

Evolution of white and megatooth sharks, and evidence for early predation on seals, sirenians, and whales

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ABSTRACT

The early white shark *Carcharodon* Smith, 1838 with the fossil *Carcharodon auriculatus* (Blainville, 1818) and the extinct megatooth shark *Otodus* Agassiz, 1843 with species *Otodus sokolovi* (Jaeckel, 1895) were both present in the European proto North Sea Basin about 47.8 - 41.3 m.y. ago (Lutetian, early Middle Eocene), as well as in the Tethys realm around the African-Eurasian shallow marine habitats. Both top predators developed to be polyphyletic, with possible two different lamnid shark ancestors within the Early Paleocene to Early Eocene timespan with *Carcharodon* (white shark line-age) and *Otodus* (megatooth shark lineage). Their sawblade teeth developed during the early Paleogene as the result of adaptation to feeding on various marine new rising mammals, coinciding with three main waves of evolutionary emergence of seals, sirenians, and whales in parallel with the evolution of these large predatory sharks. Megatooth sharks specialized in hunting whales and sirenians only on the coastal shelves of warm oceans and disappeared globally in the Pleistocene due to climate change and ocean cooling. The cold-water adapted early white sharks have survived until the present day with body temperate change adaptation in warm to temperate oceans and are proposed to have specialized on coastal seal hunting already 50 m.y. ago.

Keywords: Megatooth/White Shark Evolution; Palaeobiogeography; Marine Mammal Coevolution; Palaeoecology

1. INTRODUCTION

Large, serrated, fossil shark teeth from Tertiary sedi-

ments were generally first attributed to “white shark *Carcharodon carcharias* (Linné, 1758) ancestors”. Controversy has subsequently arisen whether they should be ascribed to the megatooth shark (“*Carcharocles*”— herein *Otodus*), or to the white shark (*Carcharodon*) lineage [1]. This controversy is partly a result of non-systematic excavation of single serrated similar looking teeth from many localities around the world, and from horizons of different ages. DNA studies have at least resolved the general position of the extant form of *Carcharodon carcharias*, placing it between the *Isurus* and *Lamna* genera [2,3], without taking into account a revision and including of extinct fossil species such as *Otodus*. The monophyletic evolutionary models that consider this genus *Otodus* to be a direct ancestor of the megatooth sharks [4] have recently received strong support, which can be supported furthermore with new Eocene tooth finds from Germany (Figure 1).

Complete megatooth and white shark skeletons, and even their teeth, are scarce in the Paleocene and Eocene around the world. A single incomplete set of teeth from *Carcharodon auriculatus* (Blainville, 1818), which is an Eocene relative of the white shark, was illustrated by Storms in 1901 [5]. Rare articulated skulls, tooth sets, or vertebral columns from megatooth sharks have been reported from the Oligocene species *Otodus angustidens* (Agassiz, 1843) [6,7], as well as from the Miocene species “*Otodus turgidus* (Agassiz, 1843)” whose latter validity is disputed herein [5] and, more commonly, from the Miocene to Pliocene species *Otodus megalodon* (Agassiz, 1843) [8,9].

The Middle Eocene shark tooth and coprolite-rich [10, 11] sites in north-western Germany, which also contain few marine mammals, recently became important following the discovery of the world’s oldest seal remains with a femur and humerus fragment [12], and newest sirenians remains with a rib and vertebra fragments [13]. Only 1% are such mammals, and 99% of the vertebrates

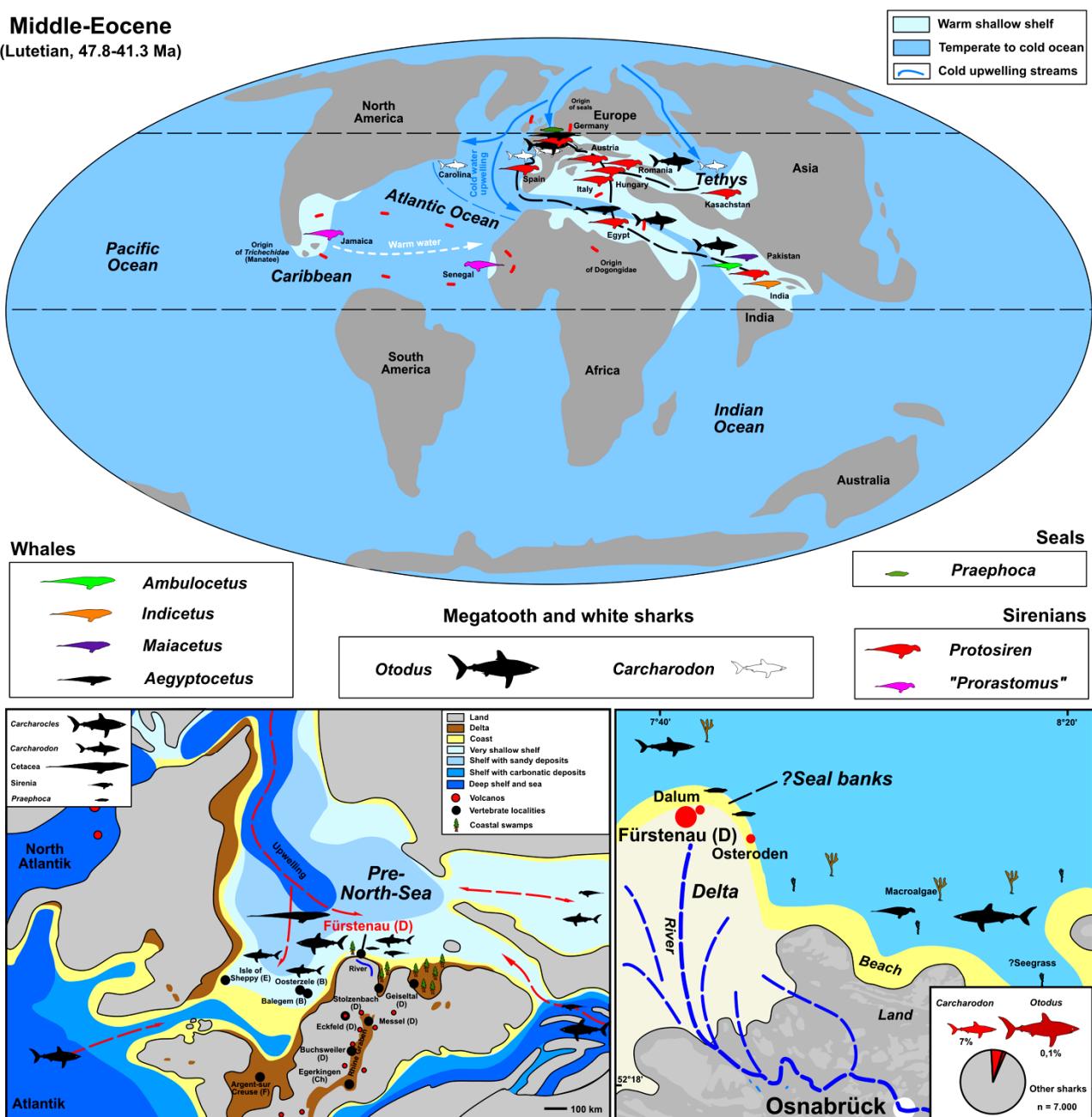


Figure 1. Global distribution of Middle Eocene (Lutetian) megatooth sharks and white sharks, and their migratory marine mammal prey. Seals were hunted along the beaches of the southern proto North Sea Basin, especially north of Osnabrück (palaeogeography of the Middle Eocene and important fossil sites of Europe compiled from [10,12,13]).

are isolated shark (mostly abundant teeth) and fish remains [10,11]. Over the past 25 years large quantities of teeth were sieved from the same layer at two smaller localities (Dalum and Osteroden) near Fürstenau (northern Germany, **Figure 1**) by two private collectors and more recent the author in a large systematic excavation campaign in 2011 [10]. Both, megatooth sharks and the ancestors of the white sharks have been unearthed from gravels with about 2000 specimens. This large amount

of finds, which are described herein with focus in the context of predator/prey relationships of marine mammals-giant sharks, are from a period that is close to the origin of both of these shark genera in the Early to Middle Eocene Lutetian [14].

