

The most northerly record of the sirenian *Protosiren* and the possible polyphyletic evolution of manatees and dugongs

Cajus G. Diedrich

Paleologic, Petra Bezruce 96, Zdice, Czech Republic; cdiedri@gmx.net, www.paleologic.eu

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ABSTRACT

Newly discovered remains of the early Middle Eocene (Lutetian) sirenian *Protosiren* (Protosirenidae) in shark tooth rich conglomerates from a coastal delta environment northwest of the European Rhenish Massif at Fürstenau (north-western Germany), represent the most northerly occurrence of this genus whose global distribution was generally restricted to warm waters. Its presence of the remains so far north can be explained by seasonal inflow of warm Tethys surface water into the cool, upwelling-influenced, basin. The existence of two discrete centers of sirenian evolution can be explained by the opening of the Atlantic and the upwelling that separated the North American warm water faunal province from those of Africa and Eurasia. A slightly modified evolutionary model is presented in which the oldest Early Eocene manatee sirenians evolved in the Caribbean of Central America. *Protosiren*, however, appears to have developed polyphyletically along the African coastline of the Tethys, and represents the oldest known dugong ancestor. Younger (Oligocene) European sirenian skeletons of *Halitherium* and *Anomotherium* are included in the phylostratigraphic model in which sirenians had generally reduced their teeth by 28 Ma as an adaptation for feeding on sea-plants (macroalgae/seagrass). Teeth from early megatooth sharks, which preyed on sirenians, have been recorded from shallow marine Eocene and Oligocene coastlines of the southern proto-North Sea Basin, and shark bite marks have been found on sirenian skeletons.

Keywords: Sirenian Remains; Early Middle Eocene;

Palaeobiogeography; Oldest Sirenians of the Proto-North Sea Basin of Central Europe

1. INTRODUCTION

Extant manatees and dugongs, together with the recently extinct Steller's seacow, are three distinct types of modern sirenian [1] that have their earliest origins in the Late Palaeocene to Early Eocene (**Figure 1**) [2-4]. The most primitive skeletons of quadrupedal sirenians (Ypresian, Early Eocene) ever found in the shallow marine palaeoenvironments of the Middle American Caribbean are of the primitive *Prorastomus* and the slightly more evolved *Pezosiren* (**Figure 1**) [5]. The global fossil record for sirenians in the Eocene is much poorer, as it is also in the Oligocene and Miocene [1], and therefore new discoveries, especially well dated material in a biodiverse and palaeoecological context, are important to our understanding of the evolution and life of the basal sirenians.

Early Middle Eocene (Lutetian) sirenian remains from the new sirenian locality at Dalum, near Fürstenau (north-western Germany, **Figure 2**) are also considered herein. The shallow coastal and slightly carbonatic Eocene sands at this locality have been bioturbated by crustaceans and are interrupted by a transgressive conglomerate bed in which phosphorite nodules and vertebrate remains are concentrated [6]. Those conglomerates within the Fürstenau Formation are extraordinarily rich in shark teeth, and also contain coprolites from several different sharks, including megatooth and white shark forms [6-8]. The rich shark biodiversity, which includes about 15 species with tooth sizes larger than 5 mm, also includes more rare large, serrated teeth up to eight centimetres from the megatooth *Otodus* and teeth up to four centimetres from the white shark *Carcharodon* [8]. The relationship between megatooth sharks and their first

