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List of skeletal material from megatooth sharks (Lamniformes, Otodontidae).

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Abstract

Otodontidae is a family of extinct sharks, commonly known as the megatooths, that includes the iconic *Otodus megalodon*. While isolated teeth are their most abundant fossils, rarer elements of the cranial and postcranial skeleton have also been recovered. Rostral nodes, jaws, and vertebrae are among these elements. This paper presents the first list of otodontid specimens that have skeletal material. It consists of 23 specimens published in the last 135 years. Knowledge of the otodontid skeleton is quantified based on the list. The phylogenetic and taxonomic implications of this material are also discussed. A sister group relationship with lamnids is supported, which is here termed the 'Lamnoidea hypothesis'.

keywords: Cretaceous, Cenozoic, *Otodus*, *Cretalamna*, *Parotodus*, crania, rostral nodes, jaws, vertebrae

Introduction

The megatooths, family Otodontidae, are a well-known clade of lamniform sharks. The most famous member is the megalodon, *Otodus megalodon*, which has left its indelible mark on both science and popular culture. This stems from its status as the largest predatory shark ever, with an estimated maximum length of 18–20 meters (Pimiento & Balk 2015; Perez et al. 2021). Besides *Otodus*, the family also includes the genera *Cretalamna*, *Kenolamna*, *Megalolamna*, *Palaeocarcharodon*, and *Parotodus* (Siversson et al. 2015; Shimada et al. 2017). Otodontids appeared in the late Albian stage of the Early Cretaceous around 100 Ma (Siversson & Machalski 2017) and went extinct during the late Pliocene between 3.6–2.6 Ma (Pimiento & Clements 2014; Boessenecker et al. 2019). Certain species like *O. megalodon* achieved cosmopolitan distributions (Pimiento et al. 2016). As a result, fossils of otodontids have been discovered on all continents, ranging from Spitsbergen in the Arctic Circle (Hansemann 1910) to Seymour Island in Antarctica (Kriwet et al. 2016). Their regional endothermy, maintaining internal body temperature through select muscles, was the key to their success. It facilitated higher metabolisms, higher swimming speeds, larger body sizes, and possibly wider temperature tolerance (Ferrón 2017; Pimiento et al. 2019; but see Harding et al. 2021 regarding the last point).

Isolated teeth are the most common shark fossils and are recognizable to paleontologists, amateur collectors, and laypeople alike (Hubbell 1996; Cappetta 2012). Their abundance is due to their enameloid hardness and high rate of production, which lead to a greater chance of fossilization. A single *O. megalodon* could produce 34,071-38,717 teeth, assuming an average replacement rate of 1.06 per day (Correia 1999) and a lifespan of 88-100 years (Shimada et al. 2021). The ubiquity of teeth has spawned the misconception that they are the only known remains from otodontids, with the cartilaginous skeleton never being preserved (pers. obs.). On the contrary, skeletal elements of sharks are partially calcified (Seidel et al. 2020, and references therein) and can be fossilized. Several otodontid specimens with skeletal material have been described, but a review of them has not been done. Here a list of these specimens with references is compiled and published for the first time. This list contains information about the taxonomy, material, provenance, and age of each specimen.

Methods

The data in the list was gathered from published literature spanning the period 1887-2022. Included were papers, books, dissertations, abstracts, and posters, for a total of 28 publications. They were found using Google Search and Google Scholar by searching generic names (‘*Otodus*’, ‘*Cretalamna*’, etc.) combined with skeletal elements (‘cranium’, ‘vertebrae’, etc.). Unpublished and/or privately-owned specimens were excluded. Only vertebrae found associated with teeth and/or other vertebrae were included. As such, isolated vertebrae like those described by Itoigawa et al. (1985), McKee (1994), Kraig (2008), and Kent (2018) were excluded. Associated vertebrae with no teeth were identified based on their size, morphology, and age. Any cranial and jaw material was included. Dermal denticles like those described by Goto et al. (1978) and Nishimoto et al. (1992) were excluded. 23 specimens fit these criteria and comprise the list. The anatomical terminology follows Compagno (1999). The taxonomy follows Shimada et al. (2017) in placing *auriculatus*, *angustidens*, and *megalodon* in *Otodus*. However, these species are instead placed in *Carcharocles* by other authors (Kent 2018; Perez et al. 2018; Miller et al. 2021). The author considers them to be congeneric with *O. obliquus* because they are most likely a lineage of chronospecies (Zhelezko & Kozlov 1999). Additionally, the absence or presence of tooth serrations is not a valid character for separating genera because it varies within other shark genera (Cappetta 2012). The authorships and publication dates of *Otodus* species follow Brignon (2021).