2. MATERIAL AND METHODS

During 2011 Europe's largest shark tooth excavations were completed by the author at two shallow marine fos-

sil sites (Dalum and Osteroden) in north-western Germany, together with geological and palaeontological surveys, as an interdisciplinary research project for the Visitor Center at the UNESCO *Terra.Vita* Geopark/that built up recently the SharkCenterBippen; German = Haizentrum Bippen = SCB) [10]. A large total of 180 cubic meters of conglomeratic material was removed from the Dalum forest site for sieving, of which little over 0.1% (250×10 litre buckets) has been sieved to date. A further 10 cubic meters were removed from the Osteroden sand pit site, but most of this remains un-sieved. The gravel from Dalum was wet-sieved into two size fractions (+4 mm and 4 – 1 mm) and examined for vertebrate, invertebrate, and other fossil remains. At this campaign about 14.400 fossils (95% are shark teeth) have been found and analysed preliminary only on this public collection of the Geopark Terra.Vita, including some material of white and megatooth teeth [10].

The large private collection owned by H. Felker (included in future in the SCB), which was accumulated over 25 years from these sites with exact stratigraphic context and acribic sorting of all grain sizes (fractioned down to 1 mm) ranging over all fossil groups: foraminifera to megatooth shark teeth, and terrestrial mammal teeth), was additionally included in this study. This large amount of material is not to obtain in a short-term excavation campaign, and both combined allowed finally statistical analyses of both collections [10]. Whereas the excavation allows clear fossil amounts, the private collection allows presenting the biodiversity (rare fossils) and analyses of selected species with better amounts. This collection contains approximately 250,000 shark teeth, about 12,000 fish otoliths [15], many different kinds of macro invertebrate, and vertebrate fossils that include a few terrestrial mammal teeth and marine mammal bone fragments [10,12,13]. From this collection, together with the newly excavated material, about 2000 serrated teeth from *Carcharodon* and *Otodus* were separated for this study. Those teeth often are only tooth crowns or incomplete teeth without roots which can not be determined even to the genus. However, this material represents the largest number of serrated teeth ever analysed globally from a single layer (Eocene condensation bed). This German Middle Eocene material was compared with other large serrated teeth from the German Oligocene sites (Doberg, Astrup, Eckelsheim, Alzey, and Espenhain) [13] in order to understand the early evolution of white and megatooth shark dentitions with focus on the proto North Sea Basin during the Paleogene and Neogene. Tooth material from the species discussed herein was also compared with material in a number of other collections, both public and private, or published on the internet. Finally, the marine mammal record from German Eocene sites has been extended with the discov-

ery of the earliest known (fragmented) seal (herein added a new humerus fragment), sirenian [13] and possible whale material (vertebra fragments and rib/longbone fragment), which is of great relevance to discussions on the predator-prey relationships, ecology and evolution around the world.

The Oligocene material used for comparisons is housed in the Geologische Museum Ostwestfalen-Lippe, Dobergmuseum Bünde (**GMOL**) and the Museum Nierstein (**MNIE**). The Eocene material described herein is in the Shark Center, Bippen: German = Haizentrum Bippen (**SCB**) of the Geopark Terra.Vita, and the private collection of H. Felker in Ankum (**HF**). The material figured herein is housed all in the SCB.

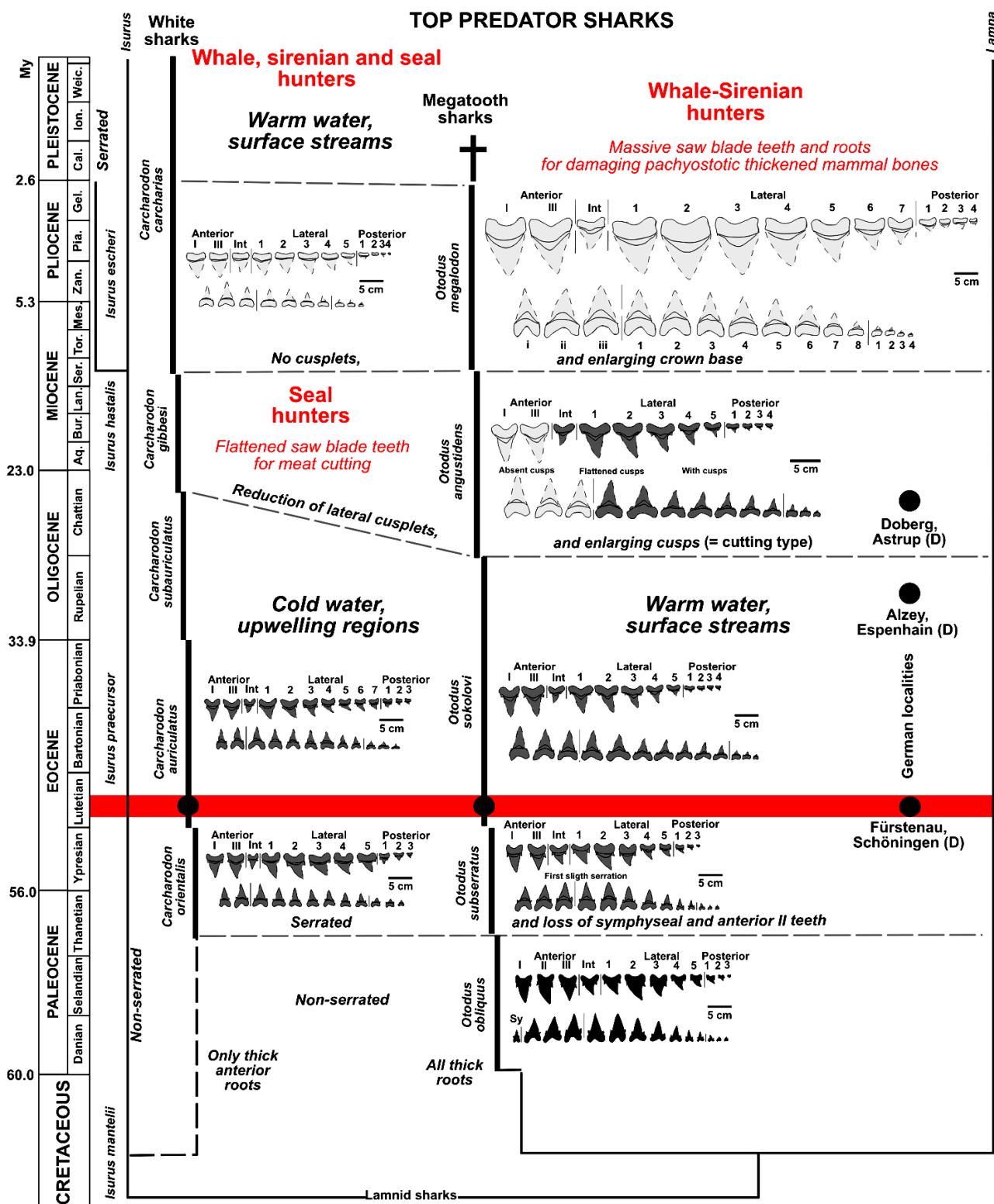
3. DISCUSSION

3.1. Origin and Evolutionary Model

DNA and cladistic analyses [2,3] have in the past failed to provide a satisfactory model for the evolution of *Carcharodon* and *Otodus*. However, consideration of climate indicators, predator/prey relationships, coevolution of predators and prey (such as possible convergent evolutionary developments), and analyses of dental morphology, combined with access to extensive new material from the Middle Eocene of Europe, has led to the development of the new model presented herein which differs in many ways to the recently compiled models [16,17], which are not repeated, because they are based on many herein used primary publications. This new and not only cladistic model is based on a polyphyletic origin for these two predatory large sharks, which already occupied different ecological niches and had different water temperature preferences by the Middle Eocene (**Figure 1**).