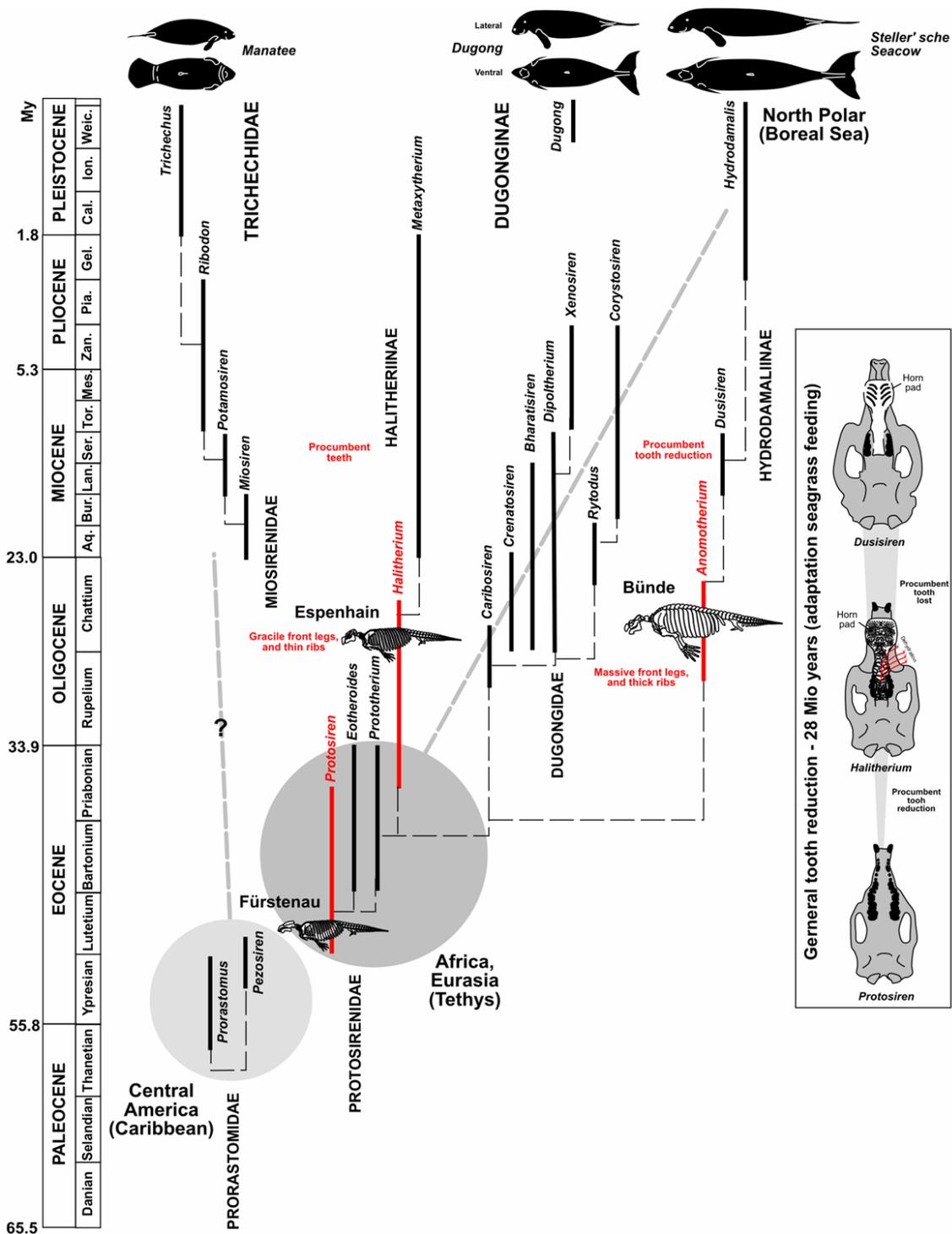


Figure 1. Polyphyletic model of sirenian evolution. General tooth reduction took place as an adaptation for feeding on sea-plants (with the greatest reduction occurring already in *Dusisiren* of the Hydrodamalinae). Northern German Proto-North Sea Basin records are marked in red, after [5-37,34-48]. The relative position of *Anomotherium* has been altered and the ancestral connection for the Trichechidae remains open. Sirenians may have coevolved, with convergent marine adaptation, in two different parts of the world.

marine mammal prey (Figure 3) has been recently discussed in detail with respect to their coevolution [8]. Megatooth sharks as extinct top predators on sirenians

are also discussed herein for the Oligocene of Germany, to explain their coincident appearances as fossils in many warm water palaeoenvironments around the world [8,9].

