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Review

A Review of the Palaeobiology of Some Neogene Sharks and the Fossil Record of Extant Shark Species

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Abstract: In the last years, new findings and new methods (stable isotopes of oxygen, zinc and nitrogen, 2D and 3D modelling, geometric morphometric analyses of the teeth) have enhanced our knowledge of the Neogene shark fauna and its palaeobiology. Several papers deal with the large *Otodus* (*Megselachus*) species, including the construction of a 3D model as well as insights into lifestyle and diet. In addition, skeletal remains of *Carcharias gustrowensis, Carcharodon hastalis, Keasius parvus* and a natural tooth set of *Carcharodon hubbelli* have been described in the last 13 years, and the dentition of the Neogene species *Carcharoides catticus, Megachasma applegatei* and *Parotodus benedenii* have been reconstructed. Stable isotope analyses of the teeth from the Neogene species of *Araloselachus*, *Carcharias*, *Carcharodon*, *Galeocerdo*, *Hemipristris*, and *Mitsukurina* have given insights into the trophic position of these genera during the Neogene, and shark teeth preserved near skeletal remains of prey animals (mammals) and shark bite traces on these remains provide direct evidence of trophic interactions. Tooth shape, fossil locality and palaeoenvironment have been used to better understand the taxa *Carcharhinus dicelmai, Megalolamna paradoxodon, Pachyscyllium dachiardii* and *P. distans.* Among extant species, *Galeorhinus galeus* can be traced back to the Eocene. The following taxa can be traced back to the Oligocene: ?*Alopias superciliosus,* and *Rhincodon typus.* Species already present in the Miocene include: *Alopias vulpinus*, *Carcharhinus amblyrhynchoides*, C. *amblyrhynchos, C. albimarginatus, C. amboinensis, C. brachyurus, C. brevipinna, C. falciformis, C. glaucus, C. leucas, C. limbatus, C. longimanus, C. macloti, C. obscurus, C. perezi, C. sealei,* ?*Carcharodon carcharias, Centrophorus granulosus, Cetorhinus maximus, Dalatias licha, Deania calcea, Galeocerdo cuvier, , Glyphis glyphis, Heptranchias perlo, Isurus paucus, Lamna nasus, Negaprion brevirostris, Odontaspis ferox, Pseudocarcharias kamoharai, Sphyrna media, S. mokarran*. First appearing in the Pliocene are: *Scymnodon ringens, Somniosus rostratus, Zameus squamulosus*. For some extant species (*Carcharias taurus, Hexanchus griseus, Isurus oxyrinchus, Notorynchus cepedianus, Sphyrna zygaena)* it is not clear if the assigned Neogene teeth represent the same species. Applying these new methods to more fossil shark taxa, a detailed search for shark fossils, as well as better knowledge of the dentition of extant species (especially those with minute-sized teeth) will further enhance knowledge of the evolution and palaeobiology of sharks.

Keywords: Neogene; teeth; fossil; Miocene; Pliocene

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1. Introduction

The earliest record of elasmobranch fishes is from isolated shark scales that date back to the late Ordovician period, about 455 million years ago (Motta et al. 2012). Apart from a different tooth shape, Palaeozoic sharks had a different anatomy than the "modern" sharks (Neoselachii), which are known since the beginning of the Mesozoic. The following differences were mentioned by Benton (2005): The jaws of neoselachians open more widely than in earlier forms because of greater mobility about the jaw joint and a highly kinetic palatoquadrate and hyomandibular. The notochord of is enclosed in, and constricted by, calcified cartilage vertebrae, whereas the primitive chondrichthyans had a simple notochordal sheath. The limb girdles in neoselachians are strengthened by fusion or firm connection in the midline, which allows more powerful muscle activity. The basal elements (the radials) in the paired fins are reduced and most of the fin is supported by flexible collagenous rods called ceratotrichia or actinotrichia. See also Cappetta (2012, pp. 84-89) for further details. The rise and diversification of the Neoselachii began in the Lower Triassic, and by the Neogene the shark fauna was similar to the Recent one. However, despite general similarities, the timing of appearance of extant morphospecies, extinction of some Paleogene-Neogene species, and potential trophic changes resulting from these origin and extinction dynamics can provide insights into the structure and occupancy of higher trophic levels in Recent oceans.

The cartilaginous skeleton of sharks is normally not preserved in the fossil record, making teeth the most abundant record of fossil sharks. Sharks replace their teeth continuously throughout their lifetime, and this high production of potential bioclasts makes fossil shark teeth the main vertebrate fossils in marine deposits of the Paleogene and Neogene. Therefore, the designation of species is mostly based on a few isolated teeth. In some cases, calcified vertebral centra can be found, as well as dermal denticles, fin spines, and gill rakers. Only under special environmental conditions (e.g., fast sedimentation, exclusion of oxygen), the skeleton or parts of it were fossilized. Accordingly, such finds are very rare. Examples can be found for example in Ehret et al. (2009; 2012); Hovestadt & Hovestadt-Euler (2010) and Hovestadt (2022).

The "classical" method to infer shark ecology from teeth is to look to extant relatives as analogues, as well as the shape of the teeth. Cappetta (2012) divided the different tooth shapes into eight adaptive dental types. In addition to tooth size and shape, the embedding sediment also gives indications of habitat preferences of Neogene sharks. In the last 20 to 30 years, new findings as well as new methods made it possible to get more detailed information on the palaeoecology of Neogene sharks. Recently, Bazzi et al. (2021) quantified the classical method by applying 2D geometric morphometrics to statistically discriminate diet based on tooth shape, and Cooper et al. (2023) determined variation in tooth morphology could be partitioned into seven key variables with which ecological roles in fossil sharks could be accurately assessed. Palaeobiology is probably best-documented for the most famous fossil shark *Otodus* (*Megaselachus*) *megalodon*, simply because there have been so many papers in the last year with this species as main subject. The aim of this paper is to provide a detailed overview of those Neogene shark species for more research was done, excluding taxa described from only one or a few teeth. Than it will be summarize what is known of the palaeobiology of this Neogene shark species, as well as to examine the Neogene (or sometimes earlier) first appearance of Recent species. The ordering of the orders and families are based on Cappetta (2012). Genera and species are arranged in alphabetical order within higher taxonomic groupings. Lastly, we provide an outlook on possible future developments concerning the research on fossil sharks. This work presents the current state of the art concerning the palaeobiology of Neogene sharks as well as the fossil record of extant species.

2. Methods used to infer the palaeobiology of fossil sharks

There are six methods commonly employed to reconstruct the palaeobiology of fossil sharks:

1. The "classical" method for inferring diet based on the teeth as mentioned above. More findings made it possible to reconstruct complete dentitions, and infer diet with greater accuracy. Complete dentitions, also called tooth sets (Welton & Farish 1993) are a more solid framework with which to reconstruct the diet of the sharks than only isolated teeth. According to these authors, there are three types of tooth sets: a) Natural tooth set: The jaw is preserved and all the teeth are on their original positions. This the best but also the rarest condition; b) An associated tooth set is one based on the teeth of an individual shark where the teeth were found displaced from their natural positions. This also rare and mostly associated with skeletal remains. See e.g. Hovestadt & Hovestadt-Euler (2010); c) An artificial tooth set can be constructed from a number of tooth types from one locality that are believed to belong to one species. The teeth probably come from different individuals. This is the main type of reconstruction.

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2. The rare discovery of preserved articulated or disarticulated skeletons or parts thereof, including body proportions, gastric contents, and data on reproductive biology (see e.g. Hovestadt 2022).

3. Bite marks on fossil bones (see e.g., Govender 2015), or shark teeth embedded next to the fossilized skeletal remnants of prey animals (see e.g. Kent 2018) can also be used to provide direct evidence of predation or scavenging.

4. Stable isotopes can be used to reconstruct trophic position; see Kast et al. 2022 and McCormack et al. 2022 for details on this method.

5. 2D or 3D computer modelling based on vertebral centra and morphometric comparisons with Recent sharks (see Cooper et al. 2020; 2022) can provide information on body size and tooth shape.

6. Shape and morphology of the placoid scales can be used to reconstruct swimming abilities (see Shimada et al. 2023).

3. Material and methods:

For this review, the literature were searched for information concerning the ecology and palaeobiology of Neogene shark species, and referral of fossil remains to extant species. Although this paper is about Neogene shark species, an earlier occurrence (Oligocene, Eocene) of some extant species is nevertheless also noted. An important source for the literature research was Pollerspöck & Straube (2023) as well as the reference lists of the cited papers. Recent species and their fossil record are described. In addition, when remarkable fossil information concerning the biology has been discovered, e.g. dietary shift, this is mentioned in the text. Otherwise, the reader is referred to the according literature for the biology of individual species, because details of the ecology of extant sharks have already been often published. For the individual Neogene shark species, one fossil tooth has been illustrated, or in the case of the extinct basking shark *Keasius parvus*, a gill raker. The latter species is known since the Oligocene (Palaeogene) and the mentioned raker is from this epoch simply because it was the best preserved one available to the authors. However, a complete preserved tooth was not available for every taxon. Extant species are not figured because photos of them can be found in nearly every scientific or coffee-table shark book.

Despite the large volume of research on fossil sharks during the last decades, there are unresolved questions and different opinions, especially concerning genus-level membership of some taxa. However, a discussion of the problems regarding Neogene taxa is beyond the scope of this paper, and is not relevant for this review. Details to this can be found in the cited literature.

4. Results

4.1. Extinct Neogene shark species

Lamniformes Berg, 1958
Mitsukurinidae Jordan, 1898
Mitsukurina lineata (Probst, 1879).