3.2. Evolution-Monophyletic or Polyphyletic?

DNA analyses have placed modern *Carcharodon* white sharks between the *Isurus* and *Lamna* lamnid sharks [3] (**Figure 2**), with their separation suggested to have occurred in the Early Eocene [2]. Although to date, there has been no material available to support this thesis, which can be added herein. The extinct Late Paleocene to Early Eocene *Otodus* genus, whose dental unserrated characteristics are more closely related to *Lamna* (also symphyseal teeth) than to *Isurus*, was included in the analyses (**Figure 2**). The massive rounded root bases of *Otodus* teeth, which is a plesiomorphic character in all lamnid teeth from the Eocene (including the lamnid *Jaeckelotodus*) [10,16], are very similar to those of all teeth (both anterior and posterior) from the megatooth shark *Otodus sokolowi*, as well as those in the anterior teeth of *Carcharodon orientalis* and *Carcharodon*



auriculatus (Figures 1 and 2). The tooth root morphology of *Carcharodon* is, however, more closely related to that of *Isurus*, whose anterior teeth have prominent but lateral teeth have flattened roots. This is the main tooth charac-

ter to distinguish those genera from each other. The overlap in anterior teeth seem to have confused in the past the exact attribution to megatooth or white shark ancestors. It is suggested herein that *Otodus* and *Car-*

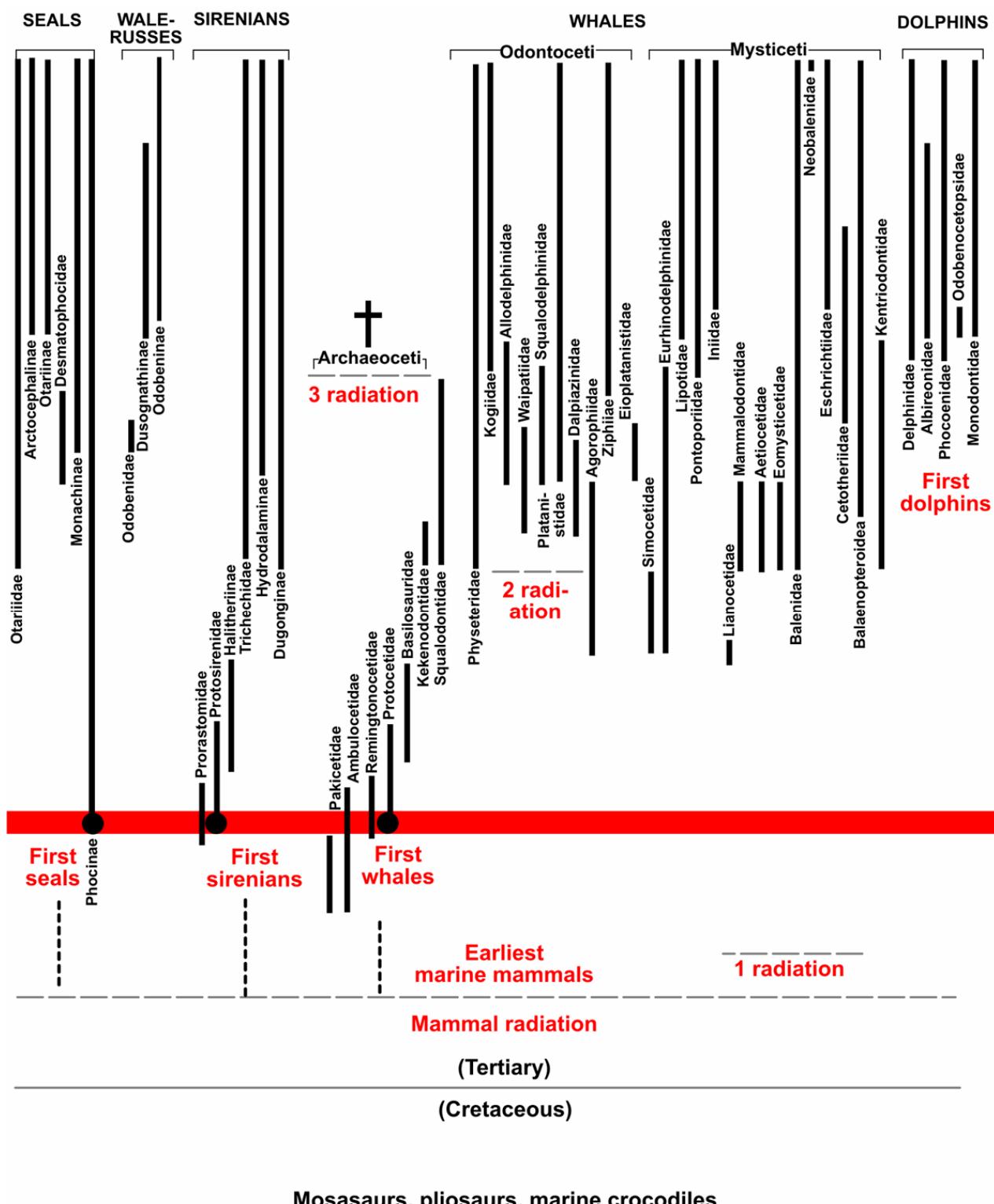


Figure 2. Evolution of the megatooth and white shark lineages, and coevolution with their largest marine mammal prey (redrawn after [2,4,7,12,13,16,17,22,24,28,42,57,58] using the international chronostratigraphical chart 2012 [59] and compiled to include the new results).

charodon each had different ancestors (Figure 2), and that their tooth serration is a convergent development

that may even have occurred twice in *Isurus* lineage (during the Paleocene in *Carcharodon orientalis*, and

again during the Pliocene in *Isurus escheri* [14,17,18]). A similar serration happened also in other shark groups in “short-terms” such as in *Squalicorax* during the Lower-Middle Cenomanian [16]. Therefore, serration of shark teeth also in the herein described megatooth and white sharks must be expected to have happened also in “short-term” as demonstrated herein in **Figure 2**. There were already two separate large shark lineages with well serrated teeth [2] (**Figures 2-4**) in the Late Paleocene and/or Early Eocene, as can be clearly obtained in fossil material from northern Germany (**Figures 2-4**). It appears, that both lineages were polyphyletic, with *Isurus* being the most probable ancestor of *Carcharodon*, having developed a little earlier during the Early Paleocene—first serration wave [2] (**Figure 2**), whereas *Otodus* only evolved a very few later during the Late Paleocene to Early Eocene to species with serrated teeth from unclear lineage more related to *Lamna* due to symphyseal teeth and dentition formula (cf. **Figure 2**). The possibility that both

(*Carcharodon* and *Otodus*) have only *Otodus* as a single monophyletic ancestor is, excluded herein by dentition formula, and tooth root characters mainly (**Figure 2**).

3.3. White Shark—*Carcharodon* Lineage

Carcharodon carcharias (Linnaeus, 1758) is the correct oldest reported genus and species with extant holotype species “*Squalus carcharias* Linnaeus, 1758”. This white shark was attributed later to the genus *Carcharodon* Smith, 1938. Therefore, it is invalid to use for megatooth/white sharks the younger synonym of fossil tooth genus *Carcharocles* Jordan and Hannibal, 1923. Their type-species is the fossil white shark “*Squalus auriculatus* Blainville 1818”, which was mentioned correctly as *Carcharodon auriculatus* by Agassiz, 1843. Younger synonyms used are *Procarcharodon* Case, 1981.

