Geologica Acta, Vol.13, Nº 3, September 2015, 181-190
DOI: 10.1344/GeologicaActa2015.13.3.1

geologica acta

Megalodon, mako shark and planktonic foraminifera from the continental shelf off Portugal and their age

M.T. ANTUNES[1,2] **P. LEGOINHA**[2,*] **A. BALBINO**[2,3]

[1]Academia das Ciências de Lisboa
R. da Academia das Ciências, 19, 1249-122 Lisboa, Portugal. Antunes E-mail: migueltellesantunes@gmail.com

[2]GEOBIOTEC, Departamento de Ciências da Terra, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa
2829-516 Caparica, Portugal. Legoinha E-mail: pal@fct.unl.pt

[3]Departamento de Geociências (ECT), Universidade de Évora
7000 Évora, Portugal. Balbino E-mail: acaceres@uevora.pt

* Corresponding author

ABSTRACT

Turbidite fragments collected by a fishing net off the central Portuguese coast (Peniche) present some fossils. The matrix is phosphatized and iron-rich with small quantities of manganese, zinc and copper. The occurrence of *Megaselachus megalodon* most probably excludes an age older than Middle Miocene. Its very advanced evolution stage is consistent with a Pliocene age. Based on planktonic foraminifera in depressions of cetacean skulls recovered in the same way, from the same area, the age of sharks and cetaceans is likely to range from latest Messinian to Early Pliocene. Condensed sedimentation is revealed by the co-occurrence of typical Late Pliocene and Quaternary foraminifera. Lack of benthic foraminifera suggests more or less deep environments, while a scallop, *Mimachlamys varia*, indicates nearby rocky substrate. The mako shark *Isurus* cf. *oxyrhinchus* is recorded in the area for the first time. The shark association represents a moderately warm environment as *M. megalodon* and Isurus are essentially temperate water dwellers, while no warm water form is known. Early Pliocene planktonic foraminifera point out to temperate to subtropical waters. Hence temperate to moderately warm conditions seem to have prevailed.

KEYWORDS **Megalodon. Mako shark. Planktonic foraminifera. Continental shelf. Age.**

INTRODUCTION

This paper deals with a hitherto unexplored theme of research that results from the study of fossil discoveries made occasionally by trawlers off the Portuguese western coast. These include cetacean skulls, shark teeth and invertebrates collected in phosphate hardground and condensed levels on the sea floor. Observations are not as accurate as those that can be made inshore, as fishermen do not disclose accurate information about the findings. Nevertheless, progress concerning age can be attained owing to foraminifera preserved in cetacean skull cavities. Otherwise, age can also be discussed on shark's teeth evidence. We are aware that fossils have been found in several localities, but in so closely similar conditions that suggest the whole theme should be dealt with together.

HARDGROUNDS

Advances on marine geology demonstrated the existence of deep bottom areas where there was nearly no sedimentation during broad time and hardgrounds occur. Phosphate vertebrate remnants fallen on the bottom stay there for long, acting as substrate for other organisms.

Phosphate matrix is present in all rock fragments recovered offshore by trawler nets. Two of the shark teeth were found in rock fragments that may be classified as turbidites.

In order to assess the nature and composition of the host rock, two samples collected from the block with a megalodon and a mako shark teeth were analysed (Table 1) for Cu, Fe, Mn, P and Zn at the REQUINTE (Rede de Química e Tecnologia) laboratory, at the Faculty of Science and Technology, New University of Lisbon (internal reference 13-I137, 22/05/2013).

It is observed that the composition of the two samples is similar. In both cases, the matrix is phosphatized and iron-rich with small quantities of manganese and zinc and even less copper.

PALEONTOLOGICAL FINDINGS

Cetacean bones, often with a dark brown patina, are dominant among the vertebrate fossils along with large megalodon shark teeth recovered in trawling nets. Fishermen spared cetacean skulls and other bones from Odontoceti and a few from Mysticeti. Some were given to the Lourinhã Museum (see Bianucci *et al.*, 2013). Two further odontocete skulls collected in the same way were sent A. Balbino at Évora University and then to M.T. Antunes.

Shark teeth

Taxonomical remarks

The discussion of taxonomical aspects is not our goal here, but it seems useful to present the following remarks, mostly according to Cappetta (1987; p. 95-96, 103-104; 2006; p. 145, 321, 329).

The giant shark was firstly scientifically described and named by Louis Agassiz (1843) as *Carcharodon megalodon*. It was thus reported to the genus Carcharodon Smith in Müller and Henle 1841, whose type species is *Carcharodon carcharias* Linnaeus, 1758, the extant white shark.

TABLE 1. Chemical analysis of two samples from the block containing the megalodon and mako shark teeth

Element	Sample	Sample 2
Cu (ppm)	15.20	13.85
Fe (%)	10.70	12.75
Mn (%)	0.095	0.077
P (%)	7.54	6.03
Zn (%)	0.021	0.026

However, *C. carcharias* does not descend from *M. megalodon* and it is generally agreed that the two must be classified in separate families (Applegate and Arrubarrena, 1996):

- *M. megalodon*, in the family Otodontidae Glückman 1964, the typical genus being Otodus Agassiz, 1843, which includes its close ancestors;
- *C. carcharias*, in the family Lamnidae.

