



NATIONAL AND KAPODISTRIAN UNIVERSITY OF ATHENS
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Investigation of the Plio-Pleistocene eastern Mediterranean Ichthyofauna and paleoenvironmental representations on Rhodes and Crete Islands

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Athens, 2013



European Union
European Social Fund



OPERATIONAL PROGRAMME
EDUCATION AND LIFELONG LEARNING
investing in knowledge society
MINISTRY OF EDUCATION, LIFELONG LEARNING AND RELIGIOUS AFFAIRS
MANAGING AUTHORITY



NSRF
2007-2013
programme for development
EUROPEAN SOCIAL FUND

Co- financed by Greece and the European Union



ΕΘΝΙΚΟ ΚΑΙ ΚΑΠΟΔΙΣΤΡΙΑΚΟ ΠΑΝΕΠΙΣΤΗΜΙΟ ΑΘΗΝΩΝ
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**Διερεύνηση της Πλειο-Πλειστοκαινικής Ιχθυοπανίδας της Ανατολικής
Μεσογείου και παλαιοπεριβαλλοντική αναπαράσταση στις νήσους Ρόδο και
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Αθήνα, 2013



Ευρωπαϊκή Ένωση
Ευρωπαϊκό Κοινωνικό Ταμείο



ΕΠΙΧΕΙΡΗΣΙΑΚΟ ΠΡΟΓΡΑΜΜΑ
ΕΚΠΑΙΔΕΥΣΗ ΚΑΙ ΔΙΑ ΒΙΟΥ ΜΑΘΗΣΗ
επένδυση στην κοινωνία της γνώσης

ΥΠΟΥΡΓΕΙΟ ΠΑΙΔΕΙΑΣ, ΔΙΑ ΒΙΟΥ ΜΑΘΗΣΗΣ ΚΑΙ ΘΡΗΣΚΕΥΜΑΤΩΝ
ΕΙΔΙΚΗ ΥΠΗΡΕΣΙΑ ΔΙΑΧΕΙΡΙΣΗΣ

Με τη συγχρηματοδότηση της Ελλάδας και της Ευρωπαϊκής Ένωσης



ΕΣΠΑ
2007-2013
Πρόγραμμα για την ανάπτυξη
ΕΥΡΩΠΑΪΚΟ ΚΟΙΝΩΝΙΚΟ ΤΑΜΕΙΟ

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This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

Η παρούσα έρευνα έχει συγχρηματοδοτηθεί από την Ευρωπαϊκή Ένωση (Ευρωπαϊκό Κοινωνικό Ταμείο - ΕΚΤ) και από εθνικούς πόρους μέσω του Επιχειρησιακού Προγράμματος «Εκπαίδευση και Δια Βίου Μάθηση» του Εθνικού Στρατηγικού Πλαισίου Αναφοράς (ΕΣΠΑ) – Ερευνητικό Χρηματοδοτούμενο Έργο: Ηράκλειτος ΙΙ . Επένδυση στην κοινωνία της γνώσης μέσω του Ευρωπαϊκού Κοινωνικού Ταμείου.

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Preface

The present dissertation was undertaken in order to fill in a significant gap in the record of the eastern Mediterranean paleoichthyofauna, for which prior studies have been scarce and fragmentary. The previous studies, on fossil fish skeletons found on Attica, Aegina, Crete and Gavdos Island, revealed the presence of very few genera and species. The fossil material was not always well preserved and the fossiliferous localities, although parts of a lengthier marine sequence, revealed fossil skeletons only in certain beds, and not above nor below. As a result, the evolution of the fauna in each area was completely unknown, while stratigraphic correlation between the fossiliferous beds became very difficult. For these reasons, I chose to study fossil fish otoliths, in hope to better reconstruct the fauna.

This thesis was assigned to me, on 15th December 2008, by the Faculty of Geology and Geoenvironment, and has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

I would like to thank the members of the examining committee for accepting this task and helping me, at this final stage, with their constructive comments and their perspective.

In my efforts to carry out this thesis, I have had a lot of help from my teachers, collaborators, friends and family, whom I would like to acknowledge and thank. First of all, I would like to thank the members of the Department of Historical Geology and Paleontology for accepting me to study and progress in its premises and offering the thrills and warmth of home to me.

Especially, I owe to my supervisor, Professor Dr. Vasileios Karakitsios, for his support and guidance during these last years.

I would also like to thank Associate Professor Dr. Maria Triantaphyllou for believing in me, instructing me and working with me to combine the data of this research with her analyses of the nannofossil assemblages.

Preface

Assistant Professor Dr. Efterpi Koskeridou has greatly advised me throughout this study, both at the University and also in the field, where she guided me, and taught me, and sampled with me during all the field trips.

Along with Professor Dr. Pierre Moissette and Dr. Jean-Jacques Cornée, they initiated me in the geology of Rhodes, and spend a great deal of time and effort to teach me in the field and sample with me in order for me to gather all the material needed for this thesis.

My teacher, collaborate and friend, Ass. Professor Dr. Angela Girone, I owe so much, because she has carefully instructed me in the systematic identification of fish otoliths, and allowed me free access to her comparative collection, but also for our endless discussions over the various issues of this thesis.

Assistant Professor Dr. Frédérique Quillévéré and Dr. Gatsby-Emperatriz López-Otálvaro greatly helped me during the 2011 field trip and have afterwards kindly provided the biostratigraphic data, based on planktonic foraminifera and calcareous nannofossils respectively, for the Rhodes Island sections. I also thank Lecturer Dr. Margarita Dimiza for aiding with the SEM photography of the samples.

Dr. Nefeli Kafousia I would like to thank for joyfully sharing our office space. To my friend Roy Apostolidi I am grateful for tirelessly helping during the Crete 2009 sampling trip.

Finally, I am very fortunate to have had the understanding and support from my friends Ioanna Balioussi and Magda Mantourlia. But most of all, I am lucky to have had the love and support from my family. I thank you.

to Eleni and Nikos,

my children,

I hope you can be as proud of me as I am of you

Εκτενής περίληψη

Ο σκοπός της παρούσας διατριβής είναι η ανασύνθεση της ιχθυοπανίδας του Πλειοκαίνου και του Πλειστοκαίνου της Ανατολικής Μεσογείου και η περαιτέρω χρήση των δεδομένων αυτών για να εκτιμηθούν οι παλαιοπεριβαλλοντικές συνθήκες στις περιοχές μελέτης. Τρεις επιμέρους στόχοι πρέπει να επιτευχθούν για το σκοπό αυτό. Αρχικά, ο προσδιορισμός των απολιθωμένων ωτολίθων των ιχθύων που βρίσκονται στα Πλειο-Πλειστοκαινικά ιζήματα των περιοχών μελέτης θα επιτρέψει την ανασύνθεση της πανίδας. Στη συνέχεια, οι συναθροίσεις αυτές θα αναλυθούν ώστε να εκτιμηθούν οι παλαιοοικολογικές παράμετροι. Μέσα από την σύγκριση με τα δημοσιευμένα δεδομένα για τις Νεογενείς και Τεταρτογενείς πανίδες ιχθύων της Μεσογείου, καθώς και με τις σύγχρονες εξαπλώσεις των ειδών παγκοσμίως, θα καθοριστεί η γεωγραφική και στρωματογραφική εξάπλωση των προσδιορισμένων ειδών και η εξέλιξη της πανίδας της ανατολικής Μεσογείου από το κατώτερο Πλειόκαινο έως σήμερα.

Οι περιοχές μελέτης επιλέχθηκαν στις νήσους Ρόδο και Κρήτη, με βάση το διαθέσιμο χρονοστρωματογραφικό πλαίσιο και τη σχετικότητα ως προς τους στόχους της έρευνας. Οι μελετημένες τομές είναι ο λόφος Υψένης, η τομή 4 στο Φαλιράκι, η ακτή Βάγια και η ακτή Καλλιθέα στη Ρόδο και η τομή Βούτες στο Νομό Ηρακλείου της Κρήτης. Τα ιζήματα των περιοχών αυτών εκτείνονται στρωματογραφικά από το Ζάγκλιο μέχρι το Μέσο Πλειστόκαινο, και οι παρατηρήσεις υπαίθρου οδηγούν στο συμπέρασμα ότι πρόκειται για παράκτια έως ιζήματα υφαλοκρηπίδας.

Η μεθοδολογία έρευνας περιλαμβάνει τα ακόλουθα στάδια: παρατηρήσεις υπαίθρου και δειγματοληψία, επεξεργασία των δειγμάτων, περιγραφή, προσδιορισμός και φωτογράφιση των ωτολίθων. Για την παλαιοπεριβαλλοντική αναπαράσταση, τα δεδομένα παρουσίας/απουσίας χρησιμοποιήθηκαν για την εκτίμηση παλαιοβάθους, και εν συνεχεία οι σχετικές αφθονίες τους αναλύθηκαν παλαιοοικολογικά, με βάση τα σύγχρονα στοιχεία οικολογίας των ειδών. Μελετήθηκαν οι παράμετροι: αναλογία πελαγικών/βενθικών-βενθοπελαγικών ειδών, σχετική αφθονία των διαφορετικών οικολογικών ομάδων (τροπικά, υποτροπικά, εύκρατα και υποπολικά είδη) στο σύνολο της συνάθροισης και στα επιμέρους πελαγικά και βενθικά-βενθοπελαγικά κλάσματα, η σχετική αφθονία χαρακτηριστικών ειδών σε κάθε δείγμα, ο συνολικός αριθμός ωτολίθων και προσδιορισμένων ειδών στο δείγμα.

Συνολικά προσδιορίστηκαν και περιγράφηκαν οι ωτόλιθοι από 81 είδη Τελεόστεων ιχθύων, που ανήκουν σε 60 γένη και 34 οικογένειες. Ιδιαίτερα σημαντικές είναι οι παρατηρήσεις στα είδη *Pseudophichthys* spp., *Rhynchoconger pantanellii*, *Chlorophthalmus agassizi*, *Diaphus* spp., *Parascombrops mutinensis*, και *Gobius* spp. Η στρωματογραφική εξάπλωση 29 ειδών επεκτάθηκε, ενώ 12 είδη αναφέρονται για πρώτη φορά στο Ζάγκλιο της ανατολικής Μεσογείου, 8 στο Γελάσιο και 21 στο Καλάβριο.

Στην περιοχή Βούτες διαπιστώνονται έξι στάδια παλαιοπεριβαλλοντικής εξέλιξης: 1) το κατώτερο μέρος της χαρακτηρίζεται από έντονες ροές βαρύτητας που αναμιγνύουν τη συνάθροιση ωτολίθων των ρηχών (0-30 m) με αυτή των βαθύτερων υδάτων (~100 m), 2) μια τροπική-υποτροπική πανίδα εγκαθίσταται σε βάθη μεταξύ 100-150 m, 3) ένα θερμό επεισόδιο χαρακτηρίζει την περιοχή με μεγάλη αφθονία του γένους *Bregmaceros*, σε βάθη 200-300 m, 4) διατομίτες που αποτέθηκαν σε βάθη 87-100 m εξακολουθούν να εμφανίζουν μια τροπική πελαγική πανίδα, που όμως περιλαμβάνει μικρότερη συμμετοχή των τροπικών ειδών, 5) μειώνεται περαιτέρω η συμμετοχή των τροπικών, ενώ ταυτόχρονα αυξάνεται η αφθονία των εύκρατων ειδών, δείχνοντας υποχώρηση των θερμών κλιματικών συνθηκών, 6) ένα νέο θερμό επεισόδιο καταγράφεται στο ανώτερο τμήμα της τομής, με αυξημένη πάλι τη συμμετοχή του *Bregmaceros* sp., ενώ το βάθος απόθεσης εκτιμάται στα 200 m.

Στο λόφο Ύψένης, έχουν καταγραφεί οκτώ στάδια παλαιοπεριβαλλοντικής εξέλιξης: 1) το κατώτερο τμήμα αποτέθηκε μεταξύ 100-200 m με τάση ελάττωσης του βάθους και εμφανίζει πλούσια πελαγική πανίδα ενισχυμένη σε τροπικά είδη και με σημαντική την παρουσία του είδους *Electrona risso*, που δείχνει θερμοκρασία 10°-15°C και παραγωγικότητα 50grC/m²/yr (Whitehead et al 1984), 2) στο στάδιο αυτό η περιοχή χαρακτηρίζεται από απότομη και βραχώδη τοπογραφία και σταδιακή ψύχρανση των επιφανειακών υδάτων, 3) η πανίδα στο στάδιο αυτό δείχνει ρηχά και ψυχρά νερά (<30 m) με ωκεάνια επίδραση και χαλαρό υπόστρωμα, 4) το βάθος αυξάνεται στα 100 m και η ψύχρανση συνεχίζει, με αξιοσημείωτη την παρουσία του *Protomyctophum arcticum*, 5) μια ημί-κλειστή λιμνοθάλασσα σχηματίζεται σε αυτή τη φάση, με βραχώδη όρια, 6) εκ νέου βάθυνση της περιοχής στα 100-150 m, 7) η περιοχή συνεχίζει να βαθαίνει με πιθανή αυξημένη ωστόσο βαθυμετρική βαθμίδα και βραχώδες υπόστρωμα, 8) στο ανώτερο τμήμα της τομής η ιχθυοπανίδα εμπλουτίζεται με υποτροπικά είδη, εις βάρος των ψυχρών.

Στην περιοχή Φαλιράκι διαχωρίστηκαν πέντε στάδια παλαιοπεριβαλλοντικής εξέλιξης: 1) αρχικά η περιοχή τοποθετείται στα ανώτερα όρια της υποτροπικής ζώνης, σε βάθη 50-100 m με χαλαρό υπόστρωμα και ανάπτυξη *Posidonia*, όπου αποτίθεται ο σχηματισμός της Κολυμπιάς, 2) το κατώτερο τμήμα του σχηματισμού της ακτής Λίνδου αποτίθεται μεταξύ 40-90 m στην περιοχή αυτή, 3) σε βάθη 75-100 m το στάδιο αυτό χαρακτηρίζεται από την είσοδο εύκρατων βενθικών και βενθοπελαγικών ειδών, 4) η απότομη τοπογραφία πιθανόν ευθύνεται για την ανάμιξη της πανίδας ρηχών νερών (0-40 m) με αυτή του βαθύτερου χώρου (150-250 m), 5) αργότερα το βάθος απόθεσης εκτιμάται στα 100-200 m με ψύχρανση των υδάτων και ελάττωση της βιοποικιλότητας σε σχέση με το προηγούμενο στάδιο.

Στην τομή ακτής Βάγια προσδιορίστηκαν πέντε στάδια παλαιοπεριβαλλοντικής εξέλιξης: 1) στα κατώτερα 2,5 m της τομής εντοπίζονται οι πρώτοι ωτόλιθοι, που δείχνουν βάθη μικρότερα από 15 m σε προστατευμένες περιοχές με βράχια και πέτρες, 2) το περιβάλλον παραμένει βραχώδες, ωστόσο η πανίδα περιλαμβάνει λίγα είδη, μόνο ορισμένα μεσοπελαγικά *Myctophidae* και το βενθικό είδος *Carapus cf. acus*, 3) στο δείγμα αμέσως μετά το ερυθρό οξειδωμένο ορίζοντα της τομής απουσιάζουν εντελώς τα επιφανειακά είδη και βρίσκονται μόνο ωτόλιθοι του απολιθωμένου είδους *Gadiculus labiatus*, το οποίο πιθανόν να ακολουθεί παρόμοιο τρόπο ζωής με το σύγχρονο *G. argenteus*, δηλαδή να βρίσκεται σε βάθη άνω των 100 m, 4) μια πλούσια πανίδα χαρακτηρίζει αυτό το στάδιο, αποτελούμενη από αντιπροσώπους μικρού βάθους (0-30 m) αναμιγμένους με μεσοπελαγικά και βενθοπελαγικά ψάρια μεγαλύτερων βαθών (>100 m), και χαρακτηριστική την παρουσία των *Engraulis cf. encrasicolus*, *Sardinella maderensis*, *Electrona risso*, *Grammonus ater* και *Atherina boyeri*, 5) στο ανώτερο τμήμα της τομής βρίσκεται μια ομοιόμορφη ιχθυοπανίδα αποτελούμενη από πελαγικά *Myctophidae*, λίγα βενθικά *Gobiidae* και το είδος *Cepola macrophthalma*, τα οποία δείχνουν βάθος 10-130 m, που αυξάνει ελαφρά προς τα πάνω, καθώς και χαλαρό υπόστρωμα.

Τα αποτελέσματα της ανάλυσης της συνάθροισης ωτολίθων από την περιοχή της Καλλιθέας επιτρέπουν την εκτίμηση του βάθους απόθεσης για το ανώτερο τμήμα του σχηματισμού της ακτής Λίνδου στα 15-50 m βάθος. Η περιοχή ήταν παράκτια με κατά τόπους πιο κλειστούς κολπίσκους και γενικά χαμηλής ενέργειας ύδατα.

Η σύγκριση των προσδιορισμένων ειδών ιχθύων από τις έως τώρα μελέτες των απολιθωμένων ωτολίθων στα ιζήματα του Πλειο-Πλειστοκαίνου του N-NA Αιγαίου, με τα αντίστοιχα προσδιορισμένα είδη από τα ευρήματα διατηρημένων σκελετών, αποκαλύπτει ότι οι ωτόλιθοι σαφώς υπερέχουν στην εκπροσώπηση της παλαιοπανίδας. Συνολικά έχουν προσδιοριστεί 67 είδη από 30 οικογένειες με βάση τους ωτόλιθους, έναντι 24 ειδών από 16 οικογένειες με βάση τα σκελετικά στοιχεία. Μόλις τρία είδη έχουν προσδιοριστεί ταυτόχρονα από ωτόλιθους και διατηρημένους σκελετούς ιχθύων.

Οι περιβαλλοντικές παράμετροι καθορίζουν την εξάπλωση, μετανάστευση και αφθονία των ψαριών στη θάλασσα. Τα σύγχρονα, ιστορικά και αρχαιολογικά δεδομένα, παρόλο που πιστοποιούν τις μεταβολές, περιοδικές και μη των ιχθυοπανίδων σε κλίμακα από εποχική έως εκατονταετίας, δεν μπορούν να δώσουν πληροφορίες για μεγαλύτερης κλίμακας μεταβολές. Ωστόσο οι μεταβολές αυτές χρίζουν περαιτέρω διερεύνησης εάν αναλογιστούμε τη σύγχρονη διαταραχή που υφίσταται το θαλάσσιο περιβάλλον λόγω της κλιματικής αλλαγής και της ανθρωπογενούς παρέμβασης. Σημαντικά ερωτήματα προκύπτουν αναφορικά με τα όρια ανοχής των ειδών και των οικοσυστημάτων και τις δυνατότητες ανάκαμψης. Στο κεφάλαιο 4 της παρούσας εργασίας παρουσιάζεται η εξέλιξη της ιχθυοπανίδας της Μεσογείου με ανάλυση σε επίπεδο βαθμίδας και ξεχωριστά για την δυτική και ανατολική υπολεκάνη. Με τον τρόπο αυτό ωστόσο δεν αποκαλύπτονται πιο λεπτομερείς μεταβολές, οι οποίες για να εντοπιστούν απαιτούν την ανάλυση σε επίπεδο τομής ή έστω περιοχής, με βάση λεπτομερέστερο χρονοστρωματογραφικό πλαίσιο. Με αυτή την προσέγγιση, ήταν δυνατό να εξεταστεί η συσχέτιση των περιβαλλοντικών παραμέτρων με την κατανομή των μικρών πελαγικών ειδών *Engraulis encrasicolus* και *Sardinella maderensis* στην ανατολική ακτή της Ρόδου από το Γελάσιο έως και το Μέσο Πλειστόκαινο.

Με βάση τα αποτελέσματα της παρούσας διατριβής προτείνεται η χρήση των δεδομένων από την μελέτη των απολιθωμένων ωτολίθων στη βαθμονόμηση μοντέλων οικολογικών θόκων, με στόχο την πρόβλεψη της εξάπλωσης των ψαριών στην ανατολική Μεσόγειο στο πλαίσιο των προβλεπόμενων μελλοντικών κλιματικών συνθηκών.

Extended abstract

This study targets to reconstruct the Plio-Pleistocene eastern Mediterranean ichthyofauna and estimate the paleoenvironmental parameters in the study area. In order to accomplish this goal, three intermediate aims must be achieved: the identification of the fossil fish otoliths contained in the study areas' sediments, the assemblage paleoecological analyses, and a thorough paleobiogeographic overview incorporating the new data.

The study areas were selected on Rhodes and Crete Islands based on the available chronostratigraphic framework and the relevance to the research aims; these are: Ypsenis hill, Faliraki 4, cape Vagia, and Kallithea section on Rhodes Island, and Voutes section on Crete Island. The sediments span the Zanclean-Middle Pleistocene interval, and the field observations indicate they were deposited in shelf to upper continental slope environments.

The methodology includes field observation and sampling, sample processing, morphological description, identification and photographing of the otoliths. The paleobathymetric estimation method of Nolf and Brzobohaty (1994) was applied and the assemblages were further paleoecologically analyzed on the basis of present-day ecological information for the identified taxa. The following parameters were calculated: pelagic/benthic-benthopelagic ratio, relative abundance of the different ecological groups (tropical, subtropical, temperate and subpolar) in the total abundance, in the pelagic and the benthic-benthopelagic component, relative abundance of characteristic species in each sample, total number of otoliths and total number of taxa per sample.

Overall, the otoliths from 81 teleost species were described and identified, placed within 60 genera and 34 families. Particularly important are the morphological observations on the species *Pseudophichthys* spp., *Rhynchoconger pantanellii*, *Chlorophthalmus agassizi*, *Diaphus* spp., *Parascombrops mutinensis*, and *Gobius* spp. The stratigraphic distribution of 29 species was expanded; 12 species are reported for the first time in the eastern Mediterranean Zanclean, 8 in the Gelasian and 21 in the Calabrian stage.

Six stages in the paleoenvironmental evolution of Voutes area are distinguished: 1) the lower part of the section, which is characterized by strong gravity flows, contains a mixed fauna from shallow (0-30 m) and deeper (~100 m) waters, 2) a tropical-subtropical fauna is established thereafter between depths 100-150 m, followed by 3) a climatic optimum, with increased abundance of *Bregmaceros* sp., and depths of deposition between 200-300 m, 4) the tropical fauna subsides somewhat, and the area is more shallow (87-100 m), 5) the temperate species invade the local area, to the expense of tropical taxa, indicating a cooling period, 6) another warm episode is recorded, again with an increased contribution of *Bregmaceros* sp. and estimated depths at 200 m.

The sediments outcropping on Ypsenis hill record eight paleoenvironmental stages: 1) the lowest part was deposited between 100-200 m depth, shallowing upwards, and presents a rich pelagic fish fauna enhanced in tropical species, 2) steep and rocky topography is evident during this next stage, when the surface waters become cooler, 3) shallow (<30 m) waters inhabited by a mostly temperate fauna with open oceanic access and soft substratum, 4) the depth increases to ~100 m and the cooling continuous, denoted by the presence of *Protomyctophum arcticum*, 5) a lagoon forms during this stage, with rocky shelters available, 6) a new deepening phases to 100-150 m is noted, which continues into the next stage, 7) characterized by a high bathymetric gradient and a mostly rocky substratum, 8) the upper part of the section includes a highly subtropical fauna.

In Faliraki 4 section five paleoenvironmental stages were determined, as follows: 1) initially the area is placed in the upper subtropical zone, in paleodepths between 50-100 m and soft substratum suitable, 2) shallowing upwards a little to 40-90 m, 3) and then back to 75-100 m, concurrent with the invasion of temperate benthic and benthopelagic taxa, 4) a mixed fauna is recorded during the next stage, containing both shallow (0-40 m) and deeper-water (150-250 m) inhabitants, 5) while later on the depth is estimated at 100-200 m, and cooling coincides with a low faunal diversity.

Also five stages were separated in the Vagia section: 1) the basal 2.5 m were barren, followed by the first remains indicating depths <15 m in sheltered areas with rocks, 2) continuing upwards, where the assemblage contains only some mesopelagic

myctophids and the benthic species *Carapus cf. acus*, 3) immediately after the red oxidized layer, the pelagic upper water column species are absent completely; only otoliths of fossil species *Gadiculus labiatus* were found, probably indicating depths greater than 100 m, 4) a rich fauna is found during this next stage, containing shallow water inhabitants (0-30 m), as well as mesopelagic and benthopelagic fish of greater depths (>100 m) and characteristic presence of *Engraulis cf. encrasicolus*, *Sardinella maderensis*, *Electrona risso*, *Grammonus ater* and *Atherina boyeri*, 5) the upper part of the section presents a uniform assemblage with pelagic myctophids, some benthic gobiids and *Cepola macrophthalma*, estimating a depth of 10-130 m, with a slight deepening trend upwards, in soft substratum.

The otolith assemblage analysis in lower part of Kallithea section suggests a depositional depth between 15-50 m for the upper part of the Lindos bay Formation. At this level, the area was a coast with several small enclosures and low energy waters.

Through comparison of the fish species identified so far by their otoliths in the Plio-Pleistocene sediments of the S-SE Aegean with those identified by their preserved skeleton, it becomes clear that the otoliths provide much more information regarding the paleofauna. On a total, 67 species from 30 families have been determined from otoliths, whereas 24 species from 16 families from skeletal material. Only three species have been identified both from otoliths and skeletons.

The environmental parameters determine the distribution, migration and abundance of marine fish. Modern, historic and archaeological data, although they verify the periodic and non-periodic variability of fish faunas, in scales from the seasonal to the centennial, cannot provide information about larger scale disturbances, which however may be very valuable considering the present-day marine environment perturbations due to climate change and anthropogenic activities. Several questions arise regarding the resilience of species and ecosystems, as well as their ability to recover from such disturbances. In chapter 4 of the present thesis, the evolution of the Mediterranean ichthyofauna is analyzed on the chronostratigraphic stage level resolution and separately for the western and the eastern sub-basin. However, the more frequent changes could not be traced through this analysis, and require a section-by-section approach, based on a more detailed chronostratigraphic framework,

Extended abstract

such as the one presented in chapter 5. This approach enables to correlate the environmental parameters with respect the distribution of small pelagic fish such as *Engraulis encrasicolus* and *Sardinella maderensis* in the eastern Rhodes Island coast from the Gelasian until the Middle Pleistocene.

1. Introduction

The scope of this research is to reconstruct the eastern Mediterranean Pliocene and Pleistocene ichthyofauna and furthermore to use this data to infer about the paleoenvironment, the paleoceanographic and paleoclimatic conditions in the selected study areas. This target will be achieved through the accomplishment of three intermediate aims. First, the systematic identification of the fossil fish otoliths found in the study areas' Pliocene and Pleistocene sediments will be used to determine the composition of the paleoichthyofauna. These assemblages will then be analyzed to provide paleobathymetric and paleoecologic estimates. Furthermore, the fossil assemblages will be considered with respect to other available data on the Neogene and Quaternary Mediterranean fish faunas, as well as the present-day faunas of the Atlantic and the Mediterranean, in order to determine the paleobiogeographic distribution of the identified taxa and its evolution from the Early Pliocene until today.

This is the first targeted and extensive study of the fossil fish assemblages of the eastern Mediterranean Basin. The Mediterranean fossil fish record so far holds data on the Eocene to middle Pleistocene of the western Mediterranean sub-basin (Sorbini and Tirapelle Rancan 1980; Landini and Sorbini 2005a,b; Carnevale et al 2008), mostly south France (Schwarzhan 1986; Nolf and Girone 2000; Nolf and Brzobohaty 2002; Reichenbacher 2004; Girone and Nolf 2009; Caputo et al 2009; Gierl et al 2013), Italy (Landini et al 1990; Carnevale et al 2006a,b; Carnevale 2008), northern Africa (Greenwood 1972; Carnevale 2004; Baciú et al 2005; Carnevale and Bannikov 2006; Carnevale 2007; Pawellek et al 2012), and Spain (Nolf et al 1998), whereas little information exist on the distribution of fish in the eastern sub-basin. Significant targeted researches have been conducted on the Ionian Sea fossil ichthyofauna, especially for the Pliocene-middle Pleistocene interval (Girone 2000; Girone and Varola 2001; Nolf and Girone 2006; Girone 2007; Landini and Sorbini 2010; Agiadi et al 2010). In addition, sporadic data exist on fish skeletal remains in the eastern Mediterranean even outside the Ionian realm, mostly of Miocene and early Pliocene age (Gaudant et al 1994; Gaudant 2001). However, the fish skeletal remains offer limited possibilities for the identification of the entire fauna and, as a result, these fish records are rather poor compared to otolith records (Landini and Sorbini 2005; Girone et al 2006). Consequently, the eastern Mediterranean fossil fish fauna, outside the

Ionian Sea realm, remains largely unknown. The examination of the Rhodes and Crete Island Pliocene and Pleistocene fish otoliths comes to fill the knowledge gap, by providing a concrete and extensive record of the stratigraphic and geographic distribution of fish in the eastern Mediterranean region.

1.1 Fossil fish otoliths

Otoliths are the aragonitic incremental stone-like structures contained within the inner ear of teleost fish, which facilitate sound and balance perception. Fish otoliths provide the most significant fossils for the study and reconstitution of the Cenozoic ichthyofauna (Nolf 1985). Since fish inhabit the entire water column, the otoliths found within marine sediments reflect the paleoceanographic conditions in the surface, intermediate, as well as the deep water levels and the bottom of the sea.

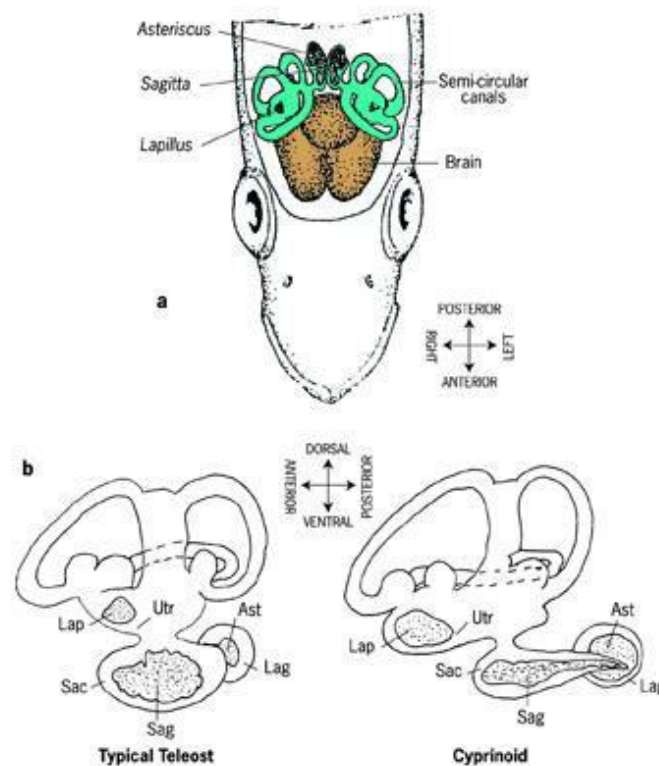


Figure 1.1 Position of the three sets of otoliths within the cranium of teleost fish (Panfili et al 2002). a. Dorsal view of the teleost head, where the upper part of the cranium has been removed. b. The otoliths' position in the labyrinth.

Otoliths provide information on the temperature, salinity, bathymetry, water oxygenation, productivity, temperature gradient, oceanic circulation, terrigenous input

and other parameters (Brzobohaty and Nolf 1994; Laurito 1997; Girone 2000; Brzobohaty and Nolf 2002; Donovan et al. 2003; Girone 2005; Brzobohaty et al. 2007; Agiadi et al. 2010; 2011; Ciaranfi et al 2010). Teleost fish otoliths are contained within the three interconnected otic sacs of the inner ear labyrinth, and function as mechanoreceptors in the auditory and vestibular system, stimulating the sensory tissue in order to detect sound waves as well as linear and angular accelerations, thus enabling sound and balance perception (Panfili et al 2002).

There are three sets of otoliths in each fish, the sagitta, lapilli, and asterisci (Figure 1.1). The sagittus is the otolith used in most applications. It exhibits species-specific morphology, which is mainly characterized by the sulcus and its two colliculi, the rostrum and antirostrum, the peripheral shape and ornamentation, which allows the description and taxonomic identification (Nolf 1985). Fossil fish otoliths are identified based on this characteristic species-specific morphology. The most significant characters to distinguish are presented in Figure 1.2.

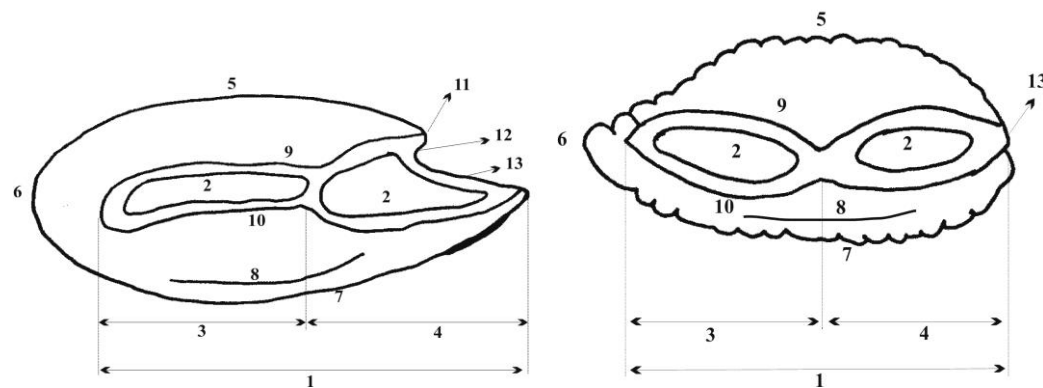


Figure 1.2 Morphological nomenclature applied for the description and systematic taxonomy of fossil fish otoliths (Nolf 1985). On the left is a schematic representation of the Acanthopterygian type of otolith, while on the right the Paracanthopterygian type. 1. Sulcus, 2. Colliculum, 3. Cauda, 4. Ostium, 5. Dorsal rim, 6. Posterior rim, 7. Ventral rim, 8. Ventral fissure, 9. Crista superior, 10. Crista inferior, 11. Antirostrum, 12. Excissura, 13. Rostrum. Both sketches correspond to a left otolith.

Internally otoliths are incremental structures formed by the accretionary deposition of concentric layers of proteins and aragonite crystallites throughout the fish's life duration (Degens et al 1969; Campana and Neilson 1985; Campana 1999). In the last few years, fish otoliths have been used in several occasions to provide high-resolution paleoclimatic representations, since their aragonite growth increments record biologic and oceanographic information in great detail (Patterson et al 1993;

Patterson 1998, 1999; Ivany et al 2000; Wurster and Patterson 2001; Andrus et al 2002a,b; Dufour et al 2000; Ivany et al 2003; Reichenbacher et al 2004; Grimes et al 2003, 2005; Tutken et al 2006; Ghosh et al 2007; Wurster and Patterson 2009; Price et al 2009; Andrus 2011; Vanhove et al 2011; Wang et al 2011; Wang et al 2013).

1.2 The Cenozoic Mediterranean fish fauna

The early Oligocene Mediterranean ichthyofauna may be characterized by the large contribution of cosmopolitan oceanic taxa, which today inhabit the Indian and Pacific Ocean (Nolf and Steurbaut 2004, Nolf and Brzobohaty 2004). From the Early Miocene until the Tortonian, but also during the Zanclean, these taxa gradually depart from the Mediterranean, to be replaced by modern Atlantic taxa (Nolf et al 1998).

Fish exhibit greater mobility with respect to other aquatic organisms, a fact which allows them to respond quite rapidly to changing environmental conditions. Indeed, Carnevale et al (2006a) report marine fish otoliths in many horizons of the “Lago-mare” sequence in Cava Serredi (central Italy), attesting the prevalence of normal marine conditions during at least the upper part of this sequence. This observation indicates that the Mediterranean flooding, after the Messinian Salinity Crisis, took place before the onset of the Pliocene period. Indeed, the presence of fish species belonging to different ecologic and trophic categories in the Messinian facies reveals the complex ecological structure of the Mediterranean during this time.

From the early Pliocene until the early Pleistocene, taxa with Indo-Pacific or, more generally tropical–subtropical affinities, were gradually replaced by temperate taxa (Girone et al. 2006). This was accomplished through a gradual increase of the Atlantic originating taxa towards the Pleistocene. These fish still exist in the present-day Mediterranean. Although currently available data on the Piacenzian fish fauna is scarce, it may be assumed that the temperate fish introduction to the Mediterranean commenced at that time (Girone 2006). The Gelasian fauna appear to be enriched by more temperate Atlantic species, such as *Notoscopelus elongatus* and *Phycis blennoides*, which inhabit the Mediterranean till today, along with a group of subpolar species, confined today to the North Atlantic region. At the same time, typical tropical – subtropical species, which inhabited the Mediterranean Sea during the Zanclean or even before the Messinian, disappeared after the Gelasian (Girone et al. 2006). A

second invasion by tropical – subtropical Atlantic species to the Mediterranean, during the Middle Pleistocene, has been recorded in the Montalbano Jonico section of Italy, possibly induced by the interglacial climatic optimum conditions (Girone and Varola 2001). Landini and Sorbini (2005a) identified three major mass ichthyofauna turnover episodes in the Mediterranean, during the Piacenzian, the Gelasian – Calabrian boundary, and the Calabrian – Middle Pleistocene boundary, while reporting a stasis during the Calabrian. These authors indicate a period of extensive and continuous environmental stress, during the Gelasian and the beginning of the Calabrian. At this time the fish species disappearances are not balanced by the new appearances in the Mediterranean Sea.

In general, the evolution of the Mediterranean fish fauna from the Oligocene until the Middle Pleistocene, according to previous authors, exhibits the following trends: a) a progressive decline in the contribution to the assemblages of the Indo-Pacific species, b) an overall increase in endemic species, c) an increase in the Atlantic species, and d) a decrease in cosmopolitan species especially throughout the Pliocene and the Pleistocene and in the deep-water assemblages. At this point, it is important to note that there is a significant and eventual gap in the fish stratigraphic distribution record, and that is in the Middle – Upper Pleistocene interval, which is due to the great difficulty in finding appropriate sediment samples of this age, in quantities suitable for otolith studies, as well as the lack of sediment outcrops of this age, which may have held skeletal remains. As such, so far at least, one may only hypothesize about this interval.

The present-day Mediterranean fish fauna is unique, comprised of 619 known species, 13% of which are endemic, 2% are introduced, and 67% are non-endemic natives. Overall, 85% of the modern Mediterranean fish species are teleosts (Lasram et al 2009). Introduced species include human introductions and Indo-Pacific/Red Sea immigrants (alien species) passing through the Suez Canal. Non-endemic natives are Atlantic, Boreal and Tropical species including amphi-Atlantic species which may periodically visit the Mediterranean Sea, or true colonizers which become permanent inhabitants (Corsini-Foka and Economidis 2007).

2. Geological Setting

Rhodes and Crete Islands (Figure 2.1 and 2.2) lie on the southern and southeastern part of the Hellenic arc, exhibiting intense active tectonism and a great variety of environments both present and past (Mutti et al. 1970; Zachariasse 1975; Dewey and Sengor 1979; Le Pichon et al. 1979; 1982; Dermitzakis and Georgiadou-Dikaiouli 1983; Frydas 1986; Meulenkamp et al. 1979; 1988; 1994; Fassoulas et al. 1994; Dermitzakis et al. 1995; Moissette and Spjeldnaes 1995; Hanken et al. 1996; Jovilet et al. 1996; 2003, 2013; Meijer and Wortel 1997; ten Veen and Meijer 1998; Thomson et al. 1998; 1999; Mascle et al. 1999; Duermeijer et al. 1998; 2000;

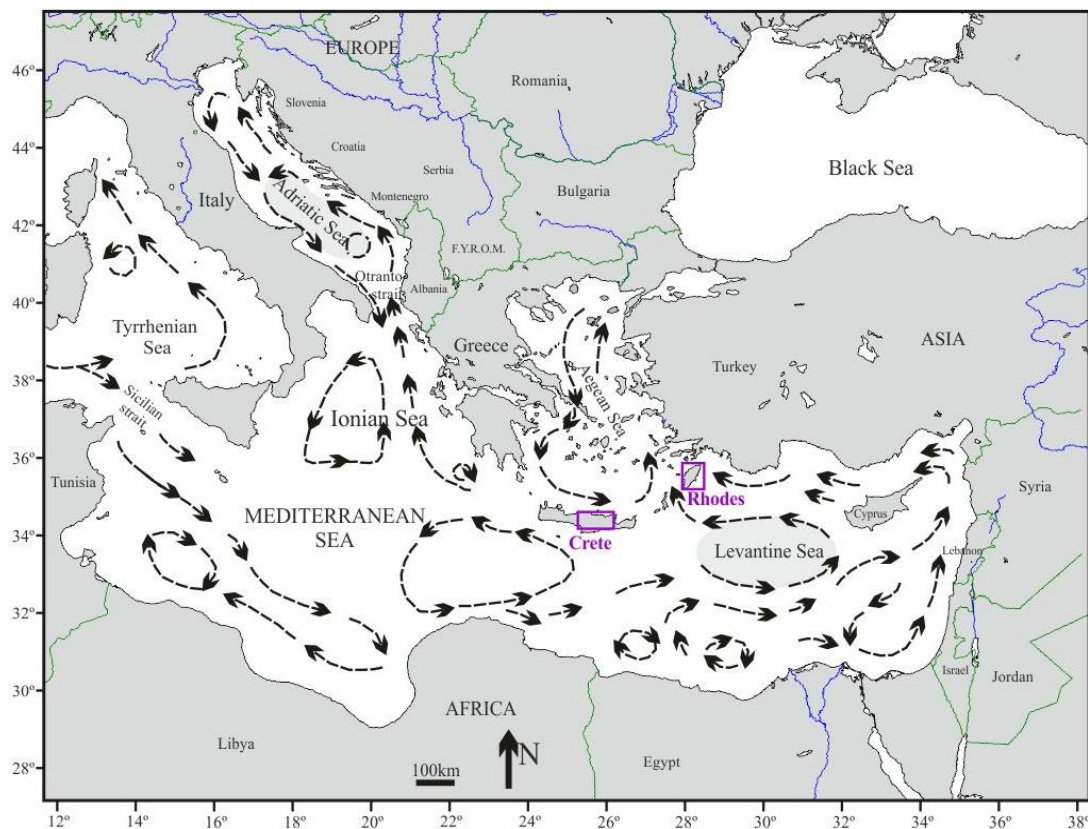


Figure 2.1 Map of the eastern Mediterranean area, showing the location of the study areas as well as the major sea water circulation patterns. The arrows illustrate the main pattern of the present-day surface circulation, whereas the shaded areas mark the present-day intermediate and deepwater formation regions (Robinson and Golnaraghi 1993, Theocharis et al. 1993).

Lekkas et al. 2000; Hansen 1999; 2001; Fassoulas 2001; ten Veen and Kleinspehn 2003; Drinia et al. 2005; Cornée et al. 2006; van Hinsbergen and Meulenkamp 2006;

van Hinsbergen et al. 2007; Joannin et al. 2007; Triantaphyllou et al. 2009; Zachariasse et al. 2008).

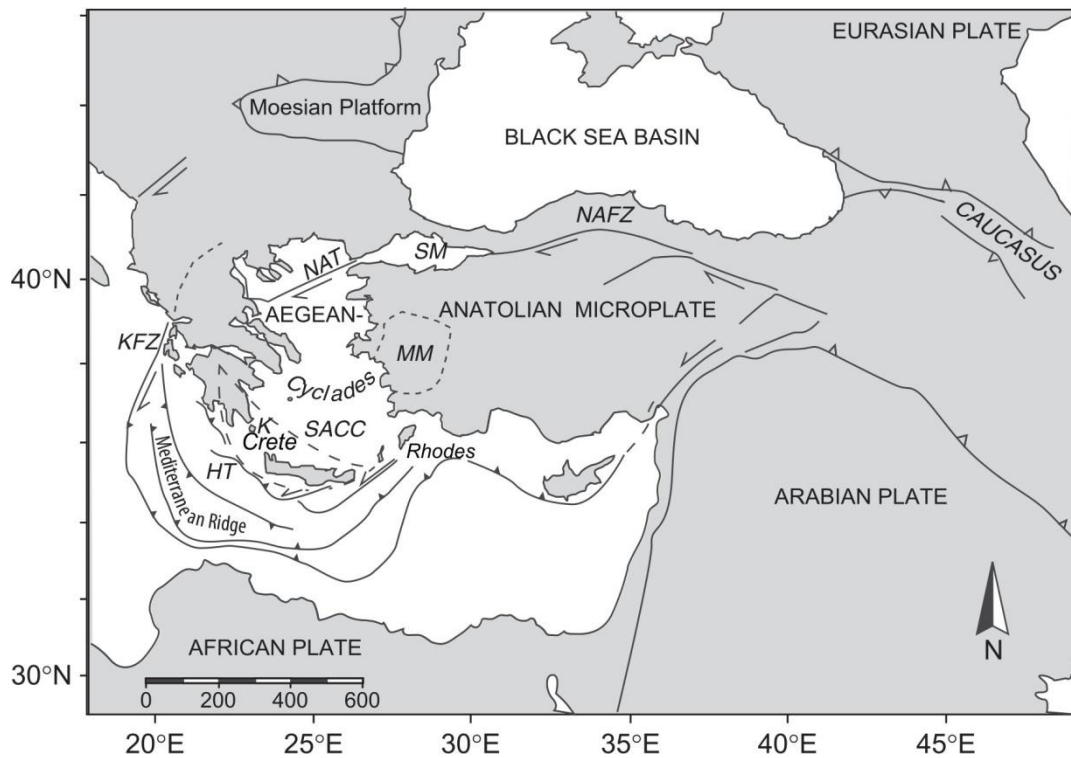


Figure 2.2 Map of the Aegean region (Zachariasse et al. 2011). HT, Hellenic Trench; NAFZ, North Anatolian Fault Zone; NAT, North Anatolian Trough; KFZ, Kephalaria Fault Zone; SACC, South Aegean Crystalline Complex; K, Kythira; MM, Menderes Massif; SM, Sea of Marmara.

2.1 Crete Island – Heraklion

Crete Island was uplifted in 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 (Angelier 1976; Bornovas and Rontogianni-Tsiabaou 1983; Meulenkamp et al. 1988, Van Hinsbergen and Meulenkamp 2006). The Neogene sediments overlie the alpine substratum (Figure 2.3), comprising a pile of nappes including the metamorphic Plattenkalk and the Phyllites - Quarzites Units followed, in discontinuity, by the Tripolis and Pindos-Ethia, as well as other minor units (Bonneau 1973; Karakitsios 1979; Jolivet et al. 2010, Zachariasse et al. 2011).

The Heraklion basin is located between the Psiloritis and Dicti mountains, within a kilometer-scale fault delimited graben structure, and it is the largest of

several multi-oriented Neogene tectonic basins in Crete (Fig. 2.3; Meulenkamp et al. 1979). It was formed most probably during the Tortonian (van Hinsbergen and Meulenkamp 2006), and was originally part of a larger basin which included the present Messara. Early Pliocene tectonic activity dissociated the two basins (Meulenkamp et al. 1994). The alpine substratum in Heraklion area consists of Pindos and Tripolis sedimentary rocks, as well as minor ophiolite exposures. The Mesozoic to Eocene limestones outcrop at the margins and as isolated horsts within the basin, whereas at the margins one may observe the Eocene flysch.

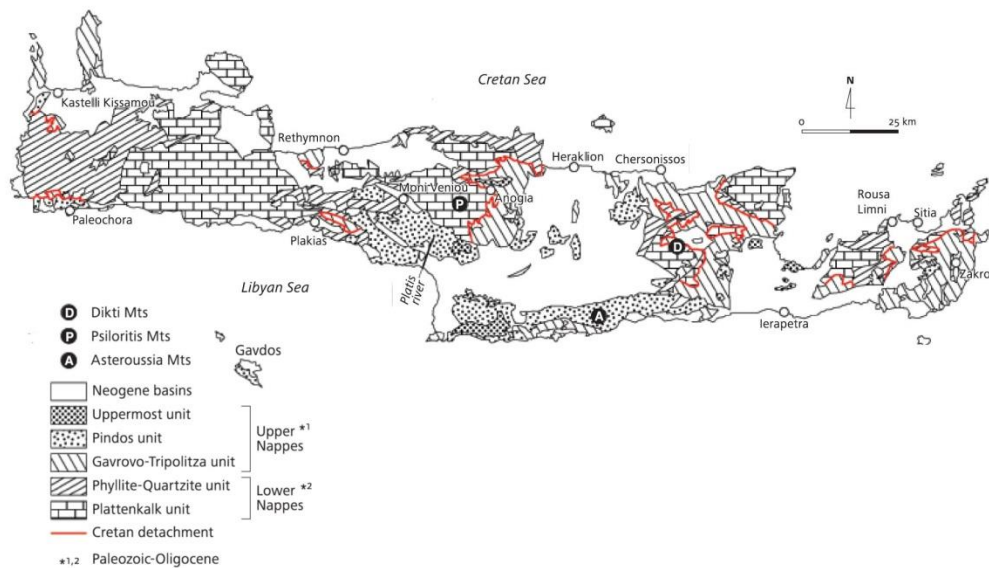
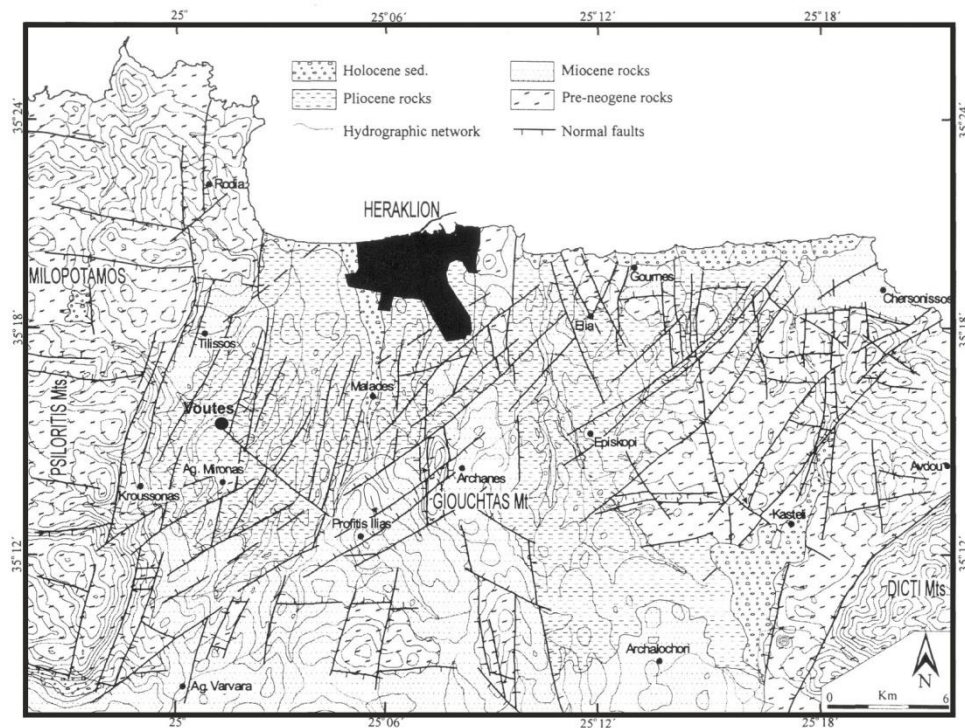


Figure 2.3 Geological map of Crete (Bornovas and Rontogianni-Tsiabaou 1983). The Cretan detachment plane corresponds to the tectonic contact between the Lower and Upper Nappes units (Zachariasse et al. 2011).

The intense neotectonic activity affecting the entire island is denoted, in the case of Heraklion Neogene deposits, through the variable sediment thickness and deformations (Fassoulas 2001). Benda et al. (1974), followed by Meulenkamp et al. (1979), eventually separated the Neogene and Quaternary sediments of Heraklion basin in six groups, based on the research of Freudenthal (1969), Meulenkamp (1969), Sissingh (1972), Drooger and Meulenkamp (1973), Gradstein (1973), Zachariasse (1975), Fortuin (1977, 1978) and their own.

At the southern margin, the basal Neogene deposits forming the Prina group are exposed, consisting of dark limestone breccias and conglomerates, deposited in a non-

marine to brackish or shallow marine environment (Fig. 2.4; Papapetrou-Zamani 1966; Anapliotis 1976).



Period	Stage	Lithostratigraphic unit
Pliocene	Piacenzian	Galini
	Zanclean	Finikia
Miocene	Messinian	Hellenikon
		Vrysses
	Tortonian	Tefeli
	Serravalian	Prina
	Langhian	
	Burdigalian	
Paleozoic-Mesozoic		alpine basement rocks

Figure 2.4 Geological map of the northern Heraklion prefecture, indicating the location of the Voutes section (modified from Fassoulas 2001). Lithostratigraphy of Crete according to Benda et al. (1974), Meulenkamp et al. (1979), Frydas (1998) and Fassoulas (2001).

The Tefeli group comprises clastic sediments of fresh-water, brackish and marine affinities. Both groups are covered by the Vrysses group marine sediments, which are bioclastic limestones and associated alternations of laminated shallow marine marls (Papapetrou-Zamani 1966; Anapliotis 1976; Dermitzakis and Georgiadou-Dikaioulia 1979). The Hellinikon group comprises non-marine conglomerates, fluvio-lacustrine and lagoonal sediments with gypsum of the latest Miocene (Benda et al. 1974; Georgiadou-Dikaioulia 1979; Meulenkamp et al. 1979). The Pliocene sediments of Heraklion basin, mainly marine marls and diatomites form the Finikia group; lay unconformably over the Miocene deposits (Georgiadou-Dikaioulia 1979; Zachariasse 1979; Frydas 1998). Delrieu et al. (1993) also reported the lago-mare facies lying unconformably over the Miocene sediments. According to Meulenkamp et al. (1979) the Heraklion basin was uplifted during this period and separated from the Messara basin, which it further supplied with the clastic material forming the Pleistocene Galini group.

2.2 Rhodes Island

The Island of Rhodes is situated on the eastern edge of the Aegean arc (Fig.2.2) and was formed during the Pliocene, concurrently with the initiation of the Aegean archipelago, due to the increased pressure in this area, incurred by the syndepositional transtensional tectonics controlled by N70° trending sinistral strike-slip faults, because of the increasing curvature of the plate. These vertical movements are still continuing today (Pirazzoli et al. 1989; Hanken et al. 1996; Kontogianni et al. 2002; Cornée et al. 2006). Alpine calcareous series and Ophiolitic complex rocks comprise the geological basement (Fig. 2.5). These are the Plattenkalk series (also known as Attaviros Unit), the Tripolis series (topically named Lindos Unit), the Pindos series (Profitis Ilias Unit) and the Pelagonian series, which includes the ophiolites.

In the Miocene, the south-southwestern part of Rhodes was emerged, as part of the Aegean realm, which collapsed during the Pliocene, when Rhodes essentially became an island. Miocene deposits on the island include fluvio-lacustrine sediments with various terrestrial fossils, such as vertebrate skeletal remains. The northeastern part of Rhodes was however submerged during the Pliocene and most of the Pleistocene. This Pliocene basin extended well into the north, until the coast of

Turkey, up until the Late Pleistocene, when northeastern Rhodes collapsed to form the present-day Rhodes basin (Nelson et al. 2001; Cornée et al. 2006), which reaches depths of up to 4400m (Woodside et al. 2000). This event is attested by the presence of post-Miocene sediments on the bottom of the modern Rhodes basin. However, during the Early – Middle Pleistocene northeastern Rhodes experienced significant uplift (Cornée et al. 2006).

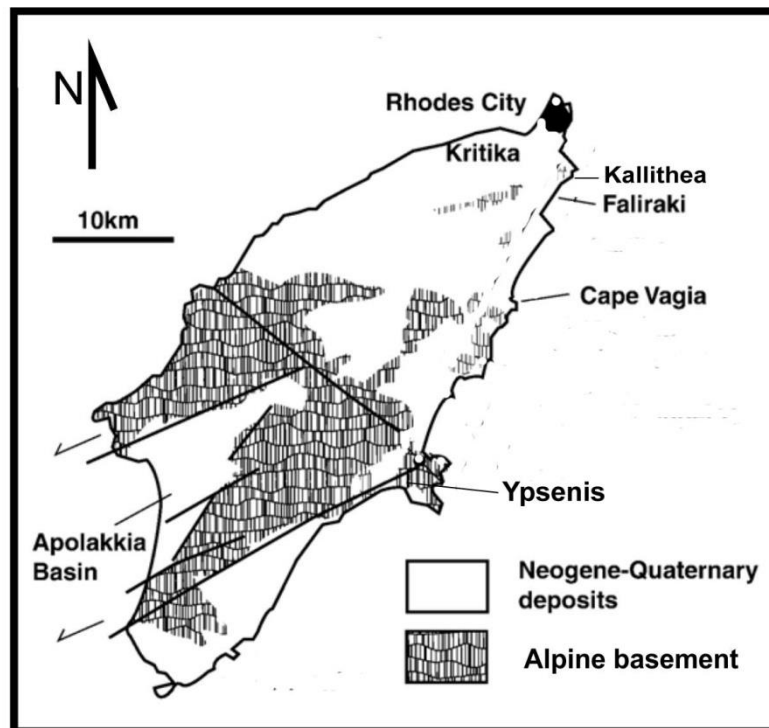


Figure 2.5 Simplified geological map of Rhodes Island based on Bornovas and Rontogianni-Tsiabaou (1983), showing the location of the samples outcrop sections on the north and northeast coast.

This complex geodynamic evolution of Rhodes area is elaborately recorded in the Pleistocene sedimentary facies outcropping on the north and northeastern coasts (Fig. 2.5). Overall, the post-alpine sediments of Rhodes were originally divided in four major lithostratigraphic units: Damatria Formation, Kritika Formation, Rhodes Formation and Lindos-Acropolis Formation (Hedenborg 1837; Bukowski 1899; Mutti et al. 1970; Meulenkamp et al. 1972; Hanken et al. 1996). Later on Cornée et al. (2006) recognized only three formations, unifying Damatria and Kritika series under Rhodes Formation, and presenting evidence of an intermediate lithostratigraphic unit, Tsampika-Ladiko Formation, between Rhodes and Lindos-Acropolis Formations. According to these authors, the Rhodes and Tsampika-Ladiko Formations' sediments

were deposited during two major sedimentary transgression – regression cycles, which are delimited by important erosional surfaces.

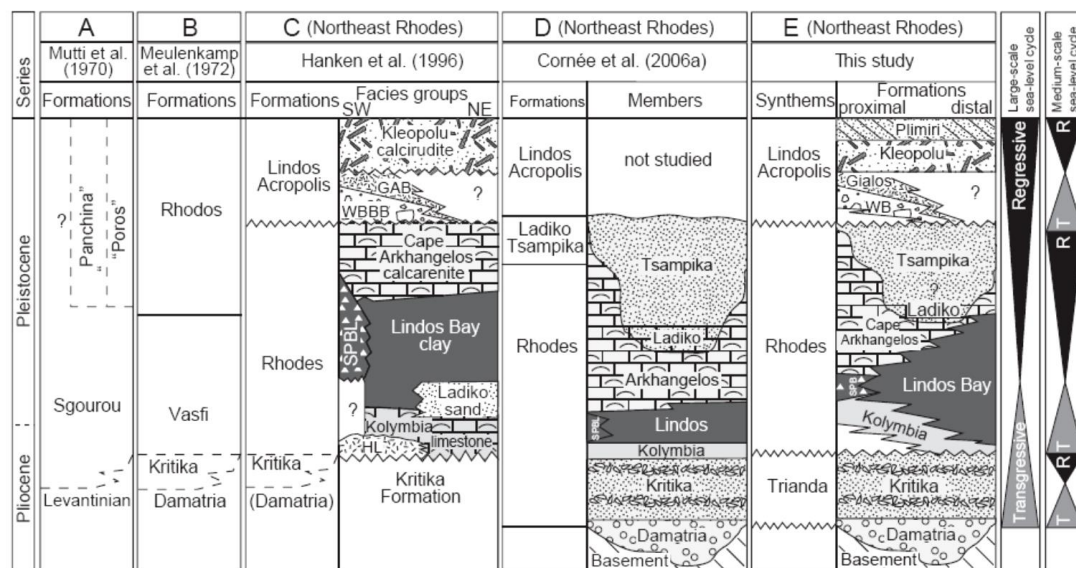


Figure 2.6 Lithostratigraphic divisions of the Plio-Pleistocene deposits on Rhodes (compiled by Titschack et al. 2012, from Hanken et al. 1996; Hansen, 1999; Nelson et al. 2001; Cornée et al. 2006, Titschack et al. 2008). HL, Haraki Limestone; SPBL, St. Paul’s Bay Limestone; WBBB, Windmill Bay Boulder Bed; GAB, Gialos Algal Biolithite.

Rhodes Formation was deposited during a cycle characterized by intense synsedimentary tectonism, lasting from the Gelasian until the Calabrian (approximately until 1.4-1.3 Ma). Tsampika-Ladiko Formation is interpreted as a transgressional system, part of a second Pleistocene sedimentary cycle, which took place between 1.3-0.3Ma, and was interrupted abruptly by the emersion of NE Rhodes. Further works by Titschack et al. (2008) and Moissette et al. (2012) led to the acceptance of four lithostratigraphic units in the Early to Late Pleistocene of Rhodes: the Rhodes, the Ladiko–Tsampika, the Lindos Acropolis, and the Plimiri Aeolianite Formations. Furthermore, the Rhodes Formation is subdivided into four members: Kritika, Kolymia Limestone, Lindos Bay Clay, and Cape Arkhangelos Calcarenite (Moissette et al. 2012). However, recently Titschack et al. (2012) altered the above division to include subdivisions of the Lindos - Acropolis Synthem, as observed in the Lardos area (Figure 2.6).

Overall, a short review of the current assessment of the Neogene deposits of Rhodes Island reveals the multi-faceted geodynamic and paleoenvironmental evolution of the area. Damatria Formation comprises fluvio-lacustrine conglomerates, 20

sands and silts, with occasional clay intercalations (Mutti et al. 1970; Willmann 1981), gradually transiting to the Kritika Formation (Meulenkamp et al. 1972). Benda et al. (1977) placed the Damatria Formation to the Gelasian stage.

The Kritika Formation includes several siliciclastic facies (Hanken et al. 1996; Cornée et al. 2006; Moissette et al. 2007), representing transgressive-regressive sedimentary cycles delimited by emersion surfaces of cemented blocks or rhizoliths (Moissette et al. 2012). The Kritika series exemplifies cyclic deposition of marine carbonates and sandstones, transiting to low-energy marine and lagoonal sandy clays, marls and coal beds, capped by shore-face deposits of marine sandstones and conglomerates (Moissette et al. 2012). These unique ancient beachrock formations, which record the Early Pleistocene relative sea-level fluctuations, are quite similar to those developing in the area today (Moissette et al. 2012).

The Kolymbia Formation, which includes the Haraki limestones, is dated in the Gelasian as well (Løvlie et al. 1989), and consists of bioclastic limestones deposited in a coastal front to outer shelf environment (Hanken et al. 1996; Spjeldnaes and Moissette 1997; Steinthorsdottir 2002). The Lindos Bay Formation comprises calcareous and muddy clays with a rich marine fauna indicating significant deepening of the area to 400-600 meters and then uplifts again (Moissette and Spjeldnaes 1995; Hanken et al. 1996). The stratigraphic placement of these beds still remains quite controversial, since older biostratigraphic studies supported a Calabrian age (Meulenkamp et al. 1972). Subsequent magnetostratigraphic data indicated an age extend from 3 Ma, at the base of the sequence, to 0.7 Ma at the top (Løvlie et al. 1989). Thomsen et al. (2001) however, suggested an early Pleistocene age, between 1.6-1.0 Ma. According to the most recent studies by Cornée et al. (2006), the Lindos marls were deposited between 2.09-1.4 Ma. The Lindos Bay Clay member also includes the limestones of the Saint Paul coast, which are biolithites with deep water corals, supposedly filling underwater canyon flanks, concurrently with clay deposition at the coasts (Hanken et al. 1996).

The Cape Arkhangelos Calcarenite Formation comprises grainstones and packstones rich in molluscs and bryozoans, forming shelf down-stepping clinofolds of 20-30 meters thickness, whose base erodes the Lindos Bay Clay (Beckman 1995;

Hanken et al. 1996; Hansen 1999). The Cape Arkhangelos Calcarenite is observed up to 70 meters above present sea level, so it has been associated with a sea level high stand, at the end of a significant regression phase. Towards the upper part, the calcarenite transits to outer shelf marls with thin-shelled Pectinidae (Hanken et al. 1996). Cornée et al. (2006) date the deposition of Cape Arkhangelos Calcarenite between 1.4-1.3 Ma.

The Tsampika and Ladiko Formations in the Ladiko area appear with at least four retrogradational – progradational coastal sequences of alternating sandy marls, sands and muds (Cornée et al. 2006), deposited in intense paleocliffs (Ferry et al. 2001). Although the Ladiko sequence appears at the same altitude, parallel to the Kritika clastic deposits, which appear in the Ladiko section some few hundred meters away, their lateral connection is buried underneath Holocene sediments. However, Cornée et al. (2006) have shown that to the west, the Ladiko sequence overlays the Kritika deposits, which have occasionally been eroded. These authors interpret the Ladiko series as a coastal, mostly high-energy sequence, formed within narrow embayments, where skeletal remains from the hard substratum and soft bottom organisms lay mingle. Their deposition most probably took place during the Pleistocene, after the Cape Arkhangelos Calcarenite and the Tsampika series.