The oldest fossil white sharks date from the Middle to Late Paleocene (Thanetian), with the earliest serrated

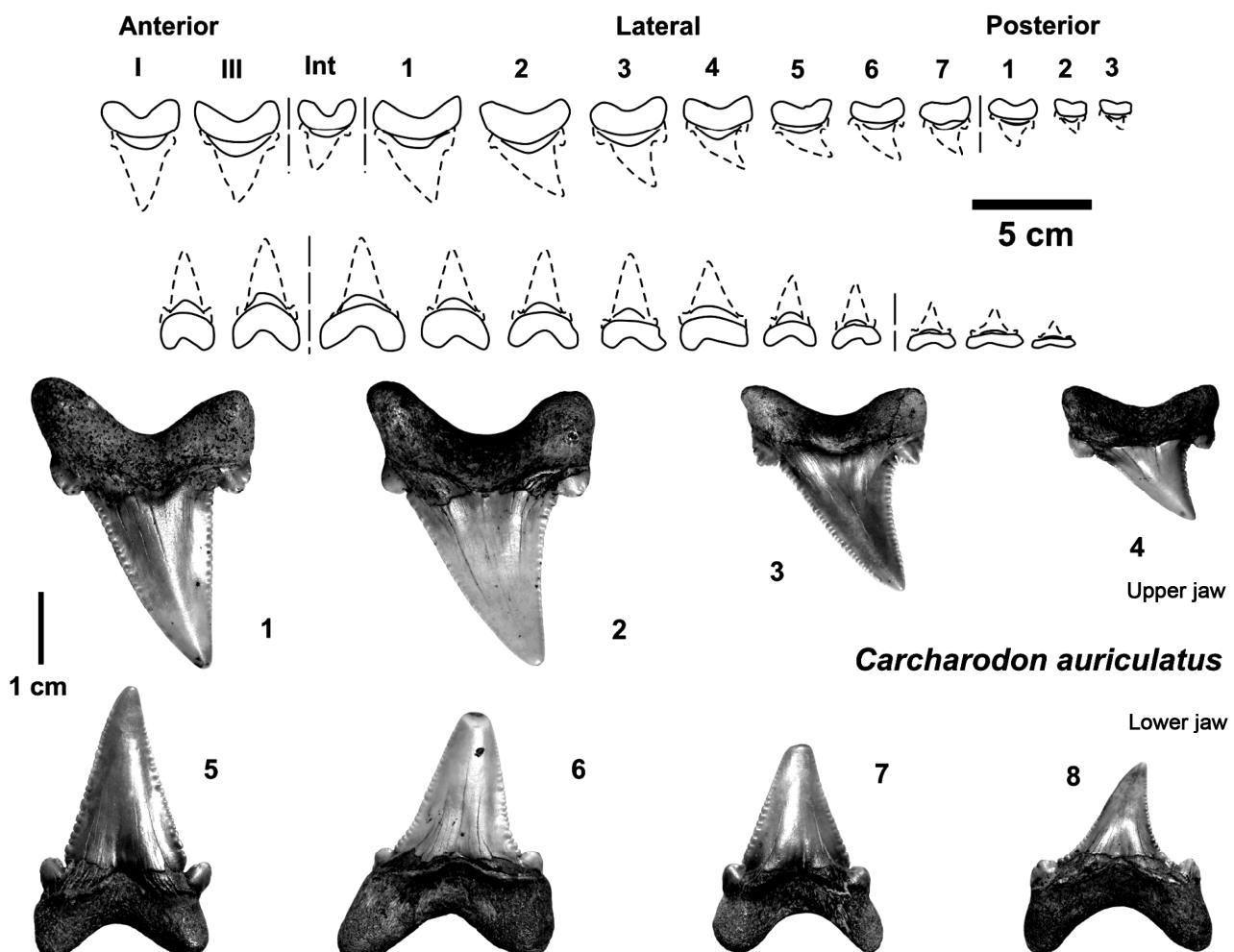


Figure 3. Parts of tooth sets from the white shark ancestor *Carcharodon auriculatus* (1 - 8 coll. SCB) from the early Middle Eocene (Lutetian) gravels of Dalum, north-western Germany, which also include reworked Late Paleocene to Early Eocene material (all in the SCB).

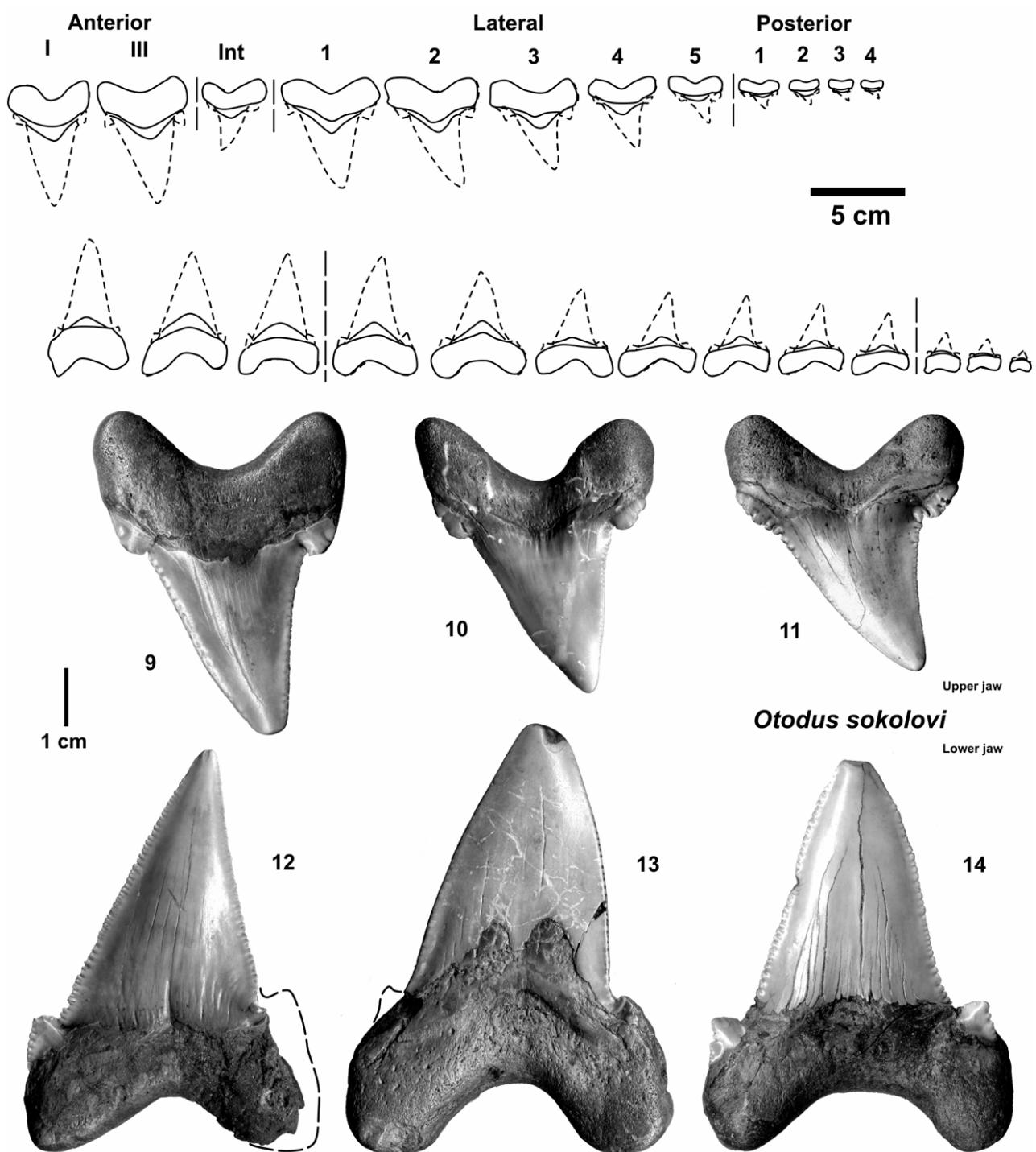


Figure 4. Parts of tooth sets from the megatooth shark ancestor *Otodus sokolovi* (9 - 12 coll. HF) from the early Middle Eocene (Lutetian) gravels of Dalum, north-western Germany, which also include reworked Late Paleocene to Early Eocene material (all in the SCB).