This is possibly the ancestor to the Recent *M. owstoni* Jordan, 1898. Teeth of the ancient *M. lineata* can be found in bathyal and neritic deposits from the Early and Middle Miocene in Europe and South Korea (Cappetta 2012; Yun 2021). δ^{66}Zn values for teeth from the Early Miocene of Baden-Württemberg, Germany show a lifestyle similar to that of *Pseudocarcharias kamoharai* (Matsubara, 1936) (see McCormack et al. 2022, Figure 2, as *P. rigida*). The latter species feeds on bony fishes, squids and shrimps (Compagno 1984) which is also the case for the Recent *M. owstoni* (Compagno 1984). Although *M. owstoni* is a mostly bathyal shark (Compagno 1984), the teeth of the ancient *M. lineata* have also been found in neritic deposits as mentioned above. The species possibly came in search for food to shallower waters or the sharks followed schools of fishes (Pfeil 1991). However, Compagno (1984) stated that the extant species rarely occurs in shallow water close inshore.

Odontaspididae Müller & Henle, 1839
Araloselachus cuspidatus (Agassiz, 1843)

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There are differing opinions if this species belongs to the genus *Carcharias* (see the extant *Carcharias taurus*) or to the extinct genus *Araloselachus* (Cappetta 2012; Hovestadt 2020; 2022). In the same way, its relationship to the species *Araloselachus vorax* (Le Hon, 1871), which had similar-shaped teeth is not yet resolved (see De Schutter 2011; Reinecke et al. 2011; Cappetta 2012; Kent 2018 and Hovestadt 2020). *Araloselachus cuspidatus* is known from Miocene neritic deposits of Europe, North America and central Asia (Cappetta 2012) as well as also from older deposits of Oligocene age (Reinecke et al. 2001; Hovestadt 2022). Its teeth are also very abundant. They have a grasping, odontaspid shape but with a broader crown and often larger size than *C. contortidens* or *C. taurus*. Following McCormack et al. (2022), δ^{66}Zn values indicate that *A. cuspidatus* was likely a higher trophic level piscivore than *M. lineata* and *Pseudocarcharias kamoharai* (*P. rigida* in McCormack et al. 2022, Figure 2), also supported by the larger tooth size of *A. cuspidatus*. Hovestadt (2022) illustrated and described a partial skeleton of *A. cuspidatus* including fetuses from the Oligocene of Germany. The author estimated a body length of c. 5 m for this specimen. Cannibalism among unborn pups of the extant *Carcharias taurus* is well known, so-called adelophagy or intrauterine cannibalism, which is characterized by larger pups preying on smaller ones (Compagno, 1984; Ebert et al., 2021; Hovestadt 2022). Following Hovestadt (2022), this might also exist in *A. cuspidatus* and could explain the large number of incomplete embryos recovered.

Carcharoides catticus (Philippi, 1846)

Two species of *Carcharoides* are known from the Neogene, *C. catticus* and *C. totuserratus* Ameghino, 1901. From the two species of this genus, an artificial tooth set was constructed by Reinecke et al. (2018, Figure 15) for *Carcharoides catticus* (Philippi, 1846). Based on the tooth morphology of *C. catticus*, Purdy et al. (2001) saw this species as a synonym of *Triaenodon obesus* (Rüppell, 1835). All the other authors dealing with this species (e.g. Reinecke et al. 2011; 2018) didn`t share this opinion and cited this species as *C. catticus*. At the moment, dried jaws or Recent teeth from *T. obesus* were not available to the authors for own comparisons, therefore the fossil teeth are treated here as *C. catticus*. The reconstruction of the dentition by Reinecke et al. (2018, Figure 15) shows similarities to the dentition of *Carcharias* and *Odontaspis*; therefore, a piscivorous diet can be also assumed for *C. catticus*. Reinecke et al. (2018) mentioned weak ontogenetic heterodonty for members of *Carcharoides*. The species *C. catticus* is already present by the Oligocene (Reinecke et al. (2018), and teeth can be found up to the Middle Miocene in neritic sediments of Europe and North America (Purdy et al. 2001; Reinecke et al. 2018). *C. totuserratus* is only known from South America.

Carchariidae Müller & Henle, 1838

Carcharias contortidens (Agassiz, 1843) (syn. *C. acutissima*) and *Carcharias gustrowensis* (Winkler, 1875)

Teeth similar in shape to those of the extant *Carcharias taurus* Rafinesque, 1810 can be found worldwide in Neogene neritic deposits. Teeth of this kind are the most abundant and often occur *en masse*. Historically, the Miocene teeth were identified as *C. contortidens*, but the relationship of this taxon to *C. taurus* is not completely clear (see Reinecke et al. 2011 for details). According teeth from the Early Pliocene were named as *C. taurus* (see Purdy et al. 2001; McCormack et al. 2022, Figure 2). One problem is that despite their abundance, the teeth are often not completely preserved and therefore important details (e.g., lateral cusplets) are often missing.

Another species with similar teeth is *Carcharias gustrowensis* (Winkler, 1875) (see Hovestadt & Hovestadt-Euler 2010, Figure 6; Figures 7.16-7.18), which existed from the Oligocene (Hovestadt & Hovestadt-Euler 2010) to at least the Lower Miocene (Reinecke et al. 2011; collection material). From the Oligocene of Baden-Württemberg, Germany, Hovestadt & Hovestadt-Euler (2010) described a partial skeleton of a gravid shark with eight fetuses along with a myliobatoid tail spine and a chimaeroid dorsal fin spine. Following these authors, the variation in length of the fin radials in *C. gustrowensis* resembles the pectoral fin skeleton of *Carcharias taurus.* The myliobatoid and chimaeroid spines are likely remains of prey that have pierced the skin or cartilage of the jaw area.

Based on δ^{66}Zn values, *Carcharias* teeth show relatively stable trophic levels and ecological niches through time and space (McCormack et al. 2022), so a similar lifestyle to that of the extant *C. taurus* can be assumed for *C. contortidens*. Details of the biology of *C. taurus* can be found in Ebert et al.

(2021). Today, this species is distributed in nearly all warm- and tropical waters apart from the eastern and central Pacific (Ebert et al. 2021). During the Miocene and part of the Pliocene, members of the genus *Carcharias*, (probably *C. taurus*) also occupied the western coast of South America, where today it is absent (Cione et al. 2007). These authors suggested that the local extinction of *Carcharias* was the consequence of a drop of global temperatures during the middle Pliocene and Pleistocene and the coeval drop in sea level that reduced the shelf area and therefore the suitable environments for this species. Due to the establishment of the Panamanian isthmus, a later migration of *C. taurus* from the north was not possible (Cione et al. 2007).

Lamnidae Müller & Henle, 1838

The *Carcharodon* complex:

The most recent systematic arrangement of tooth shape shows *Carcharodon hastalis* (Early Miocene-Pleistocene) as the oldest member of this genus, which leads to *Carcharodon hubbelli* (Late Miocene) and then to the extant species *Carcharodon carcharias* (Early Pliocene-Recent) (Ehret et al. 2009; 2012).

Carcharodon hastalis (Agassiz, 1838).

Teeth of this species are common worldwide from the Early Miocene to the Pleistocene in temperate to tropical neritic deposits (Cappetta 2012; Ebersole et al. 2017). The generic relationship of this species remains debated. There are also some uncertainties at the species level, with a narrower tooth morphotype as well as a broader one. Therefore, there is a discussion if two other "broad toothed" species (*C. plicatilis* and *C. xiphodon*) can be separated from the narrower shaped *C. hastalis* teeth (see Pfeil 1991; Purdy et al. 2001; Whitenack & Gottfried 2010; Ehret et al. 2012; Cione et al. 2012; Kent 2018). Following Ehret et al (2012), this morphological difference could represent sexual dimorphism or ontogenetic change. Assuming all the referred teeth belong to only one species, the maximum size would have been between 6 m and 7.6 m, with anterior teeth up to 8.1 cm in height (Purdy et al. 2001). Collareta et al. (2017b) documented a partially complete articulated skeleton of a juvenile *C. hastalis* including stomach contents from the Late Miocene of Peru. The total body length of the immature specimen was estimated at about 2.3-2.4 m. The Meckel`s cartilages are very similar to those of various extant Lamniformes (including *Carcharodon carcharias* and *Isurus* spp.). The teeth are distinctly more slender than the adult teeth of *C. hastalis*, in agreement with the pronounced ontogenetic heterodonty recognized in this species (Collareta et al. 2017). The stomach contents consist of fishes including the pilchard *Sardinops* sp. cf. *S. sagax*. It is possible that specimens with the narrow-toothed morphology had a piscivorous lifestyle, whereas the ones with the broader teeth had a diet primarily consisting of small-sized marine mammals (see also Collareta et al. 2017). In the Pisco Formation, sixteen teeth of *C. hastalis* were also found in close contact with a balaenopterid whale skeleton (Takakuwa 2014). Kent (2018) illustrated a tooth of *C. hastalis* from the Calvert Cliffs (USA) (Miocene, from 8 to 18 Ma) completely penetrated by a myliobatiform caudal spine early in its development. Bianucci et al. (2010) noted bite traces on a well-preserved fossil dolphin skeleton from the Pliocene of Italy. Most bite traces have been referred to a shark about 4 m long with unserrated teeth, attributed to *C. hastalis* based on shape and general disposition on the dolphin skeleton. Govender (2015) also described bite traces from *C. hastalis* on cetacean skeletons from the Zanclean (Early Pliocene) of South Africa. In contrast to the bite trace record, Kast et al. (2022) found similar $\delta^{15}N_{EB}$ values in Miocene-aged *C. hastalis* to those of Pliocene and extant *C. carcharias* but lower, more piscivore-like values in the Pliocene (see Kast et al. 2022, Figure 2). Congruently, $\delta^{66}Zn$ signals that *C. hastalis* from the Early Miocene of Malta had a higher trophic position than teeth from the Early Pliocene of North Carolina. However, conspecific teeth from the Miocene of Baden-Württemberg, Germany also indicated a lower trophic position, suggesting potentially that the regional availability of different prey types influenced diet (see McCormack et al. 2022, Figure 2). The same result is recovered for individuals of *Hemipristis serra* between the two Miocene localities; lending support to this hypothesis. However, another possibility is that the previously mentioned tooth morphotypes were driving trophic signal ("broad" or "narrow"). Based on collections material, it seems that only the narrower morphotype was present in the Early Miocene of Baden-Württemberg (see also Höltke et al. 2020, Pl. 4, Figures 3-8; Pl. 5, Figure 1). Reasons underlying the extinction of C. *hastalis* are unknown.

