

HISTORICAL AND NOMENCLATURAL REMARKS ON SOME MEGATOOCHED SHARK TEETH (ELASMOBRANCHII, OTODONTIDAE) FROM THE CENOZOIC OF NEW JERSEY (U.S.A.)

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Abstract. In the second issue of Samuel Morton's "Synopsis of the Organic Remains of the Cretaceous Group of the United States" published in June 1835, several otodontid shark teeth from Cenozoic formations of New Jersey are named with authorship of Louis Agassiz and meet the conditions of availability of the International Code of Zoological Nomenclature. It has gone largely unnoticed that some of these names were introduced in this work before their publication in Agassiz's masterpiece "Recherches sur les poissons fossiles". The specimens presented by Morton were kept in the John Price Wetherill (1794-1853) collection that found its way into the paleontological collection of the Academy of Natural Sciences of Drexel University, Philadelphia, where most of them have been rediscovered. These teeth are part of the type series upon which Agassiz introduced *Lamna obliqua* Agassiz in Morton, 1835, *Lamna lanceolata* Agassiz in Morton, 1835, *Carcharias lanceolatus* Agassiz in Morton, 1835, *Carcharias megalotis* Agassiz, 1835 and *Carcharias polygyrus* Agassiz in Morton, 1835, all of these species being referred to the genus *Otodus* in the present work. In order to secure the nomenclatural stability of the Otodontidae, it is established that *Otodus lanceolatus* is a junior synonym of *Otodus obliquus*, that "*Carcharias*" *lanceolatus* belongs to the genus *Otodus* Agassiz, 1838 and is invalid as a junior secondary homonym of *Otodus lanceolatus*, that *Otodus megalotis* is a junior synonym of *Otodus auriculatus* (Blainville, 1818), and that *Otodus polygyrus* (*Otodus polygyrus* being an incorrect subsequent spelling) is a junior synonym of *Otodus megalodon* (Agassiz, 1835). Furthermore, it is shown that the date of publication of *Otodus obliquus* (Agassiz in Morton, 1835) is 1835 and not 1838 as previously thought.

INTRODUCTION

Otodontidae, often referred to as megatoothed sharks, constitute an extinct family of apex predatory selachians that lived from the Early Paleocene to the Pliocene (Cappetta 2012; Pimiento & Clements 2014; Ehret & Ebersole 2014; Shimada et al. 2017; Perez et al. 2019; Boessenecker et al. 2019; Ballell & Ferrón 2021). This group experienced a trend towards gigantism throughout the Cenozoic

that culminated with *Otodus megalodon* (Agassiz, 1835b), the largest predatory shark ever reported to date (Gottfried et al. 1996; Purdy 1996; Godfrey & Altman 2005; Aguilera et al. 2008; Pimiento & Balk 2015; Pimiento et al. 2016; Lebrun & Canevet 2016; Collareta et al. 2017; Shimada 2019; Cooper et al. 2020; Perez et al. 2021; Shimada et al. 2021).

Several iconic names, including the genus *Otodus* and the species epithet *megalodon*, were introduced for the first time by the Swiss-born paleoichthyologist Louis Agassiz in his landmark contribution "Recherches sur les poissons fossiles" [Researches on fossil fishes], hereafter referred to as

“Recherches”. This book in five volumes was published in 18 installments (“Livraisons” in French) and a supplement (“Tableau général”) over a period of more than ten years between July 1833 and the beginning of 1844 (Everhart 2013; Brignon 2014, 2015a; Giusberti et al. 2018). Except for the first volume dealing with general considerations, each volume is devoted to a particular group of “fishes”. Each Livraison contains portions of text and plates from different volumes, which has always been a source of great confusion in determining the publication dates of the numerous genera and species first introduced in this work. The content and date of publication for each Livraison were first established by Brown (1890) and Jeannet (1928). More recently, these data have been reviewed and amended based on copies of the Livraisons still preserved in their original state (Brignon 2014: 250-252). Sometimes Agassiz also responded to requests from friends and colleagues to help them identify their discoveries. Names proposed by Agassiz in handwritten letters or manuscripts were sometimes published in his colleagues’ publications before he had the opportunity to do so in his own work (Brignon 2015a). This fact has often added further confusion in determining the publication dates of many of Agassiz’s names. This is notably the case for some otodontid names published in June 1835 by the physician and natural scientist Samuel George Morton (1799-1851) of Philadelphia in the second issue of his “Synopsis of the Organic Remains of the Cretaceous Group of the United States”, hereafter referred to as “Synopsis”. This problem was raised by Fowler (1911) who estimated that some of the names published in Morton’s work had priority over those published in Agassiz’s “Recherches”. Since then, this question has been ignored in the modern literature on fossil sharks. The aim of this paper is to review the historical context of the otodontid shark teeth illustrated and named in Morton’s work and to analyze their potential impact on otodontid nomenclature.

