeus, 1758, Voutes a. **16.** *Lesueurigobius sanzi* (de Buen, 1918), Voutes a. **17, 18.** *Lesueurigobius friesii* (Malm, 1874), Voutes a. **19.** *Aphia minuta* (Risso, 1810), Voutes 5. **20.** “*Gobidarum*” sp. 1, Voutes 6. **21.** *Arnoglossus* sp., Voutes 6. **22.** *Arnoglossus kokeni* (Bassoli, 1906), Voutes a. **23.** Bothidae indet., Voutes a. **24.** *Lesueurigobius suerii* (Risso, 1810), Voutes a. Scale bars: 200 μ m (3, 4, 7, 9, 12, 19, 20, 22, 23); 500 μ m (1, 2, 5, 6, 8, 10, 13–18, 21, 24); 1 mm (11).

Family	Genus and Species	Western Mediterranean										Eastern Mediterranean					Present-day Atlantic	Present-day Indo-Pacific	References			
		Miocene					Pliocene					Pleistocene										
		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Upper	Holocene	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian				Middle	Upper	Holocene
Sternoptychidae	<i>Maurolicus muelleri</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 2, 3, 8, 9, 12, 13, 16, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 34	
	<i>Vinciguerria poweriae</i>																				1, 3, 8, 9, 13, 22, 24, 25, 26, 28	
Phosichthyidae	<i>Ceratoscopelus maderensis</i>			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 3, 5, 6, 7, 8, 9, 11, 12, 13, 14, 15, 21, 22, 24, 25, 26, 27, 28, 29, 30, 31, 32	
	<i>Diaphus adenomus</i>			+																	3	
	<i>Diaphus cavallonis</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3, 4, 7, 8, 9, 13, 14, 15, 17, 34	
	<i>Diaphus holti</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 3, 4, 6, 7, 9, 13, 22, 23, 26, 28, 33	
	<i>Diaphus rafinesquii</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 3, 4, 6, 8, 9, 13, 14, 17, 23, 26, 27, 28, 29, 31, 34	
	<i>Diaphus aff. splendidus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3, 4, 7, 8, 9, 13, 14, 17, 23, 26, 27, 28, 32, 33, 34	
	<i>Diaphus taaningi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 4, 7, 9, 13, 26, 27, 28, 34	
	<i>Hygophum benoiti</i>																					1, 8, 13, 23, 24, 26, 27, 28
	<i>Hygophum hygomi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 3, 5, 6, 7, 8, 9, 13, 14, 15, 22, 23, 24, 26, 27, 28, 29, 31, 32, 34
	<i>Lobianchia dofteini</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 5, 7, 9, 7, 13, 14, 22, 23, 25, 26, 27, 28, 31, 34
Mycetophidae	<i>Mycetophum fitchi</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3, 5, 6, 7, 9, 13, 14, 15, 33	
	<i>Notoscopelus resplendens</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	3, 5, 6, 8, 9, 13, 15, 29	
	<i>Scopelopsis phocenicus</i>	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 3, 5, 6, 7, 8, 9, 13, 15, 26, 28, 29, 33	
	<i>Bregmaceros</i> sp.	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1, 2, 3, 8, 9, 11, 12, 13, 16, 18, 19, 20, 21, 22, 24, 29, 31, 34	