Carcharodon hubbelli Ehret, MacFadden, Jones, DeVries, Foster and Salas-Gismond, 2012

A well-preserved jaw containing 222 teeth as well as a series of 45 vertebral centra were found in the Late Miocene Pisco Formation of Peru. The teeth show similarities of those of *C. carcharias* and *C. hastalis*, and *C. hubbelli* was interpreted as an intermediate species between *C. hastalis* and *C. carcharias* (Ehret et al. 2009; 2012). *C. hubbelli* is also known form the Late Miocene of California, USA and Chile (Boessenecker 2016; Hoffmeister et al. 2023).

Examination of the vertebral centra yielded an age of the shark of at least 20 years. Based on measurements of teeth and vertebral centra, this specimen is estimated to have had a minimum total body length of 4.80–5.07 m. The growth of *C. hubbelli* appears to have been slower than that of Recent great white sharks (Ehret et al. 2009; 2012). *C. hubbelli* fed on marine mammals (Ehret et al. 2012).

Otodontidae Glickman, 1964

Megalolamna paradoxodon Shimada, Chandler, Lam, Tanaka & Ward, 2016 (Figure 2.1)

This newly described genus and species is known from teeth from the early Miocene of the USA (North Carolina, California), Japan and Peru (Shimada et al. 2016; Landini et al. 2019) as well as from Baden-Württemberg, Germany (as "*Lamna* sp.": Pfeil 1991, pl. 2, Figure 6). All the deposits represent shallow-water shelf-type coastal environments (Pfeil 1991; Shimada et al. 2016; Landini et al. 2019). The largest teeth examined by Shimada et al. (2016) came from an individual that measured at least 3.7 m in total length. Based on the shape of the anterior and lateral teeth, the diet of *M. paradoxodon* could have included relatively large prey, such as medium-sized [ca. 0.5–1 m] fishes, captured by the use of its anterior teeth and cut by the distal portion of the dentition to a size suitable for ingestion (Shimada et al. 2016).

Otodus (*Megaselachus*) *megalodon* (Agassiz, 1835) and *O.* (*M.*) *chubutensis* (Ameghino, 1901)

In the past, these extinct species have been placed in diverse genera (*Carcharodon, Procarcharodon, Carcharocles, Megaselachus*). Now they are placed in *Otodus*, and *Megaselachus* is used as a subgenus (see Cappetta 2012 and Kent 2018).

The large, triangular teeth of these likely two species are surely the most known shark teeth. *Otodus* spp. were top predators during the Miocene and early Pliocene. *Otodus* is divided into two chronospiecies: *O. (M.) chubutensis* (with lateral cusplets or only traces thereof) and *O. (M.) megalodon* (without lateral cusplets). In Early Miocene deposits, teeth with cusplets dominate over uncuspleted ones. Moving upwards through the Miocene profile, uncuspleted forms increase in relative abundance and the cuspleted ones finally disappear (pers. observ. O.H.; see also Perez et al. 2019). Following Perez et al. (2019), a definitive separation between all the teeth of the taxa *O. chubutensis* and *O. megalodon* is impossible, because a complex mosaic evolutionary continuum characterizes this transformation, particularly in the loss of lateral cusplets. The cuspleted and uncuspleted teeth of *Otodus* (*Megaselachus*) spp. are designated as chronomorphs because there is broad overlap between them both morphologically and chronologically. For details on the *O. chubutensis/megalodon* problem see Kent (1994; 2018), Perez et al. (2019), and Pollerspöck et al. (2022). For the relationships of the genus see Cappetta (2012); Ehret (2012) and Kent (2018).

Otodus teeth can be found worldwide in neritic deposits of the Neogene epoch (see Cappetta 2012). The teeth of *O.* (*M.*) *chubutensis* can reach a height of 13 cm; the ones from *O.* (*M.*) *megalodon* can reach 17 cm (Kent 1994). Based on tooth size, the maximum body length of *O.* (*M.*) *megalodon* was probably between 18 and 20 meters (Shimada et al. 2022). Following the latter authors, individuals of *O* (*M.*) *megalodon* were on average larger in cooler water than those living in warmer waters. In the shallow marine Miocene Gatun Formation of Panama, the majority of *O. (M.) megalodon* teeth are very small (Pimiento et al. 2010). According to the cited authors, the individuals from Gatun were mostly juveniles and neonates, with estimated body lengths between 2 and 10.5 meters. They therefore proposed that the Gatun Formation represented a paleo-nursery area for *O.* (*M.*) *megalodon*. However, Shimada et al. (2022) argued that while it is possible that neonatal *O. (M.) megalodon* could have utilized nursery areas, the previously identified palaeo-nursery areas may reflect temperature-dependent trends rather than inferred life history strategies.

A viviparous reproductive strategy characterized by matrotrophy via oophagy is primitive for crown-lamniform sharks (Blackburn, 2015), resulting in large size at birth. This is consistent with the inferred life history of *O.* (*M.*) *megalodon* (Shimada et al. 2021). Incremental growth bands in fossil vertebrae of a 9.2-m-long individual *O.* (*M.*) *megalodon* from the Miocene of Belgium (see below), reveal that the shark was born large at 2 m in length, and this specimen died at age 46 (Shimada et al. 2021). The authors estimated that *O.* (*M.*) *megalodon* had a lifespan of at least 88–100 years and that it had a slightly higher growth rate during the first 7 years (19–23 cm/yr) compared to the remainder of its life (11–18 cm/yr). Shimada et al. (2023) verified tessellated calcified cartilage remains next to the teeth of a ca. 11.7 m long individual from the Miocene of Japan. According to the authors, the morphology of each tessera (e.g. predominantly hexagonal) and the arrangement of tesserae as a tessellated calcified cartilage sheet in *Otodus* (*M.*) *megalodon* are practically identical to those of extant chondrichthyans. Further, they found that the size range of tesserae observed in the estimated 11.7-m-TL individual of *O.* (*M.*) *megalodon* is comparable to that of extant chondrichthyans suggests that larger body size does not necessarily produce larger tesserae. Following Shimada et al. (2023), this observation suggests that, as in extant sharks, skeletal elements sheathed by tesserae developed through biomineralization along the margins of existing tesserae to form new tesserae in *O.* (*M.*) *megalodon*, despite its gigantic body size. The first reconstruction of the skeletal anatomy of *Otodus* was done by Gottfried et al. (1996). The most recent anatomical reconstructions were made by Cooper et al. (2020; 2022). Cooper et al. (2020) made a 2D-reconstruction of *O. megalodon* based on comparisons with extant members of Lamniformes. The results suggest that a 16 m *O.* (*M.*) *megalodon* likely had a head ~4.65 m long, a dorsal fin ~1.62 m tall and a tail ~3.85 m high (Cooper et al. 2020). In 2022, Cooper et al. published a 3D-model of *O. megalodon*. The basis was a vertebral column with 141 centra, belonging to the single, 9.2-m-long individual of *O.* (*M.*) *megalodon*, mentioned above (stored in the Royal Belgian Institute of Natural Sciences in Brussels, Belgium) as well as comparisons with the skeleton of the Recent great white shark *Carcharodon carcharias*. This vertebral column was recovered from around the Antwerp basin in the 1860s; however, neither the locality nor an age has been specified beyond a Miocene range (23 to 5.3 Ma ago) (Cooper et al. 2022). The reconstruction yielded a total length of 15.9 m, and a body mass of 61 560 kg. The mean absolute speed for the model was suggested to be 1.4 –4.1 m/s (= ca. 5.0–14.8 km/h) and the mean relative cruising speed as 0.09 body lengths per second. Additionally, the gape size was determined at different angles: gape height 1.2 m at a 35° angle and 1.8 m at 75° angle. The gape width measured 1.7 m at both 35° and 75° angles. The stomach volume was estimated as 9605 liters. Prey of 8 m length could have been completely ingested, whereas larger prey (e.g. the size of the modern humpback whale *Megaptera novaeangliae)* could not (Cooper et al. 2022). The authors calculated that the modelled *O.* (*M.*) *megalodon* required 98 175 kcal per day. Concerning the cruising speed, however, Shimada et al. (2023) estimated lower values (2.0 km/h with a range of 0.9–3.0 km/h) for *O. (M.) megalodon* than the ones mentioned above, based on details of the morphology of its placoid scales. The authors also found out that the general size of placoid scales represented by the vast majority of extant pelagic lamniforms and carcharhiniforms as well as extinct lamniform taxa such as *Cretoxyrhina*, *Cretodus*, and *Squalicorax* is similar to the overall scale size of the much larger *O. megalodon*. This at least demonstrates that the exceptionally large body size seen in *O.* (*M.*) *megalodon* did not necessarily yield exceptionally large placoid scales. Rather, new placoid scales of similar small size were added as the fossil shark grew through ontogeny (Shimada et al. 2023). The authors used the chronospecies name *O. megalodon*, but there is no reason to assume that these data cannot be extrapolated to *O. chubutensis* if of similar size.