Abbreviations:

ANSP: Academy of Natural Sciences of Philadelphia, now the Academy of Natural Sciences of Drexel University, Philadelphia; **APS:** American Philosophical Society, Philadelphia; **ATL:** Alexander Turnbull Library, Wellington, New Zealand; **GSL:** Geological Society of London, UK; **ICZN:** International Commission on Zoological Nomenclature; **NHMUK:** Natural History Museum, London. Square brackets “[]” are used in transcription of manuscript letters and documents for insertions of missing words or translations in English.

HISTORICAL OVERVIEW

Archaeological data from North America indicate that pre-European Native Americans collected fossil shark teeth over the past 10,000 years (Lowery et al. 2011; Colvin 2011, 2014; Betts et al. 2012). These teeth, notably those of *Otodus megalodon*, have been found in mortuary and ritual contexts. Some of them are modified, notched, or drilled. Although most were probably used as projectile points, knives, or scraping tools, intentionally drilled holes on some fossil teeth indicate that a few were possibly used as ornaments (Lowery et al. 2011).

Otodontid teeth found in North America have been reported in publications since the early 18th century (Ray 2001; Brignon 2017). James Petiver (ca. 1663-1718), a rich London apothecary who amassed a large natural history collection, reported having received from Joseph Lord (1672-1748), two “*glossopetrae*”, i.e. fossil shark teeth, found in the Carolinas, the larger one “*being above three inches from the tip to the hollow or middle of the root*” (Petiver 1705: 1960). Joseph Lord was living in Dorchester, South Carolina and was one of several individuals in the British colonies of North America who agreed to collect natural history specimens for Petiver between 1701 and 1713 at least (Stearns 1952; Sanders & Anderson 1999; Blackwell & McMillan 2013). The Zürich physician and naturalist Johann Jakob Scheuchzer (1672-1733) was the first to publish an illustration of an otodontid shark from North America. The specimen, an incomplete tooth of *Otodus megalodon* from the Carolinas, was given him by Petiver (Scheuchzer 1708: 20, pl. 3; Gaudant & Bouillet 2008: 65). It is still preserved in the Paläontologisches Institut und Museum der Universität Zürich, under inventory number PIMUZ A/I 3600 (Leu 1999; Brignon 2020). In the catalogue of the paleontological collection of the English naturalist, antiquarian and geologist John Woodward (1665-1728), many fossil shark teeth from North America, including otodontids, are listed (Woodward 1728: 23-25). Today, these specimens are still preserved in the Woodwardian Museum, which is part of the Sedgwick Museum of Earth Science, Cambridge University, UK (Price 1989; Brignon 2019a, 2020). They were collected in Virginia by John Banister (1650-1692), and in Maryland by William Vernon (ca. 1666-1711) and the Reverend Hugh Jones (1671-1702) (Frick et al. 1987; Ray 2001).

Fig. 1 - A) John Price Wetherill (1794, Philadelphia – 1853, Philadelphia) black and white image of a painting (76.2×63.5 cm) made by Thomas Sully (1783, Horncastle, England – 1872, Philadelphia) between May 13th and June 25th, 1822 (Biddle and Fielding 1921: 315; Lewis 1922a: 161; 1922b: 165; 1924: 40-42). B) Samuel George Morton (1799, Philadelphia – 1851, Philadelphia), engraving from Wood (1853). C) Gideon Mantell (1790, Lewes – 1852, London), oil on canvas (76.2×63.5 cm) by John James Masquerier (1778, Londres – 1855, Brighton), 1837, credit: The Royal Society, inventory number P/87. D) Louis Agassiz (1807, Môtier, Switzerland – 1873, Cambridge, USA), oil on canvas (152.4×110.5 cm, figure cropped) by Frédéric Züber-Bühler (1822, Le Locle, Switzerland – 1896, Paris), 1844, credit: Harvard University Portrait Collection, Gift of G. R. Agassiz, Max Agassiz, and R. L. Agassiz, 1910, inventory number H175.