teeth (=first serration wave) [19], from *Carcharodon orientalis* (Snizow 1899) a former genus “*Procarcharodon*”, or synonymous to “*C. landanensis* Léricle, 1910”, having been found in upwelling-influenced phosphatic-rich sediments of Morocco [7, **Figure 2**]. These teeth

belong to the “small serrated tooth” type, with primitive coarse serration on all teeth as well as flattened roots in all lateral to posterior teeth which is, as mentioned, the most important character for distinguishing the mega-tooth sharks from white sharks on the basis of tooth

morphology. This is also important for understanding the origin of white sharks from *Isurus*. The most abundant white shark ancestor tooth material is slightly younger and comes from sites in north-western Germany [10], ranging in age from Early Eocene to early Middle Eocene and includes the more highly evolved *Carcharodon auriculatus* (Blainville, 1818) which occurs around the world [19,20, **Figure 1**], and to which also belong *C. disauris*—(Agassiz 1843), *C. debrayi* (Leriche 1906), and *C. nodai* (Yabumoto 1987) [20]. The large quantities of teeth recovered allow presenting nearly complete sets of teeth can be compiled according to known articulated tooth sets (**Figures 3 and 4**). A finer serration had already evolved by this time, although some teeth still exhibit coarser serration (in adult teeth), especially the lateral cusplets. The roots are still typically prominent in anterior teeth, but are flattened in all lateral to posterior teeth, typical also in *Isurus* teeth. This species is followed in the Oligocene by *Carcharodon subserratus*, and in the Lower Miocene by *Carcharodon gibbesi* (**Figure 1**) which transitions to the extant *Carcharodon carcharias*, but their remains are not yet well known due to the absence of tooth sets from those periods.

There is a general evolutionary trend in the tooth morphology of *Carcharodon* (**Figure 1**). During the Late Eocene to Late Miocene the lateral cusplets were reduced and the tooth crowns became a little enlarged, a convergent development with that of the megatooth lineage.

The same trend has also been reported in the Late Cretaceous, when *Isurus* (formerly *Cretoxyrhina*) tooth cusplets became reduced the crowns enlarged in a similar way, as an adaptation for shark predation on the evolving mosasaurs and other marine reptiles at this time (**Figure 1**) [21]. This first *Isurus* adaptation for feeding on large marine prey thus evolved in the Cenomanian (*I. denticulatus*), in the early part of the Late Cretaceous, while the lateral cusplets were reduced during the Turonian resulting in enlarged teeth with no cusplets in the Coniacian (*I. mantelli*), paralleling the evolution and diversification of the mosasaurs [21]. A second adaptation in tooth morphology appears to have been related obviously to Tertiary mammal radiation as presented herein (**Figure 2**).

That modern white sharks evolved from the Paleocene *Carcharodon orientalis* (first serration wave) can also be recognized from the ontogenetic tooth stage repetition in *C. carcharias*. The teeth of immature individuals are initially coarsely serrated (very similar to *C. orientalis*) but became more finely serrated in adult sharks [14]. Serrations can even sometimes be absent in teeth from *C. carcharias* [22], which may also be indicative of ancestors without serrated teeth (i.e. *Isurus*). Another form (*I. escheri*) with slightly serrated teeth evolved from *Isurus* in Miocene to Pliocene times (= second serration wave) [17,18], as a third adaptation to the type of prey, this time in response to marine mammal diversification during the

Middle Miocene (**Figure 1**: 3rd radiation of marine mammals, including the appearance of modern dolphins), which provides further evidence that the genus *Isurus*, was also before the ancestor of *Carcharodon* (**Figure 1**).

3.4. Megatooth Shark—*Otodus* Lineage

The oldest of these largest serrated teeth are more closely related to *Otodus* and finally also to *Lamna*, contrary to suggestions by other authors [1,13], and therefore *O. obliquus* (Agassiz, 1843) must be seen, as the oldest representative of megatooth sharks that developed also serrated teeth (as has also been proposed by other authors [5]), which strictly should be referred not to the invalid to “*Carcharocles*” genus, instead *Otodus*. These younger forms separating it especially from serrulation absence (also dentition formula few differences) are herein suggested only to be ancestral to the megatooth shark lineage (**Figure 2**), which exclusion is explained within the *Isurus* lineage and revision of Upper Cretaceous species [21]. “*Carcharocles*” is indeed a subjective younger synonym of *Carcharodon* (*C. auriculatus*, see white shark discussion) and cannot be used therefore for any other species anymore. This has an effect on the renaming herein several megatooth shark species consequently. Using this, all megatooth sharks from non serrated to full serrated teeth stages must be named as *Otodus* Agassiz, 1843 as the oldest genus name.

The new material from Germany (**Figure 4**) also contains reworked Paleocene to Early Eocene fossils [10], and it appears obvious that the full transition from non-serrated *Otodus* to slightly serrated “*Otodus*” forms can be supported through compiled tooth sets also of the German sites [cf. 10]. This evolution, involving the general development of serrations, has also been recorded from the eastern Tethys (Kazakhstan), but there, both lineages have been incorrectly interpreted as belonging to a single white shark lineage and were therefore mixed [19]. However, around the world the first serrations on *Otodus* teeth appear on teeth (anterior to posterior) with massive roots, which are herein placed within the genus *Otodus subserratus* Agassiz, 1843 [4] (also with other species names of *aksuaticus*, and *mugodzharicus* [4]). Following the better eastern Tethys stratigraphic record, *O. subserratus* first appeared in the late Thanetian (Late Paleocene) and continued into the middle Ypresian (Early Eocene; **Figure 2**) [19]. Similar *O. subserratus* teeth from the Eocene of Germany again provide evidence for this gradual transition from non-serrated *Otodus* teeth with massive roots (*O. obliquus*, Danian to early Thanetian) to early *Otodus serrated* teeth (*O. subserratus*, late Thanetian to middle Ypresian) again in a “short-time” frame. This has also been previously proposed by a number of authors but therein with the different genus names *Carcharocles/Carcharodon* [4, and references therein].

The first fully serrated megatooth shark teeth must have already been developed by the late Ypresian [19]. The material from the Middle Eocene condensed gravels of northwest Germany includes the oldest known and well dated not younger as middle Lutetian records of *Otodus sokolovi* (Jaeckel, 1895) [10] (**Figures 1 and 2**), extending its chronostratigraphic occurrence between the Middle Eocene and the Early Oligocene [13] (**Figure 1**). Complete sets of teeth would be required from this time frame to distinguish this new Middle Eocene material from younger forms. Some of the individual teeth collected in Europe from the Late Oligocene to Early Miocene “*O. angustidens*” must be ascribed to the Rupelian (Early Oligocene) species *O. sokolovi* (**Figures 1 and 2**), as seen in the material compared herein from the proto North Sea Basin (German localities at Eckelsheim and Espenhain). *O. angustidens* (Agassiz, 1843), which is known from isolated teeth from the northwest German Doberg site (Late Oligocene, proto North Sea Basin) [12, 13]. Proof of this lateral cusplets reduction is found in the complete tooth set and partial *O. angustidens* skeleton found in Ne Zealand, which either no longer has any clearly developed cusplets on the anterior teeth (or else they are very flattened), but which still has cusplets present on the more lateral and posterior teeth [7].

This tooth set represents the transition between teeth with lateral cusplets and those with either flattened cusplets or no cusps at all (**Figures 2 and 4**). The most evolved megatooth teeth are from *O. megalodon* (former “*Carcharodon/Carcharocles*”) and have no lateral cusplets which, having been fully reduced, are completely absent from all teeth (**Figure 2**). Despite this is not frequent, lateral cusplets indeed appear in posterior replacement teeth during early growth stages of the tooth. There are several late Miocene-early Pliocene examples in the records along the Pacific.

