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C. R. Palevol 4 (2005) 687–695



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Systematic Palaeontology (Vertebrate Palaeontology)

The Tortonian fish fauna of Gavdos Island (Greece)

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Received 21 April 2005; accepted after revision 17 August 2005

Available online 06 October 2005

Presented by Philippe Taquet

Abstract

Although the occurrence of fossil fishes is known since more than one century in the Neogene of Gavdos Island (Greece), its composition remained hitherto unknown. The present study demonstrates that, in the Tortonian of Gavdos, the most abundant species is *Bregmaceros albyi* (Sauvage), which constitutes two thirds of the collected material. This fish fauna is indicative of an environment of moderate depth, probably corresponding to the external edge of the neritic zone, or possibly to the upper part of the continental slope. **To cite this article: J. Gaudant et al., C. R. Palevol 4 (2005).**

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Résumé

L'ichthyofaune tortonienne de l'île de Gavdos (Grèce). Bien que l'existence de poissons fossiles soit connue depuis plus d'un siècle dans le Néogène de l'île de Gavdos (Grèce), on ne disposait jusqu'à présent d'aucune information sur la composition de cette ichthyofaune. La présente étude montre que, dans le Tortonien de Gavdos, l'espèce la plus abondante est *Bregmaceros albyi* (Sauvage), qui constitue les deux tiers du matériel recueilli. La composition de cette ichthyofaune indique un milieu de profondeur assez modérée, correspondant probablement au bord externe de la zone néritique, ou éventuellement à la partie supérieure du talus continental. **To cite this article: J. Gaudant et al., C. R. Palevol 4 (2005).**

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Keywords: Fishes; Teleosts; Tortonian; Gavdos Island; Greece

Mots clés : Poissons ; Téléostéens ; Tortonien ; Gavdos ; Grèce

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Version française abrégée

Introduction

L'île de Gavdos (Fig. 1), qui est située dans la mer de Libye, à une trentaine de kilomètres au sud de Chora Sfakion (Crète), constitue la partie émergée la plus méridionale de l'arc hellénique, connue sous le nom de ride de Gavdos. Elle comporte un soubassement alpin anté-néogène, qui s'étend du cap Kefali, au nord-ouest, jusqu'au cap Tripiti, au sud-est, constitué par une séquence calcaire, d'âge Maastrichtien, à Danien et par un flysch éocène [32], qui appartient à la série d'Athia de la zone géotectonique du Pinde.

Les sédiments néogènes, dont l'épaisseur maximale atteint 150 m, occupent les deux tiers de la surface de l'île ; reposant en discordance sur le soubassement alpin, ils ont été subdivisés en deux formations superposées : la formation Potamos, d'âge Serravallien, et la formation Metochia, dont la partie inférieure est observable dans la coupe Metochia B située à l'ouest du village de Metochia [20]. La formation Metochia débute par un paléosol, au-dessus duquel prennent place des sédiments de faciès estuarien et des sables marins peu profonds riches en échinodermes, mollusques et *Heterostegina* [24]. Le rapport élevé entre foraminifères benthiques et foraminifères planctoniques témoigne de la proximité du rivage. Au-dessus, s'observe une alternance régulière de marnes hémipélagiques et de niveaux brunâtres à structure laminaire (« sapropels » des auteurs), numérotés de M1 à M55 [17,20]. La décroissance progressive du rapport entre foraminifères benthiques et foraminifères planctoniques traduit un approfondissement progressif des dépôts au fur et à mesure qu'on s'élève dans la série. Dans la partie inférieure de cette alternance s'intercalent cinq séquences turbiditiques riches en matière organique (M7 à M11), qui remplacent parfois totalement les « sapropels ». La présence d'ichnofossiles de type *Zoophycus* et *Chondrites* indique l'existence dans le milieu de teneurs restreintes en oxygène [15], ce que confirme l'abondance de restes végétaux et de bois dans ces niveaux.