The Tsampika series has been deposited on a paleocanyon, unconformably over the eroded Kolympia limestone or the Cape Arkhangelos Calcarenite, or in some cases over the alpine basement (Cornée et al. 2006). The ages of this siliciclastic series is placed within the Pleistocene (Ferry et al. 2001) and consists of up to nine sedimentary sequences have been identified (Cornée et al. 2006). The basal sequence, which is equivalent to the Ladiko series, comprises deltaic deposits transiting to coastal marine and then deltaic/lagoonal, followed by a fluvial conglomerate bed. Overlying continue seven retrogradational-progradational sequences of conglomerates, sands, silts and silty marls. The deposition of the Tsampika – Ladiko Formations is placed between 1.3-0.3 Ma (Cornée et al. 2006).

The Lindos Acropolis Synthem comprises four sets of facies, deposited in coastal environments (Hanken et al. 1996, Titschack et al. 2012), whose base is set on an erosional surface. The Windmill Bay boulder consists of eroded Cape Arkhangelos

Calcarenite, covered with crusts formed by microbes or bryozoans. Gialos Formation is a red algal biolithite lying on top of the Windmill Formation. Kleopoulou Formation is a bioclastic limestone with algae, around 12 meters thick, with clastic material originating from the alpine basement, as well as the Pleistocene deposits (Cornée et al. 2006). Finally, Plimiri Aeolinite Formation is an autochthonous coralligene facies equivalent to the Windmil Bay Boulder Bed and Gialos Algal Biolithite (Hanken et al. 1996; Titschack et al. 2008; Moissette et al. 2012). At Plimiri, it overlies unconformably the Rhodes Formation, and comprises well-sorted fine to medium sands consisting of a mixture of quartz grains, basement clasts and reworked red algal clasts, with rhizoliths especially at the lower part (Titschack et al. 2008).

3. Material and Methods

3.1 Stratigraphic data, sample acquisition and processing

On Rhodes and Crete Islands, the Pliocene and Pleistocene sediments outcrop in numerous localities. Field observations, with the guidance of Ass. Prof. Dr. Efterpi Koskeridou, Ass. Prof. Dr. Pierre Moissette and Dr. Jean-Jacques Cornée, led to distinguish the following sections to be included in this thesis, taking into account their stratigraphic continuity and span: Voutes (Crete), Ypsenis, Faliraki, Vagia and Kalithea (Rhodes) (Figure 3.1). A published chronostratigraphic data were already available for Faliraki, Vagia and Kalithea sections. Ypsenis section was first located and sampled in 2009. The biostratigraphic analysis was conducted, in parallel to the course of this thesis, by Ass. Prof. Dr. F. Quillevère and Dr. G.E. Lopez-Otalvaro, at the University of Lyon and CNRS Montpellier, France. Dating was also not available for Voutes section, and was kindly provided by Ass. Prof. Dr. M. Triantaphyllou at the University of Athens.

Epochs	Stages	Geological sections
Holocene	Holocene	
Pleistocene	Upper	
	Middle	
	Calabrian	
	Gelasian	
Pliocene	Piacenzian	
	Zanclean	
Miocene	Messinian	

Figure 3.1 The stratigraphic span of the studied sections.

As a standard, sediment sampling for fish otolith studies requires large bulk samples. In older studies (e.g. Anfossi and Mosna 1972, 1976, 1979; Schwarzahns 1979; Aruta and Greco 1980), researchers approached the sampling procedure with the notion of horizon sampling; they generally took bulk sediment samples from horizons or beds that provided macroscopic evidence of fish otolith presence. As a

result, these studied produced sporadic fish distributions, since the stratigraphic continuity, as much as it can be obtained in any sampling, was lost altogether. In more recent studies (e.g. Nolf and Cappetta 1988; Girone and Varola 2001; Girone 2003) researchers have realized this drawback and so have since started to sample in a more organized manner, taking multiple bulk sediment samples along biostratigraphically dated outcrops. In the present study approximately 25 kg of sediment were collected per sample, along the studied outcrops, in a continuous manner. The samples were diluted in plain water and sieved using a 250 μm diameter sieve. The otoliths were then handpicked from the sediment, under a stereoscope.

CRETE ISLAND

3.1.1 Voutes section

The studied section is located southwest of the village Voutes in central Crete, south of Heraklion city (Fig. 2.2). Geologically it is situated in the western section of the Heraklion basin. The section's sediments may be placed within the Finikia lithostratigraphic group and include more than 80 meters of marls and sandy marls (Figures 3.2 and 3.3). The upper part of the section presents three diatomite horizons. Strong gravity flows have formed a series of sand lenses, on the lower part of the section, with distinctive sedimentologic attributes and characteristic fauna (Figure 3.4). On a total, nine (9) sediment samples were taken along Voutes section (Figure 3.3). Field observations were also noted, including lithological and sedimentologic remarks, as well as the macroinvertebrate fauna (identifications on the field by Ass. Prof. E. Koskeridou). Samples 1, 3 and 4 have been taken from the diatomite horizons, which are barren of other faunal remains. Sample 2 was collected from the uppermost marls, which present a rather rich macroinvertebrate fauna, including *Pycnodonta*, pectinids (e.g. *Chlamys*), Veneridae and many Lucinidae. Sample 5 was taken from the blue marls, at the middle part of the section, where pteropods, *Nucula*, thin Pectinidae and *Cadulus* could also be identified. Sample 6 came from marly sands, mostly gravity flows with Pectinidae and gastropods. Sample *a* was also collected from marls with *Pycnodonta navicularis* and pectinids. Sample *b* was taken from one of the sand gravity lenses observed at the lower part of the outcrop, and also included macrofossils such as *Natica*, Pectinidae, Veneridae, *Cardium* and *Turritella*.

From the lowermost part of the section, sample *c* came from the marls underneath and around the sand lenses and the macroscopic examination showed no evidence of other faunal remains.

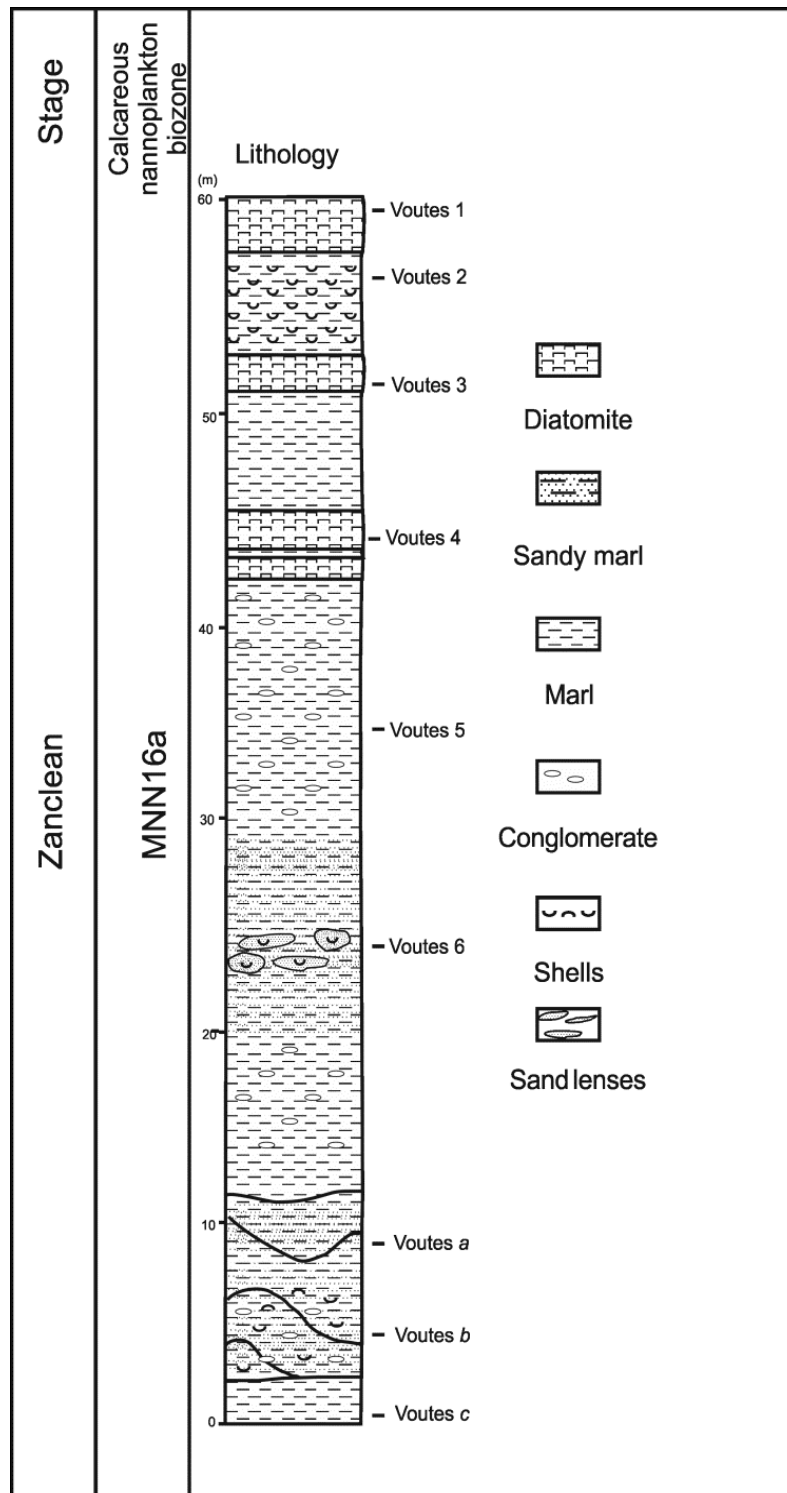


Figure 3.2 Voutes stratigraphic column and samples. Biostratigraphy is provided by Ass. Prof. M. Triantaphyllou, following the biozonation scheme of Rio et al. (1990).



Figure 3.3 Voutes section and sampling.



Figure 3.4 Gravity flows at the lower part of the Voutes outcrop section.

The relevant chronostratigraphic framework (Figure 3.2) for the evaluation of the results was provided through calcareous nannoplankton biostratigraphy, by Ass. Prof. M. Triantaphyllou, based on the biozonation scheme of Rio et al. (1990) as this has been incorporated in the magnetobiochronologic framework of Lourens et al. (2004) in Gradstein et al. (2004). Numerical ages of biozone boundaries are given according to Lourens et al. (2004) and Raffi et al. (2006). In 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*, very sporadic *D. pentaradiatus* and *D. brouweri*. Placoliths are represented mainly by very abundant *Pseudoemiliana lacunosa*. *Helicosphaera sellii* is also significantly contributing to nannofossil assemblages. *Reticulofenestra pseudoumbilicus* (>7micron) and sphenolithids are practically absent. The high abundance of both *D. tamalis* (15-35%) and *D. surculus* (15-50%) imply the correlation with nannofossil biozone MNN16 (Rio et al. 1990). Moreover, the nearly absence of *D. pentaradiatus* supports the recognition of paracme interval of this species. Therefore the studied interval from Voutes section is assigned in biozone MNN16, in particular above the highest occurrence of *R. pseudoumbilicus* and *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 uppermost Zanclean.

RHODES ISLAND

3.1.2 *Ypsenis section*

A thirty-meter sequence of marine marls and sands outcrops on the top of a hill, a few kilometres east of Ypsenis Monastery (Figures 2.4, 3.5 and 3.6). Samples *YPS3*, 4 and 5 were taken from the lower marl beds. On the eastern foothills, a sandier facies may be observed, where samples *YPS11quat*, *YPS11*, *YPS12ter*, *YPS12*, *YPS9ter* and *YPS7* were taken. Sample *YPS9ter* exhibited the best macrofossil preservation including many *Dentalium* and rhodoliths.

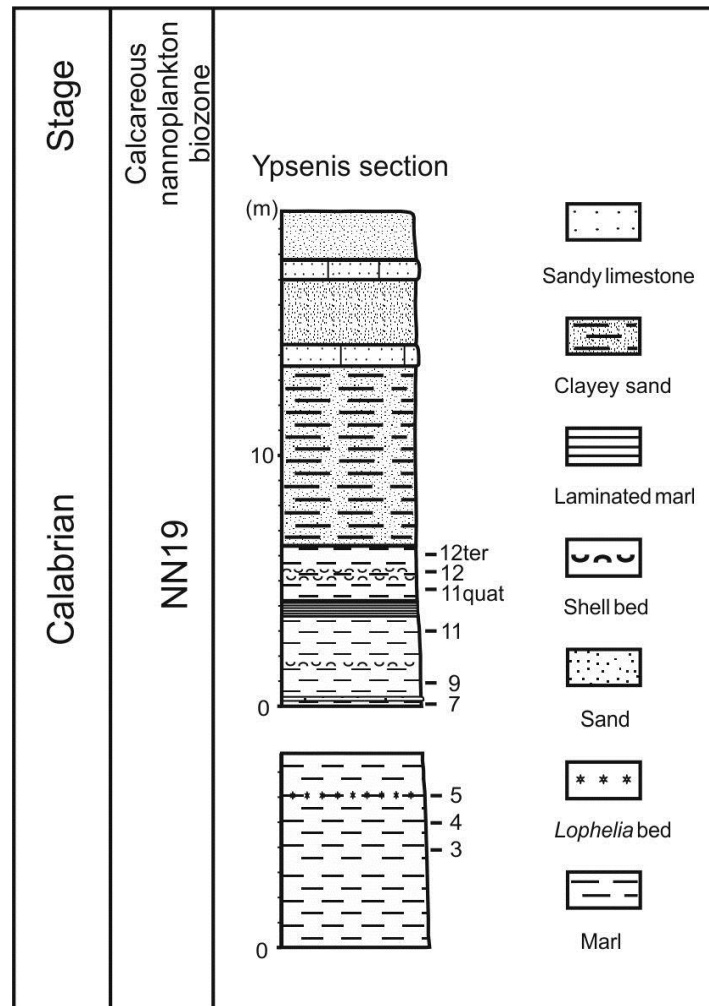


Figure 3.5 Ypsenis stratigraphic log and sampling (Moissette pers.comm.). The biostratigraphy is provided by Dr. G.-E. Lopez-Otalvaro, following the biozonation scheme of Martini (1971).



Figure 3.6 Ypsenis outcrop section: a. Ypsenis hill, b. the lower part of the Ypsenis section, corresponding to the upper part of the Lindos bay marls, c. the upper part of the section, observed in the western side of the hill.

The samples taken from the lower portion of the section were analyzed for foraminifer biostratigraphy by Ass. Prof. Dr. F. Quillevère, at the University of Lyon 1. Notably, the benthic foraminifer *Hyalinea balthica* was present in all the samples, and both *Globigerinoides extremus* and *Gs. obliquus* are both absent, indicating an age younger than 1.3 Ma for the entire section, because *H. balthica* is common in the Mediterranean since 1.4–1.5 Ma (Lourens et al. 1998). Furthermore, sinistral specimens of *Neogloboquadrina* sp. were found up to sample 4, whereas *Stilostomella* sp. was present in sample 3. *Stilostomella* sp. becomes extinct globally between 700 and 580 ka (Kawagata et al. 2005), and specifically in the Atlantic at 650 ka (Weinholz and Lutze 1989). Therefore, the lower part of the section may be considered older than 650 ka.

The Ypsenis section sediments were analyzed for calcareous nannofossil biostratigraphy by Dr. Gatsby Emperatriz Lopez Ojalvaro at the Laboratory UMR 5276 (University Lyon 1) and the Oceanic Geosciences Group (University of Salamanca). A total of seven samples were studied. The biohorizons utilized are considered to be easily identifiable and reliable in the regional context (Raffi et al. 2006). The thin slides were prepared according to the rippled standard smear technique, and examined under the light microscope. The results were correlated to the calcareous nannofossil biostratigraphic zonation (NN) of Martini (1971), and the absolute ages for the biohorizons were assigned based on the astrobiochronology of Raffi et al. (2006) for the eastern Mediterranean.

Overall, the calcareous nannofossil assemblages at Ypsenis section are characterized by their high abundance and good preservation. Biostratigraphic datums could not be identified, but the consistent occurrence of *Reticulofenestra asanoi* and medium-sized *Gephyrocapsa* (*G. omega* and *G. oceanica*) in the lower part of the section, up to YPS9, suggest an age between 985 – 901 ka for this part, within the NN19 Zone. The First Common Appearance Datum (FCAD) of *G. caribbeanica* (560 ka) was not identified. Thus, the absence of FCAD of this species strengthens the assumption that the age of YPS11, YPS11_{quart} and YPS12_{ter} is older than 560 ka. Nevertheless, the consistent occurrence of reworked upper Pleistocene biomarkers, in particular *Calcidiscus macintyreii*, *Gephyrocapsa* large >5.5 µm and *Helicosphaera sellii* are reported, but always in low percentages (>1.6%).

3.1.3 Faliraki section

The sediments outcropping along the coastal road of Faliraki area may be best observed in eight sequential geological sections, named Faliraki 1-8 (Fig. 2.4). The Faliraki composite section reveals the progressive transformation of the area, from an enclosed coastal brackish basin to a pure marine environment. Thereafter, the sequential transgression and regression of the sea renders the area subject to repeated bathymetric variations, within the coastal environment (Figure 3.7, 3.9).

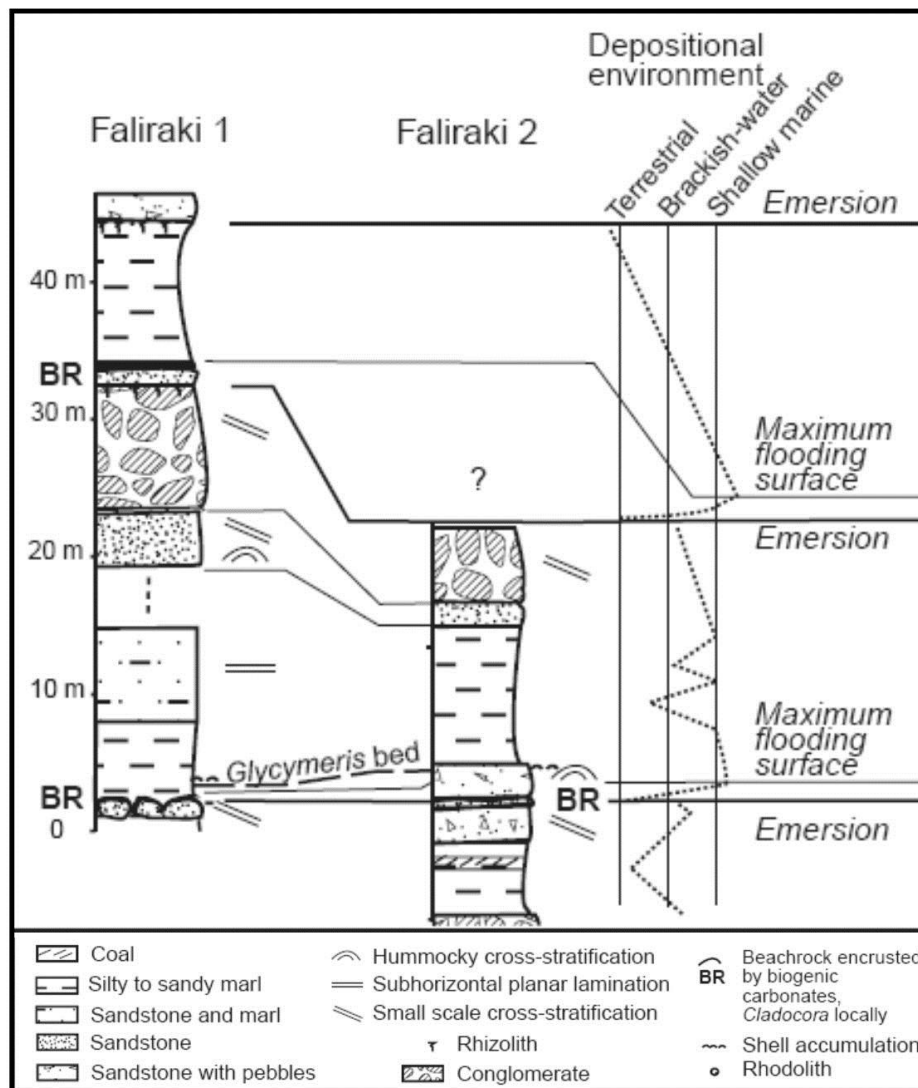


Figure 3.7 Depositional environments and simplified sequence stratigraphic subdivision of the Faliraki 1 and 2 sections (Moissette et al. 2012).

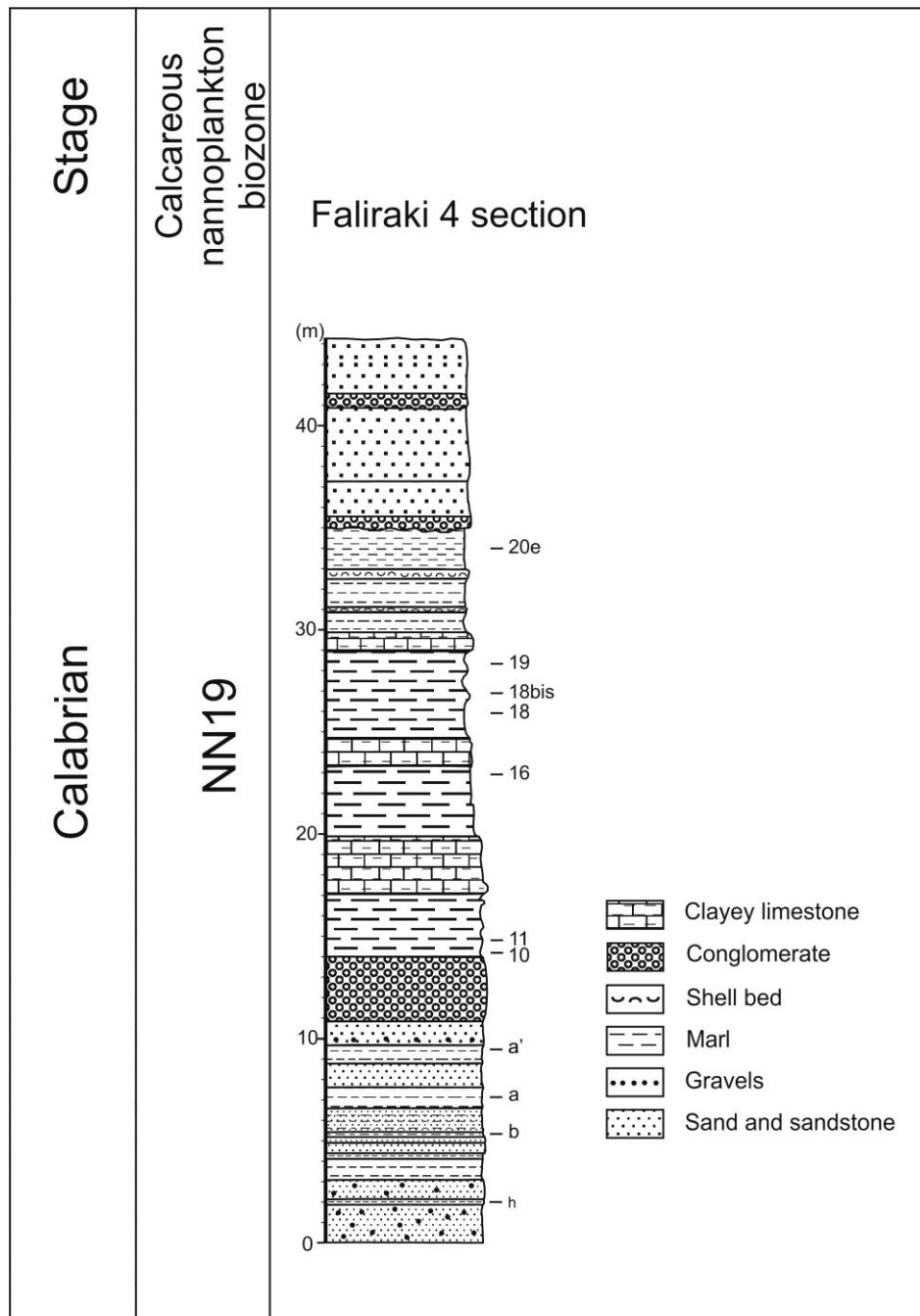


Figure 3.8 Faliraki 4 stratigraphic log (Moissette pers. commun.) and sampling. The biostratigraphy is provided by Dr. G.-E. Lopez-Otalvaro, following the biozonation scheme of Martini (1971).

This intense paleogeographic evolution is recorded in the 180-meter-thick deposition of the typical Kritika Formation (Figure 3.8) dated in the Gelasian stage (Muttý et al. 1970; Meulenkamp et al. 1972; Broekman 1973; Hanken et al. 1996; Hajjaji et al. 1998; Rasmussen et al. 2005; Cornée et al. 2006; Moissette et al. 2007; Moissette et al. 2012).

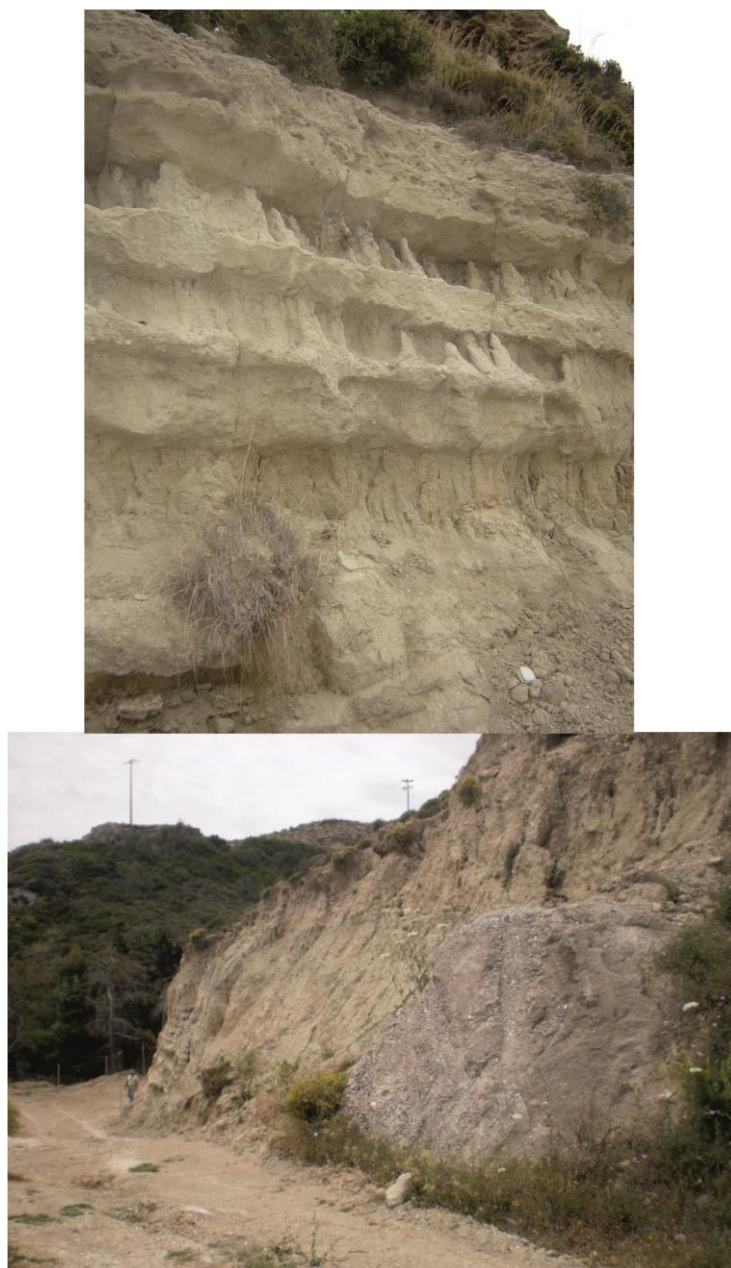


Figure 3.9 Faliraki 4 outcrop. Lower part including the brackish deposits of the Kritika Formation (lower photo), and the upper part presenting the Lindos Bay sediments (upper photo).

In particular, the base comprises siliciclastic sediments, mainly conglomerates, sands and sandstones, siltstones, clays, and a few lignite beds, which were probably deposited in a muddy, deltaic setting of wide extent (Figure 3.9). The Kritika Formation at Faliraki area is also characterized by the presence of several sandstones to conglomerates, forming concrete beds covered with dense biogenic calcareous crusts (Cornée et al. 2006; Moissette et al. 2007). Moissette et al. (2012) interpreted these hard beds as ancient beachrocks, with a rich invertebrate and vertebrate fauna,

and proposed a model for their deposition, as a result of relative sea-level variations affecting the NE Rhodes Island (Figure 3.7).

In further detail, the lithostratigraphic examination of the section logs reveals that each siliciclastic sequence comprises, from bottom to top: 1) carbonate crusts (0.05-1 m thick) rich in marine fossils, 2) sandstones (0.1-3 m thick) with hummocky cross-stratification and ripple-marks, 3) silty to sandy clays and marls (1-15 m thick) with marine to brackish or even lacustrine fossils and a few thin coal interbeds, 4) marine sandstones (0.5-3 m thick) with cross-stratification and low-angle planar bedding, and 5) sandy conglomerates (0.3-4 m thick) with small-scale cross-stratification (Moissette et al. 2012)

Section Faliraki 4 was sampled for the purposes of the current study (Fig. 3.8, 3.9). The base of the Faliraki 4 section comprises some 20-25 meters of Kritika Formation sediments, initially brackish, then conglomerates ending with a transgression. An atypical Kolymbia Formation sequence follows (Moissette et al. 2012), being mostly calcareous, indicative of a deeper shelf edge depositional environment. These limestones are followed by the Lindos Bay marls. The outcrop ends with Archangellos Formation sediments; a sequence of prograding beach deposits. High energy period result in sedimentary channels, and are accompanied by the low energy, stable beach phase deposits, with rhythmic sedimentary structures. The outcrop was sampled continuously, from the base to the top. Samples *Fal4/h*, *Fal4/b*, *Fal4/a*, *Fal4/a'* were taken from the Kritika Formation. Immediately below *Fal4/b*, there is a red oxidized layer. Samples *Fal4/10* and *Fal4/11* were taken from Kolymbia sediments. *Fal4/16*, *Fal4/18*, *Fal4/18bis*, *Fal4/19* and *Fal4/20e* were sampled from the Lindos Bay Formation.

Calcareous nannoplankton biostratigraphy at Faliraki 4 section, by Dr. G.-E. Lopez-Otalvaro, reveals three lower Pleistocene bioevents; the FO large *Gephyrocapsa*, below the level of sample *Fal4/16* (1.608-1.62 Ma), the LO large *Gephyrocapsa*, above the level of sample *Fal4/19* (1.617 Ma), and the LO *Helicosphaera sellii*, just below sample *Fal4/20e* (1.256 Ma) (Raffi et al. 2006). These observations lead to the conclusion that the Faliraki 4 section comprises Calabrian age sediments deposited between 1.7 – 1.2 Ma.

3.1.4 Vagia section

The Vagia section was initially extensively studied by Løvlie et al. (1989), Frydas (1994), Moissette and Spjeldnaes (1995), Hanken et al. (1996), Kovacs and Spjeldnaes (1999) and Streinthsordottir et al. (2006). Pleistocene sediments lie on top of the Jurassic substratum, forming paleo-tsunami deposits, nicely observed at the southern part of the bay (Fig. 2.4). Siliceous sponges as well as brachiopods are found to cut through the Mesozoic substratum.

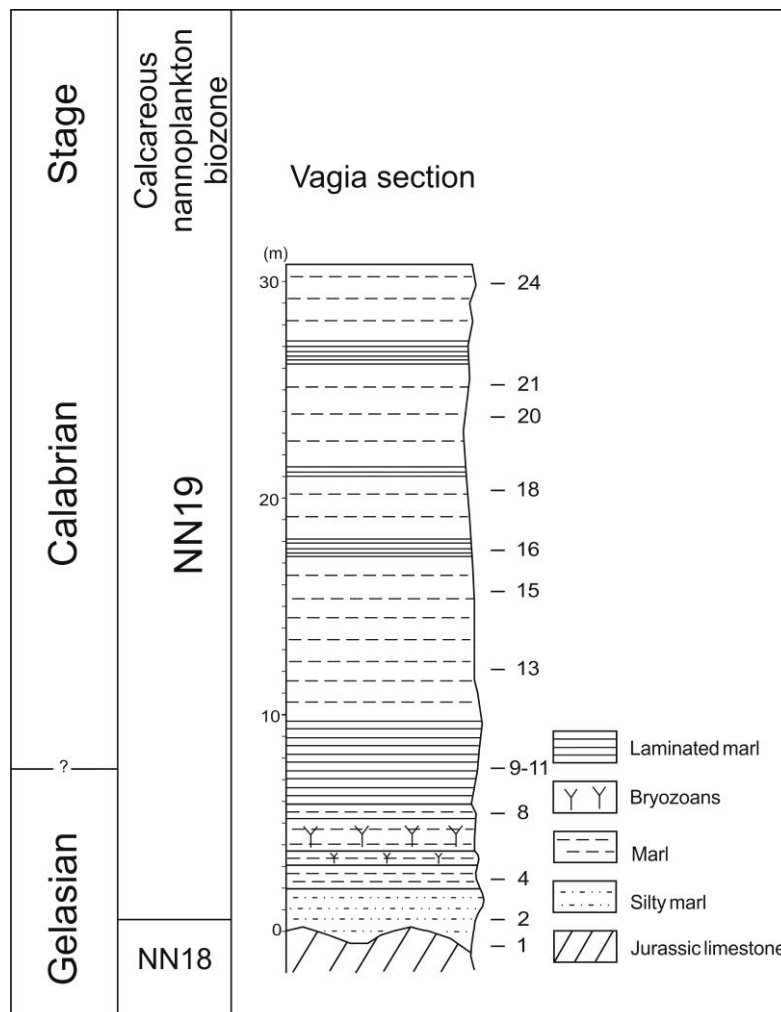


Figure 3.10 Vagia stratigraphic log (Moissette and Spjeldnaes 1995) and sampling. Biostratigraphy is provided by Dr.G.-E.Lopez-Otalvaro, after the biozonation scheme of Martini (1971).

The base of the Cenozoic sequence consists of 6 meters of the Kolymia Formation, where five regression – transgression cycles may be observed, followed by 20 meters of the Lindos Bay marls, capped by the Archangelos calcarenite (Figure 3.10).

Løvlie et al. (1989) placed the Gelasian – Calabrian boundary at 5 meters from the base of the Lindos Bay Formation in this section, based on the magnetic polarity in conjunction with the first appearance datum of *Hyalinea balthica*, just over a black horizon, which they identified as tuff. However, Cornee et al. (2006) were not able to find this horizon, but instead identified, in its place, a thin red oxidation layer. Neither these researchers, nor Frydas (1994) earlier, were able to find *H. balthica* in the same sediments. On the contrary, they report high abundances of *Globorotalia inflata* and *Bulimina marginata*, and mostly dextral specimens *Neogloboquadrina pachyderma*. Magnetic polarity is reverse for the most part of the section, and 2-3 meters of normal polarity are recorded immediately above the oxidized layer, which may correspond to Olduvai C2n subchron (1.942-1.785 Ma), in the absence of *H. balthica* (Duermeijer et al. 2000; Cornee et al. 2006).

Calcareous nannoplankton biostratigraphy at Vagia section, by Dr. G.-E. Lopez-Otalvaro, reveals the following bioevents: the HO of *Discoaster broweri* at sample Vag2 (1.950 Ma), the HO *Calcidiscus macintyreii* above sample Vag24 (1.664 Ma), and the LO large *Gephyrocapsa* (1.617 Ma) (Raffi et al. 2006). These recent results are in agreement with the previous hypothesis about the reverse magnetic polarity interval, and the overall stratigraphic placement of the section, made by Cornee et al. (2006), and lead to the conclusion that the Vagia section comprises the time interval between approximately 1.6–2 Ma.

The section was sampled continuously from the base of the Kolymbia through to the upper part of the Lindos Bay Formation sediments (Fig. 3.10). Samples *Vag1*, *Vag2* and *Vag4* were taken from the Kolymbia limestones. The horizon where *Vag2* was taken showed signs of bioturbation, whereas that of *Vag4* contained large brachiopods, many bryozoans, *Pecten*, *Ostrea* and other molluscs. *Vag8*, *Vag9-11*, *Vag13*, *Vag15*, *Vag16*, *Vag18*, *Vag20*, *Vag21* and *Vag24* were sampled from the Lindos Bay Formation. In particular, *Vag 8* was taken from massive Lindos marls, followed by a red oxidized layer (Cornee et al. 2006). Immediately afterwards, *Vag9-11* was taken from a laminated marl bed. *Vag13* was sampled from massive marls, with *Dentalium*, *Chlamys* and small deep-water bivalves. *Vag15* was taken from massive marls showing ichnofossils, *Vag16* from laminated marls, *Vag18* from

massive marls with nice sedimentary structures and slumps, *Vag20* from massive marls with bivalves, *Vag21* from laminated marls and *Vag24* from massive marls.

3.1.5 *Kalitheia section*

The Kalitheia section is located 8 km south of the city of Rhodes, on the coastal area of the homonymous thermae (Fig. 2.4). The alpine substratum here consists of well-bedded, slightly metamorphosed, grey dolomitic cherty limestones (Elaphokampos Formation; Mutti et al. 1970), of Carnian to Early Liassic age (Nielsen et al. 2006).

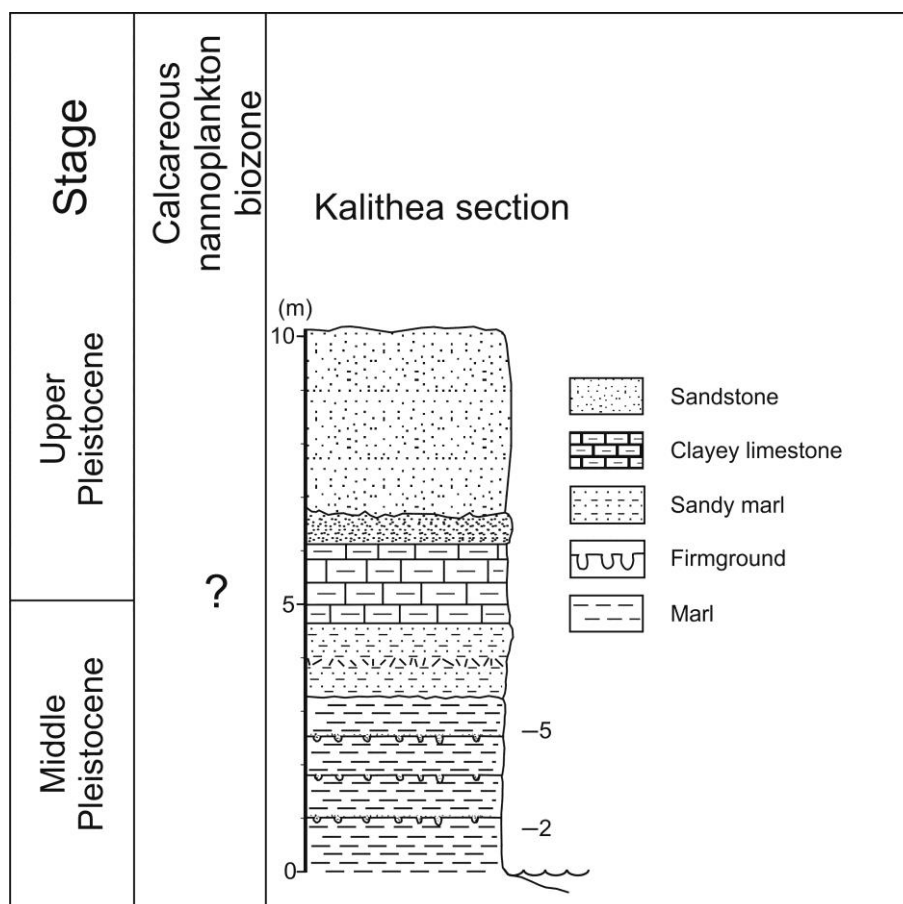


Figure 3.11 Kalitheia stratigraphic log (Moissette pers. commun.) and sampling.

Løvlie et al. (1989) and Rasmussen et al. (2005) showed that the area did not undergo transgression before the early Pleistocene. As a result, subaerial exposure caused extensive karstification, creating the nice structures observed on the Kalitheia coast, upon which were the Pleistocene sediments were deposited. The post-alpine sequence in this small section encompasses only the last 2 meters of the Lindos Bay

Formation, ending in a conglomerate bed (Figure 3.11), followed by the Archangelos Formation, where Nielsen et al. (2006) recognized five sedimentary facies: (A) the lower shoreface storm beds of calcareous tempestites and bryozoan packstones, (B) the lower shoreface, migrating bars, (C) the storm surge channels on the lower shoreface, (D) the upper shoreface storm beds of cross-bedded grainstone and rudstone, and (E) the giant-scale foresets formed during the carbonate platform progradation, interrupted by large-scale scours. Above the Archangelos Formation, lies the Windmill Bay Boulder Bed and Kleopoulou Calcirudite (Hansen 1999).

Nielsen et al. (2006) consider a Pleistocene age for the upper part of the Lindos Bay Formation, which is exposed in this section, based on the presence of pteropods *Cavolinia tridentata* and *Clio pyramidata*. In addition, findings of bivalve *Arctica islandica*, in life position, in the uppermost facies (E) of Archangelos Formation denotes a Middle Pleistocene age also for this part of the section. Furthermore, two U/Th datings have been provided for this outcrop (Nielsen et al. 2006). The first one dates facies (D) of Archangelos Formation to 108,600 BP (+ 4,000, – 3,800). The second dating referred the Windmill Bay Boulder Bed, about 10 meters south of the round thermae building, to 81,660 BP (+ 4,510, – 4,340). Considering all this data, it may safely be considered that the upper part of the Lindos Bay Formation, exposed in this section, is placed within the Middle Pleistocene (Ionian) stage, while the Archangelos Formation extends in the Upper Pleistocene (Tarantian) stage.

Only the lower part of this section was sampled (Fig. 3.11), as it would not be possible to abstract any fish otoliths from the concrete Archangelos, Windmill or Kleopoulou Formations. Sample *Kal2* was taken from the lower part of the Lindos bay marl in this section, and *Kal5* from the upper part, just below the conglomerate. In *Kal2* the presence of *Corbula gibba*, *Turritella ammonis*, and *Nucula* sp. was also noted (E. Koskeridou pers. commun.).

3.2 Otolith description and Systematics

The fish otoliths were identified based on the morphologic characteristics described by Nolf (1985). Lapilli in particular were described and identified based on the systematic paper of Assis (2005). The species' taxonomic position followed the scheme of Nelson (2006). Many recent fish species were already represented in the

Mediterranean Pliocene, and in several cases, specific identification could not be unequivocally decided; thus the abbreviation aff. (*affinis*) was inserted between the name of the genus and the name of the group species. The abbreviation cf. (*conformis*) was used whenever the condition of preservation of the otolith did not allow 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 to decide.

The examined material was identified from published descriptions and photographs, and through direct comparison with the material from the lower-middle Pleistocene sediments of Zakynthos and Kephallonia Islands published in Agiadi et al. (2010), as well as with the extensive collection of fossil and modern material at the University of Bari, with the guidance of Ass. Prof. Dr. Angela Girone.

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.

3.3 Paleobiogeographic analysis

The paleobiogeographic distributions of the identified teleost species were compared to the equivalent assemblages from the western Mediterranean realm, in order to fill the gaps in the fossil record, as well as to identify any ichthyofauna differences and similarities, which may be attributed to palaeoenvironmental factors. Their geographic and stratigraphic distribution is presented in a stage-level resolution, and separately for the eastern and western sub-basin, mentioning also the present-day distribution in the Atlantic and Indo-Pacific based on the Fishbase database (Froese and Pauly 2013).

3.4 Assemblage analysis methodology

The qualitative and quantitative analyses of the fish taxa identified in the studied sediments were based on their present-day ecology or the currently available data on their closest living relative (Table 2.1). The relative abundances were calculated following the criteria proposed for bivalves by Di Geronimo and Robba

(1976). Accordingly, the abundance of each taxon in the assemblage is the sum of the greatest number of the taxon's otoliths in the sample (either the number of left or the number of right otoliths) plus half of the smallest number. The diagenetically modified specimens, indicating transportation or reworking were completely excluded from this analysis.

3.4.1 Paleobathymetry

A series of paleobathymetric estimates was established for the studied sediments, based on the modern depth ranges of all the taxa present in each sample, according to the methodology of Nolf and Brzobohaty (1994) readjusted by Agiadi et al. (2010). The number of possible presences for each 50-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. An initial overview of the bathymetric distributions of the studied taxa indicated that the depth estimates would definitely not exceed 1000 m. Consequently, the analysis was conducted for 50-meter intervals, with the upper limit of 1000 m.

In order to apply this method, it must first be established that the systematic position of the fossil taxa has a close affinity to their modern analogues. To this end, the presence/absence data used here includes only those taxa for which present-day bathymetric information is available. This means that higher order (family/order level) identified otolith specimens were completely excluded from analysis. For the genus level identifications, the modern analogue was reconstructed from a compilation of the modern Mediterranean and/or Atlantic species' ecological data.

The modern analogue for the extinct species *Scopelopsis pliocenicus* is *Scopelopsis multipunctatus*, as its single genus level living relative. On the contrary, *Rhynchoconger* currently includes seven species, occupying either the Indo-Pacific or the western Atlantic coasts at various depths. Presently, the Mediterranean is inhabited by three Congrid species, *Ariosoma balearicum*, *Conger conger* and *Gnathophis mystax*, all of which exhibit great depth distributions, from a few tens to more than 700 meters (Whitehead et al. 1986; Mytilineou et al. 2005). Consequently,

this generalized assessment was accepted as a possible depth distribution of *R. pantanelli*.

Gonostoma includes three extant species, *G. elongatum* and *G. atlanticum* which are extra-Mediterranean and *G. denudatum* (Quero et al. 1990). Likewise, currently there are ten valid *Lampadena* species distributed worldwide, none of which may be found in the Mediterranean Sea. *Lampadena yaquinae* and *Lampadena urophaos urophaos* occupy the Pacific Ocean only. The remaining eight species may be found in various depths from 0-2400 meters (Hulley et al. 1990). Presently, there exist 123 valid *Coelorinchus* species; one only in the Mediterranean Sea, *Coelorinchus coelorinchus*, which is therefore used as the modern analogue (Reiner 1996). There are 14 valid *Gaidropsarus* species today; four in the Mediterranean, *G. biscayensis*, *G. granti*, *G. mediterraneus*, *G. vulgaris* (Svedovidov 1986). There are eight valid species of the genus *Scorpaena* currently inhabiting Mediterranean waters, *S. azorica*, *S. elongata*, *S. lopei*, *S. maderensis*, *S. notata*, *S. porcus*, *S. scrofa* and *S. stefanica* (Quero et al. 1990). Of the fifteen valid *Trachurus* species around the world today, only three inhabit the Mediterranean Sea, *T. mediterraneus*, *T. picturatus* and *T. trachurus* (Whitehead et al. 1986). There are four valid species of *Dentex* in the modern Mediterranean, *D. dentex*, *D. gibbosus*, *D. macrophthalmus* and *D. maroccanus* (Quero et al. 1990). The genus *Deltentosteus* has only two valid species today, both inhabiting the Mediterranean Sea, *D. quadrimaculatus* and *D. collonianus* (Whitehead et al. 1986). The genus *Lesueurigobus* has five modern valid species, all in the eastern Atlantic, three of them also in the Mediterranean, *L. sanzi*, *L. suerii*, *L. friesii*, *L. koumansii*, *L. heterofasciatus* (Mytilineou et al. 2005). The genus *Pomatoschistus* has ten valid species today in the Mediterranean Sea, *P. bathii*, *P. canestrinii*, *P. knerii*, *P. marmoratus*, *P. microps*, *P. minutus*, *P. norvegicus*, *P. pictus*, *P. quagga* and *P. tortonesei* (Whitehead et al. 1986).

After the above assignments, the following taxa were found to exhibit too great a bathymetric range to be useful for the present analysis, and were thus excluded: *Conger conger*, *Gonostoma* sp., *Maurolicus muelleri*, *Benthoosema glaciale*, *Lobianchia dofleini*, *Myctophum punctatum*, *Scopelopsis pliocenicus*, *Phycis blennoides*, *Grammonus ater*, *Atherina boyeri* and *Trachurus* sp. Finally, a depth range of 0-200 meters was applied for the otoliths of *Lampanyctus crocodilus*

identified in samples *YPS3*, *YPS4*, *YPS5*, *Fal4/18*, *Fal4/19* and *Fal4/20e*, which clearly belonged to juvenile individuals, because this species changes its lifestyle from mesopelagic to benthopelagic after maturation (Stefanescu and Cartes 1992).

3.4.2 *Paleoecology*

The assemblages were analyzed based on the modern depth, environmental preferences, and geographic distribution of the species that comprise them (Table 3.1). According to the depth they occupy in the water column, and their life mode, modern marine fish are separated into five main categories. Epipelagic fish live entirely in the euphotic zone (higher than 200 meters depth). Mesopelagic fish live entirely or in part between depths of 200 and 1000 meters in the water column. Bathypelagic fish occupy the lower part of the water column in the aphotic zone. Benthopelagic fish stay close to the sea bottom. Finally, benthic fish live either on or directly above the bottom of the sea. The present-day geographic distributions of the identified extant taxa range from tropical to subpolar regions.

In order to study the fishes' response to different palaeoceanographic conditions along the depth of the water column in previous works (Agiadi et al. 2011), the identified taxa were placed in one or more of the following three categories based on their depth distribution and life mode. The surface group (S) comprises taxa occupying the upper 200 meters of the water column, the intermediate water group (I) incorporates taxa living between 200 and 500 meters, and the deepwater group (D) contains taxa occupying waters below 500 meters. The benthopelagic and benthic taxa contribute only to the deepest part of the water column depending on the palaeobathymetry of the examined sediment sample (Agiadi et al. 2010; Girone 2000) since they live near or on the sea bottom. When the palaeobathymetric estimate had indicated depths of less than 500 meters, the deepwater layer's (D) conditions could not be evaluated. Accordingly shallow water assemblages, with paleodepth estimations up to 200 meters were not considered for the intermediate water group. In this case, all taxa were evaluated with respect to the surface water conditions. In all those cases, it was assumed that all otolith specimens of taxa living in the deeper zone had either been secondarily transported into the taphocoenosis, or had a different palaeobathymetric distribution at that time, than they do today.

The initial inspection of the paleodepths in the areas examined here showed that the studied sediments were deposited in shallow water marine environments, in almost all cases not exceeding depths of 200 meters. As a result, the above methodology could not be applied as such. Instead the relative abundance of the tropical, subtropical, temperate and subpolar fish taxa was calculated for each sample in the total assemblage, as well as separately again for the pelagic component of the assemblage and the benthic-benthopelagic component. These results were then evaluated to establish the surface water and the sea bottom conditions prevailing in the study areas.

In a few cases, when the estimated paleodepth exceeded 200 meters, the paleoecologic methodology was adjusted so as to include the taxa inhabiting depths greater than 200 meters in the benthic-benthopelagic component, which was taken to indicate the intermediate water conditions. In particular, in Voutes section, samples 1, 2 and 4, which were estimated to deposit in depths greater than 200 m, contained specimens of the benthic fish *Epigonus denticulatus* (usually found between 300-600 m; Whitehead et al. 1986) and *Laemonema* sp. (the modern equivalent *L. robustum* and *L. yarrelli* are found between 220-1200 m; Hureau and Monod 1979; Quero et al. 1990). The benthic-benthopelagic component of the assemblages in these samples is taken to indicate intermediate water conditions.

Certain remarks on the present-day ecology of the examined taxa are considered especially important. Indeed, the small planktivore *Bregmaceros* has been reported in open waters between 0-1260 meters depth. However, it largely maintains an epipelagic way of life and is thus most abundant in the upper 200 meters (Castellanos-Galindo et al. 2006). Also, according to Whitehead et al. (1984), the distribution of *Hygophum benoiti* may be related to the oceanographic boundaries of the North Atlantic gyre system. As for the abundant species *Maurolicus muelleri*, it is known to display seasonal vertical migrations, in the Atlantic Ocean, occupying deeper parts of the water column during the summer. However, this does not hold true for the modern Mediterranean Sea, where adult specimens maintain a depth range between 200-400 meters during the daytime and feed in the surface waters at night (Whitehead et al. 1984). In addition, the present-day geographic distribution of the tropical - subtropical *Electrona risso* is discontinuous across the cyclonic gyre region, between the South

Equatorial countercurrent and the western branch of the Benguela Current (5°S-13°S), and is limited by the 10° and 15° C isotherms at 200 meters, and by productivity of 50 grams of carbon per square meter per year (Whitehead et al. 1984). Finally, despite the fact that the otolith of *Alepocephalus* cannot be identified to the specific level, all known modern *Alepocephalus* species exhibit distributions within the boundaries of the tropical to temperate zones, and dwell in the intermediate and deeper waters. Indeed, *A. rostratus*, the only *Alepocephalus* species occupying the Mediterranean today, has a bathymetric distribution between 300-2250 meters (Carrasson & Matallanas 1998), which is also inclusive of the distributions of the other *Alepocephalus* species.

In addition to the above analysis, three values were inspected, in order to draw conclusions regarding the taphonomic condition and the local biodiversity. The total number of otoliths found in each 25kg-sediment sample is a result of the size of the fish population studied and the taphonomic processes. Furthermore, the number of identified taxa in each sediment sample is controlled by the population size, the species richness, and the degree of preservation of the otoliths in general and of each taxon in particular. Finally, the ratio of the number of identified taxa against the total number of otoliths in each sample is here used as an indicator of the fish population heterogeneity.

Chapter 3. Material and Methods

Family	Genus/Species	Depth (m)	Climate	Lifestyle	Environment	Trophic	References
Congridae	<i>Conger conger</i>	?-1171	Te	Benthic	Marine; rocky and sandy bottoms	fish, crustaceans, cephalopods	Mytilineou et al 2005; Gutheil et al 1992
	<i>Gnathopli smystax</i>	80-800	ST	Demersal	Marine; mud/sand bottoms; continental slope	benthic invertebrates, small fish	Whitehead et al 1986
	<i>Pseudophichthys splendens</i>	37-1647	ST-Tr	Bathodemersal	Marine; muddy bottoms	-	Quero et al 1990
Engraulidae	<i>Engraulis encrasicolus</i>	0-400	ST	Pelagic-neritic; oceanodromous	Marine, brackish; coastal; salinity of 5-41 ppt	planktonic organisms	Frimodt 1995; Schneider 1990
Ophidiidae	<i>Ophidion barbatum</i>	?-150	ST	Demersal	Marine	-	Nielsen et al 1999
Argentiniidae	<i>Argentina sphyraena</i>	50-700	SP-Te	Bathodemersal	Marine	polychaetes, mollusks, crustaceans, pelagic invertebrates, fishes	Mytilineou et al 2005
Gonostomatidae	<i>Gonostoma</i> spp.	-	Te-ST	Meso-Bathypelagic	Marine	-	Quero et al 1990
Sternoptychidae	<i>Polyipnus polli</i>	250-600	Tr	Benthopelagic; non-migrating	Marine	-	Harold 1994
	<i>Mauroliscus muelleri</i>	0-1524	SP-Te	Bathypelagic; demersal	Marine	Plankton: copepods, euphausiids, and hyperiid amphipods	Wheeler 1992
Clupeidae	<i>Sardinella maderensis</i>	0-80	ST	Oceanodromous	Marine; brackish; prefers 24°C, migrates correlate with seasonal upwelling	Planktonic invertebrates, fish larvae and phytoplankton	Reiner 1996; Riede 2004
Phosichthyidae	<i>Vinciguerria attenuata</i>	100-2000	ST	Bathypelagic	Marine	Small crustaceans	Yang et al 1996
	<i>Vinciguerria poweriae</i>	50-1000	ST	Bathypelagic	Marine	small crustaceans	Quero et al 1990
Alepocephalidae	<i>Alepocephalus</i> spp.	300-2250	Te-Tr	Bathodemersal	Marine; soft bottoms	pelagic crustaceans like euphausiids, decapods, mysids	Fischer et al 1981
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>	50-1000	Te-Tr	Bathypelagic; pelagic juveniles	Marine; brackish; continental shelf, upper slope; mud/clay bottom	bottom-living invertebrates, pelagic crustaceans: euphausiids, decapods, mysids	Mytilineou et al 2005
Scopelarchidae	<i>Scopelarchus analis</i>	0-820	ST-Tr	Bathypelagic; oceanodromous	Marine	midwater fishes	Quero et al 1990
Myctophidae	<i>Benthoosema glaciale</i>	0 - 1407	SP-Te	pelagic-oceanic; non-migratory	Marine	calanoid copepods, euphausiids and copepodites	Coad and Reist 2004
Myctophidae	<i>Benthoosema suborbitale</i>	50-2500	ST-Tr	bathypelagic; oceanodromous	marine	zooplankton	Riede 2004
	<i>Ceratoscopelus maderensis</i>	51-1082	Te	bathypelagic; oceanodromous	marine	Copepods, planktonic crustaceans	Riede 2004
	<i>Diaphus adenomus</i>	180-600	ST-Tr	Bathypelagic	Marine	-	Masuda et al 1984
	<i>Diaphus holti</i>	40-777	Te	bathypelagic; oceanodromous	marine	-	Riede 2004; Mytilineou et al 2005
	<i>Diaphus rafinesquii</i>	40-1200	Te	bathypelagic; oceanodromous	marine	-	Riede 2004
	<i>Diaphus splendidus</i>	0-8000	ST-Tr	Bathypelagic; oceanodromous	Marine	-	Quero et al 1990
	<i>Diaphus taaningi</i>	40-475	Tr	Meso-bathypelagic; Pseudoceanic	Marine; continental shelves and slopes	Mainly animals	Quero et al 1990
	<i>Electrona risso</i>	90-820	ST-Tr	bathypelagic; oceanodromous	Marine; 10°-15°C (200m); productivity>50g C/m ² /yr	Mainly animals	Riede 2004
	<i>Hygophum benoitii</i>	51-700	Te	bathypelagic; oceanodromous	Marine	-	Quero et al 1990
<i>Hygophum hygomii</i>	0-800	ST-Tr	Bathypelagic; oceanodromous	Marine	-	Quero et al 1990	
Myctophidae	<i>Lampantctus crocodilus</i>	0-1192; juv.0-200	Te-ST	Bathypelagic; oceanodromous	Marine	Zooplankton	Mytilineou et al 2005; Coad and Reist 2004
	<i>Lampadena</i> sp.	0-2400	Tr-Te	Bathypelagic; oceanodromous	Marine	-	Hulley et al 1990
	<i>Lobianchia dofleini</i>	0-4000	ST	Bathypelagic; oceanodromous	Marine	Copepods and ostracods	Whitehead et al 1984
	<i>Myctophum punctatum</i>	0-1000	Te-ST	bathypelagic; oceanodromous	Marine; possibly upwelling	copepods, euphausiids, fish	Muus and Nielsen 1999; Riede 2004
	<i>Notoscopelus elongatus</i>	45-1000	ST	pelagic-oceanic; oceanodromous	Marine	-	Riede 2004
	<i>Notoscopelus resplendens</i>	0-2121	ST-Tr	Bathypelagic; oceanodromous	Marine	-	Quero et al 1990
	<i>Protomyctophum arcticum</i>	90-1600	SP-Te	bathypelagic; oceanodromous	Marine	Crustaceans	Riede 2004; Coad and Reist 2004
<i>Scopelopsis multipunctatus</i>	3-2000	ST	bathypelagic; oceanodromous	Marine	-	Riede 2004	

Family	Genus/Species	Depth (m)	Climate	Lifestyle	Environment	Trophic	References
Macrouridae	<i>Coelorinchus coelorinchus</i>	90-1250	Te-ST	benthopelagic; non-migratory	Marine	Various benthic organisms	Reiner 1996
Moridae	<i>Laemonema</i> spp. (<i>L. robustum</i> & <i>L. yarrelli</i>)	220-1200	ST-Tr	Bathydemersal	Marine; outer shelf, upper & continental slope	Shrimp	Hureau and Monod 1979; Quero et al 1990
Phycidae	<i>Phycis blenoides</i>	10-1047	Te	benthopelagic; oceanodromous	Marine; sand/mud bottoms; young: coastal on the continental shelf; adults: slope	crustaceans and fishes	Riede 2004; Mytilineou et al 2005
Gadidae	<i>Gadidulus argenteus</i>	100-1000	Te	benthopelagic; non-migratory	Marine; mud/muddy sand/gravel/rock bottoms	small crustaceans, worms	Muus and Nielsen 1999
	<i>Gadidulus thori</i>	100-1000	Te	benthopelagic; oceanodromous	Marine; muddy bottoms	-	Muus and Nielsen 1999
	<i>Micromesistius poutassou</i>	150-3000	Te	bathypelagic; oceanodromous	Marine; continental slope and shelf	small crustaceans, small fish and cephalopods	Riede 2004
Bregmacerotidae	<i>Bregmaceros</i> sp.	-	Tr	pelagic-oceanic; oceanodromous	Marine	zooplankton/phyto plankton, especially crustaceans	Quero et al 1990; Castellanos-Galindo et al 2006
Lotidae	<i>Gaidropsarus</i> spp.	0-600	Te-Tr	Pelagic	Marine	-	Svedovidov 1986
	<i>Grammonus ater</i>	-	ST	Reef-associated	Marine; shallow rocky areas	-	Gothel 1992; Nielsen et al 1999
Carapidae	<i>Echiodon dentatus</i>	120-3250	ST	Demersal	Marine	-	Nielsen et al 1999
	<i>Carapus acus</i>	1-150	ST	Demersal	Marine	Small fish and benthic invertebrates	Nielsen et al 1999
Ophidiidae	<i>Ophidion barbatum</i>	?-150	ST	Demersal	Marine	-	Nielsen et al 1999
Atherinidae	<i>Atherina boyeri</i>	1-?	ST	demersal; amphidromous	Marine; freshwater; brackish	small crustaceans, worms, mollusks and fish larvae	Muus and Nielsen 1999; Riede 2004
Scorpaenidae	<i>Scorpaena</i> spp.	0-700	ST	Demersal	Marine; brackish	-	Quero et al 1990
Carangidae	<i>Trachurus</i> spp.	0-1000	ST	benthopelagic	Marine; brackish	Crustaceans or fishes	Whitehead et al 1986
Apogonidae	<i>Apogon imberbis</i>	10-200	ST	Reef-associated; non-migratory	Marine; mud/rocky bottoms and caves	Small invertebrates and fishes	Whitehead et al 1986
Epigonidae	<i>Epigonus denticulatus</i>	130-830	Te-Tr	Adults benthic; juveniles pelagic	Marine	small fishes and planktonic invertebrates	Quero et al 1990
Acropomatidae	<i>Synagrops spinosus</i>	87-544	Te	Bathypelagic	Marine; continental shelf outer parts, upper slopes	-	Mejia et al 2001
Sparidae	<i>Dentex</i> spp.	0-500	ST	Benthopelagic or demersal	Marine; hard bottoms (rock or rubble)	Crustaceans, fish, molluscs, cephalopods	Quero et al 1990
	<i>Diplodus annularis</i>	0-90	ST	Benthopelagic	Marine; brackish; on <i>Zosteraseagrass</i> or <i>Posidonia</i> beds, sandy / rocky bottom	Carnivorous, feed on worms, crustaceans, mollusks, echinoderms and hydrozoans	Quero et al 1990
Sparidae	<i>Oblada melanura</i>	?-30	ST	benthopelagic; oceanodromous	Marine; rocky bottoms/seagrass beds (<i>Zostera</i> and seaweeds)	small invertebrates	Riede 2004
	<i>Pagrus pagrus</i>	?-300	ST	Benthopelagic; oceanodromous	Marine	Crustaceans, fish, mollusks	Quero et al 1990
	<i>Pagellus bogaraveo</i>	?-700	Te	Benthopelagic	Marine; Inshore waters above various types of bottom; young near coast, adults on continental slope especially over muddy bottoms	crustaceans, mollusks, worms and small fish	Quero et al 1990
	<i>Pagellus erythrinus</i>	?-300	ST	Benthopelagic	Marine; inshore waters, on various bottom (rock, gravel, sand and mud)	benthic invertebrates and small fishes	Quero et al 1990
Centracanthidae	<i>Spicara smaris</i>	15-328	ST	benthopelagic	Marine; <i>Posidonia</i> beds/muddy bottoms	-	Mytilineou et al 2005
Merlucciidae	<i>Merluccius merluccius</i>	30-1075	Te	Demersal	Marine	Fish, squids, crustaceans	Cohen et al 1990
Cepolidae	<i>Cepola macrophthalma</i>	15-400	ST	Demersal	Marine; sand/mud bottom	small crustaceans and chaetognaths	Quero et al 1990
Pomacentridae	<i>Chromis chromis</i>	2-40	ST	Demersal; non-migratory	Marine; midwater above or near rocky reefs or seagrass meadows (<i>Posidonia</i>)	small planktonic or benthic animals	Quero et al 1990; Giakoumi and Kokkoris 2013
Blenniidae	<i>Blennius ocellaris</i>	10-400	ST	Demersal	Marine; hard bottoms	Small invertebrates	Wheeler 1992

Family	Genus/Species	Depth (m)	Climate	Lifestyle	Environment	Trophic	References
Gobiidae	<i>Aphia minuta</i>	0-97	ST	demersal	Marine; brackish; inshore and estuarine waters, over sand, mud and eel-grass	zooplankton, especially copepods, and mysids	Iglesias and Morales-Nin 2001
	<i>Deltentosteus quadrimaculatus</i>	?-333	ST	demersal; non-migratory	Marine; Epibenthic over sand or muddy sand	-	Mytilineou et al 2005
	<i>Deltentosteus</i> spp.	0-333	Te-ST	Demersal	Marine	-	Whitehead et al 1986
	<i>Gobius niger</i>	1-75	Te; 8°C - 24°C	Demersal	Marine; brackish; estuaries, lagoons, inshore waters; sand/mud; in seagrass or on algae	crustaceans, bivalves, gastropods, polychaetes, chironomid larvae, small fish	Moreira et al 1992
	<i>Gobius paganellus</i>	0-15	STI	demersal; amphidromous	Marine; freshwater; brackish; adults: inshore, intertidal waters, under stones, in pools, on sheltered rocky shores with much weed cover	Crustaceans, polychaetes	Mauge 1986
	<i>Lesueurigobius friesii</i>	10-130	ST	Demersal	Marine; Cryptobenthic, burrowing in muddy sand/mud; associated with <i>Nephrops norvegicus</i>	Polychaetes, small crustaceans, mollusks	Quero et al 1990
	<i>Lesueurigobius sanzi</i>	47-117	ST	Benthic	Marine; muddy sand/mud	-	Whitehead et al 1986
	<i>Lesueurigobius suerii</i>	0-337	ST	Demersal	Marine; inshore	-	Mytilineou et al 2005
Gobiidae	<i>Lesueurigobius</i> spp.	10-345	ST-Tr	demersal	marine	-	Mytilineou et al 2005
Gobiidae	<i>Pomatoschistus</i> spp.	1-325	Te-ST	demersal	Marine; brackish; freshwater	-	Whitehead et al 1986
Citharidae	<i>Citharus linguatula</i>	?-300	ST	Benthic	Marine; soft bottoms	small fish and crustaceans	Quero et al 1990
Bothidae	<i>Arnoglossus</i> spp.	-	-	Demersal	Marine	-	Quero et al 1990

Table 3.1 Present day ecological data compiled from Froese and Pauly (2013). Abbreviations: distribution in the climatic zones Tr: tropical, ST: subtropical, Te: temperate, SP: subpolar.

