PALEOICHTHYS 6 - 2022

Index

Shimada, K.	Phylogenetic affinity of the extinct shark family Otodontidae within Lamniformes remains uncertain - Comments on “List of skeletal material from megatooth sharks (Lamniformes, Otodontidae)” by Greenfield.	1 - 5
Greenfield, T.	Additions to “List of skeletal material from megatooth sharks”, with a response to Shimada (2022).	6-11

Phylogenetic affinity of the extinct shark family Otodontidae within Lamniformes remains uncertain – Comments on “List of skeletal material from megatooth sharks (Lamniformes, Otodontidae)” by Greenfield.

Kenshu Shimada

Department of Biological Sciences, DePaul University, Chicago, IL 60614, USA
Department of Environmental Science and Studies, DePaul University, Chicago, IL 60614, USA
Sternberg Museum of Natural History, Fort Hays State University, Hays, KS 67601, USA
kshimada@depaul.edu

Abstract

The recently proposed superfamily Lamnoidea for a clade uniting two lamniform shark families, Otodontidae and Lamnidae, as sisters is reviewed. The fact is that there is so far not even one decisive diagnostic character supporting the validity of the proposed superfamily, where the phylogenetic affinity of Otodontidae within Lamniformes remains uncertain. Therefore, the ‘Lamnoidea hypothesis’ is unfounded. This paper highlights the fact that, besides the need for valid taxonomic characters and careful consideration of the fossil record, the practice of erecting higher taxonomic categories should be conducted with caution, particularly for a phylogenetically uncertain group like Lamniformes.

keywords: evolution; fossil record, lamniform, phylogeny, systematics

Introduction

Otodontidae is an extinct shark family belonging to the order Lamniformes and represents a clade that consists of *Cretalamna*, *Kenolamna*, *Megalolamna*, and *Parotodus*, as well as the so-called megatooth shark (*Otodus*) lineage typified by *O. megalodon* (Cappetta 2012; Shimada et al. 2017; Siversson et al. 2015). Recently, Greenfield (2022) provided a list of otodontid skeletal remains and proposed a new taxonomic hypothesis. While the compilation of otodontid skeletal data is commendable, Greenfield (2022) contended that Otodontidae is sister to the family Lamnidae, that includes some extant taxa (*Carcharodon*, *Isurus*, and *Lamna*) as well as several extinct forms (*Carchariolamna*, *Carcharoides*, *Carcharomodus*, *Isurolamna*, *Karisurus*, *Lethenia*, and *Macrorhizodus*) (see Cappetta 2012; Kriwet et al. 2015). Greenfield (2022) even erected a new superfamily Lamnoidea that represents a clade consisting of Otodontidae and Lamnidae (fig. 1A). This present brief communication is to illuminate problems with Greenfield’s (2022) ‘Lamnoidea hypothesis.’

Unfounded ‘Lamnoidea hypothesis’

The most problematic aspect of Greenfield’s (2022) taxonomic proposal is the fact that there is not even one decisive diagnostic character for the new superfamily Lamnoidea. Greenfield (2022) discussed three potential characters as evidence for the close phylogenetic affinities between Otodontidae and Lamnidae. They are: 1) robust, calcified rostral cartilages with circular transverse cross-section and without fenestrae and appendices; 2) regional endothermy; and 3) “the loss of lateral cusplets and acquisition of serrations in the teeth of derived species” (p. 5). However, as discussed below, these features cannot be used to define Greenfield’s (2022) Lamnoidea uniting Otodontidae and Lamnidae.

Greenfield (2022, pp. 5–6) discussed a rostral specimen from the Pliocene of North Carolina, USA, that was originally described by Mollen & Jagt (2012) by referring to it as coming from *Otodus megalodon* or *Parotodus benedeni*. However, it must be pointed out that Mollen & Jagt (2012) explicitly noted that the exact taxonomic identity of the fossil specimen is uncertain, where it could even belong to an extinct species of Lamnidae, specifically *Carcharodon hastalis*. Greenfield (2022, fig. 2) also presented a ‘composite reconstruction’ of a generalized otodontid head with the jaws of *Cretalamna* described by Shimada (2007) combined with an outline of Mollen & Jagt’s (2012) taxonomically uncertain fossil rostral specimen; however, the scientific merit of such an artificial cranial reconstruction is highly questionable given the taxonomic uncertainty of the fossil material because the rostral specimen was an isolated find and did not accompany any teeth. In addition, the use of the robustness and calcification level of rostral cartilages cannot be a character even for Lamnidae given that such robust, ‘hypercalcified’ rostral cartilages are confined to the genus *Lamna* among the extant lamnids (Compagno 1988, 1990; Mollen et al. 2012; Maisey & Springer 2013).

Greenfield (2012) used the presence of regional endothermy to unite Otodontidae and Lamnidae. At least some taxa of Otodontidae, such as *Cretalamna* and *Otodus*, are interpreted to have been regionally endothermic (Ferrón 2017), but this thermophysiological hypothesis still needs additional support. More critically, regional endothermy apparently evolved in multiple lamniform lineages independently of one another, including the common thresher sharks, *Alopias vulpinus*, besides Lamnidae and putatively Otodontidae (Sternes et al. 2022, and references therein; vs. Pimiento et al. 2019). This taxonomic distribution of regional endothermy in Lamniformes, in turn, suggests that it is premature to use regional endothermy as evidence for the sister relationship between Otodontidae and Lamnidae. In addition, Greenfield (2022, p. 5) stated that “Previous authors (Kent 1999; Ferrón 2017; Pimiento et al. 2019) briefly suggested a sister group relationship between the families Otodontidae and Lamnidae.” However, Greenfield’s characterization of their works is inaccurate, and certainly inappropriate to use as evidence for the close phylogenetic link between the two families, particularly because none of those authors conducted any phylogenetic analysis but rather mere taxonomic discussion (Kent 1999) or character mapping (Ferrón 2017; Pimiento et al. 2019) each using an already-existing, non-comprehensive phylogenetic framework.