In his autograph collection, the naturalist and paleontologist Robert Wilson Gibbes (1809-1866) had the original of a letter dated February 11th, 1806, from Dr. William Reid to Thomas Jefferson, third president of the United States, reporting on the discovery of a fossil tooth of “*some monster unknown at this day*” from the Cenozoic beds of the Cooper river, South Carolina (Gibbes 1848). Gibbes, who had been able to observe the specimen, affirmed that it was a tooth of “*Carcharodon megalodon*”. The geologist and paleontologist Edward Hitchcock (1793-1864), professor of Chemistry and Natural History at Amherst College, illustrated in 1833 two “*megalodon*” teeth from Gay Head, now Aquinnah, on the western-end of Martha’s Vineyard island, Massachusetts (Hitchcock 1833: 193, pl. 11, fig. 11, 12). Finally, in 1834, Samuel George Morton published in his “Synopsis” illustrations of six otodontid

teeth. Found in New Jersey, they were part of the collection of his friend, John Price Wetherill.

The Wetherills were originally from the county of Durham, in England, and came to America in 1683 settling in Burlington, New Jersey. They owned a large landed estate in Burlington, Hunterdon, Morris and Essex counties (Jordan 1914: 788-790). John Price Wetherill was born on 17 October 1794 in Philadelphia, where his grandfather and his father had established a chemical and paint manufacturing business (Fig. 1A). In 1829, he took over the family company and was elected to the Common Council of the city of Philadelphia. He succeeded his father as clerk of The Religious Society of Friends, better known as the Free Quakers (Wetherill 1894). He held various advisory and executive positions in many of the city’s institutions, and was president of the Schuylkill Bank from 1846. For several years,

he was captain of the Second Troop, Philadelphia City Cavalry. He was a member of the American Philosophical Society, the Franklin Institute, the Geographical Society, an honorary member of the Boston Society of Natural History, the Mineralogical Society of St. Petersburg, the American Society for the Advancement of Science, and the New Jersey Society of Natural History. He was particularly active in the Academy of Natural Sciences of Philadelphia (ANSP), to which he had been admitted in March 1817, only five years after its foundation (Anonymous 1867). From December 1819 to 1835, John Price Wetherill was one of the curators of the Academy's museum, of which he was elected Vice-President from December 1834 until his death on July 23, 1853 (Anonymous 1877).

Wetherill built up a rich collection of fossils. He regularly donated objects of natural history, minerals and fossils to the Museum of the ANSP as mentioned in the lists of donations published in the Journal and the Proceedings of this institution (Anonymous 1818, 1822, 1824, 1827, 1854). He had notably deposited in the Museum of the Academy two major collections of fossils containing 3000 specimens. The first one was the late Henry Steinhauer's (1782-1818) collection of English specimens that Steinhauer had taken with him to America and that Wetherill acquired in 1826 (Torrens 2005). It was particularly rich in fossil plants of Yorkshire, as well as in invertebrates from the Jurassic and Cretaceous formations (Anonymous 1846). The second collection was that of the late John D. Clifford (1779-1820) of Lexington, Kentucky. It was purchased by Wetherill in 1829 (Boewe 2000: xxvii) and contained "*series of fossil remains of the Carboniferous deposits of the Valley of the Mississippi*", "*bones of the Mastodon, Elephant, Megalonyx, &c. together with numerous shells, zoophytes, &c.*" (Anonymous 1830, 1846). In his "Report of the curators for the year 1847", Joseph Leidy (1823-1891) mentioned the Wetherill collection within the ANSP Museum (Leidy 1847).

