



FURTHER REVISIONS TO THE CATALOGUE OF SKELETAL MATERIAL FROM MEGATOOTH SHARKS, WITH A RESPONSE TO STERNES ET AL. (2024)

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Greenfield, T. (2026): Further revisions to the catalogue of skeletal material from megatooth sharks, with a response to Sternes et al. (2024). – Fossil Imprint, 82(1): 91–97, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).

Abstract: One specimen of *Otodus auriculatus* and three specimens of *O. megalodon* are added to the catalogue of skeletal material from megatooth sharks. Criticisms of the Lamnoidea hypothesis and reconstruction of *Cretalamna* sp. by Sternes et al. (2024) are responded to. Included is discussion of the validity of rostra, regional endothermy, and bauplans as evidence for the Otodontidae + Lamnidae clade, as well as phylogenetic analyses incorporating these families. This is the third installment in a series of papers compiling the catalogue.

Key words: Lamnoidea, *Cretalamna*, *Otodus*, skeleton, bauplan, physiology, phylogeny, taxonomy

Received: April 3, 2025 | Accepted: June 2, 2025 | Issued: October 7, 2026

Zoobank: <http://zoobank.org/urn:lsid:zoobank.org:pub:FED1659E-C93A-44F3-8AC4-0C422ABB15A7>

Introduction

The catalogue of skeletal material from megatooth sharks was previously published in two installments (Greenfield 2022a, b). The goal of this catalogue is to compile all specimens of otodontids with skeletal material, excluding unpublished and/or privately-owned specimens and isolated vertebrae. For each entry, information about the taxonomy, material, provenance, and age is provided, as well as references. Discussion of the implications of these specimens for morphology, physiology, and phylogeny is also featured. Most notable is the Lamnoidea hypothesis, the proposed sister group relationship between Otodontidae and Lamnidae. The catalogue and its conclusions have attracted flawed critiques (e.g., Shimada 2022), so another function is responding to them. The purpose of this third installment is to update the catalogue with more specimens and reply to new criticisms from other authors.

Revisions to the catalogue

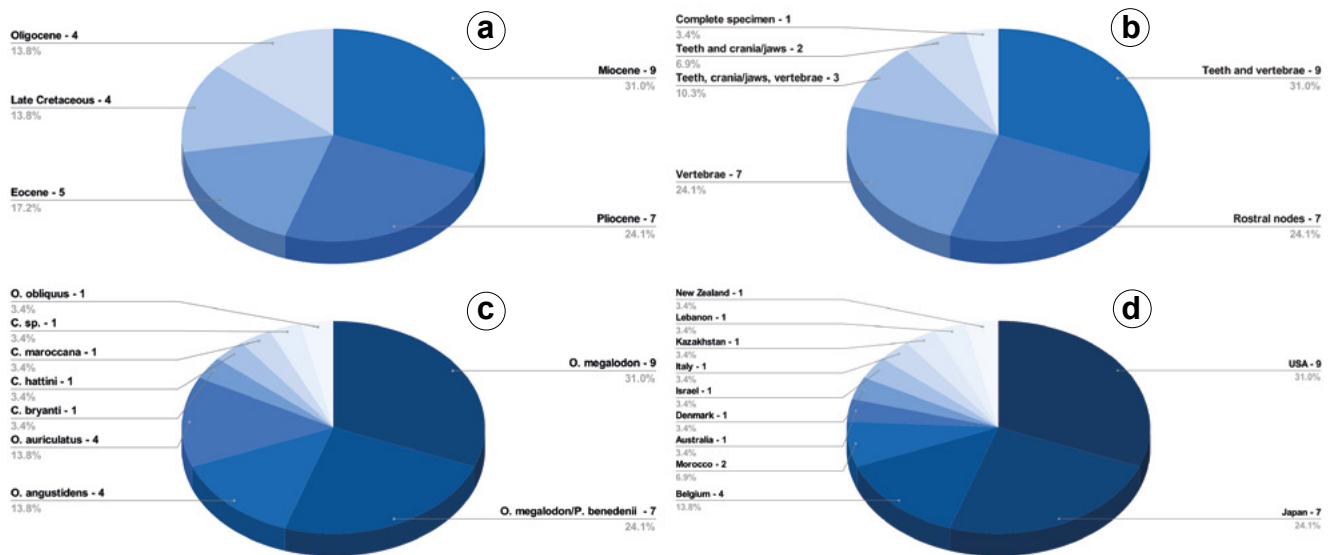
One specimen of *Otodus auriculatus* (Bassani 1895, Forti and Dal Nero 1909) and three specimens of *O. megalodon* (Uyeno et al. 1989, Watanabe et al. 2004, Shimada et al. 2024, 2025a) are here added to the catalogue, bringing the total to 29 specimens. A potential specimen of *O. megalodon*

(‘Mitchill’s monster’) was excluded because it was destroyed and associated skeletal material probably belonged to a whale (Greenfield 2023, 2024). An updated version of fig. 1 from Greenfield (2022a, b) is shown in Text-fig. 1. Additional papers relating to IRSNB P 9893, a specimen of *O. megalodon* already included in the catalogue, were recently published (Sternes et al. 2024, Shimada et al. 2025b). Another paper which is seemingly the earliest reference to the same specimen was rediscovered (Dupont 1892). It describes the mounting of a vertebral column and dentition at IRSNB like how P 9893 was first displayed there (Gottfried et al. 1996).