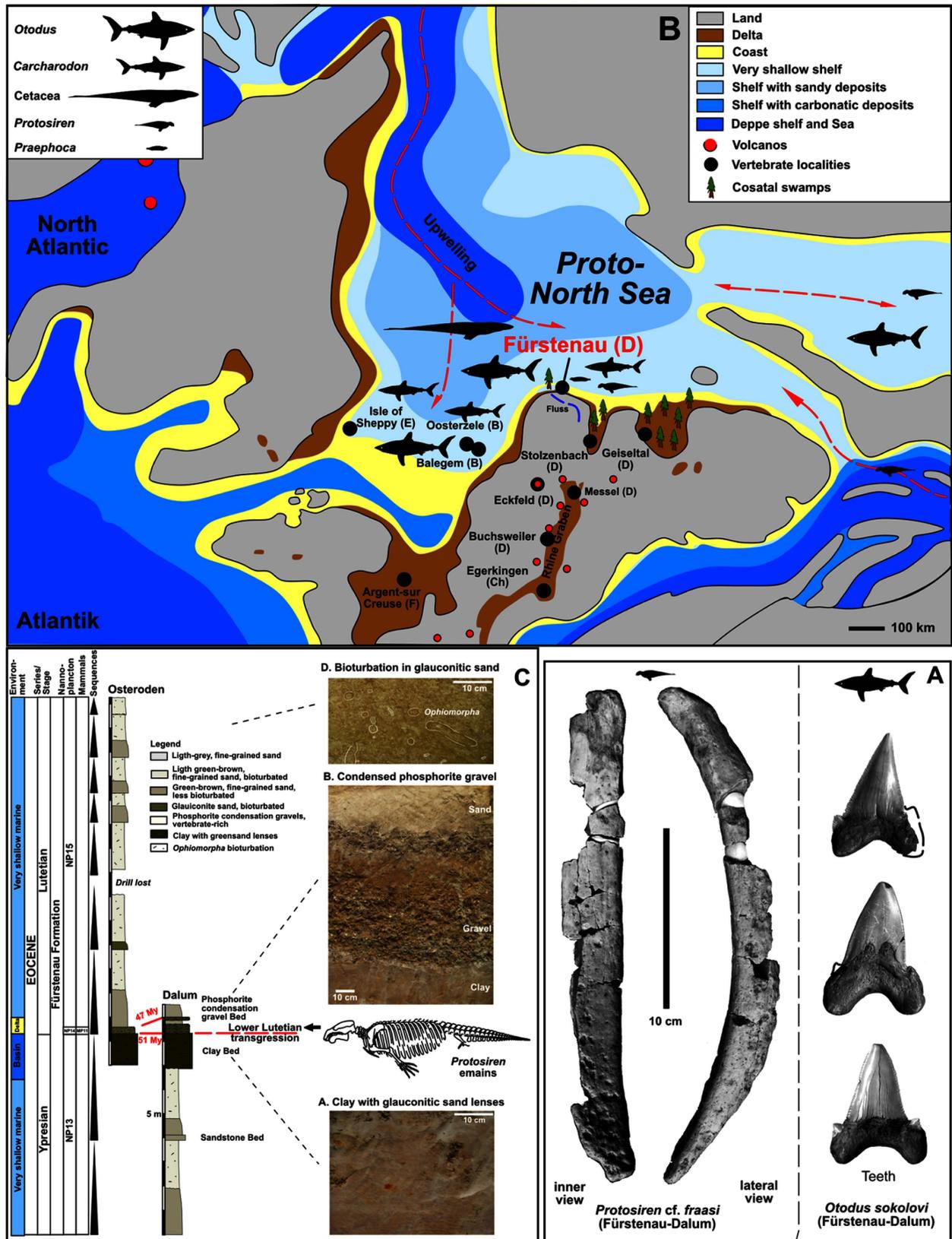
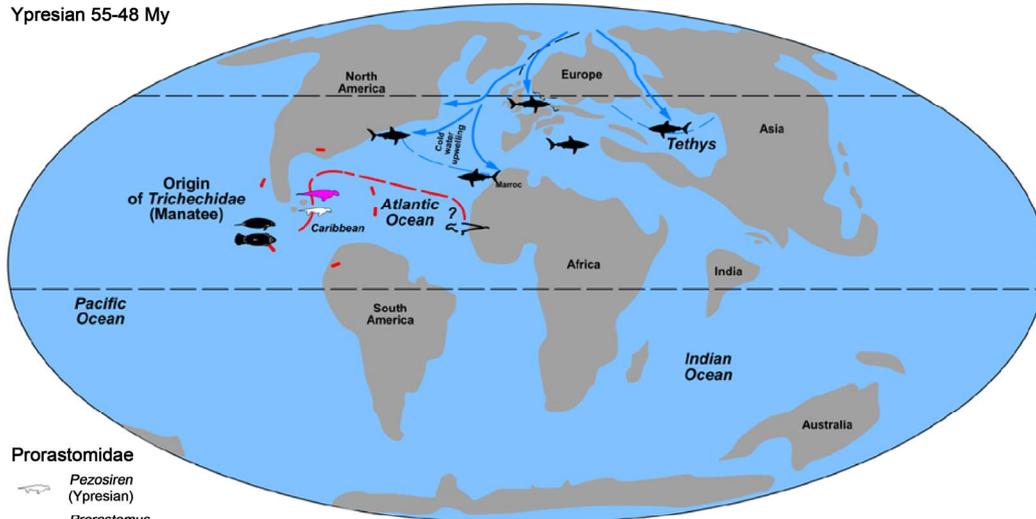


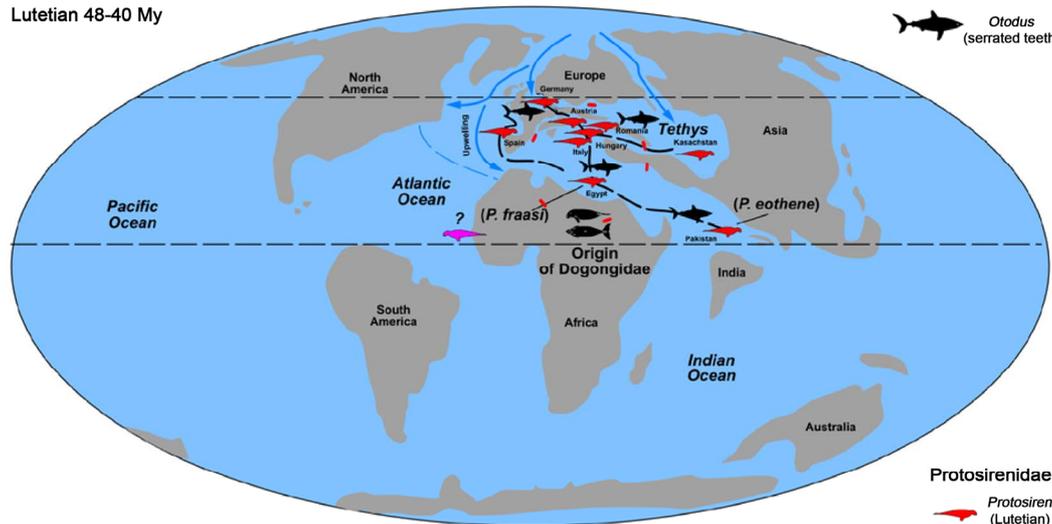
Figure 2. (A) Newly discovered and most northerly record of *Protosiren* (rib), and large teeth of *Otodus* megatooth sharks (all coll. HF), from the north-western German site at Fürstenau. (B) Map after [6]. (C) Stratigraphic position of the sirenian and shark-rich vertebrate conglomerate layer at the two Fürstenau sites.