In general, all non-serrated-serrated megatooth *Otodus* shark teeth have massive roots (anterior to posterior) that are not flattened (very different in white sharks), with fine serrations starting in the Thanetian (Late Paleocene) and a trend towards lateral cusplet reduction that started in the Early Oligocene (**Figure 2**: second radiation of marine mammals), ending with no lateral cusplets and enlarged “saw-blade” fine serrated tooth crowns in the Middle Miocene (**Figure 2**: third radiation of marine mammals). This convergent development with white shark teeth often makes them very difficult to distinguish from each other. The teeth coevolved from catching teeth to cutting teeth, driven by the three major marine mammal radiations during the Tertiary (**Figure 2**).

3.5. Early Prey Specializations in Megatooth Sharks and White Sharks

The main groups of large marine mammals can now

be reported to have been present in the Proto North Sea Basin of Europe. The gravels at Fürstenau have yielded the remains of seals (**Figure 5**) [12], and also of sirenians (ribs) [13], and whales (possibly vertebrae in very fragmentary material, **Figure 5(E)**), all of which are found within the time frame of the first marine mammal radiation which started in the Thanetian to Ypresian of the Late Paleocene or Early Eocene (**Figure 2**: first radiation of marine mammals) [12]. In the megatooth and white sharks from the Early to Middle Eocene of northwest Germany, more marked damage to the tips of many changed teeth which are non-strong transported and non-rounded (**Figure 5** [10]) such as in many other cases, suggests clearly damage from feeding on large robust prey such as larger bony fish, or marine mammals. Only fish remains have so far been found in the few shark coprolites preserved from the Early to Middle Eocene of Germany, which have been attributed to these large sharks [11] (**Figure 5**), but this is no contra-argument to exclude mammals as large shark prey at all. The chance to find in an excrement a seal, sirenian or whale bone fragment is nearly zero, because most bones (also fish) were dissolute mostly by stomach acid, or were left so small not to be identified as such. Furthermore, the recent coprolite studies on the Fürstenau shark coprolites did not allow damaging the large megatooth/white sharks attributed few specimens, where mammal bones can be expected. Not to destroy those rare specimens only bones which were visible on the excrement surface have been identified [11]. Finally, most bones built completely dissolute the phosphate matrix of the coprolites. The arguments given herein are more a combination of shark tooth tip damage, and co-occurrence with the “marine mammal fauna” such as:

Seals: The oldest *Praephoca* seal records from northwest Germany (Lutetian, early Middle Eocene, **Figure 5**) pushed back the time from Lower Oligocene to Middle Eocene when they could have been first predated by large sharks. Former fossil finds previously suggested seals to have been present not before the Late Oligocene [2], whereas DNA studies also proposed clearly the origin of pinnipeds already in the Eocene [22]. Large seal populations appear to have bread at the Middle Eocene’s sandy beaches along the southern coastline of the proto North Sea Basin in Central Europe. This is estimated by the fossil record and taphonomy of pinnipeds, which is recently studied for the Eocene to Pleistocene seal evolution and record of the Proto North Sea Basin [cf. 12]. Interestingly, in 99% of the fossil records of Eocene, and Miocene shark-tooth-bonebeds the seal remains (always less than 0.1% of the vertebrates) consist of the long-bones (mainly humerus and femur) and other massive bones, teeth are e.g. known by a single record. Furthermore the amount of seal remains was estimated per 100 cubique meter of the gravels where they were found

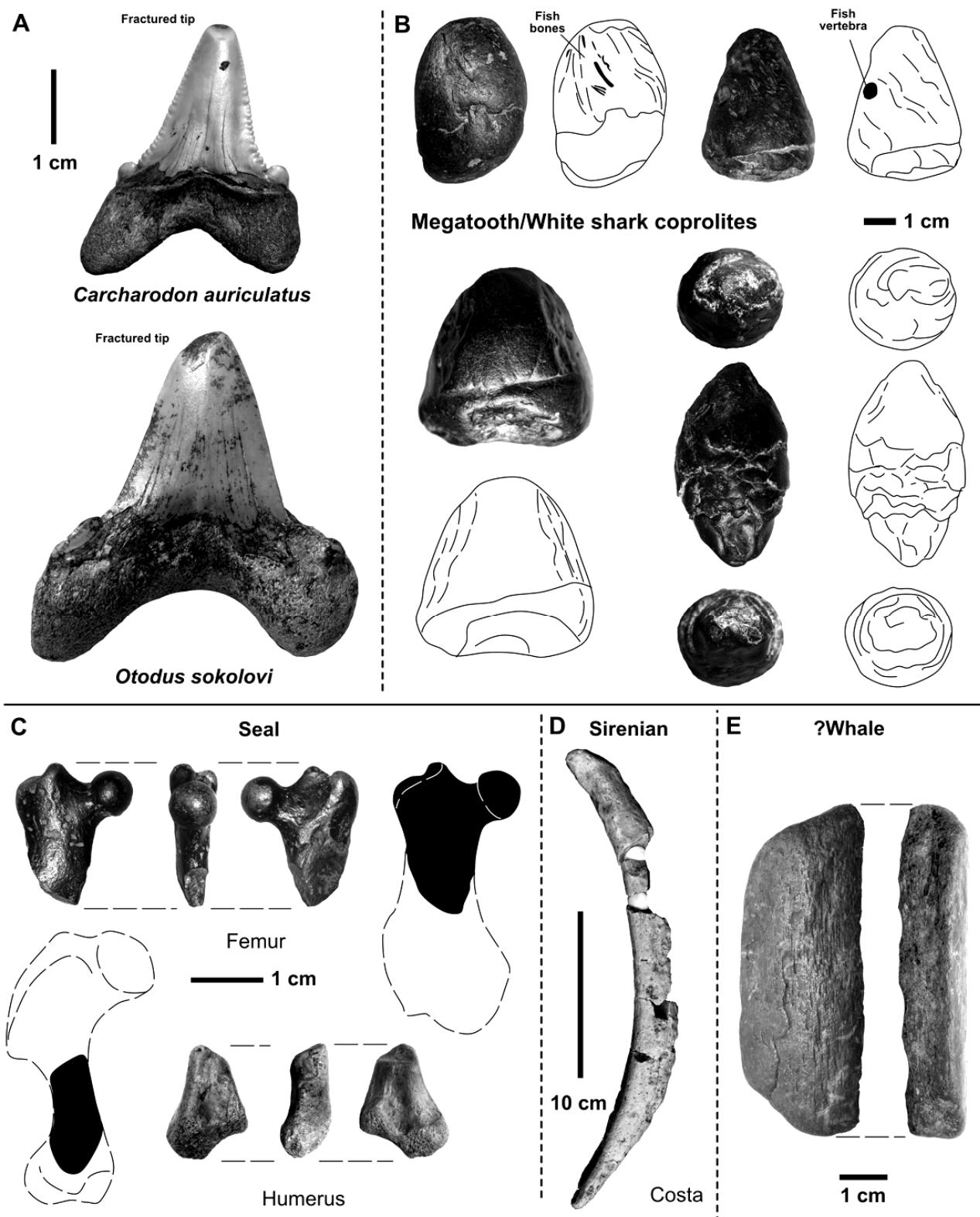


Figure 5. A) Bite damage on the tips of teeth from megatooth and white shark ancestors *Carcharodon auriculatus* and *Otodus sokolovi* (coll. SCB); B) Large coprolites from the Middle Eocene Dalum and Osteroden near Fürstenau sites (coll. HF), which contain only fish remains, can be attributed to these large sharks; C) Seal bone remains from the Middle Eocene Dalum site, femur fragment from [12]; D) *Protosiren* sp. rib from the Middle Eocene Dalum site (coll. HF), from [13]; E) Possible ?whale bone fragment remain from the Middle Eocene Dalum site (coll. SCB) (all in the SCB).