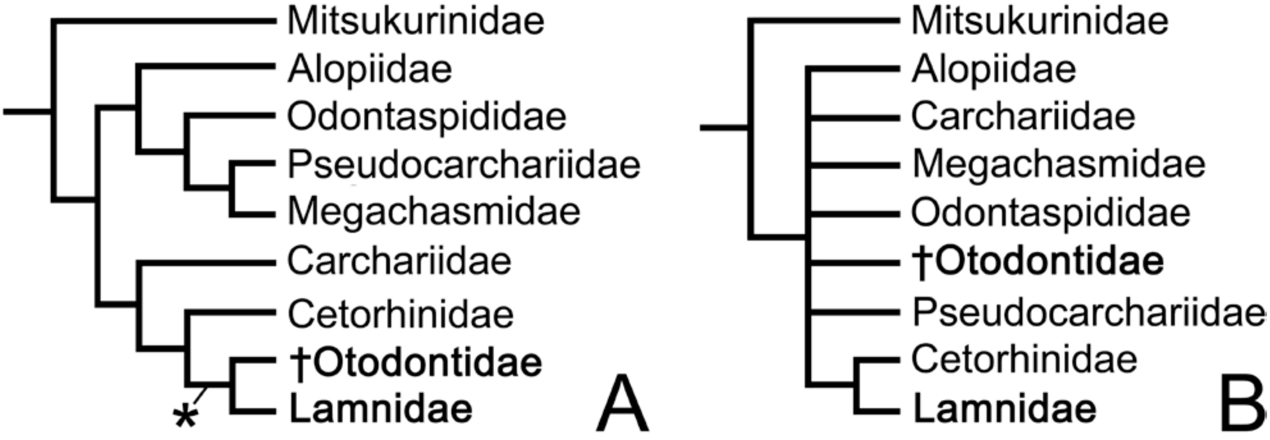


fig. 1. Simplified family-level lamniform phylogeny showing all extant clades and †Otodontidae (dagger [†] indicates extinct; note that other extinct lamniform families are not depicted). A, phylogenetic tree proposed by Greenfield (2022) showing sister relationship between †Otodontidae and Lamnidae in which the clade uniting them (asterisk [*]) represents the newly erected superfamily Lamnoidea. B, parsimonious systematic position of †Otodontidae with respect to the position of Lamnidae based on presently available evidence (see text; modified after Sternes et al. 2022; note that a large portion of the phylogenetic tree remains unresolved due to conflicting results based on various molecular and morphological studies: see Stone & Shimada 2019).

Although Otodontidae is recognized as a taxonomically distinct lamniform family (e.g., Cappetta 2012; Shimada et al. 2017), it should be noted that there has not been even one character-based phylogenetic analysis compellingly and decisively suggesting the exact phylogenetic affinity of Otodontidae within Lamniformes.

Greenfield (2022, p. 5) considered “the loss of lateral cusplets and the acquisition of serrations in the teeth of derived species”, presumably referring to the morphological trend seen from *Cretalamna* or the earliest *Otodus* to derived *Otodus* (e.g., *O. megalodon*) for Otodontidae (e.g., Ballell & Ferrón 2021) and from *Lamna* to *Carcharodon* (e.g., implicitly by Cappetta 2012, p. 210), as characters uniting Otodontidae and Lamnidae. However, such processes (‘loss’ and ‘acquisition’) must not be treated as synapomorphies or homologies (sensu Patterson 1982, 1988), especially because homologies should be framed as statements about patterns (i.e., observed conditions) and should not imply processes or mechanisms (Hall 1992, 1994). On another philosophical basis, it is worth pointing out that if the presence of lateral cusplets is plesiomorphic for a clade, the only possible evolutionary transformation, if it happens, would be a ‘loss’ of lateral cusplets as an apomorphic default. Likewise, if the absence of serrations is plesiomorphic for a clade, the only possible evolutionary transformation would be an ‘acquisition’ of serrations as an apomorphic default. Just because both families underwent the same evolutionary transformations do not necessarily indicate that they have a sister relationship.

Greenfield’s (2022, fig. 4) phylogenetic tree depicted the basking shark family Cetorhinidae to be sister to the proposed Lamnoidea consisting of Otodontidae and Lamnidae (fig. 1A). However, there is very strong support for the sister relationship between Cetorhinidae and Lamnidae based on both molecular and morphological data (Naylor et al. 2012; Stone & Shimada 2019 and references therein; Vella & Vella 2020). Molecular data have suggested that the divergence between Cetorhinidae and Lamnidae took place during the Cretaceous (e.g., Martin et al. 2002; Heinicke et al. 2009), but it is generally accepted that Cetorhinidae is a Cenozoic taxon (e.g., Friedman et al. 2010; Shimada et al. 2015) with the oldest known fossil record from the middle Eocene (Cappetta 2012; Welton 2013, 2015). Otodontidae has a geologic origin in the mid-Cretaceous represented by *Kenolamna* and *Cretalamna* (Shimada et al. 2017 and references therein), whereas the oldest taxon of Lamnidae represented by *Isurolamna* in the lower Paleocene, followed by *Macrorhizodus* in the lower Eocene (Cappetta 2012 and reference therein). If Otodontidae and Lamnidae are sister taxa that originated no later than the early Paleocene, then the evolutionary origin of Cetorhinidae should be traced back to at least the Cretaceous, but the present fossil record does not support it. Therefore, besides the fact that none of Greenfield’s (2022) characters is sufficient to justify the sister relationship between Lamnidae and Otodontidae as discussed above, more critically, the fossil record among Cetorhinidae, Lamnidae, and Otodontidae does not corroborate Greenfield’s Lamnoidea hypothesis.