Material and methods

Institutional abbreviations

IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium
MCSNV	Museo Civico di Storia Naturale di Verona, Verona, Italy
MIM	MIM Museum, Beirut, Lebanon
NBE	Nishiki Board of Education, Nishiki, Japan
SMNH	Saitama Museum of Natural History, Nagatoro, Japan



Text-fig. 1. Updated data from the catalogue represented as pie charts, modified from Greenfield (2022b). The charts are broken down by age (a), material (b), species (c), and provenance (d).

Systematic palaeontology

Order Lamniformes BERG, 1937

Superfamily Lamnoidea MÜLLER et HENLE, 1838

Family Otodontidae GLICKMAN, 1964

Note. The authorship of Lamnoidea was formerly mis-attributed to ‘Bonaparte, 1835’ (Greenfield 2022a, b), but that paper was actually published in 1840 (Bonaparte 1840, Greenfield 2025). Müller and Henle (1838) were the first to name a family after the genus *Lamna* CUVIER, 1816 (incorrectly as ‘Lamnoidea’, emended to Lamnidae; Articles 11.7.1.3 and 29.2 in ICZN 1999) and authorship of the superfamily is also attributed to them under the Principle of Coordination (Article 36.1 in ICZN 1999).

Genus *Otodus* AGASSIZ, 1838

O. auriculatus (BLAINVILLE, 1818)

Specimen. MCSNV unnumbered.

Material. 50 teeth and 32 vertebrae.

Provenance. ‘Calcare grossolano’, Italy.

Age. Lutetian, middle Eocene.

References. Bassani (1895), Forti and Dal Nero (1909).

O. megalodon (AGASSIZ, 1835)

Specimen. NBE unnumbered.

Material. Six vertebrae.

Provenance. Yamaya Formation, Japan.

Age. Tortonian-Messinian, Late Miocene.

Reference. Watanabe et al. (2004).

Note. This specimen was originally not identified to the species level, but was later referred to *O. megalodon* by Shiba et al. (2016).

Specimen. NBE unnumbered.

Material. Nine vertebrae.

Provenance. Yamaya Formation, Japan.

Age. Tortonian-Messinian, Late Miocene.

Reference. Watanabe et al. (2004).

Note. This specimen was originally not identified to the species level, but was later referred to *O. megalodon* by Shiba et al. (2016).

Specimen. SMNH-VeF-38–44, 376–378, 382.

Material. 73 teeth, cranial and jaw fragments, and dermal denticles.

Provenance. Tsuchishio Formation, Japan.

Age. middle Tortonian, Late Miocene.

References. Uyeno et al. (1989), Shimada et al. (2024, 2025a).

Response to Sternes et al. (2024)

Sternes et al. (2024) dedicated an appendix to criticizing the work of Greenfield (2022a, b). Overall, they considered a sister group relationship between Otodontidae and Lamnidae and prior reconstructions of otodontids to be unfounded. Some of their claims are repeated from Shimada (2022), including ones about the nomenclature of Lamnoidea and phylogeny of Cetorhinidae. They are not discussed here since they were already refuted in Greenfield (2022b). Other claims are new and are accordingly addressed in the following sections.

Rostral nodes and cartilages

Sternes et al. (2024) contested the morphology of the rostral cartilages as a synapomorphy of Otodontidae and Lamnidae. They highlighted other lamniforms with hypercalcified rostra, such as *Alopias superciliosus* (Lowe, 1841) and an indeterminate anacoracid (Shimada 2013). Yet, neither of them contain the specific combination of characteristics seen in otodontids and lamnids (robust, calcified rostral cartilages with circular transverse cross-sections and without fenestrae or appendices). The CT scan provided by Sternes et al. (2024) shows that only the rostral node of their *A. superciliosus* is densely calcified, while the cartilages are not. This node is flatter and its sides are more outwardly angled than those of lamnoids. Specimens with an unexpanded node have been documented (Compagno 1990, Soares and de Carvalho 2013), so the mineralized structure is individually variable. The cartilages are also flattened in transverse cross-section and bear appendices (Compagno 1990). The anacoracid nodes are crushed, fragmented, and lacking the cartilages, so the relevant features cannot be assessed in this taxon. Additionally, Anacoracidae is not confidently assignable to Lamniformes. Anacoracids do not have the typical lamni-form tooth pattern and dental bullae (Shimada and Cicimurri 2005) or vertebral radial lamellae (Newbrey et al. 2015). The absence of those traits and presence of concentric lamellae are shared with Ptychodontidae (Hamm 2020, Jambura and Kriwet 2020). Therefore, the recent allocation of ptychodontids to Lamniformes (Vullo et al. 2024) is problematic for the same reasons. Affinities are more strongly supported by the