4. Results

4.1 Systematic Paleontology

In the present study, a total of eighty-one (81) teleost fish species were identified, placed under sixty (60) genera and thirty-four (34) families. The most important distinguishing morphological characteristics for each taxon are presented in this chapter, as well as comprehensive comments on the family characters where applicable and any further comments made on the morphology of the specimens studied here, after examination of the modern and fossil comparative material. A list of synonyms is also offered; page, plate and figure numbers are only mentioned for the publications used in the identification.

Phylum Chordata (Haeckel, 1847)

Superclass Gnathostomata (Gegenbauer, 1874)

Class Actinopterygii Klein, 1885

Subclass Neopterygii Regan, 1923

Division Teleostei, Mueller, 1846

Subdivision Elopomorpha Greenwood et al., 1966

Order Anguilliformes Regan, 1909

Family **Congridae** Kaup 1856

General remarks: Congrid otoliths are elongate or sub-square shaped, non-angular, with a concave outer face and an almost flat inner face. The sulcus is undivided, in the shape of a groove, and its general direction may or may not form an angle to the posterior-anterior long distance. This channel does not reach the posterior end of the otolith, but opens either anteriorly or antero-dorsally, directly or through a neck. There are no colliculi inside the sulcus, but its borders are rimmed in some taxa.

Genus *Conger* Bosc, 1817

Conger conger (Linnaeus, 1758)

Plate I (1)

- 1758 *Muraena conger* – LINNAEUS;
- 1758 *Anguilla conger* – (LINNAEUS);
- 1758 *Leptocephalus conger* – (LINNAEUS);
- 1788 *Leptocephalus lineatus* – BONNAPARTE;
- 1789 *Leptocephalus morrisii* – GMELIN;
- 1810 *Muraena nigra* – RISSO;

- 1810 *Conger niger* – (RISSO);
1810 *Leptocephalus spallanzani* – RISSO;
1827 *Conger verus* – RISSO;
1829 *Leptocephalus gussoni* – COCCO;
1832 *Leptocephalus candidissimus* – COSTA;
1832 *Ophidium pellucidum* – COUCH;
1832 *Leptocephalus pellucidus* – (COUCH);
1832 *Conger vulgaris* – YARRELL;
1839 *Anguilla obtuse* – SWAINSON;
1839 *Ophisoma obtuse* – (SWAINSON);
1840 *Conger rubescens* – RANZANI;
1844 *Conger communis* – COSTA;
1853 *Leptocephalus vitreus* – KÖLLIKER;
1856 *Leptocephalus stenops* – KAUP;
1883 *Leptocephalus inaequalis* – FACCIOLÀ;
1998 *Conger conger* – NOLF et al., pl.1, fig.7;
2009 *Conger conger* – NOLF et al., pl.2, familie 86;
2013 *Conger conger* – NOLF, pl.20.

Remarks: The otoliths of this species are characterized by the elongate shape, and the clear, wide and deep sulcus, which forms a circular plane in the anteroventral area.

Genus *Gnathophis* Kaup, 1859

Gnathophis mystax (Delaroche, 1809)

Plate I (2)

- 1809 *Muraena mystax* – DELAROCHE;
1809 *Ariosoma mystax* – (DELAROCHE);
1809 *Bathycongrus mystax* – (DELAROCHE);
1809 *Conger mystax* – (DELAROCHE);
1809 *Congermuraena mystax* – (DELAROCHE);
1809 *Congromuraena mystax* – (DELAROCHE);
2006 *Gnathophis mystax* – NOLF & GIRONE, pl.3,fig.7;
2009 *Gnathophis mystax* – NOLF et al., pl. 3, familie 86;
2013 *Gnathophis mystax* – NOLF, pl.20.

Remarks: The fossil specimens attributed to *Gnathophis mystax* are square-shaped and have a delineated sulcus, angular, opening to the postero-dorsal area.

Genus *Pseudophichthys* Roule, 1915

General remarks: Specimens placed under the genus *Pseudophichthys* may best be described with regard to the ostium portion of the sulcus, which is only very shallow and consequently poorly definable, in contrast to other Congrids.

Pseudophichthys escavaratierensis Nolf and Cappetta, 1989

Plate I (3)

- 1986 *Pseudophichthys escavaratierensis* – SCHWARZHANS;
1989 *Pseudophichthys escavaratierensis* – NOLF & CAPPETTA;
2013 *Pseudophichthys escavaratierensis* – NOLF, pl. 24.

Pseudophichthys splendens (Lea, 1913)

Plate I (4)

- 1888 *Myrus pachyrhynchus* – (NON VAILLANT);
 1913 *Leptocephalus splendens* – LEA;
 1915 *Pseudophichthys latedorsalis* – ROULE;
 1940 *Promyllantor schmitti* – HILDEBRAND;
 2007 *Pseudophichthys splendens* – GIRONE, pl.1, fig.2;
 2010 *Pseudophichthys splendens* – GIRONE et al., fig. 5, d.

Remarks: One specimen from Voutes section is unequivocally comparable to the extant Atlantic *Pseudophichthys splendens*, also reported from the western Mediterranean Pliocene (Nolf and Girone, 2006; Girone, 2007), while the other may be better placed under the fossil species *Pseudophichthys escavaratierensis*, also known from the Pliocene of South France (Schwarzhan, 1986; Nolf and Cappetta, 1988). The two *Pseudophichthys* specimens exhibit between them a distinguishable difference in the placement of the postero-dorsal angle. Moreover, *Pseudophichthys 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 & Schubert, 1906)

Plate I (5-10)

- 1906 *Ophidium appendiculatum* – BASSOLI;
 1906 *Ophidium magnum* – BASSOLI;
 1906 *Ophidium pulcher* – BASSOLI;
 1914 *Conger duvergieri* – PRIEM;
 1988 *Rhynchoconger pantanellii* – NOLF & CAPPETTA;
 1998 *Rhynchoconger pantanellii* – NOLF et al., pl.1, fig.3;
 2006 *Rhynchoconger pantanellii* – GIRONE et al., fig. 2.1;
 2007 *Rhynchoconger pantanellii* – GIRONE;
 2013 *Rhynchoconger pantanellii* – NOLF, pl.25.

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

Subdivision Ostarioclupeomorpha Arratia, 1996

Superorder Clupeomorpha Greenwood et al., 1966

Order Clupeiformes Bleeker, 1959

Family **Engraulidae** Gill, 1861

Genus *Engraulis* Cuvier, 1816

Engraulis encrasicolus (Linnaeus, 1758)

Plate I (17-20)

- 1758 *Clupea encrasicolus* – LINNAEUS;
1758 *Engraulis encrasicolus* – (LINNAEUS);
1758 *Engraulis encrasicolus* – (LINNAEUS);
1758 *Engraulis engrasicolus* – (LINNAEUS);
1758 *Engraulis engrasicolus* – (LINNAEUS);
1758 *Engraulis engrasicolus* – (LINNAEUS);
1758 *Engraulis engrasicolus* – (LINNAEUS);
1827 *Engraulis amara* – RISSO;
1829 *Engraulis meletta* – CUVIER;
1832 *Engraulis vulgaris* – NILSSON;
1848 *Engraulis argyrophanus* – VALENCIENNES;
1913 *Engraulis capensis* – GILCHRIST;
1927 *Engraulis encrasicolus ponticus* – ALEKSANDROV;
1947 *Engraulis russoi* – DULZETTO;
1947 *Engraulis encrasicolus russoi* – DULZETTO;
1961 *Anchoiella guineensis* – ROSSIGNOL & BLACHE;
1961 *Anchoa guineensis* – (ROSSIGNOL & BLACHE);
1961 *Engraulis guineensis* – (ROSSIGNOL & BLACHE);
1846 *Engraulis japonica* – (non TEMMINCK & SCHELGEL);
1846 *Engraulis japonicas* – (non TEMMINCK & SCHELGEL);
2009 *Engraulis encrasicolus* – NOLF et al., pl. 4, familie 95;
2013 *Engraulis encrasicolus* – NOLF, pl.30.

Remarks: These very thin otoliths are elongated, oval-shaped, with a protruding rostum and antirostrum, and a deep long sulcus. The ostium opens antero-dorsally, and is deeper than the cauda; both are almost equal in length. The ventral rim is nicely curved throughout its length.

Family **Clupeidae** Rafinesque, 1810

Genus *Sardinella* Valenciennes, 1847

Sardinella maderensis (Lowe, 1838)

Plate I (15)

- 1838 *Clupea maderensis* – LOWE;
1827 *Clupea desmaresti* – RISSO;
1827 *Engraulis desmaresti* – RISSO;
1847 *Sardinella granigera* – VALENCIENNES;
1847 *Alausa eba* – VALENCIENNES;
1847 *Clupea eba* – (VALENCIENNES);
1847 *Sardinella eba* – (VALENCIENNES);
1885 *Pellonula modesta* – FISCHER;

- 1917 *Sardinella cameronensis* – REGAN;
 1998 *Sardinella maderensis*– NOLF et al., pl.1, fig.10;
 2006 *Sardinella maderensis* – NOLF & GIRONI, pl.1, fig.9;
 2009 *Sardinella maderensis* – NOLF et al., pl. 5, familie 97.

Remarks: The unique otolith from Vagia section attributed to this species is elongated in shape, with a protruding rostrum, a very small antirostrum and excissura. The sulcus opens antero-dorsally. The ostium is triangular and deeper incised than the cauda. The two parts of the sulcus are almost equal in length. The dorsal rim is approximately flat, leading to an angle in the posterior part. The posterior rim is incised around the middle. The ventral area is larger than the dorsal, and nicely curved. The ventral rim forms a characteristic angle in the anterior part, to reach the rostrum.

Subdivision Euteleostei Greenwood et al., 1967

Superorder Protacanthopterygii Greenwood et al., 1966

Order Argentiniformes Johnson and Patterson, 1996

Family **Argentinidae** Bonaparte, 1846

Genus *Argentina* Linnaeus, 1758

Argentina sphyraena Linnaeus, 1758

Plate I (16)

- 1835 *Argentina silus junior* – RISBERG;
 1839 *Osmerus hebridicus* – YARRELL;
 1839 *Argentina hebridica* – (YARRELL);
 1844 *Goniosoma argentinum* – COSTA;
 1848 *Argentina cuvieri* – VALENCIENNES;
 1848 *Argentina yarrelli* – VALENCIENNES;
 2006 *Argentina sphyraena* – GIRONI et al., fig. 2.5;
 2009 *Argentina sphyraena* – NOLF et al., pl. 12, familie 166;
 2010 *Argentina sphyraena* – GIRONI et al., fig. 5, I;
 2013 *Argentina sphyraena* – NOLF, pl.39.

Remarks: The otolith described under this species is large and robust. The sulcus is long and linear, opening antero-dorsally into a small ostium. The crista superior is clearly visible in this specimen, as a straight line. The dorsal rim tends upwards to the posterior end, where it forms a characteristic angle, so that the posterior rim runs almost straight. The ventral rim is curved in the posterior part, and angular in the anterior. The ventral area is large.

Neoteleostei (Rosen, 1973)

Superorder Stenopterygii Rosen, 1973

Order Stomiiformes Regan, 1909

Family **Gonostomatidae** Gill, 1893

Genus *Gonostoma* Rafinesque, 1810

Plate II (23)

2010 *Gonostoma* – AGIADI et al., fig.2.8.

Remarks: Modern as well as fossil otoliths of *Gonostoma* spp. exhibit the same general characters, resembling perhaps *Vinciguerria* otoliths; the small size, thin and protruding rostrum, long and linear sulcus. However *Gonostoma* otoliths have elliptical outline, in contrast to the angular shape of *Vinciguerria*.

Family **Sternoptychidae** Dumeril, 1806

Genus *Maurolicus* Cocco, 1838

Maurolicus muelleri (Gmelin, 1789)

Plate II (24)

- 1789 *Maurolicus mülleri* – (GMELIN);
1789 *Maurolicus mulleri* – (GMELIN);
1789 *Salmo muelleri* – (GMELIN);
1792 *Argentina pennanti* – WALBAUM;
1792 *Maurolicus pennanti* – (WALBAUM);
1832 *Scopelus borealis* – NILSSON;
1836 *Scopelus humboldti* – YARREL;
1838 *Microstomus amethystinopunctatus* – (non COCCO);
1850 *Scopelus maurolici* – VALENCIENNES;
1915 *Maurolicus japonicus* – (non ISHIKAWA);
1967 *Maurolicus fragilis* – LAFOND-GRELLETY, p.15, pl. 3, fig. 1a&b (?non fragilis PROCHAZKA);
1969 *Argentina fragilis* - ANFOSSI & MOSNA, p. 29, pl.5, fig. 5a, b & 6a, b;
1969 *Bonapartia spina* - HEINRICH, p.15, pl.1, fig. 4a,b & 6a,b, pl.19, fig.2a,b;
?1971 *Argentina* sp. – WEILER, p.6, pl.1, fig.1;
1971 *Argentina fragilis* – ANFOSSI & MOSNA, p.145, pl.17;
1972 *Argentina fragilis* – ANFOSSI & MOSNA, p.96, pl.15, fig.5a,b;
1975 *Bonapartia spina* – ANFOSSI & MOSNA, p.5, pl.1, fig. 1a,b, 2a,b;
1975 *Bonapartia* aff. *spina* – ANFOSSI & MOSNA, p.6, pl.1, fig.3a,b, 4a,b;
1975 *Bonapartia miocenica* – ANFOSSI & MOSNA, p.6, pl.1, fig.5a,b, 6a,b, 7a,b, 8a,b;
1975 *Bonapartia* sp.1 – ANFOSSI & MOSNA, p.7, pl.1, fig. 9a,b;
1975 *Bonapartia* sp.2 - ANFOSSI & MOSNA, p.7, pl.1, fig. 10a,b;
?1975 *Bonapartia* sp.3 - ANFOSSI & MOSNA, p.8, pl.2, fig. 1a,b;
1975 *Bonapartia* sp.4 - ANFOSSI & MOSNA, p.8, pl.2, fig. 2a,b;
?1975 *Bonapartia* sp.5 - ANFOSSI & MOSNA, p.8, pl.2, fig. 3a,b;
1975 *Bonapartia* sp.4 - ANFOSSI & MOSNA, p.9, pl.2, fig. 4a,b;
1975 *Otolithus (Gonostomidarum)* sp.1 – ANFOSSI & MOSNA, p.9, pl.2, fig.5a,b;
1975 *Otolithus (Gonostomidarum)* sp.2 – ANFOSSI & MOSNA, p.9, pl.2, fig. 6a,b;
1980 *Maurolicus muelleri* – STEURBAUT, p.57, pl.2, fig. 1-13;
1988 *Maurolicus muelleri* – NOLF & STEURBAUT, pl. 4, fig. 13-15;

- 2001 *Maurolicus muelleri* – GIRONE & VAROLA, p. 435, pl.1, fig. 3;
 2004 *Maurolicus muelleri* – CAMPANA, p. 266;
 2007 *Maurolicus muelleri* – GIRONE, p. 163, pl.1, fig. 10;
 2009 *Maurolicus muelleri* – NOLF et al., pl. 17, familie 180;
 2010 *Maurolicus muelleri* – AGIADI et al., fig.2.9;
 2010 *Maurolicus muelleri* – GIRONE et al., fig. 5, j.

Remarks: The otoliths of this species are small and have a characteristically angular shape, with sharp postero-dorsal and ventral edges. The rostrum is very pointed, and equals in length almost half the rest of the otolith. Although the fossil specimens usually preserve the pointy edges and rostrum very well, indeed eroded samples may be more difficult to discern from *Vinciguerria*. Another significant feature is the shape of the sulcus, which exhibits a cut dividing its two parts, and the cauda is lengthy, parallel to the ostium, but located higher, towards the dorsal edge.

Genus *Polyipnus* Günther 1887

Polyipnus polli Schultz, 1961

Plate II (25-26)

- 1887 *Polyipnus spinosus* – (non GUNTHER);
 1899 *Polyipnus laternatus* – (non GAMAN);
 1995 *Polyipnus polli* – SMALE et al., pl.12, fig. A;
 2001 *Polyipnus polli* – GIRONE & VAROLA, pl.1, fig.2.

Remarks: The otoliths of *P.polli* have a characteristically small posterior – anterior distance relative to the ventral – dorsal direction, making them very narrow. The rostrum is small and begins at a point a little below the middle of the otolith. The sulcus is very small and resembles a small incision just above the rostrum.

Family **Phosichthyidae** Weitzman, 1974

Genus *Vinciguerria* Jordan and Williams, 1896

Vinciguerria aff. *attenuata* (Cocco, 1838)

Plate II (28)

- 2006 *Vinciguerria* aff. *attenuata* – GIRONE et al., fig. 2.14.

Remarks: This otolith is square-shaped, with smooth angles in the margin, a long linear sulcus, and a small but pointed sharp rostrum.

Vinciguerria poweriae (Cocco, 1838)

Plate II (27)

- 1838 *Gonostomus poweriae* – COCCO;
1838 *Ichthyococcus poweriae* – (COCCO);
1838 *Maurolicus poweriae* – (COCCO);
1838 *Scopelus poweriae* – (COCCO);
1838 *Vinceguerria poweriae* – (COCCO);
1899 *Vinciguerria lucetia* – (non GARMAN);
1979 *Vinciguerria poweriae* – STEURBAUT, pl.2, fig. 18;
1988 *Vinciguerria poweriae* – NOLF & STEURBAUT, pl. 4, fig. 6-7;
2004 *Photichthys* sp. – SCHWARZHANS, p. 222, pl. 2, fig. 17;
2006 *Vinciguerria poweriae* – GIRONE et al., p. 658, fig. 2: 13;
2007 *Vinciguerria poweriae* – GIRONE, p. 163, pl. 1, fig. 9;
2010 *Vinciguerria poweriae* – AGIADI et al., fig.2.7.

Remarks: These otoliths exhibit a protruding rostrum; its length is greater than the half of the otolith body, and it is very sharp. The sulcus is undivided and elongate, with clearly developed cristae. The postero-ventral side curves nicely, but the ventral rim forms an angle in its middle. The dorsal rim is almost flat.

Subsection Eurypterygii (Rosen, 1973)

Superorder Cyclosquamata Rosen, 1973

Order Aulopiformes Rosen, 1973

Family **Chlorophthalmidae** Bonaparte, 1840

Genus *Chlorophthalmus* Bonaparte, 1840

Chlorophthalmus agassizi Bonaparte, 1840

Plate II (30-33)

- 1983 *Aulopus agassizi* – BONAPARTE;
1881 *Hyphalonedrus chalybeis* – GOODE;
1883 *Pelopsia candida* – FACCIOLOA;
1983 *Chlorophthalmus productus* – GUNTHER;
1979 *Chlorophthalmus chalybeius* – GOODE & BEAN;
1941 *Chlorophthalmus borealis* – KURONUMA & YAMAGUCHI;
1953 *Chlorophthalmus atlanticus* – POLL;
2004 *Chlorophthalmus agassizi* – CAMPANA, p.32;
2013 *Chlorophthalmus agassizi* – NOLF, pl.58.

Remarks: A unique specimen found in Voutes sediments is the only known Pliocene record of *Chlorophthalmus agassizi*. Previously references of this genus included the fossil species *Chlorophthalmus costamagnai* Schwarzhans, 1986 in the lower Pliocene of Le Puget in South France (Nolf and Cappetta, 1988) and Papiol in Spain (Nolf et al., 1998), and *Chlorophthalmus* cf. *agassizi* in the Middle Pleistocene of Kephallonia in the eastern Ionian Sea (Agiadi et al., 2010, fig.2.4). The Voutes specimen exhibits all the morphological characteristics of the modern Mediterranean

species *C. agassizi* better than the Kephallonia specimen. Namely, the Voutes specimen is elongate shaped, 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*.

Family **Scopelarchidae** Regan, 1911

Genus *Scopelarchus* Alcock, 1896

Scopelarchus analis (Brauer, 1902)

Plate II (34-35)

- 1820 *Evermannella balbo* – (non RISSO);
- 1896 *Scopelarchus guentheri* – (non ALCOCK);
- 1902 *Dissomma anale* – BRAUER, 1902;
- 1916 *Odontostomus peramatus* – ROULE;
- 1916 *Scopelarchus anale* – (BRAUER);
- 1963 *Scopelarchus beebei* – ROFEN;
- 1963 *Scopelarchus candelops* – ROFEN;
- 1963 *Scopelarchus sagax* – ROFEN;
- 1988 *Scopelarchus analis* – NOLF & CAPPETTA, pl. 18, fig. 18;
- 1995 *Scopelarchus analis* – SMALE et al., pl.14, fig. F;
- 2006 *Scopelarchus analis* – GIRONE et al., p.658, fig.2: 16;
- 2010 *Scopelarchus analis* – AGIADI et al., fig.2.3.

Remarks: The otoliths of this species are large and square-shaped. They exhibit a nearly symmetrical sulcus, closed, with two circular colliculi. The outline is decorated with several curved protrusions, while the postero-ventral angle shows a characteristic pointed knob.

Subsection Ctenosquamata (Rosen, 1973)

Superorder Scopelomorpha Rosen, 1973

Order Myctophiformes Regan, 1911

Family **Myctophidae** Gill, 1892

Genus *Benthoosema* Goode and Bean, 1896

Benthoosema glaciale (Reinhardt, 1837)

Plate III (42)

- 1789 *Benthoosema mülleri* – non GMELIN;
- 1789 *Scopelus mülleri* – non GMELIN;
- 1837 *Lampanyctus glacialis* – REINHARDT;
- 1837 *Benthoosema glacialis* – REINHARDT;
- 1837 *Myctophum glacialis* – REINHARDT;
- 1837 *Myctophum glaciale* – REINHARDT;
- 1837 *Scopelus glacialis* – REINHARDT;
- 1864 *Scopelus parvimanus* – GUNTHER;

- 1889 *Scopelus scoticus* – GUNTHER;
1918 *Myctophum glaciale thori* – TANNIG;
1939 *Myctophum glaciale knipovitschi* – SOLDATOR;
1996 *Benthoosema glaciale* – BRZOBOHATY & NOLF, pl. 1, fig. 7-10;
2004 *Benthoosema glaciale* – CAMPANA, p. 96;
2006 *Benthoosema glaciale* – GIRONE et al., fig. 5: 4;
2007 *Benthoosema glaciale* – GIRONE, pl.1, fig. 5;
2010 *Benthoosema glaciale* – AGIADI et al., fig.2.18.

Remarks: The otoliths of *Benthoosema glaciale* are narrow and high, with two to three protrusions in the ventral rim. The sulcus contains an ostium and a cauda, which are almost equal, and deep, without colliculi.

Benthoosema suborbitale (Gilbert, 1913)

- 1890 *Myctophum pterotum* – (non ALCOCK);
1897 *Benthoosema fibulata* – (non GILBERT & CRAMER);
1897 *Myctophum fibulatum* – (non GILBERT & CRAMER);
1913 *Benthoosema suborbitale* – (GILBERT);
1913 *Myctophum suborbitale*[†] – GILBERT;
1928 *Benthoosema simile* – (TANING);
1928 *Myctophum imitator* – PARR;
1928 *Benthoosema imitator* – (PARR);
1928 *Myctophum simile* – TANING;
1929 *Myctophum fibulatum proximum* – PARR;
1986 *Benthoosema suborbitale* – SCHWARZHANS, p.222, pl.2, fig. 19-21;
1988 *Benthoosema suborbitale* – NOLF & CAPPETTA, pl.5, figs. 1-4;
1995 *Benthoosema suborbitale* – SMALE et al., pl.16, fig. H;
1996 *Benthoosema suborbitale* – BRZOBOHATY & NOLF, p.156, pl.1, fig. 1-4;
2004 *Benthoosema suborbitale* – CAMPANA, p. 97;
2006 *Benthoosema suborbitale* – GIRONE et al., p.662, fig. 5: 8.

Remarks: *Benthoosema suborbitale* exhibits the same characters as *B. glaciale* but for the thicker ventral area, and the irregular outline.

Genus *Ceratoscopelus* Gunther, 1864

Ceratoscopelus maderensis (Lowe, 1839)

Plate III (43)

- 1838 *Scopelus bonapartii* – (non COCCO);
1839 *Ceratoscopelus madeirensis* – (LOWE);
1839 *Myctophum maderensis* – (LOWE);
1839 *Myctophum maderense* – (LOWE);
1839 *Macrostoma maderensis* – (LOWE);
1839 *Lampanyctus maderensis* – (LOWE);
1839 *Lampanyctus maderense* – (LOWE);
1839 *Scopelus maderensis* – LOWE;
1882 *Scopelus acanthurus* – FACCIOLA;
1882 *Scopelus doderleini* – FACCIOLA;
1971 *Ceratoscopelus maderensis* – WEILER, p.10, pl.2, fig. 10;
1972 “*Myctophida*” *aemiliana* – ANFOSSI & MOSNA;
1996 *Ceratoscopelus maderensis* – NOLF & MARTINELL, tab. 1, fig. 21-22;
1997 *Ceratoscopelus maderensis* – SCHWARZHANS, p.12, pl.3, fig. 33, 37;

- 1988 *Ceratoscopelus maderensis* – NOLF & CAPPETTA, pl.5, figs. 17-20;
 1998 *Ceratoscopelus maderensis* – SCHWARZHANS, pl.3, fig. 10;
 2000 *Ceratoscopelus maderensis* – NOLF & GIRONE, p. 9, pl.1, fig. 6-11;
 2001 *Ceratoscopelus maderensis* – GIRONE & VAROLA, p. 435, pl.1, fig. 7;
 2004 *Ceratoscopelus maderensis* – CAMPANA, p. 98;
 2010 *Ceratoscopelus maderensis* – AGIADI et al., fig.2.14.

Remarks: These specimens are oval, elongated, with a large protruding rostrum, and a small antirostrum. The sulcus is lengthy and wide. It is divided into ostium and cauda; the latter being almost half in length than the former. The caudal colliculum is circular, while the ostial one is oblate. There is a ventral fissure, more pronounced in the postero-ventral area.

Genus *Diaphus* Eigenmann and Eigenmann, 1890

General remarks: *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). Very characteristic of *Diaphus* otoliths of all species are the ventral indentations.

Diaphus aff. *adenomus* Gilbert, 1905

Plate III (44)

- 2006 *Diaphus* aff. *adenomus* – NOLF & GIRONE, pl.4, fig.2-9.

Remarks: Several specimens from Voutes section present great similarity to the small and medium size specimens from the Northern Italy (Nolf and Girone, 2006) which were identified as *Diaphus* aff. *adenomus*. These otoliths are large, robust, with a nicely curved margin. The rostrum extends only slightly more than the antirostrum, and the excissura forms a clear angle. The ostrium is elongate, with an elliptical colliculum, while the cauda is quadrate filled with an oval-shaped colliculum. These are the most elongate of the *Diaphus* species' specimens examined here.

Diaphus cavallonis Brzobohaty and Nolf, 2000

Plate III (45)

- 2000 *Diaphus cavallonis* – BRZOBOHATY & NOLF, pl.5, fig.7-14;
 2007 *Diaphus cavallonis* – GIRONE, pl.1, fig.7;
 2010 *Diaphus cavallonis* – GIRONE et al., fig. 7, a;
 2013 *Diaphus cavallonis* – NOLF, pl. 72.

Remarks: These otoliths found in the Voutes section sediments are large and robust. The posterior and ventral rims are nicely curved. The dorsal area is strong and a characteristic postero-dorsal angle may be observed. The rostrum and the antirostrum

are very small and the excissura cuts in the middle of the ostrium, instead just above it, as in the other *Diaphus* species examined here. The ostrium and its colliculum are rectangle. The cauda is square, and its colliculum is placed dorsally within it.

Diaphus holti Taning, 1918

Plate III (46)

- 1838 *Diaphus rafinesquei* – (non COCCO);
- 1890 *Diaphus theta* – (non EIGENMANN & EIGENMANN);
- 1918 *Diaphus holti* – TANING;
- 1918 *Scopelus holti* – (TANING);
- 1971 *Diaphus praerafinesquii* n.sp. – WEILER, p.11, pl.1, fig. 15;
- 1976 *Diaphus theta* – ANFOSSI & MOSNA, p.18, pl.1, fig.4a,b (non EIGENMANN & EIGENMANN, 1890);
- 1980 *Diaphus holti* – NOLF & MARTINELL, tf.2, fig. 15-20;
- 1986 *Diaphus holti* – SCHWARZHANS, p.222, pl.4, fig. 40-41;
- 1988 *Diaphus holti* – NOLF & CAPPETTA, pl.8, figs.22-24;
- 1998 *Diaphus holti* – NOLF, MANE & LOPEZ, pl.3, figs.2-4;
- 1986 *Diaphus holti* – BRZOBOHATY & NOLF, p.190, pl.3, figs.7-10;
- 2006 *Diaphus holti* – GIRONI et al., p.662, fig.5: 6;
- 2010 *Diaphus holti* – AGIADI et al., fig.2.13.

Remarks: The otoliths of *Diaphus holti* are characterized by a strongly denticulate ventral margin, well developed rostrum and a salient postero-dorsal angle. The excissura is well incised. The posterior margin may be almost straight. In addition; the sulcus of *D. holti* has a nearly rounded caudal colliculum. These otoliths are characteristically high, with respect to the other *Diaphus* species, but unlike *Diaphus kokeni* and *Diaphus debilis* the rostrum is much stronger.

Diaphus rafinesquii (Cocco, 1838)

Plate III (47)

- 1838 *Collettia rafinesquei* – (COCCO);
- 1838 *Scopelus rafinesqui* – (COCCO);
- 1838 *Nyctophus rafinesquii* – COCCO;
- 1838 *Myctophum rafinesquei* – (COCCO);
- 1838 *Myctophum rafinesquii* – (COCCO);
- 1838 *Diaphus rafinesquei* – (COCCO);
- 1838 *Collettia rafinesquii* – (COCCO);
- 1838 *Scopelus rafinesquii* – (COCCO);
- 1904 *Diaphus luetkeni* – (non BRAUER);
- 1930 *Diaphus intermedius* – BORODIN;
- 1972 *Myctophum splendidum* – ANFOSSI & MOSNA, p.101, pl.17, fig.1 (non PROCHAZKA, 1893);
- 1980 *Diaphus rafinesquei* – NOLF & MARTINELL, tf.2, fig. 21-26;
- 1985 *Diaphus rafinesquei* – BOSSIO et al., p.57, pl.2, fig.5;
- 1988 *Diaphus rafinesquei* – NOLF & CAPPETTA, pl.10, fig.21;
- 1994 *Diaphus rafinesquei* – NOLF & CAVALLO, pl.2, fig. 5;
- 2004 *Diaphus rafinesquei* – BRZOBOHATY & NOLF, p.192, pl.3, figs.11-14;
- 2004 *Diaphus rafinesquii* – CAMPANA, p. 104;

- 2006 *Diaphus rafinesquii* – GIRONE et al., p.662, fig. 5: 7;
 2007 *Diaphus rafinesquei* – GIRONE, p.165, pl.2, fig. 6;
 2009 *Diaphus rafinesquii* – NOLF et al., pl. 18, familie 200;
 2010 *Diaphus rafinesquii* – AGIADI et al., fig.2.12.

Remarks: The otoliths of *D. rafinesquii* also show a well-developed rostrum and a salient postero-dorsal angle. However these are notably lengthier than *D. holti*; the latter has a greater height/length ratio. Furthermore, the sulcus of *D. rafinesquii* is more elongated.

Diaphus aff. *splendidus* (Brauer, 1904)

Plate III (48)

- 1906 “*Berycida*” *sulcata* – BASSOLI;
 1906 “*Berycida*” *tuberculata* – BASSOLI;
 1970 *Myctophum rossiae* – ROBBA;
 1998 *Diaphus* aff. *splendidus* – NOLF et al., pl.2, fig.10.;, fig.1-5;
 2000 *Diaphus* aff. *splendidus* – BRZOBOHATY & NOLF, pl.6
 2007 *Diaphus* aff. *splendidus* – GIRONE, pl.1, fig.11;
 2010 *Diaphus* aff. *splendidus* – GIRONE et al., fig. 7, c.

Remarks: These otoliths from Voutes section sediments strongly resemble those of modern species *Diaphus splendidus*. Indeed these are large, robust specimens, oval shaped. The rostrum is larger than the antirostrum by half; the excissure incised sharply. The difference observed against the specimens from the same samples, showing affinity to *Diaphus adenomus*, lies in the existence of the salient postero-dorsal angle in the *Diaphus* aff. *splendidus* specimens. Also the ostium and its colliculum are rectangle; the crista superior is very pronounced in all its length and turns dorsally in the posterior end. In addition, these otoliths are higher than those of *D. adenomus*.

Diaphus taaningi Norman, 1930

Plate III (49)

- 1905 *Otolithus (Berycidarum) austriacus* – SCHUBERT, p. 630 (partim), pl.17, fig. 6 (non 1-5, 7, non KOKEN 1891);
 1943 *Scopelus debilis* – WEILER, p.90 (partim), pl.1, fig. 8 (non 4-7, 9-13, non KOKEN, 1891);
 1949 *Scopelus debilis* – WEILER (partim), pl.1, fig. 8 (non 4-7, pl.2, figs. 9-13, non KOKEN, 1891);
 1950 *Scopelus debilis* – WEILER, p.211, pl.1, fig.2 (non pl.9, figs. 66,67, non KOKEN, 1891);
 1958 *Scopelus debilis* – WEILER, p.327, pl.1, fig. 9 (non 10=D. kokeni, non KOKEN, 1891);
 1965 *Myctophum debile* – BRZOBOHATY, p.109, pl.1, fig.1,6 (non 2-3, non KOKEN, 1891);
 1966 *Myctophum debile* – SMIGIELSKA, p.229 (partim), pl.13, fig.1 (non pl.12, figs.6-8, non KOKEN, 1891);
 1967 *Myctophum debile* – BRZOBOHATY, p.232, pl.1D, fig.3a,b (non KOKEN, 1891);
 1972 *Myctophum debile* – BAUZA, p.63, pl.1, figs. 18-19,?20-21 (non 22,23,25-31, non KOKEN, 1891);

- 1978 *Diaphus austriacus* – BRZOBOHATY, pl.1, fig.10 (non KOKEN, 1891);
1979 *Diaphus debilis* – STEURBAUT, p.62, pl.3, figs.9-10 (NON koken, 1891);
1983 *Diaphus debilis* – BRZOBOHATY, pl.6, fig.2 (non KOKEN, 1891);
1984 *Diaphus debilis* – STEURBAUT, p.53, pl.7, figs.24,25 (non KOKEN, 1891);
1985 *Diaphus debilis* – NOLF, fig. 47G;
1989 *Diaphus* sp. ind. – NOLF & CAPPETTA, pl.10, figs. 17-20;
1994 *Diaphus debilis* – BRZOBOHATY, pl.2, figs. 5,8 (non 6,7, non KOKEN, 1891);
1998 *Diaphus* sp.2 – NOLF, MANE & LOPEZ, pl.2, figs.3-8;
2003 *Diaphus taaningi* – BRZOBOHATY & NOLF, p.193, pl.2, figs. 7-12;
2004 *Diaphus taaningi* – GIRONE & VAROLA, p. 435, pl.1, fig. 4, pl.2, fig. 14;
2006 *Diaphus taaningi* – GIRONE et al., p. 662, fig. 5: 12;
2010 *Diaphus taaningi* – AGIADI et al., fig.2.1.

Remarks: The otoliths placed under the recent Atlantic species *Diaphus taaningi* are characterized by a subquadrangular shape and a wide predorsal angle. Juvenile and young adult fossil specimens are slightly more elongate than the recent material. A similar observation is made in the adult and juvenile specimens of *D. taaningi* from the lower Pleistocene of Montalbano (western Ionian) and the lower-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 lower Pliocene of Dar Bel Hamri, Atlantic Morocco.

Diaphus sp.1

Plate III (50)

Remarks: Several specimens from Ypsenis section sediments exhibited certain common characteristics, forming a distinct morphologic group. These otoliths have a medium size, a round margin; the dorsal and posterior rim forming a salient right angle. The sulcus is elongate; the ostium is larger than the cauda by half its length; both bear oval colliculi. The crista inferior is strong in the caudal portion of the sulcus. The most pronounced character of this group is the pointy rostrum, which is formed through a slight inward curve of the ventral margin in this part. The antirostrum is also sharp, but much smaller than the rostrum, and the excissura is present on the upper part of the ostium.

Genus *Electrona* Goode and Bean, 1896*Electrona risso* Cocco, 1829

Plate III (51)

- 1829 *Electrona rissoi* – (COCCO);
 1829 *Myctophum risso* – (COCCO);
 1928 *Scopelus risso* – COCCO;
 1829 *Scopelus rissoi* – (COCCO);
 1829 *Myctophum rissoi* – (COCCO);
 1906 “*Apogonida*” *orbicularis* – PRIEM;
 1933 *Electrona risso salubris* – (WHITLEY);
 1933 *Myctophum rissoi salubris* – WHITLEY;
 1979 *Electrona anfossimosnai* – SCHQARZHANS;
 1981 *Electrona risso* – NOLF & MARTINELL, tf. 1, fig.16-17;
 1988 *Electrona rissoi* – NOLF & CAPPETTA, pl. 5, figs. 11-14;
 1998 *Electrona rissoi* – NOLF et al., pl.3, fig. 5-6;
 2004 *Electrona risso* – CAMPANA, p. 106;
 2006 *Electrona rissoi* – GIRONE et al., p.662, fig. 5: 16;
 2007 *Electrona rissoi* – GIRONE, p. 165, pl.2, fig.1;
 2009 *Electrona risso* – NOLF et al., pl. 18, familie 120;
 2010 *Electrona risso* – AGIADI et al., fig.2.11.

Remarks: The otoliths of this species have an almost circular outline, with an approximately equal dorsal and ventral area. The ventral margin forms a slight angle. The sulcus is of medium depth, divided into two equal parts. The ostial and caudal colliculi appear as stretched elevations.

Genus *Hygophum* Bolin, 1939*Hygophum benoiti* (Cocco, 1838)

Plate III (52-53)

- 1810 *Scopelus humboldti* – (non RISSO);
 1838 *Myctophum benoiti* – (COCCO);
 1838 *Scopelus benoiti* – COCCO;
 1971 *Hygophum* cf. *probenoiti* – WEILER;
 2001 *Hygophum benoiti* – GIRONE & VAROLA, p. 435, pl. 1, fig. 8;
 2004 *Hygophum benoiti* – CAMPANA, p. 107;
 2006 *Hygophum benoiti* – GIRONE et al., p. 660, fig. 3: 1,2;
 2007 *Hygophum benoiti* – GIRONE, p. 163, pl.1, fig. 6;
 2010 *Hygophum benoiti* – AGIADI et al., fig.2.6.

Remarks: It should be immediately noted that the specimens examined here, as well as the comparative material from the eastern Ionian show that the otoliths of this species undoubtedly exhibit great morphologic variability. Few factors remain common and characteristic of the species. Previously, Girone et al (2006) observed differences between the otoliths of modern Mediterranean representatives and Atlantic ones. The ventral rim is less curved in modern Mediterranean specimens and

it is developed into almost angular in older specimens. The otoliths examined here also show this characteristic.

Hygophum hygomii (Lütken, 1892)

Plate III (54)

- 1864 *Scopelus macrochir* – (non GUNTHER);
1892 *Scopelus hygomii* – LUTKEN;
1892 *Myctophum hygoni* – (LUTKEN);
1892 *Myctophum hygomii* – (LUTKEN);
1892 *Myctophum hygomi* – (LUTKEN);
1892 *Myctophum benoiti hygomi* – (LUTKEN);
1892 *Hygophum hygonii* – (LUTKEN);
1892 *Hygophum hygomii* – (LUTKEN);
1892 *Hygophum higomii* – (LUTKEN);
1896 *Myctophum remiger* – GOODE & BEAN;
1896 *Myctophum remigerum* – GOODE & BEAN;
?1924 *Otolithus (Scopelus) circularis* n.sp. – FROST, p.608, pl.61, fig.2;
?1933 *Otolithus (Scopelus) regularis* n.sp. – FROST, p.135, pl.21, fig.15,16;
?1959 *Hygophus intermedius* n.sp. – WEILER, p.152, fig.8 (non 23);
1966 *Myctophum tenue murbani* – SMIGIELSKA, p.235, pl.14, fig.1 (non WEINFURTER, 1952);
?1966 *Myctophum excavatum* – SMIGIELSKA, p.234, pl.13, fig.6 (non 4-5; non SULC 1932);
1970 *Hygophum agatense* n.sp. – ROBBA, p.113, pl.9, figs.5-7;
?1970 *Myctophum* sp. – ROBBA, p.111, pl.9, fig.1;
?1971 *Electrona?* sp. - WEILER, p.14, pl.1, fig. 18,?21;
1972 *Otolithus (Myctophidarum)* sp.1 – ANFOSSI & MOSNA, p.103, pl.17, fig.7;
non 1972 *Hygophum hygomi* – ANFOSSI & MOSNA, p.98, pl.16, fig. 1 (?=Electrona);
1979 *Hygophum agrigentensis* n.sp. – SCHWARZHANS, p.13, pl.4, fig. 41-44;
?1980 *Hygophum circularis* – SCHWARZHANS, p.44, fig. 108 (non 107,109; non FROST 1924);
?1980 *Hygophum* aff. *circularis* – SCHWARZHANS, p.44, fig. 110;
?1980 *Hygophum murbani* – SCHWARZHANS, p.44, fig.111, 112 (non WEINFURTER, 1952);
1982 *Hygophum* sp., aff. *circularis* – BRZOBOHATY, pl.1, fig.9;
1983 *Hygophum agatense* – NOLF & STEURBAUT, p. 157, pl.2, fig. 16-19;
?1984 *Hygophum circularis* – GRENFELL, p.62, fig.27, 28, 128, 129, 130;
1986 *Hygophum agrigentensis*– SCHWARZHANS, p.223, pl.2, fig.23;
1989 *Hygophum agrigentensis*– NOLF & CAPPETTA, pl.6, fig. 1-4;
1995 *Hygophum hygomi* – BRZOBOHATY & NOLF, p.157, pl.2, fig. 1-24;
1995 *Hygophum hygomi* – NOLF & BRZOBOHATY, p.89, pl.4, fig.13;
1995 *Hygophum hygomii* – SMALE et al., pl. 21, fig. B;
1996 *Hygophum hygomi* – NOLF & GIRONE, p. 9, pl.1, fig. 3;
1997 *Hygophum hygomi* – GIRONE & VAROLA, p. 435, pl.1, fig. 5;
1998 *Hygophum hygomi* – NOLF et al., pl.3, fig. 8;
2004 *Hygophum hygomii* – CAMPANA, p. 108;
2010 *Hygophum hygomii* – AGIADI et al., fig.2.16;
2013 *Hygophum hygomi* – NOLF, pl. 80.

Remarks: These otoliths differ from those of *H. benoiti* in the circular outline and ornamentation all around the margin.

Genus *Lampadena* Goode and Bean, 1893

- 1996 *Lampadena* – BRZOBOHATY & NOLF, pl.4, fig.1-16;
 2006 *Lampadena* – GIRONE et al., fig. 5.2&3.

Remarks: The otoliths of *Lampadena* have a very characteristic ventral area, which distinguishes this genus from the other Myctophids, especially *Diaphus*; the indented rim forms a nice curve up until the very posterior end. The ventral fissure is well developed.

Genus *Lampanyctus* Bonaparte, 1840*Lampanyctus crocodilus* (Risso, 1810)

Plate III (55)

- 1810 *Gasteropelecus crocodilus* – (RISSO);
 1810 *Scopelus crocodilus* – (RISSO);
 1810 *Myctophum crocodilum* – (RISSO);
 1810 *Macrostoma crocodilus* – (RISSO);
 1810 *Serpe crocodilus* – RISSO;
 1810 *Lampanictus crocodilus* – (RISSO);
 1838 *Scopelus bonapartii* – (COCCO);
 1838 *Nyctophus bonapartii* – COCCO;
 1838 *Nyctophus bonaparte* – COCCO;
 1896 *Lampanyctus gemmifer* – GOODE & BEAN;
 1896 *Scopelus gemmifer* – (GOODE & BEAN);
 1929 *Lampanyctus peculiaris* – BORODIN;
 1934 *Lampanyctus iselini* – PARR;
 2001 *Lampanyctus crocodilus* – GIRONE & VAROLA, pl. 2, fig. 1-4;
 2004 *Lampanyctus crocodilus* - CAMPANA, p. 111;
 2006 *Lampanyctus crocodilus* – GIRONE et al., p. 662, fig. 5: 10;
 2010 *Lampanyctus crocodilus* – AGIADI et al., fig.3.6.

Remarks: The otoliths of *L. crocodilus* are square-shaped, thick and robust, with a curved margin and sharp excissura, but a smooth rostrum.

Genus *Lobianchia* Gati, 1903*Lobianchia dofleini* (Zugmayer, 1911)

Plate III (56)

- 1838 *Myctophum gemellari* – (non COCCO);
 1908 *Diaphus agassizi* – (non GILBERT);
 1911 *Diaphus dofleini* – (ZUGMAYER);
 1911 *Lampanyctus dofleini* - (ZUGMAYER);
 1911 *Lobianchia dofleini* - (ZUGMAYER);
 1911 *Lobianchia dofleini* - (ZUGMAYER);
 1911 *Myctophum dofleini* - ZUGMAYER;
 1911 *Scopelus dofleini* - (ZUGMAYER);
 1979 *Lobianchia dofleini* – NOLF & STEURBAUT, p. 158, pl. 3, figs. 22-29;
 1980 *Lobianchia dofleinoidea* n.sp. – STEURBAUT, p. 52, pl. 8, figs. 3-7;
 1986 *Diaphus vonhachti* n.sp. – SCHWARZHANS, p.230, pl.3, figs. 37-38;
 1988 *Lobianchia dofleini* – STEURBAUT, pl.3, fig.17-25;

- 1995 *Lobianchia dofleini* – SMALE et al., pl.24, fig. C;
2004 *Lobianchia dofleini* – CAMPANA, p. 115;
2006 *Lobianchia dofleini* – GIRONE et al., p. 662, fig. 5: 11;
2010 *Lobianchia dofleini* – AGIADI et al., fig.3.4.

Remarks: The otoliths of this species are compact and square-shaped, but with a smooth margin. The dorsal rim is round in the posterior part, and high in the middle. The ventral rim is also curved, but indented. The rostrum is short, wide and sharp. This species may easily be confused with *Diaphus taaningi* but for the excissura, which is shallow but pronounced, as well as the larger sulcus.

Genus *Myctophum* Rafinesque, 1810

Myctophum fitchi Schwarzzhans, 1979

Plate III (57)

- 1998 *Myctophum fitchi* – NOLF et al., pl.3, fig.9;
2010 *Myctophum fitchi* – GIRONE et al., fig. 11, c;
2013 *Myctophum fitchi* – NOLF, pl.78.

Remarks: The otoliths of *M. fitchi* differ from those of *M. punctatum* in the existence of a salient postero-dorsal angle. The sulcus is rimed in the upper part; the ostium is twice the size of the cauda. The caudal colliculum is oval-shaped. The antirostrum extends equally to the rostrum and is quite sharp. The excissura cuts in the upper portion of the ostial opening.

Myctophum punctatum Rafinesque, 1810

Plate III (61)

- 1810 *Gasteropelecus humboldti* – (RISSO);
1810 *Serpe humboldti* – RISSO;
1810 *Scopelus punctatus* – (RAFINESQUE);
1810 *Scopelus crocodilus* – (non RISSO);
1810 *Myctophum humboldti* – (RISSO);
1810 *Symbolophorus humboldti* – (RISSO);
1838 *Scopelus benoiti* – (non COCCO);
1850 *Scopelus caninianus* – VALENCIENNES;
1881 *Scopelus heideri* – STEINDACHNER;
1892 *Myctophum phengodes* – (non LUTKEN);
1909 *Stylophthalmus lobiancoi* – MAZZARELLI;
1977 *Myctophum punctatum*– NOLF & MARTINELL, tf.1, fig. 18-19;
2004 *Myctophum punctatum* – CAMPANA, p. 118;
2006 *Myctophum punctatum*– GIRONE et al., p.662, fig. 5: 15;
2007 *Myctophum punctatum*– GIRONE, p.165, fig.5;
2010 *Myctophum punctatum* – AGIADI et al., fig.2.17;
2010 *Myctophum punctatum* – GIRONE et al., fig. 11, b.

Remarks: The elliptical shape, a small, round cauda and an elongated sulcus, curved in the posterior part, characterize these otoliths. The ostium is more than twice the

size of the cauda, and opens widely above a small rostrum. The antirostrum is smooth and the excissura cuts just above the ostium, but not too deep. The ventral rim is angular in the middle. Furthermore, the sulcus is deeper in comparison to *Symbolophorus veranyi*, and the ventral area larger.

Genus *Notoscopelus* Gunther, 1864

Notoscopelus elongatus (Costa, 1844)

Plate III (58-59)

- 1810 *Scopelus crodilus* – (non RISSO);
 1844 *Lampanyctus elongatus* – (COSTA);
 1844 *Myctophum elongatum* – (COSTA);
 1844 *Myctophum elongatus* – (COSTA);
 1844 *Scopelus elongatus* – COSTA;
 1891 *Scopelus psedocrocodilus* – MOREAU;
 1977 *Notoscopelus* sp. – NOLF, p.19, pl.2, figs. 20-21;
 1979 *Notoscopelus* aff. *elongatus* – HUYGHEBAERT & NOLF, p.71, pl.2, figs. 15-16;
 1979 *Notoscopelus* aff. *kroyeri* – HUYGHEBAERT & NOLF, p.71, pl.2, fig. 12;
 ?1979 *Myctophum* sp. – MENZEL, p.90, pl.2, fig.2;
 2004 *Notoscopelus elongatus* – BRZOBOHATY & NOLF, pl.7, figs. 10-11;
 2006 *Notoscopelus elongatus* – GIRONI et al., p. 661, fig.4: 1, 2;
 2010 *Notoscopelus osteolatus* – SCWARZHANS;
 2010 *Notoscopelus elongatus* – AGIADI et al., fig.3.3.

Remarks: The otoliths of *N. elongatus* are elongated, with a long ostium and a short, square cauda. The posterior rim is round, and the ventral rim indented. The rostrum extends only slightly more than the antirostrum, and the excissura is sharp.

Notoscopelus resplendens (Richardson, 1845)

Plate III (60)

- 1820 *Macrostoma angustidens* – (non RISSO);
 1844 *Lampanyctus elongatus* – (non COSTA);
 1844 *Notoscopelus elongatus* – (non COSTA);
 1844 *Scopelus elongatus* – (non COSTA);
 1845 *Lampanyctus resplendens* – RICHARDSON;
 1845 *Scopelus resplendens* – (RICHARDSON);
 1889 *Notoscopelus brachychier* – EIGENMANN & EIGENMANN;
 1904 *Notoscopelus ejectus* – WAITE;
 1934 *Serpa hoffmanni* – FOWLER;
 1968 *Myctophum splendidum* – DIENI, p.260,pl.1,fig.6;
 ?1968 *Myctophum oroseinum* n.sp. – DIENI, p. 262, pl.1, fig.8, pl.2, fig.2;
 1969 *Notoscopelus resplendens* – FITCH, p.8, pl.1, fig.m;
 1970 *Myctophum oroseinum* – ROBBA, p.106, pl.8, fig. ?4,5;
 ?1972 *Myctophum oroseinum* – ANFOSSI & MOSNA, p.99, pl.16, fig.4;
 1979 *Myctophum oroseinum* – SCWARZHANS, p.6, pl.1, figs. ?1,2, ?3, ?pl.11, fig.124;
 1980 *Notoscopelus resplendens* – SCWARZHANS, p.65, text-figs195-197;
 1983 *Notoscopelus elongatus* – NOLF & STEURBAUT, p. 159, pl.3, figs. 15-16;
 1986 *Notoscopelus resplendens* – SCHWARZHANS, p.223, pl.5, fig.54;
 1989 *Notoscopelus resplendens* – NOLF & CAPPETTA, p.219, pl.6, figs.21-24;

- 1995 *Notoscopelus resplendens* – SMALE et al., pl. 25, fig. F;
1996 *Notoscopelus resplendens* – BRZOBOHATY & NOLF, pl.6, fig.1-11;
2004 *Notoscopelus resplendens* – CAMPANA, p. 122;
2007 *Notoscopelus resplendens* – GIRONE, pl.2, fig.4;
2013 *Notoscopelus resplendens* – NOLF, pl.82.

Remarks: The otoliths of *Notoscopelus resplendens* are much shorter than those of *N. elongatus* and may thus be easily distinguished. Otherwise, the morphological characteristics of the two species's otoliths are very similar. In addition to the length, *N. resplendens* is generally more robust, and thick.

Genus *Protomyctophum* Fraser-Brunner 1949

Protomyctophum arcticum (Lütken, 1892)

Plate IV (62-63)

- 2006 *Protomyctophum arcticum* – GIRONE et al., fig. 5.5.

Remarks: These very characteristic otoliths are high, concave in the inner face, like a cone, whose apex lies in the ostium. Their shape is somewhat circular, with a prominent postero-dorsal angle. The dorsal rim may be indented in the anterior part. The rostrum and antirostrum are smooth; the rostrum is a little larger than the antirostrum. The dorsal area approximately equals the ventral portion of the otolith, although the latter is stronger in the anterior part.

Genus *Scopelopsis* Brauer, 1906

Scopelopsis pliocenicus (Anfossi and Mosna, 1976)

Plate IV (64)

- 1988 *Scopelopsis pliocenicus* – NOLF & CAPPETTA, pl. 6, figs. 11-16;
1998 *Scopelopsis pliocenicus* – NOLF et al., pl.3, fig. 11-12;
2006 *Scopelopsis pliocenicus* – GIRONE et al., p.662, fig. 5: 13;
2007 *Scopelopsis pliocenicus* – GIRONE, p.165, pl.2, fig. 3;
2010 *Scopelopsis pliocenicus* – AGIADI et al., fig.3.2.

Remarks: These are square-shaped otoliths, with curved dorsal and ventral rims. The most significant characteristic of this species is the sulcus, which is wide, and extends through the entire otolith length. It appears almost open at the posterior rim, and is divided into two, almost equal parts. The rostrum and antirostrum are equal and not very protruding. The excissura is barely noticeable, and the ostium is open and curved in the anterior part. Finally, a strong ventral fissure may be observed.

Subsection Acanthomorpha (Rosen, 1973)

Superorder Paracanthopterygii Greenwood et al., 1966

Order Gadiformes Goodrich, 1909

Family **Bregmacerotidae** Gill, 1872

Genus *Bregmaceros* Thompson, 1840

Plate II (36)

- 1909 *Otolithus* (*Xenodermichthys*?) *catulus* SCHUBERT – TOULA, p. 689-690, fig. 5a,b;
 1912 *Otolithus* (*Xenodermichthys*?) *catulus* SCHUBERT – TOULA, p. 161;
 1952 *Otolithus* (?*Xenodermichthys*) *catulus* SCHUBERT – WEINFURTER, p.155-156, tav. I, fig. 5a,b, 6a,b, 7a,b, 8a,b;
 1952 *Otolithus* (?*Xenodermichthys*) *catulus* SCHUBERT – WEINFURTER, p. 458, tav., II, fig. 7;
 1963 *Bregmaceros* cf. *catulus* (SCHUBERT) – WEILER, p. 281, tav. I, fig. 4a,b, 6, 8;
 1969 *Bregmaceros catulus* (SCHUBERT) – ANFOSSI & MOSNA, tav. VIII (IV), fig. 8a,b;
 1971 *Bregmaceros albyi* (SAUVAGE, 1880) – WEILER, taf. 2, fig. 27;
 1972 *Bregmaceros albyi* (SAUVAGE, 1880) – ANFOSSI & MOSNA, p.104, tav. IV, fig. 3a,b;
 1973 *Bregmaceros albyi* (SAUVAGE, 1880) – ANFOSSI & MOSNA, p. 150-151, fig. 11 (19-21), tav. II, fig. 25-26;
 1979 *Bregmaceros albyi* (SAUVAGE, 1880) – ANFOSSI & MOSNA, tav. IX, fig.11a,b;
 1988 *Bregmaceros* sp. – NOLF & CAPPETTA, pl. 11, fig. 7;
 2000 *Bregmaceros* sp. – NOLF & GIRONE, p. 9, pl.1, fig. 12;
 2004 *Bregmaceros* sp. – NOLF & BRZOBOHATY, pl.5, fig. 4-5;
 2004 *Bregmaceros* sp. – NOLF & STEURBAUT, pl.4, fig. 12-13;
 2007 *Bregmaceros* sp. – GIRONE, p.165, pl.2, fig.8;
 2010 *Bregmaceros* sp. – AGIADI et al., fig.3.8.

Remarks: Specific identification of fossil *Bregmaceros* otoliths is currently not possible, considering the scarcity of modern comparative material, as well as a need for revision of the previous fossil skeletal material identifications, in light of new data on the present *Bregmaceros* morphometrics. Generic placement however is unquestionable, since these otoliths are non-equivalent in their shape and morphology. *Bregmaceros* otoliths are developed in a radial manner, with three angular protrusions, one in the dorsal margin and two in the ventral. The sulcus is shallow, centrally paced with two small, circular colliculi.

Family **Macrouridae**

Genus *Coelorinchus* Giorna, 1809

Plate II (37)

Remarks: One juvenile specimen from Ypsenis section was placed under the genus *Coelorinchus*, which is characterized by the round colliculi, present in all the examined modern specimens of *C. coelorinchus*, *C. stellaris*, and *C. labiatus*. The young specimens of *C. labiatus* pictured in Nolf and Girone (2000) have a straighter ventral rim than the one examined here, possibly excluding this species.

Family **Moridae** Goode and Bean, 1896

Genus *Laemonema* Gunther in Jonhson, 1862

Plate II (38-40)

- 2006 *Laemonema* sp. – GIRONE et al., fig. 3.9;
2007 *Laemonema* sp. – GIRONE, pl.2, fig.10;
2010 *Laemonema* sp. – AGIADI et al., fig.3.10.

Remarks: These otoliths are elongated and thick. They exhibit three contact surfaces, a circular in the posterior part, and two lengthy ones in the dorsal and ventral area respectively. The sulcus is deep and triangular.

Family **Phycidae**

Genus *Phycis* Walbaum, 1792

Phycis blennoides (Brünnich, 1768)

Plate IV (65)

- 1768 *Gadus blennoides* – BRÜNNICH;
1768 *Urophycis blennioides* – (BRÜNNICH);
1789 *Gadus albidus* – GMELIN;
1792 *Gadus bifurcus* – WALBAUM;
1800 *Blennius gadoides* – LACEPEDE;
1801 *Phycis tinca* – BLOCH & SCHNEIDER;
1810 *Batrachoides gmelini* – RISSO;
1828 *Phycis furcatus* – FLEMING;
1923 *Phycis elongatus* – POSTHUMUS;
1942 *Phycis simplex miocenica* – WEILER;
2006 *Phycis blennoides* – GIRONE et al., fig.6.1-7;
2007 *Phycis blennoides* – GIRONE, pl.3, fig.11;
2009 *Phycis blennioides* – NOLF et al., pl. 24&25, familie 219;
2013 *Phycis blennioides* – NOLF, pl.105.

Remarks: Phycidae otoliths are high with a flat inner surface and a slightly concave outer surface. The sulcus is shallow and broad, practically extending to cover almost the entire inner otolith surface. *Phycis blennoides* recognized in the Ypsenis material may be separated from *Phycis museki* by its more pointed rostrum.

Family **Lotidae** Linnaeus, 1766

Genus *Gaidropsarus* Rafinesque, 1810

Plate IV (74-76)

- 2010 *Gaidropsarus* – AGIADI et al., fig.3.5.

Remarks: The otoliths of *Gaidropsarus* are triangular in shape. The dorsal margin forms an apex in the middle. The ventral rim is sub-linear, with a slight incision around the middle, and ends in the two remaining angles of the triangle. The sulcus is

diagonal, ending postero-dorsally; it is practically closed in both ends. There are no colliculi, but the ostrium and cauda are both triangular.

Family **Gadidae** Rafinesque, 1810

Genus *Gadiculus* Guichenot, 1850

Gadiculus argenteus Guichenot, 1850

Plate IV (66)

- 1894 *Gadus communis* – PROHAZKA;
 1905 *Otolithus (Macrurus) ellipticus* – SCHUBERT, p.622, pl.16, fig. 31-33;
 1905 *Macrurus excises* – SCHUBERT;
 1906 *Otolithus (Macrurus) ellipticus* – BASSOLI, p. 39, pl.1, figs. 17-18;
 1906 *Otolithus (Macrurus) ellipticus* – SCHUBERT, p.665, pl.5, figs. 8-12;
 1923 *Hymenocephalus asymmetricus* – POSTHUMUS;
 1923 *Macrurus pusillus* – POSTHUMUS;
 1942 *Macrurus ellipticus* – WEILER, p.96, pl. 5, figs. 39-,41, 45-48, 50-51;
 1950 *Macrurus ellipticus* – WEILER, p. 242, pl.5, fig. 32, 34-35;
 1966 *Macrurus ellipticus* – SMIGIELSKA, p. 244, pl. 15, figs. 5-7;
 1969 *Macrurus ellipticus* – ANFOSSI & MOSNA, p. 38, pl. 7, fig. 10;
 1970 *Glyptorhynchus communis* – ROBBIA, p.123, pl.11, fig. 5;
 1974 *Macrurus ellipticus longus* – SCHWARZHANS;
 1976 *Gadiculus ellipticus* – GAEMERS, p. 513, pl.5, fig. 6 & pl. 7, fig. 3-4;
 1978 *Gadiculus argenteus* – NOLF, p. 172;
 1979 *Gadiculus argenteus* – STEURBAUT, pl.5, fig.12-16;
 1988 *Gadiculus argenteus* – NOLF & CAPPETTA, pl. 11, figs. 4-6;
 1990 *Circagadiculus kingi* – GAEMERS;
 1990 *Circagadiculus supertruncatus* – GAEMERS;
 1990 *Circagadiculus truncatus* – GAEMERS;
 1998 *Gadiculus argenteus* – NOLF et al., pl.4, fig. 4;
 2006 *Gadiculus argenteus* – GIRONE et al., p. 660, fig. 3: 5;
 2007 *Gadiculus argenteus* – GIRONE, p.165, pl.2, fig. 7;
 2010 *Gadiculus argenteus* – AGIADI et al., fig.3.7;
 2013 *Gadiculus argenteus argenteus* – NOLF, pl. 109.

Remarks: These otoliths have a fusiform shape, ending posteriorly in a smooth angle. The sulcus is central and divided in two parts, filled with circular colliculi. The dorsal margin has multiple bulges, smooth contours. The ventral margin is curved, and there is a strong ventral fissure.

Gadiculus labiatus (Schubert, 1905)

Plate IV (67)

- 1905 *Otolithus (Hymenacephalus) labiatus* - SCHUBERT, p. 626;
 1923 *Hymenocephalus brinki* – POSTHUMUS;
 1923 *Macrurus debilis* – POSTHUMUS;
 1923 *Hymenocephalus dubius* – POSTHUMUS;
 1923 *Hymenocephalus globosus* – POSTHUMUS;
 1923 *Hymenocephalus medius* – POSTHUMUS;
 1923 *Hymenocephalus ovalis* – POSTHUMUS;
 1974 *Macrurus rectangularis* – SCHWARZHANS;

- 1976 *Gadiculus deurnensis* – GAEMERS;
1980 *Gadiculus labiatus* – NOLF & MARTINELL, tf.3, fig. 18;
1979 *Gadiculus labiatus* – NOLF, p. 172;
1988 *Gadiculus labiatus* – NOLF & CAPPETTA, pl. 11, figs. 18-21;
1998 *Gadiculus labiatus* – NOLF et al., pl.3, fig. 13;
2006 *Gadiculus labiatus* – GIRONE et al., p.660, fig.4;
2007 *Gadiculus labiatus* – GIRONE, p.165, pl.2, fig. 9;
2010 *Paratrisopterus glaber* – SCHWARZHANS;
2010 *Gaduculus labiatus* – AGIADI et al., fig.3.13;
2013 *Gadiculus glaber* – HOEDEMAKERS, pl.2, fig.3;
2013 *Gadiculus labiatus* – NOLF, pl 113.

Remarks: All the Gadidae material identified in the Voutes material undoubtedly belongs to the fossil Mediterranean species *Gadiculus labiatus*. These are rectangular otoliths, with a central divided sulcus, filled with two circular colliculi. The posterior end is almost flat; differing from the angular shape of the *G. argenteus*. There is a ventral fissure observed here as well. In addition several lapilli were present in the same samples (Plate 3.4 (70-72)). 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.