Concluding remarks

Traditionally, the phrase ‘lamnoid’ was used synonymously as ‘lamniform’ at the taxonomic rank of order (e.g., ‘lamnoid shark’ and ‘lamnoid tooth pattern’: Taylor et al. 1983; Compagno 1977, 1984, 1988, 1990, 2002; Shimada 2002). Greenfield’s (2022) ‘Lamnoidea’ concept that uses the phrase in a confined, taxonomically ambiguous way introduces considerable confusion in lamniform systematics. The fact is that a large portion of the lamniform phylogeny remains unresolved due to conflicting results based on various molecular and morphological studies of extant taxa (fig. 1B; see Stone & Shimada 2019). Nevertheless, the presently available phylogenetic data and fossil record (see above for references) suggest that it is more parsimonious to consider Cetorhinidae to be a sister of Lamnidae, which would place Otodontidae outside of the clade uniting them (fig. 1B) and concomitantly rejects Greenfield’s (2022) Lamnoidea hypothesis that was proposed based on unfounded characters. Furthermore, the reality is that exactly how close Otodontidae is phylogenetically to the Cetorhinidae-Lamnidae clade also remains uncertain (fig. 1B).

It must be emphasized that erecting a new taxonomic category, like Greenfield’s (2022) ‘superfamily Lamnoidea,’ should be avoided without valid character-based justifications and consideration of the stratigraphic record of each taxon. For example, the overwhelming amount of morphological and molecular evidence suggesting the sister relationship between Cetorhinidae and Lamnidae (Stone & Shimada 2019 and references therein; Vella & Vella 2020) is tempting to erect a new superfamily for the clade uniting them. However, if the oldest fossil record of Cetorhinidae from the mid-Eocene is considered at face value to be close to its divergence time from Lamnidae, it would mean that the cetorhinid clade is nested within Lamnidae because of the presence of the two extinct lamnid genera, *Isurolamna* and *Macrorhizodus*, that evolved before the mid-Eocene (see above for references). If so, the presently known family Lamnidae including fossil taxa is non-monophyletic (specifically paraphyletic), and the question of whether a 'superfamily' uniting Lamnidae and Cetorhinidae should include *Isurolamna* and *Macrorhizodus* must be carefully evaluated. The point of this present commentary is to highlight that, besides the importance of the need for valid taxonomic characters and consideration of the fossil record, the practice of erecting higher taxonomic categories should be conducted carefully, especially for a phylogenetically uncertain taxonomic group like Lamniformes.

Acknowledgements

I thank Phillip Sternes for reviewing an earlier version of this paper, as well as Jack Cooper and Victor Perez for their formal review that improved the quality of this paper.

References

Ballell, A. & H.G. Ferrón (2021): Biomechanical insights into the dentition of megatooth sharks (Lamniformes: Otodontidae). Scientific Reports 11: 1232 [doi]

Cappetta, H. (2012): Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: teeth. 1-512. *In*: Schultze, H.P. (ed.): Handbook of paleoichthyology, volume 3E. Munich, DE: Verlag Dr. Friedrich Pfeil.

Compagno, L.J.V. (1977): Phyletic relationships of living sharks and rays. American Zoologist 17: 303-322 [doi]

Compagno, L.J.V. (1984): Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Food and Agriculture Organization Fisheries Synoposis 125 (4): 1-655

Compagno, L.J.V. (1988): Sharks of the order Carcharhiniformes. Princeton, New Jersey: Princeton University Press

Compagno, L.J.V. (1990): Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits. National Oceanic and Atmospheric Administration Technical Report, National Marine Fisheries Service 90: 357-379

Compagno, L.J.V. (2002): Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Volume 2: bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). Food and Agriculture Organization Species Catalogue for Fishery Purposes 1 (2): 1-269

Greenfield, T. (2002): List of skeletal material from megatooth sharks (Lamniformes, Otodontidae). Paleoichthys 4: 1-9

Ferrón, H. (2017): Regional endothermy as a trigger for gigantism in some extinct macropredatory sharks. PLoS One 12: e0185185 [doi]

Friedman, M., K. Shimada, L.D. Martin, M.J. Everhart, J. Liston, A. Maltese & M. Triebold (2010): 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas. Science 327: 990-993 [doi]

Hall, B.K. (1992): Evolutionary developmental biology. London, GB: Chapman and Hall

Hall, B.K. (1994): Introduction. 1-19. *In*: Hall, B.K. (ed.): Homology: hierarchical basis of comparative biology. San Diego, US: Academic Press

Heinicke, M.P., G.J.P. Naylor & S.B. Hedges. (2009): Cartilaginous fishes (Chondrichthyes). 320-327. *In*: Hedges, S.B. & S. Kumar (eds.): The timetree of life. Oxford, GB: Oxford University Press

Kent, B.W. (1999): Speculations on the size and morphology of the extinct lamnoid shark, *Parotodus benedeni* (Le Hon). Mosasaur 6: 11-15

Kriwet, J., H. Mewis & O. Hampe (2015): A partial skeleton of a new lamniform mackerel shark from the Miocene of Europe. Acta Palaeontologica Polonica 60: 857-875

Maisey, J.G. & V.G. Springer (2013): Chondrocranial morphology of the salmon shark, *Lamna ditropis*, and the porbeagle, *L. nasus* (Lamnidae). Copeia 2013: 378-389 [doi]

Martin, A.P., A.T. Pardini, L.R. Noble & C.S. Jones (2002): Conservation of a dinucleotide simple sequence repeat locus in sharks. Molecular Phylogenetics and Evolution 23: 205-213 [doi]