At the genus level, classification has changed through time. As stated above, the rather well-known (even if synonyms are plentiful) megalodon species cannot be ascribed to Carcharodon. Some authors included it in Carcharocles Jordan and Hannibal, 1923, but this genus was regarded later as synonym of Otodus. Hence the genus is definitely Megaselachus Glückman, 1964. In conclusion, and following Cappetta (2006), the name adopted here for the concerned species is *Megaselachus megalodon* (Agassiz in Charlesworth, 1837).

As far as the mako shark is concerned, the type species of the genus Isurus (Family Lamnidae) is the extant *Isurus oxyrinchus* Rafinesque, 1810, distributed world-wide in all temperate and tropical seas (Compagno *et al.*, 2005, p. 183). According to Cappetta (2006, p. 169) it first appeared in the Late Oligocene. Rather similar teeth have been ascribed to an extinct species, Isurus desori. According to our observations, we adopt for the sole available specimen the name *Isurus cf. oxyrinchus* Rafinesque, 1810.

Megalodon teeth

Three *Megaselachus megalodon* teeth from the sea bottom off the western Portuguese coast are available. The best-preserved tooth belongs to the Lourinhã Museum and is preserved in a turbidite block, whereas another very large, somewhat incomplete one was given to one of us (M.T.A.) by Mr. Horácio Mateus. Still another, incomplete tooth in a larger turbidite block is also kept at Lourinhã Museum.

The localities where the specimens were found are not accurately known. Nevertheless two broadly defined areas can be defined for some specimens, both some 15 miles offshore: i) at the latitude of Peniche, at about 2000 meters depth, but this value seems exaggerated; ii) at the latitude of Lourinhã, at only a 80m depth.

Tooth Mm 001 (M.T.A. collection kept at Lisbon Academy of Sciences Museum)

The specimen (Figs. 1; 2) is nearly complete although severely abraded, apparently by chemical corrosion and/

or by borings of endolithic organisms. Most of the crown's enamel covering had been lost and what remains is thinned and cracked with loss of the serrations of the cutting edges. The tip of the crown still keeps a small abrasion area due to use on hard matters (prey bones).

Matter has been recently lost near the tip and mesially and distally on the root, probably during the trawling operations.

The dentine surface shows a polished aspect. It presents many pits or more or less longitudinal sulci. Much dentin has been lost, especially in the external (labial) surface of the root. Extensive surface areas are incrusted by a white, calcium carbonate matter, sometimes with tiny holes. Incrustation occurs continuously on the enameloid surface and on the dentine, which means that the tooth already was much corroded, probably a long time after the tooth's deposition on the bottom. Similar corrosion aspects have been observed by us in *M. megalodon* teeth from Portugal and Angola.

On the external surface near the crown's base there is an interesting ahermatypic hexacorallian. This suggests that the tooth lied with its lingual side on the bottom. The surface presents many hollow tubes, probably produced by serpulid worms.

FIGURE 1. *Megaselachus megalodon*, large upper (palatoquadrate) tooth, labial view.

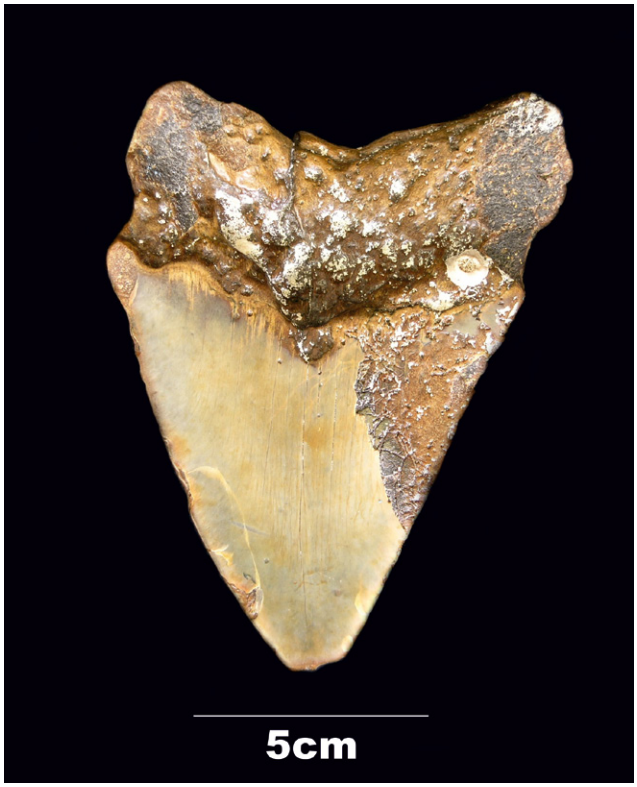

FIGURE 2. Figure 1 same, upper tooth, internal view.

The concerned tooth seems to be a first left upper (palatoquadrate) lateral from a large adult by comparison with the reconstitution of *M. megalodon* dentition made by Applegate and Espinosa-Arrubarrena (1996, p. 32, fig. 12).