Gadiculus thori Schmidt, 1913

Plate IV (68)

- 1913 *Gadiculus argenteus thori* – SCHMIDT;
1850 *Gadiculus argenteus* – (non GUICHENOT);
2006 *Gadiculus argenteus thori* – GIRONE et al., fig.3.6;
2013 *Gadiculus argenteus thori* – NOLF, pl. 109.

Remarks: These otoliths are fusiform, similar to *G. argenteus*, but for the posterior end which is not angular in this case. The sulcus is also more elongate, filled with two oval colliculi, and opens slightly in the anterior edge, and more widely in the posterior end. Thus the posterior rim is more prominent and incised around the middle. The ventral fissure is also present here.

Genus *Micromesistius* Gill, 1863

Micromesistius poutassou (Risso, 1827)

Plate IV (69)

- 1827 *Merlangus poutassou* – RISSO;
- 1827 *Boreogadus poutassou* – (RISSO);
- 1827 *Gadus poutassou* – (RISSO);
- 1827 *Gadus potassoa* – (RISSO);
- 1827 *Micromesistius poutassou* – (RISSO);
- 1827 *Merlangus vernalis* – RISSO;
- 1829 *Merlangus pertusus* – COCCO;
- 1829 *Merlangus pertussis* – COCCO;
- 1841 *Merlangus albus* – YARRELL;
- 1844 *Merlangus communis* – COSTA;
- 1855 *Gadus melanostomus* – NILSSON;
- 1982 *Micromesistius boscheineni* – SCHWARZHANS;
- 1998 *Micromesistius poutassou* – NOLF et al., pl.4, fig.5;
- 2004 *Micromesistius poutassou* – CAMPANA, p. 57;
- 2009 *Micromesistius poutassou* – NOLF et al., pl. 30, familie 220;
- 2013 *Micromesistius poutassou* – NOLF, pl. 111.

Remarks: Unlike the three *Gadiculus* species, *Micromesistius poutassou* is distinguished by the clearly divided sulcus, into a small cauda and a longer ostium. The whole otoliths are much more elongated than the *Gadus*, *Gadiculus* and *Merluccius* otoliths with which they were compared.

Order Ophidiiformes Berg, 1937

Family **Ophidiidae** Rafinesque, 1810

Genus *Ophidion* Linnaeus, 1758

Ophidion barbatum Linnaeus, 1758

Plate II (41)

- 1758 *Ophidion barbatus* – LINNAEUS;
- 1758 *Ophidium barbatum* – LINNAEUS;
- 1810 *Ophidion maculatum* – RAFINESQUE;
- 1854 *Ophidion congrus* – GRONOW;
- 2001 *Ophidion barbatum* – GIRONE & VAROLA, pl.2, fig.5;
- 2006 *Ophidion barbatum* – NOLF & GIRONE, pl.5, fig.8;
- 2009 *Ophidion barbatum* – NOLF et al., pl. 35, familie 222.

Remarks: The otoliths of *Ophidion barbatum* have a concave outer face and a convex inner face. The anterior area is strong, while the posterior end is angular. The sulcus is very shallow and divided into a small circular ostium, and a long elliptical cauda. The ventral rim is curved upwards.

Family **Carapidae** Jordan and Fowler, 1902

Genus *Carapus* Rafinesque, 1810

Carapus acus (Brünnich, 1768)

Plate IV (77-78)

2006 *Carapus acus* – GIRONE et al., fig.7.1&2;

2013 *Carapus acus* – NOLF, pl. 122.

Remarks: These otoliths are somewhat similar to the ones of *Ophidion barbatum* regarding the general outline. However, both inner and outer faces in this case are convex. The anterior area is also here much larger than the posterior, although the latter is not as angular. The sulcus is elongated as well, but undivided.

Genus *Echiodon* Thompson, 1837

Echiodon dentatus (Cuvier, 1829)

Plate IV (79-80)

1829 *Ophidium dentatum* – CUVIER;

1829 *Carapus dentatus* – (CUVIER);

1829 *Fierasfer dentatus* – (CUVIER);

1971 *Carapus praeimberbis* – WEILER;

2013 *Echiodon dentatus* – NOLF, pl.122.

Remarks: The most significant characteristic of *E. dentatus* otoliths is that they are very thick. That is the outer face is strongly convex, but the inner face is flat. The anterior area is stronger than the posterior, which run into an angle. Unfortunately the specimens examined here did not enable more detailed description of the inner face morphology.

Family **Bythitidae** Gill, 1861

Genus *Grammonus* Gill, 1896

Grammonus ater (Risso, 1810)

Plate V (96)

1810 *Oligopus ater* – RISSO;

1827 *Oligopus niger* – RISSO;

2006 *Oligopus ater* – GIRONE et al., fig.7.9.

Remarks: These otoliths are fusiform in shape, with a central, undivided, elliptical sulcus. The posterior and anterior rims end in smooth angles.

Superorder Acanthopterygii Gouan, 1770

Order Atheriniformes Rosen, 1966

Family **Atherinidae** Risso, 1827

Genus *Atherina* Linnaeus, 1758

Atherina boyeri Risso, 1810

Plate V (81-82)

- 1810 *Hepsetia boyeri* – (RISSO);
- 1810 *Atherina boaei* – RISSO;
- 1829 *Atherina mochon* – CUVIER;
- 1829 *Hepsetia mochon* – (CUVIER);
- 1831 *Atherina presbyter caspia* – EICHWALD;
- 1831 *Atherina boyeri caspia* – EICHWALD;
- 1831 *Atherina presbyter pontica* – EICHWALD;
- 1831 *Atherina mochon pontica* – EICHWALD;
- 1831 *Atherina pontica* – EICHWALD;
- 1835 *Atherina risso* – VALENCIENNES;
- 1835 *Atherina sarda* – VALENCIENNES;
- 1836 *Atherina lacustris* – BONAPARTE;
- 1838 *Atherina caspia* – EICHWALD;
- 1847 *Atherina anterina* – NARDO;
- 1861 *Atherina rissoi* – GUNTHER;
- 1885 *Atherina hyalosoma* – COCCO;
- 1902 *Atherina riqueti* – ROULE;
- 1902 *Atherina mochon riqueti* – ROULE;
- 1903 *Atherina sardinella* – FOWLER;
- 1907 *Atherina bonapartii* – BOULENGER;
- 1907 *Atherina mochon aegyptia* – BOULENGER;
- 2006 *Atherina boyeri* – GIRONE et al., fig. 6.9;
- 2009 *Atherina boyeri* – NOLF et al., pl. 41, familie 251.

Remarks: The modern *Atherina boyeri* has been discovered in the sediments from Voutes as well as Ypsenis sections. In contrast to modern specimens of *Atherinopsis* spp., which have a more rectangular shape, the modern as well as the fossil otoliths of *Atherina boyeri* are round to oval-shaped, bearing a distinctive sulcus, comprised of a small, round ostium, and a straight, medium-thickness cauda, which does not reach the posterior rim.

Order Scorpaeniformes Greenwood et al., 1966

Family **Scorpaenidae** Risso, 1827

Genus *Scorpaena* Linnaeus, 1758

Plate V (84)

- 1998 *Scorpaena* – NOLF et al., pl.6, fig.1.

Remarks: The shape of this otolith is elliptical. The sulcus is elongate, clearly divided into a triangular ostium, which opens antero-dorsally, and an oval cauda, almost equal

is size. The ostium is deeper than the cauda, and there are no colliculi. A fissure is present in the ventral area.

Order Perciformes Bleeker, 1859

Family **Acropomatidae** Gill, 1891

Genus *Parascombrops* Alcock, 1889

Parascombrops mutinensis Bassoli, 1906

Plate V (86-91)

- 1971 *Neoscombrops praeannectens* – WEILER;
- 1979 *Neoscombrops flexuosus* – STEURBAUT;
- 1998 *Parascombrops mutinensis* – NOLF et al., pl.6, fig.6-8;
- 2006 *Parascombrops mutinensis* – GIRONE et al., fig. 6.11;
- 2010 *Parascombrops mutinensis* – AGIADI et al., fig.3.11;
- 2010 *Parascombrops mutinensis* – GIRONE et al., fig. 9, e;
- 2013 *Parascombrops mutinensis* – NOLF, pl. 209.

Remarks: The otoliths of *Parascombrops mutinensis* described here have the same morphological characteristics as the Pliocene and Pleistocene material from the western Mediterranean (Nolf and Martinell, 1980; Nolf and Girone, 2006).

Parascombrops 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, a third specimen from the same section, belonging to a smaller individual, is undoubtedly lesser in this part, being similar to the Akrotiri specimens (eastern Ionian). Through direct comparison with the Akrotiri specimen and small and large specimens from Paliore river (Girone 2000) 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 **Apogonidae** Günther, 1859

Genus *Apogon* Lacepède, 1801

Plate V (85)

Remarks: The otoliths of the genus *Apogon* sp. are fusiform, with a pronounced dorsal extension, and a nice, round ostium.

Family **Epigonidae** Poey, 1861

Genus *Epigonus* Rafinesque, 1810

Epigonus denticulatus Dieuzeide, 1950

Plate V (92)

- 1810 *Pomatomus telescopus* – (non RISSO);
- 1905 *Epigonus atherinoides* – (non GILBERT);
- 1905 *Hynnodus atherinoides* – (non GILBERT);
- 1995 *Epigonus denticulatus* – SMALE et al., pl. 67, fig. G;
- 2006 *Epigonus denticulatus* – NOLF & GIRONE, pl.7, fig. 8-9;
- 2013 *Epigonus denticulatus* – NOLF, pl. 235.

Remarks: Two specimens from Voutes section show affinity to *Epigonus denticulatus*. The otoliths of this species are spindle-shaped, bearing a strong rim and an angular ventral part. The sulcus is divided into a large elliptical ostium, and an equally long, but narrow cauda, separated from each other by a strong break. Modern and fossil specimens of this species differ from *E. constantiae*, because the latter has a more oval shape.

Family **Carangidae** Rafinesque, 1815

Genus *Trachurus* Rafinesque, 1810

Plate V (94)

- 1979 *Trachurus* sp. – NOLF & STEURBAUT, pl. 2, fig. 12;
- 1979 *Trachurus* sp. – STEURBAUT, pl.8, fig. 17;
- 1999 *Trachurus* sp. – NOLF & MARTINELL, tf.4, fig. 16;
- 1988 *Trachurus* sp. – NOLF & CAPPETTA, pl. 15, fig. 13;
- 1997 *Trachurus* sp. – NOLF & MARQUE DA SILVA, pl.2, fig. 8-9;
- 2001 *Trachurus* sp. – GIRONE & VAROLA, p. 439, pl. 3, fig. 5.

Remarks: The otoliths of *Trachurus* species have a relatively flat inner face. The sulcus is long and curved in the posterior end.

Family **Sparidae** Bonaparte, 1832

Genus *Dentex* Cuvier, 1814

Plate VI (102-103)

Remarks: *Dentex* otoliths have a polygonal shape, which is very characteristic amongst the other Perciformes. Also, the ostium is large and wide. The cauda is a deep canal which leads to the posterior end, curving or not.

Genus *Diplodus* Rafinesque, 1810

Diplodus cf. *annularis* (Linnaeus, 1758)

Plate VI (101)

Remarks: This otolith is fusiform, but with a strong postero-dorsal angle. The ventral rim forms a smooth obtuse angle. The rostrum is pronounced and the excissura is barely visible. The ostium is triangular and opens antero-dorsally.

Genus *Oblada* Cuvier, 1829

Oblada melanura (Linnaeus, 1758)

Plate VI (104-105)

- 1758 *Sparus melanurus* – LINNAEUS;
- 1758 *Oblata melanura* – (LINNAEUS);
- 2009 *Oblada melanura* – NOLF et al., pl. 91, familie 378;
- 2013 *Oblada melanura* – NOLF, pl. 258.

Remarks: Long, slender-shaped *Oblada melanura* has a convex inner and a strongly concave outer face, an angular ventral rim and a rather small ostium. The dorsal rim is almost straight; the dorsal area small, while the ventral is well developed.

Genus *Pagellus* Valenciennes, 1830

Pagellus cf. bogaraveo (Brünnich, 1768)

Plate VI (107)

Remarks: The prominent posterior and ventral angles are very characteristic of all *Pagellus*. The recent otoliths of *Pagellus bogaraveo* have a triangular ostium opening antero-dorsally, a small dorsal area and a wide ventral one, and the cauda curves towards the posterior end, without reaching the margin. The cristae are well developed.

Pagellus erythrinus (Linnaeus, 1758)

Plate VI (106)

- 1758 *Sparus erythrinus* – LINNAEUS;
- 1838 *Pagellus canariensis* – VALENCIENNES;
- 2009 *Pagellus erythrinus* – NOLF et al., pl. 93, familie 378.

Remarks: *Pagellus erythrinus* otoliths are high and more angular than *P. acarne*, as well as shorter.

Genus *Pagrus* Cuvier, 1816

Pagrus pagrus (Linnaeus, 1758)

- 2009 *Pagrus pagrus* – NOLF et al., pl. 95, familie 378.

Remarks: The prominent posterior and ventral angles are more rounded in *Pagrus* than in *Pagellus*. The ostium opens antero-dorsally and has an oval shape. The dorsal

area is smaller than the ventral one. The cauda curves towards the posterior end, without reaching the margin. The cristae are well developed.

Family **Centracanthidae** Gill, 1893

Genus *Spicara* Rafinesque, 1810

Spicara smaris (Linnaeus, 1758)

Plate V (97)

- 1758 *Sparus smaris* – LINNAEUS;
 1758 *Maena smaris* – (LINNAEUS);
 1758 *Smaris smaris* – (LINNAEUS);
 1810 *Sparus alcedo* – RISSO;
 1810 *Smaris alcedo* – (RISSO);
 1810 *Spicara alcedo* – (RISSO);
 1830 *Smaris vulgaris* – VALENCIENNES;
 1836 *Smaris gracilis* – BONAPARTE;
 1836 *Smaris maurii* – BONAPARTE;
 2006 *Spicara smaris* – GIRONE et al., fig.7.10;
 2009 *Spicara smaris* – NOLF et al., pl. 101, familie 379.

Remarks: The only member of this family identified is *Spicara smaris*, which has fusiform otoliths with an angular posterior edge. The sulcus is clearly divided into a wide, open ostium. The rostrum is strong, but there is no antirostrum. The cauda is long and narrow at the end, not really curved. In comparison to *S. flexuosa* this species exhibits more angular ventral side.

Family **Cepolidae** Rafinesque, 1810

Genus *Cepola* Linnaeus, 1764

Cepola macrophthalmma (Linnaeus, 1758)

Plate V (98)

- 1758 *Ophidion macrophthalmmum* – LINNAEUS;
 1758 *Ophidion macrophthalmma* – LINNAEUS;
 1764 *Cepola rubescens* – LINNAEUS;
 1766 *Cepola taenia* – LINNAEUS;
 1800 *Cepola serpentiformis* – LACEPEDE;
 1810 *Cepola marginata* – RAFINESQUE;
 1839 *Cepola longicauda* – SWAINSON;
 1839 *Cepola novemradiata* – SWAINSON;
 1839 *Cepola attenuate* – SWAINSON;
 1839 *Cepola truncate* – SWAINSON;
 1839 *Cepola gigas* – SWAINSON;
 1839 *Cepola jugularis* – SWAINSON;
 1906 *Cepola prerubescens* – BASSOLI;
 1907 *Cepola voslauensis* – SCHUBERT;
 1984 *Cepola multicrenata* – RADWANSKA;
 1998 *Cepola rubescens* – NOLF et al., pl.7, fig. 12;
 2009 *Cepola rubescens* – NOLF et al., pl. 112, familie 407;

- 2010 *Acanthocephala sicca* – SCHWARZHANS;
2013 *Cepola macrophthalma* – NOLF, pl. 293.

Remarks: *Cepola macrophthalma* otoliths are fusiform, with a clear angular posterior end, and the rostrum forming the equivalent anterior edge. There is a clear postero-dorsal angle present, while the ventral rim is nicely curved throughout. The sulcus is very characteristic, for it is wide, divided into two equal parts with no colliculi.

Family **Pomacentridae** Bonaparte, 1831

Genus *Chromis* Cuvier, 1814

Chromis chromis (Linnaeus, 1758)

Plate V (99)

- 1758 *Sparus chromis* – LINNAEUS;
1758 *Heliastes chromis* – (LINNAEUS);
1814 *Chromis castanea* – CUVIER;
1814 *Heliastes castanea* – (CUVIER);
1817 *Chromis mediteranea* – CLOQUET;
1833 *Heliastes limbatus* – (non VALENCIENNES);
1843 *Heliastes marginatus* – (non VALENCIENNES);
2009 *Chromis chromis* – NOLF et al., pl. 111, familie 411;
2013 *Chromis chromis* – NOLF, pl. 297.

Remarks: One representative of this family has been identified in the examined material; *Chromis chromis* has large fusiform otoliths, with strong angles and a long sulcus. The ostium is only slightly shorter than the cauda. The posterior part of the sulcus is lightly curved to the ventral side, and the incision separating the ostium from the cauda is rather small. These otoliths have a strong rostrum, but no antirostrum; the sulcus opening widely to the antero-dorsal side. Through direct comparison with the modern specimens, it may be observed that *Chromis margaritis* has a larger ventral area than *Ch. chromis*.

Family **Blenniidae** Rafinesque, 1810

Genus *Blennius* Linnaeus, 1758

Blennius ocellaris Linnaeus, 1758

Plate V (100)

- 1758 *Blennius ocellaris* – LINNAEUS;
2001 *Blennius ocellaris* – GIRONE & VAROLA, pl.3, fig. 14-17;
2007 *Blennius ocellaris* – GIRONE, pl.3, fig.9;
2009 *Blennius ocellaris* – NOLF et al., pl. 120, familie 447.

Remarks: This otolith has a generally triangular shape, with an antero-dorsal opening to allow for the deep ostium. The division between the ostium and the circular cauda is an elevation. The dorsal rim is curved, the ventral more flat.

Family **Gobiidae** Bonaparte, 1832

Genus *Aphia* Risso, 1827

Aphia minuta Risso, 1810

Plate VI (115)

- 1810 *Atherina minuta* – RISSO;
- 1810 *Aphia minuta* – (RISSO);
- 1810 *Argentina aphia* – RAFINESQUE;
- 1824 *Gobius pellucidus* – NARDO;
- 1824 *Aphia pellucida* – (NARDO);
- 1824 *Brachyochirus pellucidus* – (NARDO);
- 1827 *Aphia meridionalis* – RISSO;
- 1831-37 *Gobius albus* – PAMELL;
- 1845 *Gobius stuvitzii* – DUBEN;
- 1845 *Gobius stuwitzii* – DUBEN;
- 1846 *Brachyochirus aphia* – BONAPARTE;
- 1859 *Gobius pellucidus* – KESSLER;
- 2006 *Aphia minuta* – GIRONE et al., fig.7.5&6;
- 2009 *Aphia minuta* – NOLF et al., pl. 123, familie 460;
- 2013 *Aphia minuta* – NOLF, pl. 316.

Remarks: Gobiidae otoliths with very similar morphological characteristics. The most significant distinguishing 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* are very small, oval shaped, with a concave inner surface. The sulcus is also small and undivided, while the dorsal margin is irregularly curved.

Genus *Deltentosteus* Gill, 1863

Deltentosteus quadrimaculatus Valenciennes, 1837

Plate VI (116-118)

- 1837 *Gobius quadrimaculatus* – VALENCIENNES;
- 1847 *Gobius scagioctus* – NARDO;
- 1938 *Gobius quadrimaculatus trimaculatus* – NINNI;
- 1938 *Gobius quinquemaculatus* – NINNI;
- 2009 *Deltentosteus quadrimaculatus* – NOLF et al., pl. 124, familie 460;
- 2013 *Deltentosteus quadrimaculatus* – NOLF, pl. 324.

Remarks: The most important characteristic of this species is the triangular shape of the sulcus. Otherwise these otoliths are quadrate and robust. The margin may be indented all around.

Deltentosteus aff. *quadrifaculatus* Valenciennes, 1837

- 2000 *Deltentosteus* aff. *quadrifaculatus* – NOLF & GIRONE;
2006 *Deltentosteus* aff. *quadrifaculatus* – GIRONE;
2007 *Deltentosteus* aff. *quadrifaculatus* – GIRONE;
2013 *Deltentosteus* aff. *quadrifaculatus* – NOLF, pl. 324.

Remarks: Twelve specimens from Voutes section show greater affinity to the otoliths of *Deltentosteus* aff. *quadrifaculatus* described in the early Pleistocene of Northern Italy (Nolf and Girone, 2000; 2006; Girone, 2007), which has a more blunt antero-ventral angle than modern *D. quadrifaculatus*.

Genus *Gobius* Linnaeus, 1758

Gobius niger Linnaeus, 1758

Plate VII (123-124)

- 1758 *Gobius jazo* – LINNAEUS;
1758 *Gobius niger jazo* – LINNAEUS;
1758 *Gobius iozo* – LINNAEUS;
1810 *Gobius gorgione* – RAFINESQUE;
1821 *Gobius viridis* – OTTO;
1827 *Gobius longiradiatus* – RISSO;
1837 *Gobius britannicus* – THOMPSON;
1841 *Gobius fuliginosus* – MCCOY;
1859 *Gobius jazo pontica* – KESSLER;
1862 *Gobius jazo albescens* – CANESTRINI;
1862 *Gobius jazo nigrescens* – CANESTRINI;
1884-85 *Gobius punctulatus* – COCCO;
1891 *Gobius jazo minor* – KOLOMBATOVIC;
1891 *Gobius jazo major* – KOLOMBATOVIC;
1928 *Gobius niger hispanicus* – DE BUEN;
1928 *Gobius niger nigerrimus* – DE BUEN;
non 1775 *Gobius nebulosus* – FORSSKAL;
non 1814 *Gobius quadricapillus* – PALLAS;
2009 *Gobius niger* – NOLF et al., pl. 125, familie 460.

Remarks: *Gobius niger* otoliths exhibit a convex inner face. The sulcus has a large and a smaller part clearly defined, unlike both *Gobius paganellus* and *Zosterisessor ophiocephalus*, which show two equally large sulcus parts. There is an antero-dorsal protrusion accompanied by an excissura.

Gobius cf. *paganellus* Linnaeus, 1758

Plate VII (121-122)

Remarks: The sulcus differentiates *G. paganellus* from *G. niger*, which in the first case shows two equal parts, rather than a large and a smaller one. Also, the specimens examined here seemed more compressed, in the dorso-ventral direction.

Gobius sp.1

Plate VII (125)

2000 *Gobius* sp. – NOLF & GIRONE;2006 *Gobius* sp. – NOLF & GIRONE.

Remarks: One specimen, from Voutes section, was identified as *Gobius* sp.1, strongly resembling *Gobius* sp. from the Pliocene and Pleistocene sediments of Morrone and Piemonte Alba of Northern Italy (Nolf and Girone, 2000; 2006).

Gobius sp.2

Plate VII (126-130)

Remarks: The Ypsenis and Faliraki 4 specimens assigned to *Gobius* sp.2 somewhat resemble those of *Chromogobius* spp. figured in Nolf (2013, pl.316). However the observed characteristics were insufficient to place it under this genus, and direct comparison would be necessary. In addition, *Callogobius* otoliths may also be found comparable; both fossil and modern specimens have a significantly deeper sulcus, without colliculi, which is divided in two approximately equal parts.

Gobius sp.3

Plate VII (131-132)

Remarks: Two morphotypes of *Gobius* sp.3 were distinguished in the Ypsenis material. Both morphotypes have a very small sulcus, divided into two almost equal circular parts. *Gobius* sp.3 morphotype 1 is more compressed, while morphotype 2 is higher and has a dorsal angle.

Genus *Lesueurigobius* Whitley, 1950*Lesueurigobius friesii* (Malm, 1874)

Plate VII (134)

1874 *Gobius friesii* – MALM;1874 *Gobius friesii friesii* – MALM;1874 *Lesueuria friesii* – (MALM);1874 *Lesueurigobius friesii friesii* – (MALM);1874 *Gobius friesii* – MALM;1874 *Lesueurigobius friesii* – (MALM);1874 *Lesueuria friesii* – (MALM);1874 *Lesueuria friesii friesii* – (MALM);1874 *Lesueuria friesii* – (MALM);1874 *Lesueurigobius friesii* – (MALM);1838 *Gobius gracilis* – FRIES;1891 *Gobius macrolepis* – SCHARFF;non 1789 *Gobius cruentatus* – (GMELIN);

- non 1891 *Gobius friesii macrolepis* – (KOLOMBTAVIC);
2009 *Lesueurigobius friesii* – NOLF et al., pl. 126, familie 460;
2013 *Lesueurigobius friesii* – NOLF, pl. 324.

Remarks: These otoliths exhibit a rectangular shape and a central sulcus with two colliculi. In *L. friesii* the inner face is almost flat, the sulcus is wide, and the antero-dorsal area is large.

Lesueurigobius sanzi (de Buen, 1918)

Plate VII (135)

- 1918 *Gobius sanzi* – DE BUEN;
1918 *Lesueuria sanzoi* – DE BUEN;
1918 *Lesueurigobius sanzoi* – DE BUEN;
non 1758 *Bathygobius paganellus* – (LINNAEUS); fig. 13;
1998 *Lesueurigobius sanzoi* – NOLF et al., pl.7
2006 *Lesueurigobius sanzoi* – GIRONE;
2010 *Lesueurigobius sanzoi* – GIRONE et al., fig. 10, a.

Remarks: The smaller colliculus is not as well observed in *L. sanzi*, as in the other species. The otoliths of *L. sanzoi* from the Lower Pliocene of Montalbo Roero (Girone, 2006) present many similarities to *L. friesii*, but for the smaller sulcus and the more robust dorsal area.

Lesueurigobius suerii (Risso, 1810)

Plate VII (136)

- 1810 *Gobius suerii* – RISSO;
1810 *Lesueuria meuri* – (RISSO);
1810 *Lesueurigobius suerii* – (RISSO);
1824 *Gobius lunve* – NARDO;
1827 *Gobius lunie* – NARDO;
1827 *Gobius lesuerii* – RISSO;
1827 *Gobius lesueurii* – RISSO;
1827 *Lesueuria lesueurii* – (RISSO);
2009 *Lesueurigobius suerii* – NOLF et al., pl. 126, familie 460.

Remarks: *Lesueurigobius suerii* otoliths are asymmetrically higher, and the posterior as well as the anterior incision are very pronounced.

Genus *Pomatoschistus* Gill, 1863

Plate VI (119-120)

Remarks: Four specimens from Ypsenis section were placed under the genus *Pomatoschistus*, without any specific identification further. These small otoliths resembled those of *Aphia minuta* in size; their shape is almost square, and the sulcus off-centered, undivided.

genus «Gobidarum» sp.1

Plate VI (133)

Remarks: One gobiid specimen, from Voutes section, exhibits very characteristic morphology, but cannot be specifically identified, and is referred to here as *genus «Gobidarum» sp.1*. 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 Pleuronectiformes (Regan, 1910)

Family **Citharidae** Hubbs, 1845

Genus *Citharus* Röse, 1793

Citharus linguatula (Linnaeus, 1758)

Plate VI (110)

- 1758 *Pleuronectes linguatula* – LINNAEUS;
- 1787 *Pleuronectes macrolepidotus* – BLOCH;
- 1787 *Citharus macrolepidotus* – (BLOCH);
- 1807 *Pleuronectes citharus* – SPINOLA;
- 1847 *Pleuronectes patarachia* – NARDO;
- 1906 *Citharus schuberti* – BASSOLI;
- 1955 *Eucitharus balearicus* – BAUZA;
- 1973 *Eucitharus lusitanicus* – JONET;
- 1998 *Citharus linguatula* – NOLF et al., pl.7, fig.4-9;
- 1999 *Citharus linguatula* – SCHWARZHANS, pg. 73, figs.59-64;
- 2009 *Citharus linguatula* - NOLF et al., pl. 134, familie 490;
- 2013 *Citharus linguatuls* – NOLF, pl. 340.

Remarks: These otoliths are oval shaped, with a smooth curved margin. The sulcus is elongated, with a very small circular ostium and a thinner elongated cauda. The rostrum is slightly more protruding than the antirostrum, and the excissura cuts in the middle of the ostial opening.

Family **Bothidae** Regan, 1910

Genus *Arnoglossus* Bleeker, 1862

Arnoglossus kokeni (Bassoli, 1906)

Plate VI (111)

- 1906 *Solea kokeni* – BASSOLI, pl.2, fig.3;
- 1950 *Arnoglossus bauzai* – SANZ, pl. 55, fig1.3;
- 1964 *Arnoglossus bauzai* – BAUZA-RULLAN, pl. 4, fig. 4;
- 1973 *Arnoglossus laterna* – ANFOSSI & MOSNA, pl. 12, figs. 11-13;
- 1980 *Arnoglossus bauzai* – NOLF & MARTINELL, pl. 5, figs 26-29;
- 1983 *Arnoglossus kokeni* – NOLF & STEURBAUT, pl. 7, fig. 24;
- 1999 *Arnoglossus quadratus* – SCHWARZHANS;

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- 1999 *Laeops rhabensis* – SCHWARZHANS;
1999 *Arnoglossus kokeni* – SCHWARZHANS, pg. 172,174, figs.360-364;
2000 *Arnoglossus kokeni* – NOLF & GIRONE, pl.3, fig.13-14;
2001 *Arnoglossus kokeni* – GIRONE & VAROLA, pl.1, fig.15;
2013 *Arnoglossus kokeni* – NOLF, pl. 348.

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 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.

4.2 Teleost fish paleobiogeography

4.2.1 Revision of the geographic and stratigraphic distributions

The present study yielded the identification of eighty-one (81) species, belonging to sixty (60) genera and thirty-four (34) families. Thirty-two (32) of these are pelagic species, placed under twenty-one (21) genera and ten (10) families, while the majority of forty-nine (49) species are benthic or benthopelagic fish, belonging to thirty-nine (39) genera and twenty-six (26) families. The stratigraphic and geographic distributions of the identified taxa are presented in Tables 4.1 and 4.2. Overall, the stratigraphic distribution of twenty-nine (29) taxa is significantly extended. In particular, twelve (12) species are reported for the first time in the Zanclean of the eastern Mediterranean realm. In the Gelasian stage, eight (8) species are reported as new for this area. The Calabrian record is enriched by twenty-one (21) taxa.

The pelagic fish include members of the families Engraulidae, Gonostomatidae, Sternoptychidae, Phosichthyidae, Clupeidae, Scopelarchidae, Gobiidae, Bregmacerotidae; Myctophids however are by far the most diverse and abundant family. Based on already published data and the present record five pelagic species can safely be assumed to inhabit the Mediterranean Sea up until the Gelasian: *Scopelarchus analis*, *Diaphus* aff. *adenomus*, *Diaphus cavallonis*, *Diaphus* aff. *splendidus* and *Myctophum fitchi*. Also, *Notoscopelus resplendens*, *Scopelopsis pliogenicus* and *Bregmaceros* sp. may be found until the Middle Pleistocene stage/age. Importantly, the arctic mesopelagic species *Protomyctophum arcticum* is reported here for the first time in the eastern Mediterranean Calabrian. This species is presently distributed in the arctic regions but, along with *Benthoosema glaciale*, they are known to spawn both south and north of the Atlantic Polar Front (Mecklenburg et al. 2011). Girone et al. (2006) previously reported *P. arcticum* from the Upper Pleistocene of the western Mediterranean.

The most numerous and diverse deep-water groups are congrid, gadids, sparids and gobiids. According to the data known until now (Table 4.2), the following notes are made. Five congrid species have inhabited the eastern Mediterranean from the early Pliocene until now; *Conger conger* and *Pseudophichthys splendens* appear present the entire time, until today. *Gnathopis mystax* is first here recorded in the Calabrian stage sediments of Ypsenis.

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Family	Taxon	western Mediterranean										eastern Mediterranean							Present-day Atlantic	Present-day Indo-Pacific	Studied material	References								
		Mio-cene		Plio-cene		Pleistocene				Holocene	Mio-cene		Plio-cene		Pleistocene			Holocene												
		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Upper		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle						Upper							
PELAGIC TAXA																														
Engraulidae	<i>Engraulis encrasicolus</i>			+	+	+	+	+												+	+			+	+	+		Y,Va,Ka	36	
Clupeidae	<i>Sardinella maderensis</i>			+																								Va	3,7	
Gonostomatidae	<i>Gonostoma</i> sp.	+	+	+					+	+																		Y	36	
Sternoptychidae	<i>Maurolicus muelleri</i>	+	+	+	+	+	+	+																				Vo,Y,F,Va	1,2,3,8,9,12,13,14,16,18,19,21,22,23,24,25,26,27,28,34	
Phosichthyidae	<i>Vinciguerra cf. attenuata</i>					+	+		+																			Y	36	
	<i>Vinciguerra poweriae</i>	+	+	+	+	+	+	+																				Vo,F,Va	1,3,8,9,13, 22, 24,25,26,28,36	
Scopelarchidae	<i>Scopelarchus analis</i>	+	+	+		+	+	+																				Va	34,36	
Myctophidae	<i>Benthoosema glaciale</i>		?	+	+	+	+	+	+	+																		Y,F,Va	36	
	<i>Benthoosema suborbitale</i>			+	+	+	+																					Y	36	
	<i>Ceratoscopelus maderensis</i>			+	+	+	+	+		+																		Vo,Y,F,Va,Ka	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 aff. adenomus</i>				+																							Vo	3	
	<i>Diaphus cavallonis</i>	+	+	+	+																							Vo	3,4,7,8,9,13,14,15,17,34	
	<i>Diaphus holti</i>	+	+	+	+	+	+			+																		Vo,Y,F,Va	1,3,4,6,7,9,13,2,2,23,26,28,33,36	
	<i>Diaphus rafinesquii</i>	+	+	+	+	+	+			+																		Vo,Y,F,Va	1,3,4,6,8,9,13,1,4,23,26,27,28,29,31,34,36	
	<i>Diaphus aff. splendidus</i>	+	+	+	+	+		+																				Vo	3,4,7,8,9,13,14,17,23,26,27,28,32,33,34	
	<i>Diaphus taaningi</i>	+	+	+	+	+	+																					Vo,Y,F,Va	1,4,7,9,13,26,27,28,34	
	<i>Electrona risso</i>			+	+	+	+	+	+	+																			F,Va	36
	<i>Hygophum benoitii</i>					+				+																			Vo,Y,F,Va,Ka	1,8,13,23,24,26,27,28
	<i>Hygophum hygomii</i>	+	+	+	+	+	+	+		+																			Vo,Y,F	1,3,5,6,7,8,9,13,14,15,22,23,24,26,27,28,29,31,32,34
	<i>Lampadena</i> sp.	+		+	+	+	+	+	+	+																			F	34,36
	<i>Lampanyctus crocodilus</i>					+	+	+		+																			F,Va	36
	<i>Lobianchia dofleini</i>	+	+	+	+	+	+			+																			Vo,Y,F,Va	1,5,7,9,7,13,14,22,23,25,26,27,28,31,34
Myctophidae	<i>Myctophum fitchi</i>	+		+	+	+																						Vo	3,5,6,7,9,13,14,15,33,34	
	<i>Myctophum punctatum</i>			+	+	+	+	+		+																		Y,F,Ka	36	
	<i>Notoscopelus elongatus</i>	+				+	+	+		+																		Y,F,Va	36	
	<i>Notoscopelus resplendens</i>	+		+	+																							Vo	3,5,6,8,9,13,15,29	
	<i>Protomyctophum arcticum</i>								+																			Y,F	36	
	<i>Scopelopsis pliocenicus</i>	+		+	+		+																					Vo,Y,F	1,3,5,6,7,8,9,13,15,26,28,29,33,34	
Bregmacerotidae	<i>Bregmaceros</i> sp.	+	+	+	+	+	+																					Vo	1,2,3,8,9,11,12,13,16,18,19,20,21,22,24,29,31,34	
Gobiidae	<i>Aphia minuta</i>		+				+	+		+																		Vo,Y,F,Va,Ka	13,27,34	

Table 4.1 Geographic and stratigraphic distribution of the identified pelagic fish taxa. The respective sedimentary outcrops where the identified material, in this study, has been found is indicated in the column ‘studied material’; Vo: Voutes, Y: Ypsenis, Va: Vagia, F: Faliraki 4, Ka: Kalitheia. Present-day distributions are according to the Fishbase database (Froese & Pauly, 2013). **Dark grey** indicates those taxa whose record in the present study marks the first in the eastern Mediterranean Sea for the interval noted. **Light grey** indicates the taxa which have been reported in the eastern Mediterranean before, for the time interval noted, but only in the Ionian realm. Present-day Indo-Pacific distribution of *Maurolicus muelleri* is confined to the eastern part of the Pacific Ocean.

Pseudophichthys escavaratierensis shows no record in the post-Zanclean sediments studied, and was only identified in the Voutes section. Also, the extinct species *Rhynchoconger pantanellii* is recorded until the Calabrian.

Furthermore, the Atlantic species *Polyipnus polli*, departed today from the Mediterranean realm, is identified in the Calabrian stage, while it has previously been found in the Middle Pleistocene of Montalbano Jonico section (Girone and Varola, 2001). The presently abundant deep-water *Chlorophthalmus agassizi*, which has only a single previous record in the Middle Pleistocene age sediments of Kephallonia (Ionian Sea), is found again in the Calabrian (Faliraki section) and the Zanclean (Voutes section).

Gadidae are present in the record with four species: *Gadiculus argenteus*, *G. labiatus*, *G. thori* and *Micromesistius poutassou*. *Gadiculus argenteus* and *M. poutassou* appear to have been present in the Mediterranean realm from the early Pliocene continuously through today. The fossil record on *Gadiculus thori* is rather poor, and it seems to have inhabited the Mediterranean from the Gelasian to the Calabrian age. On the other hand, *G. labiatus* also exhibits a continuous record from the Tortonian until the Calabrian.

In addition, *Epigonus denticulatus* is identified for the first time in the eastern Mediterranean Zanclean. *Oblada melanura*, *Pagellus cf. bogaraveo*, *Pargus pargus*, *Sardinella maderensis* and *Gobius cf. paganellus* are reported in the eastern Mediterranean realm, outside the Ionian Sea, for the first time. Finally, *Lesueurigobius sanzi* is first found in the Calabrian of Faliraki section.

4.2.2 Comments on the evolution of the Teleost fish eastern Mediterranean fauna

Older reviews of the evolution of the Cenozoic Mediterranean fish fauna (Nolf et al. 1998; Gaudant 2002; Landini and Sorbini 2005a & b; Girone et al. 2006; 2010) highlight the necessity for a niche-based approach to this problem. In general, the Pliocene deep-water faunas are composed of circumglobal oceanic species, but gradually the strictly Atlantic fish prevail (Nolf et al. 1998; Landini and Sorbini 2005). Girone et al. (2006) documented this Atlantic invasion of deep-water fish in the Mediterranean Sea from the Late Pliocene lasting until the Late Pleistocene. In the neritic realm, the inhabitants are restricted to the Mediterranean and mostly prevail

until today, even since the Rupelian (Nolf and Girone 2008) and certainly since before the Messinian crisis (Girone et al. 2010). Table 4.3 presents the fish taxa identified through this study, sorted according to their modern or hypothesized niche, including their stratigraphic distribution. Please note that this Table is far from any sense of complete, and comments may only be safely drawn in specific cases. Much more data would be required to fill in the fossil record and provide a more thorough overview of the fish taxa per niche for the Mediterranean Sea through time. Bearing this in mind, the following observations are facilitated:

Already by Girone et al. (2006) the transition from the warmer Pliocene to an overall colder Pleistocene climatic regime was transferred to the fish assemblages, through the replacement of pelagic tropical-subtropical by subtropical-subpolar species. Very characteristic is the example of *Notoscopelus* spp. Currently subtropical *Notoscopelus elongatus* inhabits the Aegean Sea (Lambropoulou and Papaconstantinou 2000), which until recently had erroneously been considered a synonym of the North Atlantic temperate species *N. kroyeri*. Girone et al. (2006) supported that *N. elongatus* s.l. (including at the time *N. kroyeri*) replaced the tropical-subtropical *N. resplendens*. Indeed, it appears that *N. resplendens* and *N. kroyeri* are meso-bathypelagic species distributed in oceanic areas, whereas *N. elongatus* is a pelagic-oceanic fish adapted to the Mediterranean habitats. *Notoscopelus elongatus* presents a stratigraphic distribution, in the eastern Mediterranean Sea, from the Zanclean until the Calabrian; *N. resplendens* has been identified since the Gelasian. Girone et al. (2006) also report *Notoscopelus (elongatus) aff. kroyeri* in the Calabrian sediments of Vrica and Fiumefreddo. It is perceived that the replacement of the co-generic species did not occur in a single process. *Notoscopelus resplendens* was replaced sometime in the Calabrian age, probably initially by *N. kroyeri* which quickly evolved to the more adapted form of *N. elongatus*.

Tropically distributed pelagic taxa appearing through the Pliocene have now departed from the Mediterranean. Examples include *Bregmaceros* sp., recently re-entering as *B. atlanticus*, also *Diaphus taaningi*, *Scopelarchus analis*, *Scopelopsis pliogenicus*, *Benthosema suborbitale*, *Diaphus adenomus* and *Diaphus splendidus*. *Myctophum fitchi*, presumably a subtropical (- tropical) species, was gradually

Chapter 4. Results

Preferred habitat		Miocene	Zanclean	Piacenzian	Gelasian	Calabrian	Middle [*] Pleistocene	Holocene	
Coastal, pelagic	ST, marine/brackish				<i>E. encrasicolus</i>	<i>E. encrasicolus</i>		<i>E. encrasicolus</i>	
					<i>S. maderensis</i>			<i>S. maderensis</i>	
Pelagic, neritic	ST, marine/brackish, sand/mud/eel-grass		<i>A. minuta</i>		<i>A. minuta</i>	<i>A. minuta</i>		<i>A. minuta</i>	
Pelagic-oceanic and Meso-bathypelagic	Tr	<i>Bregmaceros</i> sp.	<i>Bregmaceros</i> sp.	<i>Bregmaceros</i> sp.	<i>Bregmaceros</i> sp.	<i>Bregmaceros</i> sp.			
	Tr, continental shelf and slope	<i>D. taaningi</i>	<i>D. taaningi</i>	<i>D. taaningi</i>	<i>D. taaningi</i>	<i>D. taaningi</i>	<i>D. taaningi</i>		
	ST-Tr			<i>S. pliocenicus</i>	<i>S. pliocenicus</i>	<i>S. pliocenicus</i>	<i>S. pliocenicus</i>	<i>S. pliocenicus</i>	
				<i>D. aff. adenomus</i>					
			<i>D. aff. splendidus</i>	<i>D. aff. splendidus</i>	<i>D. aff. splendidus</i>	<i>D. aff. splendidus</i>			
			<i>E. risso</i>	<i>E. risso</i>	<i>E. risso</i>	<i>E. risso</i>	<i>E. risso</i>	<i>E. risso</i>	<i>E. risso</i>
			<i>H. hygomii</i>	<i>H. hygomii</i>	<i>H. hygomii</i>	<i>H. hygomii</i>	<i>H. hygomii</i>	<i>H. hygomii</i>	<i>H. hygomii</i>
			<i>N. resplendens</i>	<i>N. resplendens</i>	<i>N. resplendens</i>	<i>N. resplendens</i>	<i>N. resplendens</i>		
	ST			<i>V. poweriae</i>	<i>V. poweriae</i>	<i>V. poweriae</i>	<i>V. poweriae</i>	<i>V. poweriae</i>	<i>V. poweriae</i>
			<i>L. dofleini</i>	<i>L. dofleini</i>	<i>L. dofleini</i>	<i>L. dofleini</i>	<i>L. dofleini</i>	<i>L. dofleini</i>	<i>L. dofleini</i>
				<i>M. fitchi</i>	<i>M. fitchi</i>	<i>M. fitchi</i>			
					<i>N. elongatus</i>	<i>N. elongatus</i>	<i>N. elongatus</i>	<i>N. elongatus</i>	<i>N. elongatus</i>
	Te-ST				<i>M. punctatum</i>	<i>M. punctatum</i>	<i>M. punctatum</i>	<i>M. punctatum</i>	<i>M. punctatum</i>
					<i>L. crocodilus</i>	<i>L. crocodilus</i>	<i>L. crocodilus</i>	<i>L. crocodilus</i>	<i>L. crocodilus</i>
	Te		<i>C. maderensis</i>	<i>C. maderensis</i>	<i>C. maderensis</i>	<i>C. maderensis</i>	<i>C. maderensis</i>	<i>C. maderensis</i>	<i>C. maderensis</i>
		<i>D. holti</i>	<i>D. holti</i>	<i>D. holti</i>	<i>D. holti</i>	<i>D. holti</i>	<i>D. holti</i>	<i>D. holti</i>	
		<i>D. rafinesquii</i>	<i>D. rafinesquii</i>	<i>D. rafinesquii</i>	<i>D. rafinesquii</i>	<i>D. rafinesquii</i>	<i>D. rafinesquii</i>	<i>D. rafinesquii</i>	
		<i>H. benoiti</i>	<i>H. benoiti</i>	<i>H. benoiti</i>	<i>H. benoiti</i>	<i>H. benoiti</i>	<i>H. benoiti</i>	<i>H. benoiti</i>	
						<i>P. arcticum</i>			
SP-Te	<i>B. glaciale</i>	<i>B. glaciale</i>	<i>B. glaciale</i>	<i>B. glaciale</i>	<i>B. glaciale</i>	<i>B. glaciale</i>	<i>B. glaciale</i>		
SP-ST	<i>M. muelleri</i>	<i>M. muelleri</i>	<i>M. muelleri</i>	<i>M. muelleri</i>	<i>M. muelleri</i>	<i>M. muelleri</i>	<i>M. muelleri</i>		
Pelagic	Te-Tr				<i>Gaidropsarus</i> sp.	<i>Gaidropsarus</i> sp.	<i>Gaidropsarus</i> sp.		
Coastal, benthic	ST, <u>soft</u> bottoms				<i>C. acus</i>	<i>C. acus</i>	<i>C. acus</i>	<i>C. acus</i>	
			<i>D. quadrimaculatus</i>	<i>D. quadrimaculatus</i>	<i>D. quadrimaculatus</i>	<i>D. quadrimaculatus</i>	<i>D. quadrimaculatus</i>	<i>D. quadrimaculatus</i>	
		<i>L. sanzii</i>	<i>L. friesii</i> , <i>L. sanzii</i>		<i>L. friesii</i>	<i>L. friesii</i> , <i>L. sanzii</i>	<i>L. friesii</i>	<i>L. friesii</i>	
			<i>L. suerii</i>	<i>L. suerii</i>	<i>L. suerii</i>	<i>L. suerii</i>	<i>L. suerii</i>	<i>L. suerii</i>	
			<i>C. linguatula</i>	<i>C. linguatula</i>	<i>C. linguatula</i>	<i>C. linguatula</i>	<i>C. linguatula</i>	<i>C. linguatula</i>	
		<i>A. kokeni</i>	<i>A. kokeni</i>	<i>A. kokeni</i>	<i>A. kokeni</i>			<i>Arnoglossus</i> spp.	
	ST, <u>rocky</u> bottoms		<i>G. ater</i>		<i>G. ater</i>	<i>G. ater</i>			
		<i>Apogon</i> sp.	<i>Apogon</i> sp.					<i>Apogon imberbis</i>	
	ST, marine/ <u>brackish</u>		<i>A. boyeri</i>	<i>A. boyeri</i>		<i>A. boyeri</i>	<i>A. boyeri</i>	<i>A. boyeri</i>	
					<i>Trachurus</i> spp.	<i>Trachurus</i> spp.	<i>Trachurus</i> spp.	<i>Trachurus</i> spp.	
				<i>G. cf. paganellus</i>		<i>G. cf. paganellus</i>		<i>G. paganellus</i>	
			<i>G. niger</i>	<i>G. niger</i>	<i>G. niger</i>	<i>G. niger</i>	<i>G. niger</i>	<i>G. niger</i>	
						<i>C. chromis</i>	<i>C. chromis</i>		
Coastal, benthopelagic	ST, <u>hard</u> bottoms, inverts	<i>Dentex</i> spp.	<i>Dentex</i> spp.	<i>Dentex</i> spp.	<i>Dentex</i> spp.	<i>Dentex</i> spp.			
	ST, <u>rock/seagrass</u> , inverts		<i>O. melanura</i>		<i>O. melanura</i>	<i>O. melanura</i>			
	ST, <u>brackish/marine</u> , <u>rock/seagrass</u> , inverts					<i>D.cf.annularis</i>	<i>D. annularis</i>		
Coastal, benthopelagic	ST, <u>Posidonia</u> beds/ <u>muddy</u> bottoms		<i>S. smaris</i>	<i>S. smaris</i>	<i>S. smaris</i>	<i>S. smaris</i>	<i>S. smaris</i>		
	ST, <u>inshore</u> , inverts/fish		<i>P. erythrinus</i>	<i>P. erythrinus</i>			<i>P. erythrinus</i>		
	Te, <u>inshore</u> , <u>muddy</u> bottoms, woms/inverts/fish					<i>P.cf.bogaraveo</i>	<i>P.bogaraveo</i>		
	ST, inverts/fish					<i>P. pagrus</i>	<i>P. pagrus</i>		
Coastal/deep-water, benthic	ST, <u>sand/mud</u> bottoms, inverts	<i>C. macrophthalma</i>	<i>C. macrophthalma</i>	<i>C. macrophthalma</i>	<i>C. macrophthalma</i>	<i>C. macrophthalma</i>	<i>C. macrophthalma</i>		
	ST, <u>hard</u> bottoms, inverts					<i>B. ocellaris</i>	<i>B. ocellaris</i>		
	Te, <u>rocky/sandy</u> bottoms, fish/inverts		<i>C. conger</i>	<i>C. conger</i>		<i>C. conger</i>	<i>C. conger</i>		

Preferred habitat		Miocene	Zanclean	Piacenzian	Gelasian	Calabrian	Middle* Pleistocene	Holocene
Continental slope, benthic	ST, muddy/sandy bottoms, fish/inverts					<i>G.mystax</i>		<i>G.mystax</i>
	ST-Tr	<i>R. pantanellii</i>	<i>R. pantanellii</i>	<i>R. pantanellii</i>	<i>R. pantanellii</i>	<i>R. pantanellii</i>		
Deep-water, benthic	ST-Tr, muddy bottoms, fish/inverts	<i>P.splendens</i>	<i>P.splendens</i> , <i>P.escavaratiere nsis</i>		<i>P. splendens</i>	<i>P. splendens</i>		
	ST-Te, polych./fish/inv	<i>A. sphyraena</i>	<i>A. sphyraena</i>	<i>A. sphyraena</i>		<i>A. sphyraena</i>		<i>A. sphyraena</i>
	ST-Tr, outer shelf/continental slope, shrimp	<i>Laemonema</i> spp.	<i>Laemonema</i> spp.	<i>Laemonema</i> spp.	<i>Laemonema</i> spp.	<i>Laemonema</i> spp.		
	ST		<i>E.dentatus</i>			<i>E.dentatus</i>	<i>E.dentatus</i>	<i>E.dentatus</i>
	Te-Tr, fish/inverts		<i>E.denticulatus</i>					<i>E.denticulatus</i>
Deep-water, bathypelagic	Te-Tr, muddy bottom, oligotrophic		<i>C. agassizi</i>			<i>C. agassizi</i>	<i>C. agassizi</i>	<i>C. agassizi</i>
	Te, inverts/worms	<i>G. argenteus</i>	<i>G. argenteus</i>	<i>G. argenteus</i>	<i>G. argenteus</i>	<i>G. argenteus</i>	<i>G. argenteus</i>	<i>G. argenteus</i>
	Tr-ST	<i>G. labiatus</i>	<i>G. labiatus</i>	<i>G. labiatus</i>	<i>G. labiatus</i>	<i>G. labiatus</i>		
	Te, muddy bottoms				<i>G. thori</i>	<i>G. thori</i>		
	Te, continental slope/shelf		<i>M. poutassou</i>	<i>M. poutassou</i>	<i>M. poutassou</i>	<i>M. poutassou</i>	<i>M. poutassou</i>	<i>M. poutassou</i>
	Tr-ST, continen. shelf/slope	<i>P. mutinensis</i>	<i>P. mutinensis</i>	<i>P. mutinensis</i>	<i>P. mutinensis</i>			
Deep-water, bathypelagic	Tr					<i>P. polli</i>	<i>P. polli</i>	
	Te-ST	<i>Coelorinchus</i> spp.	<i>Coelorinchus</i> spp.	<i>Coelorinchus</i> spp.	<i>Coelorinchus</i> spp.	<i>Coelorinchus</i> spp.	<i>Coelorinchus</i> spp.	<i>Coelorinchus</i> spp.
	Te, sandy/muddy bottoms, fish/inverts				<i>P. blennoides</i>	<i>P. blennoides</i>		<i>P. blennoides</i>

Table 4.3 The eastern Mediterranean Teleost fish; taxa per niche. The niche descriptions are presented in correlation to and referenced in Table 2.1. Fossil species and their hypothesized ecological niche are shown in **bold**. Most of these fish are found in marine environments. Otherwise it is specified. Distribution in the present climatic zones: SP. subpolar, Te. temperate, ST. subtropical, Tr. tropical. *no reference is made to the Upper Pleistocene age, because there are not sufficient data for this interval.

replaced by the subtropical-temperate *Myctophum punctatum* in the meso-bathypelagic domain. Likewise, *Rhynchoconger pantanellii* is hypothetically a subtropical – tropical species of the continental slope. From the Calabrian, the purely subtropical congrid *Gnathophis mystax* occupies this continental slope, possibly displacing *R. pantanellii*. In the deep-water, *Gadiculus labiatus* and *Parascombrops mutinensis* have also departed during the Calabrian and Gelasian respectively, but their replacement could not be singled out at this point.

Interesting is the occurrence of *Chlorophthalmus agassizi* in the eastern Mediterranean Pliocene and Pleistocene. This species has not been reported in the western sub-basin. Currently *Chlorophthalmus agassizi* dominates the present-day eastern Ionian Sea, whereas *Gadiculus argenteus* prefers the western Ionian (Mytilineou et al. 2005). Anastasopoulou and Kaporis (2008) suggested that *C. agassizi* is well-adapted to oligotrophic environments, exploiting a wide variety of available niches. If indeed *C. agassizi* is an oligotrophy indicator, then its presence since the Calabrian, but also in the Zanclean is very suggestive of the eastern Mediterranean oceanographic conditions at these times.

4.3 Paleoenvironmental reconstruction

CRETE ISLAND

4.3.1 *Voutes*

4.3.1.1 Paleobathymetry

The paleodepth analysis and estimates are presented in Figures 4.1 and 4.2. In sample *Voutes b*, only three species may be considered, which provided a paleobathymetric estimate between 10-130 m, *Cepola macrophthalma*, *Deltentosteus* aff. *quadrimaculatus* and *Lesueurigobius friesii*. In *Voutes 3* the analysis delivered an estimate of 50-350 m. However, this range is affected by the 50-meter intervals used in the analysis. After closer examination, it may be observed that the actual paleodepth estimate ought to be that where both *Aphia minuta* and *Diaphus adenomus* could coexist, and that is between 87-100 m depth. The presence of *D. holti*, *H. hygomii* and *Laemonema* sp. in *Voutes 4* leads to a paleodepth estimate between 200-800 m, with no greater accuracy available for this level. The fish taxa identified in sample *Voutes 1* did not allow for the paleobathymetric estimation. In particular, in this sample the following taxa have been identified: Myctophidae indeterminable (ind.), *Bregmaceros* sp., *Laemonema* sp., *Gadiculus labiatus*, Sparidae ind. and Perciformes ind. The great abundance of *Bregmaceros* sp., in conjunction with the presence of Myctophids and deep-water benthopelagic taxa such as *Laemonema* sp., *Gadiculus labiatus* and Perciformes, may indicate a rather deep marine environment, generally exceeding 200 m.

A mixed fauna is revealed through the paleobathymetric analysis in sample *Voutes c*. Indeed, although at first observation the results seem straightforward to provide an estimate between 300-337 m, delimited by the maximum depth distribution of *L. suerii*, the presence of *Oblada melanura* is problematic. This benthopelagic fish today inhabits rocky bottom of depths up to 30 m, in the coasts of the eastern Atlantic and the Mediterranean Sea. In addition, reef-associated taxa *Grammonus ater* and *Apogon* sp. were also present in sample *Voutes c*. Two faunal units may thus be separated in this level, a deeper neritic unit from an environment reaching depths around 300-337 m, and a shallow unit from depths between 0-30 m.

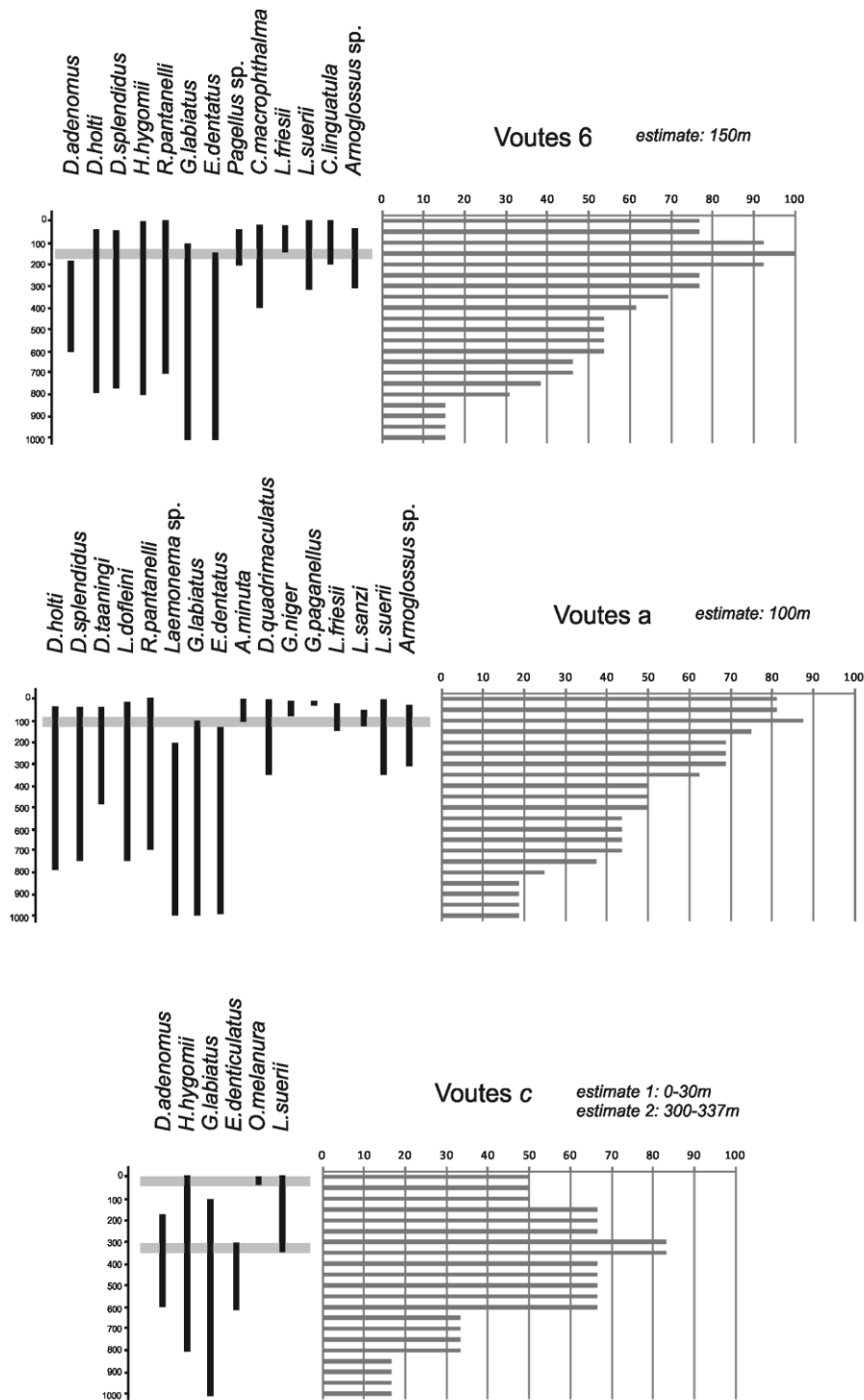


Figure 4.1 Voutes paleobathymetric analysis and estimates.

Although the paleobathymetric method does yield a conclusive result for sample *a*, it is noted that the cumulative percentage is very low; only 88% for the 100 meters depth value. In addition, *Echiodon dentatus* as well as *Laemonema spp.* inhabit deeper waters, whereas *Aphia minuta*, *Gobius niger* and *Gobius paganellus* require shallower environments than the proposed 100 m common depth for the entire

assemblage. Consequently, it is proposed that this sample also features a mixed fauna comprised of a shallow component inhabiting depths 15-30 m, and a deeper-water constituent from depths greater than 100 m. This hypothesis is in agreement with the appearance of the gravity flows observed at this level of the outcrop.

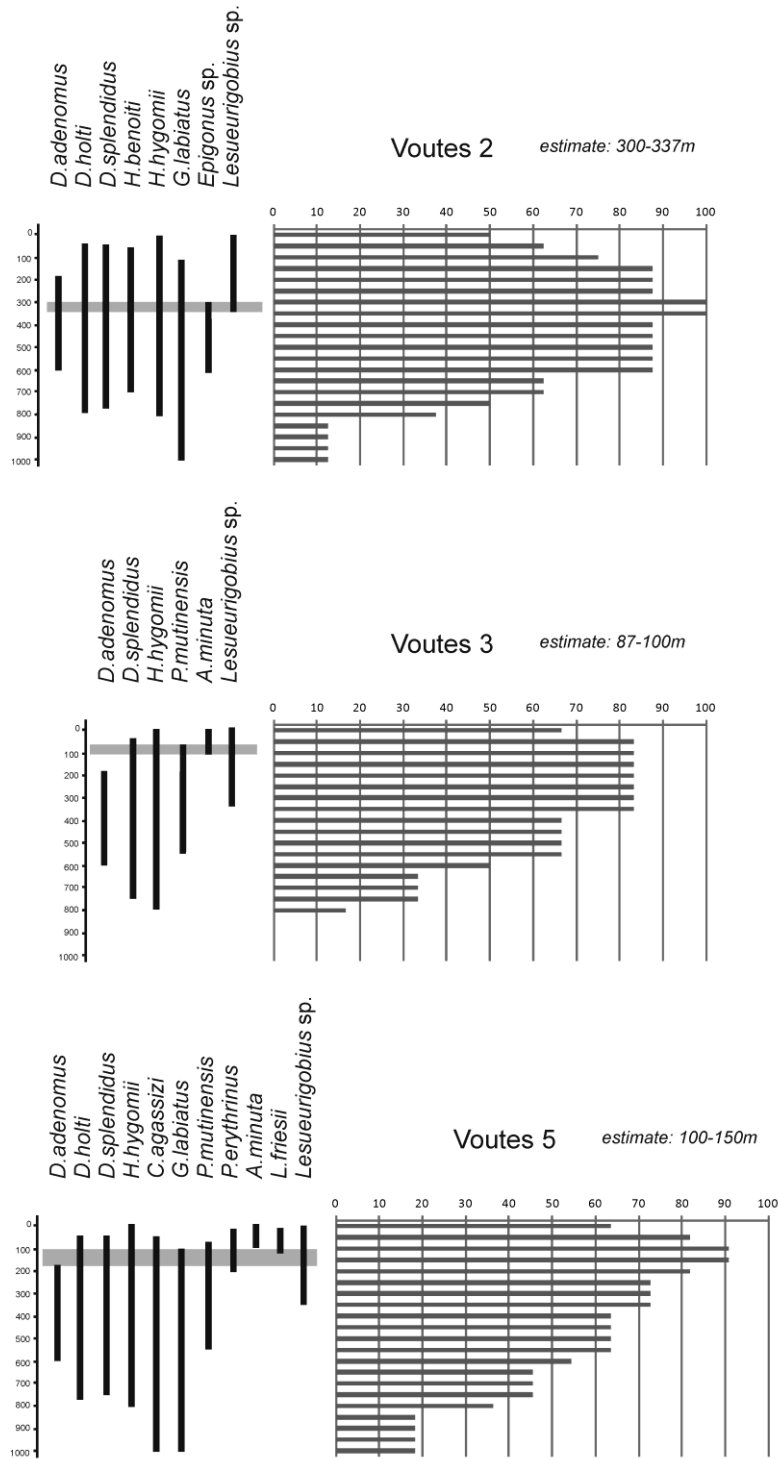


Figure 4.2 Voutes paleobathymetric analysis and estimates (continuation).

4.3.1.2 Paleoecology

The following observations result from the quantitative analysis of the Voutes teleost fish assemblages (Figures 4.3 and 4.4):

- The Pliocene Voutes ichthyofauna exhibits tropical to subtropical affinities. No general tendencies may be observed in the group abundances (Fig. 4.4).
- Subpolar taxa are scarce throughout the section. The only subpolar-temperate species present in the pelagic component of the Voutes assemblages is *Maurolicus muelleri*, which has a small relative abundance of 1.52% and 0.55%, in samples 3 and *a* respectively (Table 4.4). No benthic-benthopelagic subpolar species is present in the assemblages.

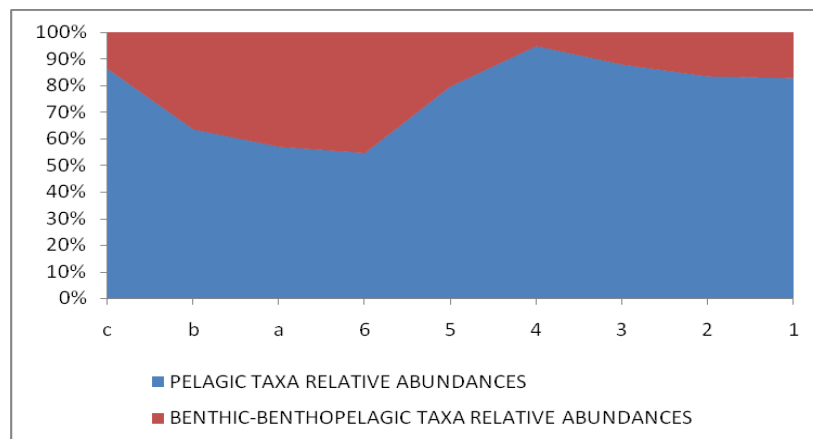


Figure 4.3 Contribution of the pelagic and the benthic-benthopelagic taxa to the Voutes taphocoenoses.