Mollen, F.H. & J.W.M. Jagt (2012): The taxonomic value of rostral nodes of extinct sharks, with comments on previous records of the genus *Lamna* (Lamniformes, Lamnidae) from the Pliocene of Lee Creek Mine, North Carolina (USA). Acta Geologica Polonica 62: 117-127

Mollen, F.H., S.P. Wintner, S.P. Iglesias, S.R. Van Sommeran & J.W.M. Jagt (2012): Comparative morphology of rostral cartilages in extant mackeral sharks (Chondrichthyes, Lamniformes, Lamnidae) using CT scanning. Zootaxa 3340: 29-43 [doi]

Naylor, G.J.P., J.N. Caira, K. Jensen, K.A.M. Rosana, N. Straube & C. Lakner (2012): Elasmobranch phylogeny: a mitochondrial estimate based on 595 species. 31-57. *In*: Carrier, J.C., J.A. Musick & M.R. Heithaus (eds.): The biology of sharks and their relatives. Boca Raton, US: CRC Press

Patterson, C. (1982): Morphological characters and homology. 21-74. *In*: Joysey, K.A. & A.E. Friday (eds.): Problems of phylogenetic reconstruction. London, GB: Academic Press.

Patterson, C. (1988): Homology in classical and molecular biology. Molecular Biology and Evolution 5: 603-625 [doi]

Pimiento, C., J.L. Cantalapiedra, K. Shimada, D.J. Field & J.B. Smaers (2019): Evolutionary pathways towards shark gigantism. Evolution 73: 588-599 [doi]

Shimada, K. (2002): Dental homologies in lamniform sharks (Chondrichthyes: Elasmobranchii). Journal of Morphology 251: 38-72 [doi]

Shimada, K. (2007): Skeletal and dental anatomy of lamniform shark, *Cretalamna appendiculata* from Upper Cretaceous Niobrara Chalk of Kansas. Journal of Vertebrate Paleontology 27: 584-602 [doi]

Shimada, K., R.E. Chandler, O.L.T. Lam, T. Tanaka & D.J. Ward (2017): A new elusive otodontid shark (Lamniformes:

Otodontidae) from the lower Miocene, and comments on the taxonomy of otodontid genera, including the 'megatoothed' clade. Historical Biology 29: 704-714 [doi]

Shimada, K., E.V. Popov, M. Siversson, B.J. Welton & D.J. Long (2015): A new clade of putative plankton-feeding sharks from the Upper Cretaceous of Russia and the United States. Journal of Vertebrate Paleontology 35 (5): e981335 [doi]

Siversson, M., J. Lindgren, M.G. Newbrey, P. Cederström & T.D. Cook (2015): Late Cretaceous (Cenomanian–Campanian) mid-palaeolatitude sharks of *Cretalamna appendiculata* type. Acta Palaeontologia Polonica 60: 339-384 [doi]

Sternes, P.C., J.J. Wood & K. Shimada (2022): Body forms of extant lamniform sharks (Elasmobranchii: Lamniformes), and comments on the morphology of the extinct megatooth shark, *Otodus megalodon*, and the evolution of lamniform thermophysiology. Historical Biology [doi]

Stone, N.R. & K. Shimada. (2019): Skeletal anatomy of the bigeye sand tiger shark, *Odontaspis noronhai* (Lamniformes: Odontaspididae), and its implications to lamniform phylogeny, taxonomy, and conservation biology. Copeia 107: 632-652 [doi]

Taylor, L.R., L.J.V. Compagno & P.J. Struhsaker (1983): Megamouth - a new species, genus, and family of lamnoid shark (*Megachasma pelagios*, Family Megachasmidae) from the Hawaiian Islands. Proceedings of the California Academy of Science 43: 87-110

Vella, N. & A. Vella (2020): The complete mitogenome of the critically endangered smalltooth sand tiger shark, *Odontaspis ferox* (Lamniformes: Odontaspididae), Mitochondrial DNA Part B 5 (3): 3301-3304 [doi]

Welton, B.J. (2013): A new archaic basking shark (Lamniformes: Cetorhinidae) from the Late Eocene of western Oregon, U.S.A., and description of the dentition, gill rakers and vertebrae of the Recent basking shark *Cetorhinus maximus* (Gunnerus). New Mexico Museum of Natural History and Science Bulletin 58: 1-48

Welton, B.J. (2015): A new species of late Early Miocene *Cetorhinus* (Lamniformes: Cetorhinidae) from the Astoria Formation of Oregon, and coeval *Cetorhinus* from Washington and California. Contributions in Science (Natural History Museum of Los Angeles County) 523: 67-89

Shimada, K. (2022):
Phylogenetic affinity of the extinct shark family Otodontidae within Lamniformes remains uncertain – Comments on “List of skeletal material from megatooth sharks (Lamniformes, Otodontidae)” by Greenfield.
Paleoichthys 6: 1-5

authors’ IDs & affiliations Shimada

Additions to “List of skeletal material from megatooth sharks”, with a response to Shimada (2022).

Tyler Greenfield

Independent researcher. 414 Oakwood Drive, Webster City, IA 50595, USA
tgreenfield999@gmail.com

Abstract

More specimens are added to the list of skeletal material from megatooth sharks. These include one of the most complete otodontids to date, an exceptional skeleton of *Cretalamna* with preserved soft tissues. It has important implications for the body form and phylogenetic position of otodontids. Criticisms of the Lamnoidea hypothesis by Shimada (2022) regarding taxonomy, phylogeny, and anatomical and physiological characters are addressed. Contrary to his paper, a sister group relationship between Otodontidae and Lamnidae remains the most parsimonious explanation.

keywords: Lamnoidea, *Cretalamna*, *Otodus*, skeleton, bauplan, physiology, phylogeny, taxonomy

Institutional abbreviations

IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium
MIM	MIM Museum, Beirut, Lebanon
SDM	State Darwin Museum, Moscow, Russia
USNM	National Museum of Natural History, Washington, District of Columbia, USA