Il est à noter que les poissons fossiles provenant de la coupe Metochia B ont été recueillis dans les niveaux de sapropels numérotés de M16 à M22. Anastasakis et al. [2], qui en ont étudié les nannofossiles calcaires, ont daté ces niveaux du Tortonien inférieur, et plus précisément de la partie inférieure de la zone de nannoplancton NN9, définie par Martini [22].

Selon Hilgen et al. [17], Krijgsman et al. [20] et Antonarakou [4], la coupe Metochia B correspond à l'intervalle de 9,7 Ma à environ 8,2 Ma. Quant aux niveaux qui renferment l'ichthyofaune, ils sont caractérisés par la première abondance relative de la forme 4 de *Globorotalia menardii* dans le cycle M15, datée d'environ 9,3 Ma, et par la présence de *Globoquadrina dehiscens* dans le cycle M29, daté d'environ 9,0 Ma [4].

Un second affleurement de marnes hémipélagiques alternant avec des lits brunâtres à structure laminaire, situé à quelques centaines de mètres de Karave (Fig. 1), a également livré quelques squelettes de poissons. Il constitue l'équivalent des niveaux de la partie inférieure de la coupe Metochia B, situés au-dessus des sables à *Heterostegina*.

L'ichthyofaune

En se fondant sur l'étude d'environ 135 spécimens plus ou moins complets recueillis dans le Tortonien inférieur de l'île de Gavdos, l'ichthyofaune de ces niveaux apparaît composée comme suit :

Famille Clupeidae

Genre *Sardina* Antipa ?

Sardina ? crassa (Sauvage)

(Fig. 2, 1)

Une région operculaire isolée indique la présence de cette espèce dans le Tortonien de Gavdos. Cette région operculaire, qui provient des environs de Karave, montre notamment un opercule sub-rectangulaire caractéristique, dont le champ antéro-ventral est orné de rides divergentes en relief.

Famille Myctophidae

Genre « *Myctophum* » Rafinesque (s.l.)

« *Myctophum* » *licatae* (Sauvage)

(Fig. 2, 5)

Deux individus indiquent la présence de cette espèce dans le Tortonien de Metochia. La longueur standard du plus grand (Fig. 1, 5) égale 62 mm. Ce sont des poissons au corps allongé, dont la hauteur maximale du corps égalait environ un quart de la longueur standard. La longueur standard du second est de seulement 42,5 mm. Un troisième spécimen incomplet a été récolté à Aghios Georgios.

Famille Bregmacerotidae

Genre *Bregmaceros* Thompson

Bregmaceros albyi (Sauvage)

(Fig. 2, 6)

Cette espèce caractérise à elle seule le Tortonien de Metochia, car elle constitue 71% des spécimens récoltés. Elle est principalement représentée par des individus dont la longueur standard maximale est comprise entre 30 et 60 mm, avec deux maxima observés entre 30 et 40 mm et entre 50 et 55 mm. L'état de conservation généralement médiocre de ces poissons ne permet pas d'en donner une description anatomique détaillée.

Famille Syngnathidae

Genre *Syngnathus* L.

Syngnathus cf. *albyi* Sauvage

(Fig. 2, 4)

Cette espèce est représentée par douze spécimens fragmentaires, soit 8,9% du matériel récolté, dans le Tortonien de Metochia. Plusieurs d'entre eux montrent des opercules ovoïdes, dont la surface présente une ornementation réticulée caractéristique. Sur d'autres pièces sont conservés des toits crâniens plus ou moins complets, montrant un allongement remarquable de la région pré-orbitaire.

Famille Acanthuridae

Gen. et sp. indet.

(Fig. 2, 2)

Un petit spécimen dont la longueur standard égale 12,5 mm provient du Tortonien des environs de Karave. Il est très semblable au matériel de l'Oligo-Miocène de la série de Maikop (Caucase), décrit par Danilch'enko [14] comme *Caprovesposus parvus* Danilch'enko, dont Bannikov et Tyler [6] ont montré qu'il s'agissait réellement du stade larvaire *acronurus* pélagique d'un Acanthuridae.