Ypresian 55-48 My



Prorastomidae
 Pezosiren (Ypresian)
 Prorastomus (Ypresian-Lutetian)

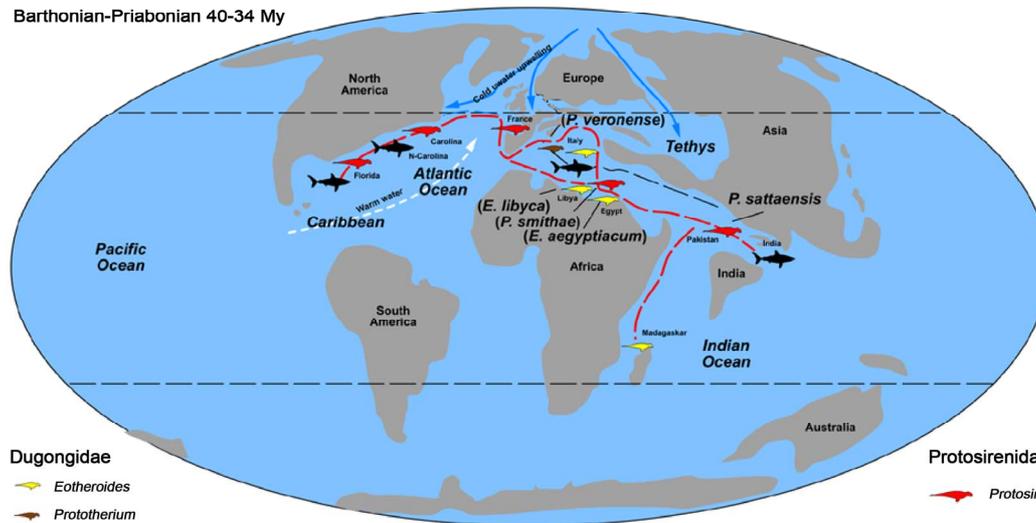
Lutetian 48-40 My



Megatooth sharks
 Otodus (serrated teeth)

Protosirenidae
 Protosiren (Lutetian)

Barthonian-Priabonian 40-34 My



Dugongidae
 Eotheroides
 Prototherium

Protosirenidae
 Protosiren

Figure 3. Global paleobiogeography of Eocene sirenians, which was dependent on the distribution of warm waters and on ocean upwelling (after [6-40,47,48]), with the *Protosiren* genus having the widest range. The distribution of the sirenians overlapped with that of the early megatooth shark *Otodus* [8].

A small number of Tertiary sirenian fossils have been described from central Europe, from the proto-North Sea Basin [10-14]. Three different Paleogene (Eocene to Oligocene) genera from northern Germany are reviewed herein: *Protosiren* (Middle Eocene, single bones), *Halitherium* (lower/basal Upper Oligocene, several skeletons), and *Anomotherium* (Upper Oligocene, two skeletons) from the proto-North Sea Basin are placed within the cladistic models based on former descriptions [1-5]. An extended model of sirenian evolution that includes a phylostratigraphic and possibly polyphyletic evolution of manatees and dugongs is presented, reviewing most of the known important global material and including new Eocene (Lutetian) fossil remains from northern Germany (**Figure 2**). These most northern global records of the *Protosiren* genus are also significant in the reconstruction of ancient, climate-influenced palaeocurrents (e.g., cold upwellings and warm surface currents), and of global paleobiogeography.

2. MATERIAL AND METHODS

About 250,000 shark teeth, 12,000 fish otoliths, some terrestrial mammal teeth, marine seal remains, shark coprolites, teleostean fish remains, and invertebrate fossils have been collected by H. Felker (**HF**) from two Eocene fossil sites at Bippen and Dalum, near Fürstenau (**Figure 2**), over the past 30 years. This collection has now been examined for marine mammal remains. About 60 higher vertebrate bone fragments are present, including some mosasaur remains reworked from Upper Cretaceous horizons, making small fragments difficult to determine macroscopically using only their osteological morphology. The sirenian material from Dalum is represented by at least one almost complete sirenian rib (**Figure 1**), a few other rib fragments, and a possible vertebral neural arch fragment. Possible whale remains are also present but these bone fragments, especially the vertebra fragments, can as yet not be firmly distinguish from those of sirenians. The cross sections of the fractured sirenian ribs were examined in order to verify that they were pachyostotic ribs, with concentric growth rings. The material was then compared with a *Protosiren fraasi* skeleton from the Stuttgart State Museum for Natural History (**SMNS**), with skeletons or bones (from younger Oligocene horizons) of *Halitherium schinzii* from the Senckenberg Museum in Frankfurt (**SMF**), and with *Anomotherium langewieschei* remains from the Dobergmuseum Geological Museum of Ostwestfalen-Lippe in Bünde (**DMB**). Megatooth shark teeth in the private collection of U. Beye (**UB**) are from Barleben, near Magdeburg. Finally, the teeth of predatorial megatooth sharks from Fürstenau and sirenian skeletons with evidence of shark-bites have also been included in these investigations in order to understand the relationships

between, and palaeobiogeographical distributions of, these predators and their prey.