Additions to the list

One specimen of *Otodus auriculatus* (Zhelezko & Kozlov 1999) and one specimen of *Cretalamna* sp. (Pfeil 2021) are added to the list, bringing the total to 25 specimens. Other specimens described by Pfeil (2021) were excluded because they were deposited in private collections. Another specimen of *Cretalamna* sp. (Trbušek 1999) was excluded because it too was deposited in a private collection. An updated version of Figure 1 from Greenfield (2022) is shown in Figure 1. An additional paper describing IRSNB P 9893, a specimen of *O. megalodon* already included in the list, was recently published (Cooper et al. 2022).

genus *Cretalamna* Glickman, 1958

species *C.* sp.

specimen: MIM unnumbered
material: mostly complete and articulated specimen consisting of the dentition and jaws, cranium and vertebral column with soft tissue outline, and first dorsal and one pectoral fins
provenance: Hjoula lagerstätte, Sannine Formation, Lebanon
age: middle Cenomanian, Late Cretaceous
reference: Pfeil 2021
note: This specimen was originally assigned to *C. appendiculata*, but that species has only been confidently identified in the Cenomanian-Turonian of Europe (Siversson et al. 2015). Given the preliminary state of its preparation and the likelihood that it is a new species, it is not referred to any named species here.

genus *Otodus* Agassiz, 1838

species *O. auriculatus* (Blainville, 1818)

specimen:	SDM Zh-U1/E12
material:	unspecified number of teeth, Meckel's cartilage fragment, and unspecified number of vertebrae
provenance:	Shorym Formation, Kazakhstan
age:	middle Bartonian, middle Eocene
reference:	Zhelezko & Kozlov 1999
note:	This specimen was originally designated as a paratype of *O. poseidoni poseidoni*. However, most species and subspecies named by Zhelezko & Kozlov have been rejected (Ehret & Ebersole 2014). *O. p. poseidoni* is here considered a junior synonym of *O. auriculatus*.

Response to Shimada (2022)

Status of Lamnoidea

Shimada mistakenly claimed that Lamnoidea was a new taxon that I erected. The subfamily 'Lamnini' was named by Bonaparte (1835), with its suffix later corrected to Lamninae following Articles 11.7.1.3 and 29.2 of the *Code* (ICZN 1999). The Principle of Coordination, Article 36.1 of the *Code*, states that "a name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at all other ranks in the family group". These names have "the same authorship and date at every rank". Thus, Bonaparte also established the family Lamnidae and superfamily Lamnoidea, even though he did not use these names. While Lamnoidea was first used by Jordan & Gilbert (1882), its authorship must be attributed to Bonaparte (1835). I simply redefined Lamnoidea to apply to the Otodontidae+Lamnidae clade, repurposing it after its infrequent and inconsistent usage in the past. This was done specifically to avoid creating a new name for a tentative hypothesis. All of this information was outlined in Greenfield (2022), but was overlooked nonetheless.

Rostral nodes and cartilages

Shimada questioned my identification of six rostral nodes (USNM 474994-99) from the early Pliocene Yorktown Formation of North Carolina. I identified them as either *Otodus megalodon* or *Parotodus benedenii*, the two otodontids currently known from this formation. Mollen & Jagt (2012) previously identified them as a member of Otodontidae or Lamnidae. An assignment to Lamnidae can be dismissed, regardless of Shimada's unjustified suggestion otherwise.

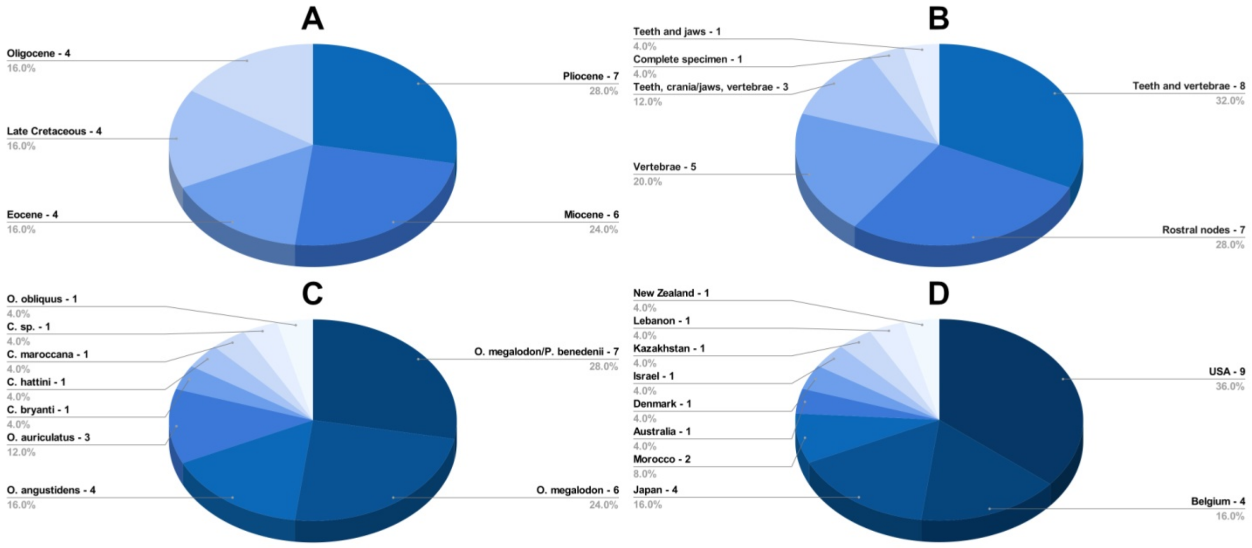


fig. 1. Updated data from the list represented as pie charts. The charts are broken down by age (A), material (B), species (C), and provenance (D).