Famille Trichiuridae

Genre *Lepidopus* Gouan

Lepidopus sp.

(Fig. 2, 3)

Le Tortonien de la coupe de Metochia a livré treize fragments, soit 9,6 % du matériel récolté, indiquant la présence du genre *Lepidopus* Gouan. Le plus caractéristique est un opercule isolé, dont la largeur égale pratiquement deux fois la hauteur et dont la surface est ornée de rides qui rayonnent à partir de son angle antéro-dorsal.

Signification paléocéologique de l'ichthyofaune tortonienne de Gavdos

En résumé, l'ichthyofaune tortonienne de Gavdos, dans laquelle l'espèce *Bregmaceros albyi* (Sauvage) est

fortement prédominante, suggère l'existence, à cette époque, d'un milieu de profondeur modérée qui correspondait vraisemblablement à la zone externe du domaine néritique, ou éventuellement à la partie supérieure du talus continental. L'aire de sédimentation de Gavdos devait avoir alors une connexion assez réduite avec la mer ouverte, comme l'indique le fait que les Myctophidae sont rares dans le gisement. On soulignera également l'importante similitude observée entre l'ichthyofaune tortonienne de Gavdos et celle de Ierapetra [5,10,16,28].

Il est à noter que l'étude des foraminifères benthiques a permis de mettre en évidence l'existence, sur le fond, d'un déficit en oxygène, mais conduit par ailleurs à une interprétation bathymétrique un peu différente, en suggérant que le dépôt se serait produit dans la partie supérieure de la zone bathyale.

1. Introduction

Gavdos Island is located approximately 30 km south of Chora Sfakion, Crete (Fig. 1). It is the emergent part of the Gavdos ridge, a topographic height in the floor of the Libyan Sea, which is the southernmost emerged part of the Hellenic arc system. The pre-Neogene Alpine

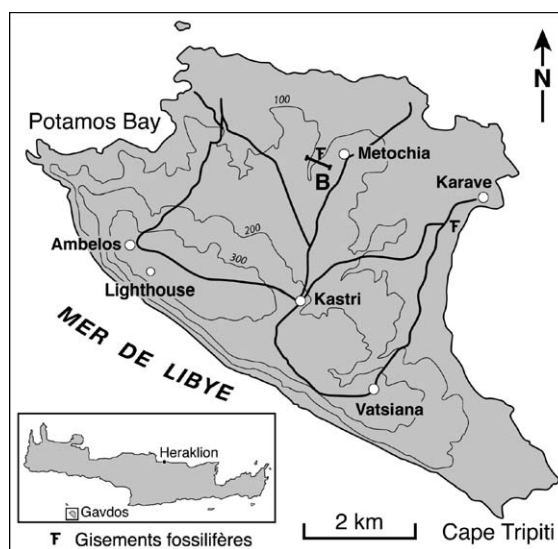


Fig. 1. Schematic map of Gavdos Island showing the location of the Metochia B section and of the Tortonian outcrop in the vicinity of Karave.

Fig. 1. Carte schématique de l'île de Gavdos montrant l'emplacement de la coupe de Metochia B et du gisement proche de Karave.

basement of the island, which extends from Cape Kefali, in the northwest, to Cape Tripiti, in the southeast, constitutes the southern part of the island and is known as the Kefali–Tripiti ridge. It consists of a Maastrichtian–Danian calcareous sequence and of an Eocene flysch [32], belonging to the Pindos–Ethia geotectonic zone, which is well developed in Crete [19]. The Neogene sediments, which have a maximum thickness of 150 m, cover the two thirds of the surface of the island, overlying unconformably the Alpine basement ([1,4,32], etc). According to the study of planktonic foraminifera, calcareous nannofossils and mollusc assemblages, they are not older than the Serravallian [2]. They are subdivided into two lithostratigraphic formations: the Potamos and Metochia Fm., the second one including the fossiliferous layers yielding fossil fishes and tree leaves. The occurrence of these fossils had been reported more than one century ago by Simonelli [27]. A more extensive investigation started in 1994 when one of us (N.T.) began a detailed geological study of the Neogene sediments of Gavdos, during which many fossil fishes were found in the laminated marls exposed in the badlands occurring west of the Metochia village, in the Metochia B section of Krijgsman et al. [20].