Concerning diet, there are many finds of marine mammal bones with bite traces from *Otodus* teeth, e.g., of small-sized baleen whales, cetaceans, and pinnipeds in the upper Miocene Pisco Formation (southern Peru: Collareta et al. 2017a) or baleen whale caudal vertebra from the Pliocene of North Carolina (Purdy 1996). Following McCormack et al. (2022), however, in the majority of cases, it remains unclear if these feeding events on mammals document active hunting or scavenging. With the help of enameloid-bound $\delta^{15}N$ ($\delta^{15}N_{EB}$) in *Otodus* teeth, Kast et al. (2022) determined that *Otodus* (*M.*) *megalodon* as well as *O.* (*M.*) *chubutensis* occupied a higher trophic level than known for any marine species, extinct or extant. The $\delta 15_{\mathrm{NEB}}$ values show a large range for *O. (M). megalodon* which may reflect a fundamental aspect of its ecology, specifically a generalist diet, with individuals feeding across many prey types and different trophic levels (Kast et al. 2022). Many extant apex predatory sharks are also opportunistic in their prey selection (McCormack et al. 2022). Despite the bite traces on baleen whale bones mentioned above, the high $\delta^{15}N_{\mathrm{EB}}$ values indicate that baleen whales were not the dominant prey of *O. megalodon*, as extant baleen whales have a low trophic level and a correspondingly low δ^{15} N (Kast et al. 2022). McCormack et al. (2022) used the δ^{66}Zn values in the tooth enameloid of *O. megalodon* and found support for the previous conclusion that *Otodus* spp. were apex predators feeding at a very high trophic level. However, during the Early Pliocene, the *Otodus* lineage represented by O. (*M*). *megalodon* showed a considerable increase in the mean δ^{66}Zn value for the Atlantic populations, hinting at a reduced trophic position for the megatooth shark lineage in the Atlantic. This could indicate a dietary shift, specifically that lower trophic level mammalian prey such as mysticetes (and perhaps herbivorous sirenians) may have been an important food item for Atlantic populations of *O.* (*M*). *megalodon*. Now extinct small- and medium-sized mysticetes (e.g., Cetotheriidae and various small-sized Balaenidae and Balaenopteridae) were abundant during the Early Pliocene and were thus available as prey (McCormack et al. 2022). As can be seen, the two isotopes show two partly different results concerning trophic level.

Another important point concerning the palaeobiology of Neogene *Otodus* spp. is thermophysiology. Griffiths et al. (2023) examined the question of endothermy in Neogene *Otodus* sharks using $\delta^{18}O_{P}$ values (P = phosphate). Their measurements show the presence of endothermy in *Otodus* (*M.*) *megalodon* and O. (*M.*) *chubutensis*. Based on their lower estimation of the cruising speed, Shimada et al. (2023) suggested that the relative importance of the functional roles of regional endothermy possibly shifted from maintaining high cruising speeds to visceral food processing through the evolution of gigantism in otodontids.

Regarding the extinction of *Otodus* (*M.*) *megalodon*, two dates are reported in the newer literature:

1. Before c. 2.6 Ma (Pliocene/Pleistocene boundary) (Pimiento & Clements 2014); 2. Before c. 3.6 Ma (early-late Pliocene boundary) (Boessenecker et al. 2019). There are different opinions concerning competition with great white sharks as a possible driver for the extinction, as well as the extinction of small to mid-sized baleen whale prey species (Pimiento et al. 2016; Kast et al. 2022; McCormack 2022). Competition with carnivorous odontocetes may have also played a role in the extinction process (see Pimiento et al. 2016; McCormack et al. 2022). Concerning the influence of climatic changes on the extinction, Pimiento et al. (2016) found no evidence for direct effects of global temperature. Griffiths et al. (2023) mentioned the possibility that the gigantic body size with the high metabolic cost of maintaining a high body temperatures may have contributed to the vulnerability of *Otodus* species to extinction when compared to other sympatric sharks that survived the Pliocene epoch. To sum up, the reasons for the extinction of O. (*M.*) *megalodon* are still unknown.

Parotodus benedenii (Le Hon, 1871)

Teeth of *Parotodus benedenii* can be up to 6 cm high. This species has been widely reported from early Oligocene through early Pliocene fossil beds of Europe (Belgium, Germany, Hungary, Italy, Malta, the Netherlands, Portugal, Slovakia, and Switzerland), Africa (Angola and South Africa), the Azores, and the United States along with Australia, Japan, and New Zealand in the western Pacific (Kent 2018 and references therein). Despite its broad geographical distribution, this species is rare in Neogene deposits. During the Neogene, a clear increase of size occurred, accompanied by a very notable thickening of the root, which became very stout and globular (Cappetta 2012). Kent (1994, Figure B.11); Kent & Powell (1999, Figure 3) and Purdy et al. (2001, Figure 23) illustrated an artificial tooth set. Collareta et al. (2023) also dealt closely with this species. Following these authors, *P. benedenii* may be reconstructed as a large-sized, carnivorous shark that inhabited pelagic settings and fed primarily on large, soft prey and scavenged items. Thus, some ecological partitioning did likely exist between *P. benedenii* and other elasmobranch apex predators of the Neogene mid-latitude seas (including the extant species *Carcharodon carcharias*, *Carcharhinus leucas* and *Galeocerdo cuvier* during the Pliocene). Collareta et al. (2023) estimated the body length of *P. benedenii* at over 7 m; Purdy et al. (2001) estimated a maximum length between 6 and 7.5 m.

Cetorhinidae Gill, 1861

Keasius parvus (Leriche, 1908)

This species was original placed in the basking shark genus *Cetorhinus*. In 2013, Welton placed the species in his newly erected genus *Keasius* (see Welton 2013a), based on the shape of the gill rakers, the vertebral centra as well as the dentition. *K. parvus* existed from the Middle Eocene to Middle Miocene (Hovestadt & Hovestadt-Euler 2011). Remains have been found in Europe, Mexico and Japan (see Welton 2013 and references therein). Hovestadt & Hovestadt-Euler (2011) described a partial skeleton of *K. parvus* from the Oligocene (Rupelian) of Germany. Following these authors, *K. parvus* possessed a filter feeding apparatus similar to that of the extant *Cetorhinus maximus*, and it can be assumed that the species share the same feeding habits. The aforementioned skeleton came from a ca. 2 m long animal (Hovestadt & Hovestadt-Euler 2011). The maximum length of *K. parvus* is estimated at 4.5 – 5 m (Hovestadt & Hovestadt-Euler 2011).

Megachasmidae Taylor, Compagno & Struhsaker, 1983

Megachasma applegatei Shimada, Welton and Long, 2014

The teeth of this extinct megamouth shark are known from late Oligocene–early Miocene marine deposits of the western USA (Krak & Shimada 2023). *M. applegatei* could have commonly measured approximately 6 m in total length and likely had a broad diet, possibly including small fishes and planktonic invertebrates. The fossil record indicates that either *M. applegatei* was broadly adapted to a wide bathymetric tolerance or was a nektopelagic feeder over both deep and shallow water habitats (Shimada et al. 2014). Krak & Shimada (2023) examined the possible dentition of this species via landmark-based geometric morphometric analysis. The teeth were more variable in shape than those of the extant *Megachasma pelagios* Taylor, Compagno & Struhsaker, 1983. The teeth of the fossil species were probably arranged in the typical heterodont "lamnoid tooth pattern" (see Shimada 2002), as in predatory lamniform sharks.

Carcharhiniformes Compagno, 1977

Scyliorhinidae Gill, 1862

Pachyscyllium distans (Probst, 1879) and *Pachyscyllium dachiardii* (Lawley, 1876)

Both catshark species lived contemporaneously and their teeth are widespread in the Miocene and Early Pliocene of Europe (e.g. Germany, Belgium, France, Netherlands, Portugal, Italy) (see Reinecke et al. 2011; Höltke et al. 2020 and Collareta 2020 for the different localities). The only known information about the paleoecology of these taxa is that both were thermophilic sharks (Reinecke et al. 2011; Collareta 2020).

Hemigaleidae Hasse 1878

Hemipristris serra (Agassiz, 1843)

The species is very widely distributed from the late Oligocene (Chattian) through Pleistocene formations in warmer-water regions of the Atlantic Ocean, Caribbean Sea, Mediterranean Sea, Indian Ocean, and Pacific Ocean (Kent 2018). Purdy et al. (2001, Figures 46-47) published an artificial tooth set for this species. Whether *H. serra* is the direct ancestor to the Recent *H. elongata* (Klunzinger, 1871) is questionable. Based on histological differences of the teeth compared to those of extant *H. elongata* (Klunzinger, 1871), Ward and Bonavia (2001) suggested that generic reassignment of *H. serra* is warranted.

H. serra probably reached a length of c. 6 m (Pimiento et al. 2019), whereas the Recent species only attains lengths of 2.3–2.4 m (Ebert et al. 2021). There are some differences in tooth size through time and space. Teeth from the Early Miocene of southern Germany have a maximum size of 31 mm height and 25 mm width (Feichtinger & Pollerspöck 2021), but teeth from the Early Pliocene of North Carolina, USA reached a height of 41 mm and a width of 43 mm (Purdy et al. 2001).