Fig. 9. Geographic and stratigraphic distribution of the identified pelagic fish taxa. Present-day distributions are according to the Fishbase database (Froese and Pauly, 2012). Dark grey cells indicate those taxa with first eastern Mediterranean Sea record in the corresponding time interval; light grey cells indicate taxa already reported in the Eastern Mediterranean for the corresponding time interval, but only in the Ionian realm. Present-day Indo-Pacific distribution of *M. muelleri* is confined to the eastern part of the Pacific Ocean. References: 1. Agiadi et al., 2011; 2. Landini and Sorbini, 1993; 3. Nolf and Girone, 2006; 4. Brzobohaty and Nolf, 2000; 5. Brzobohaty and Nolf, 1996; 6. Nolf and Martinell, 1980; 7. Nolf et al., 1998; 8. Girone, 2007; 9. Nolf and Cappetta, 1988; 10. Carnevale et al., 2006; 11. Markopoulou-Diakantoni and Kagiouzis, 2001; 12. Gaudant, 2002; 13. Landini and Sorbini, 2005; 14. Nolf and Cavallo, 1995; 15. Schwarzahns, 1979; 16. Anfossi et al., 1982; 17. Anfossi and Mosna, 1979; 18. Landini et al., 1990; 19. Gaudant, 2001; 20. Gaudant et al., 1994; 21. Sorbini, 1988; 22. Landini and Menesini, 1986; 23. Landini and Menesini, 1978; 24. Sorbini and Landini, 2003; 25. Landini and Varola, 1983; 26. Girone, 2000; 27. Girone and Varola, 2001; 28. Girone, 2003; 29. Anfossi and Mosna, 1972; 30. Aruta and Greco, 1980; 31. Bossio et al., 1986; 32. Nolf and Girone, 2000; 33. Anfossi and Mosna, 1976; 34. Girone et al., 2010; 35. Hoedemakers and Batllori, 2005.

Sphenolithus spp. following the MNN14/15–MNN16 boundary (3.84 Ma, Lourens et al., 2004; Raffi et al., 2006) and just below the top of *D. pentaradiatus* paracme (3.61 Ma, Lourens et al., 2004), within the latest Zanclean.

5.2. Stratigraphic and biogeographic affinities

This study represents the first otolith-based reconstruction of a Zanclean fish paleofauna in the Eastern Mediterranean. The

Family	Genus and Species	Western Mediterranean												Eastern Mediterranean						Present-day Atlantic	Present-day Indo-Pacific	References			
		Miocene			Pleistocene			Holocene			Miocene			Pleistocene			Holocene								
		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Upper	Holocene	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Upper	Holocene						
Congridae	<i>Pseudoplichthys splendens</i>																							3, 8, 34	
	<i>Pseudoplichthys escavaratterensis</i>																								3, 9, 13, 14
	<i>Rhynchoconger pantanellii</i>																								3, 7, 8, 9, 14, 15, 16, 17, 33
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>																								1
	<i>Laemonema</i> sp.																								1, 8
Gadidae	<i>Gadiculus labiatus</i>																								1, 2, 3, 6, 7, 8, 9, 13, 14, 16, 17, 19, 21, 29, 34
	<i>Grammonus ater</i>																								27
Carapidae	<i>Echiodon dentatus</i>																								13, 27, 32
	<i>Atherina boyeri</i>																								12, 34
Apogonidae	<i>Apogon</i> sp. (ref. <i>A. lozanoi</i>)																								6, 9, 13, 14, 17, 34
	<i>Epigonus</i> aff. <i>denticalatus</i>																								3
Acropomatidae	<i>Parascombrops mutinensis</i>																								1, 3, 6, 7, 8, 9, 13, 14, 15, 16, 17, 29, 33, 34
	<i>Oblada melanura</i>																								3
Sparidae	<i>Pagellus erythrinus</i>																								3, 6, 9, 13, 14, 18, 32
	<i>Cepola macrophthalmia</i>																								3, 6, 7, 8, 9, 13, 14, 17, 18, 26, 27, 29, 32, 33, 34, 35
Cepolidae	<i>Aphia minuta</i>																								13, 27, 34
	<i>Deltentosteus</i> aff. <i>quadrifasciatus</i>																								1, 3, 13, 26, 27, 32
Gobiidae	<i>Gobius niger</i>																								3, 10, 13, 18, 32
	<i>Gobius paganelus</i>																								3, 8, 17, 26, 27, 32
	<i>Lesueurigobius friesii</i>																								3, 7, 34
	<i>Lesueurigobius sanzii</i>																								3, 14, 27, 32
Citharidae	<i>Lesueurigobius suerii</i>																								3, 7, 9, 13, 14, 26, 27, 32, 35
	<i>Citharus linguatula</i>																								3, 6, 9, 13, 14, 17, 26, 27, 32, 35
Bothidae	<i>Armoiglossus kokeni</i>																								