THE GENESIS OF MORTON'S "SYNOPSIS" AND THE QUESTION OF THE FOSSIL SHARK TEETH

In 1830, Samuel George Morton (Fig. 1B) published in the American Journal of Science and Arts

a paper in two parts dealing with the fossils from the Ferruginous Sand Formation of the United States (Morton 1830). Soon after, Morton decided to prepare a second edition of this work in a separate form that would become his famous "Synopsis of the organic remains of the Cretaceous group of the United States". Morton was in communication with various scientists in Europe, and in particular with the English obstetrician, geologist and paleontologist, Gideon Mantell (1790-1852) (Fig. 1C) (Cooper 2010; Everhart 2013). Mantell was renowned at the time for his books on the geology of Sussex, as well as for the discovery and description of *Iguanodon* (Mantell 1822, 1825, 1827; Dean 1999). The letters between Morton and Mantell are preserved in the Alexander Turnbull Library, Wellington, New Zealand (ATL; letters from Morton to Mantell) and the American Philosophical Society, Philadelphia (APS; letters from Mantell to Morton) (Brignon 2019a). The unpublished handwritten letters from Morton reveal the genesis of his "Synopsis" and give valuable bibliographical information on it. This work appears to have been published in two different issues, one year apart from another (Morton 1834, 1835a). This is far from anecdotal and has consequences on the publication dates of the nomenclatural acts it contains. The oldest letter from Morton to Mantell dates back to August 1831 (ATL, MS-Papers-0083-072). On May 19, 1832, Morton announced to Mantell that he was working on his "Synopsis" and that only seven plates were then planned:

"I have now in progress a second edition of my Synopsis of the Organic remains of the ferruginous sand which will be illustrated by at least seven plates, & upwards of an hundred figures. As soon as completed you shall receive a copy" (Morton to Mantell, Philadelphia, 19 May 1832, ATL, MS-Papers-0083-072).

Morton added a few months later:

"I have anticipated your suggestion with respect to my "Synopsis" and have occupied my leisure hours for some months past in preparing a second edition in a separate form. It will be illustrated by at least nine plates, and will be otherwise rendered as complete as I can make it. But, as without your reiterated approval of my labours I never should have ventured on a second edition, I am going to give you a share of the onus by dedicating the work to you. It is not likely, however, that I can get ready for publication before March or April next - leaving time for you to enter any

protest against my intentions of giving you a portion of the responsibility. But, my dear Sir, to the serious, I shall feel much flattered by your acceptance of this small acknowledgement of your many kindnesses to one who followed so far behind you in the path of science” (Morton to Mantell, Philadelphia, 16 September 1832, ATL, MS-Papers-0083-072).

This excerpt tells us that Mantell had been instrumental in motivating his American colleague to accomplish this project. This explains why Morton dedicated the book to Mantell, as can be read on the dedication leaf inserted just after the title of the published book (Morton 1834: [iii]). In September 1832, Morton planned to accompany his “Synopsis” with nine plates. He had at his disposal several fossil vertebrate remains of which he had already made drawings and plate proofs. Among these specimens were in particular teeth of mosasaurs of which he had sent casts to his English correspondent:

“I am highly pleased with your unequivocal recognition of the “mosasaurus” cast I sent you. I wish you could examine some of the saurian remains we have here; they are paradoxes to me, for want of means of comparisons. We find, as yet, few teeth in our marls; and all these will be figured, together with some bones in my forthcoming Synopsis”.

Morton also sent Mantell the proofs of four plates, two of which represent teeth of sharks, bony fishes and reptiles. The two other ones correspond to plates 1 and 2 of the “Synopsis”, and depict fossil invertebrates. Admitting that he did not know enough about the teeth of living sharks, Morton sought Mantell’s advice to identify them:

“I send herewith copies of four of the plates for the next edition of my “Synopsis” in the hope that you will be able to give me some further light on the teeth & bones. I am not enough acquainted with the recent Squali to note the analogies [between] their teeth & my fossil ones”.