Based on δ^{66}Zn composition, *H. serra* from the Early Miocene of Malta occupied a higher trophic position than individuals from the Early Miocene of Baden-Württemberg, Germany. This is the same relative result recovered for individuals of *Carcharodon hastalis* between the two localities; different prey availability or a shorter trophic chain in the German Molasse Basin may also be driving the pattern in this case. The Maltese specimens have a similar trophic position to *Galeocerdo aduncus* (see McCormack et al. 2022, Figure 2).

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Galeocerdonidae Poey, 1875

Galeocerdo aduncus (Agassiz, 1835)

This ancient tiger shark is found worldwide in neritic sediments of Oligocene to late Miocene age (Türtscher et al. 2021). A preserved jaw fragment from the Miocene (8 to 18 Ma) of Calvert Cliffs, USA was illustrated by Kent (2018, Figure 2.21.G). The teeth are similar to those of the extant tiger shark *G. cuvier*, apart from differences concerning the serration as well as the size (Türtscher et al. 2021). *G. aduncus* teeth are smaller. However, Purdy et al. (2001) placed this species in synonymy with the extant *G. cuvier* on the basis of similarities in morphology.

Feichtinger et al. (2021) found fossil evidence from the middle Miocene of the Styrian Basin (Austria) that *G. aduncus* fed on a *Metaxytherium* carcass. Godfrey and Smith (2010) were also able to match tooth marks on a crocodilian coprolite to this species. According to McCormack et al. (2022), Zinc isotope values in the *Galeocerdo* lineage show no statistical variability with either age or locality, suggesting tiger sharks occupied a similar trophic level and ecological role in the marine ecosystem since at least the Early Miocene. *G. aduncus* likely had a similar lifestyle to that of the extant *G. cuvier*, despite having smaller teeth.

Physogaleus contortus (Gibbes, 1849)

Teeth are known from the early and middle Miocene of the eastern Unites States (Maryland, North Carolina, and Virginia),Cuba, Panama, Peru, Germany, and Hungary (Kent 2018 and references therein). The paleobiology of *P. contortus* is largely unknown, although the slender twisted tooth crowns are consistent with a largely piscivorous diet (Kent 2018). A sperm whale from the lower Calvert Formation of Popes Creek, Maryland, USA (Early to Middle Miocene) was associated with 37 *P. contortus* teeth (Kent 2018). Although the teeth are exceptionally large, these sharks were far too small to have attacked and killed such substantial prey. Typically, such an association of teeth would be attributed to scavenging, although this is difficult to confirm. On the basis of tooth morphology, it seems equally plausible that this tooth concentration represents *Physogaleus* preying on small scavenging fishes attracted by the carcass (Kent 2018).

Carcharinidae Jordan & Evermann, 1896

Carcharhinus dicelmai Collareta, Kindlimann, Baglioni, Landini, Sarti, Altamirano, Urbina & Bianucci, 2022

This newly described species is known from the Lower Miocene Chilcatay Formation of Peru (type locality) and from the Lower- to mid Miocene (Burdigalian to lower Langhian) Cantaure Formation of Venezuela. The latter locality suggests a trans-Panamanian distribution for this ancient species (Collareta et al. 2022a). Given the dimensions of the teeth, *C. dicelmai* was likely a diminutive carcharhinid and may have relied on small-sized prey items (including, e.g., small bony fishes and invertebrates) that were individually captured and ingested through feeding actions that involved clutching (Collareta et al. 2022a). Following the latter authors, *C. dicelmai* may also have been an essentially thermophilic and very littoral shark.

Additional comments regarding fossil *Carcharhinus*: In the Pliocene of Tuscany, Italy Collareta et al. (2022b) found a fossil cetacean rib pierced by a partial requiem shark tooth (*Carcharhinus* sp.). Evidence for *Carcharhinus* sharks (mostly broad-toothed members of the genus) foraging upon cetaceans is preserved in the Mediterranean Pliocene fossil record in the form of bite traces and teeth associated with bones (Collareta et al. 2022b). Identifications to the species level were not provided.

4.2. Extant shark species and their fossil record:

Hexanchiformes de Buen, 1926

Hexanchidae Gray, 1851

Hexanchus griseus (Bonnaterre, 1788)

Fossils of very large *Hexanchus* teeth (at least 25 mm in width) have been widely, if rarely, collected from the early Miocene to Pliocene sediments of Belgium, Chile, Italy, Japan, Malta, Peru, Portugal, Spain as well as California and North Carolina in the USA (Kent 2018 and references therein). These were named as *Hexanchus gigas* (Sismonda, 1861) by Kent (2018) or as *Hexanchus* sp. by Purdy et al. (2001). Apart from the large size, they are similar to the teeth of the extant *H. griseus*.

As yet it is unclear whether they represent separate species or are conspecific. A large *Hexanchus* tooth was associated with a cetacean skeleton (*Cephalotropis coronatus* Cope, 1896) from the Late Miocene of Maryland, although it is uncertain whether this represents active predation or scavenging. Merella et al. (2021; 2022) mentioned shark bite traces on a sirenian skeleton from Pliocene shoreface deposits of Tuscany (Italy) which can probably be attributed to an immature *H. griseus.*

Notorynchus cepedianus (Péron, 1807)

The fossil record of this extant species is not clear. Teeth of similar shape to those of *N. cepedianus* can be found from the late Oligocene (Chattian) through late Miocene of Florida(?), Maryland, North Carolina, and Virginia, as well as Australia, Austria, Azores, Belgium, Denmark, France, Germany, Japan, the Netherlands, Poland, Portugal, Slovakia, Spain, and Switzerland (Kent 2018 and references therein). These fossil teeth were mostly named as *Notorynchus primigenius* (Agassiz, 1843) (see e.eg. Höltke et al. 2020). There are, however, differing opinions if *N. primigenius* is a separate species (Kent 2018) or synonym to *N. cepedianus* (Purdy et al. 2001). Interestingly, the geographic distribution of Recent *N. cepedianus* is quite unlike that of *Notorynchus* in the Neogene, with Recent members of this species generally restricted to cool temperate waters, whereas in the Neogene the genus was also widely distributed in warm temperate and tropical waters (Reinecke et al. 2011).

Heptranchias perlo (Bonnaterre, 1788)

Fossil record: Early Miocene: Costa Rica (Laurito et al. 2014); Middle Miocene: Italy (Abruzzo, Parma) (Cigala-Fulgosi 1977; Carnevale 2005); Late Miocene: Panama (Northern Panama) (Carrillo-Briceño et al. 2015a); Portugal (Lisbone) (Antunes & Jonet 1970, as “cf”); Late Miocene to early Pliocene: Venezuela (Northeastern Venezuela) (Aguilera & de Aguilera 2001).

Squaliformes Goodrich, 1909

Centrophoridae Bleeker, 1859

Centrophorus granulosus (Bloch & Schneider, 1801)

Fossil record: Early to Middle Miocene: France (Vaucluse) (Ledoux 1972); Pliocene: Italy (Tuscany, Piedmont) and France (Le-Puget-sur-Argens) (Landini 1977; Cappetta & Nolf 1991; Cigala Fulgosi et al. 2009). In the Miocene deposits of Europe and South America, a lot of teeth were named as *Centrophorus* cf. *granulosus* (see e.g. Carrillo-Briceño et al. 2020; Höltke et al. 2023). The reason for this is that the according teeth show similarities with the extant *C. granulosus.* However, the dentition of the other 10 extant *Centrophorus* species (Pollerspöck & Straube 2023) is insufficiently known. Therefore the assignment of isolated *Centrophorus* teeth to species is not without problems.

Deania calcea (Lowe, 1839)

Fossil record: Early to Middle Miocene: France (Vaucluse) (Ledoux 1972), Middle Miocene: Spain (Southeastern Spain) (Martínez-Pérez et al. 2018), Japan (Nagano Prefecture) (Suzuki 2012, as “cf”);

Early Pliocene: Italy (Parma) (Cigala Fulgosi 1986, as "cf").

Dalatiidae Gray, 1851

Dalatias licha (Bonnaterre, 1788)

Fossil record: Miocene: Italy (Sardinia) (Comaschi Caria 1973); Early to Middle Miocene: France (Vaucluse, Southern France) (Ledoux 1972; Cappetta 1975; Brisswalter 2009), Colombia (Guajira Peninsula) (Carrillo-Briceño et al. 2016b; 2019, both as "cf."); Middle Miocene: South Korea (Yun 2021), Early Miocene to early Pliocene: Japan (Itoigawa et al. 1985; Yabe & Hirayama 1998; Tanaka 2001; Suzuki 2005), Late Miocene: Panama (Carrillo-Briceño et al. 2015a); Pliocene: Japan (Uyeno & Matsushima 1975); Early Pliocene: France (Le-Puget-sur-Argens) (Cappetta & Nolf 1991); Late Pliocene: Italy (Tuscany) (Cigala Fulgosi et al. 2009).

Somniosidae Jordan, 1888

Scymnodon ringens du Bocage & Capello, 1864

Fossil record: Early Pliocene: Italy (Parma) (Cigala-Fulgosi 1996); Middle Pliocene: Italy (Romagna Apennines) Marsili & Tabanelli 2007 as "cf").

Somniosus rostratus (Risso, 1827)

Fossil record: Early Pliocene: Italy (Parma) (Cigala-Fulgosi 1988a).