Order Sirenia Illiger 1811

Family Protosirenidae Sickenberg 1934

Protosiren Abel 1907

Protosiren cf. *fraasi* Abel 1904

Material: One almost complete rib 27 cm long (**Figure 2**), some small rib fragments, and a possible vertebral neural arch fragment (**HF** collection).

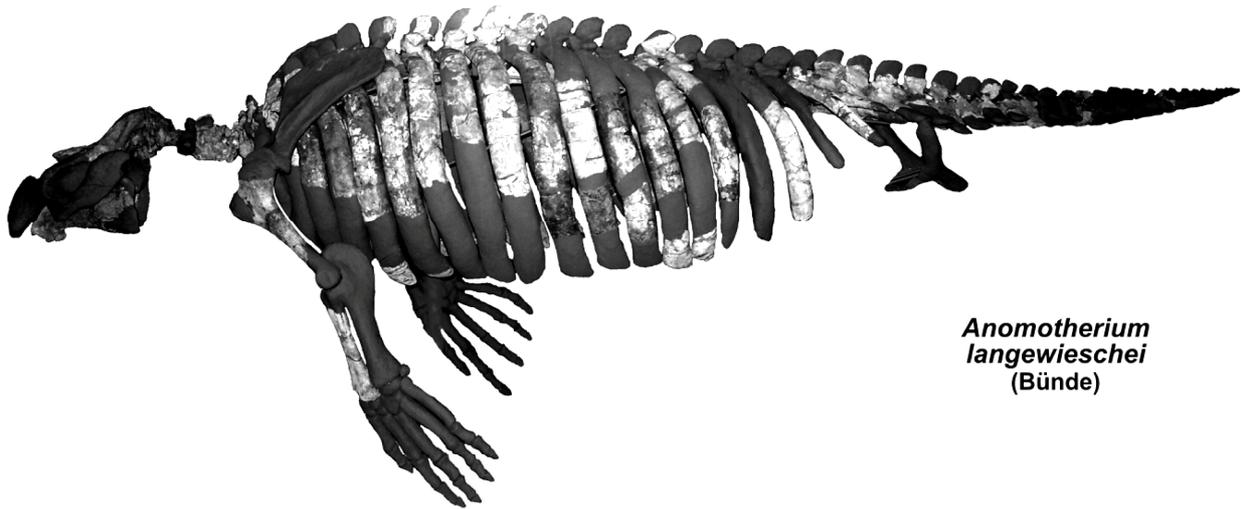
Comparison: Material from this genus is scarce and no complete skeletons are known. All material is therefore fragmentary, but several "species" of the Eocene *Protosiren* have been established in different parts of the world, such as *P. eoethene* Zalmout *et al.* (2003) [15], *P. fraasi* Abel (1904) [16,17], *P. sattaensis* Gingerich *et al.* (1995) [18], *P. smithae* Domning and Gingerich (1994) [19], and *P. minima* Desmarest (1822) [15-17], which are clearly in need of global revision. The almost complete rib from Germany illustrated herein (**Figure 2**) is very similar in shape and cross section to a middle thoracic rib from *P. cf. fraasi* (**SMNS** 11090), which is of similar age, coming from the early Middle Eocene of Egypt [16], but the surface of the German rib has been corroded by ocean waters. The inner side of the pachyostotic rib is flattened, while the outer side is convex. The articular facet on the rib capitulum is relatively flat to concave, which is typical of *Protosiren* ribs [16-20]. Some other fragments are also from ribs, but the exact number of ribs is difficult to estimate for the freshly fractured material. A neural arch fragment is also possibly preserved, but it is too small to permit positive identification.