Measurements (mm) are as follows: total height, >110.2, or *ca.* 124 if complete; total width, >89.9, or *ca.* 97 as estimated if complete.

It is distinctly larger than all rather numerous Miocene specimens of comparable morphology from Portugal and Angola (Antunes, 1978).

Tooth ML 646 (Lourinhã Museum)

Another specimen, ML 646 (Fig. 3), is kept at Lourinhã Museum. It is attached to a block of detrital turbidite rock, *ca.* 12cm maximum dimension, composed of irregularly-shaped, angular, little-rolled, 3 to 70mm at most clasts. There are several voids between clasts, which apparently underwent a brief transportation. The detrital elements are glued together by a darker, brownish to black, less than one mm thick layer, maybe made up of Fe-Mn matter. Broken surfaces show a fine grained, apparently high density greenish rock, maybe a dolerite. Part of the matter may be a compact, yellowish phosphate. On the surface of some clasts there are the bases of a few isolated, ahermatypic

FIGURE 3. *Megaselachus megalodon*, small upper tooth, external view.

hexacorallians, poorly preserved. Tiny areas present a much reduced evidence of calcareous crust, as well as of boring organisms. This seems to mean a long exposure on the bottom.

ML 646 is nearly complete. It is smaller but much better preserved than the preceding one. Measurements (mm): total height, ~55.3 as measured in somewhat unfavourable conditions because of the matrix covering; total width, 44.3.

Only the external (labial) surface is exposed. As a whole, mechanical abrasion was unimportant. The triangular crown is nearly symmetrical. The crown apex is a little abraded by use; hence the tooth has been operational. It can have been lost in life, maybe after a little use. Corrosion is minimal. Fine, regular serrations are preserved on both edges. Serrations are undoubtedly distinct from those of *C. carcharias* teeth. As much as it can be ascertained, the crown is rather broad and flat, with its enameloid cover well preserved except for a small part at its base on the mesial side, where there is a small area that has been hit by a mechanical action resulting into some loss of matter. This is similar to what happened to the root near its proximal-distal extremity; a straight, *ca*. 8mm limit is a sort of boundary for a lost, detached splinter. This is also a consequence of a mechanical action that does not seem very recent either.

On the mesial part of the crown, there is some enameloid loss at the proximal end. No serrations remain, a feature that may be due to abrasion by use or post mortem abrasion.

The root does not present any noteworthy features. There are no distinct foramina nutrientia.

Interesting characters may be clearly seen on the distal side: it is distinctly wrinkled and looks like an incomplete vestigial lateral denticule. Wrinkling also seems to have occurred on the mesial side. This apparently archaic condition recalls ancient *M. megalodon*'s characters, better seen in "*M. chubutensis*" specimens (Applegate, 1996; Cappeta, 2006).

As far as position in the mouth is concerned, ML 646 seems to be a second right upper palatoquadrate lateral tooth as pointed out by its symmetry (Applegate and Espinosa-Arrubarrena, 1996: 32/Fig. 12).

The whole shape, size, as well as the characters of denticles are typical of an adult *M. megalodon*. However, some doubt could remain about its geologic age. In terms of size, it could be compatible either with a rather archaic *M. megalodon* shark, late Early to Middle Miocene in age, or to a Late Miocene or Pliocene one from a very young individual. If this is the case, let us recall that *M. megalodon* nursery areas have been recognized in warm coastal environments (Purdy, 1996: 76-77).

Tooth ML 1918 (Lourinhã Museum)

The third specimen, ML 1918 (Fig. 4), is part of a larger than the preceding block of turbidite rock that looks similar to the one enclosing the ML 646: the rock includes angular elements of basic rock and phosphatic (?) matter covered by a thin Fe-Mn layer. Its maximum dimensions are about 27x22.5cm.

On certain surfaces there are small, dispersed, rather fine, sand-sized grains of glauconite. Glauconite originates in continental shelf with low sedimentation rates and under reducing conditions in sediments. It is abundant in sea-floor areas that are isolated from large supplies of land-derived sediment, on submarine elevations from about 30 to 1000m deep. Glauconite also occurs on certain surfaces of the previously referred block.

FIGURE 4. *Megaselachus megalodon,* lower tooth, lingual view.

The block includes invertebrates: encrusting Bryozoa; some calcareous fixed valves craniid Brachiopoda adhering to the rock; and serpulid worms' calcareous tubes, all of which may be more recent. The brachiopods are represented by broad, rather rounded ventral, *ca.* 11 to 12mm wide valves strongly attached to a hard-substrate. These brachiopods (as for Crania anomala) commonly occur in shallow to moderately deep waters (15-165m) but have been collected much deeper (1500m) (de Kluijver *et al.* 2000). Craniids are still found in the Atlantic from Shetland to Canary's Islands (Moore, 1965).

The *M. megalodon* (ML 1918) is moderately large, but less than the large upper tooth described above (ML 646). Only its internal (buccal) side is exposed. It is not complete, as much root matter has been lost owing to corrosion and especially by intense boring. The apex is distinctly worn by use; the tooth has been lost in life.