Fig. 10. Geographic and stratigraphic distribution of the identified benthic and benthopelagic fish taxa. At present, *G. ater* may be found in the Mediterranean, from the western sub-basin to the Adriatic Sea. Grey cells and reference numbers: see Fig. 9.

stratigraphic and geographic distributions of the identified taxa are presented in Figs. 9 and 10. Overall, the stratigraphic distribution of 31 species is significantly extended. In particular, 12 species are reported for the first time in the Zanclean of the Eastern Mediterranean realm, while 19 species are reported for the first time in the Eastern Mediterranean outside the Ionian Sea. They illustrate a teleost fauna including both neritic and oceanic fishes.

The only previous reference to fossil fish otoliths in the Pliocene of the Eastern Mediterranean, outside the Ionian Sea, is the short note by Markopoulou-Diakantoni and Kagiouzis (2001). Unfortunately, the material examined in that paper is not available for re-evaluation. Revisiting the Rethymnon section, outside the village Prassies, allowed the identification of the outcrop where the Late Miocene and Early Pliocene sediment samples were presumably taken by these authors. Systematic identification of the studied specimens could only be evaluated through the provided figures and photographs. As such, the specimens referred to *Diaphus* spp. can be positively identified at the generic level, *Ceratoscopelus maderensis* may be safely considered to be present, *Bregmaceros albyi* should best be referred to as *Bregmaceros* sp. due to the lack of data on the otolith morphological characteristics of the present-day species, and the specimens identified as *Gobius vicinalis* are better considered to belong to *Lesueurigobius* sp. based on their description and figures.

A significant observation made on Figs. 9 and 10 is that the Middle–Upper Pleistocene fish distribution is almost completely unknown. This is caused by lack of data due to the practical difficulty in finding appropriate specimens for this period.

Overall, the Pliocene Eastern Mediterranean ichthyofauna, as preserved in the Voutes area, presents a rich pelagic and a rather diverse benthopelagic and benthic component. The pelagic taxa include members of four families: Myctophidae, which is the most abundant and diverse, Sternoptychidae, Phosichthyidae, and Bregmacerotidae. The pelagic fish fauna does not present any striking differences neither from the western sub-basin fauna, nor from the Messinian fauna (Fig. 9).

Gobiids are by far the most diverse and abundant benthic fish family in the studied assemblages (Fig. 10). Six, out of the nine species identified, inhabit the Eastern Mediterranean coasts until today. *Lesueurigobius sanzi* may only be found today in the Atlantic Ocean and the western sub-basin, although it was present in both Mediterranean sub-basins prior to the Messinian salinity crisis. Gobiids generally appear to be quite resilient to the various environmental disturbances, persisting until today. The very limited data on the Eastern Mediterranean fish fauna is the most likely reason behind the striking gobiid absence from the Miocene assemblages. Judging from the state of the Western Mediterranean record however, it may be safely assumed that *D. quadrimaculatus*, *G. paganellus*, *L. friesii* and *L. suerii* are indeed Pliocene-introduced species.

In addition, the sparids *Oblada melanura* and *Pagellus erythrinus* first seem to enter the Mediterranean after the Messinian/Zanclean boundary. Furthermore, the presence of *Chlorophthalmus agassizi* in the Zanclean Eastern Mediterranean basin is notable since this very abundant extant species has only been recorded before, in the Middle Pleistocene sediments of the Ionian Sea (Agiadi et al., 2011). So far, *Grammonus ater* has only been found in the eastern sub-basin from the Gelasian–Calabrian Ionian Sea (Girone and Varola, 2001). Finally, this is also the first post-Messinian Salinity Crisis Eastern Mediterranean record of the presently abundant species *Atherina boyeri* (Girone et al., 2006, 2010).