Institutional abbreviations

FMNH	Field Museum of Natural History, Chicago, Illinois, USA
GMNH	Gunma Museum of Natural History, Tomioka, Japan
HU	Hebrew University of Jerusalem, Jerusalem, Israel
INM	Ibaraki Nature Museum, Bando, Japan
IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium
LACM	Natural History Museum of Los Angeles County, Los Angeles, California, USA
NHMD	Natural History Museum of Denmark, Copenhagen, Denmark
NHMT	Natural History Museum, Tokai University, Shizuoka, Japan
NHMUK	Natural History Museum, London, UK
NMV	Museums Victoria, Melbourne, Australia
OU	University of Otago, Dunedin, New Zealand
SMNH	Saitama Museum of Natural History, Nagatoro, Japan
UF	Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA
USNM	National Museum of Natural History, Washington, District of Columbia, USA

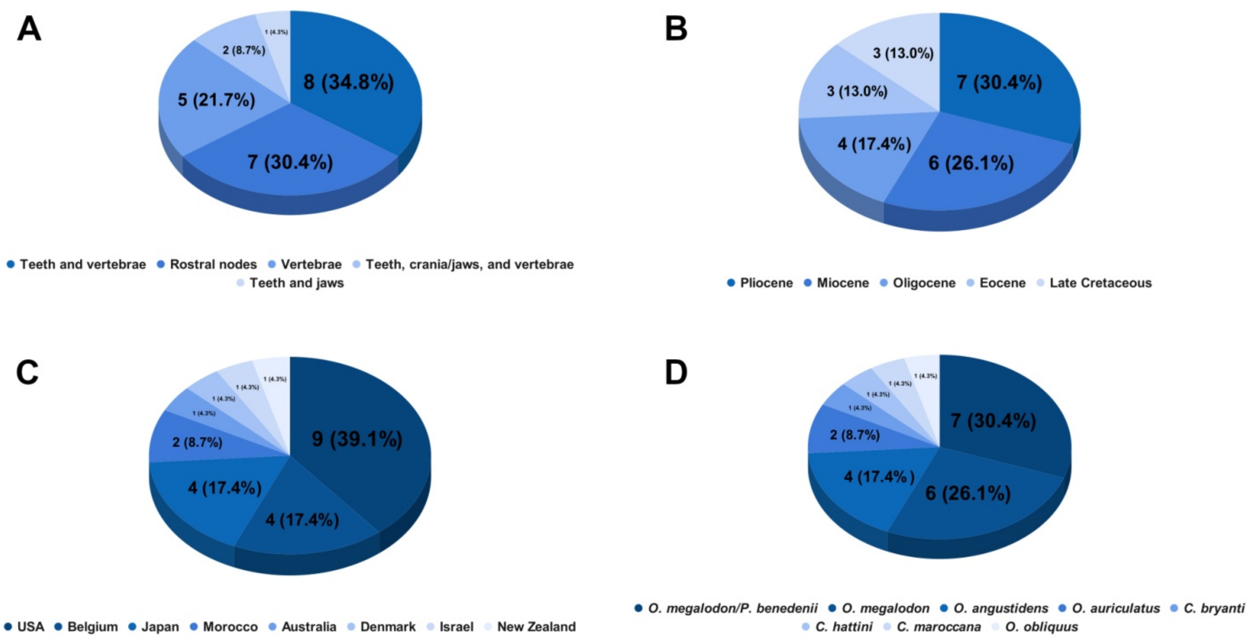

fig. 1. Data from the list represented as pie charts. The numbers on each slice are the number of specimens and percentage of total specimens, respectively. The charts are broken down by material (A), age (B), provenance (C), and species (D).

List

order **Lamniformes** Berg, 1937

superfamily **Lamnoidea** Bonaparte, 1835
- included families: Lamnidae Bonaparte, 1835 and Otodontidae Glickman, 1964
- phylogenetic definition: The least inclusive clade containing *Lamna* Cuvier, 1816 and *Otodus* Agassiz, 1838.
- note: The Principle of Coordination (Article 36.1 in ICZN, 1999) dictates that the authorship of Lamnoidea and Lamnidae is the same.

family **Otodontidae** Glickman, 1964
- phylogenetic definition: The most inclusive clade containing *Otodus* Agassiz, 1838 but not *Lamna* Cuvier, 1816.