The two plates depicting fossil vertebrate teeth sent by Morton, on September 16, 1832, are still preserved in the Mantell’s papers kept in the Alexander Turnbull Library (Fig. 2). They are provisionally numbered 8 and 9, and represent what would be the plates XI and XII in the first issue of the “Synopsis” published in 1834 (Morton 1834). With these plates, Morton communicated to Mantell the following succinct explanations (Fig. 3):

*“Pl. 8 of Do [ditto, i.e., the “Synopsis”]
Fig. 1.2.3.4.5.6.11. sharks teeth - what species think you?
Fig. 8 - Parts of two teeth attached to a portion of bone, without alveoli.
Fig. 7. Tooth of something like Mosasaurus - appears to be a shell of enamel, filled with bone.
9. Mosasaurus - (from your cast)
10. Geosaurus? - Two teeth - one emerging from the jaw.
12. Striated tooth of crocodile, from Lower marl.
13. smooth do [ditto] from calcareous strata.
Pl. 9 [fig. 1] what is this tooth? Two convex surfaces terminating in acute serrated edges.
2.3.4.5 Squali.”*

In the following letter, dated November 14, 1832, Morton urged Mantell to give him his opinion on the drawings of the teeth he had sent him along with his previous letter:

“I also very much desire you to give me, as far as possible, your opinion respecting the drawing of fossil shark and other tooth sent you on a former occasion; It appears to me that your figure of Sq. galeus (South Downs) does not differ from a figure on one of my plates (pl. 8, fig. 6) & again the large tooth pl. 9, fig. 2, is almost precisely the same as the fig. by Parkinson pl 19, fig. 11, but no name is given”. (Morton to Mantell, Philadelphia, 14 November 1832, ATL, MS-Papers-0083-072).

Morton found the tooth he depicted on “pl. 8, fig. 6” (Fig. 2; Morton 1834, 1835a: pl. 11, fig. 6) to be similar to those illustrated by Mantell (1822: 227, 318, pl. 32, fig. 12-16) in his “Fossils of the South Downs” as *Squalus galeus*. In both cases, they are indeed teeth of Anacoracidae but whereas Mantell’s specimens are attributable to *Squalicorax falcatus* (Agassiz, 1843) and come from the “Lower Chalk” (Cenomanian) (Woodward 1889: 424), the tooth illustrated by Morton can be identified as *Squalicorax pristodontus* (Agassiz, 1835a) and come from Maastrichtian deposits. Morton also noted that the tooth he showed on “pl. 9, fig. 2” (Fig. 2; Morton 1834, 1835a, pl. 12, fig. 2) was similar to the one presented by the English surgeon and apothecary James Parkinson (1755-1824) in his “Organic remains of a former world” (Parkinson: pl. 19, fig. 11). Morton was right because both teeth belong to *Otodus megalodon* (Agassiz, 1835b). In November 1832, his “Synopsis” consisted of 10 plates. He recognized that his project was behind schedule. He wanted to include new geological observations that his collea-