The Voutes fish fauna comprises both Messinian relics, as well as Pliocene introductions. When examining the stratigraphic distribution of the various fish taxa identified in this section, it is perceived that few are those Miocene species which seem to

persist into the Pliocene, but do not last until today; these are *D. cavallonis*, *M. fitchi*, *S. pliocenicus*, *G. labiatus*, *Apogon* spp., *P. mutinensis*. Apart from *Apogon* spp., these are presently extinct taxa. In addition, it becomes more evident that some species were indeed first introduced to the Mediterranean after the salinity crisis, and maintained their place in the ecosystem until the present day; these are *V. poweriae*, *C. maderensis*, *H. benoiti*, *C. agassizi*, *G. ater*, *E. dentatus*, *E. denticulatus*, *O. melanura*, *P. erythrinus*, *D. quadrimaculatus*, *G. paganellus*, *L. friesii*, *L. suerii*, and *C. linguatula*. The present-day distributions of these latter species are either circum-global or Atlantic. The previously reported Indo-Pacific affinity of the Pliocene Mediterranean fauna (Gaudant, 2002) does not seem to apply in the case of the Voutes assemblages.

6. Conclusion

The added value provided through the examination of the Voutes fish fauna lies in the fact that this is the first systematic study of the evolution of the fish paleofauna in the Eastern Mediterranean. Indeed, *Chlorophthalmus agassizi*, an extant circum-global species very abundant in the Eastern Ionian Sea today, is documented for the first time outside the Ionian basin and in the Early Pliocene. This significantly affects any preconceptions regarding the Eastern Mediterranean deep-dwelling faunas, which may not be as much affected by climatic regimes, but rather more by other paleoceanographic factors such as circulation patterns, as already proposed by Agiadi et al. (2011). In addition, several systematic remarks are made on the otoliths of selected taxa. Finally, notable is the great diversity of the neritic benthic component, mostly comprised of gobiids, presumably reflecting locally different sea bottom conditions, but also of the mesopelagic myctophids. It can be safely assumed that the Voutes area offered several diverse habitats for different faunal components, but also that the environmental perturbations did not permit for a few species to competitively overwhelm others and dominate.

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References

- Agiadi, K., Triantaphyllou, M., Girone, A., Karakitsios, V., Dermizakis, M., 2010. Paleobathymetric interpretation of the fish otoliths from the lower-middle Quaternary deposits of Kephallonia and Zakynthos Islands (Ionian Sea, western Greece). *Rivista Italiana di Paleontologia e Stratigrafia* 116 (1), 63–78.
- Agiadi, K., Triantaphyllou, M., Girone, A., Karakitsios, V., 2011. The early Quaternary palaeobiogeography of the eastern Ionian deep-sea Teleost fauna: a novel palaeocirculation approach. *Palaeogeography Palaeoclimatology Palaeoecology* 306, 228–242.
- Anfossi, S., Brambilla, G., Mosna, S., 1982. La fauna del Pliocene di Taino (Varese). *Atti dell' Istituto Geologico dell' Università di Pavia* 30, 83–102.
- Anfossi, G., Mosna, S., 1972. Otoliti del Pliocene inferiori di Lugagnano (Piacenza). *Atti dell' Istituto Geologico dell' Università di Pavia* 23, 90–118.
- Anfossi, G., Mosna, S., 1976. Otoliti del Pliocene inferiore della Liguria occidentale. *Atti dell' Istituto geologico della Università di Pavia* 26, 15–29.
- Anfossi, G., Mosna, S., 1979. La fauna ittologica di Monteu Roero (Alba, Italia NW). *Otoliti. Atti dell' Istituto Geologico della Università di Pavia* 27, 111–132.
- Aruta, L., Greco, A., 1980. Otoliti dell' Emiliano di località Olivella (PA) e del Pliocene superior di contrada Pipitone (AG) (Sicilia occidentale). *Il Naturalista Siciliano ser 4* 4 (3–4), 101–117.