The quite complete crown is nearly symmetrical and rather thick. Although the specimen is firmly attached to the matrix and not entirely observable, it may be considered as a right, probably the 4th or 5th lateral, mandibular tooth.

Measurements (mm): crown height at its middle part, 46.1 and probably somewhat higher; maximum height as estimated, ~81.3; estimated maximum width, more than 63; thickness at the crown's base, about 20.0.

Although large-sized, the concerned tooth does not seem especially large in comparison with others.

A mako shark tooth (Lourinhã Museum)

The same turbidite block that contains ML1918 also includes an isolated, incomplete mako shark tooth (Fig. 5), a few centimetres from the *M. megalodon* one. The root seems lost. The quite twisted crown with sharp, non-denticulated cutting edges attains a *ca.* 27.4mm median height. Comparisons with extant *Isurus oxyrinchus* dentition (three specimens, one juvenile and two adults from M.T.A. collection kept at Lisbon Academy of Sciences Museum) suggest it is a left, first upper (palatoquadrate) tooth from a very large individual.

Evidence is enough to report the concerned tooth to the genus Isurus, but determination at the species's level is risky on this data only. It seems close to the Atlantic mako, and maybe to the extinct species *Isurus desori*. It can be ascribed to an *Isurus cf. oxyrinchus* which, as far as we know, is recognized for the first time in the Portuguese marine area.

An ancient scallop (Lourinhã Museum)

The larger turbidite block with *M. megalodon* and Isurus teeth also shows an external mould of a pectinid valve (Fig 6). The general shape, the distinct ribs wider than the interspacing channels, at least 26 as preserved, maybe some further ones (up to 35 ribs maximum); as well as size (somewhat more than 42mm in height, maximum 70mm), seem to point out to a very common and widely

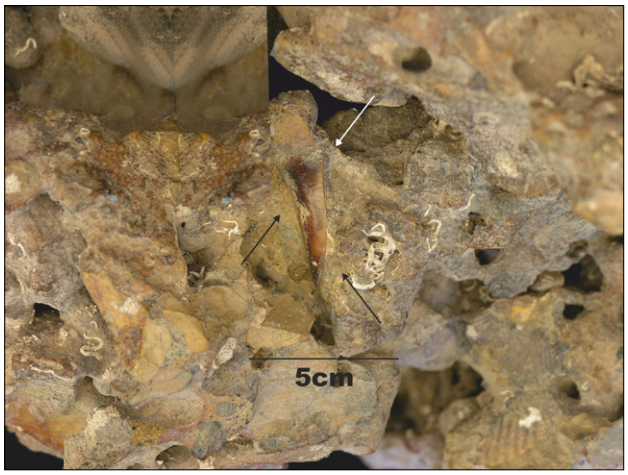

FIGURE 5. *Isurus cf. oxyrinchus*, upper tooth, internal view; the same block as Figure 4.

distributed species since at least the lower Miocene, *i.e. Mimachlamys varia* (Linnaeus, 1758). It mainly occurs along rocky coasts (de Bruyne, 2003).

Foraminifera from sediment infilling cetacean skulls cavities

Sediment from the cetacean skulls depressions, almost completely constituded by planktonic foraminifera shells, was scratched and washed on 125μm mesh sieve. Two samples were obtained: one from a skull collected by trawlers off Peniche and given to Lourinhã Museum; another one from a skull collected at about 600m depth, from unknown location, by trawlers based at the Setúbal harbour, and conserved at Évora University.

No meaningful difference was found between both planktonic assemblages (kept in Earth Sciences Department, FCT/UNL). Several of the identified forms are chronostratigraphically interesting (Fig. 7). Account is taken of the known stratigraphic range and the first and last appearance data for key species, as well as paleoecological data (Kennet and Srinivasan, 1983).

Three sub-associations can be recognized, pointing out different ages (Table 2).

An at least late Messinian to Early Pliocene age is shown by *Globorotalia conomiozea*, FAD 6.1Ma (Berggren *et al*., 1995); *Globorotalia puncticulata*, FAD 4.8Ma in the southern hemisphere, entering in the North Atlantic and Mediterranean at 4.5Ma (Scott *et al*. 2007: 235-253); *Globorotalia cibaoensis*, LAD 4.4Ma (Berggren *et al*., 1995). *Globorotalia margaritae* is rare. Neverthless, there are references about its rarity or even its absence in uppermost Miocene and basal Pliocene in the North Atlantic realm (Huddlestun, 1984). These planktonic foraminifera suggest that the fossilization of the skulls probably occurred at an age range from 6.1 to 4.4Ma.