3. DISCUSSION

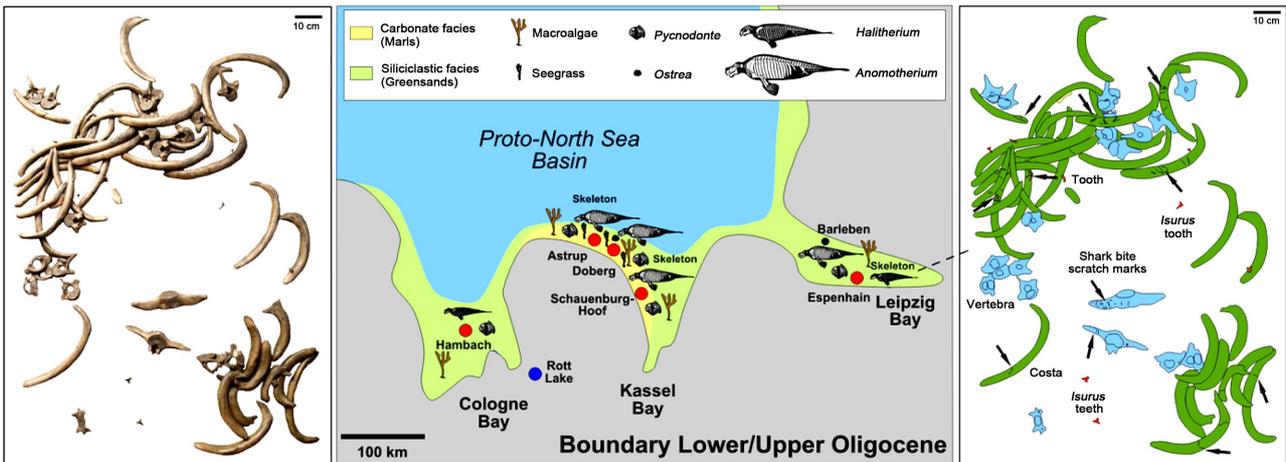
3.1. Sirenian Species during the Eocene

The substantial morphological diversity and global distribution of the Eocene sirenians *Prorastomus*, *Pezosiren*, *Protosiren*, *Eotheroides* and *Prototherium* (**Figures 1** and **3**) [1-5,15-41,47] suggests that they must have already evolved from terrestrial mammals by the late Paleocene [1-5].

Early Eocene (Ypresian): The oldest known sirenians are the Prorastomidae, of Early Eocene age. *Prorastomus sirenooides* Owen, 1855 and *Pezosiren portelli* Domning, 2011, in the late Ypresian/early Lutetian, are still primitive and quadrupedal, with fully developed legs. Both have been recorded from Jamaica, in the Caribbean [1,5] (**Figures 1** and **3**). If the newest described remain from Senegal (*Prorastomidae* indet.) [47] does not belong into this time-frame must remain unclear, because this strongly damaged vertebra could also have been reworked marine from older layers. It would then, indicate the exchange between Caribbean and West-African populations (cf. **Figure 3**).



Anomotherium langewieschei
(Bünde)



Halitherium schinzii
(Espenhain)



Halitherium schinzii
(Eckelsheim)

Otodus angustidens

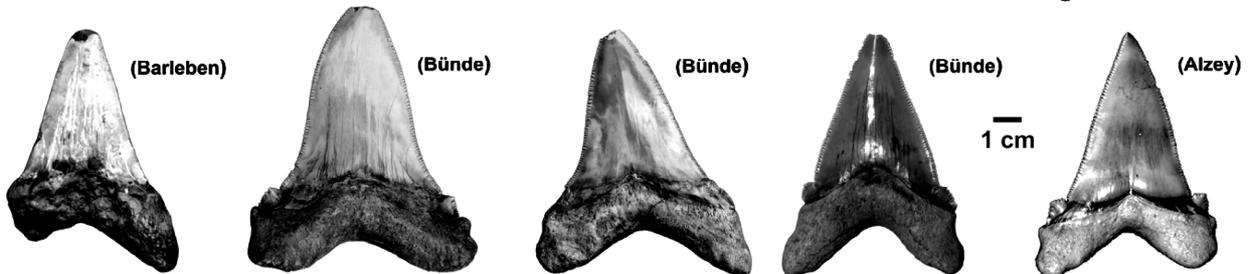


Figure 4. Sirenian species from the Lower/Upper Oligocene boundary of the proto-North Sea Basin and a *Halitherium* skeleton with large shark bite marks on many ribs and vertebrae (after [14]). *Anomotherium* skeleton (in DMB), *Halitherium* skeleton (in SMF). Large serrated teeth from the megatooth shark *Otodus angustidens*, from the German Oligocene (teeth in DMB, HB, UB, and PMN).

Early Middle Eocene (Lutetian): The best-preserved and most abundant sirenian specimens with a similar age to the Fürstenau material are the Protosirenidae from Egypt (*Protosiren fraasi*) [16,18,34], and Pakistan (*Protosiren eoethene*) [15,37] (**Figures 1 and 3**). Most of the material from Hungary, Germany, and Spain, as well as that from Kazakhstan, should probably be attributed to *P. fraasi* Abel, 1904 [16-17,19,23]. There may have been only a single species distributed throughout the Tethys (**Figure 3**), but the fossil record is sparse and fragmentary.

Upper Middle Eocene to lower Late Eocene (Bartonian): The protosiren *P. sattaensis*, which is represented mainly by ribs and a small quantity of other Protosirenidae material found along the east coast of North America (Carolina, Florida), and which has also been suggested from Pakistan (**Figures 1 and 3**), has been accurately dated from the North American discoveries [27]. Other protosiren remains from *P. smithae* have been reported from Egypt [19]. The possible *P. minima* remains from France are problematic as far as species identification and dating are concerned. Two other Dugongidae genera also developed during the Bartonian, these being *Eotheroides* [1,21], which has been found along the northern coastline of Africa [37,42], and *Eosiren* Andrews 1902, which is from the Late Eocene (Bartonian to Priabonian) (**Figures 1 and 3**) [1].

Late Eocene (Priabonian): The dugongid *Prototherium veronense* de Zigno, 1875 has been found in Italy [28] and ranged from the upper Middle to the Late Eocene (**Figures 1 and 3**). The *E. libyca* Andrews, 1902 has been recorded from the Late Eocene of Egypt [42] (**Figures 1 and 3**).