- Assis, C.A., 2005. The utricular otoliths, *lapilli*, of teleosts: their morphology and relevance for species identification and systematics studies. *Scientia Marina* 69 (2), 259–273.
- Benda, L., Meulenkamp, J.E., Zachariasse, W.J., 1974. Biostratigraphic correlations in the eastern Mediterranean Neogene. Part I: Correlation between planktonic foraminiferal, uvigerinid, sporomorph and mammal zonations of the Cretan and Italian Neogene. *Newsletters on Stratigraphy* 3, 205–217.
- Bossio, A., Landini, W., Mazzei, R., Salcatorini, G., Varola, A., 1986. Studi sul Neogene e Quaternario della Penisola Salentina. I. La sequenza pliocenica di S. Andrea (Lecce) e il suo contenuto in pesci, ostracodi, foraminiferi e nannofossili. *Atti della Società Toscana di Scienze Naturali Memoire series A* 92, 35–93.
- Brzobohaty, R., Nolf, D., 1996. Otolithes de myctophides (poissons teleosteens) des terrains tertiaires d'Europe: revision des genres *Benthosema*, *Hygophum*, *Lampadena*, *Notoscopelus* et *Symbolophorus*. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 66, 151–176.
- Brzobohaty, R., Nolf, D., 2000. *Diaphus* otoliths from the European Neogene (Myctophidae, Teleostei). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 70, 185–206.
- Carnevale, G., Landini, W., Sarti, G., 2006. Mare versus Lago-mare: marine fishes and the Mediterranean environment at the end of the Messinian Salinity Crisis. *Journal of the Geological Society London* 163, 75–80.
- Delrieu, B., Saint Martin, J.-P., Merle, D., 1991. Un modèle d'évolution tectono-sédimentaire dans le domaine sud-égréen du Miocène supérieur: l'accident d'Aghia Varvara (Crète centrale, Grèce). *Comptes Rendus de l'Académie des Sciences de Paris* 313, 1043–1049.
- Di Geronimo, I., Di Geronimo, R., Girone, A., La Perna, R., Rosso, A., 2003. Autochthonous and allochthonous assemblages from Lower Pleistocene sediments (Palione river, Sicily). *Bollettino della Società Paleontologica Italiana* 42, 133–138.
- Fassoulas, C., 2001. The tectonic development of a Neogene basin at the leading edge of the active European margin: the Heraklion basin, Crete, Greece. *Journal of Geodynamics* 31, 49–70.
- Froese, R., Pauly, D., 2012 (Eds.). *Fishbase*. World Wide Web electronic publication. www.fishbase.org, version (10/2012).
- Gaudant, J., 2001. Ammissos: un gisement clé pour la connaissance de l'ichthyofaune du Pliocène supérieur de Crète. *Annales des Naturhistorischen Museums in Wien* 102A, 131–187.
- Gaudant, J., 2002. La crise messinienne et ses effets sur l'ichthyofaune Néogène de la Méditerranée: le témoignage des squelettes en connexion de poissons téléostéens. *Geodiversitas* 24 (3), 691–710.
- Gaudant, J., Delrieu, B., Dermizakis, M., Symeonidis, N., 1994. Découverte d'une ichthyofaune marine dans les diatomites du Pliocène supérieur (Piacenzien) des environs d'Heraklion (Crète centrale, Grèce). *Comptes rendus de l'Académie des Sciences, Paris*, ser. 2 319, 589–596.
- Girone, A., 2000. The use of fish otoliths for paleobathymetric evaluation of the Lower to Middle Pleistocene deposits in Southern Italy. *Bollettino della Società Paleontologica Italiana* 39 (2), 235–242.