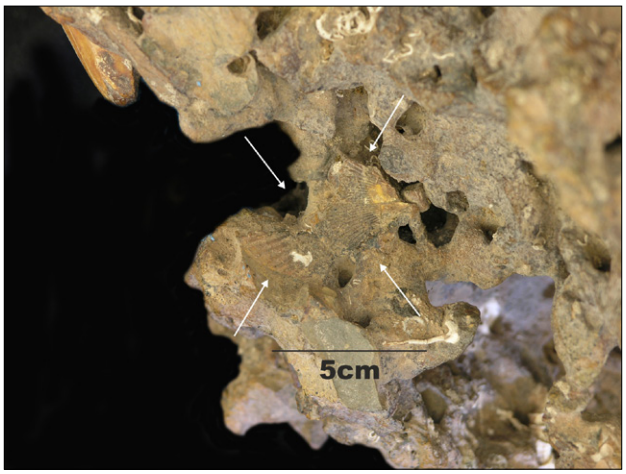

FIGURE 6. Pectinid valve external mould, internal view; the same block as the previous specimen.

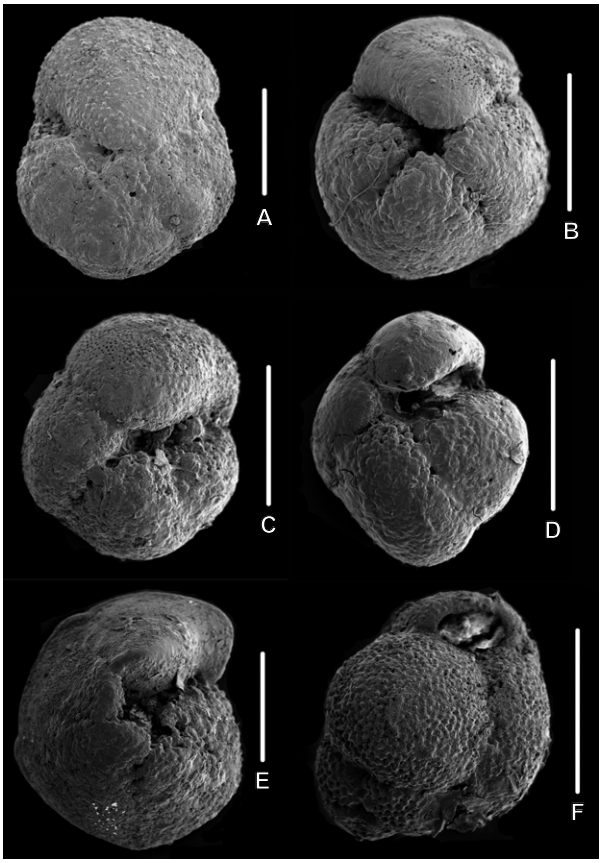

FIGURE 7. Key biostratigraphic species of planktonic foraminifera from the sediment in the cetacean skulls cavities. Bar=300µm: A: Globorotalia (Hirsutella) cibaoensis Bermúdez; B: Globorotalia (Globoconella) conomiozea Kennett; C: Globorotalia (Globoconella) puncticulata (Deshayes); D: Globorotalia (Globoconella) inflata D'Orbigny; E: Globorotalia (Truncorotalia) truncatulinoides (D'Orbigny); F: Globigerinoides extremus Bolli.

Furthermore, a Late Pliocene age is pointed out by *Globorotalia inflata* (FAD 3.0Ma) and a Pleistocene to Recent age by Globorotalia truncatulinoides (FAD 1.93Ma; Lourens *et al*., 2004) representing a period of condensation.

AGE

Fossils from different ages can accumulate together in hardgrounds. The age span of these hardgrounds can be assessed from the study of foraminiferal assemblages. On the other hand, megalodon's evolution stage as pointed out by its maximum size can also provide an approximate age determination.

Rarely an extinct animal from after the "Age of Dinosaurs" attracted so much public attention as the largest

TABLE 2. Planktonic foraminifera from sediment infilling cetacean skulls cavities. Stratigraphic range, N zones, Bottom (BT)/Top occurence, and paleoecological data based on Kennet and Srinivassen (1999). Three sub-associations can be recognized, as shown by chronologic order of key species (Fig. 7)

LATE MIOCENE/ EARLY PLIOCENE, 4.5Ma (+1.5,-0.1). Subtropical–Temperate			
Globorotalia (Hirsutella) cibaoensis Bermúdez.	Late Miocene, N17A–Early Pliocene, N19; TOP 4.4Ma	Tropical–temperate.	Fig. A
Globorotalia (Globoconella) conomiozea Kennett	L. Miocene–Early Pliocene, N19; 6.1–3.0Ma	Warm subtropical–temperate.	Fig. B
Globorotalia (Globoconella) puncticulata (Deshayes)	Early–Late Pliocene, BT. 4.8Ma; 4.5Ma–Mediterranean	Temperate–warm subtropical.	Fig. C
Globigerina concinna Reuss	Frequent throughout the Pliocene in western Emilia/northern Italia		
Globorotalia (Hirsutella) margaritae Bolli	Early Pliocene, N19–20	Tropical to temperate.	
LATE PLIOCENE, 3Ma. Warm subtropical			
Globorotalia (Globoconella) inflata D'Orbigny	Late Pliocene–Recent BT. 3.0Ma	Sub-antarctic–warm subtropical	Fig. D
Globigerina (Zeaglobigerina) apertura Cushman	N16–N21	Warm subtropical–temperate.	
Globigerinoides extremus Bolli	N16–N21	Tropical–cool subtropical.	Fig. F
Neogloboquadrina acostaensis (Blow)	N16–N21	Tropical–warm subtropical.	
Globigerinoides conglobatus (Brady)	N17B–Recent	Tropical–warm subtropical.	
QUATERNARY, 1.93 Ma. Warm subtropical–Temperate			
Globorotalia (Truncorotalia) truncatulinoides (D'Orbigny)	BT. 1.93Ma–N22 Early Pleistocene–Recent	Warm subtropical–tropical.	Fig. E
Globigerinella aequilateralis (Brady)	N12–Recent	Tropical–temperate.	
Orbulina spp.	N9–Recent		