(Eocene, Miocene shark-bonebed gravels) where less than 1 specimen is found. The relation is about 1 seal remain to 250,000 shark teeth remains, e.g. at the Fürstenau (Germany) Eocene site, or the Rumst (Belgium) Miocene site. Even the Pleistocene bones from the North-sea Floor (found by fisherman) are rare. Few or single bones in the fossil record, therefore, can indeed indicate “larger populations”, which however are represented by taphonomic sorting (e.g. most robust and larger humeri/femora) are more sensitive for water transport (currents), such as tiny teeth. The gravels in the Eocene/Miocene have a sorting (around 2 cm gravel sizes)—and this water energy sorting might explain best the scarcity of “larger seal bones” and their sorting in shark-tooth-rich gravels in the Proto North Sea Basin. In the shallow shelf sediments of Fürstenau *Carcharodon auriculatus* teeth are the second most abundant (455 specimens = 7%, **Figure 1**) after sand shark (*Striatolamia macrota*) teeth (5901 specimens = 85%), based on a total of 6946 systematically excavated teeth [10]. At other sites in Belgium that are rich in shark teeth but from which marine mammals have not yet been reported [20], *C. auriculatus* teeth are present in much smaller quantities (not statistically presented) in the coastal sands [20]. The correlation between the occurrence of seals and abundant teeth from the white shark ancestor *C. auriculatus* provides the main evidence of the oldest known seal-hunting specialization in the fossil record of the northern hemisphere. Sharks probably hunted along the seals’ breeding beaches (**Figure 1**) in much the same way that modern sharks do (**Figure 5**) [23]. Sadly, there are no comparative taphonomic studies that demonstrate the modern abundance of seal bones and shark teeth at modern seal breeding beaches. Small white shark ancestor teeth are also abundant at more recent fossil sites in other parts of the world in which seals have been recorded [24], especially in cold marine regions influenced by upwelling [1]. Even today, seal hunts fulfil an important role in the feeding of mature white sharks. Whereas immature white sharks (up to 2 meters in length) feed mainly on fish, as well as on other sharks, when they reach adulthood they switch to seal hunting [25]. Such predation on seals has best been documented in seal colonies along the coast of California [23]. The photo sequence of great white sharks hunting the cape fur seal *Arctocephalus pusillus* on the South African coast, (**Figure 5**) demonstrates their attack technique, in which the white sharks generally attack from below, throwing the seal prey out of the water (**Figure 5**) [23] and then biting into any part of the body to prevent their agile prey escaping [23].

Sirenians: were reported with oldest Early Eocene (*Pezosiren*) to basal Middle Eocene (*Prorastomus*) forms from Jamaica and the Caribbean [26-30]. The new model of polyphyletic evolution split now the siren origins with manatees in the Caribbean Central America (basal Early

Eocene), and dugongs on the northern African Tethys coasts (early Middle Eocene) [13].

In the Lutetian only *Protosiren* was distributed within the Thetyan realm represented possibly even by a few species around the warmer Tethys oceans, only (**Figure 1**) [13]. The newly discovered *Protosiren* rib and further fragments from the early Middle Eocene proto North Sea Basin conglomerates of Fürstenau correlate with the influence of warm Tethys water and megatooth shark migration for predation. In younger Early Oligocene horizons of Europe several fossil sirenian *Halitherium* skeletons document by bite scratch marks on ribs/vertebrae that these animals were quite commonly scavenged by sharks, and probably even killed by warm water species such as *O. angustidens* in the Rhine Graben, the Proto North Sea Basin [31], and the Alpine Molasse Basin [32] of Europe.

Whales: Primitive archaeoceti toothed whales (the Pakicetidae, Ambulocetidae) were first recorded from the Thanetian/Ypresian (Early Eocene), and with the first radiation and Remingtonocetidae which developed in the Early to Middle Eocene (**Figure 1**) [33-50]. During the early Middle Eocene (Lutetian) at least four whales (or groups) were present around the world, although again only in warm oceans, these being *Ambulocetus*, *Indicetus*, *Maiacetus* and *Aegyptocetus* [36-38,42,49]. Well known discoveries of *Basilosaurus* skeletons have been reported from Australia and Egypt, within marine sediments of Upper Eocene age [51-53]. Some “archaeocetid whale” bone fragments from Fürstenau [13] might represent the most northern records of these mammals (**Figure 1**), but more finds from Fürstenau must confirm this in future. The whale and megatooth shark distributions again overlap globally, both being present in shallow coastal shelf zones of the Tethys realm, and the northern southern hemisphere (**Figure 1**) [54,55]. Megatooth sharks (*O. subseratus*, and *O. sokolovi*, **Figure 2**) also coevolved with their largest whale/sirenian prey during the Thanetian and Lutetian (Late Paleocene to Early Eocene; **Figures 1 and 2**). The oldest record of their feeding on whale carcasses is evidenced by large shark bite marks on the thoracic region (ribs) of *Aegyptocetus tarfa*, a middle Eocene archaeocetid from Egypt [49]. Similar tooth marks on immature whales are also known from younger Pliocene strata [56], but these appear to have been produced by megatooth sharks, and not by white sharks as has previously been speculatively reported. Similar large bite damage also appears on Pliocene whale vertebrae from the east coast of North America [1]. Modern white sharks are known to have taken over the ecological niche of megatooth sharks, and to also scavenge on whales all around the world [25].

Dolphins with modern forms appeared as far as we know up to date during the Middle/Late Miocene (Serravalian/Tortonian) [42] and then spread around the

world (**Figure 1**). From the Miocene to the Pleistocene their main shark predators were *O. megalodon* (until its extinction in Pleistocene) and *C. carcharias*. In addition to these sharks, a separate evolution with secondary and not to the *C. carcharias* lineage developing tooth-serration development clearly took place within the *Isurus* lineage during this period, from *I. hastalis* to *I. escheri* (**Figure 2**) [17], which are not seen herein as the ancestors of the modern white sharks (being another serrulation process, different seen in [17]). The radiation of modern dolphins (3rd radiation of marine mammals, **Figure 2**) and other marine mammals was probably the motor behind the prey-related adaptations and tooth morphology changes in large scavengers on marine mammals. There is one fossil dolphin recorded as showing evidence of scavenging, in the form of large shark bite marks; this specimen is from the Pliocene of southern Europe [57].

3.6. Prey Migrations, Water Temperatures, and Shark Paleobiogeography

The new sieving of Middle Eocene material from northwest Germany yielded 2 teeth from the German megatooth shark *O. sokolovi* [10] (but more than 100 larger teeth are present from another collection of HF), supporting the theory, that megatooth sharks in general were occasionally present in colder oceans/waters and may have migrated through these upwelling and temperate basin areas [1]. The *O. sokolovi* megatooth sharks were far less abundant (2 teeth recovered) in the Eocene proto North Sea Basin than the *C. auriculatus* white sharks (455 teeth recovered) [10]. The megatooth sharks may have followed large, migratory mammal prey such as whales and sirenians, which are likely to have made use of the seasonal warm surface-water currents of the Tethys for north- and east-westward migration (**Figure 1**). Further support for this theory can be found in the same region, but from the Late Oligocene. The northern German Doberg fauna contains remains of the toothed whale *Eosqualodon*, as well as remains of the siren *Anomotherium* [31] and the large teeth from its megatooth shark predator *O. angustidens* [13], but white shark teeth are unknown in the Late Oligocene of northern Germany, yet, also because there are shark-tooth enriched condensation bonebeds absent (teeth are “rare”). Thus the abundant white shark *C. auriculatus* must have lived in cold-water areas of upwelling, as demonstrated in the Proto North Sea Basin [10]. This temperature control on the distribution of these predatory sharks has also been recorded in more recent periods (extending from the Oligocene to the Pliocene) all around the world [1]. There is a clear correlation in the fossil record between the scarcity of both, megatooth shark ancestors and their prey (whales and sirenians) [1] in areas of cold water upwelling, and the abundance of white sharks, together with seals in some

of those areas [1], such as demonstrated herein for the Proto North Sea basin of Europe.

4. RESULTS

The early white shark *Carcharodon auriculatus* and the megatooth shark *Otodus sokolovi* were both present in the European proto North Sea Basin about 47.8 - 41.3 m.y. ago (Lutetian, early Middle Eocene), as well as in the Tethys realm only around the world. At the same time, early seals may have been common in cold waters, and remains of a few rare early warm water adapted sirenians and basal toothed whales are known from the sandy beach areas and shelf regions of the proto North Sea Basin, which had primary cold water temperatures and was influenced by upwellings but was also subject to the periodic influence of warm surface waters from the Tethys realm.