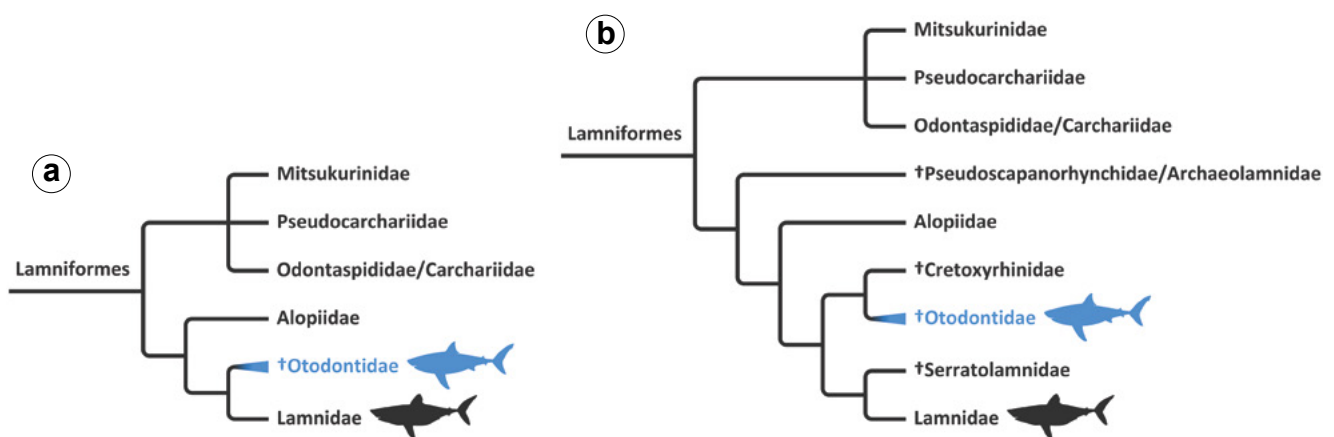
transitional form *Ptychocorax* GLICKMAN et ISTCHENKO in GLICKMAN, 1980, which has anacoracid-like anterior teeth grading into ptychodontid-like posterior teeth (Glickman 1980, Cappetta 2012). The two families could belong to a separate order, the oldest name for which would be Anacoraciformes HERMAN et VAN WAES, 2012. In any case, these examples are not comparable; they do not challenge rostral morphology as a synapomorphy of Lamnoidea or the taxonomic status of the otodontid rostra.

Regional endothermy

Sternes et al. (2024) disputed regional endothermy as another synapomorphy of Otodontidae and Lamnidae. They pointed out the recent discoveries of endothermy in *Cetorhinus maximus* (GUNNERUS, 1765) (Dolton et al. 2023a; but see also Klöcker et al. 2025) and *Odontaspis ferox* (Risso, 1810) (Dolton et al. 2023b). The newfound occurrence of this physiology in cetorhinids and odontaspidids, combined with its previous recognition in otodontids, lamnids, and alopiids, reinforces a single origin in lamniforms (Pimiento et al. 2019, Dolton et al. 2023b). That contradicts proposals of two convergences by Greenfield (2022b) and three convergences by Shimada (2022), which are now less parsimonious given the increased prevalence of the character. Consequently, regional endothermy is most likely not a synapomorphy of Lamnoidea, but instead a plesiomorphy of Lamniformes.

Phylogenetic analyses

Sternes et al. (2024) stated that Otodontidae and Lamnidae have never been tested together or recovered as sister taxa in a phylogenetic analysis. Nonetheless, Kuga (1984) included both in an analysis and achieved that very result (Text-fig. 2a). Alopiidae was the sister to Otodontidae+Lamnidae and the ‘*Odontaspis* group’ was the sister to Alopiidae+Lamnoidea. Kuga (1985) clarified that the ‘*Odontaspis* group’ was composed of Mitsukurinidae, Pseudocarchariidae, and Odontaspididae (with *Carcharias*/Carchariidae lumped into the latter after Compagno 1984). He elaborated on the characters used and



Text-fig. 2. The phylogenetic placement of Otodontidae, modified from Greenfield (2022a). The topologies of these trees are based on Kuga (1984) (a) and Kuga (1985) (b), with the taxonomy changed as explained in the text. 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).

broadened the dataset, leading to a somewhat different topology (Text-fig. 2b). In this revised iteration, Cretoxyrhinidae was the sister to Otodontidae and ‘plesion *Cretalamna*’ was the sister to Lamnidae. ‘Plesion *Cretalamna*’ consisted of species that were transferred to *Serratolamna*/Serratolamnidae (Landemaine 1991), while true *Cretalamna* was placed in Otodontidae. Cretoxyrhinidae+Otodontidae and Serratolamnidae+Lamnidae were sisters, with Alopiidae being the sister to that clade. Under this scheme, lamnids would still be the nearest living relatives to otodontids, even though they are no longer sisters. Basal to them was the wastebasket genus *Plicatolamna* (sensu Herman 1977), whose species have been reassigned to *Cretodus*/Pseudoscapanorhynchidae (Cappetta 1987, Shimada and Everhart 2019) and *Archaeolamna*/Archaeolamnidae (Siverson 1992, Underwood and Cumbaa 2010), among others. Unfortunately, the accuracy of these results is uncertain due to the following limitations of the analyses. They have neither been independently confirmed nor ruled out by subsequent testing. As outlined, some of the OTU’s were coded based on obsolete identifications. The characters were entirely dental, which are prone to homoplasy, and skeletal elements and soft tissues were not factored in. Cetorhinidae and Megachasmidae (synonymized after Maisey 1985) were omitted because of their specialized teeth. Kuga’s work does not conclusively demonstrate a close relationship between otodontids and lamnids, but it disproves the notion that the Lamnoidea hypothesis has never been phylogenetically analyzed. He at least deserves recognition as the earliest author to posit the idea.