3.2. Origin, Palaeobiogeography and Habitat of Early European Sirenians

The distribution of early sirenians is related to that of warm ocean waters with seagrass meadows [1,2,4,14]. These aquatic mammals may have had polyphyletic development from two separate centers (**Figure 3**). Classical models [1-5] describe an origin in the warm shallow waters of Central America [5], and a subsequent dispersal to Eurasia. The palaeoceanography of the Early Eocene (Ypresian), however, indicates that the opening of the North Atlantic resulted in massive upwellings of cold, arctic bottom currents, which are likely to have inhibited any such migration.

These upwellings extended not only into the proto-North Sea Basin, but also as far south as north-western Morocco, where the absence of any sirenian remains in shark-rich phosphatic bonebeds lends support to the idea that the upwellings presented a barrier to sirenian migration (**Figure 3**). The modern Trichechidae and Dugongi-

dae are therefore more likely to have had different origins and ancestors (**Figures 1 and 3**), one in the Caribbean, and the other in the very different habitat provided by the shallow, warm, marine waters off northern Africa (**Figure 3**). The monophyletic model is based on classical monophyly [1-5], but the “evolution of the sirenians” presented herein is a little different (**Figures 1 and 3**), bringing together all of the data, and leaving open any gaps in the fossil record or unclear phylogenetic relationships between families and subfamilies.

The Middle Eocene *Protosiren* (Protosirenidae) is believed herein to be known after reviewing the descriptions and figures of single finds in the Lutetian from Italy, Spain [26], Hungary [16], Romania [32], Egypt [17,19], Kazakhstan, and Pakistan [15-40], and now also from Germany. These early sirenians have recently been recorded from along the equator and further north in the Tethys, the northern Indian Ocean, the proto-North Sea Basin, and the western coastlines of the already opened North Atlantic (**Figure 3**) [15-40], but they always appear to have been in shallow marine habitats of warm oceans, or in areas influenced by warm surface waters. The remains from the proto-North Sea Basin, which are the most northerly sirenian record for that time, are from a slightly different environment from other discoveries in that this was primarily a cold shallow marine basin, influenced by upwelling (**Figure 2(B)**) [6].

Periodic influxes of warm surface waters from the Tethys are, however, clearly documented by the presence of the remains of sirenians, whales, and megatooth sharks (**Figure 2**) [8], that must have come into the area from the east or southeast, at least during the Lutetian (**Figure 3**).

The early Lutetian *Protosiren* appears from the recently discovered fossil record not to have originated in Central America, but from the coastline of northern Africa [1,27], as is also the case for the Early Eocene primitive quadrupedal sirenians (ancestors of Trichechidae). Their distribution appears to have been clearly restricted by the cold water upwelling, which had already started in the Paleocene. The North Atlantic therefore would have been a barrier to dispersal, which would also explain another polyphyletic development—the emergence of the Dugongidae in Eurasian coastal Tethys habitats (**Figures 1 and 3**). These did not arrive on the east coast of North America before the Bartonian [1,27], which would again appear to support an origin in Eurasia (**Figures 1 and 3**). Their original habitat was more likely to have been along the more gently sloping coastlines covered with seagrass (and possibly also macroalgae) that had already become the main food source for sirenians during the Eocene [1-5,14,45]. Adaptation to feeding on seagrass caused a general tooth reduction in sirenians between the Eocene and the Pliocene (**Figure 1**). Com-

plete incisor, premolar, and anterior molar tooth reduction occurred within the Trichechidae and the Dugonginae, but the greatest reduction (including the anterior procumbent teeth) occurring in the Hydrodamalinae (**Figure 1**). Further support for a polyphyletic development is provided by the major sirenian radiation in Eurasia (**Figures 1** and **3**). Within the Bartonian, the Dugongidae *Eotheroides* and *Prototherium* developed on the shallow marine shelves of northern Africa, and in the Tethys area in general (**Figure 3**), as did the Protosireniidae (a little later) which are believed to have been distant non-ancestors of modern Dugongs [1-5].

3.3. Younger Sirenian Records from the Proto-North Sea Basin

Focusing only on the proto-North Sea Basin of central Europe, Miosireniidae and Halitheriinae are now known from horizons of various ages (**Figure 2**), which include the Early to lower Late Oligocene *Halitherium schinzii* Kaup, 1838 [10,11,44] (also distributed in the Cologne and Leipzig bays, in northern Germany at Doberg, in the Molasse Basin, and in the Rhine Graben: **Figure 4** [14, 46]), and the large Upper Oligocene form *Anomotherium langewieschei* Siegfried, 1965 [12,14] (only recorded in the southern proto-North Sea Basin, **Figure 4**, with two skeletons found near Bünde [14] and Schaumburg-Hof [13,14]).

The *Anomotherium* discoveries coincide with the distribution of a carbonate facies in which indirect evidence for macroalgae and seagrass is provided by the xenomorphic attachment surfaces of various oysters [14,45] (**Figure 4**).