Three lamnids are known from teeth found in the Yorktown Formation: *Isurus oxyrinchus*, *Carcharodon carcharias*, and *Carcharodon hastalis* (Purdy et al. 2001; Maisch et al. 2018). The rostral nodes of *Isurus* and *Carcharodon* are not as calcified and robust as the Yorktown specimens. Their lateral rostral cartilages attach to the node after conjoining with each other at an angle, instead of attaching separately and parallel to each other like the Yorktown specimens (Mollen & Jagt 2012; Mollen et al. 2012). The Yorktown specimens are most similar to *Lamna* in their degree of calcification and robusticity, but are still distinguished by the separate and parallel lateral rostral cartilages (Mollen & Jagt 2012; Mollen et al. 2012). These differences were discussed in the text and illustrated in Figure 3 of Greenfield (2022). The most parsimonious option is that the Yorktown rostral nodes belonged to an otodontid. Their morphology does not match the lamnids, or any other lamniforms, from the formation. Assigning them to Lamnidae would require the extra assumptions that an extinct lamnid genus unknown from teeth existed in the formation and that it had a rostral character which is not present in any extant lamnids. This is especially unlikely because known extinct lamnid genera (e.g., *Carchariolamna*, *Carcharoides*, *Lethenia*) all disappeared before the Pliocene (Cappetta 2012).

Shimada also disputed the validity of robust, calcified rostral cartilages lacking fenestrae or appendices as a synapomorphy of Otodontidae and Lamnidae. He is correct that *Isurus* and *Carcharodon* have less calcified and robust rostral cartilages than *Lamna*. However, this does not negate the fact that the character is only found in Lamnidae among extant lamniform families. Additionally, *Lamna* is recovered as the basalmost lamnid in both morphological and molecular analyses (Veléz-Zuazo & Agnarsson 2011; Naylor et al. 2012; Stone & Shimada 2019; Vella & Vella 2020). This indicates that the reduced calcification and robusticity in *Isurus* and *Carcharodon* is a derived state, while *Lamna*-like rostral cartilages were the ancestral state for lamnids. Combined with the identification of the Yorktown nodes as an otodontid, it suggests that the most recent common ancestor of Otodontidae and Lamnidae had robust, calcified rostral cartilages without fenestrae or appendices. Since no other lamniforms have that character, and there is no evidence of homoplasy, it is a valid synapomorphy that supports the Lamnoidea hypothesis.

Regional endothermy

Shimada doubted regional endothermy as another synapomorphy of Otodontidae and Lamnidae. He noted that it evolved independently twice in extant lamniforms, in Alopiidae and Lamnidae, so its appearance in Otodontidae could likewise be homoplasic. Although this scenario is possible, it is less parsimonious to assume that regional endothermy evolved three times rather than two (Ferrón 2017). If it developed only twice, this means that Otodontidae would have to be the sister group to either Alopiidae or Lamnidae. No other characters uniting alopiids and otodontids to the exclusion of other lamniforms have been proposed. The aforementioned rostral morphology of otodontids also contradicts a close relationship with alopiids. Therefore, it is still most likely that otodontids are the sister group to lamnids. Physiological characters in extinct taxa are admittedly more uncertain than skeletal characters due to the absence of direct observation. Yet, the available evidence supports regional endothermy as a synapomorphy of Otodontidae and Lamnidae.

Relationships of Cetorhinidae

Shimada stated that a sister group relationship between Cetorhinidae and Lamnidae was recovered in morphological and molecular analyses. He reasoned that this point refutes the Lamnoidea hypothesis, but that notion is incorrect. Firstly, all of the cited analyses (Naylor et al. 2012; Stone & Shimada 2019; Vella & Vella 2020) excluded otodontids. They did not actually test if Otodontidae is outside of the Cetorhinidae+Lamnidae clade. Secondly, cetorhinids and lamnids being sister groups is not as well supported as Shimada implied. At least two molecular analyses have placed *Cetorhinus* as sister to ‘sand tiger’ sharks, one to *Odontaspis*/Odontaspididae (Veléz-Zuazo & Agnarsson 2011) and one to *Carcharias*/Carchariidae (Naylor et al. 2012; this analysis was miscited by Shimada). *Caucasochasma zherikhini*, a basal cetorhinid from the early Oligocene of Russia (Prokofiev & Sychevskaya 2018), also substantiates a relationship to sand tigers. It is the oldest cetorhinid known from a fairly complete body including most of the fins. *Caucasochasma* combines *Cetorhinus*-like, filtering gill rakers with a benthic bauplan more akin to *Odontaspis* and *Carcharias*. It has an elongated body with a high vertebral count and a caudal fin with a low angle upper lobe and small lower lobe.

This demonstrates that the high angle, lunate caudal fin of *Cetorhinus,* which is comparable to lamnids, was convergently evolved. Thirdly, a divergence time for Cetorhinidae in the Cretaceous is not as unlikely as Shimada asserted. The gill rakers and minute teeth diagnostic of cetorhinids appeared in the Eocene

(Welton 2013), but that does not mean the family originated then. Extrapolating from *Caucasochasma* and sand tigers, it is plausible that the earliest cetorhinids had larger, tearing type teeth and lacked prominent gill rakers, reflecting no specialization for filter feeding. It would render them virtually unrecognizable and easily misidentified as an odontaspidid or carchariid (pers. obs.).