Bauplan of *Cretalamna*

Sternes et al. (2024) questioned the restoration of *Cretalamna* sp. in fig. 2 of Greenfield (2022b). They alleged that taphonomic deformation was not taken into account when creating it. However, multiple specimens with varying completeness and angles of preservation were compared and used to reconstruct the body. Extant sharks, especially *Lamna* which is most similar in appearance, were consulted to further correct for distorted and missing parts. The constraints of this approach were noted, with the head in particular said to be the most speculative (p. 9). Sternes et al. (2024) also asserted that the specimens are ambiguously catalogued and conclusions drawn from them are not replicable. While others are privately held, one is located at the MIM Museum in Beirut, Lebanon, as acknowledged by Pfeil (2021) and Greenfield (2022b). This institution likewise houses the holotypes of the following species: the dragonflies *Libanoliupanshaniania mimi* AZAR et al., 2019 and *Libanocordulia debiei* AZAR et al., 2019 (MIM F63 and F64; Azar et al. 2019), pterosaur *Mimodactylus libanensis* KELLNER et al., 2019 (MIM F1; Kellner et al. 2019), snake *Eupodophis descouensi* (RAGE et ESCUILLÉ, 2000) (MIM F49; Zaher et al. 2022), and fish traces *Pinnichnus haqilensis* POKORNÝ et al., 2025 and *P. emmae* POKORNÝ et al., 2025 (MIM F1001 and F1021; Pokorný et al. 2025). Although the MIM *Cretalamna* is unnumbered, it is in a publicly-accessible repository and thus can be scientifically evaluated like the other taxa stored there. *Cretalamna* clearly has a tachypelagic bauplan akin to lamnids, characterized by a fusiform shape, enlarged first dorsal (anteriorly positioned), pectoral, and caudal (semilunate to lunate) fins, and reduced

second dorsal, pelvic, and anal fins. This morphotype remains as possible evidence for the Lamnoidea hypothesis and it still has important implications for the body forms of derived otodontids. If cretoxyrhinids are closely related to lamnoids, their tachypelagic aspects (Shimada 1997, Shimada et al. 2006) indicate it might be a synapomorphy of a wider clade of lamniforms than formerly suggested.

Conclusions

In summary, the catalogue of skeletal material from mega-tooth sharks is revised by the addition of four specimens, for a total of 29. The arguments of Sternes et al. (2024) are examined and found to be mostly erroneous. The rostra of alopiids and anacoracids do not dispute the identity of otodontid rostra or their shared characters with lamnids. Regional endothermy is conceded to not be a synapomorphy of Lamnoidea. A sister group relationship between Otodontidae and Lamnidae has been recovered in a phylogenetic analysis. The legitimacy of the reconstruction of *Cretalamna* and accessibility of one of the utilized specimens are defended.

Acknowledgements

Reviewer Oriol Foix Sillero, an anonymous reviewer, and editor Jiří Kvaček are thanked for their feedback which revised the manuscript.

References

- Agassiz, J. L. R. (1835): Recherches sur les poissons fossiles. Cinquième livraison. – Petitpierre et Prince, H. Nicolet, Neuchâtel, 130 pp.
<https://doi.org/10.3931/e-rara-11962>
- Agassiz, J. L. R. (1838): Recherches sur les poissons fossiles. Onzième livraison. – Petitpierre, H. Nicolet, Neuchâtel, 78 pp.
<https://doi.org/10.3931/e-rara-11962>
- Azar, D., Maksoud, S., Huang, D., Nel, A. (2019): First Lebanese dragonflies (Insecta: Odonata, Aeshnoptera, Cavilabiata) from the Arabo-African mid-Cretaceous paleocontinent. – Cretaceous Research, 93: 78–89.
<https://doi.org/10.1016/j.cretres.2018.08.025>
- Bassani, F. (1895): Avanzi di *Carcharodon auriculatus* scoperti nel calcare eocenico di Valle Gallina presso Avesa (provincia di Verona) [Remains of *Carcharodon auriculatus* discovered in the Eocene limestone of Valle Gallina near Avesa (province of Verona)]. – Memorie della Accademia di Verona (Agricoltura, Scienze, Lettere, Arti e Commercio), Serie III, 71(1): 1–11. (in Italian)
- Berg, L. S. (1937): A classification of fish-like vertebrates. – Izvestiya Akademii Nauk SSSR, Otdeleniye Matematicheskikh i Yestestvennykh Nauk, Seriya Biologicheskaya, 1937(4): 1277–1280. (in English and Russian)
- de Blainville, H. M. D. (1818): Sur les ichthyolites ou les poissons fossiles. – In: Nouveau dictionnaire d’histoire