The basal part of the Metochia B section is made of a palaeosol that is overlain by sediments deposited in an estuarine environment and shallow marine sands rich in *Heterostegina*, echinoderms and molluscs [24]. The lower part of the marine section is characterized by a high benthic/planktonic foraminifera ratio, which is indicative of a close proximity to the shore. Above the marine sands takes place an alternation of hemipelagic marls and brownish laminated beds (the so-called ‘spropels’), which are numbered from M1 to M96 [17,20], although the Metochia B section ends with bed M 55. The upward decrease of the benthic/planktonic ratio suggests a gradual deepening [24] starting from the first spropel level (M1), which is also suggested by the correlative replacement of marine sands by hemipelagic marls. In the lower part of the Metochia B section, five successive turbiditic sequences (M7 to M11) occur within or completely replace the laminated intervals. According to Ekdale et al. [15], the occurrence in these sequences of the ichnofossils *Zoophycus* and *Chondrites* is indicative of restricted aerobic conditions. This is confirmed by the abundance of plant and wood remains in these levels. The fish-fauna which is

preserved as articulated skeletons was found in the lower part (M16–M22 cycles) of the Metochia B section.

From a biostratigraphical point of view, although the majority of samples are, according to Anastasakis et al. [2], devoid of nannofossils, the occurrence of *E. calcaris* and *E. hamatus* is indicative of a Lower Tortonian age, corresponding more precisely to the lower part of the NN9 zone of Martini [22].

According to Hilgen et al. [17], Krijgsman et al. [20] and Antonarakou [4], the Metochia B section corresponds to a period ranging from 9.7 Ma to about 8.2 Ma. The use of significant bioevents such as the regular occurrence of *Neogloboquadrina acostaensis* from dextral to sinistral, the lowest common occurrence of *Globorotalia menardii* 4, the last common occurrence of large sized *Globorotaloides falconarae*, the frequency shift of *Globorotaloides falconarae* from nearly absent to commonness, has shown that the Metochia B section belongs to the N16 biozone of Blow [9], biozone of *Neogloboquadrina acostaensis* of Zachariasse [33]. More precisely, the stratigraphical interval in which the fish fauna was found is characterized by the lowest common occurrence of the *Globorotalia menardii* form 4 at cycle M15, dated at about 9.3 Ma, at the stratigraphical level of 29.35–29.76 m and the occurrence of *Globoquadrina dehiscens* at about 9.0 Ma in cycle M29 at the stratigraphical interval of 40.91–41.15 m of the section [4].

Additionally to the Metochia B section, it should be noted that fish skeletons were also found at some hundred metres southwest of Karave. This section consists of alternations of hemipelagic marls and brownish laminated beds, which can be correlated with the lower part of the Metochia B section, above the fossiliferous sand bed rich in *Heterostegina*.

2. The fish fauna

According to the study of 135 more or less fragmentary specimens collected in the Lower Tortonian of Gavdos, it is possible to give an account of the composition of this fish fauna.

Family Clupeidae

Genus *Sardina* Antipa ?