known marine predator, the giant shark *Megaselachus megalodon*. Let us recall its appearance about the end of the Early Miocene (Leriche, 1926). Since then, a distinct evolutionary trend has been recognised for this species: Late Miocene and even more Pliocene teeth seemingly attain a much larger maximum size. This contrasts with the distinctly smaller, Early Miocene ones (Antunes, 1978). Maximum body length and weight are really impressive, as they have been estimated to attain 24 to 25 meters and about 103 tons respectively (Gottfried *et al*., 1996).

Antunes (1978) discussed this size increase from the rich Pliocene ichthyologic faunas from Angola and elsewhere, among which the association of very large *Megaselachus megalodon* with the still extant *Carcharodon carcharias* is characteristic. In Portugal and Spain, *C. carcharias* was never found in rocks older than Pliocene (Antunes and Balbino, 2003; Antunes and Balbino, 2010), and therefore the joint occurrence of both seems a good Pliocene indicator (Adnet *et al*., 2009; García *et al*., 2009). We are aware that *C. carcharias* has been referred to the Miocene, however, there have been errors in identification, mostly resulting from confusion with juvenile megalodon teeth, as well as errors relative to the sample location, or on chronology. As an example, the Pliocene beds of Farol das Lagostas in Angola had previously been ascribed to Early Miocene, "Burdigalian" (Antunes, 1978).

Another point is *M. megalodon* extinction. This has been discussed with focus mainly on climate changes, and specially on ocean cooling (Purdy, 1996: 71-77). This was related to the closing of Panama's isthmus in Pliocene, *ca*. 3Ma former Atlantic-Pacific communication and the settling of new ocean current patterns, including the beginning of the Gulf Stream. Atlantic currents were therefore forced northward with dramatic consequences

on climate and oceanography. Other changes concern sea level drops and decline on food supply.

Lowering sea water temperatures and good adaptation of large cetaceans to colder areas out of megalodon's range concurred to the population decrease of this great predator (Gottfried *et al.*, 1996; p. 65):

«A seeming anomaly in the above speculation, which implies that the distribution of megatooth sharks was closely linked to the presence of cetaceans, pinnipeds and possibly other large marine vertebrates as food resources, is the observation that megatooth sharks apparently became extinct before the end of the Pliocene. The extinction of *C. megalodon* near the end of the Cenozoic was, therefore, likely due to another factor, or combination of factors, such as climatic change, competition from large odontocetes, or a distributional shift of large marine mammals to colder, high-latitude conditions for which the megatooth was unsuited».

Did *M. megalodon* really survive in Quaternary times? This question seems to have been answered long ago, as a *M. megalodon* tooth had been recovered from red mud at the sea bottom during HMS Challenger 1872 oceanographic expedition. On this basis and scant further data, the chronological distribution of the species was recognized between Early Miocene and Quaternary, as stated in the classical memoir by Leriche (1926) and other papers (Leriche, 1942, 1957). Recently, it has been supposed that the extinction took place during the Pleistocene, about 1.5Ma, but this may not be entirely taken for granted. According to Purdy (1996) the survival of megalodon in the Pleistocene is questionable, while Applegate and Espinosa-Arrubarrena (1996: fig. 14) place its last occurrence in the Late Pliocene, 2.5 to 1.6Ma.

Pimiento and Clements (2014) applied Optimal Linear Estimation in order to probabilistically infer the extinction time of megalodon. They obtained an age older than 2,6Ma (modal value) for 50% of the simulations, and from 2,6 to 0,1Ma for the remaining 50% of the simulations. However, these results are open to discussion, as the time range of calculated ages is very broad and cannot be taken for granted. Hence the results do not really advance much beyond what was already known.

All in all, the advanced stage of evolution of *M. megalodon* teeth is consistent with the latest Miocene–Early Pliocene age inferred from planktonic foraminifera.

PALEOECOLOGY

M. megalodon had a broad distribution in warm, tropical to subtropical waters. Forms close to *Isurus oxyrinchus* may co-occur but generally avoid tropical, warm seas and may therefore be taken as good indicators of temperate waters. In Gottfried *et al.* (1996) there is a synthesis on this subject:

«The nearly panoceanic occurrence of *C. megalodon* in nearshore deposits at subtropical to moderately high-temperature latitudes indicates that it occurred in environmental conditions broadly similar to those favored by the living species, *C. carcharias*: biologically rich nearshore and coastal shelf areas where large prey are relatively abundant. Megatooth sharks may also have occurred in other environments, including more tropical habitats, that have gone unrecognized due to preservation and/or collecting bases».