- naturelle, appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc. Nouvelle édition. Tome XXVII. Deterville, Paris, pp. 310–395.
- Bonaparte, C. L. (1840): *Prodromus systematis ichthyologiae*. – *Nuovi Annali delle Scienze Naturali*, 2(4): 181–196, 272–277.
- Cappetta, H. (1987): *Handbook of paleoichthyology*. Volume 3B. *Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii*. – Gustav Fischer Verlag, Stuttgart, 193 pp.
- Cappetta, H. (2012): *Handbook of palaeoichthyology*. Volume 3E. *Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth*. – Verlag Dr. Friedrich Pfeil, Munich, 512 pp.
- Compagno, L. J. V. (1984): *FAO species catalogue*. Vol. 4. *Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 1. Hexanchiformes to Lamniformes*. – Food and Agriculture Organization of the United Nations, Rome, 249 pp.
- Compagno, L. J. V. (1990): Relationships of the megamouth shark, *Megachasma pelagios* (Lamniformes: Megachasmidae), with comments on its feeding habits. – In: Pratt, H. L. Jr., Gruber, S. H., Taniuchi, T. (eds), *Elasmobranchs as living resources: Advances in the biology, ecology, systematics, and the status of the fisheries*. NOAA Technical Report NMFS 90. U.S. Department of Commerce, Washington, pp. 357–379.
- Cooper, J. A., Pimiento, C., Ferrón, H. G., Benton, M. J. (2020): Body dimensions of the extinct giant shark *Otodus megalodon*: A 2D reconstruction. – *Scientific Reports*, 10: 14596 (9 pp.).
<https://doi.org/10.1038/s41598-020-71387-y>
- Cuvier, J. L. N. F. (1816): *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée*. Tome II, contenant les reptiles, les poissons, les mollusques et les annélides. – Deterville, Paris, 532 pp.
<https://doi.org/10.5962/bhl.title.41460>
- Dolton, H. R., Jackson, A. L., Deaville, R., Hall, J., Hall, G., McManus, G., Perkins, M. W., Rolfe, R. A., Snelling, E. P., Houghton, J. D. R., Sims, D. W., Payne, N. L. (2023a): Regionally endothermic traits in planktivorous basking sharks *Cetorhinus maximus*. – *Endangered Species Research*, 51: 227–232.
<https://doi.org/10.3354/esr01257>
- Dolton, H. R., Snelling, E. P., Deaville, R., Jackson, A. L., Perkins, M. W., Bortoluzzi, J. R., Purves, K., Curnick, D. J., Pimiento, C., Payne, N. L. (2023b): Centralized red muscle in *Odontaspis ferox* and the prevalence of regional endothermy in sharks. – *Biology Letters*, 19(11): 20230331 (5 pp.).
<https://doi.org/10.1098/rsbl.2023.0331>
- Dupont, É. (1892): Sur de nouveaux groupes d'ossements fossiles installés dans les galeries du Musée royal d'histoire naturelle. – *Bulletins de l'Académie royale des sciences, des lettres et des beaux-arts de Belgique*, 3^{me} série, 24(11): 462–466.
- Forti, A., Dal Nero, V. (1909): *Catalogo illustrativo della collezione petrografica e paleontologica del Cav. Enrico Nicolis* [Illustrated catalogue of the petrographic and palaeontological collection of Cav. Enrico Nicolis]. – Madonna Verona: Bollettino del Museo Civico di Verona, 3(4): 188–212. (in Italian)
- Glickman, L. S. (1964): *Akuly Paleogena i ikh stratigraficheskoye znachenie* [Paleogene sharks and their stratigraphic significance]. – Nauka, Moscow, 229 pp. (in Russian)
- Glickman, L. S. (1980): *Evolutsiya melovykh i kaynozoyevykh lamnoidnykh akul* [Evolution of Cretaceous and Cenozoic lamnoid sharks]. – Nauka, Moscow, 248 pp. (in Russian)
- Gottfried, M. D., Compagno, L. J. V., Bowman, S. C. (1996): Size and skeletal anatomy of the giant “megatooth” shark *Carcharodon megalodon*. – In: Klimley, A. P., Ainley, D. G. (eds), *Great white sharks: The biology of Carcharodon carcharias*. Academic Press, San Diego, pp. 55–66.
<https://doi.org/10.1016/B978-012415031-7/50008-2>
- Greenfield, T. (2022a): List of skeletal material from megatooth sharks (Lamniformes, Otodontidae). – *Paleoichthys*, 4: 1–9.
- Greenfield, T. (2022b): Additions to “List of skeletal material from megatooth sharks”, with a response to Shimada (2022). – *Paleoichthys*, 6: 6–11.
- Greenfield, T. (2023): The mystery of Mitchell’s monster: An *Otodus megalodon* skeleton, or an associated *O. megalodon* and whale?. – *The Mosasaur*, 13: 15–23.
<https://doi.org/10.5281/zenodo.7903372>
- Greenfield, T. (2024): Addendum to “The mystery of Mitchell’s monster”. – *The Mosasaur*, 14: 9–11.
<https://doi.org/10.5281/zenodo.13285787>
- Greenfield, T. (2025): Notes on the nomenclature of spinorays (Chondrichthyes, Batomorphii, Apolothabatiiformes). – *Bionomina*, 43(2): 9–13.
<https://doi.org/10.11646/bionomina.43.2.2>
- Gunnerus, J. E. (1765): *Brugden (Squalus maximus)*. – *Det Trondhiemske Selskabs Skrifter*, 3:33–49.
- Hamm, S. A. (2020): Stratigraphic, geographic and paleoecological distribution of the Late Cretaceous shark genus *Ptychodus* within the Western Interior Seaway, North America. – *New Mexico Museum of Natural History and Science Bulletin*, 81: 1–96.
- Herman, J. (1977): *Les Sélaciens des terrains néo crétacés & paléocènes de Belgique & des contrées limitrophes. Éléments d'une biostratigraphie intercontinentale*. – *Mémoires pour servir à l'explication des Cartes géologiques et minières de la Belgique*, 15: 1–450.
- Herman, J., Van Waes, H. (2012): Observations diverses et déductions concernant l'évolution et la systématique de quelques Euselachii, Neoselachii et Batoidei (Pisces – Elasmobranchii), actuels et fossiles. – *Géomorphologie Belgique*, 2(1): 1–89.
- ICZN (1999): *International code of zoological nomenclature* (4th ed.). – International Trust for Zoological Nomenclature, Natural History Museum, London, xxix + 306 pp.
<https://doi.org/10.5962/bhl.title.50608>
- Jambura, P. L., Kriwet, J. (2020): Articulated remains of the extinct shark *Ptychodus* (Elasmobranchii, Ptychodontidae) from the Upper Cretaceous of Spain provide insights into gigantism, growth rate and life history of ptychodontid sharks. – *PLoS One*, 15(4): e0231544 (16 pp.).
<https://doi.org/10.1371/journal.pone.0231544>