genus ***Cretalamna*** Glickman, 1958

species ***C. bryanti*** Ebersole & Ehret, 2018
- specimen: FMNH PF 3515
- material: 13 teeth and 50 vertebrae
- provenance: Mooreville Chalk Formation, Alabama, USA
- age: late Santonian–early Campanian, Late Cretaceous
- reference: Applegate 1970
- note: This specimen was originally assigned to *C. appendiculata*, but Siversson et al. (2015) restricted that species to the Cenomanian-Turonian of Europe. Ebersole & Ehret (2018) named *C. bryanti* for teeth from the Mooreville Chalk Formation, to which this specimen is probably referrable.

species ***C. hattini*** Siversson, Lindgren, Newbrey, Cederström, & Cook, 2015
- specimen: LACM 128126 (holotype)
- material: ~120 teeth, both palatoquadrates, both Meckel's cartilages, and 35 vertebrae
- provenance: Smoky Hill Chalk Member, Niobrara Formation, Kansas, USA
- age: late Santonian–early Campanian, Late Cretaceous
- references: Shimada 2007; Siversson et al. 2015

species ***C. maroccana*** (Arambourg, 1935)
- specimen: NHMUK PV P 73610
- material: 69 teeth, cranial and jaw fragments, and 59 vertebrae
- provenance: 'Couche III', Ouled Abdoun phosphates, Morocco
- age: late Maastrichtian, Late Cretaceous
- reference: Donnelly et al. 2014

genus ***Otodus*** Agassiz, 1838

species ***O. angustidens*** (Agassiz, 1835)
- specimen: IRSNB P 928
- material: 134 teeth and 93 vertebrae
- provenance: Boom Clay Formation, Belgium
- age: Rupelian, early Oligocene
- references: Dollo 1887; Leriche 1910; Nolf 1988

- specimen: IRSNB P 929
- material: 97 teeth and 77 vertebrae
- provenance: Boom Clay Formation, Belgium
- age: Rupelian, early Oligocene
- references: Dollo 1887; Leriche 1910; Ehret 2010

- specimen: NMV P253864
- material: 33 teeth and one vertebra
- provenance: Jan Juc Formation, Australia
- age: late Chattian, late Oligocene
- reference: Ziegler et al. 2019

- specimen: OU 22261
- material: ~165 teeth and 32 vertebrae
- provenance: Otekaike Limestone Formation, New Zealand
- age: middle Chattian, late Oligocene
- references: Gottfried & Fordyce 2001; Labs-Hochstein & MacFadden 2006

species *O. auriculatus* (Blainville, 1818)

specimen: HU 21771
material: four vertebrae
provenance: unspecified formation, Israel
age: Lutetian, middle Eocene
reference: Avnimelech 1962
note: This specimen was originally referred to *O. angustidens*, but its age instead supports an assignment to *O. auriculatus*. Any identification is highly tentative given its unusual preservation as an internal cast.

specimen: IRSNB P 809
material: 34 teeth and 50+ vertebrae
provenance: Brussels Formation, Belgium
age: Lutetian, middle Eocene
references: Storms 1901; Nolf 1988; Labs-Hochstein & MacFadden 2006; Ehret 2010

species *O. megalodon* (Agassiz, 1835)

specimen: GMNH-PV-3246
material: 30+ teeth and jaw fragments
provenance: Haraichi Formation, Japan
age: Serravallian–Tortonian, middle–late Miocene
references: Goto et al. 1983; Takakuwa 2021

specimen: INM-4-012886 - 932
material: 54 teeth and four vertebrae
provenance: Kokozura Formation, Japan
age: Burdigalian, early Miocene
references: Koda et al. 2007, 2008

specimen: IRSNB P 9893 (formerly IRSNB 3121)
material: 141 vertebrae
provenance: unknown formation, Belgium
age: uncertain, likely middle–late Miocene
references: Leriche 1926; Gottfried et al. 1996; Ehret 2010; Cooper et al. 2021; Shimada et al. 2021

specimen: NHMD 157890
material: ~20 vertebrae
provenance: Gram Formation, Denmark
age: Tortonian, late Miocene
reference: Bendix-Almgreen 1983
note: Most of this specimen was accidentally discarded by museum staff and only fragments remain (Bonde and Steemann, pers. comms.).