Zameus squamulosus (Günther, 1877)

Fossil record: Early Pliocene: Italy (Parma) (Cigala-Fulgosi 1996).

Orectolobiformes Applegate, 1974

Rhincodontidae Garman, 1913

Rhincodon typus Smith, 1829

Fossil record: Late Oligocene: USA (South Carolina) (Cicimurri & Knight 2009, as “cf.”). Early Miocene: ?France (region Monpellier) (Cappetta 1970, as *Rhincodon* sp.).Early to Middle Miocene: USA (Maryland, North Carolina) (Purdy et al. 2001; Visaggi & Godfrey 2010); Late Miocene-Early Pliocene: Costa Rica (Laurito 1999).

Lamniformes Berg, 1958

Cetorhinidae Gill, 1862

Cetorhinus maximus (Gunnerus, 1765)

Fossil record: Following Hovestadt & Hovestadt-Euler (2010) this extant species first occurs in the Middle Miocene, whereas Welton (2013b) cited Late Miocene as the earliest occurrence.

Fossil record: Early to Middle Miocene: Japan (Saitama) (Uyeno et al. 1983); Middle Miocene: Czech Republic (Kienberg) (Schultz et al. 2010); Late Miocene: USA (Oregon) (Welton 2013b, as "cf"), USA (California) (Powell et al. 2019); Late Miocene: ?Germany (Sylt, Lower Saxony) (Lienau 1987; Menzel et al. 1994); Late Miocene to Early Pliocene: Chile (El Rincón) (Long 1993), Netherlands (Winterswijk-Almelo) (Van den Bosch et al. 1975); Early Pliocene: Belgium (Kallo) (Herman 1979), France (Le-Puget-sur-Argens, Anvers) (Leriche 1908; Cappetta & Nolf 1991); Late Pliocene: Italy (Tuscany) (Cigala-Fulgosi et al. 2009).

Carchariidae Müller & Henle, 1838

Carcharias taurus Rafinesque, 1810

See *C. contortidens*.

Odontaspididae Müller & Henle, 1839

Odontaspis ferox (Risso, 1810)

Fossil record: Early Miocene: Chile (Central Chile); Middle Miocene: USA (North Carolina) (Purdy et al. 2001), (Suárez et al. 2006); Middle Miocene-Pliocene: Chile (Northern Chile) (Hoffmeister & Villafaña 2023); Late Miocene-Early Pliocene: Venezuela (Aguilera & de Aguilera 2001); Early Pliocene: USA (North Carolina) (Purdy et al. 2001); Late Pliocene: Italy (Tuscany) (Cigala Fulgosi 2009).

Pseudocarchariidae Taylor, Compagno & Struhsaker, 1983

Pseudocarcharias kamoharai (Matsubara, 1936)

Fossil record: Early Miocene: Germany (Baden-Württemberg, Bavaria) (Schultz 2013; Höltke et al. 2020), Austria (Upper Austria) (Schultz 2013), Hungary (Kordos & Solt 1984), Switzerland (Schaffhausen) (Schalch 1881); Middle Miocene: Italy (Parma) (Cigala-Fulgosi 1992): Late Miocene: Portugal (Alvalade) (Antunes et al. 1999, as "cf"); Late Miocene-Early Pliocene: Venezuela (Aguilera & de Aguilera 2001).

Alopiidae Bonaparte, 1835

Alopias superciliosus Lowe, 1841

Fossil record: Oligocene: Germany (Bavaria) (Pfeil 1981, as "cf.").

Early Miocene: USA (North Carolina) (Case 1980), : Peru (Landini et al. 2019), Colombia (Carrillo-Briceño et al. 2016b, as "cf"); Early Miocene to early Middle Miocene Japan (Itoigawa et al. 1985); Middle Miocene: Netherlands (Bor et al. 2012); Middle Miocene to lower Pliocene: USA (Florida) (Boyd 2016); Late Miocene: Panama (Carrillo-Briceño et al. 2015a; Perez et al. 2017), Portugal (Alvalade Basin, Lisbon) (Balbino 1996; Antuness & Balbino 2003, both as "cf"); France (Luberon) (Brisswalter 2009, as "cf"); Late Miocene-Early Pliocene: Venezuela, Costa Rica (Laurito 1999; Aguilera & de Aguilera 2001); Pliocene: Italy (Tuscany) (Cigala-Fulgosi 1988b).

Alopias vulpinus (Bonnaterre, 1788)

Fossil record: Miocene: Myanmar (Noetling 1901), India (Orissa) (Bhalla & Dev 1975): Early Miocene: Portugal (Algarve) (Antunes et al. 1981). There are also a lot of entries in the literature with “cf” or “aff” for deposits dating from the Oligocene (see e.g, Balbino 1996; Reinecke et al. 2005; Cicimurri & Knight 2009; Landini et al. 2019). Therefore, the fossil record requires reassessment.

Lamnidae Müller & Henle, 1838

Lamna nasus (Bonnaterre, 1788)

Fossil record: Late Miocene: Netherlands (Liessel) Mollen 2010); Early Pliocene: Belgium (Kallo) (Herman 1979); Late Pliocene Italy (Tuscany) (Collareta et al. 2018).

Isurus oxyrinchus Rafinesque, 1810

This species is mentioned in sediments dating from the Oligocene (Reinecke et al. 2005). It is known from many deposits in Germany, Belgium, France, Italy, Switzerland, USA, Japan, Chile, and Africa (see Cappetta 2012 and references therein). Fossil teeth similar in shape to the extant *I. oxyrinchus* were sometimes named as *Isurus desori* (Agassiz, 1843) (see Feichtinger & Pollerspöck 2021). At the moment, it is not clear if *I. desori* is a valid species or synonym of *Isurus oxyrinchus.*

Isurus paucus Guitart-Manday, 1966

Fossil record: Early Miocene to early Middle Miocene: Japan (Central Japan) (Itoigawa et al. 1985, as "cf"; Itoigawa 1993); Middle Miocene-Pliocene: possibly Chile (Northern Chile) (see Hoffmeister & Villafaña 2023 and references therein for details).

Carcharodon carcharias (Linnaeus, 1758)

The extant great white shark is known since the early Pliocene or Miocene (Cappetta 2012; Kent 2018). For details on the biology of extant *C. carcharias* see Domeier (2012). The teeth occur worldwide in neritic sediments.

In a few cases the predatory/scavenging habits of fossil *C. carcharias* have been documented in the fossil record, and as with observations on extant *C. carcharias*, attacks are principally on cetaceans (Govender 2015; Kent 2018 and references therein). Cigala-Fulgosi (1990) described a skeleton of an extinct dolphin with bite traces attributed to *C. carcharias* from the Pliocene of Italy (Piacenza). To date, there are no studies documenting piscivory by *C. carcharias* in the fossil record (Kent 2018). The δ^{66}Zn results indicate an increase in trophic position for *C. carcharias* from the Early Pliocene to Recent (McCormack et al. 2022). In a comparison between Recent and fossil data concerning the diet of *Carcharodon carcharias*, in the Pliocene both mysticetes and odontocetes are assumed to have been equally represented. In contrast, extant great white sharks principally attack small toothed whales and only rarely mysticete baleen whales. This change could be due to both the general reduction in body size of the living great white shark over time, and the diminished diversity of the cetacean assemblage (Bianucci et al. 2002).

The occurrence of fossil teeth from Spain indicate that large *C. carcharias* close to 7 m long or larger were not scarce in the Early Pliocene (Adnet et al. 2010). Villafaña et al. (2020) described a palaeo-nursery area of the great white shark in the Pliocene of Chile. Fossil teeth of *C. carcharias* can often be found in the same deposits as the extinct megatooth shark *Otodus* (*Megalselachus*) *megalodon*, for example in the Late Miocene/Early Pliocene of Chile (Long 1993). This suggests that both sharks co-existed (Adnet et al. 2010). However, no interaction or competition between these two apex predators has been documented.

Carcharhiniformes Compagno, 1977

Triakidae Gray, 1851

Galeorhinus galeus (Linnaeus, 1758)

Fossil record: Late Eocene: USA (North Carolina) (Case & Borodin 2000); Early Miocene: USA (North Carolina) (Case 1980); Late Miocene: Panama (Carrillo-Briceño 2015a, as “cf”); Late Miocene-Early Pliocene: Chile (Bahía Inglesa) (Long 1993); Early Pliocene: South Australia (Pledge 1985, as *Galeorhinus* cf. *australis*); Late? Pliocene: USA (California) (Fitch & Reimer 1967, as *Galeorhinus zyopterus*); Late Pliocene: Chile (Valparaíso) (Carrillo-Briceño et al. 2013).

Galeocerdonidae Poey, 1875

Galeocerdo cuvier (Péron & Lesueur, 1822)

Fossil record: Early Miocene: India (Gujarat) (Sharma et al. 2021), Middle Miocene: Hungary (Nyirád) (Szabó et al. 2023), USA (Florida) (Türtscher et al. 2021); Middle Miocene-Middle Pliocene: Venezuela (Carrillo-Briceño et al. 2015b); Late Miocene: Panama (Lago Bayano), (Perez et al. 2017); Late middle to early late Miocene: Panama (Central Panama) (Alberti & Reich 2018); Late Miocene: Borneo (Brunei Darussalam) (Kocsis et al. 2021); Pliocene: USA (Florida, North Carolina) (Webb &

Tessmann 1968; Maisch et al. 2018), Angola (Antunes 1978); Early Pliocene: Libya (Pawellek et al. 2012); late early/early late Pliocene: Italy (Tuscany) (Collareta et al. 2021b).