- Kellner, A. W. A., Caldwell, M. W., Holgado, B., Dalla Vecchia, F. M., Nohra, R., Sayão, J. M., Currie, P. J. (2019): First complete pterosaur from the Afro-Arabian continent: Insight into pterodactyloid diversity. – *Scientific Reports*, 9: 17875 (9 pp.).
<https://doi.org/10.1038/s41598-019-54042-z>
- Klöcker, C. A., Schlindwein, A., Arostegui, M. C., Bruvold, I. M., Wernström, J. V. Martin-Armas, M., Sims, D. W., Straube, N., Altenburger, A., Junge, C. (2025): Giants in the cold: Morphological evidence for vascular heat retention in the viscera but not the skeletal muscle of the basking shark (*Cetorhinus maximus*). – *Journal of Fish Biology*: 10.1111 (20 pp.).
<https://doi.org/10.1111/jfb.70052>
- Kuga, N. (1984): Kaseki nezumizame-me gyorui no keitō bunrui [Phylogenetic taxonomy of fossil lamniform sharks]. – In: Abstracts, 91st Annual Meeting of the Geological Society of Japan, Tokyo, Japan, p. 328. (in Japanese)
https://doi.org/10.14863/geosocabst.1984.0_328
- Kuga, N. (1985): Japanese Cenozoic elasmobranchs with special reference to Lamniforme [sic] phylogeny and ecological diversification of elasmobranchs; DSc. Dissertation. – MS, Kyoto University, Kyoto, Japan, 272 pp. (copy in National Diet Library, Seika, Japan)
- Landemaine, O. (1991): Sélaciens nouveaux du Crétacé supérieur du sud-ouest de la France. Quelques apports à la systématique des élasmobranches. – *SAGA Information*, 1: 1–45.
- Lowe, R. T. (1841): On new species of fishes from Madeira. – *Proceedings of the Zoological Society of London*, 8: 36–39.
<https://doi.org/10.1111/j.1469-7998.1840.tb00689.x>
- Maisey, J. G. (1985): Relationships of the megamouth shark, *Megachasma*. – *Copeia*, 1985(1): 228–231.
<https://doi.org/10.2307/1444816>
- Müller, J. P., Henle, F. G. J. (1838): On the generic characters of cartilaginous fishes, with descriptions of new genera. – *The Magazine of Natural History, New Series*, 2(13-14): 33–37, 88–91.
- Newbrey, M. G., Siversson, M., Cook, T. D., Fotheringham, A. M., Sanchez, R. L. (2015): Vertebral morphology, dentition, age, growth, and ecology of the large lamniform shark *Cardabiodon ricki*. – *Acta Palaeontologica Polonica*, 60(4): 877–897.
<https://doi.org/10.4202/app.2012.0047>
- 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. – In: Pradel, A., Denton, J. S. S., Janvier, P. (eds), *Ancient fishes and their living relatives: A tribute to John G. Maisey*. Verlag Dr. Friedrich Pfeil, Munich, pp. 101–182.
- Pimiento, C., Cantalapiedra, J. L., Shimada, K., Field, D. J., Smaers, J. B. (2019): Evolutionary pathways toward gigantism in sharks and rays. – *Evolution*, 73(3): 588–599.
<https://doi.org/10.1111/evo.13680>
- Pokorný, R., Nohra, R., Abi Saad, P., Vallon, L. H. (2025): Death on “live broadcast” – fish mortichnia from the Upper Cretaceous plattenkalk of Lebanon. – *Paleobiology*, 50(4): 627–640.
<https://doi.org/10.1017/pab.2024.28>
- Rage, J.-C., Escuillié, F. (2000): Un nouveau serpent bipède du Cénomanien (Crétacé). Implications phylétiques. – *Comptes rendus de l’Académie des sciences, Série IIa, Sciences de la terre et des planètes*, 330(7): 513–520.
[https://doi.org/10.1016/S1251-8050\(00\)00146-4](https://doi.org/10.1016/S1251-8050(00)00146-4)
- Risso, A. (1810): *Ichthyologie de Nice, ou histoire naturelle des poissons du département des Alpes Maritimes*. – F. Schoell, Paris, 388 pp.
<https://doi.org/10.5962/bhl.title.7052>
- Shiba, M., Sekiguchi, T., Ogawa, Y. (2016): Fossil vertebrae of *Carcharocles megalodon* (Agassiz) from the Kurami Group at Kikugawa City, in Shizuoka Prefecture. – *Science Reports of The Museum, Tokai University*, 13: 1–13. (in English and Japanese)
- Shimada, K. (1997): Skeletal anatomy of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*, from the Niobrara Chalk in Kansas. – *Journal of Vertebrate Paleontology*, 17(4): 642–652.
<https://doi.org/10.1080/02724634.1997.10011014>
- Shimada, K. (2013): Chondrichthyan origin for the fossil record of the tselfatiiform osteichthyan fish, *Thryptodus zitteli* Loomis, from the Upper Cretaceous Mooreville Chalk of Alabama. – *Alabama Museum of Natural History Bulletin*, 31(1): 72–77.
- 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.
- Shimada, K., Cicimurri, D. J. (2005): Skeletal anatomy of the Late Cretaceous shark, *Squalicorax* (Neoselachii: Anacoracidae). – *Paläontologische Zeitschrift*, 79(2): 241–261.
<https://doi.org/10.1007/BF02990187>
- Shimada, K., Everhart, M. J. (2019): A new large Late Cretaceous lamniform shark from North America, with comments on the taxonomy, paleoecology, and evolution of the genus *Cretodus*. – *Journal of Vertebrate Paleontology*, 39(4): e1673399 (25 pp.).
<https://doi.org/10.1080/02724634.2019.1673399>
- Shimada, K., Cumbaa, S. L., Van Rooyen, D. (2006): Caudal fin skeleton of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*, from the Niobrara Chalk of Kansas. – *New Mexico Museum of Natural History and Science Bulletin*, 35: 185–192.
- Shimada, K., Motani, R., Wood, J. J., Sternes, P. C., Tomita, T., Bazzi, M., Collareta, A., Gayford, J. H., Türtcher, J., Jambura, P. L., Kriwet, J., Vullo, R., Long, D. J., Summers, A. P., Maisey, J. G., Underwood, C. J., Ward, D. J., Maisch, H. M. IV, Perez, V. J., Feichtinger, I., Naylor, G. J. P., Moyer, J. K., Higham, T. E., da Silva, J. P. C. B., Bornatowski, H., González-Barba, G., Griffiths, M. L., Becker, M. A., Siversson, M. (2025b): Reassessment of the possible size, form, weight, cruising speed, and growth parameters of the extinct megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae), and new evolutionary insights into its gigantism, life history strategies, ecology, and extinction. – *Palaeontologia Electronica*, 28(1): a12.
<https://doi.org/10.26879/1502>