- The pelagic group relative abundances generally follow those of the total contributions. This is probably related to the overall lower participation of the benthic-benthopelagic taxa in the taphocoenosis (Fig. 4.3). As a result, the total relative abundances of the different climatic groups are mainly determined by the pelagic contribution.
- Samples 4 and 1, taken from the diatomite beds, exhibit the highest tropical group abundances in the benthic-benthopelagic component, 50% and 25% respectively. However, the benthic-benthopelagic taxa amount to only 5.21% of the total fauna in sample 4. Indeed, the scarce two otolith specimens of subtropical-tropical *Laemonema* sp. found in this sample are responsible for the 50% tropical taxa relative abundance (Table 4.4). Thus, clearly the group

abundances in the benthic-benthopelagic component of sample 4 are overestimated.

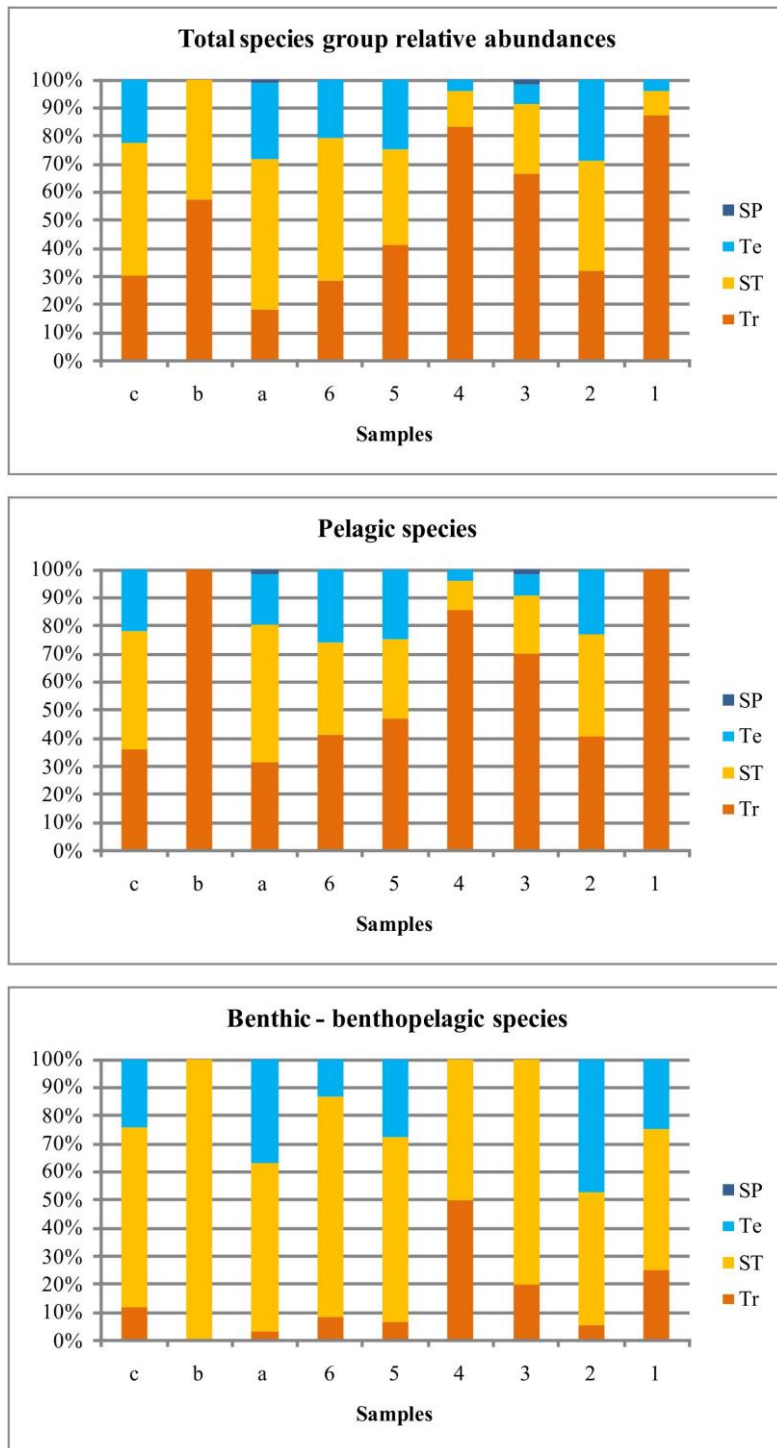


Figure 4.4 The relative contribution of the different ecological groups in Voutes assemblages. Tr: tropical, ST: subtropical, Te: temperate, SP: subpolar.

Taxonomic placement		Sample								
Family	Genus/Species	c	b	a	6	5	4	3	2	1
PELAGIC TAXA										
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)	0.00	0.00	0.55	0.00	0.00	0.00	1.52	0.00	0.00
Phosichthyidae	<i>Vinciguerra poweriae</i> (Cocco, 1838)	3.45	0.00	0.82	2.20	2.33	0.00	0.00	0.00	0.00
Myctophidae	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	8.05	0.00	2.19	12.33	11.05	2.08	6.06	11.76	0.00
	<i>Diaphus</i> aff. <i>adenomus</i> Gilbert, 1905	1.72	0.00	0.00	1.76	5.23	0.00	5.30	1.07	0.00
	<i>Diaphus cavallonis</i> (Brzobohaty and Nolf, 2000)	6.32	0.00	6.85	4.41	3.49	2.08	8.33	11.23	0.00
	<i>Diaphus holti</i> Taaning, 1918	0.00	0.00	3.29	3.08	12.21	2.08	0.00	1.07	0.00
	<i>Diaphus rafinesquii</i> (Cocco, 1838)	2.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Diaphus</i> aff. <i>splendidus</i> (Brauer, 1904)	0.00	0.00	1.37	4.85	6.98	0.00	1.52	3.74	0.00
	<i>Diaphus taaningi</i> Norman, 1930	0.00	0.00	2.47	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Diaphus</i> sp.	48.85	17.57	27.40	7.49	7.56	0.00	6.06	37.43	0.00
	<i>Hygophum benoitii</i> (Cocco, 1838)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.00
	<i>Hygophum hygomii</i> (Lotken, 1892)	5.17	0.00	0.00	0.88	2.91	4.17	4.55	2.67	0.00
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)	0.00	0.00	2.19	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Myctophum fitchi</i> (Schwarzhans, 1979)	1.15	0.00	4.66	1.32	0.00	2.08	0.00	3.21	0.00
	<i>Notoscopelus resplendens</i> (Richardson, 1845)	2.30	0.00	0.00	4.41	4.07	0.00	0.00	0.00	0.00
	<i>Notoscopelus</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	2.27	0.00	0.00
	<i>Scopelopsis pliocenicus</i> (Anfossi & Mosna, 1976)	0.00	0.00	0.00	0.00	1.74	2.08	0.00	0.00	0.00
indet.	5.17	5.41	5.21	3.52	0.00	0.00	1.52	4.28	13.79	
Bregmacerotidae	<i>Bregmaceros</i> sp.	1.72	40.54	0.00	8.37	22.09	80.21	50.76	5.88	68.97
BENTHIC AND BENTHOPELAGIC TAXA										
Congridae	<i>Pseudophichthys splendens</i> (Lea, 1913)	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
	<i>Pseudophichthys escavaratierensis</i> (Nolf and Cappetta, 1988)	0.00	0.00	0.00	0.00	0.00	0.00	1.52	0.00	0.00
	<i>Rhynchoconger pantanellii</i> (Bassoli, 1906)	0.00	0.00	0.55	2.20	0.00	0.00	0.00	0.00	0.00
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i> Bonaparte, 1840	0.00	0.00	0.00	0.00	1.16	0.00	0.00	0.00	0.00
Moridae	<i>Laemonema</i> sp.	0.00	0.00	0.55	0.00	0.00	3.13	0.00	0.00	3.45
Gadidae	<i>Gadiculus labiatus</i> (Schubert, 1905)	1.72	0.00	1.37	3.96	3.49	0.00	0.00	8.02	3.45
	Indet. lapilli	4.60	0.00	0.00	0.00	6.98	0.00	0.00	1.60	3.45
Bythitidae	<i>Grammonus ater</i> (Risso, 1810)	2.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Carapidae	<i>Echiodon dentatus</i> (Cuvier, 1829)	0.00	0.00	0.55	0.88	0.00	0.00	0.00	0.00	0.00
Atherinidae	<i>Atherina boyeri</i> Risso, 1810	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Apogonidae	<i>Apogon</i> sp.	1.15	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Epigonidae	<i>Epigonus</i> aff. <i>denticulatus</i> Dieuzeide, 1950	1.72	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Epigonus</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.00
Acropomatidae	<i>Parascombrops mutinensis</i> (Bassoli, 1906)	0.00	0.00	0.00	0.00	1.74	0.00	3.03	0.00	0.00
Sparidae	<i>Oblada melanura</i> (Linnaeus, 1758)	1.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Pagellus erythrinus</i> (Linnaeus, 1758)	0.00	0.00	0.00	0.00	1.16	0.00	0.00	0.00	0.00
	<i>Pagellus</i> sp.	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
	Indet.	0.00	2.70	3.84	0.88	0.00	2.08	0.00	0.00	3.45
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)	0.00	2.70	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Perciformes	Indet.	0.00	0.00	1.10	3.52	0.00	0.00	4.55	1.07	3.45

Taxonomic placement		Sample								
Family	Genus/Species	c	b	a	6	5	4	3	2	1
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)	0.00	0.00	0.82	0.00	2.33	0.00	1.52	0.00	0.00
	<i>Deltentosteus</i> aff. <i>quadrimaculatus</i> (Valenciennes, 1837)	0.00	8.11	3.56	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Gobius niger</i> Linnaeus, 1758	0.00	0.00	10.41	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Gobius</i> cf. <i>paganellus</i> Linnaeus, 1758	0.00	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Gobius</i> sp.1	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
	<i>Gobius</i> sp.	0.00	0.00	1.37	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Lesueurigobius friesii</i> (Malm, 1874)	0.00	18.92	7.95	9.25	1.16	0.00	0.00	0.00	0.00
	<i>Lesueurigobius sanzi</i> (de Buen, 1918)	0.00	0.00	2.19	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Lesueurigobius suerii</i> (Risso, 1810)	1.15	0.00	0.82	7.49	0.00	0.00	0.00	0.00	0.00
	<i>Lesueurigobius</i> sp.	0.00	0.00	0.00	0.00	1.16	0.00	1.52	3.74	0.00
	genus « <i>Gobidarum</i> » sp.1	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
	Indet.	0.00	4.05	6.30	9.25	1.16	0.00	0.00	0.00	0.00
Trichiuridae	Indet.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.07	0.00
Citharidae	<i>Citharus linguatula</i> (Linnaeus, 1758)	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
Bothidae	<i>Arnoglossus kokeni</i> (Bassoli, 1906)	0.00	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Arnoglossus</i> sp.	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00
	Indet.	0.00	0.00	0.55	0.00	0.00	0.00	0.00	0.00	0.00
Total number of otoliths		105	45	224	135	102	57	79	113	34

- The benthic-benthopelagic component in sample 1 amounts for the 17.24% of the total assemblage; the 25% tropical participation is caused by the presence of *Laemonema* sp. as well as *Gadiculus labiatus*. Since the paleodepth estimate for sample 1 exceeds 200 m, the benthic-benthopelagic component of the assemblage in this sample is indicative of intermediate water conditions in the general study area. The high participation therefore of the tropical group in sample 1 suggests warm intermediate water during this interval.
- The sample 3, also taken from diatomites, shows a high relative abundance of *Parascombrops mutinensis* (Table 4.4). The closest modern relative of this fossil Mediterranean species is *Synagrops spinosus*, which inhabits continental shelf areas in the temperate regions of the Atlantic Ocean (Mejia et al. 2001). Accepting this as an equivalent of *P. mutinensis* means that the temperate group relative abundances in samples 3 and 5 are increased. If, as an alternative, this species is considered to be a warmer-water fish, adapted to the Pliocene Mediterranean Sea, where it is commonly found, its relative abundance in the studied assemblages would be added to the subtropical group

of the benthic-benthopelagic component. This is accepted as more plausible herein, and presented in Figure 4.4.

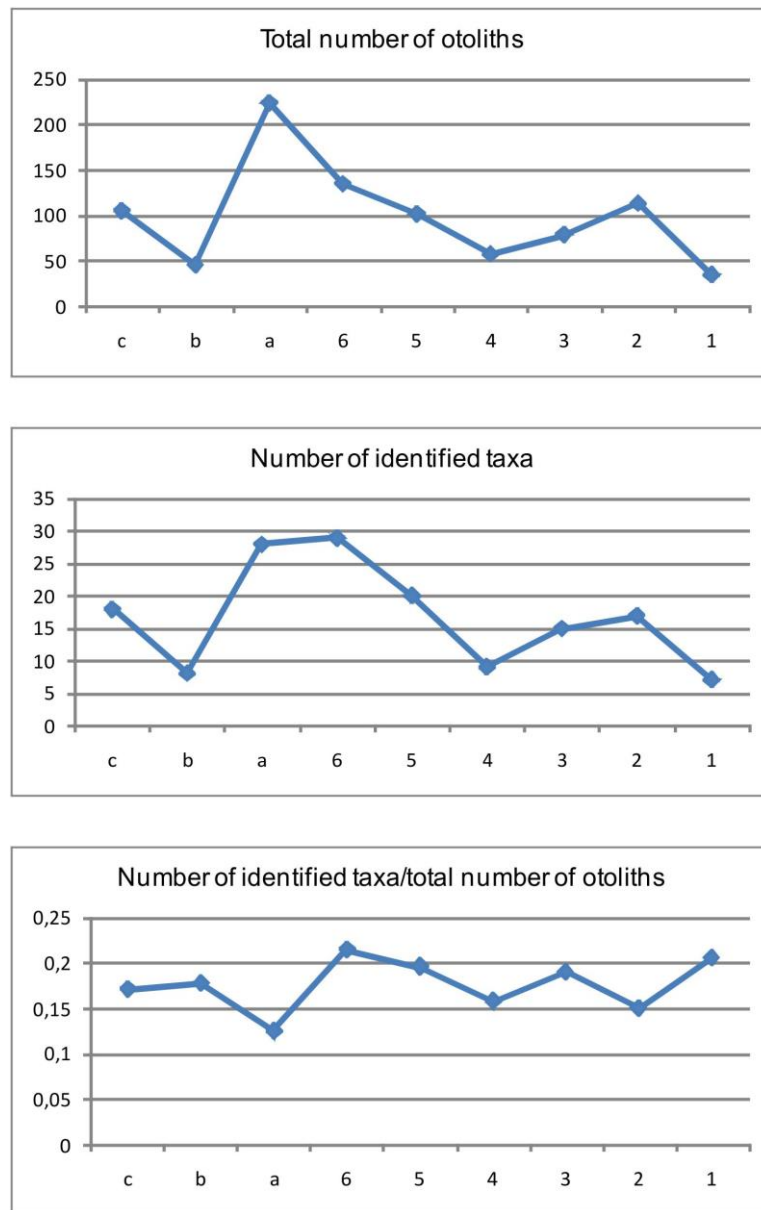


Figure 4.5 The total number of identified taxa in each Voutes sample compared to the total number otoliths found in the sample.

- The highest temperate group contribution in the benthic-benthopelagic component is observed in sample 2 and coincides with a low in the tropical group contribution. Sample 2 was taken from the uppermost marls of the section, which include a rich macrofauna.
- The only temperate benthic species present in the assemblages, *Gobius niger*, also has a high relative abundance of 10.41% in sample *a*. However, sample *a*

also contains a 2.47% relative abundance of the tropical pelagic species *Diaphus taaningi*.

- *Bregmaceros* sp. is very abundant in the studied Voutes assemblages. It has an especially high relative abundance in the diatomite sediments (sample 4: 80.21%, sample 3: 50.76% and sample 1: 68.97%). It is worth noting, at this point, that skeletal material from this fish is commonly found in the Pliocene diatomite deposits around the Mediterranean region.
- The total number of otoliths varied greatly between the samples (Figure 4.5); sample *a* was the most rich, while samples *1* and *b* were the most poor in findings. The number of identified taxa in each sample was in direct relation to the total number of otoliths found in the same sample, providing a mean ratio of 0.18.

4.3.1.3 Paleoenvironmental reconstruction of the Voutes area

The paleobathymetric curve produced through the analysis of the fish otolith fauna uncovered in the Voutes outcrop sediments present an interesting input in the paleogeographic evolution of the Central Crete area, namely the Heraklion basin (Figure 4.6). Indeed, the paleodepths estimated for the late Zanclean deposits indicate that the paleoenvironment underwent severe changes. Generally, depths throughout this interval do not exceed 350 m, although the lower part of the section exhibits much shallower estimates, up to 150 m. Indeed the presence of *Atherina boyeri* in sample 6 indicates a lagoon environment (Danilova 1991) established in the study area during the corresponding time interval. The deeper environments are found on the upper part of the section. However, no specific trend may be safely concluded from the estimated values. Rather several depth variations are visualized (Figure 4.6). In addition, the lower part of the Voutes outcrop reveals a mixture of the fish faunas from two realms, a deep water probably autochthonous faunal component, and a shallow allochthonous fauna. This is in accordance with the gravity flows observed at the lower part of the section, which seem to have incurred this mixing. Overall, during the late Zanclean, Voutes area was a coast, habitat for a rich shallow neritic ichthyofauna.

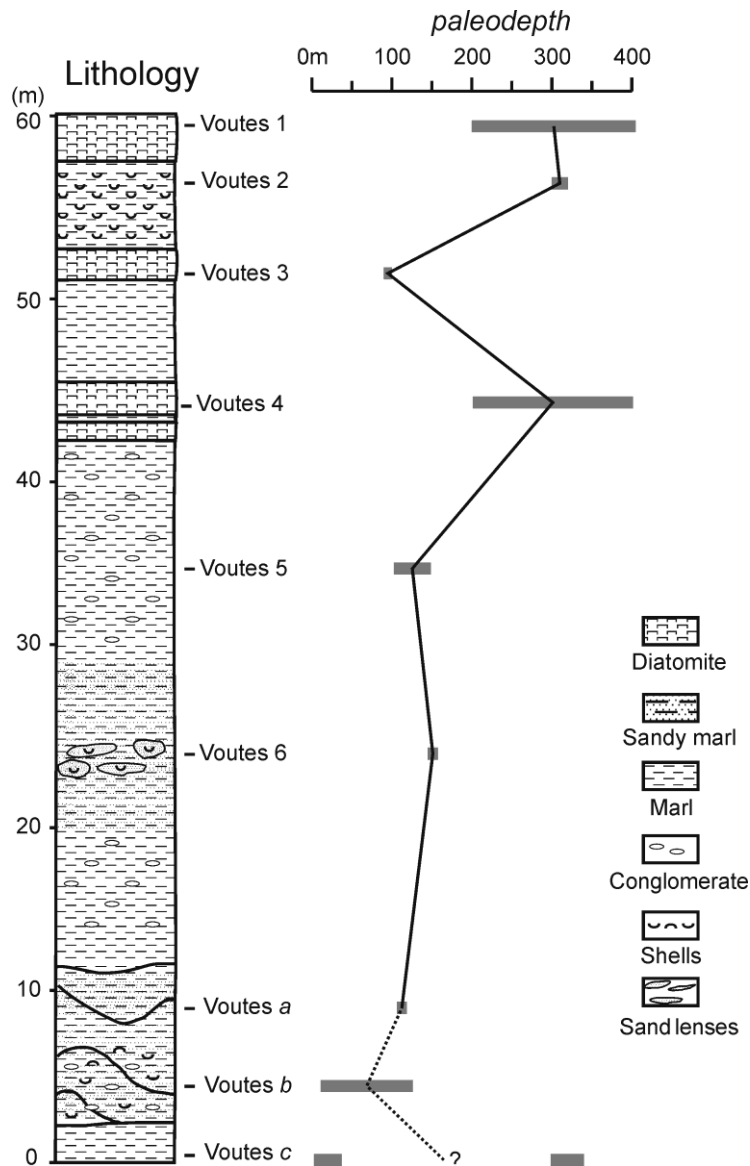


Figure 4.6 Voutes section lithology and otolith-based paleobathymetric curve.

Six stages in the paleoenvironmental evolution of the Voutes study area can be distinguished based on the fish otolith assemblages' analysis.

i. The lower portion of the section, encompassing sample levels *a*, *b*, *c* and 6, is characterized by the strong gravity flows, which cause a mixing of the faunas. Two separate fish assemblages are distinguished in this part occupying shallower (0-30 m) and deeper (~100 m) coastal depths respectively. Furthermore, this interval is enriched in benthic and benthopelagic fish remains in comparison to the upper portion of the section, perhaps because it incorporates several different micro-environments. Alternatively, the upper section portion is depleted in benthic-benthopelagic taxa, perhaps as a result of oxygen-deficiency at the sea bottom.

ii. A more stable tropical to subtropical fauna, throughout the water column, is gradually established. At 100-150 m, in the sample 5 level, the benthic-benthopelagic component amounts for approximately 20% of the total fauna; the subtropical taxa add up to 65.51% of this, while the temperate taxa to 27.6%. The pelagic component, which makes the 80% of the total fauna, comprises 47.24% tropical, 28.22% subtropical and 24.54% temperate taxa.

iii. The paleodepth was estimated between 200-800 m for the sample 4 level, through the above analysis. However, a more conservative value around 200-300 m is probably better, because a transition greater than 50-150 m in the time interval of 0.25 Ma, within the uppermost Zanclean, represented by the section sediments would be most unlikely. The deepening of the area is evident also in the drastic increase of the pelagic to benthic-benthopelagic ratio in sample 4. The bottom dwelling fish remains become extremely scarce. The tropical taxa become very abundant, forming the 85.58% of the pelagic component, while the overall abundance of this group increases to 83.5% of the fauna. The ichthyofauna at this stage indicates warm conditions throughout the water column.

iv. The sample 3 diatomite bed was deposited in a shallower environment, estimated at 87-100 m; warm conditions subside, although still the fauna may be characterized as a tropical one. Notable is the relative abundance of *Bregmaceros* sp., which drops, from 80.21% in sample 4, to 50.76% in sample 3.

v. A further drastic drop in the tropical component, at all levels, appears in the sample 2 stratigraphic level, also marked by a decrease in the relative abundance of *Bregmaceros* sp. to only 5.88%. Furthermore the temperate taxa relative contribution increases significantly at all levels. The total temperate group participation rises from 7.09% to 28.86%.

vi. The uppermost part of the Voutes section signifies a further warm episode in the uppermost Zanclean. Total tropical group contribution increases to 87.5%, clearly modulated by the *Bregmaceros* sp. abundance. In addition, the paleodepth estimate below 200 m for sample 1, making this probably the deeper part of the section, enables to decipher intermediate water conditions by the benthic-benthopelagic assemblage composition. Indeed, the high relative abundance of tropical deep-dwelling taxa suggests warm intermediate water in the general study area at this time.

RHODES ISLAND

4.3.2 *Ypsenis*4.3.2.1 Paleobathymetry

The results of the paleobathymetric analysis based on the fish otolith finds are illustrated in Figures 4.7 and 4.8. The paleodepth estimate for sample *YPS3* at 150-200 m is delimited by the *Lampanyctus crocodilus* juvenile depth distribution, between 0-200 m, since all the identified specimens are small and thus belong to non-adult individuals, and the uppermost depth range of *Micromesistius poutassou*, at 150 m. The same holds true for the *L.crocodilus* specimens in sample *YPS4*. This in combination with the presence of *G.argenteus*, inhabiting depths of more than 100 m, provides the overall estimate for *YPS4* of 100-200 m.

The fish taxa identified in sample *YPS5* do not have a uniform depth distribution. The paleobathymetric analysis provides a low percentage peak (80%) for 0-350 m, requiring further inspection. The fish assemblage consists of a pelagic – mesopelagic component, mostly myctophids and gadids, as well as a rich benthic – benthopelagic member, which includes: *Conger conger*, *Gnathophis mystax*, *Rhynchoconger pantanelli*, *Polyipnus polli*, *Scorpaena* sp., *Dentex* sp., *Cepola macrophthalma*, *Chromis chromis*, *Deltentosteus quadrimaculatus*, *Gobius niger*, and *Leseurigobius suerri*. *Chromis chromis* and *Dentex* spp. require hard, rock bottoms. *L. crocodilus* specimens once more belong to juvenile individuals. It is perceived that the fossil assemblage of *YPS5* represents a mixed fauna indicating coastal steep underwater morphology with easy access to the open ocean. The depositional depth for sample *YPS7* is estimated at 0-30 m, based on the modern distribution of *Oblada melanura*.

The simultaneous presence of *Aphia minuta* and *Gadiculus argeneus* provides a depth of 100m for samples *YPS9* and *YPS11*, which may go a little further to 100-150 m, to include the upper distribution boundary of *Micromesistius poutassou*, in sample *YPS11quat*. The paleodepth is estimated between 100-350 m, based on the concurrent presence of *G.argenteus*, and *Deltentosteus* sp, in sample *YPS12*. However the presence of *Atherina boyeri* denotes a rather shallow, lagoon environment.

Finally, *Deltentosteus quadrimaculatus*, *Blennius ocellaris* and *Pomatoschistus* sp. provide a wide estimate of 10-350 m for sample *YPS12ter*.

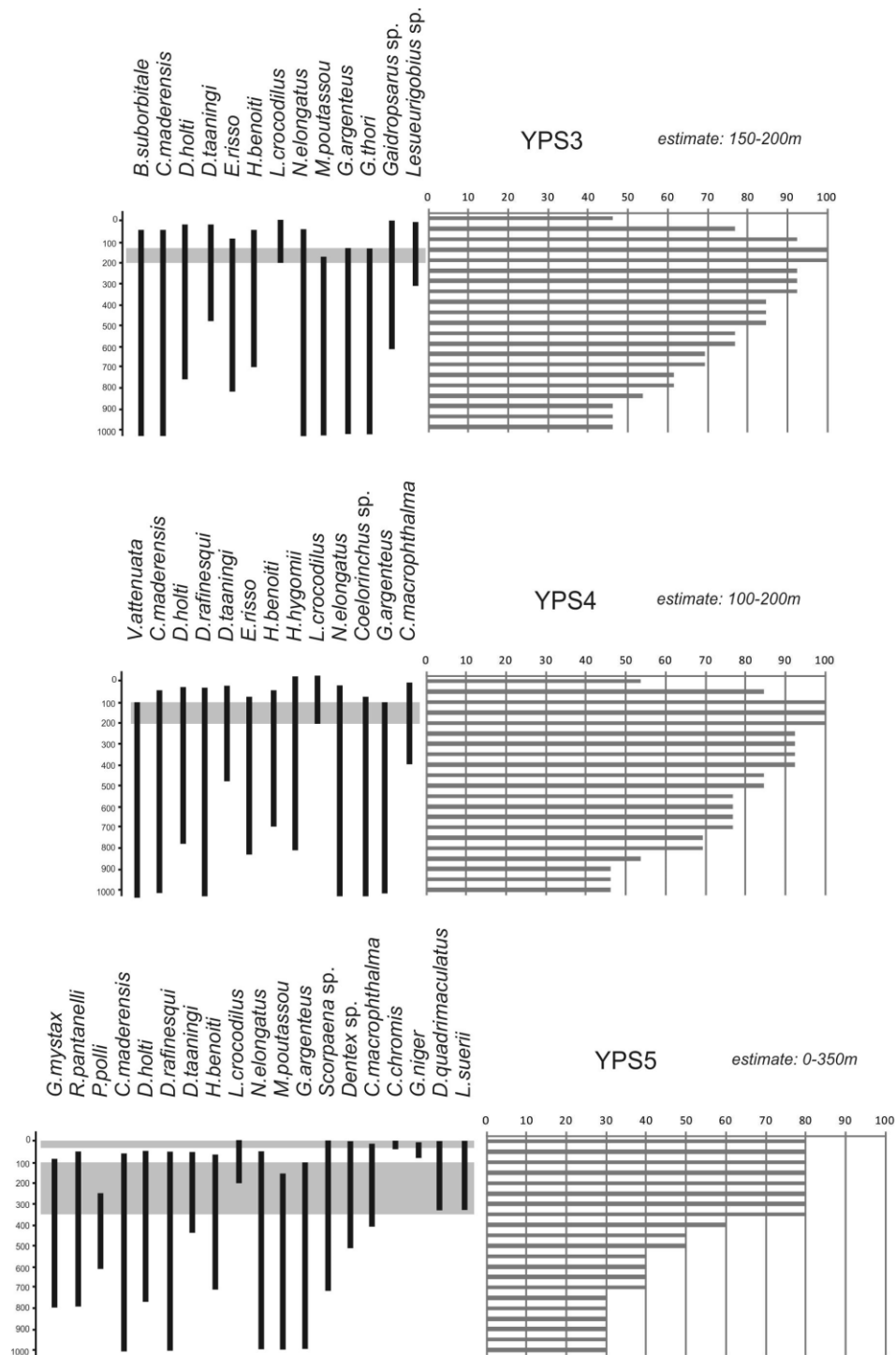


Figure 4.7 Ypsenis paleobathymetric analysis and estimates.

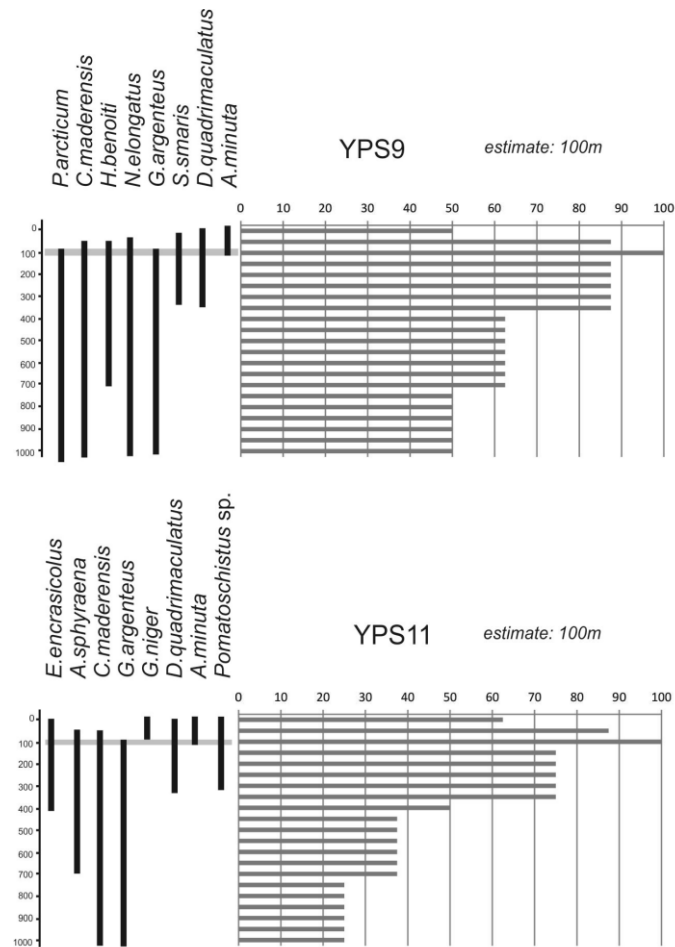


Figure 4.8 Ypsenis paleobathymetric analysis and estimates (continuation).

4.3.2.2 Paleoecology

The paleoecological analysis results for the teleost fish assemblages in the Ypsenis sediments are presented in Figures 4.9, 4.10 and 4.11.

- Overall, the fish assemblages identified in the Ypsenis sediments reveal a temperate to subtropical fauna occupying the area during the Calabrian.
- As in the case of the Voutes assemblages, the pelagic component makes up more than half of the total assemblage, and modulates the total group abundances.
- Tropical taxa, both pelagic and benthic-benthopelagic, appear only in the lower half part of the section (samples 3, 4 and 5).

- Subpolar taxa appear only in the pelagic component, throughout the section, and have their highest abundance in the upper part of the section, in samples *YPS11quat* (30.1%) and *YPS12* (22.6%).
- In the benthic-benthopelagic component, the subtropical taxa exhibit the highest relative abundances in all of the samples apart from the lowermost part of the section, where there is only a very small percentage of benthic and benthopelagic taxa (6.2% in sample 3 and 4.01% in sample 4) comprised mostly of temperate fish.

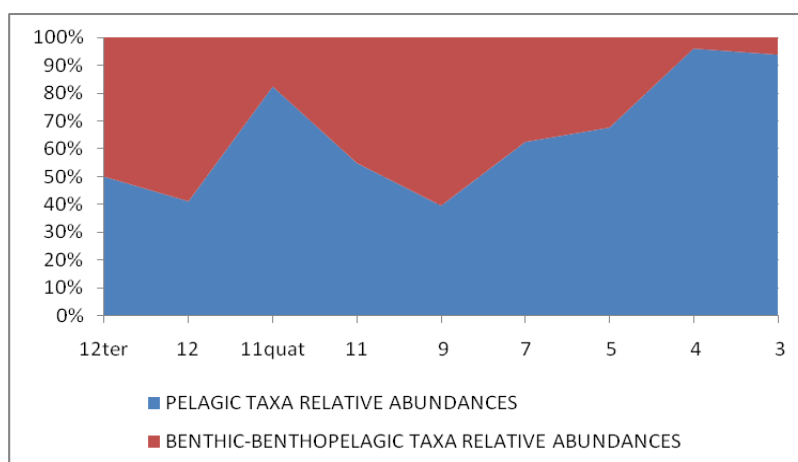


Figure 4.9 Contribution of the pelagic and the benthic-benthopelagic taxa to the Ypsenis taphocoenoses.

- The benthic-benthopelagic component in sample 9 is dominated by subtropical taxa; this sample exhibits the highest abundance of this group. Closely examining the assemblage composition however reveals that in this sample several specimens have not been identified at the species or even genus level. The benthic-benthopelagic taxa comprise 60.38% of the total assemblage, including 7.54% *Gobius* sp. morphotypes, 3.77% indeterminable Perciformes, 3.77% indeterminable Sparidae; meaning that a quarter of the benthic-benthopelagic taxa have not been included in the paleoecological analysis. It is possible, therefore, that the group abundances presented in Figure 4.10, for the benthic-benthopelagic component of sample 9, are distorted, and should not be evaluated.

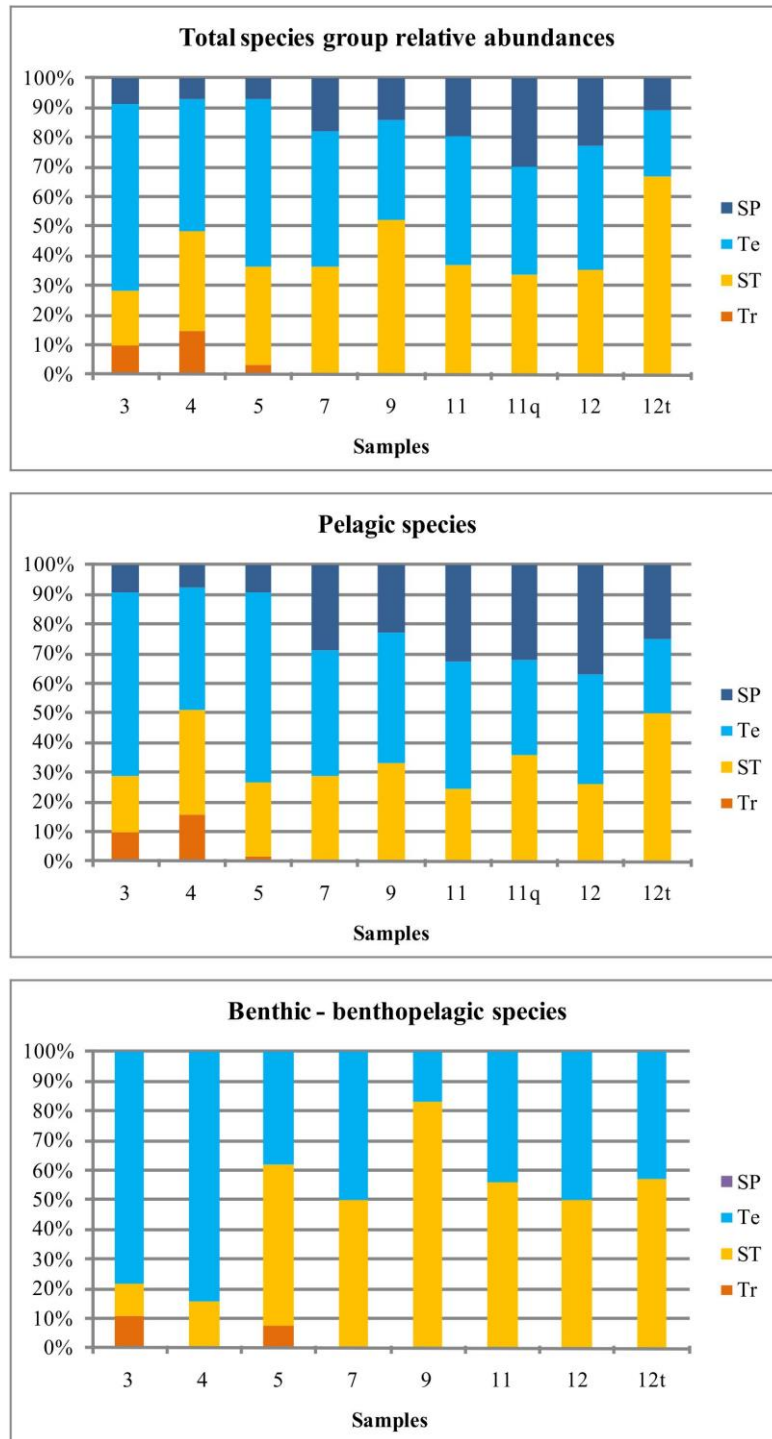


Figure 4.10 The relative contribution of the different ecological groups in Ypsenis assemblages.

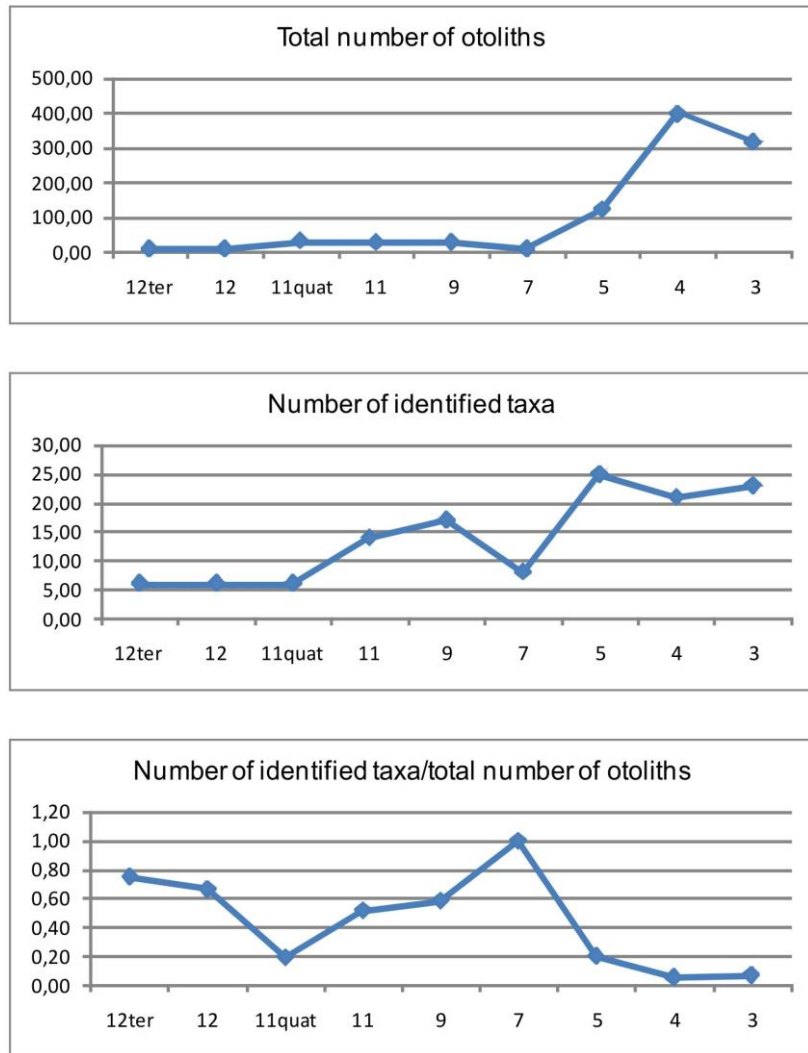


Figure 4.11 The total number of identified taxa in each Ypsenis sample compared to the total number of otoliths found in the sample.

- Examination of the selected taxa distribution in the section samples reveals that the temperate species *Maurolicus muelleri* gradually increases its relative abundances upwards in the section, from 0.8% in sample 3 to 66.67% in sample 11quat, and then down to 12.5% in sample 12ter. Furthermore, the tropical mesopelagic myctophid *Diaphus taaningi* appears only in the lower part of the section (samples 3, 4 and 5).
- Notable is also the appearance of *Atherina boyeri* in samples 9 and 12. *Atherina boyeri* is a subtropical euryhaline demersal fish, inhabiting mainly coastal areas and estuaries, but also freshwater environments (Francisco et al. 2008).

- The total number of otoliths, as well as the number of identified taxa in each sample vary greatly, with the higher values observed in the lower part of the section. The most heterogeneous assemblages are collected however in samples 7, 12 and 12ter (Table 4.5).

4.3.2.3 Paleoenvironmental reconstruction of the Ypsenis area

The overall assessment of the depositional depth in Ypsenis area is presented in Figure 4.12. A deepening trend is observed from sample 7 to 11quat. The uppermost samples do not permit more precise depth estimations. In the lower segment of the section, sample 5 provides dual depth estimation, which is at first problematic. However, abundant coral specimens are found in the same bed. Bromley (2005), studying these particular deposits, identified *Lophelia* and *Madrepora* fragments and reported their short-distance transportation, suggesting that the active tectonism of this area created steep seafloor topography and proximity of shallow-water environments. Furthermore, in agreement with Wisshak et al. (2005), he proposed that these ‘deep-water’ corals found suitable habitat in the Rhodes Pleistocene coasts, because the steep bathymetric gradients and the confined topography forced deep water to the near surface. Indeed, the mixed fish fauna identified in sample 5 further supports such an assumption.

Eight stages in the paleoenvironmental evolution of the Ypsenis area can be distinguished based on the fish otolith assemblages’ analysis. It should be indicated that according to the provided chronostratigraphic framework (Dr. Lopez-Otalvaro, pers. comm.) the levels, where samples 3-9 were taken, encompass an interval between 985-901 ka. The upper part of the section, i.e. sample-levels 11, 11quat, 12 and 12ter are older than 560 ka.

i. The lowermost part of the section (samples 3 and 4) has been deposited in a marine environment around 100-200 m, shallowing upwards. The rich pelagic fish fauna comprises mostly of myctophids, while the benthic and benthopelagic assemblage includes gadids, *Cepola macrophthalmia*, *Lesueurigobius* sp. and *Gaidropsarus* sp. The entire fish assemblage exhibits high tropical group relative abundance. Indeed the increased contribution of *Diaphus taaningi* (1% in s.3 and 2.89% in s.4) indicates rather warm conditions. Very characteristic also is the high relative abundance of *Electrona risso* (8.4% in s.3 and 2.09% in s.4). Its present-day distribution is

delimited by the 10°-15°C at 200 m, and productivity of 50 grams of Carbon per m² per year (Whitehead et al. 1984).

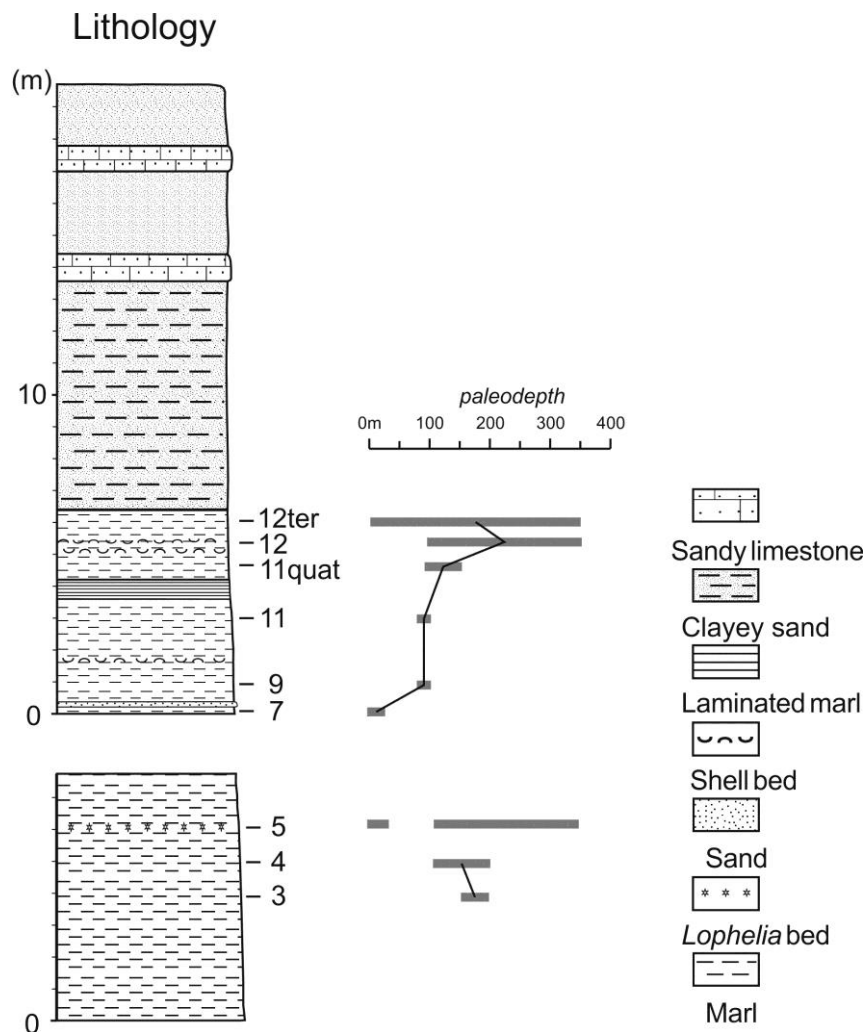


Figure 4.12 Ypsenis section lithology and otolith-based paleobathymetric curve.

ii. A steep paleocoast is evident in the sample 5 level, where a shallow water fauna from depths between 0-30 m is mixed with deeper inhabitants (>100m), supported by the presence of deep-water corals *Lophelia* and *Madrepora* (Bromley 2005).

Gradually cooling takes place also at this stage; the tropical taxa diminish overall (from 10.6% in s.3 to 7.39% in s.4 and to 3.92% in s.5) and in the pelagic component (from 9.8% in s.3 to 7.39% in s.4 and to 1.47% in s.5). The temperate *Maurolicus muelleri* increases gradually (from 0.8% in s.3 to 8.33 in s.5). It is postulated that the paleoenvironment, in Ypsenis area at this time, presented great variety, offering habitat to shallow and deeper-dwelling fish. Indeed, the same level includes specimens of subtropical-tropical deep-water fish like *Polyipnus polli*, as well as

several congrid (*Conger conger*, *Gnathopis mystax* and *Rhynchoconger pantanellii*), and the temperate benthic fish *Gobius niger*, which is known to occupy estuaries, lagoons and inshore water, preferring sand and muddy bottoms, sea-grass or even algae (Whitehead et al. 1986).

iii. A very shallow coast, with depths not exceeding 30 m, is established in the area during the next stage (sample 7-level). The tropical taxa are no longer present, and the cooling proceeds. The pelagic fauna is rich in *M.muelleri*, mesopelagic myctophids and gadids, indicating still easy access to the open ocean. *Conger conger*, which is present here, prefers rocky and sandy bottoms (Guthel 1992). The study of the present-day representatives of this species (Maigret and Lu 1986) demonstrates that juveniles generally stay near the coasts, whereas adults migrate to deeper waters. The *Ypsenis otolith* specimens are rather small (up to ~3 mm length). Consequently it is assumed that they belonged to young individuals. Furthermore, *Aphia minuta* is also present in this assemblage, indicating sea surface temperatures between 13-16°C (Iglesias and Morales-Nin 2001). This gobiid prefers inshore and estuarine waters, over sand, mud and eel-grass (Maugé 1986).

iv. Deepening to 100 m and further cooling is indicated during the next stage (sample 9-level), based on the concurrent presence of *Aphia minuta* (13°-16° C at surface waters; Iglesias and Morales-Nin 2001) and *Gadiculus argenteus* (temperate distribution, depth >100 m; Muus and Nielsen 1999), as well as the initiation of temperate North Atlantic species *Protomyctophum arcticum*, generally found in depths greater than 90 m (Coad and Reist 2004), but more usually between 250-850 m (Mauchline 1988). The very euryhaline fish *Atherina boyeri* is also present in the *YPS9* assemblage; currently it is frequent in brackish waters (Wildekamp et al. 1986), estuaries and lagoons (Danilova 1991), and is known to prefer still or slow flowing waters when inhabiting freshwaters (Kottelat and Frayhof 2007). Finally increased is also the abundance of *Spicara smaris* (15.09%), known to inhabit *Posidonia* beds and muddy bottoms (Tsangridis and Filippousis 1992).

v. In the next stage, at sample 11-level, the climate still deteriorates, as the subpolar abundance increases and the subtropical taxa diminish. The depth of deposition is still at around 100 m. *Aphia minuta* is present at this level also, indicating temperatures between 13°-16° C at surface (Iglesias and Morales-Nin 2001). The existence of a

small semi-closed lagoon in the vicinity is indicated by the abundance of *Gobius niger* (3.92%) and *Engraulis encrasicolus* (5.88%; Whitehead et al. 1986; 1988; Frimodt 1995), with occasional access to the continental shelf, which is indicated by the presence of *Argentina sphyraena* (Muus and Nielsen 1999).

vi. In this stage (sample *11quat*-level) the fish fauna is dominated by *Maurolicus muelleri* (66.67%); *M. muelleri* and *A. minuta* are the only pelagic fish present in this assemblage. *Maurolicus muelleri* generally lives close to the bottom, but feeds on plankton, which it finds at the surface through daily vertical migrations (Gorelova and Krasil'nikova 1990). The benthic-benthopelagic environment is occupied by *Gadiculus argenteus*, *Micromesistius poutassou* and a few Perciformes, showing a deepening trend to 100-150 m and more open oceanic access.

vii. The further deepening of the area probably continuous, although there is insufficient data to accurately estimate the paleodepth (sample *12*-level). The presence of *Atherina boyeri* however allow for very deep environment, but rather for a high bathymetric gradient. The epibenthic temperate *Gobius niger* is replaced by subtropical *Deltentosteus quadrimaculatus*, and *Micromesistius poutassou* does not appear in the greater depths, at this stage. *Maurolicus muelleri* and *Benthosema glaciale* share the pelagic domain, still suggesting temperate conditions.

viii. During the final stage determined here, the paleobathymetric method did not provide a good estimation for sample *12ter*-level. However, the overall assemblage is clearly enriched in warm water, subtropical fish, at the expense of subpolar and temperate taxa. Characteristically, *Maurolicus muelleri* and *Benthosema glaciale* diminish drastically. There is no contribution of temperate gadids in the assemblage. Also, the subtropical mesopelagic myctophids increase once more. On the whole, the pelagic and benthic realm shows signs of warmer conditions than those prevailing during the previous stages. Peculiar, however is the presence of both subtropical species *Deltentosteus quadrimaculatus*, which prefers sand to muddy sand bottoms (Quero et al. 1990), and *Blennius ocellaris*, found on hard substratum (Breder and Rosen 1966). This co-existence once more may show a certain degree of mixing during deposition of remains from adjacent small-scale ecosystems, developed during the same time in a greatly variable paleocoast.

4.3.3 Faliraki

4.3.3.1 Paleobathymetry

The results of the paleobathymetric analysis based on the fossil otolith assemblages for Faliraki 4 section are presented in Figures 4.13 and 4.14. The depositional depth for sample *Fal4/10* may reach 337 m, delimited only by the depth range of *Lesueurigobius suerii*. Also, in sample *Fal4/18* the concurrent presences of *Deltentosteus quadrimaculatus* and juvenile specimens from *Lampanyctus crocodilus* permit to estimate a depth below 200 m.

The paleodepth for sample *Fal4/11* ranges from 50-100 m, estimated for only 90.46% of the abundances, due to the presence of *Chromis chromis* (2-40 m) and *Echiodon dentatus* (120-3250 m). This accommodation of taxa preferring different environmental settings, in the same sediment sample, possibly shows the existence of such conditions nearby, indicating rather steep sea bottom topography.

In sample *Fal4/19*, the paleobathymetric method was inconclusive, yielding a maximum participation of the abundances of 79.31% between 50-150 m depth. In particular, the taphocoenosis may be split into two groups. Group A comprises shallow water benthic-benthopelagic taxa, namely *Ophidion barbatum*, *Diplodus annularis*, *Chromis chromis*, *Gobius niger*, *Gobius paganellus* and *Lesueurigobius friesii*. Whereas Group B consists of *Pseudophichthys splendens*, *Polyipnus polli*, *Vinciguerria poweriae*, *Laemonema*, *Chlorophthalmus agassizi*, gadids, and myctophids, which may be found in deeper water levels.

Few taxa were identified, which could be found in both settings (Group C), such as *Lampanyctus crocodilus*, *Gaidropsarus* sp., *Pagellus bogaraveo*, *Spicara smaris*, *Cepola macrophthalma*, *Deltentosteus quadrimaculatus* and *Lesueurigobius suerii*. Consequently, two paleodepth estimates are provided, between 0-40 m and 150-250 m. This mixing of the fauna again indicates a high bathymetric gradient in the study area at this time.

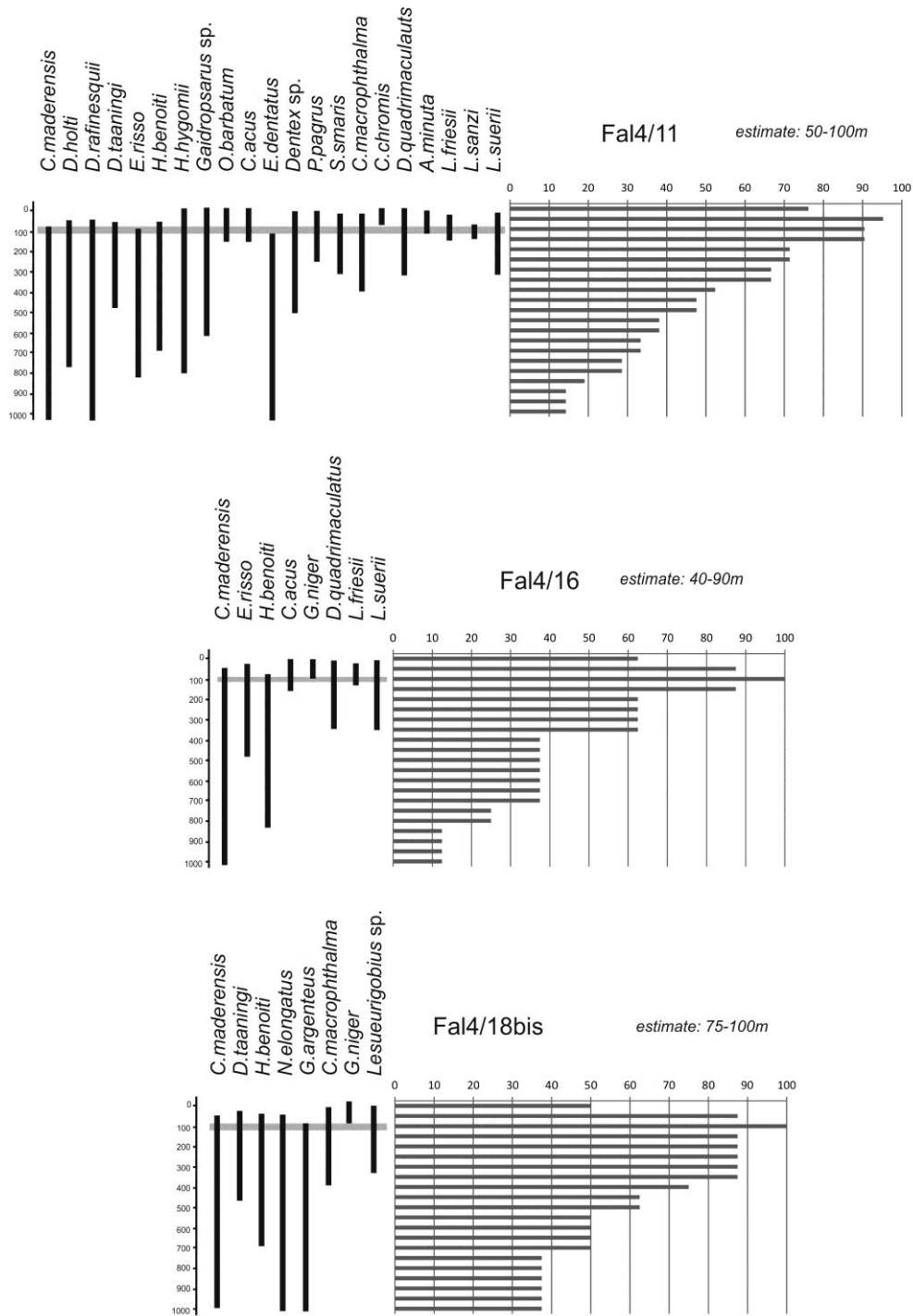


Figure 4.13 Faliraki 4 paleobathymetric analysis and estimates.

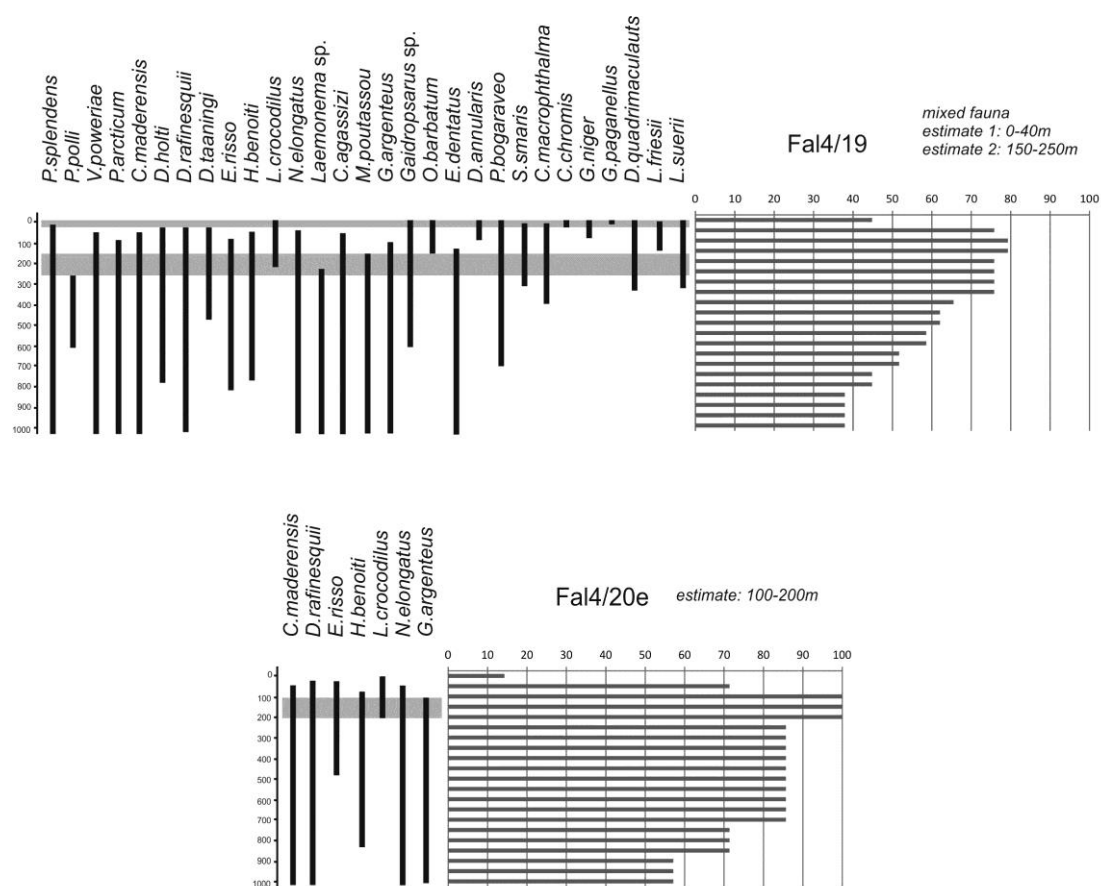


Figure 4.14 Faliraki 4 paleobathymetric analysis and estimates (continuation).

4.3.3.2 Paleoecology

The paleoecological analyses for the Faliraki 4 otolith assemblages are presented in Figures 4.15, 4.16 and 4.17. In particular it is noted that:

- The Faliraki 4 assemblages denote a subtropical to temperate fish fauna established during the Calabrian, between 1.7-1.2 Ma. Indeed, the total group relative abundances (Fig. 4.15) indicate that subtropical fish dominated the area at 1.7 Ma (sample 10-level) and were gradually overcome by the temperate fish relative abundances (sample 20e-level) at around 1.2 Ma.
- The taphocoenoses are mostly comprised of benthic-benthopelagic taxa in the lower part of the section (samples 10-18), and thereafter the pelagic contribution increases.
- The benthic-benthopelagic component of the assemblages is initially rich in subtropical taxa, but the temperate group gains weight (samples 18bis and

20e), mostly due to the introduction of gadids *Gadiculus argenteus* and *Micromesistius poutassou*.

- The sample *Fal4/19* exhibits the most diverse assemblage, in both the pelagic and the deep-water domain, with representatives of all four groups.
- The pelagic component is dominated by temperate taxa on the whole, with the exception of sample *Fal18bis*, which shows an almost equal distribution between warm and cold water species.

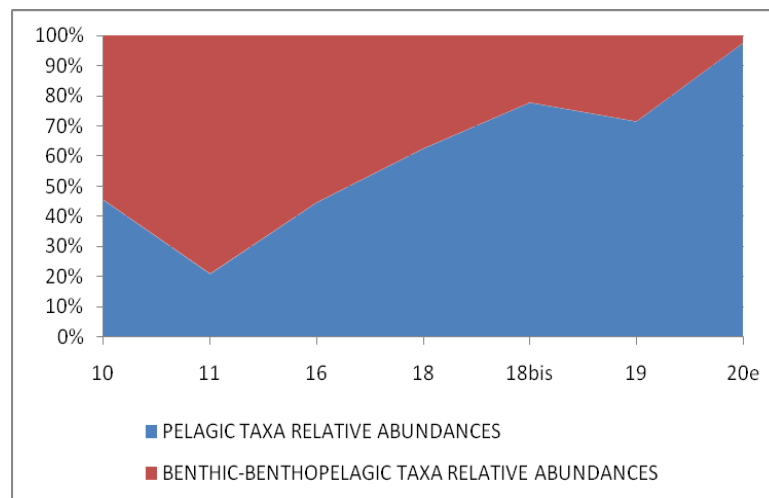


Figure 4.15 Contribution of the pelagic and the benthic-benthopelagic taxa to the Faliraki 4 taphocoenoses.

- The sample *Fal4/20e* contains only 1.03% of tropical and subtropical taxa each. The most abundant category is the temperate fish (85.02%), followed by the subtropical group (12.91%). Clearly this sample exhibits the establishment of cold-water conditions at all levels.
- The benthic-benthopelagic taxa group abundances for sample *Fal4/19* were further investigated separately for the two assemblage portions, shallow and deeper-water, which were determined above through the paleobathymetric analysis. Both assemblages are dominated by subtropical taxa, with slight differentiations.
- The lower samples *10*, *11* and *16* show a strongly subtropical benthic-benthopelagic component, which appears disproportionate in contrast with the pelagic group distributions. The strong subtropical contribution is caused by

the high abundances of *Lesueurigobius* spp. in these samples (18.18% in sample 10, 7.77% in s.11, 10.71% in s.16), and the low abundance of temperate gobiid *Gobius niger* (Table 4.6).