Carcharinidae Jordan & Evermann, 1896

Carcharhinus amblyrhynchoides (Whitley, 1934)

Fossil record: Late Miocene: Borneo (Brunei Darussalam) (Kocsis et al. 2019).

Carcharhinus amblyrhynchos (Bleeker, 1856)

Fossil record: Late Miocene: Borneo (Brunei Darussalam) (Kocsis et al. 2019)

Carcharhinus albimarginatus (Rüppell, 1837)

Fossil record: Late Miocene-Early Pliocene: Chile (North Coast) (Long 1993), Ecuador (Camarones River) (Carrillo-Briceňo et al. 2014); Middle Miocene-Pliocene: Chile (Northern Chile) (Hoffmeister & Villafaña 2023); Pliocene: Chile (Bahía Inglesa) (Long 1993).

Carcharhinus amboinensis (Müller & Henle, 1839)

Fossil record: Late Miocene: Borneo (Brunei Darussalam) (Kocsis et al. 2019).

Carcharhinus brachyurus (Günther, 1870)

Remarks and fossil record: This species can be traced back to the Early Miocene, see Landini et al. 2020 for the large lists of Neogene and Pleistocene deposits in Europe, North and South America, Australia and Japan. According to these authors, the species has an early Miocene East Pacific-central West Atlantic center of origin. The present-day distributional pattern of *C. brachyurus* is the product of historical biogeographic processes and likely reflects major changes in the global ocean system, including the closure of major seaways and the emergence of new oceanic circulation patterns (Landini et al. 2020). Landini et al. (2017a; 2019; 2020) also identified the oldest copper shark nursery area in the East Pisco Basin of Peru, from the early Miocene of the Chilcatay Formation and in the late Miocene of the Pisco Formation.

Carcharhinus brevipinna (Müller & Henle, 1839)

Fossil record: Miocene: India (Orissa) (Bhalla & Dev 1975); Late Miocene: Panama (Lago Bayano) (Perez et al. 2017); Middle Miocene to early Pliocene: USA (Florida) (Boyd 2016, as "cf").

Carcharhinus falciformis (Bibron, 1841, in Müller & Henle, 1838-1841)

Fossil record: Early to Late Miocene: Malta (Ward & Bonavia 2001); Middle Miocene: India (Kutch) (Singh et al. 2022), USA (North Carolina) (Purdy et al. 2001). Middle Miocene to early Pliocene: USA (Florida) (Boyd 2016); Late Miocene: Borneo (Brunei Darussalam) (Kocsis et al. 2019), Panama (Northern Panama, Lago Bayano) (Pimiento et al. 2013; Perez et al. 2017); Late Miocene-Early Pliocene: Costa Rica (Laurito 1999); Pliocene: USA (North Carolina) (Maisch et al. 2018); Early Pliocene: Italy (Tuscany) (Carnevale et al. 2006).

Carcharhinus glaucus (Linnaeus, 1758) (syn. *Prionace glauca*, see da Silva Rodrigues-Filho et al. 2023).

Fossil record: Miocene: Sri Lanka (Deraniyagala 1969); Middle Miocene-Pliocene: Chile (Northern Chile) (Hoffmeister & Villafaña 2023); Late Miocene: ?Belgium (Antwerp International Airport) (Goolaerts et al. 2020); Late Miocene to Early Pliocene: Chile (Northern Chile) (Villafaña et al. 2022); Early Pliocene: Italy (Parma) (Cigala Fulgosi 1986); Late Pliocene: Italy (Umbria, Tuscany) (Bellocchio et al. 1991; Cigala-Fulgosi et al. 2009).

Carcharhinus leucas (Valenciennes, 1839, in Müller and Henle, 1838-1841)

Fossil record: Early Miocene: Egypt (Moghra) (Cook et al. 2014), Peru (Zamaca) (Landini et al. 2019); Middle Miocene: India (Kutch) (Singh et al. 2022), USA (North Carolina) (Purdy et al. 2001); Middle Miocene to lower Pliocene: USA (Florida) (Boyd 2016); Middle Miocene-Middle Pliocene: Venezuela (Carrillo-Briceño et al. 2015b); Late Miocene: Panama (Northern Panama) (Pimiento et al. 2013), Portugal (Alvalade Basin) (Antunes et al. 1999, as "cf"); Late Miocene: Peru (Pisco Basin) (Bianucci et al. 2016); Pliocene: Italy (Tuscany) (Marsili 2007), USA (Florida) (Webb & Tessmann 1968; Early Pliocene: USA (North Carolina (Purdy et al. 2001); Canary Islands (Gran Canaria, Fuerteventura) (Betancort et al. 2016), South Africa (Langebaanweg) (Govender & Chinsamy 2013).

Carcharhinus limbatus (Müller & Henle, 1839)

Fossil record: Miocene: India (Orissa) (Bhalla & Dev 1975); Early Miocene: USA (Delaware) (Purdy 1998); Early Miocene to Late Pliocene: Colombia (Guajira Peninsula) (Carrillo-Briceño et al.

2019, as "cf"); Middle Miocene to early Pliocene: USA (Florida) (Boyd 2016); Early Pliocene: Italy (Tuscany) (Collareta et al. 2021a).

Carcharhinus longimanus (Poey, 1867)

Fossil record: Early Miocene: India (Kathiawar, Piram island, Orissa) (Sahni & Mehrotra 1981; Sharma & Patnaik 2014); Pliocene: Italy (Tuscany) (Marsili 2007), Spain (Alicante) (Mora Morote 1996). Cappetta (1987:125-126, Figure 106D) identified a tooth from the Pliocene of North Carolina, USA as *Pterolamiops longimanus*. *Pterolamiops* is a junior synonym of *Carcharhinus* (Compagno, 1988), but according to Purdy et al. (2001), Cappetta's tooth may belong to *C. leucas.*

Carcharhinus macloti (Müller and Henle, 1839)

Fossil record: Miocene: India (Orissa) (Bhalla & Dev 1975); Early Miocene: Brazil (Northeastern Amazonia) (Costa et al. 2009, as “cf”), Peru (East Pisco Basin) (Collareta et al. 2022); Middle Miocene: USA (North Carolina) (Purdy et al. 2001); Late Miocene: Peru (Cerro Colorado) (Landini et al. 2017b), Portugal (Lisbon) (Antunes & Jonet 1970).

Carcharhinus obscurus (Lesueur, 1818)

Fossil record: Early Miocene: Egypt (Moghra) (Cook et al. 2014); Mexico (Baja California) (Applegate 1986, as “cf”); Venezuela (Sánchez-Villagra et al. 2000, as " cf"); Early to middle Miocene: Cuba (Iturralde-Vinent et al. 1996); Middle Miocene: Grenada (Carriacou) (Portell et al. 2008), Middle to late Miocene: Ecuador (Carretera Flavio Alfaro) (Carrillo-Briceňo et al. 2014); Middle Miocene-Middle Pliocene: Venezuela (Carrillo-Briceño et al. 2015b); Middle Miocene-Pliocene: Chile (Northern Chile) (Hoffmeister & Villafaña 2023); Late Miocene: Portugal (Alvalade Basin) (Antunes et al. 1999, as "cf"), Panama (Northern Panama, Lago Bayano) (Pimiento et al. 2013; Perez et al. 2017); Pliocene: Italy (Tuscany) (Marsili 2007); Early Pliocene: USA (North Carolina) (Purdy et al. 2001).

Carcharhinus perezi (Poey, 1876)

Fossil record: Early Miocene: Brazil (North Brazil) (Aguilera et al. 2017), USA (Delaware) (Purdy 1998); Early to ?Middle Miocene: Venezuela (Falcón Basin) (Carrillo-Briceño et al. 2016a); Early Miocene to Late Pliocene: Colombia (Guajira Peninsula) (Carrillo-Briceño et al. 2019 as "cf"); Middle Miocene: USA (North Carolina) (Purdy et al. 2001); Early to middle Miocene: Cuba (Iturralde-Vinent et al. 1996), Late Miocene: Panama (Northern Panama) (Pimiento et al. 2013), Portugal (Alvalade Basin) (Antunes et al. 1999, as "cf"); Pliocene: Italy (Tuscany) (Marsili 2007); Early Pliocene: USA (North Carolina) (Purdy et al. 2001).

Carcharhinus plumbeus (Nardo, 1827)

Fossil record: Early Miocene: Italy (Piedmont) (Caretto 1972); Middle Miocene: USA (North Carolina) (Purdy et al. 2001); Middle Miocene to early Pliocene: USA (Florida) (Boyd 2016); Middle Miocene-Middle Pliocene: Venezuela (Carrillo-Briceño et al. 2015b); Late Miocene: Panama (Pimiento et al. 2013), Portugal (Alvalade Basin) (Antunes et al. 1999, as "cf"); Pliocene: Italy (Tuscany) (Marsili 2007); Early Pliocene: USA (North Carolina) (Purdy et al. 2001).

Carcharhinus sealei (Pietschmann, 1913)

Fossil record: Late Miocene: Borneo (Brunei Darussalam) (Kocsis et al. 2019).

Glyphis glyphis (Müller & Henle, 1839)

Fossil record: Early Miocene to Pliocene: Portugal (Fialho et al. 2021); Late Miocene: Borneo (Brunei Darussalam) (Kocsis et al. 2019, as “cf.”); Pliocene: Italy (Toscana) (de Stefano 1909).