- Shimada, K., Yamaoka, Y., Kurihara, Y., Takakuwa, Y. (2025a): Notice of formal repository of the remaining teeth of an associated fossil specimen of the megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae), to the Saitama Museum of Natural History, Japan. – *Historical Biology*, 37(1): 154–155.
https://doi.org/10.1080/08912963.2024.2344813
- Shimada, K., Yamaoka, Y., Kurihara, Y., Takakuwa, Y., Maisch, H. M. IV, Becker, M. A., Eagle, R. A., Griffiths, M. L. (2024): Tessellated calcified cartilage and placoid scales of the Neogene megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae), offer new insights into its biology and the evolution of regional endothermy and gigantism in the otodontid clade. – *Historical Biology*, 36(7): 1259–1273.
https://doi.org/10.1080/08912963.2023.2211597
- Siverson, M. (1992): Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristianstad Basin, Sweden. – *Palaeontology*, 35(3): 519–554.
- Soares, M. C., Carvalho, M. R. de (2013): Mandibular and hyoid muscles of galeomorph sharks (Chondrichthyes: Elasmobranchii), with remarks on their phylogenetic intrarelationships. – *Journal of Morphology*, 274(10): 1111–1123.
https://doi.org/10.1002/jmor.20166
- Sternes, P. C., Jambura, P. L., Türtscher, J., Kriwet, J., Siverson, M., Feichtinger, I., Naylor, G. J. P., Summers, A. P., Maisey, J. G., Tomita, T., Moyer, J. K., Higham, T. E., da Silva, J. P. C. B., Bornatowski, H., Long, D. J., Perez, V. J., Collareta, A., Underwood, C. J., Ward, D. J., Vullo, R., González-Barba, G., Maisch, H. M. IV, Griffiths, M. L., Becker, M. A., Wood, J. J., Shimada, K. (2024): White shark comparison reveals a slender body for the extinct megatooth shark, *Otodus megalodon* (Lamniformes: Otodontidae). – *Palaeontologia Electronica*, 27(1): a7 (20 pp.).
https://doi.org/10.26879/1345
- Underwood, C. J., Cumbaa, S. L. (2010): Chondrichthyans from a Cenomanian (Late Cretaceous) bonebed, Saskatchewan, Canada. – *Palaeontology*, 53(4): 903–944.
https://doi.org/10.1111/j.1475-4983.2010.00969.x
- Uyeno, T., Sakamoto, O., Sekine, H. (1989): Description of an almost complete tooth set of *Carcharodon megalodon* from a middle Miocene bed in Saitama Prefecture, Japan. – *Bulletin of the Saitama Museum of Natural History*, 7: 73–85. (in English and Japanese)
- Vullo, R., Villalobos-Segura, E., Amadori, M., Kriwet, J., Frey, E., González González, M. A., Padilla Gutiérrez, J. M., Ifrim, C., Stinnesbeck, E. S., Stinnesbeck, W. (2024): Exceptionally preserved shark fossils from Mexico elucidate the long-standing enigma of the Cretaceous elasmobranch *Ptychodus*. – *Proceedings of the Royal Society B: Biological Sciences*, 291(2021): 20240262 (12 pp.).
https://doi.org/10.1098/rspb.2024.0262
- Watanabe, H., Masuda, K., Miyasaka, Y., Sato, R., Sato, M., Kuroda, H. (2004): Fossil vertebrae of shark from Nishikimura, Senboku-gun, Akita Prefecture. – *Annual Report of Akita Prefectural Museum*, 29: 25–32. (in English and Japanese)
- Zaher, H., Augusta, B. G., Rabinovich, R., Polcyn, M. J., Tafforeau, P. (2022): A review of the skull anatomy and phylogenetic affinities of marine pachyophiid snakes. – In: Gower, D. J., Zaher, H. (eds), *The origin and early evolutionary history of snakes*. Systematics Association Special Volume 90. Cambridge University Press, Cambridge, pp. 180–206.
https://doi.org/10.1017/9781108938891.012