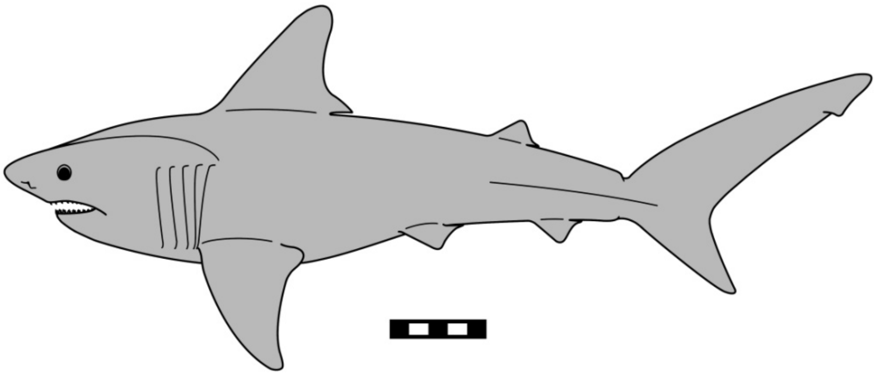


fig. 2.

A life reconstruction of *Cretalamna* sp. from Hjoula based on specimens figured in Pfeil (2021). Missing or obscured parts were restored after *Lamna* (Ebert et al. 2021). The head is the most conjectural region since it is not preserved in lateral view in any specimens. The scale bar is 10 centimeters.

Bauplan of *Cretalamna*

Remarkable specimens of *Cretalamna* sp. (MIM unnum. and others in private collections) from the Cenomanian Hjoula lagerstätte of Lebanon were recently described by Pfeil (2021, p. 167 & pl. 25). These are the first otodontids known from nearly complete skeletons with extensive soft tissues. They increase the skeletal completeness previously quantified (Greenfield 2022) to almost 100% in every metric. Most importantly, they reveal the bauplan of *Cretalamna* and by extension the ancestral bauplan of Otodontidae. It is most similar to lamnids (Ebert et al. 2021), having a fusiform body with large first dorsal, pectoral, and caudal fins but very reduced second dorsal, pelvic, and anal fins. The body compactness and relative sizes of the fins are closest to *Lamna* in particular. A notable difference from lamnids is the first dorsal fin, which is positioned directly above the pectoral fins instead of behind them. Another difference is the caudal fin, which has a less steeply inclined upper lobe and a proportionally smaller lower lobe. Its shape is semilunate compared to the lunate caudal fins of lamnids. A life reconstruction of *Cretalamna* is depicted in Figure 2. Overall, its bauplan fits the tachypelagic ecomorphotype that characterizes fast swimming, endothermic, pelagic sharks (Compagno 1990). In extant lamniforms, only lamnids are truly tachypelagic. *Cetorhinus* shares some features, but it is a slower cruiser and lacks regional endothermy. As mentioned before, the fossil record of cetorhinids shows that these features are convergent. The new specimens of *Cretalamna* suggest that a tachypelagic bauplan is an additional synapomorphy of Otodontidae and Lamnidae. Their exceptionally preserved bodies are presently the strongest evidence for the Lamnoidea hypothesis. Furthermore, they align with prior proposals of a lamnid-like body form in otodontids (Gottfried et al. 1996; Cooper et al. 2020, 2022)

Acknowledgements

Jack Cooper is thanked for his constructive review which refined this paper.

References

Agassiz, J.L.R. (1838): Recherches sur les poissons fossiles. Onzième livraison. Neuchatel, CH: Petitpierre et Prince, H. Nicolet

Blainville, H.M.D., de (1818): Sur les ichthyolites ou les poissons fossiles. 310-395. *In*: Nouveau dictionnaire d'histoire naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Tome XXVII. Paris, FR: Deterville

Bonaparte, C.L. (1835): Prodromus systematis ichthyologiae. Nuovi Annali delle Scienze Naturali 2 (4): 181-196, 272-277

Cappetta, H. (2012): Handbook of palaeoichthyology. Volume 3E. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. Munich, DE: Verlag Dr. Friedrich Pfeil

Compagno, L.J.V. (1990): Alternative life-history styles of cartilaginous fishes in time and space. Environmental Biology of Fishes 28: 33-75 [doi]

Cooper, J.A., J.R. Hutchinson, D.C. Bernvi, G. Cliff, R.P. Wilson, M.L. Dicken, J. Menzel, S. Wroe, J. Pirlo & C. Pimiento (2022): The extinct shark *Otodus megalodon* was a transoceanic superpredator: Inferences from 3D modeling. Science Advances 8 (33): eabm9424 [doi]

Cooper, J.A., C. Pimiento, H.G. Ferrón & M.J. Benton (2020): Body dimensions of the extinct giant shark *Otodus megalodon*: A 2D reconstruction. Scientific Reports 10: 14596 [doi]

Ebert, D.A., M. Dando & S. Fowler (2021): Sharks of the world: A complete guide. Princeton, US: Princeton University Press [doi]

Ehret, D.J. & J. Ebersole (2014): Occurrence of the megatoothed sharks (Lamniformes: Otodontidae) in Alabama, USA. PeerJ 2: e625 [doi]

Ferrón, H.G. (2017): Regional endothermy as a trigger for gigantism in some extinct macropredatory sharks. PLoS ONE 12 (9): e0185185 [doi]

Glickman, L.S. (1958): O tempakh evolyutsii lamnoidnykh akul [On the rate of evolution of lamnoid sharks]. Doklady Akademii Nauk SSSR 123 (3): 569-571

Gottfried, M.D., L.J.V. Compagno & S.C. Bowman (1996): Size and skeletal anatomy of the giant “megatooth” shark *Carcharodon megalodon*. 55-66. *In*: Klimley, A.P. & D.G. Ainley (eds.): Great white sharks: The biology of *Carcharodon carcharias*. San Diego, US: Academic Press [doi]

Greenfield, T. (2022): List of skeletal material from megatooth sharks (Lamniformes, Otodontidae). Paleoichthys 4: 1-9

ICZN (1999): International code of zoological nomenclature (4th ed.). London, GB: International Trust for Zoological Nomenclature, Natural History Museum

Jordan, D.S. & C.H. Gilbert (1882): Synopsis of the fishes of North America. Bulletin of the United States National Museum 16: 1-1018 [doi]