Sardina ? *crassa* (Sauvage)

(Fig. 2, 1)

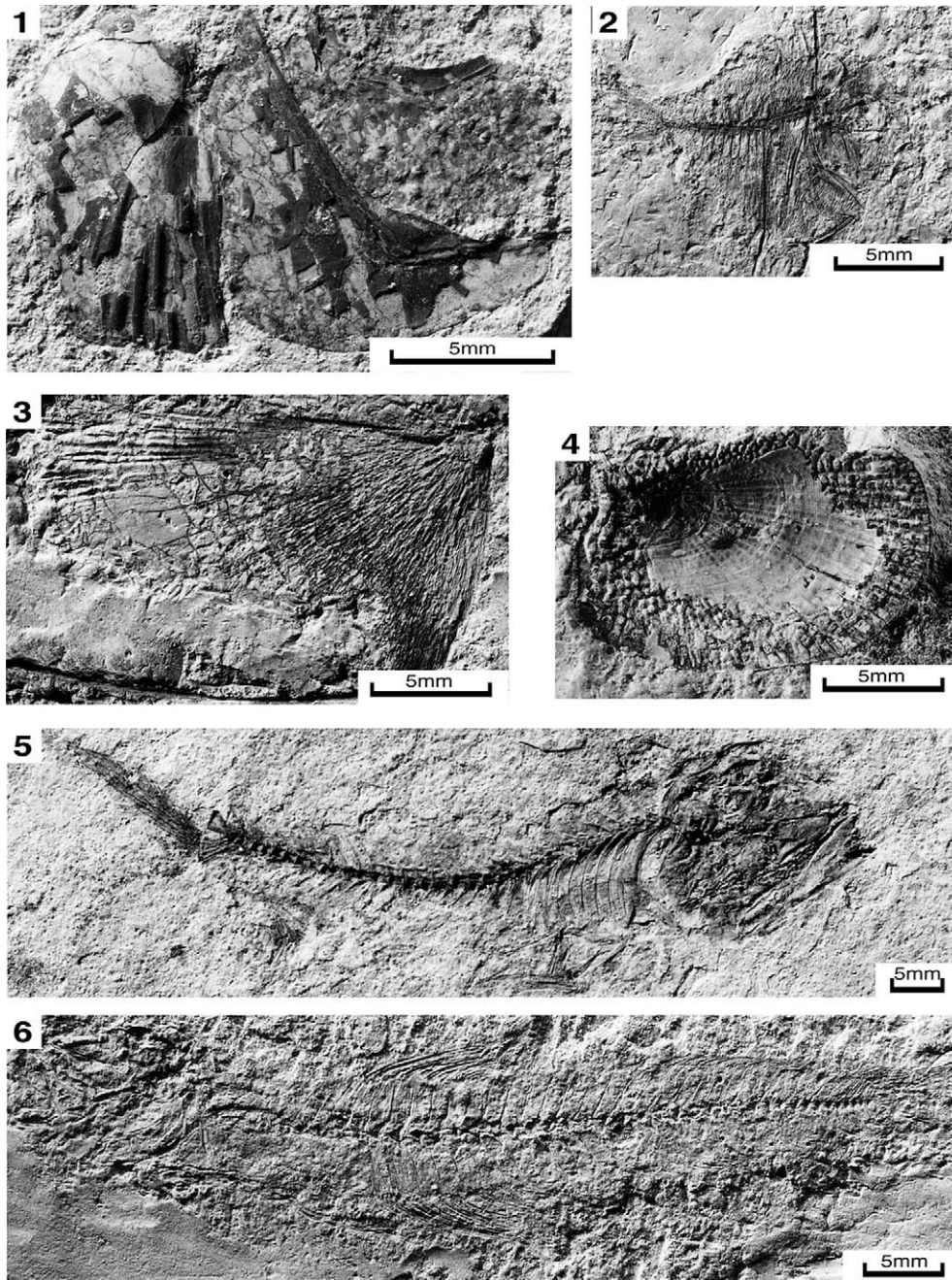


Fig. 2. Tortonian fish fauna of Gavdos Island. **1.** *Sardina ? crassa* (Sauvage). Operculum and preoperculum, vicinity of Karave. **2.** Acanthuridae, gen. et sp. indet., vicinity of Karave **3.** *Lepidopus* sp. Operculum, Metochia. **4.** *Syngnathus* cf. *albyi* Sauvage. Operculum, Metochia. **5.** '*Myctophum*' *licatae* (Sauvage). Metochia. **6.** *Bregmaceros albyi* (Sauvage). Metochia.