The new excavated serrated teeth presented from the German Eocene (Lutetian) are not of one species, nor do they only represent different individual ages of one species. Compared to modern white shark ontogenetic tooth morphology stages, the juvenile teeth in white sharks are much more coarsely serrated first, and the later are more densely—which is studied in the fossil record only for the fossil Palaeocene white shark forms partly. Another and most important character is the root form, massive-thick in *Otodus* and thin-flattened in *Carcharodon* (anterior teeth that are intermediate and more difficult to separate)—a main character, that distinguishes the similar serrated teeth (especially lateral ones) of grown up individuals in several cases, and which ontogenetic stages of Eocene species remain unclear. These similar looking serrated teeth exactly confused their separation in the past, but their maximum size in each genus also differs much being nearly twice large in Eocene *Otodus* with up to 8 cm height teeth fitting to the known general body sizes of white and megatooth sharks finally.

The two types of giant sharks, which were the main predators along these coastlines, were polyphyletic with two different lamnid shark ancestors within the Early Paleocene to Early Eocene time-span, which are *Carcharodon* (*Isurus*—white shark lineage) and *Otodus* (*Lamna*—megatooth shark lineage). Both, megatooth and white shark lineages exhibited convergent serrated saw-blade teeth, but with different (massive or non-massive) roots in the lateral teeth, different dental formulas, and different maximal sizes. The “saw-blade” teeth were the result of adaptation to feeding on various marine mammals, and their development coinciding with the emergence of seals, sirenians, and whales in parallel with the evolution of these large predatory sharks during the Late Paleocene to Early Eocene.

Megatooth sharks specialized in hunting whales and sirenians on the coastal shelves of warm oceans, but also migrated with warm surface currents into northern areas

of upwelling in which fishes were abundant, which has been shown from the northernmost records of the Proto North Sea Basin shelf, in northern Europe.

The white sharks, however, were adapted to cold and temperate waters. While the immature white sharks may have hunted in fish-rich areas, the adult sharks must have fed mainly on the early seal populations, along the coasts

lines of their reproduction beaches which also appear to have been located in cool to temperate waters (southern proto North Sea Basin). This specialization of white sharks in hunting seals, especially in the vicinity of seal colonies, has continued to the present, for example with the great white sharks hunting seals along the Californian and South African coastlines (**Figure 6**).

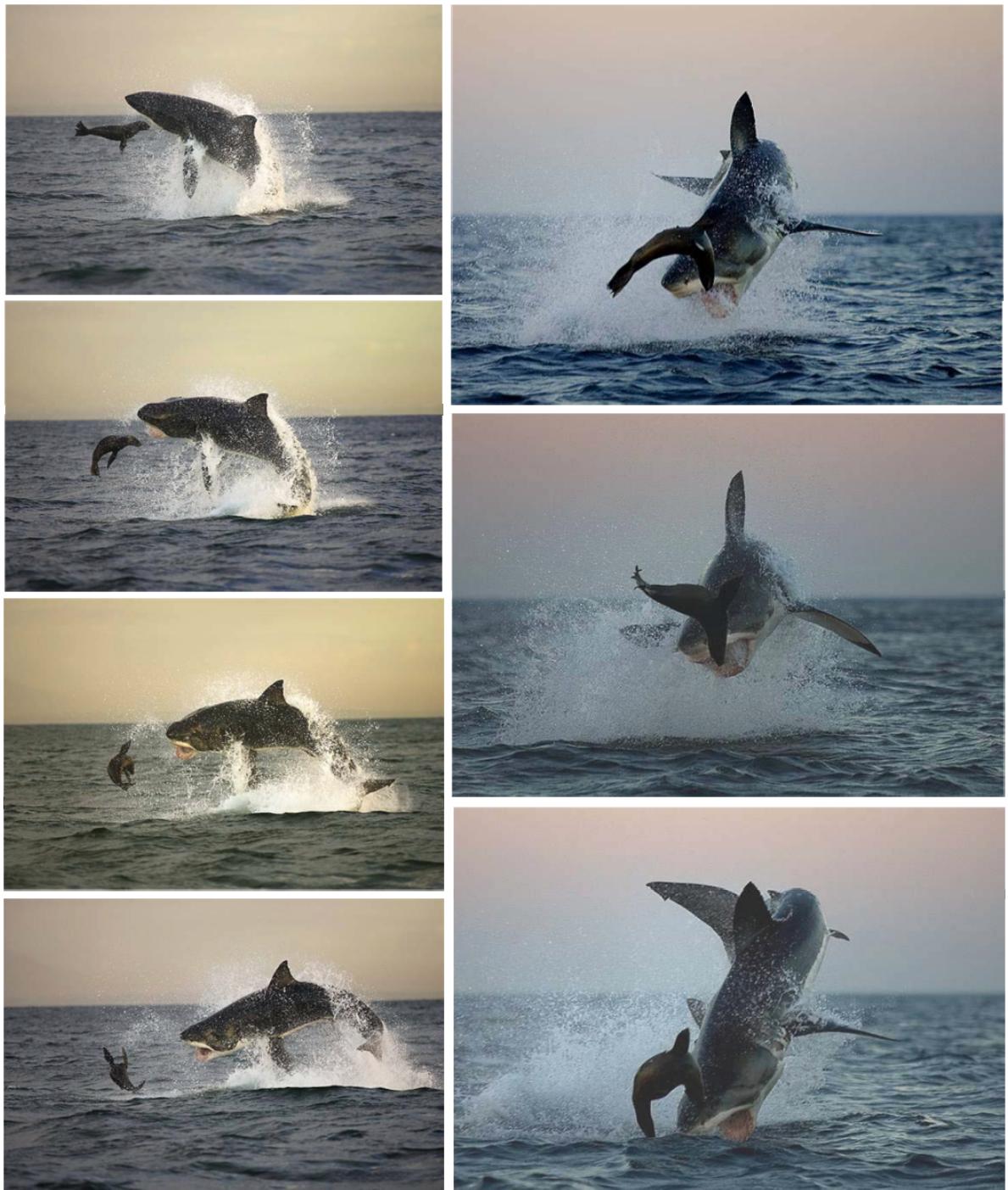


Figure 6. Photographic sequences of a modern white shark *Carcharodon carcharias* hunting a cape fur seal *Arctocephalus pusillus* in warm waters along the South African coast (Photos C. & M. Fallows).

With a second marine mammal radiation in the mid-Oligocene and a third radiation during the Middle Miocene, the tooth morphology of megatooth sharks and white sharks developed further, with both lineages again showing similar types of adaptation. The lateral tooth cusplets became smaller, while oppositely the crown base widened and even the overall tooth size enlarged (= “saw blade type”), but this development was much more marked in the megatooth sharks, as they grew in size proportional to their large whale prey during the Neogene, during which time whales became larger, marine mammals radiated once again, and the modern dolphins emerged (in the Serravallian/Tortonian of the Middle/Late Miocene). In parallel with the third marine mammal radiation, a secondary serration evolution again took place again in “short-term” within the *Isurus* lineage (from *I. hastalis* to *I. escheri*), which later became extinct at the beginning of the Pleistocene “Ice Age”, as did the megatooth sharks.

Whereas the warm-water adapted megatooth sharks disappeared globally in the Pleistocene due to climate change and ocean cooling, the cold-water adapted white sharks have survived more than 57 m.y. until the present day as specialized coastal seal hunters. Adult great white sharks today feed on modern seals in temperate to warm seawaters, indicating that they must have modified their habitat during the Ice Age, and even their body temperatures, to take over the niche vacated by the extinction of the megatooth sharks. Mature individuals now also feed on whales and sirenians but still predominantly on seals, as they have started to feed on a new marine mammal prey source for more than 50 million years.

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