Maisch, H.M., IV, M.A. Becker & J.A. Chamberlain, jr. (2018): Lamniform and carcharhiniform sharks from the Pungo River and Yorktown Formations (Miocene–Pliocene) of the submerged continental shelf, Onslow Bay, North Carolina, USA. Copeia 106 (2): 353-374 [doi]

Mollen, F.H. & J.W.M. Jagt (2012): The taxonomic value of rostral nodes of extinct sharks, with comments on previous records of the genus *Lamna* (Lamniformes, Lamnidae) from the Pliocene of Lee Creek Mine, North Carolina (USA). Acta Geologica Polonica 62 (1): 117-127 [doi]

Mollen, F.H., S.P. Wintner, S.P. Iglésias, S.R. Van Sommeran & J.W.M. Jagt (2012): Comparative morphology of rostral cartilages in extant mackerel sharks (Chondrichthyes, Lamniformes, Lamnidae) using CT scanning. Zootaxa 3340: 29-43 [doi]

Naylor, G.J.P., J.N. Caira, K. Jensen, K.A.M. Rosana, N. Straube & C. Lakner (2012): Elasmobranch phylogeny: A mitochondrial estimate based on 595 species. 31-56. *In*: Carrier, J.C., J.A. Musick & M.R. Heithaus (eds.): Biology of sharks and their relatives (2nd ed.). Boca Raton, US: CRC Press [doi]

Pfeil, F.H. (2021): The new family Mesiteiidae (Chondrichthyes, Orectolobiformes), based on *Mesiteia emiliae* Kramberger, 1884. A contribution to the Upper Cretaceous (early Cenomanian) shark fauna from Lebanon. 101-182. *In*: Pradel, A. , J.S.S. Denton & P. Janvier (eds.): Ancient fishes and their living relatives: A tribute to John G. Maisey. Munich, DE: Verlag Dr. Friedrich Pfeil

Prokofiev, A.M. & E.K. Sychevskaya (2018): Basking shark (Lamniformes: Cetorhinidae) from the lower Oligocene of the Caucasus. Journal of Ichthyology 58 (2): 127-138 [doi]

Purdy, R.W., V.P. Schneider, S.P. Applegate, J.H. McLellan, R.L. Meyer & B.H. Slaughter (2001): The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. 71-202. *In*: Ray, C.E. & D.J. Bohaska (eds.): Geology and paleontology of the Lee Creek Mine, North Carolina. III. Smithsonian Contributions to Paleobiology 90. Washington, US: Smithsonian Institution Press [doi]

Shimada, K. (2022): Phylogenetic affinity of the extinct shark family Otodontidae within Lamniformes remains uncertain – Comments on “List of skeletal material from megatooth sharks (Lamniformes, Otodontidae)” by Greenfield. Paleoichthys 6: 1-5

Siversson, M., J. Lindgren, M.G. Newbrey, P. Cederström & T.D. Cook (2015): Cenomanian-Campanian (Late Cretaceous) mid-palaeolatitude sharks of *Cretalamna appendiculata* type. Acta Palaeontologica Polonica 60 (2): 339-384 [doi]

Stone, N.R. & K. Shimada (2019): Skeletal anatomy of the bigeye sand tiger shark, *Odontaspis noronhai* (Lamniformes: Odontaspididae), and its implications for lamniform phylogeny, taxonomy, and conservation biology. Copeia 107 (4): 632-652 [doi]

Trbušek, J. (1999): Upper Cretaceous sharks and rays from the Prokop opencast mine at Březina near Moravská Třebová. Acta Universitatis Palackianae Olomucensis, Facultas Rerum Naturalium, Geologica 36: 51-61

Veléz-Zuazo, X. & I. Agnarsson (2011): Shark tales: A molecular species-level phylogeny of sharks (Selachimorpha, Chondrichthyes). Molecular Phylogenetics and Evolution 58 (2): 207-217 [doi]

Vella, N. & A. Vella (2020): The complete mitogenome of the critically endangered smalltooth sand tiger shark, *Odontaspis ferox* (Lamniformes: Odontaspididae). Mitochondrial DNA, Part B: Resources 5 (3): 3319-3322 [doi]

Welton, B.J. (2013): A new archaic basking shark (Lamniformes: Cetorhinidae) from the late Eocene of western Oregon, U.S.A., and description of the dentition, gill rakers and vertebrae of the recent basking shark *Cetorhinus maximus* (Gunnerus). New Mexico Museum of Natural History and Science Bulletin 58: 1-48

Zhelezko, V.I. & V.A. Kozlov (1999): Elasmobrankhii i biostratigrafiya paleogena Zaural'ya i Sredney Azii [Elasmobranchii and Palaeogene biostratigraphy of Trans Urals and Central Asia]. Yekaterinburg, RU: Russian Academy of Sciences, Ural Branch

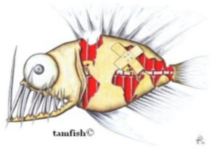
---

Greenfield, T. (2022):
Additions to “List of skeletal material from megatooth sharks”, with a response to Shimada (2022).
Paleoichthys 6: 6-11

available as pdf-file at www.pecescriollos.de since 22.Nov.2022

authors’ IDs & affiliations Greenfield

PALEOICHTHYS is being archived for permanent record by the German National Library.



logo copyright

The logo of PALEOICHTHYS has been generously relinquished for this purpose by Sascha Thamm.

Details of Sascha’s piece of art:
“Europakrise”, 40x30 cm, crayon on water color paper

Find more fishy art at Projekt TAMFISH. Please support the artist.

support & grant

Since 2003 PecesCriollos is a long-term project supported by the German Ichthyological Society (GfI).

This project, including PALEOICHTHYS, would not have been possible without GfI’s granting.