Fig. 2. Ichthyofaune tortonienne de l'île de Gavdos. **1.** *Sardina ? crassa* (Sauvage). Opércule et pré-opercule. Environs de Karave. **2.** Acanthuridae, gen. et sp. indet. Environs de Karave **3.** *Lepidopus* sp. Opércule. Metochia. **4.** *Syngnathus* cf. *albyi* Sauvage. Opércule, Metochia. **5.** « *Myctophum* » *licatae* (Sauvage). Metochia. **6.** *Bregmaceros albyi* (Sauvage). Metochia.

An isolated opercular region found in the vicinity of Karave bears witness of the occurrence of this species in the Tortonian of Gavdos, as it exhibits a characteristic sub-rectangular operculum, the antero-ventral surface of which is ornamented by a series of ridges radiating from a point situated near the articulation, between the operculum and the hyomandibular.

Family Myctophidae

Genus '*Myctophum*' Rafinesque (s.l.)

'*Myctophum*' *licatae* (Sauvage)

(Fig. 2, 5)

Two specimens bear witness of the occurrence of Myctophids in the Tortonian of Metochia. The largest one (Fig. 2, 5) has a standard length reaching 62 mm. It has an elongate body, the maximum height of which reaches a quarter of the standard length.

The second one is an incomplete specimen, which has been found in the vicinity of Karave. It lacks the caudal region. It exhibits a very long mouth opening, so that the length of the oral edge of the upper jaw reaches about two thirds of the head length.

Family Bregmacerotidae

Genus *Bregmaceros* Thompson

Bregmaceros albyi (Sauvage)

(Fig. 2, 6)

This species is by far the most abundant found at Gavdos. The amount of collected specimens reaches 71% of the material found in the Tortonian of the Metochia Formation. They are generally rather poorly preserved to such a point that it is not possible to give a detailed anatomical description of this species.

The standard length of the fishes ranges from 30 to 60 mm with two maxima observed between 30 and 40 mm and between 50 and 55 mm. The body is elongated, its maximum height being included 7 to 9 times in standard length. The vertebral column includes about 45 vertebrae, 34–36 (37) of which being postabdominal. Because of the rather poor state of preservation, it is not possible to know the composition of the dorsal and anal fins. The occurrence of long pelvic fins reaching at least the origin of the anal fin is demonstrated by several specimens.

Family Syngnathidae

Genus *Syngnathus* L.

Syngnathus cf. *albyi* Sauvage

(Fig. 2, 4)

Twelve specimens (i.e. 8.9% of the collected material) bear witness of the occurrence of the genus *Syng-*

nathus L. in the Tortonian of Gavdos. Some of them exhibit isolated opercula having a more or less ovoid shape; their maximum height approximately equals 70% of their length. The surface of the bones is ornamented by ridges exhibiting a honeycomb pattern similar to the ornamentation observed in the Messinian species *S. albyi* Sauvage. Some incomplete skull roofs show a typically elongated pre-orbital region.

Family Acanthuridae

Gen. et sp. indet.

(Fig. 2, 2)

A small specimen, the standard length of which equals 12.5 mm, was found in the vicinity of Karave. It looks very similar to the material from the Oligocene and Lower Miocene of the Maikop series of the Caucasus described by Danilch'enko [14] as *Caprovesposus parvus* Danilch'enko.

This specimen is somewhat oval-shaped, as its maximum depth equals two thirds of the standard length. The head is more or less rounded, its height being slightly larger than its length. Little is known of the cephalic anatomy, except that the frontals are projected upwards above the hind part of the orbit. The mouth is small, the length of the lower jaw being included three times in the head length. The preoperculum is rather slender. The anterior edges of its two branches determine an angle of 120°. Its lower branch is short, its length being about two thirds of that of the upper one.