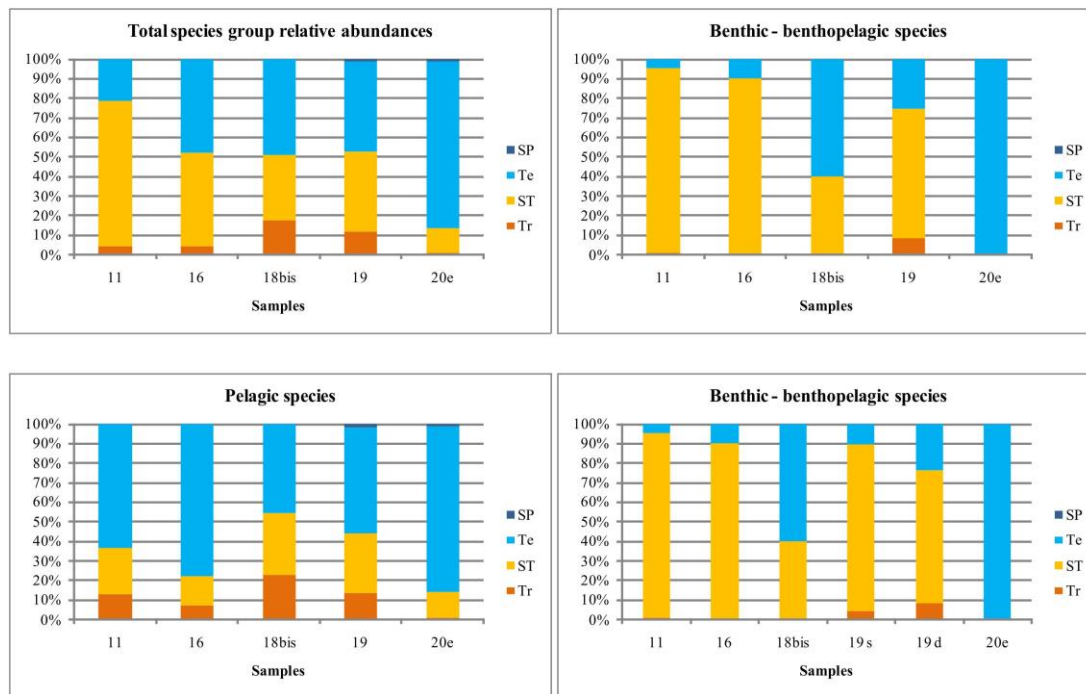


Figure 4.16 The relative contribution of the different ecological groups in Faliraki assemblages. The group abundances for samples 10 and 18 have been excluded from the diagrams, because these samples contained very few otolith specimens (less than 20 each) and consequently presented a much distorted picture of the fish assemblage. Individual data from these samples are commented in the text. The down-most, right diagram contains two group distributions in the sample *Fal4/19*, one for the shallow-water assemblage (*19 s*) and one for the deeper-water assemblage (*19 d*) as determined through the previous paleobathymetric analysis.

- However, a high contribution of *Gobius* sp.2 is observed in these same samples, for which no ecological analogue has been inferred. Therefore, this species has been excluded from the paleoecological analysis, pending further specific identification. It is possible that this lack of further data on the paleoecological significance of the identified gobiids in the lower part of the Faliraki 4 section may have led to underestimate the temperate group relative abundance in this part.

Table 4.6 Faliraki 4 section relative abundances								
Taxonomic placement		Sample						
Family	Genus/Species	10	11	16	18	18bis	19	20e
PELAGIC TAXA								
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)	0.00	0.00	0.00	0.00	0.00	0.62	0.00
Phosichthyidae	<i>Vinciguerria poweriae</i> (Cocco, 1838)	0.00	0.00	0.00	0.00	0.00	0.31	0.00
Myctophidae	<i>Benthoosema glaciale</i> (Reinhardt, 1837)	0.00	0.00	0.00	0.00	0.00	0.62	0.74
	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	45.45	10.88	19.64	0.00	24.44	13.79	40.20
	<i>Diaphus holti</i> Taaning, 1918	0.00	0.52	0.00	0.00	0.00	1.34	0.00
	<i>Diaphus rafinesquii</i> (Cocco, 1838)	0.00	1.30	0.00	0.00	0.00	1.13	0.74
	<i>Diaphus taaningi</i> Norman, 1930	0.00	0.52	0.00	0.00	17.78	5.14	0.00
	<i>Electrona risso</i> (Cocco, 1829)	0.00	0.52	3.57	0.00	0.00	4.12	0.74
	<i>Hygophum benoiti</i> (Cocco, 1838)	0.00	2.07	17.86	18.75	11.11	12.35	16.87
	<i>Hygophum hygomii</i> (Lütken, 1892)	0.00	2.07	0.00	0.00	0.00	0.00	0.00
	<i>Lampadena</i> sp.	0.00	0.52	0.00	0.00	0.00	2.37	0.00
	<i>Lampanyctus crocodilus</i> (Risso, 1810)	0.00	0.00	0.00	25.00	0.00	1.34	1.99
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)	0.00	0.00	0.00	18.75	0.00	4.53	1.99
	<i>Myctophum punctatum</i> (Rafinesque, 1810)	0.00	1.30	3.57	0.00	15.56	6.69	3.47
	<i>Notoscopelus elongatus</i> (Costa, 1844)	0.00	0.00	0.00	0.00	4.44	1.03	0.50
	<i>Protomyctophum arcticum</i> (Lütken, 1892)	0.00	0.00	0.00	0.00	0.00	0.51	0.00
	<i>Scopelopsis pliocenicus</i> (Anfossi & Mosna, 1976)	0.00	0.00	0.00	0.00	4.44	0.51	0.50
Indet.		0.00	0.00	0.00	0.00	0.00	15.12	29.78
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)	0.00	1.30	0.00	0.00	0.00	0.00	0.00
BENTHIC AND BENTHOPELAGIC TAXA								
Phycidae	<i>Gaidropsarus</i> sp.	0.00	0.52	0.00	0.00	0.00	0.93	0.00
Carangidae	<i>Trachurus</i> sp.	0.00	0.00	0.00	12.50	0.00	0.00	0.00
Centracanthidae	<i>Spicara smaris</i> (Linnaeus, 1758)	0.00	0.52	0.00	0.00	0.00	0.31	0.00
Congridae	<i>Conger conger</i> (Linnaeus, 1758)	0.00	2.33	0.00	0.00	0.00	0.41	0.00
	<i>Pseudophichthys splendens</i> (Lea, 1913)	0.00	0.00	0.00	0.00	0.00	0.51	0.00
Sternoptychidae	<i>Polyipnus polli</i> Schultz, 1961	0.00	0.00	0.00	0.00	0.00	0.21	0.00
Chlorophthalmidae	<i>Chlorophthalmus</i> aff. <i>agassizi</i> Bonaparte, 1840	0.00	0.00	0.00	0.00	0.00	0.21	0.00
Moridae	<i>Laemonema</i> sp.	0.00	0.00	0.00	0.00	0.00	0.31	0.00
Gadidae	<i>Gadiculus argenteus</i> Guichenot, 1850	0.00	0.00	0.00	0.00	8.89	3.91	1.49
	<i>Micromesistius poutassou</i> (Risso, 1827)	0.00	0.00	0.00	0.00	0.00	0.41	0.00
Ophidiidae	<i>Ophidion barbatum</i> Linnaeus, 1758	0.00	0.78	0.00	0.00	0.00	0.21	0.00
Carapidae	<i>Carapus acus</i> (Brünnich, 1768)	0.00	0.78	5.36	0.00	0.00	0.00	0.00
	<i>Echidion dentatus</i> (Cuvier, 1829)	0.00	1.55	0.00	0.00	0.00	0.62	0.00
Bythitidae	<i>Grammonus ater</i> (Risso, 1810)	0.00	0.00	0.00	0.00	0.00	0.51	0.00
Sparidae	<i>Dentex</i> sp.	0.00	1.04	0.00	0.00	0.00	0.00	0.00
	<i>Diplodus</i> cf. <i>annularis</i> (Linnaeus, 1758)	0.00	0.00	0.00	0.00	0.00	0.21	0.00
	<i>Pagellus</i> cf. <i>bogaraveo</i> (Brünnich, 1768)	0.00	0.00	0.00	0.00	0.00	0.31	0.00
	<i>Pagellus</i> sp.	0.00	0.00	0.00	0.00	0.00	0.21	0.00
	<i>Pagrus pagrus</i> (Linnaeus, 1758)	0.00	0.52	0.00	0.00	0.00	0.00	0.00
Indet.		0.00	2.85	0.00	0.00	0.00	0.00	0.00

Taxonomic placement		Sample						
Family	Genus/Species	10	11	16	18	18bis	19	20e
Clupeidae	Indet.	0.00	0.00	0.00	0.00	0.00	0.31	0.00
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)	0.00	8.55	0.00	0.00	4.44	3.29	0.00
Pomacentridae	<i>Chromis chromis</i> (Linnaeus, 1758)	0.00	0.52	0.00	0.00	0.00	0.51	0.00
Perciform indet.	Indet.	18.18	0.00	3.57	0.00	0.00	3.91	0.50
Gobiidae	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)	0.00	35.75	17.86	25.00	0.00	9.36	0.00
	<i>Gobius niger</i> Linnaeus, 1758	0.00	0.00	3.57	0.00	4.44	0.51	0.00
	<i>Gobius cf. paganelus</i> Linnaeus, 1758	0.00	0.00	0.00	0.00	0.00	0.21	0.00
	<i>Gobius</i> sp.1	0.00	0.00	0.00	0.00	0.00	0.00	0.50
	<i>Gobius</i> sp.2	18.18	14.25	3.57	0.00	0.00	0.21	0.00
	<i>Gobius</i> sp.3morphotype2	0.00	0.00	7.14	0.00	0.00	0.00	0.00
	<i>Lesueurigobius friesii</i> (Malm, 1874)	0.00	2.59	3.57	0.00	0.00	0.21	0.00
	<i>Lesueurigobius sanzj</i> (de Buen, 1918)	0.00	1.30	0.00	0.00	0.00	0.00	0.00
	<i>Lesueurigobius suerii</i> (Risso, 1810)	18.18	3.89	7.14	0.00	0.00	0.21	0.00
	<i>Lesueurigobius</i> sp.	0.00	0.00	0.00	0.00	4.44	0.00	0.00
	Indet.	0.00	0.00	0.00	0.00	0.00	0.51	0.00
Bothidae	<i>Arnoglossus</i> sp.	0.00	1.30	3.57	0.00	0.00	0.00	0.00
Total number of otoliths		6	237	32	9	26	616	263

- The total number of otoliths found differs greatly between the samples (Fig. 4.17). In addition, richer samples exhibit more diverse assemblages. However, the number of identified taxa is not a direct function solely of the total number of otoliths in the sample. Indeed, the very rich samples (*11*, *19* and *20e*) don't include a proportionately high number of taxa. As a result, the ratio between these two measures (Fig. 4.17), expressing sample heterogeneity, also varies.

4.3.3.3 Paleoenvironmental reconstruction of the Faliraki area

Overall, the Faliraki 4 otolith assemblages illustrate the varying paleoenvironmental conditions and the important of taphonomical factors in the preservation of the fossil material. The Calabrian Faliraki area presents five stage of paleoenvironmental evolution, as identified through the study of fish otoliths in the Faliraki 4 section (Figure 4.18).

i. At around 1.7-1.62 Ma, the area is placed in the subtropical to temperate zone; a marine environment between 50-100 m (based on the sample *11* estimation), where deposition of the Kolymbia sediments took place. The fish fauna includes a well-

developed subtropical-temperate benthic-benthopelagic component, and a few temperate pelagic myctophids. Notable is the presence of *Aphia minuta* in sample 11, which denotes inshore or estuarine waters, preferring sand, mud or eel-grass (Mauge 1986) and water temperatures between 13°-16° C (Iglesias and Morales-Nin 2001). The juvenile specimens of *Conger conger* also indicate coastal waters (Maigret and Ly 1986). Furthermore, *Spicara smaris* generally inhabits *Posidonia* beds and muddy bottoms (Tsangridis and Filippousis 1992). In sample 11, there is also *Electrona risso*, indicating productivity at 50 grC/m²/yr (Whitehead et al. 1984).

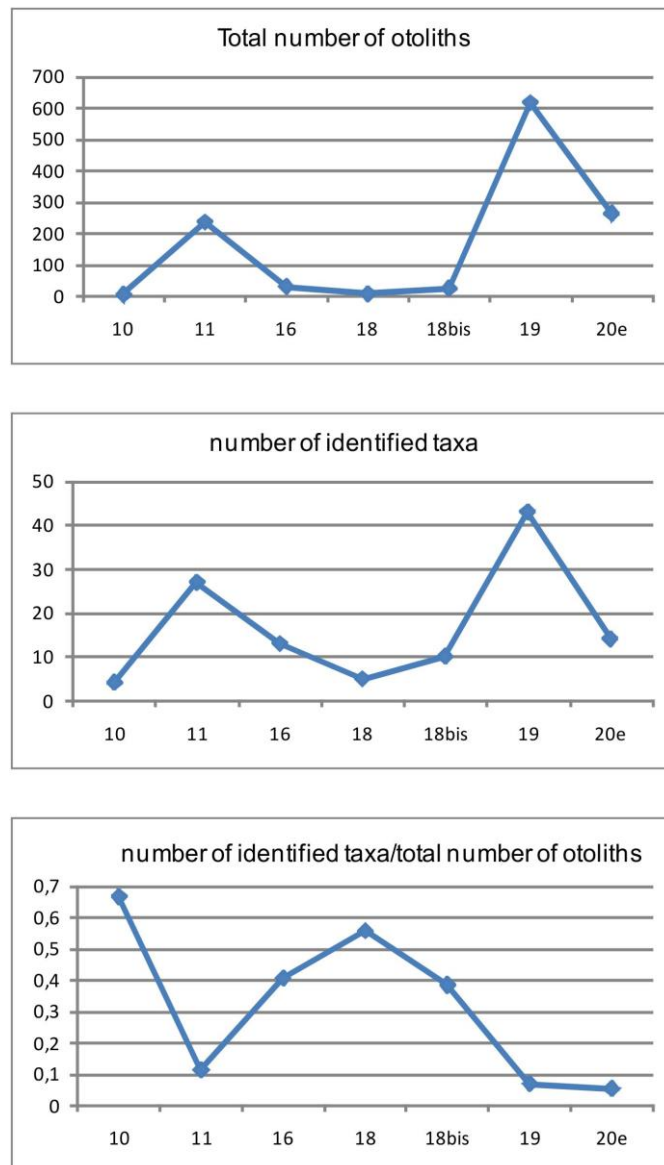


Figure 4.17 The total number of identified taxa in each Faliraki 4 sample compared to the total number otoliths found in the sample.

ii. The beginning of the Lindos bay Formation takes place in a depth between 40-90 m in the Faliraki area, in a subtropical-temperature marine environment (sample 16-level). The pelagic and the benthic-benthopelagic taxa contribute almost equally to the assemblage; the pelagic fauna is slightly more enhanced in temperate fish, whereas the benthic-benthopelagic assemblage is mostly subtropical. *Electrona risso* is present as before, and the appearance of *Gobius niger* denotes a more enclosed marine environment as well as the existence of a rich benthic invertebrate fauna (Whitehead et al. 1986).

iii. During this next stage, the sea bottom depth increases to 75-100 m, and the pelagic contribution becomes greater than the benthic-benthopelagic one. The temperate gadid *Gadiculus argenteus* first appears in high abundance (8.89%) in sample 18bis. In the benthic domain, subtropical gobiid *Deltentosteus quadrimaculatus* (sample 18) gives way to the temperate *Gobius niger* (sample 18bis).

iv. A steep coastal area incorporating associations from the shallow (0-40 m) as well as the deeper realm (150-250 m) is established during this stage (sample 19-level). A very diverse fauna is observed, with the maximum number of taxa found in sample 19. *Electrona risso*, *Spicara smaris* and *Conger conger* reappear. The deep water is dominated by *Gadiculus argenteus*, *Micromesistius poutassou*, *Chlorophthalmus agassizi*, *Pagellus bogaraveo* and *Polyipnus polli*. In the shallow domain the benthic niche is still filled by *Gobius niger*. This paleoenvironmental stage lasts until 1.617 Ma.

v. Later on, at around 1.25 Ma, the Lindos bay Formation is found, in Faliraki 4 section, to be deposited between 100-200 m. The pelagic component is very high, and a temperate fish fauna is established at all levels with characteristic species, such as *Benthoosema glaciale* (0.74%). As a result of this climatic deterioration, the observed diversity is much smaller than before (Begon et al. 1996).

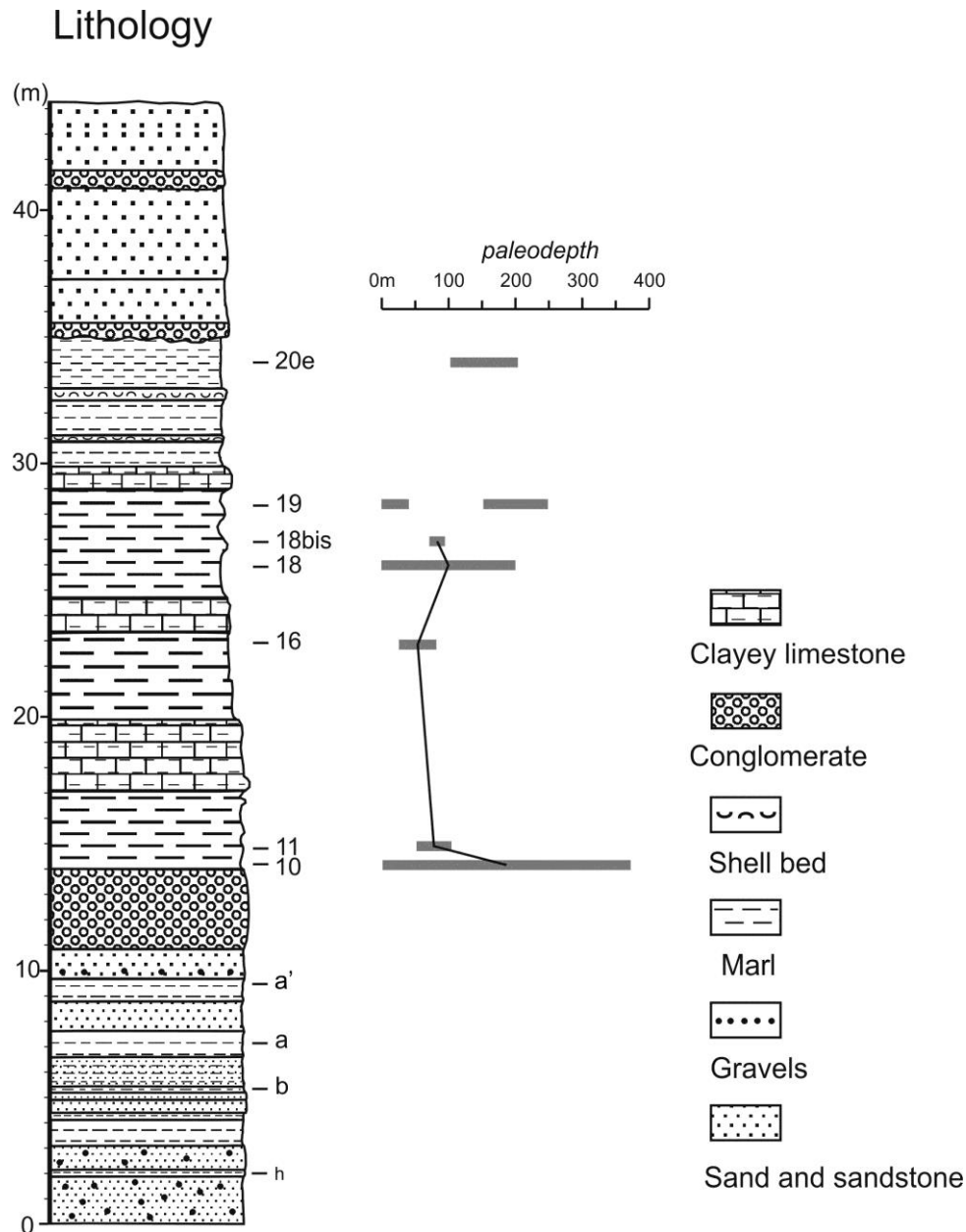


Figure 4.18 Faliraki 4 section lithology and otolith-based paleobathymetric curve.

4.3.4 Vagia

4.3.4.1 Paleobathymetry

The paleodepth estimations for the lower part of Vagia section (sample *Vag4*) placed it on the coastal zone below 15 m of depth, based on the concurrent presence of *Gobius cf. paganellus* as well as *Carapus cf. acus*. Sample *Vag8* exhibits a higher mesopelagic component and is placed deeper, between 50-150 m (Figure 4.19). Sample *Vag9-11* contains only specimens of *Gadiculus labiatus*, whose modern

equivalent is taken to be *Gadiculus argenteus*, yielding an estimated depth of above 100 m.

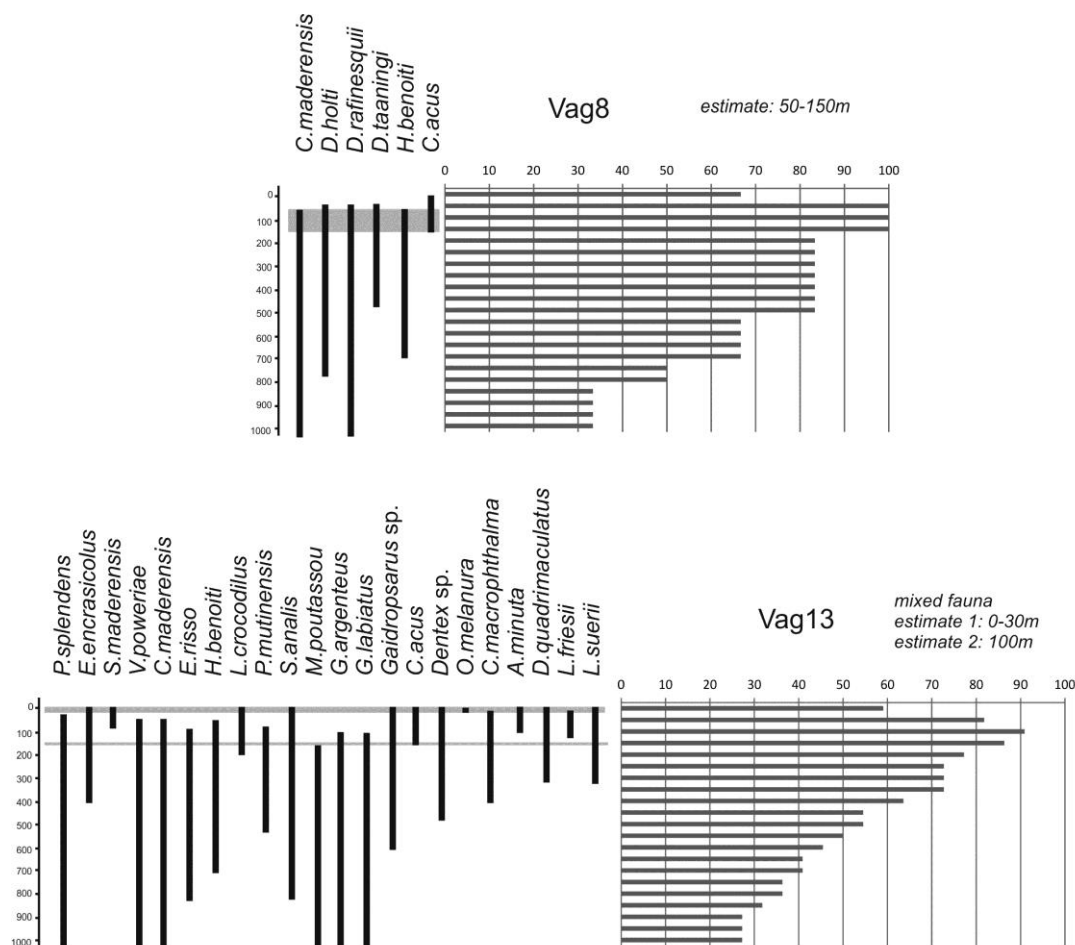


Figure 4.19 Vagia paleobathymetric analysis and estimates.

The paleobathymetric analysis was inconclusive for sample *Vag13*, yielding a maximum participation at only 90.9% (Fig. 4.19). Again sea bottom topography may cause this apparent mixing of the faunas. The shallow water group (0-30 m) is comprised of *Sardinella maderensis*, *Oblada melanura*, *Carapus cf. acus* and several gobiids, whilst the deeper water inhabitants (>100 m) is characterized by gadids.

The depth of deposition for sample *Vag15* may be contained between 10-130 m, based solely on the presence of *Lesueurigobius friesii*. It is worth mentioning also that in sample *Vag15* a leaf imprint was found during the processing. Sample *Vag20* contains *Diaphus rafinesquii*, *Notoscopelus elongatus* and *Cepola macrophthalma* otoliths, which give a rough depth estimate between 15-400 m, as does sample *Vag21*

with only *Ceratoscopelus maderensis* otoliths, and sample Vag24 with *C. maderensis*, *Hygophum benoiti* and *C. macrophthalma*.

4.3.4.2 Paleoecology

The paleoecological analysis for the Vagia otolith assemblages are presented in Figures 4.20, 4.21 and 4.22. In particular it is noted that:

- The pelagic taxa generally overwhelm the benthic-benthopelagic fauna, except in sample 4, which consists of gobiids and *Carapus cf. acus*, and sample 9-11, which presented only six otolith specimens all belonging to the deep-dwelling *Gadiculus labiatus*. Notably sample 9-11 was taken from the laminated marls immediately after the red oxidized layer (Cornee et al. 2006), where *Pinus* wood remains have been uncovered (Moissette and Spjeldnaes 1995).

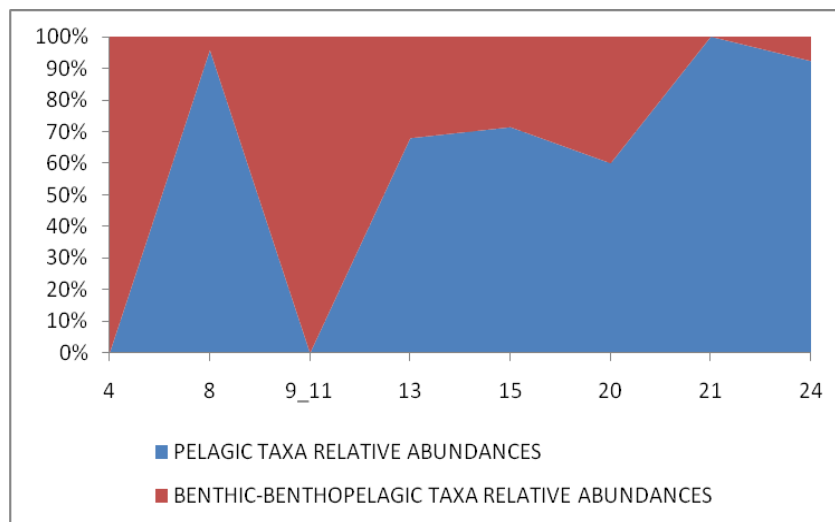


Figure 4.20 Contribution of the pelagic and the benthic-benthopelagic taxa to the Vagia taphocoenoses.

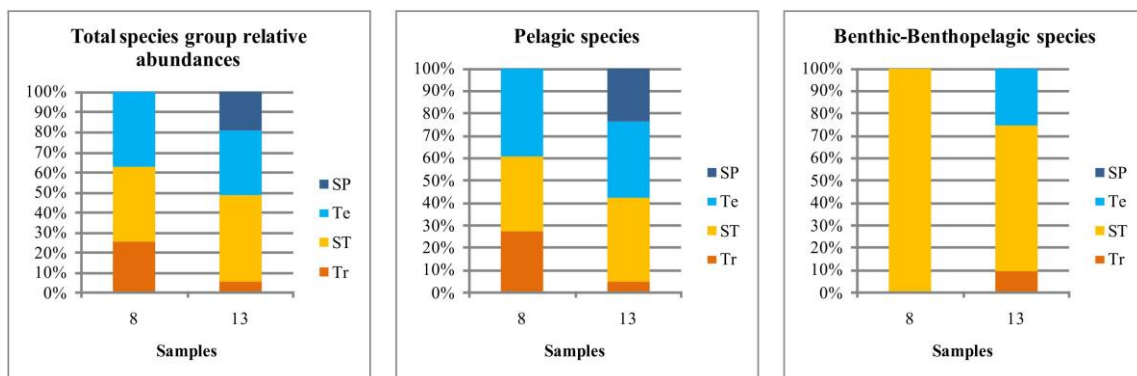


Figure 4.21 The relative contribution of the different ecological groups in Vagia assemblages.

- Only samples 8 and 13 could be analyzed with the present paleoecological method, since the rest of the samples gave very few otolith specimens.
- Sample 8, taken from the lower part of the Lindos bay Formation, presents a subtropical fauna with high tropical and temperate group relative abundances (25.72% and 37.14% of the total assemblage respectively). This results directly from the pelagic contribution, which amounts for the 95.74% of the assemblage.

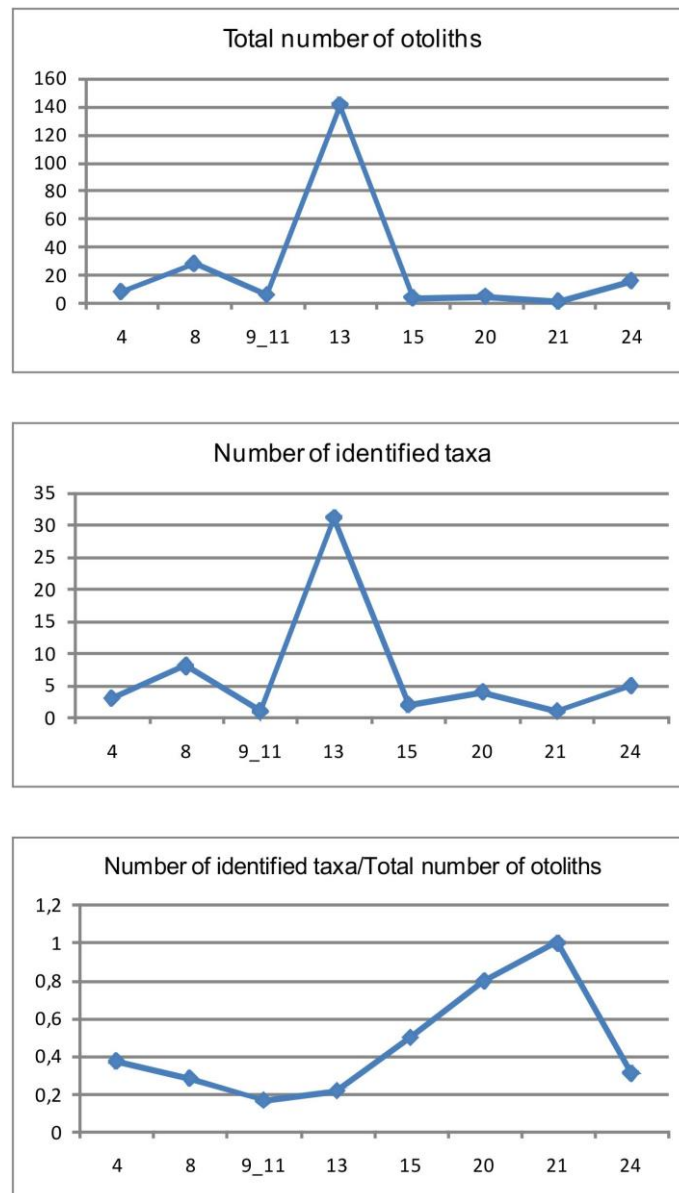


Figure 4.22 The total number of identified taxa in each Vagia sample compared to the total number otoliths found in the sample.

Table 4.7 Vagia section relative abundances									
Taxonomic placement		Sample							
Family	Genus/Species	4	8	9_11	13	15	20	21	24
PELAGIC TAXA									
Nettastomatidae	Indet.	0.00	0.00	0.00	1.71	0.00	0.00	0.00	0.00
Engraulidae	<i>Engraulis cf. encrasicolus</i> Linnaeus, 1758	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
Clupeidae	<i>Sardinella maderensis</i> (Lowe, 1838)	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
Sternoptychidae	<i>Maurolucus muelleri</i> (Gmelin, 1789)	0.00	0.00	0.00	28.63	0.00	0.00	0.00	0.00
Phosichthyidae	<i>Vinciguerria poweriae</i> (Cocco, 1838)	0.00	0.00	0.00	5.98	0.00	0.00	0.00	0.00
Scopelarchidae	<i>Scopelarchus analis</i> (Brauer, 1902)	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
Myctophidae	<i>Benthoosema glaciale</i> (Reinhardt, 1837)	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	0.00	10.64	0.00	9.40	0.00	0.00	100.00	30.77
	<i>Diaphus holti</i> Taaning, 1918	0.00	4.26	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Diaphus rafinesquii</i> (Cocco, 1838)	0.00	4.26	0.00	0.00	0.00	20.00	0.00	0.00
	<i>Diaphus taaningi</i> Norman, 1930	0.00	19.15	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Diaphus</i> sp.	0.00	25.53	0.00	2.56	0.00	0.00	0.00	46.15
	<i>Electrona risso</i> (Cocco, 1829)	0.00	0.00	0.00	5.13	0.00	0.00	0.00	0.00
	<i>Hygophum benoitii</i> (Cocco, 1838)	0.00	8.51	0.00	1.71	0.00	0.00	0.00	7.69
	<i>Lampanyctus crocodilus</i> (Risso, 1810)	0.00	0.00	0.00	1.28	0.00	0.00	0.00	0.00
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)	0.00	23.40	0.00	0.00	0.00	0.00	0.00	7.69
	<i>Notoscopelus elongatus</i> (Costa, 1844)	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00
Indet.		0.00	0.00	0.00	5.13	71.43	20.00	0.00	0.00
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00
BENTHIC AND BENTHOPELAGIC TAXA									
Congridae	<i>Pseudophichthys splendens</i> (Lea, 1913)	0.00	0.00	0.00	1.71	0.00	0.00	0.00	0.00
Phycidae	<i>Gaidropsarus</i> sp.	0.00	0.00	0.00	1.28	0.00	0.00	0.00	0.00
Gadidae	<i>Gadiculus argenteus</i> Guichenot, 1850	0.00	0.00	0.00	5.13	0.00	0.00	0.00	0.00
	<i>Gadiculus labiatus</i> (Schubert, 1905)	0.00	0.00	100.00	1.71	0.00	0.00	0.00	0.00
	<i>Micromesistius poutassou</i> (Risso, 1827)	0.00	0.00	0.00	1.71	0.00	0.00	0.00	0.00
Carapidae	<i>Carapus acus</i> (Brünnich, 1768)	15.38	4.26	0.00	1.71	0.00	0.00	0.00	0.00
Bythitidae	<i>Grammonus ater</i> (Risso, 1810)	0.00	0.00	0.00	1.28	0.00	0.00	0.00	0.00
Atherinidae	<i>Atherina boyeri</i> Risso, 1810	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
Acropomatidae	<i>Parascombrops mutinensis</i> (Bassoli, 1906)	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
Sparidae	<i>Dentex</i> sp.	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
	<i>Oblada melanura</i> (Linnaeus, 1758)	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)	0.00	0.00	0.00	3.42	0.00	40.00	0.00	7.69
Perciform indet.	Indet.	0.00	0.00	0.00	3.42	0.00	0.00	0.00	0.00
Gobiidae	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)	0.00	0.00	0.00	1.71	0.00	0.00	0.00	0.00
	<i>Gobius cf. paganellus</i> Linnaeus, 1758	23.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	<i>Lesueurigobius friesii</i> (Malm, 1874)	0.00	0.00	0.00	1.28	28.57	0.00	0.00	0.00
	<i>Lesueurigobius suerii</i> (Risso, 1810)	0.00	0.00	0.00	2.56	0.00	0.00	0.00	0.00
Indet.		61.54	0.00	0.00	0.00	0.00	0.00	0.00	
Bothidae	<i>Arnoglossus kokeni</i> (Bassoli, 1906)	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00
total number of otoliths		8	28	6	141	4	5	1	16

- Sample 13 shows a well diversified fauna at all levels; the pelagic component contains representatives of all four climatic groups, whereas the benthic realm is occupied by subtropical and temperate taxa mostly, but also a few subpolar and tropical fish contribute as well.
- Sample 13 is, by far, the richest, with 141 otolith specimens collected and 31 taxa identified. Next, sample 8 only held 28 specimens attributed to 8 taxa (Table 4.7).

4.3.4.3 Paleoenvironmental reconstruction of the Vagia area

The otolith-based paleoenvironmental representation here is commented with regard to this previous work, in order to draw more refined conclusions. In particular, five stages in the area's paleoenvironmental evolution are recognized through the study of fish otoliths (Figure 4.23):

i. The first fish remains are found around 2.5 m from the base of Vagia section; eight specimens were recovered and identified as *Carapus cf. acus*, *Gobius cf. paganellus* and some indeterminable gobiid. Both *Carapus acus* and *Gobius paganellus* are modern subtropical demersal fishes, which inhabit shallow waters not exceeding 15 m. In fact, the latter is found regularly in sheltered rocky sites in pools or intertidal waters under stones.

ii. The next stage refers to sample 8 which includes a sufficient number of otolith specimens to allow for a pelagic quantitative paleoecological analysis. The fish fauna is composed only of mesopelagic tropical to temperate myctophids, indicating easy oceanic access, while *C. cf. acus* still present is now the only benthic species. From this information, it can be assumed that the environment was a rocky coast, with few shelters in between the rocks.

iii. Sample 9-11 was taken from the marl beds immediately after the oxidized layer, and this is important because the remains in this sample may indicate towards the conditions and/or events leading to the layer's formation. This sample contains otolith specimens exclusively from the fossil Mediterranean species *Gadiculus labiatus*. Notably, surface water inhabitants were not found altogether. *Gadiculus labiatus* has

one modern living relative in the Mediterranean Sea, *Gadiculus argenteus*, a temperate pelagic-oceanic, non-migratory fish, which inhabits water depths below 100 m, over various substrata (Muus and Nielsen 1999). *Gadiculus labiatus* may be considered to lead a similar lifestyle, although its occurrences in the fossil record (Landini and Sorbini 2005; Girone et al. 2006) allow to assume a subtropical rather than temperate distribution. Based on the above, it is hypothesized that Vagia coast, described during the previous paleoenvironmental stage, gave place to a deeper shelf environment (over 100 m depth). Furthermore, the lack of other fish finds in sample 9-11, raises questions as to the origin of the red oxidized layer just below this level, the oceanographic implications of whatever mechanism and/or event caused its deposition, and the resilience of *G. labiatus* to them.

iv. During this stage (sample-level 13) the Vagia coast holds a rich and well-diversified fish fauna. Very shallow coastal fish (0-30 m) are mixed with mesopelagic and benthopelagic taxa (>100 m) in the taphocoenosis, indicating topographical steepness. The assemblage includes representatives of all categories, from subtropical to tropical. Particularly, *Engraulis* cf. *encrasicolus* indicates a coastal marine environment, with salinity varying between 5-41 ppt. The modern *Engraulis encrasicolus* occasionally enters lagoons, estuaries and lakes during the spawning season especially (Whitehead et al. 1988; Frimodt 1995). Also, *Electrona risso* presently tolerates temperatures between 10-15° C at 200 m depth, and productivity of 50 grC/m²/yr (Whitehead et al. 1984). *Grammonus ater* inhabits shallow rocky areas (Whitehead et al. 1986). *Atherina boyeri* is very euryhaline, regularly found in estuaries and lagoons (Danilova 1991), frequently in brackish water (Wildekamp et al. 1986), but also in low-energy freshwater (Kottelot and Frayhof 2007). Finally, *Sardinella maderensis* is a coastal pelagic species that tolerates low salinities in estuaries and prefers sea surface temperature of 24 ° C (FAO-FIGIS 2005).

v. The remaining part of the section exhibits a uniform fish assemblage, comprised mainly of pelagic myctophids, which dominate, a few benthic gobiids at the lower part, and *Cepola macrophthalma*. The depositional depth is estimated between 10-130 m in the lower part, slightly increasing towards the upper part. The consistent presence of *C. macrophthalma* during this stage indicates sandy and muddy substratum (Sanches 1991). Also, its modern depth distribution is mostly bound

between 70-200 m (Stergiou and Papaconstantinou 1993), but in the western Aegean Sea it is found between 100-200 m (Stergiou 1993).

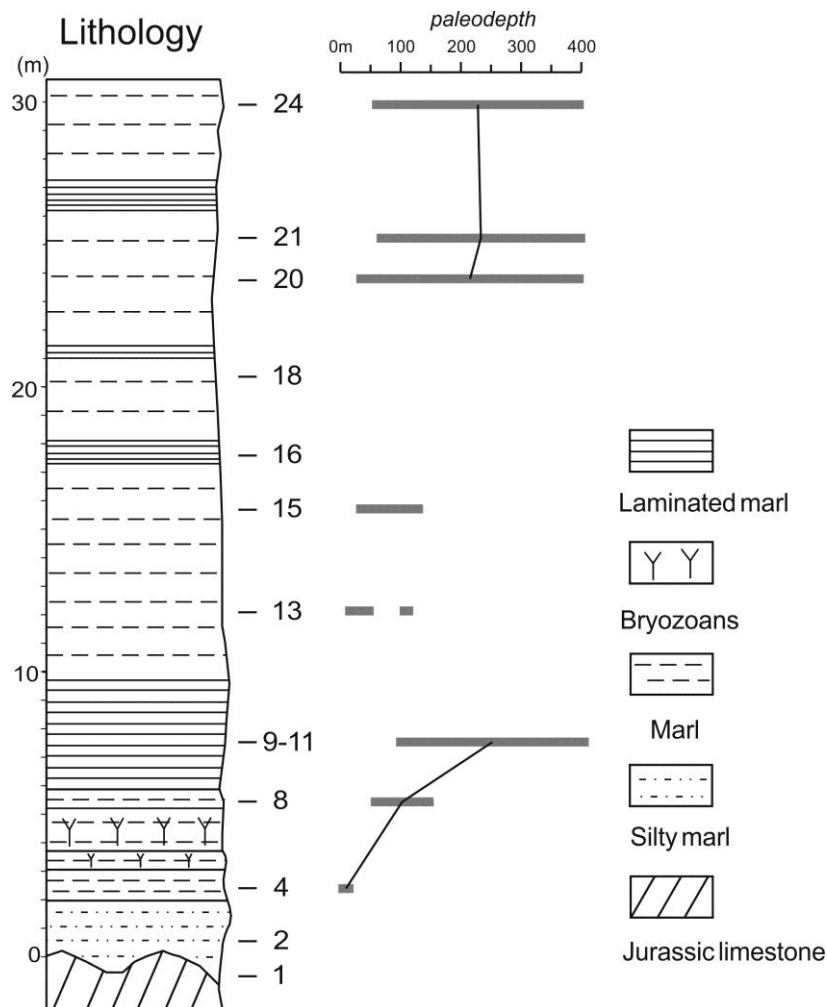


Figure 4.23 Vagia section lithology and otolith-based paleobathymetric curve.

Older paleoenvironmental studies of the Cape Vagia post-alpine sediments were conducted based on the chronostratigraphic framework proposed by Løvlie et al. (1989). This accepted the presence of a thin layer of volcanic ash, at a horizon between sample-levels 8 and 9, through which they had placed the Gelasian-Calabrian boundary at approximately 5 m above the base of the section. Later on, the bryozoan paleobathymetric study of Moissette and Spjeldnaes (1995) allowed these authors to hypothesize a transgressional phase of more than 600 m, initiated just below the Gelasian-Calabrian boundary, and followed by slow regression thereafter.

The present analysis of the otolith assemblages indicate a steep rocky coast established after 2 Ma at Vagia area, with occasional small sheltered parts. Gradually

the access to the open ocean becomes more important. In a break, the event responsible for the red oxidized layer before sample 9-11 seems to have affected the surface pelagic fauna as well as the bottom-dwellers, which are there absent. Afterwards, the ecosystem becomes rich once more; the fish fauna is very diverse, and the topography remains steep, allowing the mixing of the assemblages in the taphocoenosis. The fish identified in the sediments from the upper portion of Vagia section indicate that later on this area became deeper, but the depth gradient was significantly smaller, allowing for a sand or even mud sea bottom to establish.

4.3.5 *Kallithea*

4.3.5.1 Paleobathymetry

The paleobathymetric methodology was applied to the uppermost sample from Kallithea section (*Kal5*) and is presented in Figure 4.24. The depth of deposition is estimated between 15-50 m, based on the concurrent presence of *Gobius* cf. *paganellus*, *Vinciguerria* sp. and juvenile specimens of *C.maderensis* and *H.benoiti*.

4.3.5.2 Paleoecology

The total pelagic taxa relative abundance in sample *Kal5* assemblage amounts to 58.97%; these are mostly temperate mesopelagic myctophids (Table 4.8). The presence of subtropical *Engraulis encrasicolus* indicates coastal marine environment (Frimodt 1995), whereas *Aphia minuta* tolerates temperatures between 13-16°C (Iglesias and Morales-Nin 2001) and generally prefers more low-energy waters (Mauge 1986).

The remaining 41.03% of the assemblage refers to the benthic-benthopelagic taxa in sample *Kal5*, which include the subtropical gobiids *Gobius* cf. *paganellus*, *Deltentosteus quadrimaculatus* and *Lesueurigobius suerii* as well as *Cepola macrophthalma*. *Atherina boyeri* is also present, suggesting enclosed coastal areas with still or generally low-energy waters (Kottelat and Frayhof 2007).

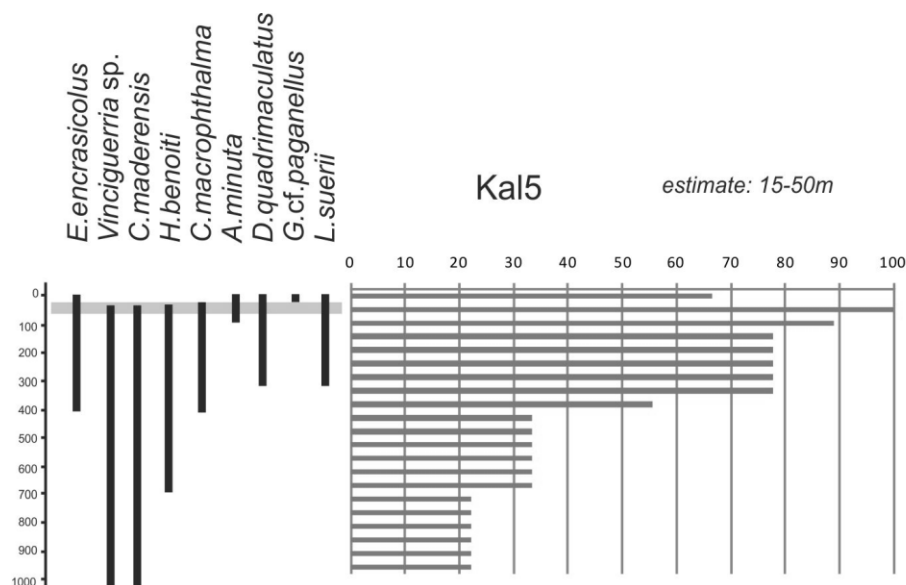


Figure 4.24 Kallithea paleobathymetric analysis and estimate.

Table 4.8 Kallithea section relative abundances		
Taxonomic placement		sample
Order/Family	Genus/Species	5
Engraulidae	<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	12.82
Phosichthyidae	<i>Vinciguerria</i> sp.	5.13
Myctophidae	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	17.95
	<i>Hygophum benoiti</i> (Cocco, 1838)	12.82
	<i>Myctophum punctatum</i> (Rafinesque, 1810)	5.13
Atherinidae	<i>Atherina boyeri</i> Risso, 1810	5.13
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)	10.26
Gobiidae	<i>Gobius</i> cf. <i>paganellus</i> Linnaeus, 1758	5.13
	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)	7.69
	<i>Lesueurigobius suerii</i> (Risso, 1810)	12.82
	<i>Aphia minuta</i> (Risso, 1810)	5.13
Total number of otoliths		22

4.3.5.3 Paleoenvironmental reconstruction of the Kallithea area

The previous works conducted in the Kallithea section (Hansen 1999; Nielsen 1999; Nielsen et al. 2006) suggested that the Lindos bay Formation in this area, was deposited in the upper circa-littoral zone, under fully marine conditions, in a well-oxygenated environment, with low sedimentation rate. The occurrence of pteropods and plant remains were interpreted as a result of the coastal vicinity (Nielsen et al. 2006). Although the Lindos bay marls in other outcrops are considered as deep-water deposits (Hanken et al. 1996), in the Kallithea section, the invertebrate fauna

indicated a depth of deposition between 8-120 m, mostly between 24-95 m (Nielsen et al. 2006). The results of the otolith assemblage analysis refine the paleobathymetric estimation for the upper part of the Lindos bay Formation, at 15-50 m. Furthermore the composition of the fish assemblage indicates that the Kallithea area, during the later part of the Lindos bay Formation deposition, was a marine coastal area with enclosed sites, free open ocean access and generally low-energy waters.

5. Discussion

5.1 The otolith-based versus the skeleton-based Pliocene – Pleistocene eastern Mediterranean fish record

A review of the available data on the teleost fish taxa identified either through skeletal remains or from their otoliths, in the south Aegean Sea, within Pliocene and Pleistocene sediments, is offered in Table 5.1. A total of eighty-eight (88) species from thirty-eight (38) families have been identified; sixty-seven (67) species from thirty (30) families have been identified based on their otoliths, while twenty (24) species from sixteen (16) families have been identified based on the preserved skeletal parts. Only three (3) species are commonly represented in the otolith and the skeleton-based record and only eight (8) families are reported by both. This comparison clearly demonstrates that the otolith-based record is much richer, than the skeleton-based record. However, it must be noted that clupeids are especially favored in the skeleton-based record, in contrast to the otolith data which is rather poor for this family, possibly because clupeid otoliths are very thin and fragile and therefore more difficult to be preserved in the sediment or after the sampling and preparation procedures.

Fish skeleton preservation results in a biased fossil record. The fish whose skeletons are preserved belong to those taxa which are tolerant of the environmental conditions necessary for their preservation. On the other hand, otoliths are preserved in a wider range of settings and thus represent the paleofauna more appropriately. In their review of the skeletal remain versus the otolith record of the Messinian teleost fish, Girone et al. (2010) argued that a) the skeletal fossil material has been studied far longer and more intensively than the otoliths, and b) the otoliths found in situ are usually very badly preserved. Furthermore, these authors indicated great discrepancies between the otolith-based and skeleton-based faunas, at the generic and specific level, and hypothesized the reasons behind them, such as the climatic latitudinal differences from south to north within the Mediterranean Sea. In addition, they noted that the otolith identifications are much more reliable than those for the skeletal record. The same observations apply in the Pliocene and Pleistocene eastern Mediterranean fish record.

Table 5.1 Comparison between the published skeleton-based versus the otolith-based record on the Plio-Pleistocene teleost fish fauna of the south Aegean Sea.			
Family	Taxa		References
	Skeletal material	Otoliths	
Congridae		<i>Conger conger</i>	This study
		<i>Gnathophis mystax</i>	This study
		<i>Pseudoplichthys escavaratierensis</i>	This study
		<i>Pseudoplichthys splendens</i>	This study
		<i>Rhynchoconger pantanelli</i>	This study
Engraulidae		<i>Engraulis encrasicolus</i>	This study
Clupeidae	<i>Alosa cf. elongata</i>		Gaudant 2001
	<i>Alosa</i> sp.		Gaudant et al. 1994
	<i>Sardina cf. pilchardus</i>		Gaudant 2001
	<i>Sardina</i> sp.		Gaudant et al. 1994
		<i>Sardinella maderensis</i>	This study
		<i>Spratelloides gracilis</i>	Gaudant et al. 1994; Gaudant & Symeonidis 1995
	<i>Spratelloides cf. gracilis</i>		Gaudant 2001; Gaudant et al. 2010
Belonidae	<i>Belone</i> sp.		Gaudant et al. 1994; Gaudant 2001
Scomberesocidae	<i>Scomberesox</i> sp.		Gaudant et al. 1994; Gaudant 2001
Centriscidae	<i>Ampisile cf. strigata</i>		Gaudant 2001
Syngnathidae	<i>Syngnathus albyi</i>		Gaudant et al. 1994
	<i>Syngnathus cf. albyi</i>		Gaudant 2001
Argentinidae		<i>Argentina sphyraena</i>	This study
Gonostomatidae		<i>Gonostoma</i> sp.	This study
Sternoptychidae	<i>Maurolicus cf. muelleri</i>		Gaudant 2001
		<i>Maurolicus muelleri</i>	This study
		<i>Polyipnus polli</i>	This study
Phosichthyidae		<i>Vinciguerria attenuata</i>	This study
		<i>Vinciguerria poweriae</i>	This study
Chlorophthalmidae		<i>Chlorophthalmus agassizi</i>	This study
Scopelarchidae		<i>Scopelarchus analis</i>	This study
Myctophidae		<i>Bentosema glaciale</i>	This study
		<i>Bentosema suborbital</i>	This study
		<i>Ceratoscopelus maderensis</i>	Markopoulou-Diakantoni & Kagiouzis 2001; Lavorati 2002; This study
Myctophidae		<i>Diaphus aff. adenomus</i>	This study
		<i>Diaphus cavallonis</i>	This study
		<i>Diaphus holti</i>	Lavorati 2002; This study
		<i>Diaphus rafinesquii</i>	This study
		<i>Diaphus aff. splendidus</i>	This study
		<i>Diaphus taaningi</i>	This study
		<i>Electrona risso</i>	Lavorati 2002; This study
		<i>Hygophum benoiti</i>	This study
		<i>Hygophum hygomii</i>	This study
		<i>Lampadena</i> sp.	This study
		<i>Lampanyctus crocodilus</i>	This study
		<i>Lobianchia dofleini</i>	Lavorati 2002; This study
		<i>Myctophum fitchi</i>	This study
		<i>Myctophum punctatum</i>	Lavorati 2002; This study
		<i>Notoscopelus elongatus</i>	Lavorati 2002; This study
		<i>Notoscopelus resplendens</i>	This study
	<i>Protomyctophum arcticum</i>	This study	
	<i>Scopelopsis pliocenicus</i>	This study	
Bregmacerotidae	<i>Bregmaceros albyi</i>		Gaudant et al. 1994
	<i>Bregmaceros cf. albyi</i>		Gaudant 2001
		<i>Bregmaceros</i> sp.	Markopoulou-Diakantoni & Kagiouzis 2001; This study
Macrouridae		<i>Coelorinchus artinaberi</i>	Lavorati 2002
		<i>Coelorinchus</i> sp.	This study
Moridae	<i>Gadella</i> sp.		Gaudant & Symeonidis 1995; Gaudant 2001
		<i>Laemonema</i> sp.	This study
Phycidae		<i>Phycis blennoides</i>	This study
Lotidae		<i>Gaidropsarus</i> sp.	This study
Gadidae		<i>Gadiculus argenteus</i>	Lavorati 2002; This study
		<i>Gadiculus labiatus</i>	This study
		<i>Gadiculus thori</i>	This study

Table 5.1 Comparison between the published skeleton-based versus the otolith-based record on the Plio-Pleistocene teleost fish fauna of the south Aegean Sea (continuation).			
Family	Taxa		References
	Skeletal material	Otoliths	
Gadidae		<i>Micromesistius poutassou</i>	Lavorati 2002; This study
	<i>Micromesistius</i> sp.		Gaudant 2001
Ophidiidae		<i>Ophidion barbatum</i>	This study
Carapidae		<i>Carapus acus</i>	This study
		<i>Echiodon dentatus</i>	This study
Bythitidae		<i>Grammonus ater</i>	This study
Atherinidae		<i>Atherina boyeri</i>	This study
Dactylopteridae	<i>Dactylopterus</i> sp.		Gaudant et al. 1994; Gaudant 2001
Scorpaenidae		<i>Scorpaena</i> sp.	This study
Acropomatidae		<i>Parascombrops mutinensis</i>	This study
Apogonidae		<i>Apogon</i> sp.	This study
Epigonidae		<i>Epigonus</i> aff. <i>denticulatus</i>	This study
Serranidae	<i>Serranus</i> sp.		Gaudant 2001
Carangidae	<i>Caranx</i> sp.		Gaudant 2001
		<i>Trachurus mediterraneus</i>	Lavorati 2002
	<i>Trachurus</i> sp.	<i>Trachurus</i> sp.	Gaudant & Symeonidis 1995; Gaudant 2001; This study
Sparidae	<i>Boops</i> cf. <i>boops</i>		Gaudant et al. 1994
	<i>Boops</i> sp.		Gaudant 2001
		<i>Dentex</i> sp.	This study
		<i>Diplodus</i> cf. <i>annularis</i>	This study
		<i>Oblada melanura</i>	This study
		<i>Pagellus bogaraveo</i>	This study
		<i>Pagellus erythrinus</i>	This study
	<i>Pagrus pagrus</i>	This study	
Centracanthidae		<i>Spicara smaris</i>	This study
Cepolidae		<i>Cepola macrophthalmia</i>	This study
Pomacentridae		<i>Chromis chromis</i>	This study
Blennidae		<i>Blennius ocellaris</i>	This study
	<i>Blennius</i> cf. <i>pavo</i>		Gaudant et al. 1994
Trichiuridae	<i>Lepidopus</i> cf. <i>caudatus</i>		Gaudant 2001
	<i>Lepidopus</i> sp.		Gaudant et al. 1994; Gaudant 2001
Scombridae	<i>Scomber</i> sp.		Gaudant 2001
	<i>Scomberomorus</i> sp.		Gaudant 2001
Gobiidae		<i>Aphia minuta</i>	This study
		<i>Deltentosteus quadrimaculatus</i>	This study
		<i>Gobius niger</i>	Lavorati 2002; This study
		<i>Gobius</i> cf. <i>paganellus</i>	This study
		<i>Lesueurigobius friesii</i>	This study
		<i>Lesueurigobius sanzi</i>	This study
		<i>Lesueurigobius suerii</i>	This study
		<i>Pomatoschistus</i> sp.	This study
Citharidae		<i>Citharus linguatula</i>	This study
Bothidae		<i>Arnoglossus kokeni</i>	This study
		<i>Arnoglossus laterna</i>	Lavorati 2002

Considering the different ecological and facies parameters affecting fossil preservation, the Voutes section offers a good example. Indeed the diatomite beds, which also contain skeletal remains, include otolith assemblages depleted in benthic and benthopelagic fish, but enriched in mesopelagic myctophids, gadids and *Bregmaceros* sp. On the contrary, marl beds exhibit rich and well diversified faunas at all water levels. The same phenomenon was observed, by Girone et al. (2010), in Tanaro section (Italy). There, it was noted that articulated skeletons were found in laminated clays and diatomites, indicating perhaps anoxic or hypersaline conditions

during deposition. The faunas, both skeleton-based and otolith-based, found in laminated or diatomitic depositions lack a strong benthic and benthopelagic component. On the contrary, otolith-based faunas identified within other types of sediments, are rather rich in bottom-dwelling fish.

5.2 Advantages and limitations in the paleoenvironmental reconstructions through the use of fossil otolith assemblages

In chapter 4 of this thesis, the identified fish otolith assemblages were used to reconstruct the paleoenvironment in the Zanclean Heraklion basin and the Gelasian – Middle Pleistocene eastern coast of Rhodes and Rhodes basin. The following observations may be noted regarding the advantages of this application:

- a. A major advantage in the use of fish otoliths as paleoenvironmental indicators is the fact that fish inhabit all possible water environments (Nolf 1985). In the sea, they are found in all water depths, throughout the water column. As such, they may provide information about environmental parameters, such as depth, temperature, oxygenation, nutrient content, at all levels and habitats.
- b. Fish otoliths are found in various sediments and facies, and, in contrast to the fossil skeletal remains, they may be sampled across entire outcrop sections, providing stratigraphic continuity at a reasonable resolution. It is noticeable that although specific stratigraphic distributions within the Mediterranean and the eastern sub-basin in particular, may appear continuous (see Tables 4.1, 4.2 and 4.3), observation in detail, at the section level shows that regionally these distribution often adjust depending on the climatic and oceanographic general and local conditions (see chapter 4). This may be observed when studying complete section data.
- c. In sedimentary research, studying the fossil otolith assemblages provides a good indication of primary and secondary mixing of the sediments as well as the origin and character of the allochthonous facies (see comments and results in chapter 4).

- d. Fish are the highest link in the trophic chain of water environments. The paleoenvironmental perturbations effect on their assemblages equals that on land mammals.

The fossil otolith sampling size is the most important drawback in the paleoenvironmental reconstructions through this methodology. It makes it difficult to sample in remote and inaccessible locations, and limits the sampling resolution. However, otoliths still provide more information than fossil fish skeletons, which are found only accidentally and span a few beds at most.

5.3 Climate-related changes in the fish distribution during the Pliocene and Pleistocene in the eastern Mediterranean

Environmental variability determines the distribution, migration and abundance of fish (Lehodey et al. 2006). The close link between climate and fish populations has been observed in modern times, from seasonal to centennial time scales (Alheit and Hagen 1997; Genner et al. 2004; Perry et al. 2005; Koutrakis et al. 2005; Sabates et al. 2006; Tsikliras 2008; Alheit et al. 2012; Alheit et al. 2013). However, the effect of long term environmental changes and variability on the fish populations is little known, since that would require longer time series historical data than currently available. Significant questions arise regarding the tolerance limits to rapid and non-rapid environmental perturbations of fish and their assemblages and the possibilities for recovery after the environment has been restored.

In the paleobiogeographic analysis presented in chapter 4 the spatial and temporal distribution of teleost fish was examined at the stage/age and sub-basin resolution. New input stretched the species' distribution in several cases. However, this resolution step hid the smaller scale variability both in space and time. It is possible to observe this variability when examining each of the studied sections separately or in groups, bearing in mind the provided chronostratigraphic framework for the relevant sediments. An example of these smaller-scale climate-related distribution changes are presented in the following paragraph.

5.3.1 *The distribution of small pelagic fish in the Pleistocene Rhodes coast*

Small pelagic fish generally have short life spans, and their abundances are thus strongly driven by the annual recruitment of young fish, a process well understood to be modulated at present by ocean climate (Lehodey et al. 2006). For example, in the northern Aegean Sea, sardine was found to be selective for warm waters, contrary to the anchovy (Giannoulaki et al. 2005). Globally, upwelling systems are known to support abundant populations of small pelagic fish, such as the anchovy *Engraulis encrasicolus* and sardines (Lehodey et al. 2006). Seasonal variability affects these systems through its atmospheric effects. Very characteristic is the influence of the ENSO oscillation on small pelagic fish, like anchovies and sardines along the Peruvian coast; during an El Niño event the coastal temperature in the Peruvian upwelling system rises up to 8°C, while plankton productivity is drastically reduced, by the lowering of the thermocline. Initially, anchovies try in vain to migrate away from the warm water; to depth or different areas altogether. A further effect of the development of an El Niño event is that predator fish also migrate to depths occupied by the anchovies, increasing predator pressure on their eggs, juveniles and adults (Alheit and Niquen 2004). The observations since the early 1970's so far show that after the event the populations do recover. Similarly, small pelagic fish have been known to be affected by climatic phenomena on different scales, such as the herring migration to the Swedish coast during cold climatic periods (Lamp 1972). Likewise, sardine biomass climate-related multi-decadal fluctuations have been recorded in the Santa Barbara basin sediments (S. California, US), spanning 1.6ky with a 500-600yr periodicity, positively correlated with major warming episodes like the Medieval Warm Period (950-1350 A.D.), and negatively responding to cooling events, such as the Little Ice Age (1400-1800 A.D.).

The fossil record on the anchovy in the Mediterranean ranges back to the Piacenzian. In the Rhodes basin it is recorded, through the present study, during the Gelasian and Calabrian. In Ypsenis section, *Engraulis encrasicolus* is found in two samples, Yps11 and Yps12t, which correspond to the uppermost part of the Lindos Bay Formation dated in the Calabrian, between 901-560 ka. A climatic minimum is suggested for the Yps11-level (paleoenvironmental stage ν), with sea surface temperatures at the Rhodes coast between 13-16°C, based on the presence of *Aphia*

minuta (Iglesias and Morales-Nin 2001). The local conditions are estimated as a semi-closed basin or lagoon, with sea bottom depths up to 100 meters (analysis in chapter 4). However, as the cold conditions prevail during the following paleoenvironmental stages (*vi* and *vii*), the anchovy population seems to disperse, probably also due to the change in the topographic setting; the area deepens and ocean access is much more enhanced. At the Yps12t-level, during stage *viii*, the climate improves again and notably the area becomes again more enclosed, allowing the anchovy to return. The same occurrence is observed also in Kallithea section, where *Engraulis encrasicolus* is present at the uppermost part of Lindos Bay Formation, estimated in Kallithea to be within the Middle Pleistocene (Ionian) stage. Again the concurrent presence of *Aphia minuta* in these coastal waters indicates surface temperatures between 13-16°C.

Engraulis cf. encrasicolus otoliths were also found together with *Sardinella maderensis* in the sample 13-level of Vagia section, located after the Gelasian/Calabrian boundary and dated between 2-1.6 Ma. The Madeiran sardinella is also a small subtropical pelagic fish whose movements are associated with seasonal upwelling (Whitehead et al. 1985). It forms schools in coastal areas and prefers temperatures around 24°C (FAO-FIGIS 2005). Sample Vag13 contains the most rich and diversified fish fauna in this section. The paleoenvironment after this level becomes deeper and both the anchovy and the sardinella are absent.

5.3.2 *The use of paleontological data in predicting fish distribution in the eastern Mediterranean under climate change scenarios*

The present-day Mediterranean Sea is the home for 619 fish species, among which 13% are endemic, 2% are introduced and 67% are non-endemic natives; 85% of these fish are teleosts (Lasram et al. 2009). Zenetos et al. (2012) report 775 alien marine species in the eastern Mediterranean Sea, 48 more were added between 2011 and 2012. These are macrophytes, mollusks, polychaetes, crustaceans and fish. On average, these authors estimate that 6 non-indigenous fish species are incorporated into the Mediterranean ecosystem every year. More than half (54%) of the marine alien species in the Mediterranean were probably introduced through corridors (mainly the Suez Canal).

Observations and theory suggest that marine species respond to ocean warming by shifting their latitudinal range (Perry et al. 2005) and depth range (Dulvy et al 2008), which is locally translated to extinctions and invasions. Temperature undoubtedly plays a pivotal role in the geographic range of marine species. However, the complicated species-species and species-ecosystem interactions hamper any future prediction (Belyea 2007). Predicting future geographic ranges of marine species, requires an a priori assessment of their environmental response mechanisms, which would best be obtained through knowledge of their spatial distribution during the climate fluctuations of the Pleistocene glaciations (Kettle et al. 2011). As an example, Kettle et al. (2011) used archaeological data to calibrate an ecological niche model and predicted the geographic ranges of four North Atlantic fish species during the Last Glacial Maximum. Similarly, the new data presented here may be used to infer the distributions of fish in the eastern Mediterranean under a different set of future conditions.