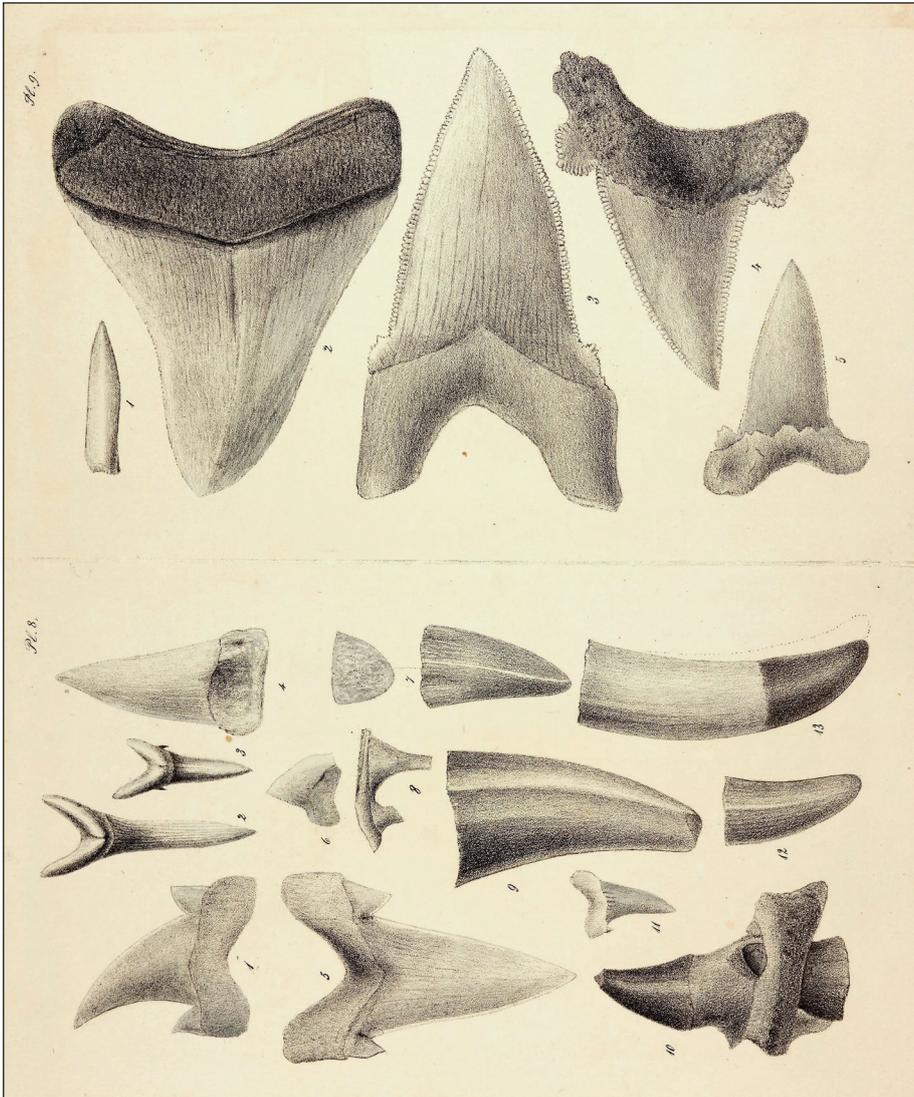


Fig 2 - Proofs of plates 8 and 9, to become plates XI and XII, of the first issue of Morton's "Synopsis". Plates in first state (stone engraving) sent by Morton to Gideon Mantell on September 16, 1832 and studied by Louis Agassiz in the fall of 1834 (Alexander Turnbull Library, Wellington, N.Z., MS-Papers-0083-072).

gue Timothy Abbott Conrad (1803-1877) planned to make in the Southern States:

"My Synopsis gets along slowly; the artist is now engaged in lithographing the 10th plate. I only regret that I have not lately met with any striking fossil of our Cretaceous group to which I could give your name. [...] The reason of my delay in publishing the new edition of the Synopsis is that Mr. Conrad is on the [verge] of going to the South on a geological expedition, & I am desirous to include his observations on the upper secondary deposits. In fact I wish to notice & illustrate every thing, worthy of attention". (Morton to Mantell, Philadelphia, 14 November 1832, ATL, MS-Papers-0083-072).