- Girone, A., 2003. The Pleistocene bathyal Teleostean fauna of Archi (Southern Italy): palaeoecological and palaeobiogeographic implications, *Rivista Italiana di Paleontologia e Stratigrafia* 109 (1), 99–110.
- Girone, A., 2007. Piacenzian otolith assemblages from northern Italy (Rio Merli section, Emilia Romagna). *Bollettino della Società Paleontologica Italiana* 45 (2–3), 159–170.
- Girone, A., Nolf, D., Cappelletta, H., 2006. Pleistocene fish otoliths from the Mediterranean Basin: a synthesis. *Geobios* 39, 651–671.
- Girone, A., Nolf, D., Cavallo, O., 2010. Fish otoliths from the pre-evaporitic (Early Messinian) sediments of northern Italy: their stratigraphic and palaeobiogeographic significance. *Facies* 56, 399–432.
- Girone, A., Varola, A., 2001. Fish otoliths from the Middle Pleistocene deposits of Montalbano Jonico (Southern Italy). *Bollettino della Società Paleontologica Italiana* 10 (3), 431–443.
- Gradstein, F., Ogg, J., Smith, A., 2004. *A Geological Time Scale*. Cambridge University Press, 610 p.
- Hoedemakers, K., Battlori, J., 2005. Fish otoliths from the Early and Middle Miocene of the Penedis (Catalunya, Spain). *Batallerna* 12, 105–134.
- Landini, W., Menesini, E., 1978. L'ittiofauna Plio-Pleistocenica della sezione della Vrica (Crotona – Calabria). *Nota preliminare. Atti della Società Toscana di Scienze Naturali Memorie SerieA* 84, 1–14.
- Landini, W., Menesini, E., 1986. L'ittiofauna pliocenica della Sez. di Stuni e suoi rapporti con l'ittiofauna plio-pleistocenica della Vrica (Crotona, Calabria). *Bollettino della Società Paleontologica Italiana* 25 (1), 41–63.
- Landini, W., Menesini, E., Ragaini, L., 1990. Paleocomunità a molluschi e otoliti nel Pliocene di Castelfiorentino (Firenze, Italia). *Atti della Società Toscana di Scienze Naturali Memoire*, ser. A 97, 175–202.
- Landini, W., Sorbini, C., 1993. Biogeographic and palaeoclimatic relationships of the Middle Pliocene ichthyofauna of the Samoggia Torrent (Bologna, Italy). *Ciencias da Terra (UNL)* 12, 83–89.
- Landini, W., Sorbini, C., 2005. Evolutionary dynamics in the fish faunas of the Mediterranean basin during the Plio-Pleistocene. *Quaternary International* 140–141, 64–89.
- Landini, W., Varola, A., 1983. L'ittiofauna del Pleistocene inferior di Matera. *Thalassia Salentina* 13, 16–45.
- Lourens, L., Hilgen, F., Shackleton, N., Laskar, J., Wilson, D., 2004. The Neogene Period. In: Gradstein, F.M., Ogg, J.G. (Eds.), *A Geologic Time Scale 2004*. Cambridge University Press, pp. 409–440.
- Markopoulou-Diakantoni, A., Kagiouzis, G., 2001. Otoliths from the lower Pliocene of the section Prassies (Rethymon, NW-Crete). *Systematics - Paleocology. Bulletin of the Geological Society of Greece* 34 (2), 577–584.
- Meulenkamp, J.E., Dermizakis, M., Georgiadou-Dikaoulia, E., Jonkers, H.A., Boerger, H., 1979. Field Guide to the Neogene of Crete. *Publications of the Geology and Paleontology Department, University of Athens, Athens*, 32 p.
- Meulenkamp, J.E., Wortel, M.J.R., Van Wamel, W.A., Spakman, W., Hoogerduyn Strating, E., 1988. On the Hellenic subduction zone and the geodynamical evolution of Crete since the late Middle Miocene. *Tectonophysics* 146, 203–215.