The vertebral column is short, as it includes only about nine abdominal vertebrae and probably 13 post-abdominal vertebrae.

The caudal fin is small: its length is about one fifth of standard length. It seems to have been paddle-shaped and to have been built up of 16 principal rays, 14 of them being branched.

The dorsal fin begins just behind the head. Anteriorly, one observes a rather long spine, the length of which equals a quarter of the maximum height of body. A very short spine was apparently present just in front of it. At least six other spines having a decreasing length are located behind the longest one. The number of soft dorsal rays is unknown.

The anal fin begins at a rather short distance behind the vertical of the base of the longest spine of the dorsal fin. Anteriorly, there are three spines: a very short anterior one, a second which is the longest, although it is slightly shorter than the longest dorsal spine, and a third one, which is shorter than the second one. Poste-

riorly, an undetermined number of soft rays is visible, although their pterygiophores are present, except in the hind part of the fin.

The pectoral fins are placed between the lower third and the middle of the flank. They include about 10 rays. The cleithrum is the best-preserved bone of the pectoral girdle. A very long ventral postcleithrum is also present. Its distal end almost reaches the ventral edge of the body, shortly in front of the first pterygiophore of the anal fin.

The pelvic fins are rather small. They are supported by narrow, elongate pelvic bones. They take place slightly in front of the origin of the pectoral fins.

The body is covered by elongate scales, which are mainly disposed more or less transversally.

It should be emphasized that Bannikov and Tyler [6] have shown that the so-called ‘*Caprovesposus parvus*’ of Danilch’enko [14] is really a pelagic *acronurus* stage of an Acanthurid. The juvenile specimen found at Aghios Georgios can be interpreted in the same way.

Family Trichiuridae

Genus *Lepidopus* Gouan

Lepidopus sp.

(Fig. 2, 3)

Thirteen fragments (i.e. 9.6% of the collected material) found in the Tortonian of the Metochia section indicate the occurrence of a representative of the genus *Lepidopus* Gouan. The most characteristic piece is the operculum. Although it is imperfectly preserved, it has clearly a general quadrangular outline, its maximum height being approximately two thirds of its length. Its ventral edge exhibits a rather well-developed concavity, which begins near its anterior quarter. The external surface of the bone is ornamented with many ridges radiating from its upper anterior angle.

3. Palaeoecological significance of the Tortonian fish fauna from Gavdos

First of all, the fish fauna preserved in the Tortonian marls outcropping in the lower part of the Metochia Formation of Gavdos Island is strongly dominated by *Bregmaceros albyi* (Sauvage), which constitutes more than two thirds of the collected material. This species belongs to a recent genus, which is mainly widespread in the intertropical regions of the Pacific, Indian and Atlantic Oceans. Although its recent species have an

epi- to mesopelagic way of life, the study of their bathymetric distribution shows that the most important populations are generally restricted to the upper 300 m [3]. Additionally, as noted by Cohen et al. [11], some species are present in coastal, very shallow areas, and even in estuaries (as demonstrated by the fact that the type species of the genus *Bregmaceros* Thompson is based on a specimen caught in the Ganges Delta).

With 8.9% of the collected material, *Syngnathus* L. is the second most abundant genus found in the Tortonian of Gavdos. However, it is only known by isolated neurocrania, opercula, and dermal scutes. This demonstrates that this material was transported from the shallow sea-grass meadows that were the probable environment of these fishes.

The genus *Lepidopus* Gouan is known by isolated bones and fragments of dislocated skeletons, which, altogether, represent up to 9.6% of the collected material. According to the biology of the recent Mediterranean species *Lepidopus caudatus* (Euphrasen), these fishes were probably living at depths mainly ranging from 100 to 400 m [29].