Its dependence on cetaceans, pinnipeds, and possibly other large marine vertebrates as food resources has been stressed (ibidem). The association of cetacean remnants and shark teeth in the concerned portuguese offshore areas seems to confirm that such areas were rather rich in prey and predators, during the latest Miocene to early Pliocene. The planktonic foraminifera from this age interval indicate a subtropical to temperate province.

CONCLUSIONS

Our study on samples recovered from the continental shelf off Portugal led to the following conclusions:

Fossil shark teeth are found in turbidite fragments. The turbidite matrix is phosphatised and rather iron-rich with small quantities of manganese and zinc and copper.

Planktonic foraminifera in cetacean skull cavities point out to a late Messinian to Early Pliocene age, from 6.1 to 4.4Ma. The cetaceans and sharks, in the same areas offshore central Portugal and with identical lithological matrix, is likely to have occurred during the same chronologic span.

A process of condensation is revealed by the mixed occurrence of typical Late Pliocene and Quaternary foraminifera; however, such a process may have begun earlier, possibly in latest Miocene.

Extremely scarce benthic foraminifera suggests more or less deep environments, while an ancient scallop, Mimachlamys varia, might indicate nearby rocky substrate.

The occurrence of *M. megalodon* excludes an age older than Miocene. The very advanced evolution stage attained, as shown by the huge size, is consistent with a Pliocene age.

Although well known elsewhere, the occurrence of a mako shark, *Isurus cf. oxyrhinchus* is recorded for the first time in the Portuguese marine area. Isurus tooth is not very useful as an age indicator since species whose dentitions are similar to that of *Isurus oxyrinchus* as *I. desori* occur since the Early Miocene or earlier (Cappetta, 1987, 2006).

The so far rather poorly known shark association comprises a seemingly moderately warm indicator as *Megaselachus megalodon* and Isurus are essentially temperate water dwellers, whereas no real stenothermic, warm water form is known; temperate to moderately warm conditions prevailed.

ACKNOWLEDGMENTS

Our best thanks are due to: the late Mr. Horácio Mateus, from Lourinhã, and Professor Hernani Mergulhão (President GEAL/ Museu da Lourinhã) for their support; Dr. Octávio Mateus, who searched megalodon specimens at the same Museum and provided part of the samples for foraminiferal research; Professor L. Aires-Barros, who examinated macroscopically the rock sample associated to one of the teeth under study; Carla Rodrigues under the responsibility of Professor José Moura, for chemical analyses obtained at the "REQUINTE/Rede de Química e Tecnologia" laboratory (Faculty of Science and Technology, New University of Lisbon); the anonymous referees and section editor, who provided useful comments and suggestions.

REFERENCES

Adnet, S., Balbino, A.C., Antunes, M.T., Marín-Ferrer, J.M., 2009. New fossil teeth of the White Shark (Carcharodon carcharias) from the Early Pliocene of Spain. Implication for its paleoecology in the Mediterranean. Neues Jahrbuch für Geologie und Paläontologie, 256(1), 7-16.

Agassiz, L., 1843. Recherches sur les poissons fossils. Neuchâtel, 1-390.

Antunes, M.T., 1978. Faunes ichthyologiques du Néogène supérieur d'Angola, leur âge, remarques sur le Pliocène marin en Afrique australe. Lisboa, Ciências da Terra (UNL), 4, 59-90.

Antunes, M.T., Balbino, A.C., 2003. Uppermost Miocene Lamniform Selachians (Pisces) from the Alvalade basin (Portugal). Lisboa, Ciências da Terra (UNL), 15, 141-154.

Antunes, M.T., Balbino, A.C., 2010. The great white shark Carcharodon carcharias (Linné, 1758) in the Pliocene of Portugal and its Early distribution in western Atlantic. Revista Española de Paleontología, 25(1), 1-6.

Applegate, S.P., Espinosa-Arrubarrena, L., 1996. The fossil history of Carcharodon and its possible ancestor, Cretolamna: a study in tooth identification. In great white sharks. The biology of Carcharodon carcharias. San Diego CA, USA, Peter Klimley and David Ainley eds. Academic Press, 4, 19-36.

Bianucci, G., Miján, I., Lambert, O., Post, K., Mateus, O., 2013. Bizarre fossil beaked whales (Odontoceti, Ziphiidae) fished from the Atlantic Ocean floor off the Iberian Peninsula. Geodiversitas, 35(1), 105-153.

Berggren, W.A., Kent, D.V., Swisher III, C.C., Aubry, M.P., 1995. A revised Cenozoic geochronology and chronostratigraphy. In: Berggren, W.A., Kent, D.V., Aubry, M.-P., Hardenbol, J. (eds.), Geochronology, Time Scales and Global StratigraphicCorrelation: A Unified Temporal Framework for an Historical Geology, SEPM Spececial Publication, 54, 129-212.

Bruyne, R.H.de, 2003. The complete Encyclopedia of shells. REBO Publishers, Lisse, 336pp.