Addendum

After this paper entered the proofing stage, Naoki Torikai kindly informed the author about another skeletal specimen of *O. megalodon* and sent a copy of its description (Kato 1973).

It is housed in the Atsumi Town Hall, Atsumi, Japan (ATH unnumbered) and comprises 40 vertebrae. It originates from the Nezugaseki Formation, Japan and dates to the Langhian–Tortonian, Middle–Late Miocene. An additional skeletal specimen of *O. megalodon* was recently published (Nagasawa et al. 2025). It is housed in the Yamagata Prefectural

Museum, Yamagata, Japan (YPM 13759–1–3) and comprises one tooth and two vertebrae. It originates from the Furukuchi Formation, Japan and dates to the Tortonian–Messinian, Late Miocene. These two specimens are added to the catalogue and bring the total to 31. One more *O. megalodon* specimen (Kamei 1969) was excluded because its repository was not specified.

Kamei, T. (1969): Notohantō no jōbu Nakashin Osamu yori same sekitsui-kotsu kaseki no sanshutsu (yohō) [Discovery of fossil shark vertebrae from the Upper Miocene of the Noto Peninsula (preliminary report)]. – *Kaseki Kenkyūkai Kaishi*, 2: 20–23. (in Japanese)

Kato, T. (1973): Atsumichō no chishitsu [The geology of Atsumi Town]. – In: Atsumichō-shi-hen-san iinkai [Atsumi Town History Compilation Committee] (eds), *Atsumichō no shizen* [The nature of Atsumi Town]. Atsumichō-shi-hen-san iinkai, Atsumi, pp. 37–106. (in Japanese)

Nagasawa, K., Seto, H., Kaihoko, Z. (2025): Fossil tooth and vertebrae of giant sharks, *Otodus megalodon*, from the Furukuchi Formation in Hanesawa, Sakegawa Village, Yamagata, northeastern Japan. – *Bulletin of the Yamagata Prefectural Museum*, 43: 13–22. (in English and Japanese)