Negaprion brevirostris (Poey, 1868)

Fossil record: Early Miocene: India (Orissa) (Sharma & Patnaik 2014); Peru (Zamaca) (Landini et al. 2019); Early to middle Miocene: Cuba (Iturralde-Vinent et al. 1996); Middle to late Miocene: Ecuador (Carrillo-Briceňo et al. 2014); Middle Miocene -Middle Pliocene: Venezuela (Carrillo-Briceño et al. 2015b); Middle Miocene to early Pliocene: USA (Florida) (Boyd 2016); Late Miocene: Panama (Northern Panama, Lago Bayano) (Pimiento et al. 2013; Perez et al. 2017), Peru (Cerro Colorado,) (Landini et al. 2017b); Pliocene: Angola (Antunes 1978, as “cf”), USA (Florida, North Carolina) (Webb & Tessmann 1968; Maisch et al. 2018).

Sphyrnidae Gill, 1872

Sphyrna media (Linnaeus, 1758)

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Fossil record: Early Miocene: Brazil (Northeastern Amazonia) (Costa et al. 2009, as "cf"), Middle Miocene: USA (North Carolina) (Purdy et al. 2001, as "cf"); Late Miocene: Peru (Cerro Colorado) (Landini et al. 2017b).

Pliocene: USA (North Carolina) (Purdy et al. 2001, as "cf"), Ecuador (Carrillo-Briceṅo et al. 2014)

Late Pliocene-Pleistocene: Ecuador (Punta Canoa) (Carrillo-Briceṅo et al. 2014).

Sphyrna mokarran (Rüppell, 1837)

Fossil record: Early Miocene: Cuba (Domo de Zaza) (Macphee et al. 2003); Middle Miocene to early Pliocene: USA (Florida) (Boyd 2016); Late Miocene: Panama (Lago Alajuela, Northern Panama, Lago Bayano) (Pimiento et al. 2013; Macfadden et al. 2017; Perez et al. 2017; Alberti & Reich 2018), Borneo (Brunei Darussalam) (Kocsis et al. 2019, as "cf").

Sphyrna zygaena (Linnaeus, 1758)

Teeth similar to this species can be found since the Early Miocene (see Reinecke et al. 2011). However, there is debate as to whether these teeth belong to *S. zygaena* or to *Sphyrna laevissima* (Cope, 1867), described from the Miocene of Maryland, USA (see Purdy et al. 2001 and Reinecke et al. 2011).

5. Outlook and Conclusions

Despite a fossil record consisting mostly of teeth, new finds and methods have increased our knowledge of fossil species and the fossil record of extant species. In particular, isotopic analyses as well as computer-based 2D and 3D reconstructions are valuable tools for examining fossil shark teeth. In total, more is known than only the descriptions of the teeth for a total of 19 extinct Neogene shark species, with the most focus on the famous large *O. megalodon*. Apart from the latter taxon, there are no theories to date as to what caused the extinctions of these sharks, however climate change and habitat loss have been suggested (Villafaña et al. 2023). Concerning the fossil record of the more than 500 extant shark species, 38 could be verified in the Neogene record. Four species of these 38 (11%) (*Alopias superciliosus Alopias vulpinus, Galeorhinus galeus, Rhincodon typus*) were also verified from the Palaeogene. For five extant species (*Carcharias taurus, Hexanchus griseus, Isurus oxyrinchus, Notorynchus cepedianus, Sphyrna zygaena*), the relationship of the extant and fossil forms is not clear. Figures 4-5 show the phylogenetic relationships and summarize the stratigraphic ranges of species discussed in the text. The separation in Charchariniformes (Figure 5) and non-Carcharhiniformes (Figure 4) were simply done for a better clarity. Determining a concrete number of existing shark species in the Neogene is highly speculative if not impossible, although it can be assumed that ancient diversity was similar to extant diversity with the addition of taxa extinct today. Reasons for this lack of knowledge are collecting bias (especially concerning minute sized teeth), incomplete preservation of the teeth, as well as poorly known dentition of extant relatives (here also especially the small species with minute-sized teeth and also the presence or absence of different forms of heterodonty). Sometimes only one tooth with a different shape can be found in a sample, which is not enough for a reliable taxonomic diagnosis (see for example "*Carcharhinus* sp." in Höltke et al. 2022a).

The usage of the new methods mentioned here, extensive collecting (especially concerning minute teeth) as well as detailed examination of the dentition of Recent species will enhance the knowledge of shark evolution and the palaeobiology of fossil sharks.

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Abbervations

LACM: Natural History Museum of Los Angeles County, Los Angeles, California
MUSM: Museo de Historia Natural de la Universidad
Nacional Mayor de San Marcos, Jesús María, Lima, Peru
SMNS: Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany
UCMP: University of California at Berkeley, Museum of
Paleontology Berkeley, California, USA.

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Legend:

Figure 1. Stratigraphic table.

Figure 2. 1. *Megalolamna paradoxodon* Shimada, Chandler, Lam, Tanaka & Ward, 2016. UCMP 112146, Miocene, Jewett Sand, Kern County, California, USA. a. lingual view; b. labial view. Scale: 20 mm. Images courtesy of K. Shimada, used with permission. 2. *Otodus* (*Megaselachus*) *megalodon* (Agassiz, 1835). SMNS 97266, Miocene, Malta. a. lingual view; b. labial view. Scale: 20 mm. 3. *Otodus* (*Megaselachus*) *chubutensis* (Ameghino, 1901). SMNS 97267, Miocene, Lake Constance, Germany. a. lingual view; b. labial view. Scale: 20 mm. 4. *Parotodus benedenii* (Le Hon, 1871). Miocene, Rengetsweiler, Baden-Württemberg, Germany. Specimen housed in a private collection. a. lingual view; b. labial view. Scale: 20 mm. Photos courtesy of Jürgen Pollerspöck, used with permission. 5. *Keasius parvus* (Leriche, 1908). SMNS 80740/16, gill raker from the Bodenheim Formation, Oligocene. Rauenberg, Baden-Württemberg, Germany. Scale: 20 mm. 6. *Mitsukurina lineata* (Probst, 1879). SMNS 97016/10, Miocene, Rengetsweiler, Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 10 mm. 7. *Megachasma applegatei* Shimada, Welton and Long, 2014. LACM 122190, Miocene, Pyramid Hill Sand Quarry in southeastern San Joaquin Valley, California. Photos courtesy of Kenshu Shimada, used with permission. a. lingual view; b. labial view. Scale: 5 mm. 8. *Carcharias contortidens* (Agassiz, 1843). SMNS 17455, Miocene, Siessen near Bad Saulgau, , Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 10 mm.

Figure 3. 1. *Carcharias gustrowensis* (Winkler, 1875). SMNS 97015/55, Miocene, Rengetsweiler, Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 10 mm. 2. *Araloselachus cuspidatus* (Agassiz, 1843). SMNS 97269, Miocene, Kühnring, Lower Austria. a. lingual view; b. labial view. Scale: 10 mm. 3. *Carcharoides catticus* (Philippi, 1846). SMNS 97015/42, Miocene, Rengetsweiler, Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 10 mm. 4. *Carcharodon hastalis* (Agassiz, 1838). "Broad toothed" morphotype. SMNS 97270, Miocene, Atacama desert, Chile. a. lingual view; b. labial view. Scale: 20 mm. 5. *Carcharodon hastalis* (Agassiz, 1838). "Narrow toothed" morphotype. SMNS 55505, Miocene, Baltringen, Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 20 mm. 6. *Carcharodon hubbelli* Ehret, MacFadden, Jones, DeVries, Foster and Salas-Gismond, 2012. SMNS 97271, Miocene, Peru. a. lingual view; b. labial view. Scale: 20 mm. 7. *Pachyscyllium dachiardii* (Lawley, 1876). SMNS 56753, Miocene, Ursendorf, Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 5 mm. 8. *Hemipristris serra* (Agassiz, 1843). SMNS 85944/1, Miocene, Baltringen, Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 10 mm. 9. *Carcharhinus dicelmai* Collareta, Kindlimann, Baglioni, Landini, Sarti, Altamirano, Urbina & Bianucci, 2022. MUSM 4697, Miocene, Peru. a. lingual view; b. labial view. Scale: 5 mm. Photos courtesy of Alberto Collareta, used with permission. 10. *Galeocerdo aduncus* (Agassiz, 1835). SMNS 97268, Miocene, Rammingen, Baden-Württemberg, Germany. a. lingual view; b. labial view. Scale: 10 mm. 11. *Physogaleus contortus* (Gibbes, 1849). SMNS 97272, Miocene, Will Beach, Maryland, USA. a. lingual view; b. labial view. Scale: 15 mm.

Figure 4. Relationships and stratigraphic ranges of non-carcharhiniform species discussed in the text. Topology derived from Stein et al. (2018) for extant species, with position of extinct taxa following the review presented here. Branch arrows indicate phylogenetic uncertainty; range arrows indicate taxa that appeared prior to the Late Oligocene, and dashed range lines indicate stratigraphic or taxonomic uncertainty. Node positions not to scale. C, Carcharhiniformes; H, Hexanchiformes; L, Lamniformes; O, Orectolobiformes; S, Squaliformes. .

Figure 5. Relationships and stratigraphic ranges of carcharhiniform species discussed in the text. Topology derived from Stein et al. (2018) for extant species, with position of extinct taxa following the review presented here. Branch arrows indicate phylogenetic uncertainty; range arrows indicate taxa that appeared prior to the Late Oligocene, and dashed range lines indicate stratigraphic or taxonomic uncertainty. Node positions not to scale. C, Carcharhiniformes; H, Hexanchiformes; L, Lamniformes; O, Orectolobiformes; S, Squaliformes.

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