Ecological niche models assume a lack of biotic interactions, evolutionary change, and species dispersal, and accept that the observed distributions are in equilibrium with their environment (Cheung et al. 2009; Nogues-Bravo 2009). It is hypothesized that the fish responded to paleoenvironmental conditions in the same way as at present (Kettle et al. 2011). However, there have been cases, usually associated with human interference or climate change, in historic and pre-historic time, when the fish populations changed their habitat preferences in order to adjust to outside pressures (e.g. Pickard and Bonsall 2004; Morales and Rosello 2004; Planque et al. 2010). By using the paleontological data, in conjunction with other paleoecologic and sedimentologic information, such modifications could be detected.

Furthermore, correlations of present-day data have demonstrated that climate-related variability of fish populations is the rule rather than the exception, but species distribution recovery is not always certain, even if the supposed preferred climate regime is reverted (Lehodey et al. 2006). The reasons behind this occurrence could be several: a completely depleted stock, the replacement by a better-adapted species, a fundamental change in the entire ecosystem, or an indication of anthropogenic interference. The overall assessment of the Mediterranean paleobiogeographic data on the teleost fish species (see chapter 3 for the analysis) indicates that local recovery is

not very common and is subject to the modified paleogeographic conditions in each case. However, on the basin or even sub-basin level, the Mediterranean holds various settings and possibilities for fish to adapt and inhabit. Overall recovery, after major environmental perturbations is very high, and usually more than a single event is needed to expatriate a fish species.

6. Conclusions

The target of this research is to reconstruct the eastern Mediterranean Pliocene and Pleistocene ichthyofauna and furthermore to use this data to infer about the paleoenvironment, the paleoceanographic and paleoclimatic conditions in selected study areas. This is the first significant study of the fossil fish assemblages of the eastern Mediterranean basin. The results and discussion presented here highlight the value of fish otoliths in the reconstruction of the paleoichthyofauna, and their use as paleoenvironmental indicators. The major conclusions accruing from this study are summarized as follows.

Fossil fish otoliths are by far the best medium for the identification of past fish faunas. In the present study, a total of eighty-one (81) teleost fish species were identified, placed under sixty (60) genera and thirty-four (34) families. Morphological comments were made on all identified taxa. Of particular interest are the new observations on the species *Pseudophichthys* spp., *Rhynchoconger pantanellii*, *Chlorophthalmus agassizi*, *Diaphus* spp., *Parascombrops mutinensis*, and *Gobius* spp. These results illustrate once more that the study of otoliths yields much better results than previous studies based on preserved skeletons.

The fish assemblages identified on Rhodes and Crete Islands were used to reconstruct the paleoenvironment in the studied areas, providing information on depth, water temperature at surface and at depth, salinity, nutrient content, oxygenation, topography and substratum. In particular, six paleoenvironmental stages were distinguished in the uppermost Zanclean Heraklion basin, with two climatic optimums recorded in the upper part of Voutes section, by the intrusion of tropical taxa at all water levels. Characteristic phases of steep underwater topography at the eastern Rhodes coast during the early – middle Pleistocene were detected through the paleobathymetric estimation method in Ypsenis, Vagia and Faliraki section. Cold and warm episodes were recorded in each Rhodes section, and upwelling events were inferred through the presence of *Engraulis encrasicolus* and *Sardinella maderensis* remains during the Gelasian (Vagia section), the Calabrian (Ypsenis section) and the Middle Pleistocene stage (Kallithea section). Overall, the Pleistocene Rhodes coastal waters held similar a fish fauna as today, with the only exception of the occasional

presence of taxa such as *Scopelarchus analis*, *Benthoosema suborbitale*, *Lampadena* sp., *Pseudophichthys splendens*, *Polyipnus polli*, *Laemonema* sp., *Phycis blennoides*, *Gadiculus thori* and *Lesueurigobius sanzi*, due to the change in the paleogeographic setting or the climatic conditions at the time. Conclusively, the most important environmental parameter which has affected the studied past assemblages is water depth. Sea surface temperature is a major modifier only for the pelagic component. Substratum also plays an important role in determining the coastal fauna composition. Salinity changes, in the marine environment, lead to the local invasion or extinction of certain euryhaline species. In addition, it was revealed in several cases, during the paleoecological analysis that, when a taphocoenosis combines inhabitants from different adjacent environmental settings, the mixing of the faunas can be inferred. Finally, bottom water anoxia leads to fossil assemblages which are highly depleted in benthic and benthopelagic taxa, and contain only upper oceanic fish.

In the paleobiogeographic investigation, the stratigraphic distribution of twenty-nine (29) taxa is significantly extended. In particular, twelve (12) species are reported for the first time in the Zanclean of the eastern Mediterranean realm. In the Gelasian stage, eight (8) species are reported as new for this area, while the Calabrian record is enriched by twenty-one (21) taxa. The broad paleobiogeographic overview presented in chapter 4, which distinguishes presence/absence during each chronostratigraphic stage from the Miocene until today, separately for the eastern and western Mediterranean sub-basins, provides information on the general evolutionary trends, introductions and extinctions, but fails to pinpoint smaller scale paleoclimatic perturbations or local events. These can be viewed only when examining the fish fauna on a section-by-section basis.

A niche-based approach is considered more appropriate to evaluate the evolution of the late Cenozoic eastern Mediterranean fish fauna. The data presented here could be further used to calibrate ecological niche models, in order to predict the fish distribution in the eastern Mediterranean under warmer climate conditions, such as those suggested for the Pliocene, as well as under higher-frequency climatic variability, based on the Pleistocene data.

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Appendix I

Plates I-VII

Photographs of the identified and comparative material

Plate I

Family CONGRIDAE

1. *Conger conger* (Linnaeus, 1758), Yps9,
2. *Gnathophis mystax* (Delaroche, 1809), Yps5,
3. *Pseudophichthys escavaratierensis* (Nolf & Cappetta, 1988), Voutes 3,
4. *Pseudophichthys splendens* (Lea, 1913) Voutes 6,
- 5-10. *Rhynchoconger pantanelli* (Bassoli, 1906), 5. Voutes 6, 6. Voutes a, 7-8. Voutes 6, 9-10. Yps5,
- 11-12. Congridae indet. Vag13.

Family NETTASTOMATIDAE

- 13-14. Nettastomatidae indet., 13. Vag13, 14. Akrotiri section, Gelasian Ionian Sea.

Family CLUPEIDAE

15. *Sardinella maderensis* (Lowe, 1838), Vag13.

Family ARGENTINIDAE

16. *Argentina sphyraena* Linnaeus, 1758, Yps11.

Family ENGRAULIDAE

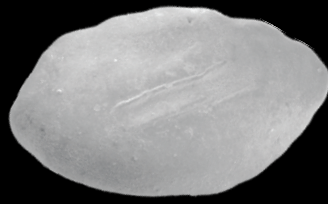
- 17-20. *Engraulis encrasicolus* (Linnaeus, 1758), 17-18. Yps11, 19. Vag13, 20. Kal5.



1

200µm

Conger conger



2

500µm

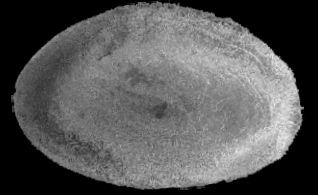
Gnathophis mystax



3

200µm

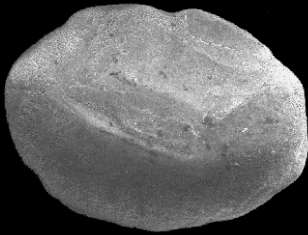
*Pseudophichthys
escavaratierensis*



4

200µm

*Pseudophichthys
splendens*



5

500µm



6

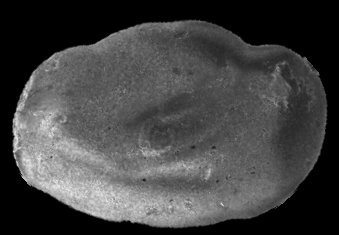
500µm

Rhynchoconger pantanelli



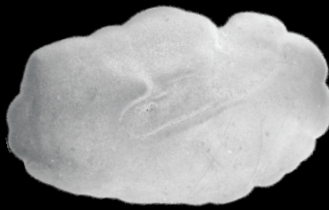
7

200µm



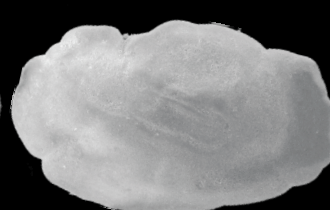
8

200µm



9

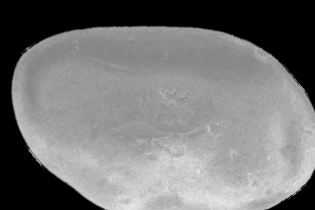
500µm



10

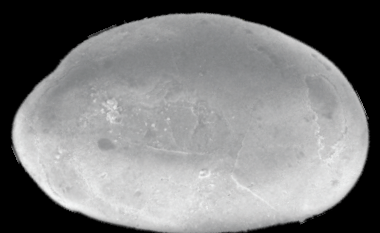
500µm

Rhynchoconger pantanelli



11

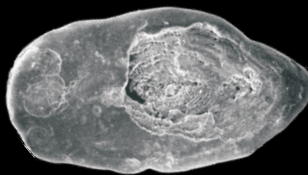
200µm



12

100µm

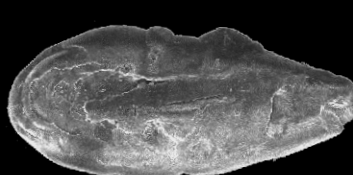
Congridae indet.



13

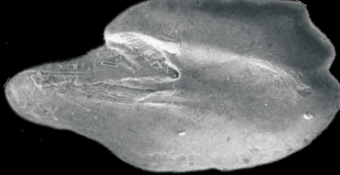
200µm

Nettastomatidae indet.



14

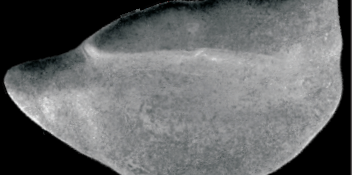
100µm



15

100µm

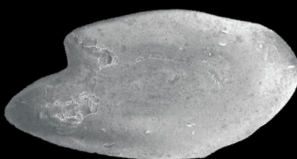
*Sardinella
maderensis*



16

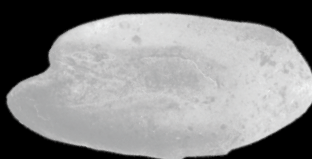
1mm

Argentina sphyraena



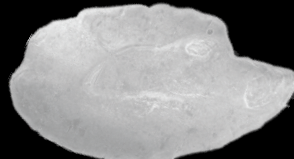
17

200µm



18

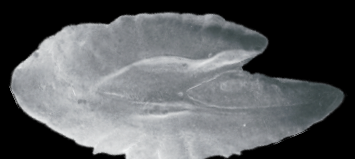
200µm



19

100µm

Engraulis encrasicolus



20

500µm

Plate II

Family MICROSTOMATIDAE

21. *Nansenia groenlandica* (Reinhardt, 1840), Akrotiri section, Gelasian Ionian Sea.

Family ALEPOCEPHALIDAE

22. *Alepocephalus* sp., Akrotiri section, Gelasian Ionian Sea.

Family GONOSTOMATIDAE

23. *Gonostoma* sp., Yps4.

Family STERNOPTYCHIDAE

24. *Maurolicus muelleri* (Gmelin, 1789), Vag13,

- 25-26. *Polyipnus polli* Schultz, 1961, Yps5.

Family PHOSICHTHYIDAE

27. *Vinciguerria poweriae* (Cocco, 1838), Vag13,

28. *Phosichthys* sp., Yps4.

Family STOMIIDAE

29. *Chauliodus sloani* Schneider, 1801, Gerakas section, Calabrian Ionian Sea.

Family CHLOROPHTHALMIDAE

30. *Chlorophthalmus* cf. *agassizi* Bonaparte, 1840, Akrotiri section, Middle Pleistocene stage Ionian Sea,

31. *Chlorophthalmus* aff. *agassizi* Bonaparte, 1840, Fal4/19,

- 32-33. *Chlorophthalmus agassizi* Bonaparte, 1840, 32. Voutes 5, 33. recent eastern Ionian Sea.

Family SCOPELARCHIDAE

- 34-35. *Scopelarchus analis* (Brauer, 1902), 34. Akrotiri section, Gelasian Ionian Sea, 35. Vag13.

Family BREGMACEROTIDAE

36. *Bregmaceros* sp., Voutes 5.

Family MACROURIDAE

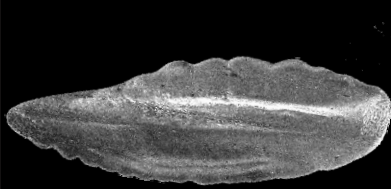
37. *Coelorinchus* sp., Yps4.

Family MORIDAE

- 38-40. *Laemonema* sp., 38-39. Voutes 4, 40. Akrotiri section, Gelasian Ionian Sea.

Family OPHIDIIDAE

41. *Ophidion barbatum* Linnaeus, 1758, Fal4/19.



21

500µm

Nansenia groenlandica



22

200µm

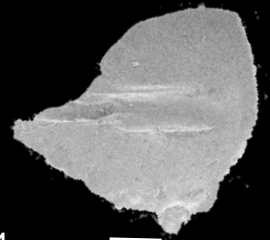
Alepocephalus sp.



23

200µm

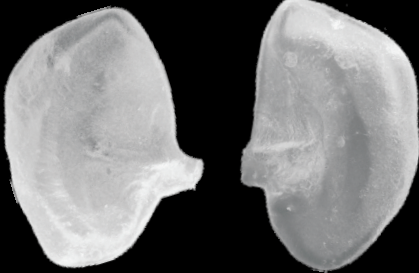
Gonostoma sp.



24

200µm

Maurolicus muelleri



25

500µm

Polyipnus polli

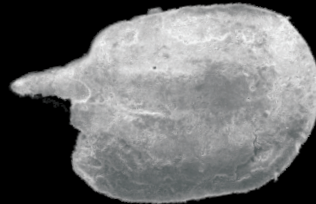


26

27

200µm

Vinciguerria poweriae



28

100µm

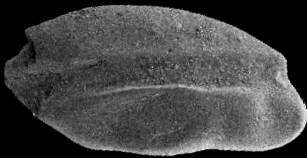
Phosichthys sp.



29

200µm

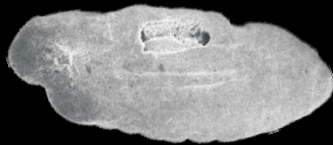
Chauliodus sloani



30

500µm

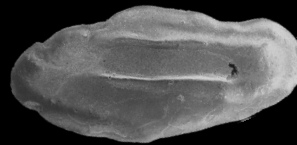
Chlorophthalmus
cf. *agassizi*



31

500µm

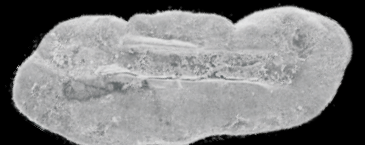
Chlorophthalmus
aff. *agassizi*



32

500µm

Chlorophthalmus agassizi



33

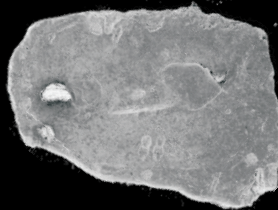
500µm



34

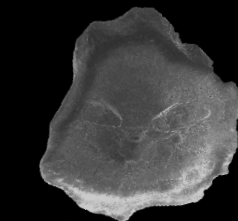
500µm

Scopelarchus analis



35

1mm



36

500µm

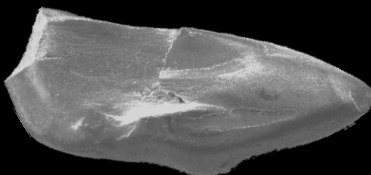
Bregmaceros sp.



37

500µm

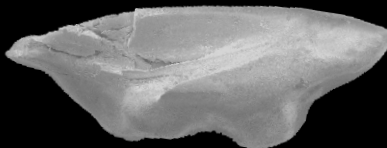
Coelorinchus sp.



38

500µm

Laemonema sp.



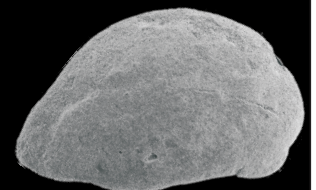
39

500µm



40

500µm



41

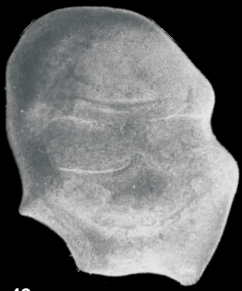
1mm

Ophidion barbatum

Plate III

Family MYCTOPHIDAE

42. *Benthoosema glaciale* (Reinhardt, 1837), Yps3,
43. *Ceratoscopelus maderensis* (Lowe, 1839), Yps3,
44. *Diaphus* aff. *adenomus* Gilbert, 1905, Voutes 2,
45. *Diaphus cavallonis* (Brzobohaty and Nolf, 2000), Voutes 2,
46. *Diaphus holti* Taaning, 1918, Yps5,
47. *Diaphus rafinesquii* (Cocco, 1838), Yps4,
48. *Diaphus* aff. *splendidus* (Brauer, 1904), Voutes 5,
49. *Diaphus taaningi* Norman, 1930, Voutes a,
50. *Diaphus* sp.1, Yps3,
51. *Electrona risso* (Cocco, 1829), Akrotiri section, Gelasian Ionian Sea,
- 52-53. *Hygophum benoitii* (Cocco, 1838), 52. Vag13, 53. Yps5,
54. *Hygophum hygomii* (Lotken, 1892), Voutes 3,
55. *Lampanyctus crocodilus* (Risso, 1810), Yps4,
56. *Lobianchia dofleini* (Zugmayer, 1911), Yps4,
57. *Myctophum fitchi* (Schwarzahns, 1979), Voutes c,
- 58-59. *Notoscopelus elongatus* (Costa, 1844), 58. Yps5, 59. Akrotiri section, Gelasian Ionian Sea,
60. *Notoscopelus resplendens* (Richardson, 1845), Voutes c,
61. *Myctophum punctatum* (Rafinesque, 1810), Yps3.



42
500µm

Benthosema glaciale



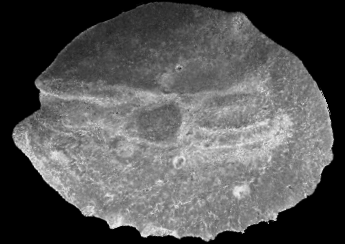
43
500µm

Ceratoscopelus maderensis



44
1mm

Diaphus aff. adenomus



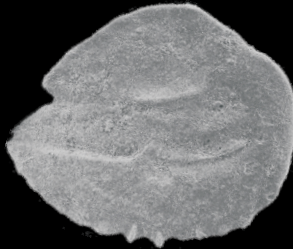
45
1mm

Diaphus cavallonis



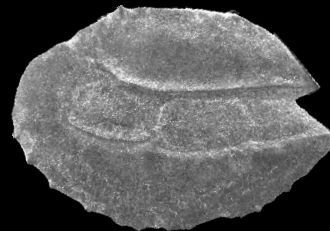
46
500µm

Diaphus holti



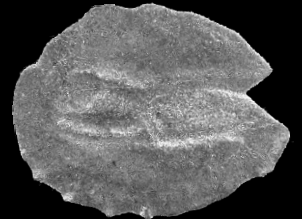
47
1mm

Diaphus rafinesqui



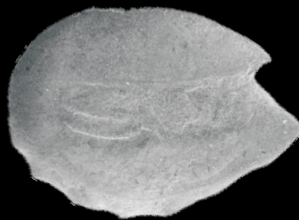
48
1mm

Diaphus aff. splendidus



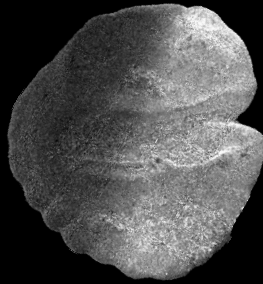
49
500µm

Diaphus taaningi



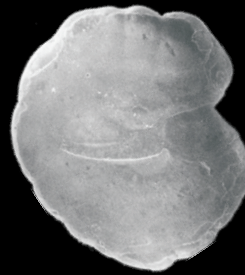
50
500µm

Diaphus sp.1



51
500µm

Electrona risso

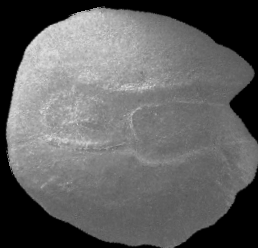


52
500µm

Hygophum benoitii

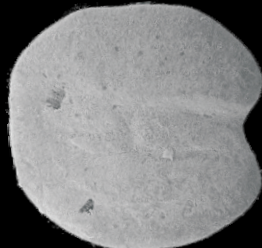


53
200µm



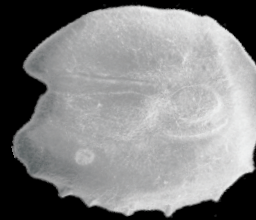
54
500µm

Hygophum hygomii



55
500µm

Lampanyctus crocodilus



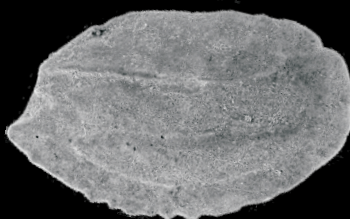
56
500µm

Lobianchia dolfeini



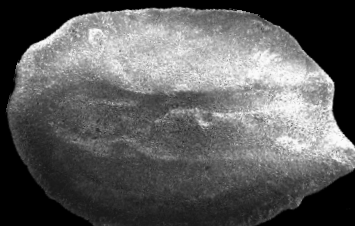
57
1mm

Myctophum fitchi



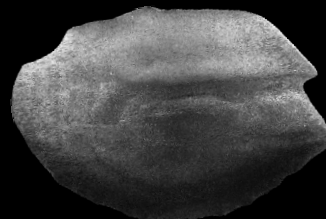
58
500µm

Notoscopelus elongatus

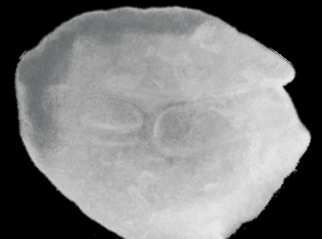


59
500µm

Notoscopelus respiciens



60
1mm



61
500µm

Myctophum punctatum

Plate IV

Family MYCTOPHIDAE (continuing...)

62-63. *Protomyctophum arcticum* (Lütken, 1892), Yps9,

64. *Scopelopsis pliocenicus* (Anfossi&Mosna, 1976), Yps4.

Family PHYCIDAE

65. *Phycis blemoides* (Brünnich, 1768), Yps5.

Family GADIDAE

66. *Gadiculus argenteus* Guichenot, 1850, Yps11,

67. *Gadiculus labiatus* (Schubert, 1905), Voutes 2,

68. *Gadiculus thori* Schmidt, 1913, Yps3,

69. *Micromesistius poutassou* (Risso, 1827), Vag13,

70-73. Gadidae indet. lapillus, 70. Voutes 5, 71-72. Voutes 2, 73. Yps4.

Family LOTIDAE

74-76. *Gaidropsarus* sp., 74. Akrotiri section, Gelasian Ionian Sea, 75-76. Vag13.

Family CARAPIDAE

77-78. *Carapus acus* (Brünnich, 1768), 77. Vag8, 78. Vag13,

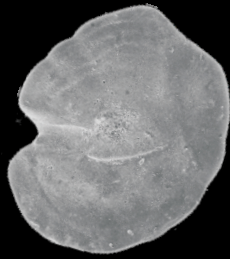
79-80. *Echiodon dentatus* (Cuvier, 1829), 79. Fal4/19, 80. Voutes a.



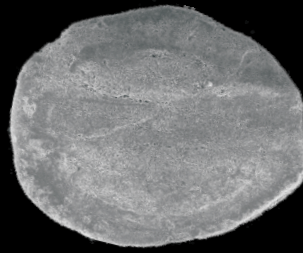
62



Protomyctophum arcticum



63



64



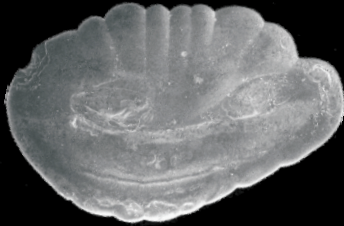
Scopelopsis pliogenicus



65



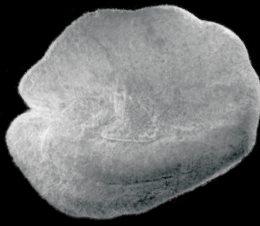
Phycis blennoides



66



Gadicus argenteus



67



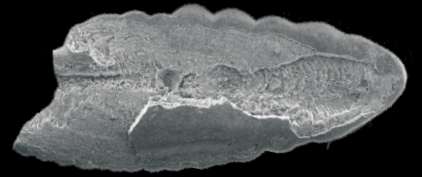
Gadicus labiatus



68



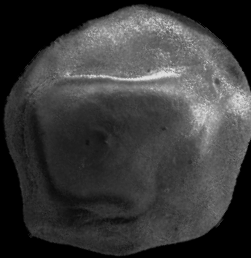
Gadicus thori



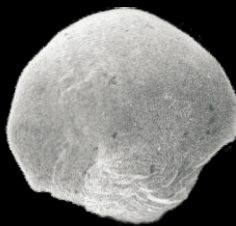
69



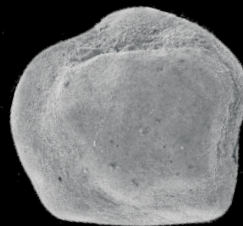
Micromesistius poutassou



70



71



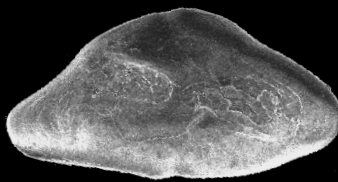
72



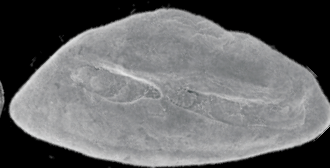
73



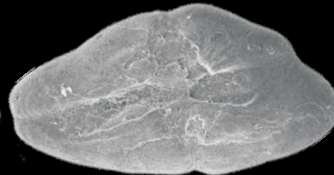
Gadidae indet. lapilli



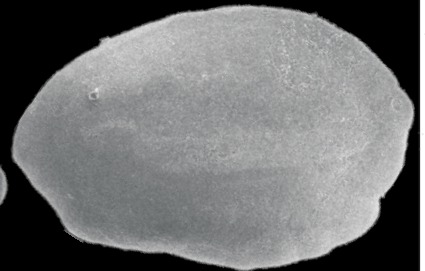
74



75



76

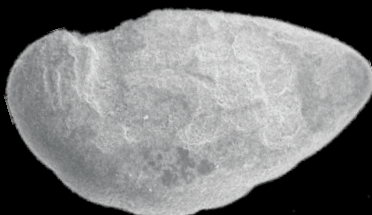


77

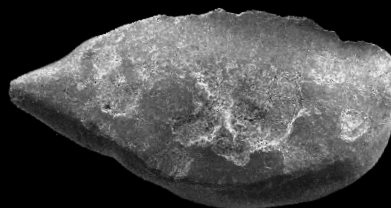


Gaidropsarus sp.

Carapus acus



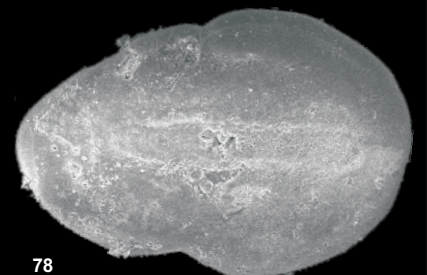
79



80



Echiodon dentatus



78



Plate V

Family ATHERINIDAE

81-82. *Atherina boyeri* Risso, 1810, 81. Vag13, 82. Voutes 6,

83. *Atherina* cf. *boyeri* Risso, 1810, Yps9.

Family SCORPAENIDAE

84. *Scorpaena* sp., Yps5.

Family APOGONIDAE

85. *Apogon* sp., Voutes 6.

Family ACROPOMATIDAE

86-91. *Parascombrops mutinensis* (Bassoli, 1906), 86. Vag13, 87 and 90. Paliore river (Di Geronimo et al., 2003), 88-89. Akrotiri section, Gelasian Ionian Sea, 91. Voutes 5.

Family EPIGONIDAE

92. *Epigonus* aff. *denticulatus* Dieuzeide, 1950, Voutes c,

93. *Epigonus* sp., Voutes 2.

Family CARANGIDAE

94. *Trachurus* sp., Yps9.

Family BYTHITIDAE

95. *Bellottia* cf. *apoda* Giglioli, 1883, Gerakas section, Gelasian Ionian Sea,

96. *Grammonus ater* (Risso, 1810), Voutes c.

Family CENTRACANTHIDAE

97. *Spicara smaris* (Linnaeus, 1758), Yps9.

Family CEPOLIDAE

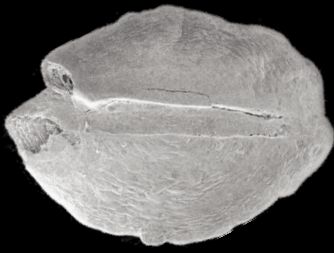
98. *Cepola macrophthalma* (Linnaeus, 1758), Voutes 6.

Family POMACENTRIDAE

99. *Chromis chromis* (Linnaeus, 1758), Yps5.

Family BLENNIIDAE

100. *Blennius ocellaris* Linnaeus, 1758, Yps12ter.



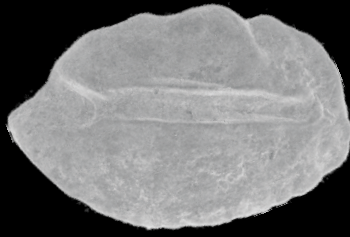
81

200µm



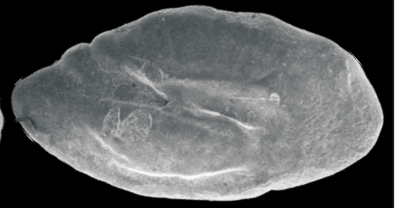
82

500µm



83

500µm



84

500µm

Atherina boyeri

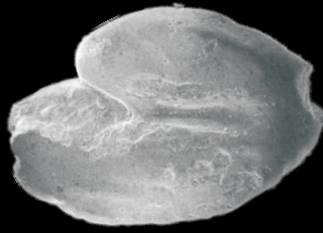
Atherina cf. boyeri

Scorpaena sp.



85

200µm



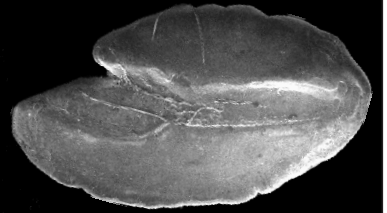
86

200µm



87

1mm

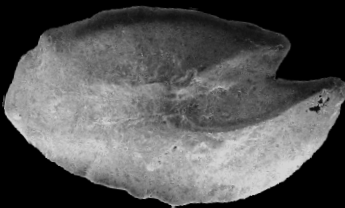


88

500µm

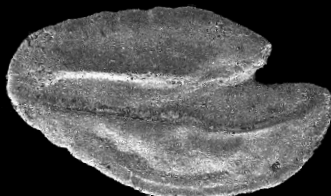
Apogon sp.

Parascombrops mutinensis



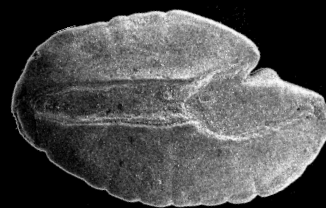
92

500µm



89

500µm



90

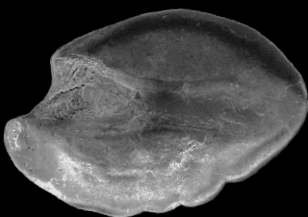
500µm



91

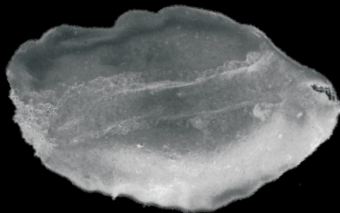
1mm

Epigonus denticulatus



93

200µm



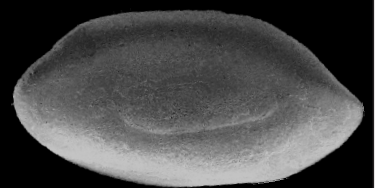
94

200µm



95

200µm



96

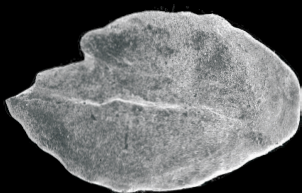
500µm

Epigonus sp.

Trachurus sp.

Bellottia cf. apoda

Grammonus ater



97

500µm



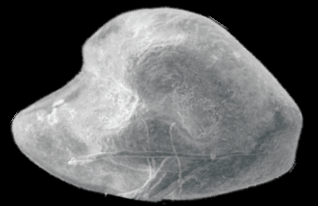
98

500µm



99

500µm



100

200µm

Spicara smaris

Cepola macrophthalma

Chromis chromis

Blennius ocellaris

Plate VI

Family SPARIDAE

101. *Diplodus cf. annularis* (Linnaeus, 1758), Fal4/19,
102-103. *Dentex* sp., 102. Vag13, 103. Yps5,
104-105. *Oblada melanura* (Linnaeus, 1758), 104. Voutes c, 105. Vag13,
106. *Pagellus erythrinus* (Linnaeus, 1758), Voutes 5,
107. *Pagellus cf. bogaraveo* (Brünnich, 1768), Fal4/19,
108. *Pagellus* sp., Voutes 6.

Family TRICHIURIDAE

109. *Aphanopus aff. carbo* Lowe, 1839, Akrotiri section, Gelasian Ionian Sea.

Family CITHARIDAE

110. *Citharus linguatula* (Linnaeus, 1758), Voutes 6.

Family BOTHIDAE

111. *Arnoglossus kokeni* (Bassoli, 1906), Voutes a,
112-113. *Arnoglossus* sp., 112. Voutes 6, 113. Vag13,
114. Bothidae indet., Voutes a.

Family GOBIIDAE

115. *Aphia minuta* (Risso, 1810), Yps7,
116-118. *Deltentosteus quadrimaculatus* (Valenciennes, 1837), 116. Yps9, 117. Vag13, 118. Fal4/11,
119-120. *Pomatoschistus* sp., Yps11,



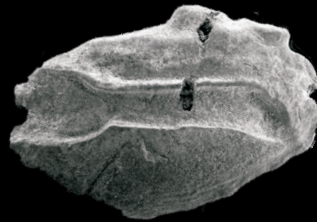
101
500µm

Diplodus cf. annularis



102
500µm

Dentex sp.

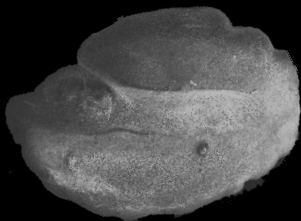


103
1mm



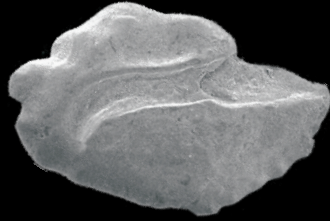
104
1mm

Oblada melanura



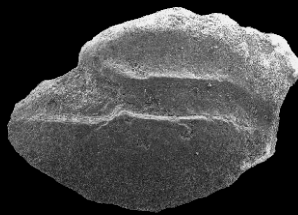
106
200µm

Pagellus erythrinus



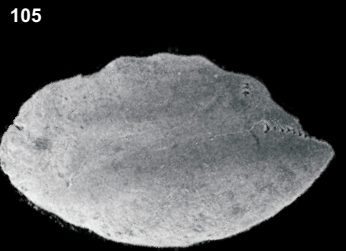
107
500µm

Pagellus cf. bogaraveo

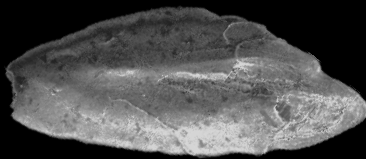


108
500µm

Pagellus sp.

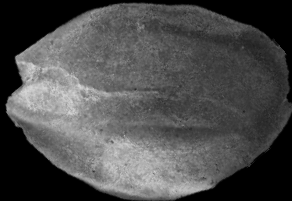


105
500µm



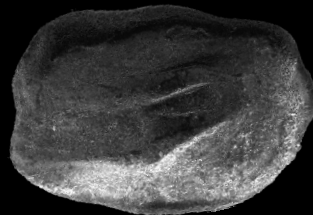
109
200µm

Aphanopus aff. carbo



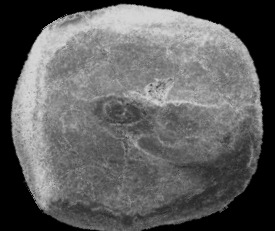
110
500µm

Citharus linguatula



111
200µm

Arnoglossus kokeni



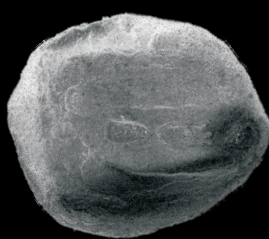
114
200µm

Bothidae indet.

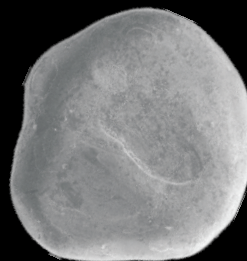


112
500µm

Arnoglossus sp.

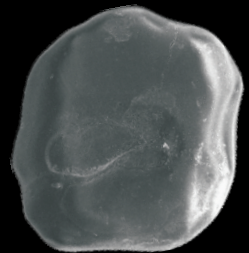


113
200µm



119
200µm

Pomatoschistus sp.



120
200µm



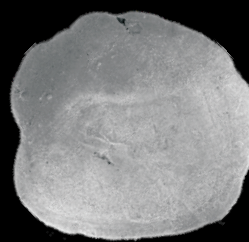
115
200µm

Aphia minuta

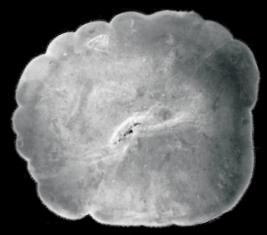


116
200µm

Deltentosteus quadrimaculatus



117
500µm



118
500µm

Plate VII

Family GOBIIDAE (continuing...)

121-122. *Gobius* cf. *paganellus* Linnaeus, 1758, 121. Voutes a, 122. Fal4/19,

123-124. *Gobius niger* Linnaeus, 1758, 123. Yps5, 124. Voutes a,

125. *Gobius* sp.1, Voutes 6,

126-130. *Gobius* sp.2, 126-127. Yps11, 128-130. Fal4/11,

131. *Gobius* sp.3 morphotype 1, Yps9,

132. *Gobius* sp.3 morphotype 2, Yps9,

133. genus «*Gobidarum*» sp.1, Voutes 6,

134. *Lesueurigobius friesii* (Malm, 1874), Voutes a,

135. *Lesueurigobius sanzi* (de Buen, 1918), Voutes a,

136. *Lesueurigobius suerii* (Risso, 1810), Yps5.



121



122



123

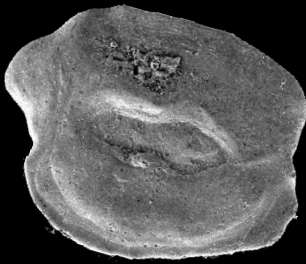


124

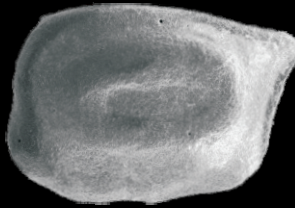


Gobius cf. paganellus

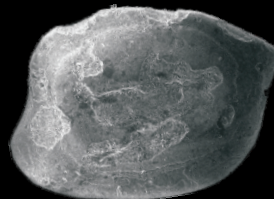
Gobius niger



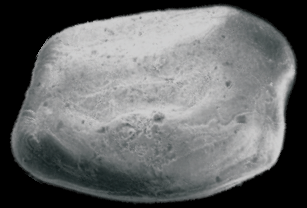
125



126



127

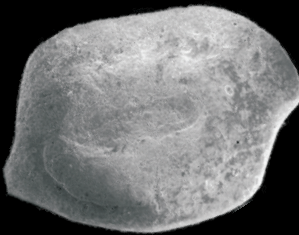


128

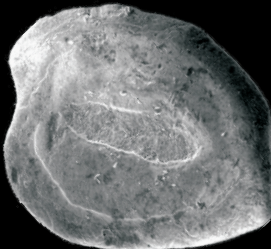


Gobius sp.1

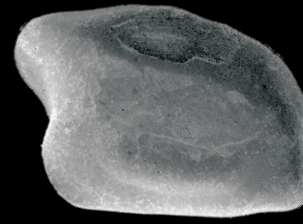
Gobius sp.2



129



130



131



132



Gobius sp.2

Gobius sp.3
morphotype 1

Gobius sp.3
morphotype 2



133



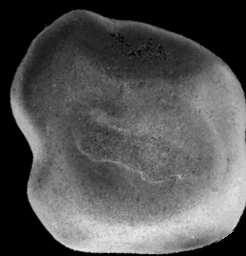
genus «*Gobidarum*»
sp.1



134



Lesueurigobius
friesii



135



Lesueurigobius
sanzi



136



Lesueurigobius
suerii

Appendix II

Material catalogue

Voutes section otolith material										
Taxonomic placement		Sample								
Family	Genus/Species	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>Ceratoscopelus 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 benoiti</i> (Cocco, 1838)								1	
	<i>Hygophum hygomii</i> (Lotken, 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	24
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)			2		2		1		
BENTHIC AND BENTHOPELAGIC TAXA										
Congridae	<i>Pseudophichthys splendens</i> (Lea, 1913)				1					
	<i>Pseudophichthys</i> <i>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

Voutes section otolith material (continuation)										
Taxonomic placement		Sample								
Family	Genus/Species	c	b	a	6	5	4	3	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>Deltentosteus</i> aff. <i>quadrifasciatus</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				
Trichiuridae	Indet.								1	
Citharidae	<i>Citharus linguatula</i> (Linnaeus, 1758)				1					
Bothidae	<i>Arnoglossus kokeni</i> (Bassoli, 1906)			1						
	<i>Arnoglossus</i> sp.				1					
	Indet.			1						
Total number of otoliths in the sample		105	45	224	135	102	57	79	113	34

Ypsenis section otolith material										
Taxonomic placement		Sample								
Family	Genus/Species	3	4	5	7	9	11	11	12	12t
PELAGIC TAXA										
Engraulidae	<i>Engraulis encrasicolus</i> (Linnaeus, 1758)						2			
	<i>Engraulis cf. encrasicolus</i> (Linnaeus, 1758)									1
Gonostomatidae	<i>Gonostoma</i> sp.	2	1							
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)	2	5	11	1	5	4	22	3	1
Phosichthyidae	<i>Vinciguerria attenuata</i> (Cocco, 1838)		2							
Myctophidae	<i>Benthoosema glaciale</i> (Reinhardt, 1837)	27	6		1		3		1	
	<i>Benthoosema suborbitale</i> (Gilbert, 1913)	1								
	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	88	28	30		1	2			
	<i>Diaphus holti</i> Taaning, 1918	4	5	3	1					
	<i>Diaphus rafinesquii</i> (Cocco, 1838)		5	2						
	<i>Diaphus taaningi</i> Norman, 1930	3	11	2						
	<i>Diaphus</i> sp.1	3								
	<i>Diaphus</i> sp.	4								
	<i>Electrona risso</i> (Cocco, 1829)	27	8							
	<i>Hygophum benoiti</i> (Cocco, 1838)	56	22	18		2				
	<i>Hygophum hygomii</i> (Lotken, 1892)		9							
	<i>Lampanyctus crocodilus</i> (Risso, 1810)	6	3	1						
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)	2	25	2						
	<i>Myctophum punctatum</i> (Rafinesque, 1810)	16	2	6						
	<i>Notoscopelus elongatus</i> (Costa, 1844)	6	3	7	1	1				
	<i>Protomyctophum arcticum</i> (Lütken, 1892)					2				
	<i>Scopelopsis pliocenicus</i> (Anfossi & Mosna, 1976)		4							
	indet.	50	24 5	4			2			2
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)				1	1	2	2		
BENTHIC AND BENTHOPELAGIC TAXA										
Congridae	<i>Conger conger</i> (Linnaeus, 1758)			2	1	1				
	<i>Gnathophis mystax</i> (Delaroche, 1809)			4						
	<i>Rhynchoconger pantanellii</i> (Bassoli, 1906)			2						
Argentinidae	<i>Argentina sphyraena</i> Linnaeus, 1758						1			
Sternoptychidae	<i>Polyipnus polli</i> Schultz, 1961			3						
Carangidae	<i>Trachurus</i> sp.					1				
Macrouridae	<i>Coelorinchus</i> sp.		1							
Centracanthidae	<i>Spicara smaris</i> (Linnaeus, 1758)					5				

Ypsenis section otolith material (continuation)										
Taxonomic placement		Sample								
Family	Genus/Species	3	4	5	7	9	11	11	12	12t
Phycidae	<i>Gaidropsarus</i> sp.	1								
	<i>Phycis blennoides</i> (Brünnich, 1768)	1		2						
Gadidae	<i>Gadiculus argenteus</i> Guichenot, 1850	11	12	3		1	1	1	1	
	<i>Gadiculus thori</i> Schmidt, 1913	1								
	<i>Micromesistius poutassou</i> (Risso, 1827)	3		1				3		
	indet. lapilli		1							
	indet.				1					
Bythitidae	<i>Grammonus ater</i> (Risso, 1810)					1				
Atherinidae	<i>Atherina</i> cf. <i>boyeri</i> Risso, 1810								1	
	<i>Atherina boyeri</i> Risso, 1810					1				
Scorpaenidae	<i>Scorpaena</i> sp.			1						
Sparidae	<i>Dentex</i> sp.			1						
	<i>Oblada melanura</i> (Linnaeus, 1758)				1					
	indet.					1			1	
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)		1	2						
Pomacentridae	<i>Chromis chromis</i> (Linnaeus, 1758)			1						
Blennidae	<i>Blennius ocellaris</i> Linnaeus, 1758									1
Gobiidae	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)			8		3	2			2
	<i>Deltentosteus</i> sp.								2	
	<i>Gobius niger</i> Linnaeus, 1758			6			1			
	<i>Gobius</i> sp.1 morphotype 1					1				
	<i>Gobius</i> sp.1 morphotype 2					1				
	<i>Gobius</i> sp.2						2			
	<i>Lesueurigobius suerii</i> (Risso, 1810)			2						
	<i>Lesueurigobius</i> sp.	1								
	<i>Pomatoschistus</i> sp.						2			1
Perciformes	indet.					1	2	1		
Total number of otoliths in the sample		31	39	12	8	29	27	31	9	8

Faliraki 4 section otolith material								
Taxonomic placement		Sample						
Family	Genus/Species	10	11	16	18	18b	19	20e
PELAGIC TAXA								
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)						4	
Phosichthyidae	<i>Vinciguerria poweriae</i> (Cocco, 1838)						2	
Clupeidae	Indet.						2	
Myctophidae	<i>Benthoosema glaciale</i> (Reinhardt, 1837)						4	2
	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	3	25	7		7	87	106
	<i>Diaphus holti</i> Taaning, 1918		1				8	
	<i>Diaphus rafinesquii</i> (Cocco, 1838)		3				7	2
	<i>Diaphus taaningi</i> Norman, 1930		1			5	30	
	<i>Electrona risso</i> (Cocco, 1829)		1	1			25	2
	<i>Hygophum benoiti</i> (Cocco, 1838)		5	6	2	3	75	44
	<i>Hygophum hygomii</i> (Lütken, 1892)		5					
	<i>Lampadena</i> sp.		1				15	
	<i>Lampanyctus crocodilus</i> (Risso, 1810)				2		8	5
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)				2		29	5
	<i>Myctophum punctatum</i> (Rafinesque, 1810)		3	1		4	40	9
	<i>Notoscopelus elongatus</i> (Costa, 1844)					1	6	1
	<i>Protomyctophum arcticum</i> (Lütken, 1892)						3	
	<i>Scopelopsis pliocenicus</i> (Anfossi & Mosna, 1976)					1	3	1
	Indet.						97	80
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)		3					
BENTHIC AND BENTHOPELAGIC TAXA								
Congridae	<i>Conger conger</i> (Linnaeus, 1758)		5				2	
	<i>Pseudophichthys splendens</i> (Lea, 1913)						3	
Sternoptychidae	<i>Polyipnus polli</i> Schultz, 1961						1	
Chlorophthalmidae	<i>Chlorophthalmus</i> aff. <i>agassizi</i> Bonaparte, 1840						1	
Carangidae	<i>Trachurus</i> sp.				1			
Centracanthidae	<i>Spicara smaris</i> (Linnaeus, 1758)		1				2	
Moridae	<i>Laemonema</i> sp.						2	
Phycidae	<i>Gaidropsarus</i> sp.		1				6	
Faliraki 4 section otolith material (continuation)								

Taxonomic placement		Sample						
Family	Genus/Species	10	11	16	18	18b	19	20e
Gadidae	<i>Gadiculus argenteus</i> Guichenot, 1850					2	23	4
	<i>Micromesistius poutassou</i> (Risso, 1827)						2	
Ophidiidae	<i>Ophidion barbatum</i> Linnaeus, 1758		2				1	
Carapidae	<i>Carapus cf. acus</i> (Brünnich, 1768)		2	2				
	<i>Echidion dentatus</i> (Cuvier, 1829)		3				4	
Bythitidae	<i>Grammonus ater</i> (Risso, 1810)						3	
Sparidae	<i>Dentex</i> sp.		2					
	<i>Diplodus cf. annularis</i> (Linnaeus, 1758)						1	
	<i>Pagellus cf. bogaraveo</i> (Brünnich, 1768)						2	
	<i>Pagellus</i> sp.						1	
	<i>Pagrus pagrus</i> (Linnaeus, 1758)		1					
	Indet.		7					
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)		20			1	21	
Pomacentridae	<i>Chromis chromis</i> (Linnaeus, 1758)		1				3	
Perciform indet.	Indet.	1		1			25	1
Gobiidae	<i>Deltentosteus</i> <i>quadrifasciatus</i> (Valenciennes, 1837)		88	6	2		58	
	<i>Gobius niger</i> Linnaeus, 1758			1		1	3	
	<i>Gobius cf. paganellus</i> Linnaeus, 1758						1	
	<i>Gobius</i> sp.1							1
	<i>Gobius</i> sp.2	1	35	1			1	
	<i>Gobius</i> sp.3morphotype2			2				
	<i>Lesueurigobius friesii</i> (Malm, 1874)		6	1			1	
	<i>Lesueurigobius sanzi</i> (de Buen, 1918)		3					
	<i>Lesueurigobius suerii</i> (Risso, 1810)	1	9	2			1	
	<i>Lesueurigobius</i> sp.					1		
	Indet.						3	
Bothidae	<i>Arnoglossus</i> sp.		3	1				
Total number of otoliths in the sample		6	237	32	9	26	616	263

Vagia section otolith material									
Taxonomic placement		Sample							
Family	Genus/Species	4	8	9-11	13	15	20	21	24
PELAGIC TAXA									
Nettastomatidae	Indet.				2				
Engraulidae	<i>Engraulis</i> cf. <i>encrasicolus</i> Linnaeus, 1758				1				
Sternoptychidae	<i>Maurolicus muelleri</i> (Gmelin, 1789)				41				
Phosichthyidae	<i>Vinciguerria poweriae</i> (Cocco, 1838)				9				
Clupeidae	<i>Sardinella maderensis</i> (Lowe, 1838)				1				
Scopelarchidae	<i>Scopelarchus analis</i> (Brauer, 1902)				1				
Myctophidae	<i>Benthoosema glaciale</i> (Reinhardt, 1837)				1				
	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)		3		13			1	5
	<i>Diaphus holti</i> Taaning, 1918		1						
	<i>Diaphus rafinesquii</i> (Cocco, 1838)		1				1		
	<i>Diaphus taaningi</i> Norman, 1930		6						
	<i>Diaphus</i> sp.		7		3				8
	<i>Electrona risso</i> (Cocco, 1829)				8				
	<i>Hygophum benoiti</i> (Cocco, 1838)		2		2				1
	<i>Lampanyctus crocodilus</i> (Risso, 1810)				2				
	<i>Lobianchia dofleini</i> (Zugmayer, 1911)		7						1
	<i>Notoscopelus elongatus</i> (Costa, 1844)						1		
	Indet.				8	3	1		
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)				6				
BENTHIC AND BENTHOPELAGIC TAXA									
Congridae	<i>Pseudophichthys splendens</i> (Lea, 1913)				2				
Phycidae	<i>Gaidropsarus</i> sp.				2				
Gadidae	<i>Gadiculus argenteus</i> Guichenot, 1850				8				
	<i>Gadiculus labiatus</i> (Schubert, 1905)			6	2				
	<i>Micromesistius poutassou</i> (Risso, 1827)				2				
Carapidae	<i>Carapus</i> cf. <i>acus</i> (Brünnich, 1768)	1	1		2				
Bythitidae	<i>Grammonus ater</i> (Risso, 1810)				2				
Atherinidae	<i>Atherina boyeri</i> Risso, 1810				1				
Acropomatidae	<i>Parascombrops mutinensis</i> (Bassoli, 1906)				1				

Vagia section otolith material (continuation)									
Taxonomic placement		Sample							
Family	Genus/Species	4	8	9-11	13	15	20	21	24
Sparidae	<i>Dentex</i> sp.				1				
	<i>Oblada melanura</i> (Linnaeus, 1758)				1				
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)				5		2		1
Perciform indet.	Indet.				5				
Gobiidae	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)				2				
	<i>Gobius</i> cf. <i>paganellus</i> Linnaeus, 1758	2							
	<i>Lesueurigobius friesii</i> (Malm, 1874)				2	1			
	<i>Lesueurigobius suerii</i> (Risso, 1810)				4				
	Indet.	5							
Bothidae	<i>Arnoglossus kokeni</i> (Bassoli, 1906)				1				
Total number of otoliths in the sample		8	28	6	141	4	5	1	16

Kalithea section otolith material			
Taxonomic placement		Sample	
Family	Genus/Species	2	5
PELAGIC TAXA			
Engraulidae	<i>Engraulis encrasicolus</i> Linnaeus, 1758		3
Phosichthyidae	<i>Vinciguerria</i> sp.		1
Myctophidae	<i>Ceratoscopelus maderensis</i> (Lowe, 1839)	1	4
	<i>Hygophum benoiti</i> (Cocco, 1838)		3
	<i>Myctophum punctatum</i> (Rafinesque, 1810)		1
Gobiidae	<i>Aphia minuta</i> (Risso, 1810)		1
BENTHIC AND BENTHOPELAGIC TAXA			
Gadidae	Indet. Lappilus		1
Atherinidae	<i>Atherina</i> cf. <i>boyeri</i> Risso, 1810		1
Cepolidae	<i>Cepola macrophthalma</i> (Linnaeus, 1758)		2
Gobiidae	<i>Deltentosteus quadrimaculatus</i> (Valenciennes, 1837)		2
	<i>Gobius</i> cf. <i>paganellus</i> Linnaeus, 1758		1
	<i>Lesueurigobius suerii</i> (Risso, 1810)		3
Total number of otoliths in the sample		1	23

Appendix III

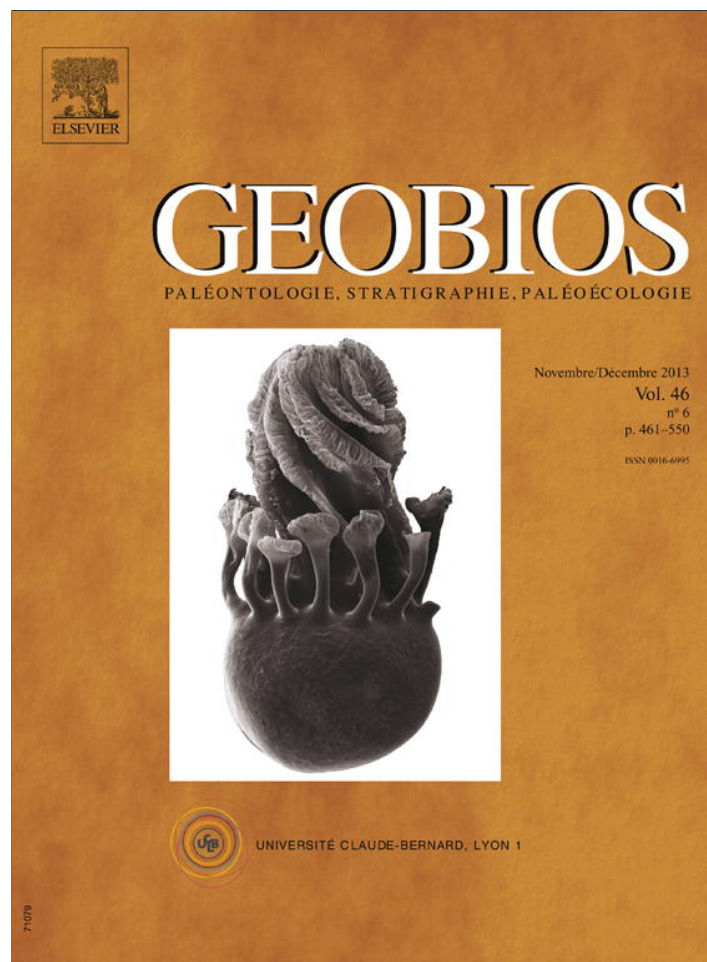
Published papers

- 1) Agiadi, K., Karakitsios, V., 2012.- Quaternary climatic variability modulates *Bregmaceros* Mediterranean distribution range. Proceeding of the 10th Hellenic Symposium on Oceanography and Fisheries, 6pp.
- 2) Agiadi, K., Koskeridou, E., Triantaphyllou, M., Karakitsios, V., 2013. Paleobathymetry of a Late Pliocene Voutes coast (Heraklion basin, Crete). Bull. Geol. Soc. Greece, XLVII.
- 3) Agiadi, K., Koskeridou, E., Triantaphyllou, M., Girone, A., Karakitsios, V., 2013.- Fish otoliths from the Pliocene Heraklion basin (Crete, eastern Mediterranean), Geobios, 46(6), in press.

Conference presentations

- 1) Agiadi, K., Karakitsios, V., 2012.- Quaternary climatic variability modulates *Bregmaceros* Mediterranean distribution range. 10th Hellenic Symposium on Oceanography and Fisheries, May 2012, Athens.
- 2) Agiadi, K., Koskeridou, E., Moissette, P., Lopez-Otalvaro, G.E., Quillévéré, F., Cornée, J.J., 2012.- A middle Pleistocene eastern Mediterranean fish refuge: the Tsampika Bay (Rhodes, Greece). EGU General Assembly 2012, April 2012, Vienna, Geophysical Research Abstracts, Vol. 14, EGU2012-8280.
- 3) Agiadi, K., Koskeridou, E., Giamali, Ch., Karakitsios, V., 2012.- Reef fish dynamic response to climatic variability in a warm eastern Mediterranean semi-enclosed basin. EGU General Assembly 2012, April 2012, Vienna, Geophysical Research Abstracts, Vol. 14, EGU2012-7728.
- 4) Agiadi K., Karakitsios V., 2013.- Fish geographic distribution range shifts as recorded in the eastern Mediterranean during the last 5 Ma. EGU General Assembly 2013, April 2013, Vienna, Geophysical Research Abstracts, Vol. 15, EGU2013-650, 2013.
- 5) Agiadi, K., Koskeridou, E., Triantaphyllou, M., Karakitsios, V., 2013.- Paleobathymetry of a Late Pliocene Voutes coast (Heraklion basin, Crete). 13th International Congress of the Geological Society of Greece, September 2013, Chania.

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Original article

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



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ARTICLE INFO

Article history:

Received 24 February 2013

Accepted 31 July 2013

Available online 22 October 2013

Keywords:

Teleostei

Systematics

Palaeobiogeography

Zanclean

Pliocene

Eastern Mediterranean

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 Konstantinidis, 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;

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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

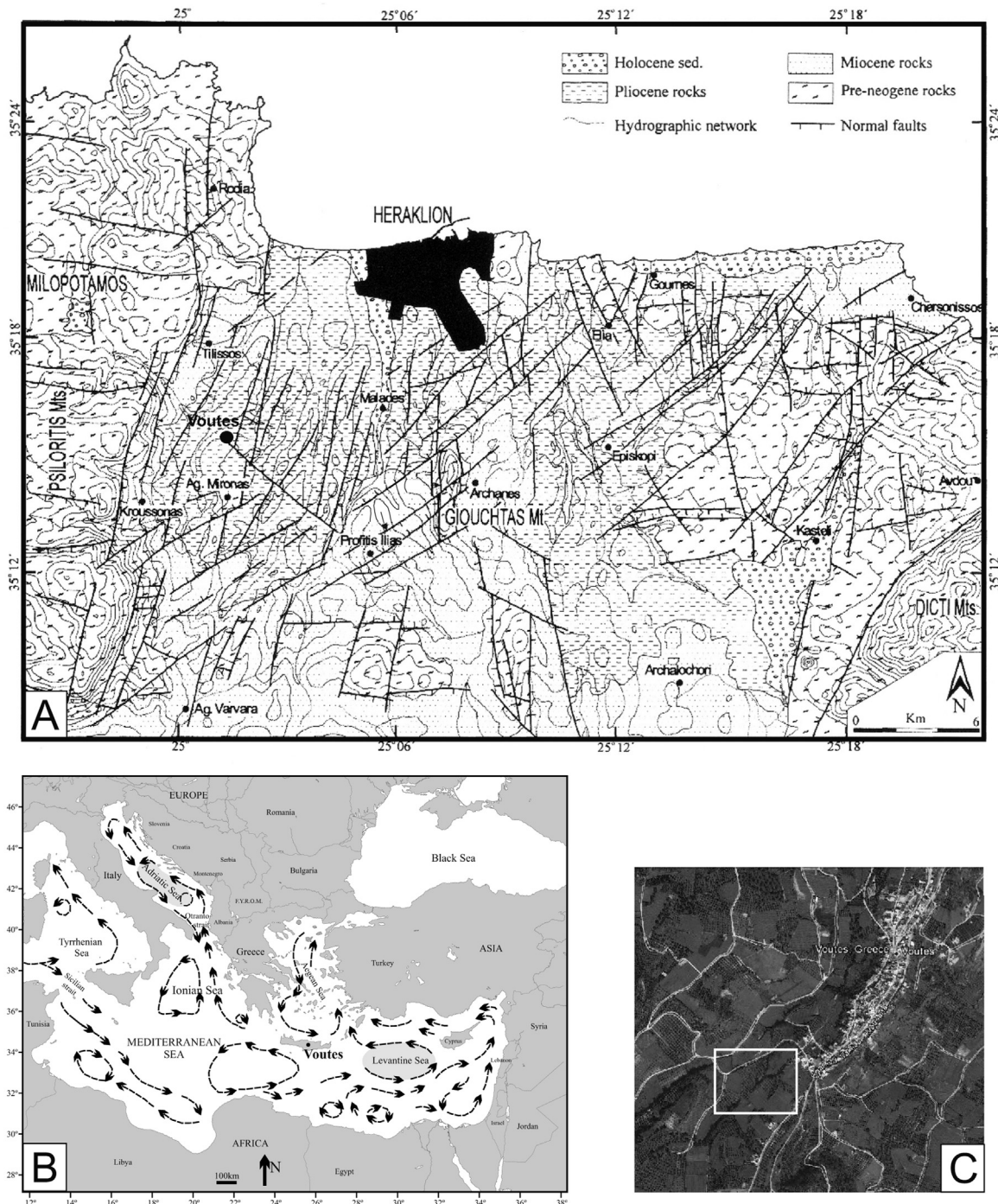


Fig. 1. Location of the study area. **A.** Geological map of the Heraklion area (simplified after Fassoulas, 2001), indicating the Voutes village. **B.** Map of the Eastern Mediterranean including the major circulation patterns. Grey sea areas denote deep-water formation regions. **C.** Photograph of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

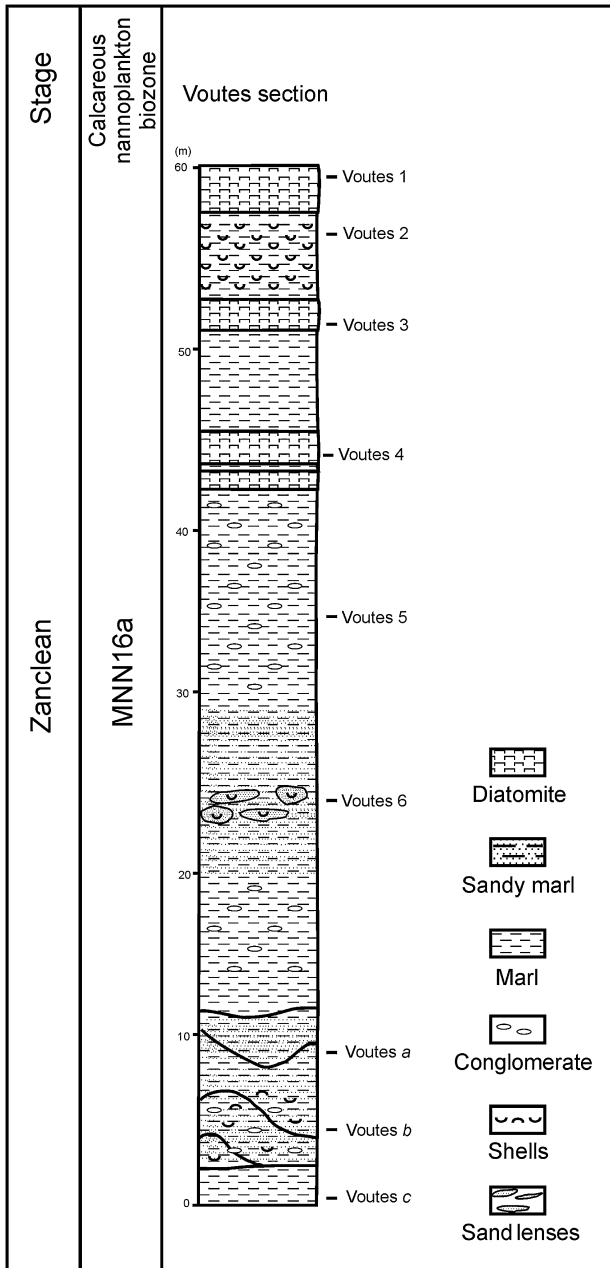


Fig. 2. Stratigraphic column of the Voutes section, indicating sample location. Calcareous nannofossil biozonation following Rio et al. (1990).