The new phylogenetic position suggested herein for *Anomotherium* within the evolutionary model is a preliminary step based on characteristics such as the extremely massive thickened ribs, which are 6 - 8 cm in width (as typically seen in hydrodamalines, and similar to those in *Hydrodamalis*). The much larger-proportioned and more massive forelegs in *Anomotherium* and *Hydrodamalis* (in contrast to the reduced forelegs of *Halitherium*; **Figure 4**) are also important. These postcranial skeleton characteristics allow the parallel-living *Anomotherium*/*Halitherium* genera to be separated from each other, especially in the proto-North Sea Basin [14]. This distinction is thus based on the large robust general habitus and body size, which in the case of *Anomotherium* is close to that of the Steller's seacow (*Hydrodamalis*). Cranial characteristics can not be used due to the high degree of damage to the skull: the presence or absence of procumbent teeth would help to position *Anomotherium* more accurately within the systematics, which are mainly based on cranial characteristics. However, the systematic position will need to be revised in the future using the two known *Anomotherium* skeletons

from Germany. The holotype is currently spread over three collections and many bone fragments have not yet been included in the skeleton but are still in boxes: the reassembled skeleton presented herein in **Figure 4** is therefore not fully representative of the holotype skeleton. Finally, the palaeobiogeography of *Anomotherium*, which is only present globally in the northern proto-North Sea Basin, seems to suggest a large sirenian already adapted to seagrass feeding and temperate waters—a habitat that was already occupied by the hydrodamalines.

3.4. The Sirenians' Predators

The megatooth shark ancestor *Otodus sokolovi* was already present in the Middle Eocene as a large form (with teeth up to 8 cm long, **Figure 2(A)**), indicating the parallel evolution of these large sharks with their main prey, the whales and sirenians [8]. Several large teeth have also been found at Fürstenau, suggesting a spatial correlation with their prey, the sirenians (and probably whales) [8], and also reflecting their presence in warm waters only.

The same spatial correlation can also be reported from the Upper Oligocene horizons in the proto-North Sea Basin, where toothed whales (*Eosqualodon*) and sirenians (*Anomotherium*) again appear together with megatooth shark remains, but in this case from the more highly evolved *Otodus angustidens* (**Figure 4**) [8,14]. The bite marks that are commonly found on the ribs and vertebrae of *Halitherium* (**Figure 4**) and other sirenians [14,46] indicate that they were scavenged, and possibly preyed upon, by large sharks. In contrast, the smaller white shark ancestor *Carcharodon auriculatus*, from which some thousands of teeth have been found in the Middle Eocene gravels at Fürstenau, was adapted to cold water, as were its main prey, the seals [8].

4. RESULTS

Early Eocene (Ypresian) sirenians (the world's oldest sirenians) appear to have already developed in the Caribbean by the Late Paleocene (Thanetian), in tropical shallow coastal waters and freshwater river environments. Two different sirenian genera, *Pezosiren* and *Prorastomus*, which are known from "New World" skeletons, did possibly not spread over the Atlantic to the "Old World", because the continents were separated by cold upwelling currents in the northern Atlantic. These quadrupedal basal sirenian forms are likely to have been the ancestors of the modern manatees (and their predecessors), which have a similar geographical distribution and also live in coastal brackish and freshwater environments. The relationship between the oldest sirenians and the manatees remains unresolved and the phylostratigraphic model is

therefore not yet complete.

The newly discovered marine Middle Eocene (Lutetian) sirenians (including *Protosiren*), which may have had a polyphyletic development, appear to have been evolved on the shallow marine coastlines of the Tethys, such as along northern Africa, or between Eurasia and India. The most northern discoveries (from Germany, in the proto-North Sea Basin) resulted from seasonal variations between warm surface waters of the Tethys and cold upwelling currents from the North Atlantic that were responsible for a rich fish fauna and the presence of three types of mammal: seals, sirenians, and whales. The Protosirenidae are seen herein to appear to be possible polyphyletic or even “ancestors” of the Dugongidae (**Figure 1**), which was seen different by other authors.

Within this lineage, it is placed herein as the massive European Oligocene form *Anomotherium* from the proto-North Sea Basin, which has only been recorded from temperate carbonate seagrass-meadow environments. This little-reported form, which is only recorded from the northern hemisphere, is best placed on the basis of anatomy (from postcranial characteristics of massive, thickened ribs and large massive forelimbs) and palaeogeography within the Hydrodamalinae lineage, with its adaptation to temperate and cold waters. The tooth reduction and horny pad development started in the Eocene as an adaptation to feeding on seagrass/macroalgae, continued in tooth reduction by 28 Ma in the Oligocene, and is best evolved in the Hydrodamalinae; in contrast to the other forms, that the Hydrodamalinae-*Dusosiren* already had no procumbent teeth by the early Miocene (23 Ma).

The first indirect evidence of sirenians having been hunted by megatooth sharks is found in the Middle Eocene of north-western Germany, where they are both (occasionally) present in the same horizons. The coincidental occurrence of both sirenians and megatooth sharks at several different locations around the globe in Paleogene to Neogene sediments also provides supporting evidence for early development of a predator-prey co-evolutionary relationship. The best examples of bite damage on ribs and vertebrae are found on skeletons of *Halitherium*, the most common Oligocene sirenian in Europe. Sirenians in general appear to have been hunted and killed (in a similar way to whales) by megatooth sharks (*Otodus*), but were also scavenged by other sharks (*Isurus*, and others).

5. ACKNOWLEDGEMENTS

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