specimen: NHMT-V501
material: 12 vertebrae
provenance: Towata Formation or Matsuba Formation, Japan
age: Burdigalian, early Miocene
reference: Shiba et al. 2016

specimen: SMNH 120
material: five vertebrae
provenance: Nagura Formation, Japan
age: Langhian-Serravallian, middle Miocene
references: Uyeno & Sakamoto 1984; Labs-Hochstein & MacFadden 2006

species *O. obliquus* (Agassiz in Morton, 1835)

specimen: UF 162732
material: 20 teeth and 10 vertebrae
provenance: unspecified unit, Ouled Abdoun phosphates, Morocco
age: Ypresian, early Eocene
references: MacFadden et al. 2004; Labs-Hochstein & MacFadden 2006; Ehret 2010
note: The numbers of teeth and vertebrae have not been published before and were sourced from the UF Vertebrate Paleontology Database [link].

genus uncertain - *Otodus* Agassiz, 1838 or *Parotodus* Cappetta, 1980

species uncertain - *O. megalodon* (Agassiz, 1835) or *P. benedenii* (Le Hon, 1871)

specimens: USNM 474994-99
material: six rostral nodes
provenance: Yorktown Formation, North Carolina, USA
age: Zanclean, early Pliocene
references: Purdy et al. 2001; Mollen & Jagt 2012
note: Mollen & Jagt (2012) narrowed down the taxon of these specimens to three candidates: *O. megalodon*, *P. benedenii*, and '*Cosmopolitodus*' *hastalis*. *C. hastalis* is now considered a species of *Carcharodon* (Ehret et

	al. 2012), so it can be ruled out based on the separate and parallel lateral rostral cartilages (see discussion).
specimen:	UF 287616
material:	one rostral node
provenance:	Peace River Formation, Florida, USA
age:	Zanclean, early Pliocene
reference:	Perez 2022
note:	This specimen was originally identified as an indeterminate lamniform, but it has separate and parallel lateral rostral cartilages like other otodontid nodes (see discussion).

Discussion

This list allows the current knowledge of otodontid skeletal anatomy to be quantified. A summary of the data is visualized in Figure 1. The most complete vertebral column, IRSNB P 9893 (*O. megalodon*), has 141 vertebrae (Cooper et al. 2021). Gottfried et al. (1996) estimated that this species had at least 200 vertebrae total. *Cretoxyrhina mantelli*, which is not an otodontid but possibly a close relative (Ferrón 2017), had an estimated 230 vertebrae (Shimada 1997). Assuming a count of 200-230 for *O. megalodon* means that 61-71% of the vertebral column is known. The most complete jaws, LACM 128126 (*Cretalamna hattini*), have both palatoquadrates and both Meckel's cartilages (Shimada 2007). Both hyomandibulae, both ceratohyals, the basihyal, and the labial cartilages are not preserved. It is unknown whether or not otodontids possessed labial cartilages; extant lamniforms have between zero and four (Shimada et al. 2009). Taking this variation into account, 31-44% of the jaws are known by element count. Besides indeterminate cranial fragments in NHMUK PV P 73610 (*C. maroccana*), six rostral nodes, USNM 474994-99 (*O. megalodon* or *Parotodus benedeni*), are the only known part of the cranium. In extant lamnids, the rostral cartilages make up 34-48% of the total length of the cranium (Mollen et al. 2012). Based on their similar morphology, the rostral cartilages of otodontids probably had similar proportions. Figure 2 shows a reconstruction of the known cranial and jaw material. None of the elements from the branchial arches or fins have been discovered yet.

Despite the limitations of the fossil record, known elements indicate the phylogenetic relationships of otodontids. The rostral cartilages are calcified and robust, being circular in transverse cross-section, and lack fenestrae and appendices. This combination of characters is shared with lamnids but no other lamniforms (Mollen & Jagt 2012). However, the lateral rostral cartilages connect to the rostral node separately and parallel to each other, which is a unique character not found in lamnids (Mollen & Jagt 2012). Figure 3 has a comparison of the rostral nodes of otodontids and lamnids. Other, non-skeletal characters are shared with lamnids, namely regional endothermy (Ferrón 2017; Pimiento et al. 2019) and the loss of lateral cusplets and acquisition of serrations in the teeth of derived species (Perez et al. 2018; Ballell & Ferron 2021). Previous authors (Kent 1999; Ferrón 2017; Pimiento et al. 2019) briefly suggested a sister group relationship between the families Otodontidae and Lamnidae. This hypothesis and the clade containing these two families have gone unnamed. Accordingly, the superfamily Lamnoidea and the term 'Lamnoidea hypothesis' are proposed here.