Cappetta, H., 1987. Chondrichthyes II/Mesozoic and Cenozoic Elasmobranchii. Handbook of Paleoichthyology. Edited by Prof. Dr. H.-P. Schultze, Lawrence. Gustav Fischer Verlag. Stuttgart. New York. 38, 123pp.

Cappetta, H., 2006. Elasmobranchii Post-Tradici (Index specierum et generum). Fossilium Catalogus I. Animalia. Edited by Wolfgang Riegraf. Pars 142. Backhuys Publishers, Leiden, 472pp.

Charlesworth, E., 1837. Notice of the teeth of Carcharias megalodon occurring in the Red Crag of Suffolk. Magazine of Natural History, 1(2), 225-227.

Compagno, L., 2005. Check list of living Chondrichthyes. In: W.C. Hamlett (Ed.), Reproductive biology and phylogeny of Chondrichthyes: sharks, batoids and chimaeras. Science Publishers, Enfield, 503-548.

De Kluijver, M.J., Ingalsuo, S.S., de Bruyne, R.H., 2000. Macrobenthos of the North Sea [CD-ROM]: 1. Keys to Mollusca and Brachiopoda. World Biodiversity Database CD-ROM Series. Expert Center for Taxonomic Identification (ETI), Amsterdam.

García, E.X.M., Antunes, M.T., Balbino, A.C., Muñoz, F.R., Llovera, J.C., 2009. Los tiburones Lamniformes (Chondrichthyes, Galeomorphii) del Plioceno inferior de la Formación Arenas de Huelva, suroeste de la cuenca del Guadalquivir, España. Revista Mexicana de Ciências Geológicas, 26(3), 674-686.

Glückman, L.S., 1964. Class Chondrichthyes, Subclass Elasmobranchii. In: Obruchev D. V. (Ed.) Fundamentals of Paleontology. Acad. Nauk SSSR 11, 196-237.

Gottfried, M. D., Compagno, L.J.V., Bowman, S.C., 1996. Size and Skeletal Anatomy of the Giant "Megatooth" Shark Carcharodon megalodon. Great White Sharks/The Biology of Carcharodon carcharias. San Diego CA, USA, Peter Klimley and David Ainley eds. Academic Press, 7, 55-66.

Huddlestun, P., 1984. Planktonic foraminiferal biostratigraphy, Deep Sea Drilling Project Leg 81. IN DSDP vol. LXXXI, 429-438.

Jordan, D.S., Hannibal, H., 1923. Fossil sharks and rays of the Pacific slope of North America. Bulletin of the Southern California Academy of Sciences, 22, 27-68.

Kennett, J.P., Srinivasan, M.S., 1983. Neogene Planktonic Foraminifera-A Phylogenetic Atlas. Stroudsburg: Hutchinson Ross, 265pp.

Leriche, M., 1926. Les Poissons néogènes de la Belgique. Mémoires du Musée royal d'histoire naturelle de Belgique, VIII(32), 364-472.

Leriche, M., 1942. Contribution à l'étude des faunes ichthyologiques marines des terrains tertiaires de la plaine côtière atlantique et du centre des États-Unis. Le synchronisme des formations tertiaires des deux côtés de l'Atlantique. Mémoires de la Société géologique de France, nouvelle série, XX(45), 111pp.

Leriche, M., 1957. Les Poissons néogènes de la Bretagne, de l'Anjou et de la Touraine. Mémoires de la Société géologique de France, nouvelle série, XXXVI(81), 64pp.

Lourens, L.J., Hilgen, F.J., Shackleton, N.J., Laskar, J., Wilson, D., 2004. The Neogene Period. In: Gradstein, F. M., Ogg, J.G. and Smith, A.G. (eds.). Geological Time Scale 2004. Cambridge University Press, 409-440.

Moore, R.C., 1965. Brachiopoda. Treatise on Invertebrate Paleontology. Part H., Volume 1. Boulder, Colorado/ Lawrence, Kansas: Geological Society of America/University of Kansas Press, H6-H93.

Müller, J., Henle, F.G.J., 1841. Systematische Beschreibung der Plagiostomen. Berlin, Veit, 1-200.

Pimiento, C., Clements, C.F., 2014. When did Carcharocles megalodon become extint? A new analysis of the fossil record. PLoS ONE, 9(10): e111086.

Purdy, R.W., 1996. Paleoecology of Fossil White Sharks. Great White Sharks/The Biology of Carcharodon carcharias. San Diego CA, USA, Peter Klimley and David Ainley eds. Academic Press, 8: 67-78.

Rafinesque, C.S., 1810. Caratteri di alcuni nuovi generi e nuovi specie di animali e piante della Sicilia, con varie asservationi sopra di medesimi. Palermo, 1-105.

Scott, G.H., Kennett, J.P., Wilson, K.J., Hayward, B.W., 2007. Globorotalia puncticulata: Population divergence, dispersal and extinction related to Pliocene–Quaternary water masses, Marine Micropaleontology, 62(4), 235-253.

Manuscript received July 2014;
revision accepted May 2014;
published Online July 2015.