- Meulenkamp, J.E., Zwaan, G.J., van der Wamel, W.A., 1994. On late Miocene to recent vertical motions in the Cretan segment of the Hellenic Arc. *Tectonophysics* 234, 57–72.
- Nelson, J.S., 2006. *Fishes of the World*, 4th ed. John Wiley & Sons Inc, New Jersey, 600 p.
- Nolf, D., 1985. Otolithi Piscium. In: Schlutze H.P. (Ed.) *Handbook of Paleoichthyology*. vol. 10, p. 1–145. Stuttgart.
- Nolf, D., Cappelletta, H., 1988. Otolithes de poissons pliocènes du Sud-Est de la France. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 58, 209–271.
- Nolf, D., Cavallo, O., 1995. Otolithes de poissons du Pliocène inférieur de Monticello d'Alba (Piemont, Italie). *Rivista Piemontese di Storia Naturale* 15, 11–40.
- Nolf, D., Girone, A., 2000. Otolithes de Poissons du Pléistocène inférieur (Santerrien) de Morrona (Sud Est de Pisa). *Rivista Piemontese di Storia Naturale* 21, 3–18.
- Nolf, D., Girone, A., 2006. Otolithes de poissons du Pliocène inférieur (Zancléen) des environs d'Alba (Piemont) et de la côte Ligure. *Rivista Piemontese di Storia Naturale* 27, 77–114.
- Nolf, D., Mane, R., Lopez, A., 1998. Otolithes de poissons du Pliocène inférieur de Papiol, près de Barcelone. *Palaeovertebrata* 27 (1–2), 1–17.
- Nolf, D., Martinell, J., 1980. Otolithes de Téléostéens du Pliocène des environs de Figueras (Catalogne). *Geologica et Palaeontologica* 14, 209–234.
- Raffi, I., Backman, J., Fornaciari, E., Paliike, H., Rio, D., Lourens, L., Hilgen, F., 2006. A review of calcareous nanofossil astrobiochronology encompassing the past 25 million years. *Quaternary Science Reviews* 25 (23–24), 3113–3137.
- Rio, D., Raffi, I., Villa, G., 1990. Pliocene-Pleistocene calcareous nanofossil distribution patterns in the western Mediterranean. In: Kastens, K.A., Mascle, J., et al. (Eds.), *Proceedings of the ODP, Scientific Results*, vol. 107. College Station TX, ODP, pp. 513–533.
- Schwarzans, W., 1979. Otolithen aus dem Unter-Pliozan von Sud-Sizilien und aus der Toscana. *Berliner geowissenschaft Abhand* 8, 1–52.
- Schwarzans, W., 1986. Die Otolithen des Unter-Pliozan von Le Puget, S-Frankreich. *Senckenbergiana Lethaea* 67 (1–3), 219–273.
- Sorbini, C., 1988. Biogeography and climatology of Pliocene and Messinian fossil fish of Eastern-Central Italy. *Bollettino del Museo Civico di Storia Naturale di Verona* 14, 1–85.
- Sorbini, C., Landini, W., 2003. A new fish fauna in the Plio-Pleistocene of Monte Singa (Calabria, southern Italy). *Bollettino della Società Paleontologica Italiana* 42 (1–2), 185–189.
- Symeonidis, N., Konstadinidis, D., 1967. Observations on the Neogenic formations of Central Crete. *Annales Géologiques des Pays Helléniques* 19, 657–688.
- Van Hinsbergen, D.J.J., Meulenkamp, J.E., 2006. Neogene supra-detachment basin development on Crete (Greece) during exhumation of the South Aegean core complex. *Basin Research* 18, 103–124.
- Zachariasse, W.J., Hinsbergen, D.J.J., Fortuin, A.R., 2011. Formation and fragmentation of a late Miocene supradetachment basin in central Crete: implications for exhumation mechanisms of high-pressure rocks in the Aegean forearc. *Basin Research* 23, 678–701.