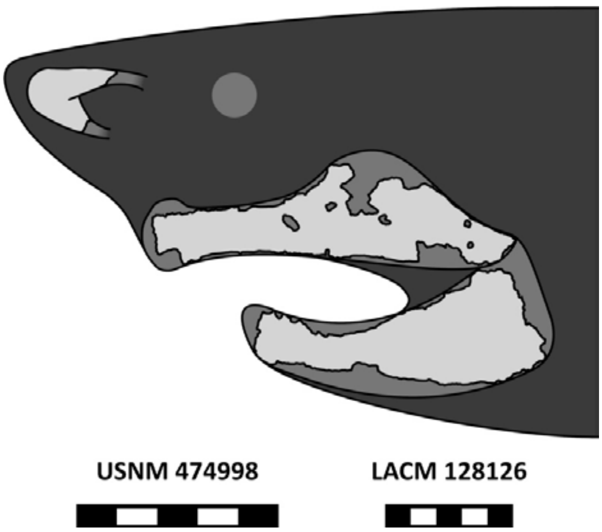

fig. 2.

A composite reconstruction of cranial and jaw material from otodontids in left lateral view. Lightest gray represents preserved areas and darker grays represent reconstructed areas. The right palatoquadrate (reversed) and left Meckel's cartilage of *Cretalamna hattini* (LACM 128126) are redrawn from Shimada (2007). The rostral node of either *Otodus megalodon* or *Parotodus benedenii* (USNM 474998) is redrawn from Mollen & Jagt (2012). Both scale bars are 10 centimeters.

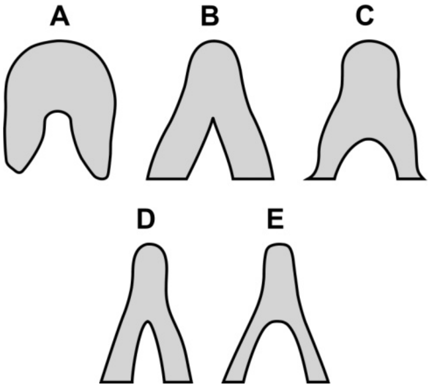

fig. 3.

The rostral nodes of otodontids and lamnids in dorsal view, demonstrating the different arrangements of the lateral rostral cartilages. The node of either *Otodus megalodon* or *Parotodus benedenii* (A, USNM 474998) is redrawn from Mollen & Jagt (2012). The nodes of *Lamna nasus* (B), *L. ditropis* (C), *Isurus oxyrinchus* (D), and *I. paucus* (E) are redrawn from Mollen *et al*. (2012). Not to scale.

A phylogenetic definition is provided in the list and a corresponding tree is shown in Figure 4. While Lamnoidea has occasionally been used by prior authors, it has been applied to inconsistent, polyphyletic groups (Jordan & Gilbert 1882; Müller & Diedrich 1991) or left undefined (MacFadden et al. 2004; Labs-Hochstein & MacFadden 2006). Restricting this name to the otodontid-lamnid clade gives it a monophyletic usage and avoids unnecessarily creating a new name.

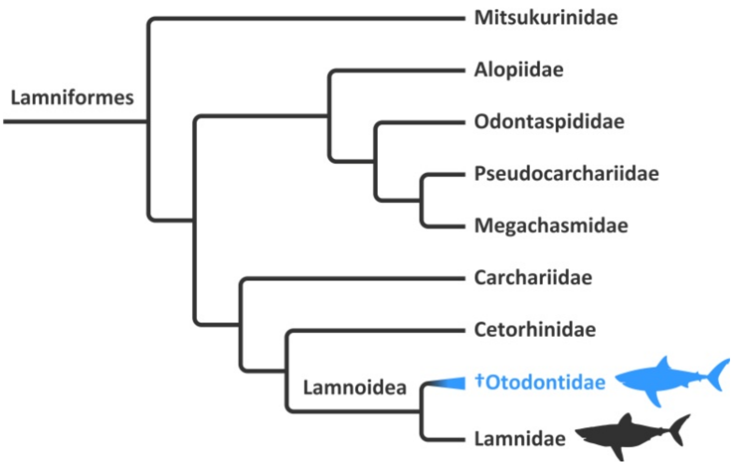

fig. 4.

The phylogenetic placement of Otodontidae according to the Lamnoidea hypothesis. The topology of this tree is mostly based on the analysis of Vella & Vella (2020). The *Otodus megalodon* silhouette is redrawn from Oliver Demuth's reconstruction in Cooper *et al*. (2020) (CC BY 4.0). The *Lamna nasus* silhouette is by Ignacio Contreras (PhyloPic, CC BY 3.0).

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