Among the other components of the Tortonian fish fauna from Gavdos are two Myctophids identified as ‘*Myctophum*’ *licatae* (Sauvage) (1.5% of the collected material). These mesopelagic fishes have very small light organs (photophores), which are not preserved on our material. They bear witness of the occurrence in the vicinity of Gavdos of a rather deep sea (at least several hundred metres). However, it should be noted that this sea exerted a rather limited influence into the sedimentary basin, as shown by the small number of Myctophids collected at Gavdos.

Additionally, one fragmentary Clupeid fish, which is tentatively referred to the genus *Sardina* Antipa, was collected in the Tortonian of Aghios Georgios. The distribution of this genus mainly corresponds to the neritic zone. Finally, an Acanthurid *acronurus* larva was also found at Aghios Georgios.

To sum up, the Tortonian fish-fauna of Gavdos, in which *Bregmaceros albyi* (Sauvage) is strongly predominant, is indicative of an environment of moderate depth, which probably corresponds to the external part of the neritic zone, or eventually to the upper part of the continental slope. The sedimentary basin had, at that time, a rather restricted connection with the open deep sea, as shown by the fact that Myctophids are rather scarce in the collected material. It should be

emphasized that the Tortonian fish fauna from Gavdos exhibits a striking similarity with that from Ierapetra [5,10,16,28], where the genus *Bregmaceros* Thompson is also predominant (more than 70% of the collected material), whereas the genera *Lepidopus* Gouan and *Syngnathus* L. are also present.

However, it should be noted that an apparent contradiction exists when comparing the palaeoecological interpretation deduced from the fishes to that relying on benthic foraminifera. The composition of the benthic foraminiferal assemblage of one sample of fish bearing sapropel was studied by one of us (H.D.). It includes 24 species belonging to 20 genera: *Anomalinoidea cicatricosa*, *Bulimina aculeata*, *Bolivina reticulata*, *Bolivina scalprata miocenica*, *Bolivina spathulata*, *Cancris oblongus*, *Cibicidoides italicus*, *Cibicidoides kullenbergi*, *Cibicides refulgens*, *Chilostomella oolina*, *Fursenkoina schreibersiana*, *Gyroidina orbicularis*, *Lenticulina rotulata*, *Neoconorbina* sp., *Pullenia bulloides*, *Planulina ariminensis*, *Praeglobobulimina ovata*, *Pyrgo* sp., *Rosalina globularis*, *Rectuvigerina siphogeneroides*, *Sphaeroidina bulloides*, *Siphonina reticulata*, *Uvigerina striatissima*, *Valvulineria complanata*.

This assemblage is dominated by *Cancris oblongus* (34%), whereas four other species are rather abundant: *Chilostomella oolina* (12%), *Valvulineria complanata* (8%), *Planulina ariminensis* and *Rectuvigerina siphogeneroides* (both 6%).

These species, which have been frequently reported from disaerobic bottoms and sapropelitic layers, typically occur in environments with high organic matter input, as they can tolerate reduced oxygen concentrations [8,23,25,26].

More specifically, *Cancris oblongus* has often been considered as a species preferring the shelf environment of the open ocean [31]. However, it is really indifferent to depth-related factors, and is tolerant to slightly hyposaline and mesotrophic to eutrophic conditions. Moreover, several authors have convincingly shown that *Chilostomella oolina* usually occurs in deep infaunal habitats, often in completely anoxic conditions [7,8,12,13,21]. Additionally, *Valvulineria complanata* can be interpreted as a shallow infaunal species, tolerant to low oxygen contents, which proliferates in relation to high food content at the sediment-water interface [18,30]. Finally, the occurrence in this assemblage of *Uvigerina*, *Bolivina*, and *Bulimina* may suggest a deposition in upper bathyal conditions.

Acknowledgments

The senior author acknowledges Prof. Dr. Michael Dermitzakis, presently vice-rector of the National and Capodistrian University of Athens, who has financially supported his visit to Athens, needed by the preparation of the present paper.

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