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

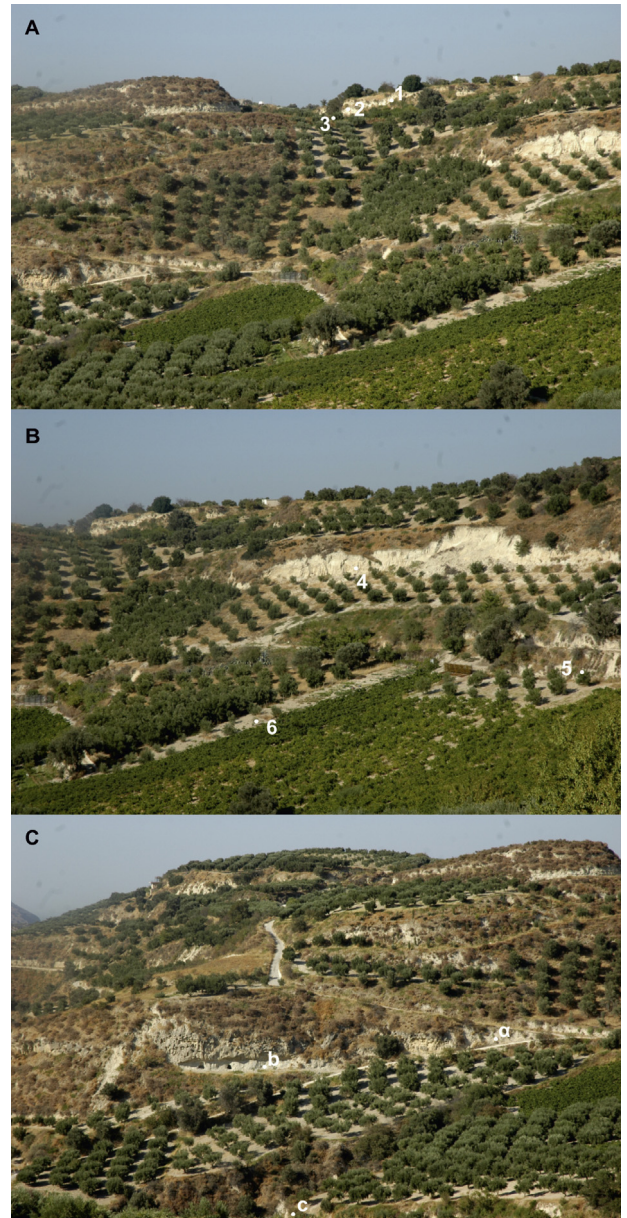


Fig. 3. Photographs of the Voutes section, with sample location. A. Upper part of the section (samples 1–3). B. Intermediate part (samples 4–6). C. Lower part (samples a–c).

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

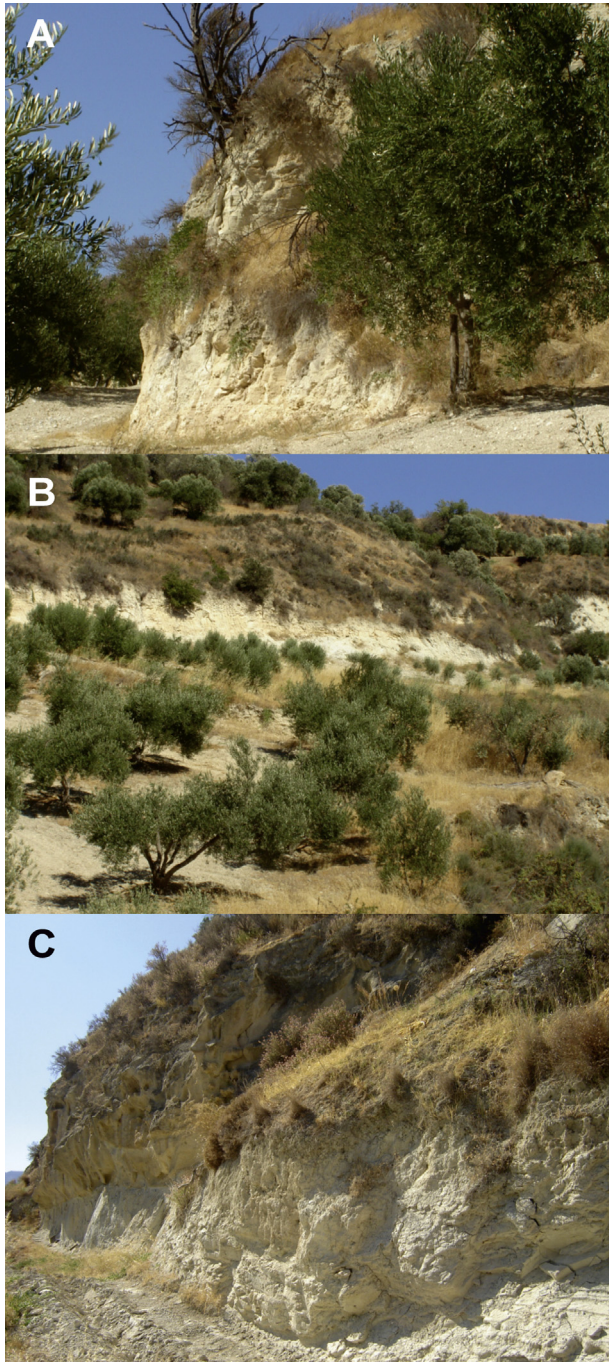


Fig. 4. Photographs of the sampled outcrops, showing different studied intervals. **A.** Upper diatomite horizon. **B.** Middle part of the section. **C.** Lower part of the section, incorporating the sand lenses.

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	24
	BENTHIC AND BENTHOPELAGIC TAXA										
Congridae	<i>Pseudophichthys splendens</i> (Lea, 1913)	–	–	–	1	–	–	–	–	–	
	<i>Pseudophichthys 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>quadrimalculatus</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	Indet.	–	–	–	–	–	–	–	–	–	
Citharidae	<i>Citharus linguatula</i> (Linnaeus, 1758)	–	–	–	1	–	–	–	–	–	
Bothidae	<i>Arnoglossus kokeni</i> (Bassoli, 1906)	–	–	1	–	–	–	–	–	–	
	<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

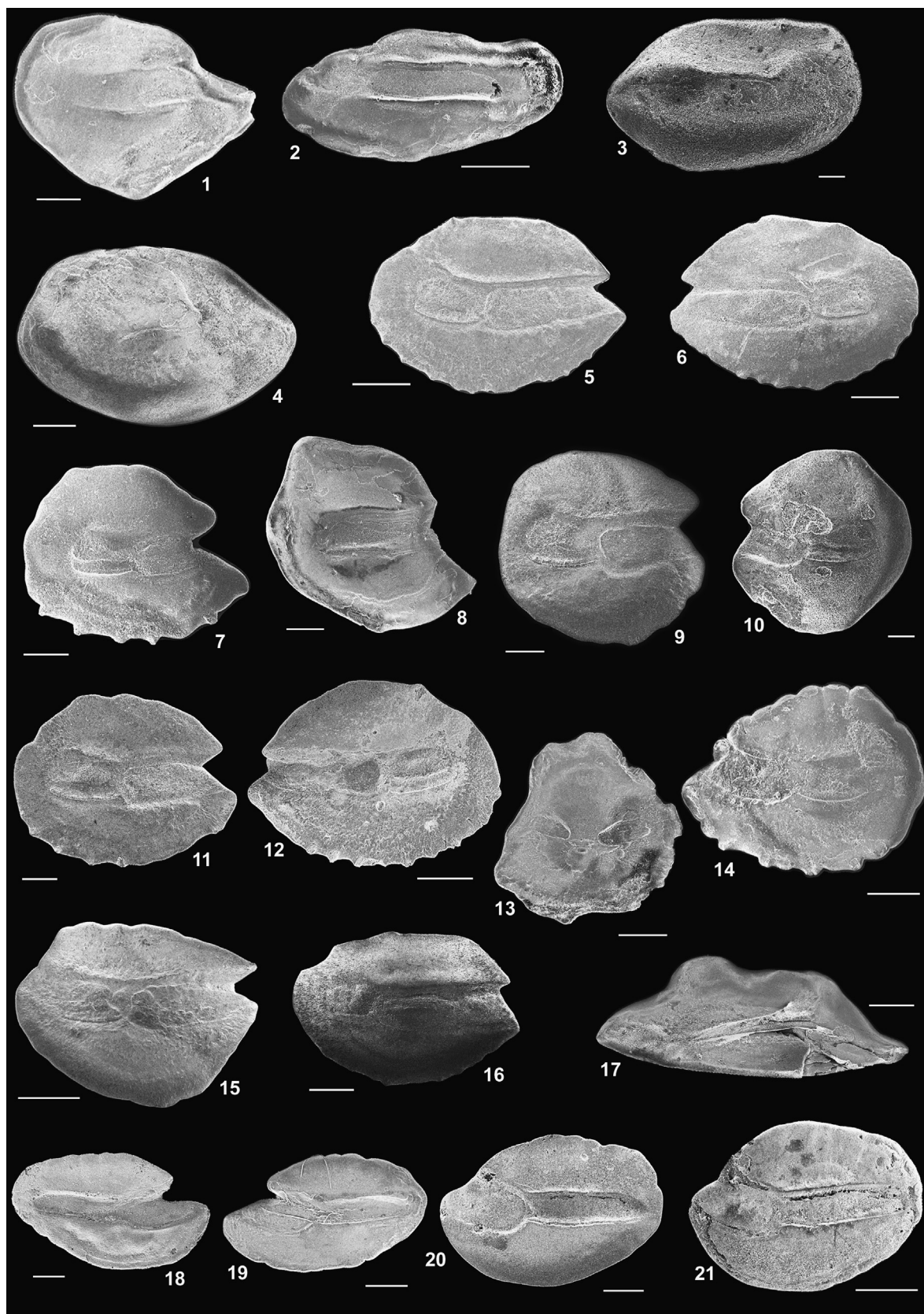


Fig. 7. SEM photographs of the studied otolith material. **1.** *Vinciguerria poweriae* (Cocco, 1838), Voutes 5. **2.** *Chlorophthalmus agassizi* Bonaparte, 1840, Voutes 5. **3.** *Pseudophichthys escavariatierensis* (Nolf and Cappetta, 1988), Voutes 3. **4.** *Rhynchoconger pantanellii* (Bassoli, 1906), 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* (Schwarzahans, 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).

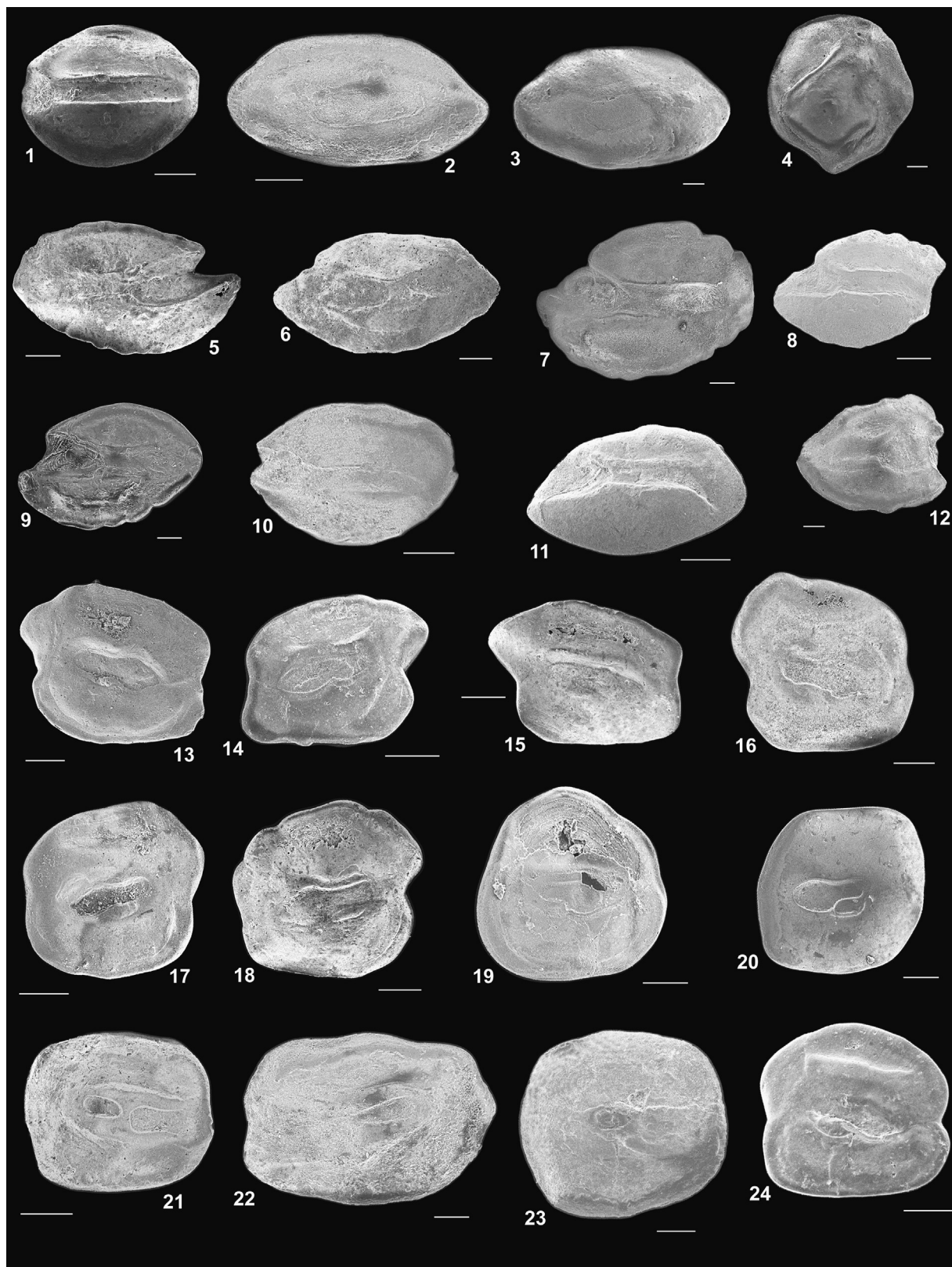


Fig. 8. SEM photographs of the studied otolith material. **1.** *Atherina boyeri* Risso, 1810, Voutes 6. **2, 3.** *Grammonus ater* (Risso, 1810), Voutes c. **4.** Gadidae indet. Lapillus, Voutes 5. **5.** *Epigonus* aff. *denticulatus* Dieuzeide, 1950, Voutes c. **6.** *Cepola macrophthalma* (Linnaeus, 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 μm (3, 4, 7, 9, 12, 19, 20, 22, 23); 500 μm (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				Miocene				Pliocene							
		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Upper	Holocene	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle				Upper
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, but only in the Ionian realm. 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			Pliocene			Pleistocene			Holocene			Miocene			Pliocene						Pleistocene			Holocene			
		Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Upper	Holocene	Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle	Upper	Holocene				Tortonian	Messinian	Zanclean	Piacenzian	Gelasian	Calabrian	Middle
Congridae	<i>Pseudoplichthys splendens</i> <i>Pseudoplichthys escavaratterensis</i> <i>Rhynchoconger pantanellii</i>																												3, 8, 34 3, 9, 13, 14 3, 7, 8, 9, 14, 15, 16, 17, 33
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i> <i>Laemonema</i> sp.																												1 1, 8
Gadidae	<i>Gadiculus labiatus</i>																												1, 2, 3, 6, 7, 8, 9, 13, 14, 16, 17, 19, 21, 29, 34
Bythitidae	<i>Grammonus ater</i>																												27
Carapidae	<i>Echiodon dentatus</i>																												13, 27, 32
Atherinidae	<i>Atherina boyeri</i>																												12, 34
Apogonidae	<i>Apogon</i> sp. (ref. <i>A. lozanoi</i>)																												6, 9, 13, 14, 17, 34
Epigonidae	<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
Sparidae	<i>Oblada melanura</i> <i>Pagellus erythrinus</i>																												3 3, 6, 9, 13, 14, 18, 32
Cepolidae	<i>Cepola macrophthalmia</i> <i>Aphia minuta</i> <i>Deltentosteus</i> aff. <i>quadrifasciatus</i>																												3, 6, 7, 8, 9, 13, 14, 17, 18, 26, 27, 29, 32, 33, 34, 35 13, 27, 34
Gobiidae	<i>Gobius niger</i> <i>Gobius paganelus</i> <i>Lesueurigobius friesii</i> <i>Lesueurigobius sanzii</i> <i>Lesueurigobius suerii</i>																												3, 10, 13, 18, 32 3, 8, 17, 26, 27, 32 3, 7, 34 3, 14, 27, 32
Citharidae	<i>Citharus linguatula</i>																												3, 7, 9, 13, 14, 26, 27, 32, 35
Bothidae	<i>Armoiglossus kokeni</i>																												3, 6, 9, 13, 14, 17, 26, 27, 32, 35

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 vicinialis* 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.

Acknowledgements

The authors thank Bruno Delrieu for the introduction to the studied section, as well as Dr. Gilles Escarguel, Dr. Giorgio Carnevale and Dr. Rostislav Brzobohaty for reviewing the manuscript. This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program “Education and Lifelong Learning” of the National Strategic Reference Framework (NSRF) – Research Funding Program “Heracleitus II. Investing in knowledge society through the European Social Fund”.

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PALEOBATHYMETRY OF A PLIOCENE VOUTES COAST (HERAKLION, CRETE)

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Abstract

The fish otolith assemblages identified in the Zanclean sediments of Voutes section (Heraklion, Crete) are analyzed in order to estimate the depth of deposition. The assemblages indicate that Voutes area was in fact a coast inhabited by a neritic fish fauna with significant mesopelagic component, mostly Myctophids. The benthic and benthopelagic group exhibits great diversity. In the late Zanclean, the study area corresponds to a deep neritic environment, which gradually uplifts. At the end of the Zanclean, Voutes area becomes a very shallow coast, as shown by the increased contribution to the assemblage by members of the Gobiid family, as well as the notable presence of Bothidae. Thereafter, the area deepens again, as the shallow benthic-benthopelagic component significantly decreases. This is consistent with the appearance of Pteropods and reaches a peak during the deposition of diatomites at maximum depth. At the upper part of the section, the sea bottom depth decreases again to allow for the deposition of marls with various molluscs remains, where Gadids and Gobiids again reappear. Finally, the upper diatomitic horizon is characterized by a rather poor fish fauna. These observations allow reconstructing the evolution of Voutes coastal area during the latest Zanclean until the Piacenzian.

Key words: Fish, otoliths, Zanclean, Teleosts, Mediterranean.

Περίληψη

Στην παρούσα εργασία παρουσιάζεται η παλαιοβαθυμετρική ανάλυση των συναθροίσεων ωτολίθων Ιχθύων, που προσδιορίστηκαν στα ιζήματα ηλικίας Ζαγκλίου στην τομή Βούτες (Ηράκλειο, Κρήτη). Η περιοχή Βούτες αποτελούσε μία ακτή με νηριτική Ιχθυοπανίδα, με υψηλή συμμετοχή μεσοπελαγικών ειδών, κυρίων *Myctophidae*. Τα βενθικά και βενθοπελαγικά ψάρια εμφανίζουν επίσης μεγάλη ποικιλότητα. Κατά το ανώτερο Ζάγκλιο, η περιοχή μελέτης αντιστοιχούσε σε βαθύ νηριτικό περιβάλλον. Σταδιακά η περιοχή ανυψώθηκε σε πολύ μικρά βάθη, όπως φαίνεται από την αυξημένη συμμετοχή στην πανίδα των *Gobiidae*, αλλά και την παρουσία *Bothidae*. Στη συνέχεια, η περιοχή βάθυνε ξανά, καθώς παρατηρείται σημαντική μείωση της συμμετοχής των ρηχών βενθικών-βενθοπελαγικών ειδών. Το συμπέρασμα αυτό ενισχύεται από την παρουσία στο επίπεδο αυτό των Πτεροπόδων, αλλά και την απόθεση διατομιτών. Σε ανώτερο τμήμα της τομής, το βάθος της θάλασσας μειώνεται και πάλι, πριν τον ανώτερο διατομιτικό ορίζοντα, ο οποίος ωστόσο εμφανίζει ιδιαίτερα φτωχή συναθροίση ωτολίθων.

Λέξεις κλειδιά: Ιχθύες, ωτόλιθοι, Ζάγκλιο, Τελεόστεοι, Μεσόγειος.

1. Introduction

Crete Island was created 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 present 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 melange 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 Konstantinidis, 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 late Late Tortonian the activation of the eastern – western oriented Agia Varvara fault differentiated the two realms, which evolved separately since then (Delrieu et al., 1991).

The Pliocene deposits of the Heraklion basin are the most extensive on the Island. The marine sediments of the lowermost Pliocene generally overlie the late Messinian deposits (Delrieu et al., 1991; Meulenkamp et al., 1979), 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.

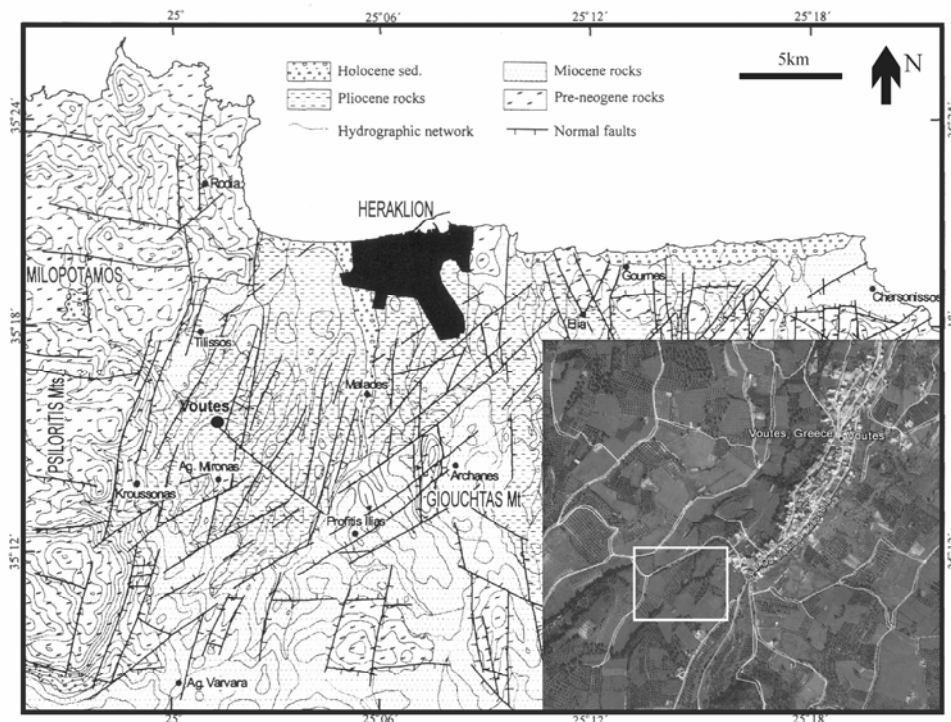


Figure 1. Heraklion area geological map (Fassoulas, 2001), indicating Voutes village.

Fish otoliths provide a unique tool in the investigation of the fish teleostean 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). In addition, they

constitute very valuable paleoecological and paleobathymetrical indicators (Nolf and Brzobohaty, 1994; Girone, 2000; Agiadi et al., 2010; et al., 2011). In the present study, fish otoliths from the Pliocene sediments of Voutes (Heraklion, Crete) are used as indicators in order to reconstruct the depositional depth.

2. Material and Methodology

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 (Figure 1). The section's sediments may be placed within the Finikia lithostratigraphic group (of Benda et al., 1974 and Meulenkamp et al., 1979) and include more than 60 meters of marls and sandy marls. Strong gravity flows have formed a series of sand lenses, on the lower part of the section, with distinctive sedimentologic attributes and characteristic fauna. The upper part of the section presents three diatomite horizons. On a total, nine (9) sediment samples were taken along Voutes section. Systematic identifications of the fish otoliths found within these samples are presented in Agiadi et al. (2013).

The relevant chronostratigraphic framework (Agiadi et al., 2013) for the evaluation of the results was provided through calcareous nannoplankton biostratigraphy, based on the biozonation scheme of Rio et al. (1990) as this has been incorporated in the magnetobiochronologic framework of Lourens et al. (2004) in Gradstein et al. (2004). The studied interval from Voutes section is assigned to the biozone MNN16, in particular above the highest occurrence of *R. pseudoumbilicus* and *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.

The depth of deposition, through the analysis of the fish otolith assemblage, was estimated using the method of Nolf and Brzobohaty (1994) for bathyal and deep neritic assemblages with a significant mesopelagic component, as it was re-adjusted by Agiadi et al. (2010). According to this methodology, based on the modern depth ranges of all the taxa in each sample (Table 1), the number of possible presences for each 50-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.

The only requirement for the application of this method is that the systematic position of the fossil taxa has a close affinity to their modern analogues. The presence/absence data used includes only those taxa for which present-day bathymetric information is available. This means that higher order identified otolith specimens were completely excluded from analysis. Out of the 43 taxa present in Voutes sediments, only eight are extinct today, *Diaphus cavallonis*, *Myctophum fitchi*, *Scopelopsis pliogenicus*, *Pseudophichthys escavaratierensis*, *Rhynchoconger pantanelli*, *Parascombrops mutinensis*, *Gadiculus labiatus* and *Arnoglossus kokeni*. The present-day distributions assigned to these species were those of their most close living relative. To this end, genus level affinity was used, in conjunction with the corresponding present record in the Aegean Sea. These analogies are presented in Table 1. In particular, *Scopelopsis pliogenicus* has only one living species with a genus-level affinity, *Scopelopsis multipunctatus* (Hulley, 1990), to which it was assigned. At present, *P. splendens* is the only *Pseudophichthys* species occupying the Mediterranean Sea (Bañon et al., 2011). Consequently, *P. escavaratierensis* was also assigned to *P. splendens*. *Rhynchoconger* currently includes seven species, occupying either the Indo-Pacific or the western Atlantic coasts at various depths (Whitehead et al., 1986). In addition, congrids in the present Mediterranean include three species *Ariosoma balearicum*, *Conger conger* and *Gnathophis mystax* (Whitehead et al., 1986).

Table 1 - Present-day bathymetric distribution of the fish taxa identified in Voutes outcrop sediments or their modern equivalent. The data has been acquired from FishBase (Froese and Pauly, 2012).

Taxonomic placement		Bathymetric range (m)	References
Family	Genus/Species		
PELAGIC TAXA			
Sternoptychidae	<i>Maurollicus muelleri</i>	50->1524	Okiyama 1971
Phosichthyidae	<i>Vinciguerria poweriae</i>	50-1000	Yang et al 1996
Myctophidae	<i>Ceratoscopelus maderensis</i>	51-1082	Mytilineou et al 2005
	<i>Diaphus adenomus</i>	180-600	Hulley 1990
	<i>Diaphus holti</i>	40-777	Mytilineou et al 2005
	<i>Diaphus metopoclampus</i> (equiv. <i>D.cavallonis</i>)	90-1085	Mytilineou et al 2005
	<i>Diaphus rafinesquii</i>	40-1200	Bogutskaya 2007
	<i>Diaphus splendidus</i>	40-750	Hulley 1990
	<i>Diaphus taaningi</i>	40-475	Hulley 1990
	<i>Hygophum benoiti</i>	51-700	Hulley 1990
	<i>Hygophum hygomii</i>	0-800	Hulley 1990
	<i>Myctophum punctatum</i> (equiv. <i>M.fitchi</i>)	0-1000	Muus and Nielsen 1999
	<i>Lobianchia dofleini</i>	20-750	Hulley 1990
	<i>Notoscopelus resplendens</i>	0-2000	Hulley 1990
		<i>Scopelopsis multipunctatus</i> (equiv. <i>S.pliocenicus</i>)	3-2000
Bregmacerotidae	<i>Bregmaceros</i> spp.	?-1260m	Castellanos-Galindo et al 2006
BENTHIC AND BENTHOPELAGIC TAXA			
Congridae	<i>Pseudophichthys splendens</i> (equiv. <i>P.escavaratierensis</i>)	37-1647	Bañon et al 2011
	Modern Mediterranean Congrids (equiv. <i>R.pantanelli</i>)	0-700	Whitehead et al 1986
Chlorophthalmidae	<i>Chlorophthalmus agassizi</i>	50-1000	Whitehead et al 1986
Moridae	<i>Laemonema</i> spp.	200-1200	Whitehead et al 1986
Gadidae	<i>Gadiculus argenteus</i> (equiv. <i>G. labiatus</i>)	100-1000	Muus and Nielsen 1999
Bythitidae	<i>Grammonus ater</i>	reef-associated	Whitehead et al 1986
Carapidae	<i>Echiodon dentatus</i>	120-3250	OBIS 2006
Atherinidae	<i>Atherina boyeri</i>	coastal, very euryhaline	Maugé 1990
Apogonidae	<i>Apogon</i> spp.	reef-associated	Whitehead et al 1986
Epigonidae	<i>Epigonus denticulatus</i> (equiv. <i>Epigonus</i> sp.)	300-600	Whitehead et al 1986
Acropomatidae	<i>Synagrops spinosus</i> (equiv. <i>P.mutinensis</i>)	87-544	Mochiuzuki and Gultneh 1989
Sparidae	<i>Oblada melanura</i>	?-30	Bauchot and Hureau 1990
	<i>Pagellus erythrinus</i> (equiv. <i>Pagellus</i> sp.)	20-200	Bauchot and Hureau 1990
Cepolidae	<i>Cepola macrophthalma</i>	15-400	Whitehead et al 1986
Gobiidae	<i>Aphia minuta</i>	0-97	Iglesias and Morales-Nin 2001
	<i>Deltentosteus quadrimaculatus</i>	?-333	Mytilineou et al 2005
	<i>Gobius niger</i>	1-75	Whitehead et al 1986
	<i>Gobius paganellus</i>	?-15	Azevedo and Simas 2000
	<i>Lesueurigobius friesii</i>	10-130	Miller 1990
	<i>Lesueurigobius sanzi</i>	47-117	Miller 1990
	<i>Lesueurigobius suerii</i> (equiv. <i>Lesueurigobius</i> sp.)	?-337	Mytilineou et al 2005
Citharidae	<i>Citharus linguatula</i>	?-200	Nielsen 1981
Bothidae	<i>Arnoglossus</i> spp.	15-300	Whitehead et al 1986

All three species exhibit great depth distribution, from a few tens to more than 700 meters, which was thus used as a generalized assessment of the depth distribution of *R. pantanelli*. There is no living species placed within the genus *Parascombrops*, nor is there an Acropomatidae representative occupying the Mediterranean Sea at present. From the comparative morphological similarities between the North Atlantic species *Synagrops spinosus* (Campana, 2004) and the *P. mutinensis* otoliths of this and previous studies (Agiadi et al., 2011; Agiadi et al., 2013), it may be considered that this is an appropriate modern analogue to the fossil species. The only *Gadiculus* Mediterranean inhabitant today is *G. argenteus* (Muus and Nielsen, 1999), which was accepted here as the modern equivalent of *G. labiatus*. Finally, *Arnoglossus* spp. depth values encompass the distribution of all six extant *Arnoglossus* Mediterranean species (Whitehead et al., 1986).

An initial inspection of the depth distribution of the identified taxa in the samples indicated that the paleodepths did not surpass 1000 meters. Consequently, the analyses were conducted until that depth. In addition, *Mauroliticus muelleri*, *Vinciguerria poweriae*, *Ceratoscopelus maderensis*, *Diaphus metopoclampus*, *Diaphus rafinesquii*, *Myctophum punctatum*, *Notoscopelus resplendens*, *Bregmaceros* sp., *Gadiculus argenteus*, *Scopelopsis multipunctatus* and *Pseudophthichthys splendens* were excluded from the analyses because their modern depth distribution range is great and encompasses almost entirely the 0-1000 meter interval. Their presence were considered only to clarify ambivalent depth estimates.

3. Paleobathymetric analysis

The paleodepth analysis and estimates are presented in Figures 2 and 3. In sample Voutes b, only three species may be considered, which provided a paleobathymetric estimate between 10-130 meters, *Cepola macrophthalmia*, *Deltentosteus* aff. *quadrimaculatus* and *Lesueurigobius friesii*. In Voutes 3 the analysis delivered an estimate of 50-350 meters. However, this range is affected by the 50-meter intervals used in the analysis. After closer examination, it may be observed that the actual paleodepth estimate ought to be that where both *Aphia minuta* and *Diaphus adenomus* could coexist, and that is between 87-100 meters depth. The presence of *D. holti*, *H. hygomii* and *Laemonema* sp. in Voutes 4 leads to a paleodepth estimate between 200-800 meters, with no greater accuracy available for this level. The fish taxa identified in sample Voutes 1 did not allow for any paleobathymetric estimation. In particular, in this sample the following taxa have been identified (Agiadi et al., 2013): Myctophidae indeterminate (ind.), *Bregmaceros* sp., *Laemonema* sp., *Gadiculus labiatus*, Sparidae ind. and Perciformes ind. The great abundance of *Bregmaceros* sp., in conjunction with the presence of Myctophids and deep-water benthopelagic taxa such as *Laemonema* sp., *Gadiculus labiatus* and Perciformes, may indicate a rather deep marine environment, generally exceeding 200 meters.

A mixed fauna is revealed through the paleobathymetric analysis in sample Voutes c. Initially, the graphical results provide an estimate between 300-337 meters, delimited by the maximum depth distribution of *L. suerii*. However, the presence of *Oblada melanura* is problematic. This benthopelagic fish today inhabits rocky bottom of depths up to 30 meters, in the coasts of the eastern Atlantic and the Mediterranean Sea (Bauchot and Hureau, 1990). In addition, reef-associated taxa *Grammonus ater* and *Apogon* sp. (Whitehead et al., 1986) also present in sample Voutes c. Two faunal units may thus be separated in this level, a deeper neritic unit from an environment reaching depths around 300-337 meters, and a shallow unit from depths between 0-30 meters.

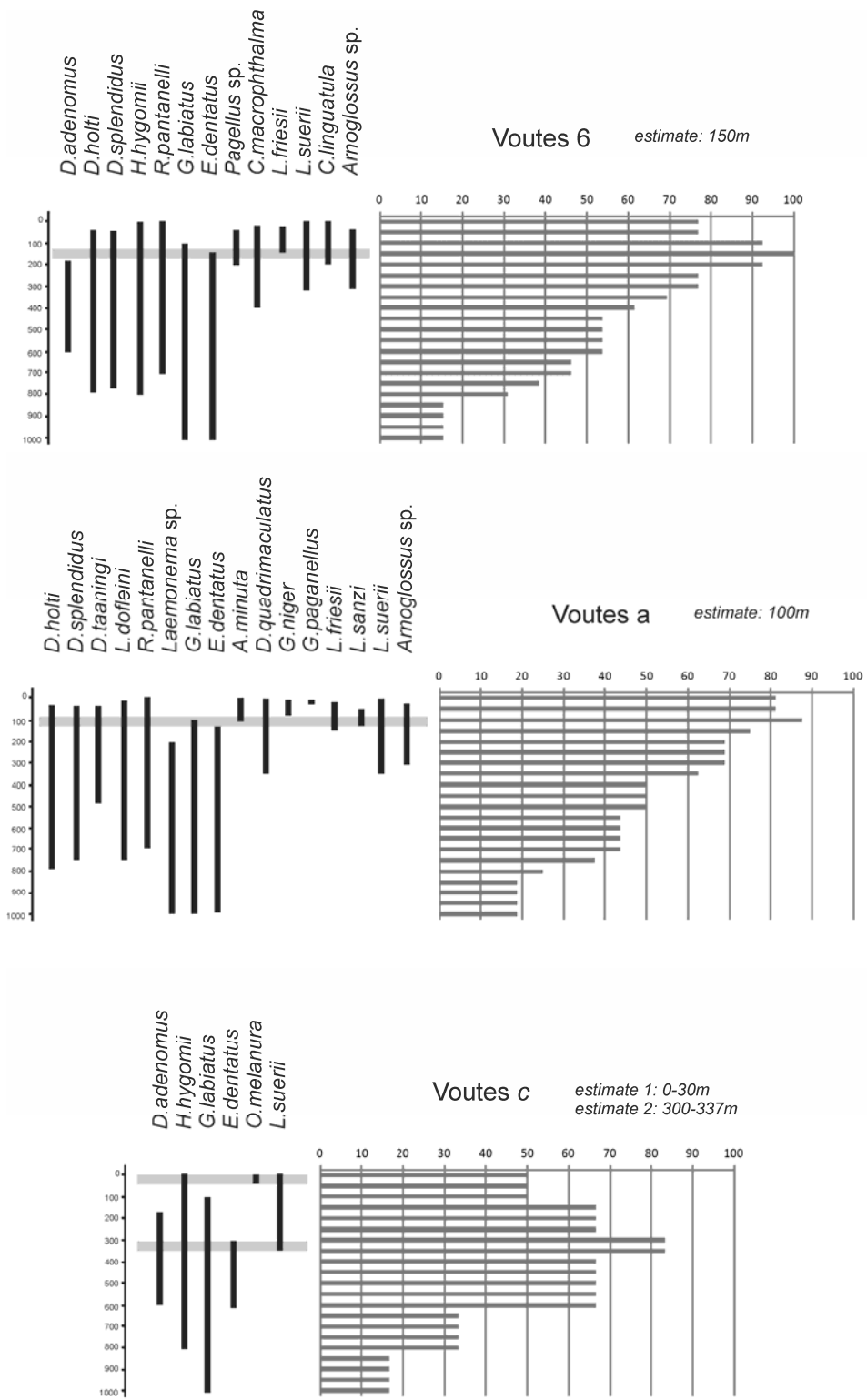


Figure 2. Paleobathymetric analysis and estimates.

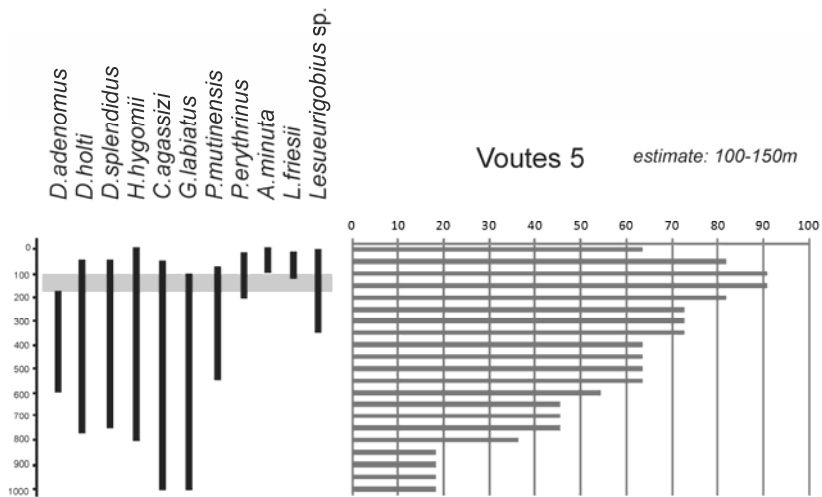
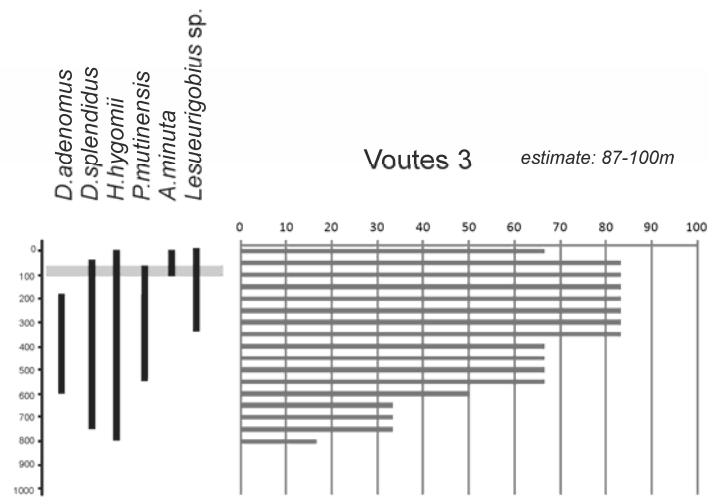
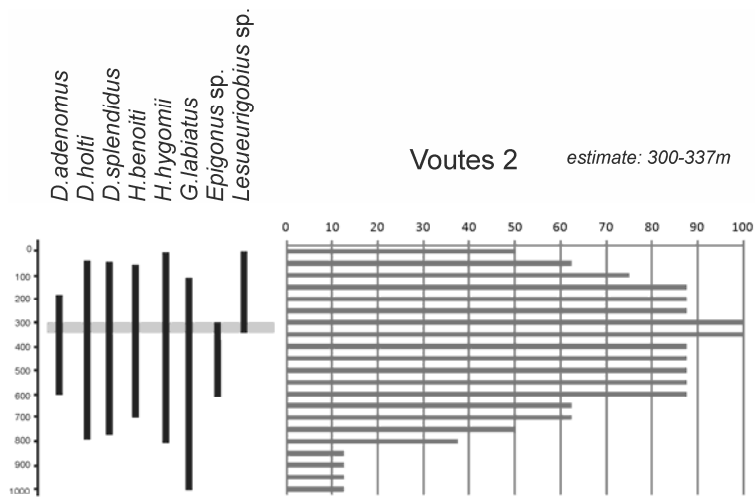


Figure 3. Paleobathymetric analysis and estimates (continuation).

4. Discussion and Conclusions

The paleobathymetric curve created from the analysis of the fish otolith fauna uncovered in the Voutes outcrop sediments present an interesting input in the paleogeographic evolution of the Central Crete area, namely the Heraklion basin (Figure 4).

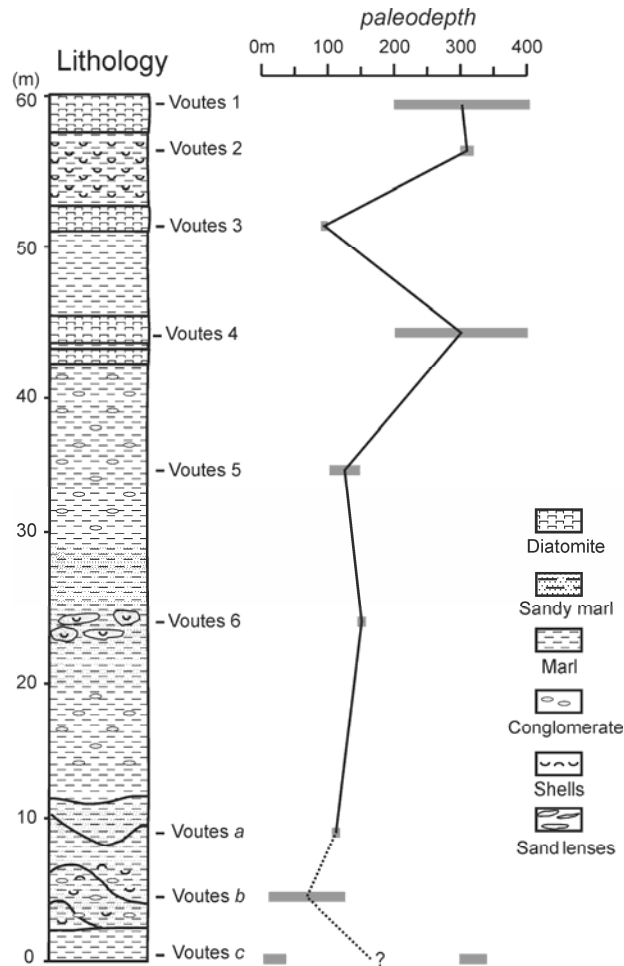


Figure 4. Voutes section lithology and paleobathymetric curve.

Generally, depths throughout this interval do not exceed 350 meters, although the lower part of the section (Figure 2) exhibits much shallower estimates, up to 150 meters. The deeper environments are found on the upper part of the section (Figure 3). However, no specific trend may be safely concluded from the estimated values. Rather several depth variations are visualized (Figure 4). In addition, the lower part of the Voutes outcrop reveals a mixture of the fish faunas from two realms, a deep water probably autochthonous faunal component, and a shallow allochthonous fauna. This is in accordance with the gravity flows observed at the lower part of the section, which seem to have incurred this mixing. Overall, during the late Zanclean, Voutes area was a coast, habitat for a rich shallow neritic Ichthyofauna. The results presented here offer new input on the tectonic – eu-static coupling effect on the paleogeography of central Crete, between 3.84 and 3.61Ma.

5. Acknowledgments

This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

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QUATERNARY CLIMATIC VARIABILITY MODULATES *BREGMACEROS* MEDITERRANEAN DISTRIBUTION RANGE

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Abstract

The Mediterranean geographic distribution of the genus *Bregmaceros* (Perciformes, Teleostei) is reviewed with respect to major palaeoclimatic and palaeoceanographic perturbations from the late Pliocene until today. New and reviewed data are examined based on the skeletal and otolith-based fossil record. *Bregmaceros* managed to survive the glacial/interglacial variability during the Early and Middle Pleistocene, by adjusting its distribution range in the Mediterranean. The reviewed database places its final departure from the Mediterranean at around 0.7 Ma. In addition, the data suggests that, during anoxic/dysoxic episodes benthic and benthopelagic fish shifted their distribution ranges to more favorable localities in northwestern Mediterranean, leaving the pelagic and mesopelagic fish, including *Bregmaceros* behind. These were then well preserved as fossils because of the lamination of the deposits. When sea floor oxygenation returned to normal levels, the benthic and benthopelagic fish returned to the southeastern Mediterranean, but taphonomic conditions were no longer favorable for their articulated skeletons to be preserved, so only their otoliths may be found.

Keywords: Pleistocene, fish, otoliths, palaeobiogeography, taphonomy

1. Introduction, Material and Methods

Bregmaceros THOMPSON 1840 is a small subtropical pelagic fish belonging to the Order Gadiformes and comprises fourteen (14) valid species of worldwide distribution (Froese & Pauly, 2011). Of these, only *Bregmaceros atlanticus* GOODE & BEAN 1886 is truly circumglobal, being distributed, apart from the Indo-Pacific, in the North Atlantic as well. Records of its presence in the modern Mediterranean Sea are scarce, and it is mostly considered an invasive species. The small planktivore *Bregmaceros* has been reported in open Atlantic waters between 0 and 1260 meters depth. However, it largely maintains an epipelagic way of life and is thus most abundant in the upper 200 meters (Castellanos-Galindo et al., 2006). Fossil remains attributed to the genus *Bregmaceros* are well recorded in the Mediterranean Neogene and Quaternary. In the present paper, the fossil record is reviewed with regard to the distribution range of *Bregmaceros* in the Pliocene and Pleistocene Mediterranean Sea, leading up to its final departure from the basin. In accordance with the work by previous authors (e.g. Girone et al 2006), Pliocene otolith based identifications provisionally remain at the genus level, since modern morphological descriptions of otoliths are almost non-existent. The Pliocene identified *Bregmaceros albyi* are based on descriptions of articulated skeletons.

There are two types of fish fossil-bearing deposits, those containing articulated fish skeletons and those containing non-articulated skeletal parts and mostly otoliths, each requiring a different sampling and studying methodology. Hence, the fish fossil record is roughly divided into locality assemblages and continuous stratigraphically correlated otolith databases. Here we review the data on *Bregmaceros* spp., from both types of deposits, in the central and eastern Mediterranean Pliocene and Pleistocene, and discuss the possible cause(s) of its apparent extinction.

2. Palaeobiogeography

The Pliocene – Pleistocene fossil record of *Bregmaceros* in the Mediterranean realm is presented in Table 1; sections and localities are shown in Figure 1. Markopoulou & Kagiouzis (2001)

Table 1. Quaternary *Bregmaceros* localities in the Mediterranean.

Figure ref.	Site/Section	Identification	Material	Age	Reference
1	Girgenti	<i>Bregmaceros</i> sp.	Otoliths	Zanclean	Weiler 1971
2	Lugagnano	<i>Bregmaceros albyi</i>	Otoliths	Zanclean	Anfossi & Mosna 1979
3	Monteu Roero	<i>Bregmaceros albyi</i>	Otoliths	Zanclean	Anfossi & Mosna 1979
4	Alba	<i>Bregmaceros</i> sp.	Otoliths	Zanclean	Nolf & Girone 2006
5	Prassies	<i>Bregmaceros</i> sp.	Otoliths	Zanclean	Markopoulou & Kagiouzis 2001 - revised
6	Monte Bauso	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Landini & Sorbini 2005b
7	Taino	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Anfossi et al 1982
8	Val d'Arda	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Anfossi & Mosna 1972
9	Castelfiorentino	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Landini et al 1990
10	Roufas	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Gaudant 2001
11	Poggibonsi	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Landini & Sorbini 2005b
12	Orciano Pisano	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Landini & Sorbini 2005b
13	Voutes	<i>B. albyi</i> <i>Bregmaceros</i> sp.	skeletal otoliths	Pliocene	Gaudant 2001 Agiadi et al. 2009
14	Gournes	<i>B. albyi</i> <i>Bregmaceros</i> sp.	skeletal otoliths	Pliocene	Gaudant et al 1994 Agiadi et al. 2009
15	Stavromenos	<i>B. cf. albyi</i>	skeletal	Pliocene	Gaudant et al 1994
16	Prassas	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Gaudant et al 1994
17	Singa	<i>Bregmaceros albyi</i>	skeletal	Pliocene	Sorbini & Landini 2003
18	Amnissos	<i>B. cf. albyi</i> <i>Bregmaceros</i> sp.	skeletal otoliths	Piacenzian	Gaudant 2001 Agiadi et al. 2009
19	Agios Thomas	<i>Bregmaceros albyi</i>	skeletal	Piacenzian	Argyriou & Theodorou 2011
20	Marecchia River	<i>Bregmaceros albyi</i>	skeletal	Piacenzian	Sorbini 1988
21	Sforzacosta	<i>Bregmaceros albyi</i>	skeletal	Piacenzian	Sorbini 1988
22	Sant' Andrea	<i>Bregmaceros albyi</i>	otoliths	Piacenzian	Bossio et al 1986
23	Stuni	<i>Bregmaceros albyi</i>	skeletal otoliths	Piacenzian	Landini & Menesini 1985
24	Samoggia Stream	<i>Bregmaceros albyi</i>	Skeletal otoliths	Piacenzian	Bedini & Landini 1986; Landini & Sorbini 1993
25	Metauro River	<i>Bregmaceros albyi</i>	Skeletal	Piacenzian	Sorbini 1988
26	Rio Merli	<i>Bregmaceros</i> sp.	Otoliths	Piacenzian	Girone 2006
27	Morrone	<i>Bregmaceros</i> sp.	Otoliths	Gelasian - Calabrian	Nolf & Girone 2000
28	Gerakas	<i>Bregmaceros</i> sp.	Otoliths	Gelasian - Ionian	Agiadi et al. 2010
29	Fiumefreddo	<i>Bregmaceros</i> sp.	Otoliths	Calabrian - Ionian	Girone et al 2006

attributed a single otolith, found in Early Pliocene sediments of Prassies section (Crete), to *Bregmaceros albyi*. Our field work data and re-sampling of the area confirm through lithostratigraphic correlation the age of Early Pliocene for the sediments in question. However, the otoliths do not exhibit any significant characteristic that justifies the previous identification, and should be considered hereafter as *Bregmaceros* sp.

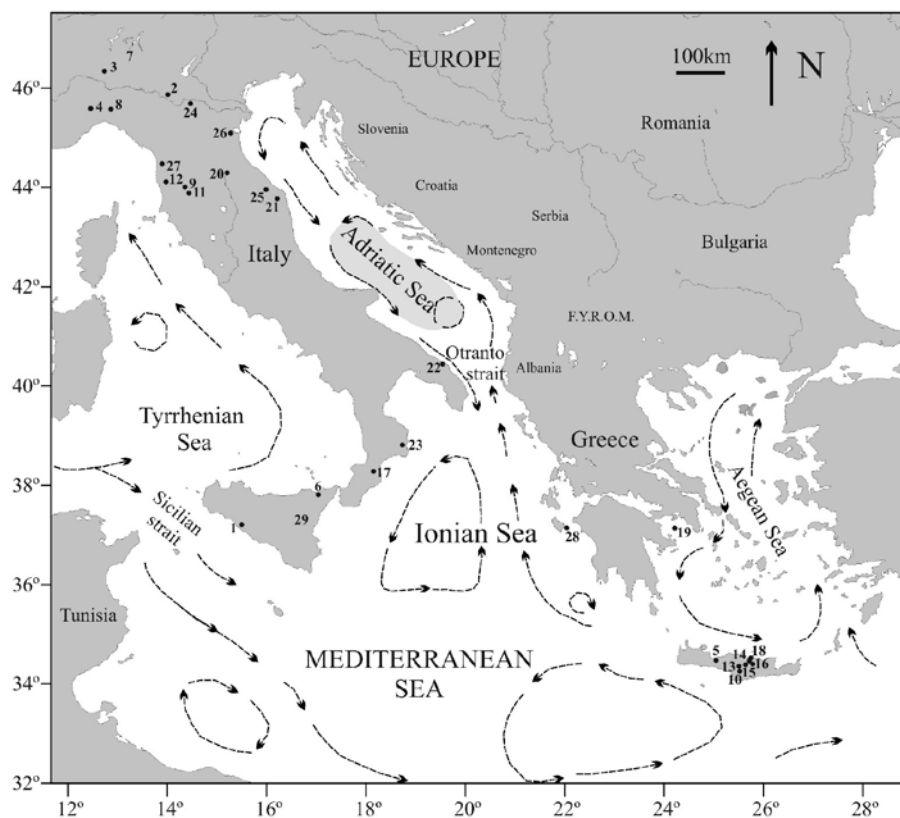


Figure 1 Localities and sections where *Bregmaceros* spp. was uncovered in Pliocene and Pleistocene sediments. The numbering corresponds to the list in Table 1.

Landini & Menesini (1988) were the first to address the distribution of the *Bregmaceros* assemblage in the Neogene sediments of the Mediterranean Sea. Two Miocene species, *Bregmaceros albyi* and *Bregmaceros catulus*, were considered valid, but no particular palaeoecologic significance was attributed to them. According to the available record on *Bregmaceros*, to that date, the genus fell extinct from the Mediterranean Sea by 2.2Ma. Furthermore these authors considered that the *Bregmaceros* assemblage occurred under very specific local palaeoenvironmental conditions of depth and palaeogeography. *Bregmaceros* populations were first ecologically displaced, during the first Pliocene climatic crisis (Landini &

Menesini, 1988), probably by 2.8Ma (Colleoni et al 2012), and were limited to more isolated palaeoenvironments. These authors believed that the Early Pleistocene (sensu Gibbard et al., 2009) further climatic deterioration, connected to the increased polar influence at ~2.2Ma, completely eliminated the *Bregmaceros* populations. More recent findings (Table 1), especially those in Fiumefreddo and Gerakas sections, extend the presence of *Bregmaceros* in the Mediterranean well into the Middle Pleistocene, placing its extinction event around 0.7 Ma before present.

The initial review of the distribution of the genus *Bregmaceros* in the Mediterranean (Landini & Menesini, 1988) considered the Miocene – Pleistocene fossil record, suggesting that during the Pliocene, *Bregmaceros* was endemic to the eastern Mediterranean, a hypothesis that was thereafter disputed by data from Nolf & Girone (2000). Landini & Sorbini (1993) also suggested that fish taxa with subtropical Indo-Pacific affinities may also survived other climatic crises in the Late Pliocene and the Quaternary.

Records of *Bregmaceros* remains in sediments sampled across complete stratigraphic sections are very few. The *Bregmaceros* fauna is usually located in short geologic sections, where there is usually not a continuous record of the fish assemblage evolution through time. Exceptions to these are the sections Stuni (Italy; Landini & Menesini 1985), Gerakas (Zakynthos Island, Ionian Sea; Agiadi et al 2010, 2011), and Voutes (Crete; Agiadi et al 2009). In Gerakas section, the high abundance of *Bregmaceros* found in Gelasian stage sediments is interpreted as a palaeotemperature maximum, as well as an indication of increased oceanic input in the area of southern Zakynthos. The glacial/interglacial Pleistocene climatic variability shifts the distribution range of *Bregmaceros*, so that the fish can adjust to the new conditions.

3. Taphonomy

A combination of palaeoecologic and taphonomic conditions determine the type of fish fossil bearing deposition. The laminated levels in Samoggia Torrent (Landini & Sorbini, 1993) contain abundant fish skeletal remains, well preserved and generally intact. However these authors noted that the assemblage exhibited a very low benthic component; only 2%. In fact, the few identified benthic taxa indicated dysoxic to anoxic conditions on the sea floor, a hypothesis also affirmed by the accompanying fauna and flora. Similarly, Girone et al. (2010) noted significant ecological and facies differences between fish assemblages preserved inside the Mediterranean Miocene sediments, either as skeletal or as otolith material. Articulated fish skeletons were usually preserved under very specific sedimentological and palaeoceanographic conditions. Indeed, Messinian fish often discovered inside laminated clays and diatomites, seemed to have died in anoxic or hypersaline waters. On the contrary normal marine clays and silts contained large numbers of otoliths, but did not allow for the preservation of articulated skeletal parts. The same situation is observed in Stuni and Voutes sections. In fact, it appears that laminated deposits, diatomites, diatomitic marls and laminated marls, in the Mediterranean Pliocene – Pleistocene (Table 1); usually preserve articulated skeletons of the *Bregmaceros* fauna. This includes taxa high pelagic and mesopelagic taxa, *Bregmaceros* spp. have a strong abundance, and lacks benthic – benthopelagic species almost completely. Otherwise, normal marine marls containing a large number of otoliths, may contain *Bregmaceros* sp. (e.g. Voutes, Gerakas sections) and its accompanying fauna, but also include a significant benthic portion. Considering these observations, it appears that during anoxic/dysoxic episodes, benthic and benthopelagic fish shift their distribution ranges to more favorable localities on the northwestern Mediterranean, leaving the pelagic and mesopelagic fish, mainly *Bregmaceros*, *Spratelloides*, Gonostomatidae, and

Myctophidae, which are then well preserved as fossils because of the lamination of the deposits. When sea floor oxygenation returns to normal level, the benthic fauna re-inhabits the southeastern Mediterranean, and can be discovered through its fossilized otoliths.

4. Conclusions

Sampling methodologies and strategies in previous years have separated the fish skeletal record from the otolith database. Here we integrate these with regard to the genus *Bregmaceros*. During anoxic events it seems that *Bregmaceros* along with other high pelagic and mesopelagic taxa are favored and become extremely abundant in the sediments. Through the contraction and expansion of its Mediterranean distribution, during the Pliocene and Pleistocene, *Bregmaceros* managed to survive the glacial events, until at least 0.7 Ma.

5. Acknowledgements

This research was co-financed by the European Union (European Social Fund – ESF) and Greek national funds, through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II Investing in knowledge society through the European Social Fund.

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Fish geographic distribution range shifts as recorded in the eastern Mediterranean during the last 5 Ma

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Marine fish species geographic distribution is known to reflect the individuals' response to changes in oceanic circulation, temperature, salinity, local geography, other species presence and/or abundance, food availability and other biotic and abiotic factors¹. New and published records on the eastern Mediterranean fish, from the end of the Messinian salinity crisis to the present, are here examined, in correlation with palaeoenvironmental data, in order to draw conclusions regarding the abiotic parameters most affecting the fish distribution during the last 5 Ma in this area. This investigation shows that the environmental variables do not affect the fish fauna in a uniform way. Rather, three faunal components may be separated, each occupying a different depth range in the water column. Pelagic fish dwell for the most part on the uppermost 200 m, and their distribution seems to be affected mainly by climatic variability. Mesopelagic fish occupy mostly intermediate depths and their distribution is regulated by the prevailing water circulation patterns. Benthic and benthopelagic fish, which live close or in contact with the sea bottom, are mostly affected by the nature and depth of the substratum. Furthermore, examples from the Ionian^{2,3} and the Aegean Sea indicate that, during the last 5 Ma, large-scale range shifts, similar to those occurring today, frequently took place in this area. This observation significantly alters previously views on the stability of fish assemblages and the processes occurring today.

Acknowledgments. This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

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Reef fish dynamic response to climatic variability in a warm eastern Mediterranean semi-enclosed basin

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Recent studies on the effects of global warming on fish populations reveal that the resulting hypoxia-based habitat compression due to the expansion of the oxygen minimum zone may lead to the restriction of fish depth distributions to the oxygenated near-surface layer¹. Here we postulate that similar phenomena may have affected the fish distribution in the early Pliocene Heraklion semi-enclosed sea (Crete, eastern Mediterranean). Fish otoliths from Voutes section are systematically identified and the data is examined from a palaeoecologic perspective in response to the Pliocene climatic variability. *Bregmaceros* and *Diaphus taaningi* otoliths' relative abundances are used as reliable palaeoclimatic indicators².

The Voutes section sediments contain a very rich fish fauna. *Diaphus* spp., *Bregmaceros* sp., *Sardinella maderensis*, *Phosichthyidae* and *Sternoptychidae* form the pelagic component. Mesopelagic taxa belong mostly to *Myctophids*. The benthopelagic and benthic component of the fish fauna is very well diversified and is comprised of *Gobiids*, such as *Gobius cf. niger*, *Callogobius* sp., *Lesueurigobius aff. sanzoi*, and *Aphya* sp., as well as *Gadiculus labiatus*, *Laemonema* sp., *Oblada melanura*, *Parascombrus mutinensis*, *Barbourisia rufa*, *Blennius* sp., *Ammodytes* sp., *Solea aff. solea*. The presence of *Oligopus* sp., *Spratelloides* sp., and *Brotula cf. mutlibarbata* in the middle part of the section indicate the development of a reef in the study area. The palaeoecologic analysis of the surface, intermediate and deep water faunal groups indicate that the pelagic fish populations in the semi-enclosed early Pliocene Heraklion basin directly reflect the climatic variability. However, the intermediate and deep water fish did not respond to climate change in the same manner. Indeed, two dysoxic events are recorded in this section, where the pelagic component of the fauna is almost exclusively comprised of *Bregmaceros* sp., few *Myctophids* are present, and the benthic and benthopelagic taxa are nearly non-existent. These events are intermitted by the development of a reef system near the study area, marked by the intense diversification of the fish fauna on all water levels. The mollusc fauna turnover reinforces the above results. Conclusively, the present study clearly presents the fish populations' dynamic characteristics of in response to climatic variability.

Acknowledgments

This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

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A middle Pleistocene eastern Mediterranean fish refuge: the Tsampika Bay (Rhodes, Greece)

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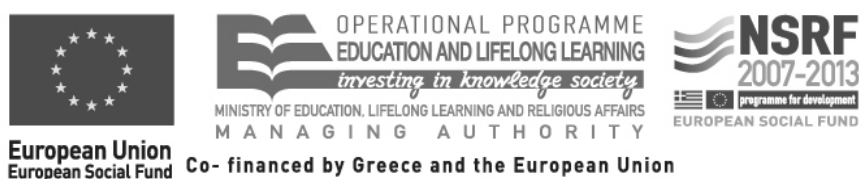
Extensive sampling of the Tsampika marly diatomites reveals the presence of at least three very important fish species, *Bregmaceros* sp., *Sygnathus acus* and *Spratteloides* sp.. Previous records of *Bregmaceros* sp. in the Mediterranean have suggested that this characteristic Pliocene warm-water circumglobal pelagic fish disappeared from the Mediterranean basin due to the climatic deterioration, after the Gelasian age^{1,2,3,4}. The Tsampika fish-bearing deposits, mainly marly diatomites, are younger than 268 Ka, based on the occurrence of *Emiliana huxleyi*. Consequently, this is so far the youngest record of *Bregmaceros* sp. in the Mediterranean, suggesting that typical Pliocene fish may have found refuge in selected localities, such as Tsampika Bay, at least until the Ionian. Evidence for its presence in the Mediterranean basin today is ambiguous. Isolated records of *Bregmaceros atlanticus* place it in the Sicily Strait⁵, and off the Israeli and south Turkish coasts⁶. Although it appears more likely that *Bregmaceros atlanticus* has been introduced to the modern Mediterranean from the Red Sea, through the Suez Canal, the possibility that it is part of a small population native to the Mediterranean can not be excluded based on present-day data⁶. Indeed the late Pleistocene Mediterranean fish record is obsolete, due to the lack of appropriate sampling on this subject. Furthermore, the majority of Pleistocene *Bregmaceros* samples pertain to otoliths, which cannot be unambiguously identified on the species level. As a result, the present findings pose the considerable possibility that the Pleistocene *Bregmaceros* records belong to two species, *B. albyi*, the well known post-Messinian Mediterranean fish, and *B. atlanticus*, which may have invaded the Mediterranean Sea from Gibraltar along with several other warm-water taxa during recurring interglacial periods. The specific identification of the Tsampika fish will undoubtedly shed light to this possibility, and enhance our knowledge on the resilience of fish populations to significant environmental perturbations.

Acknowledgments

This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.

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This research has been co-financed by the European Union (European Social Fund – ESF) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF) - Research Funding Program: Heracleitus II. Investing in knowledge society through the European Social Fund.



Η παρούσα έρευνα έχει συγχρηματοδοτηθεί από την Ευρωπαϊκή Ένωση (Ευρωπαϊκό Κοινωνικό Ταμείο - ΕΚΤ) και από εθνικούς πόρους μέσω του Επιχειρησιακού Προγράμματος «Εκπαίδευση και Δια Βίου Μάθηση» του Εθνικού Στρατηγικού Πλαισίου Αναφοράς (ΕΣΠΑ) – Ερευνητικό Χρηματοδοτούμενο Έργο: Ηράκλειτος II. Επένδυση στην κοινωνία της γνώσης μέσω του Ευρωπαϊκού Κοινωνικού Ταμείου.