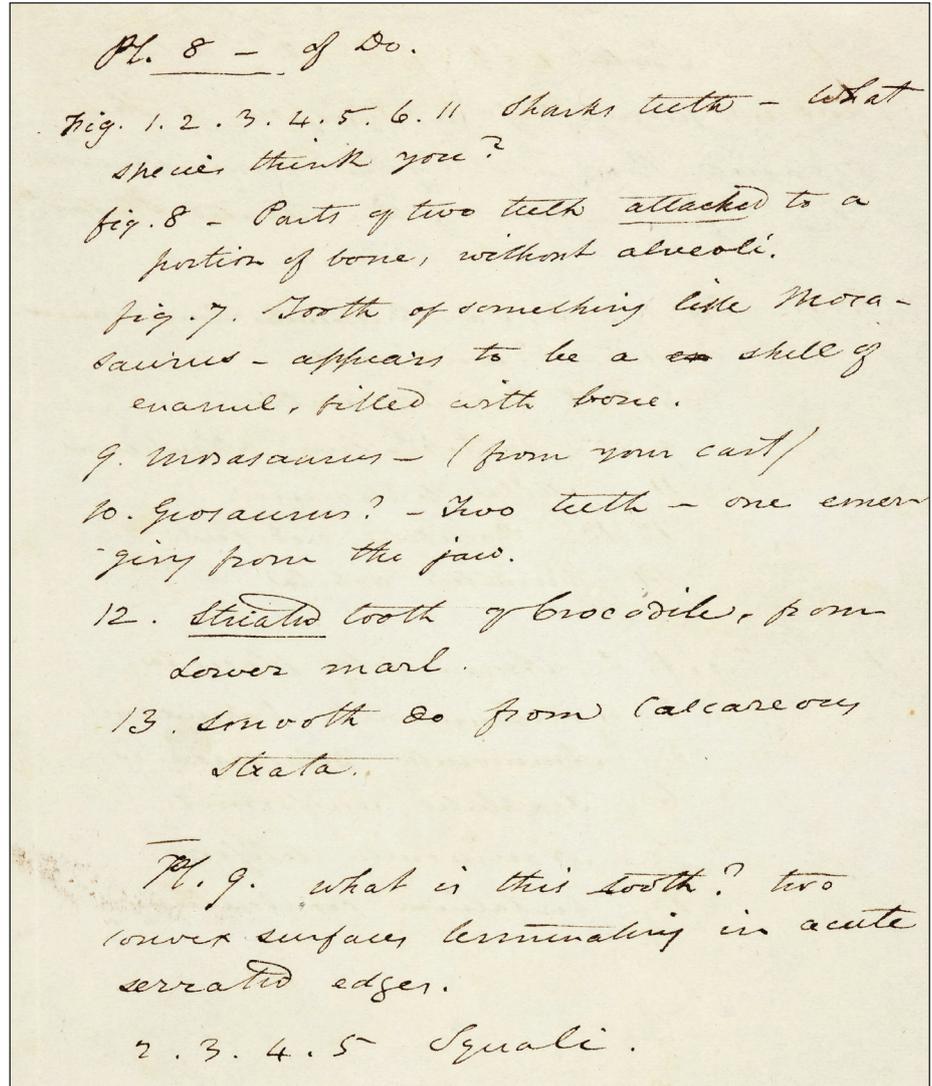
In two letters written in May 17-19, 1833 and September 30, 1833, Morton kept Mantell informed of the progress of Conrad's geological expedition. The wealth of Cretaceous and Cenozoic fossils that the latter collected in Alabama exceeded Morton's

expectations. With the addition of this new material, Morton did not see how his book could contain less than 17 plates:

"M. Conrad has been actively engaged in exploring the southern strata of this country, especially in Alabama where he now is. He has made a vast collection of Tertiary fossils, many of which are new; he has also discovered many new remains in the Cretaceous group, which will of course form part of my Synopsis. [...] I have been induced to delay publishing that essay, altho my manuscript has been ready, & twelve plates finished for more than three months past. [...] It is already evident that the illustrations of my Synopsis cannot be comprised in less than seventeen plates." (Morton to Mantell, Philadelphia, 17-19 May 1833, ATL, MS-Papers-0083-072).

"With respect to my Synopsis, you may will inquire what has become of it. I can at length assure you that the painter is at work upon it; and the delay, as I have more than one mentioned,

Fig. 3 - Morton's manuscript explanation of the plates shown in Fig. 2. This document was sent by Morton to Gideon Mantell on September 16, 1832, Alexander Turnbull Library, Wellington, N.Z. (MS-Papers-0083-072).



has arisen from anxiety to add to it all Mr. Conrad's new discoveries in the Cretaceous group of Alabama. That gentleman being a thousand miles off, and the communication slow by sea (the only way of forwarding specimens) you will readily imagine that my work has met with many impediments. No less that three new species of Hamites, portions of an Inoceramus, & a few chambered shells will now be added to my Synopsis" (Morton to Mantell, Philadelphia, 30 September 1833, ATL, MS-Papers-0083-072).

From January to May 1834, Morton made a trip to the West Indies (Wood 1853), which further delayed the progress of his book. On his return, he wrote to Mantell that it should be completed by early August. The number of plates was then eighteen:

"I left on the first day of January, & return home on the 5th of May. Before I left a part of my Synopsis was in press, and some additional fossils in the hands of the engraver; but all was necessarily suspended, nor has it been resumed until within the past

week; but now the work is fairly under progress again. I feel absolutely mortified at the delays that have occurred in the publication of a work so long since announced. But I have one great consolation: Mr. Conrad has lately returned home from his southern tour, and all his observations on the Cretaceous group of Alabama have been placed at my disposal, together with a number of new and beautiful fossils: two species of Inoceramus, three of Hamites, a perfect Trigonia, and some five chambered shells are among the number. The plates are now increased to eighteen, & the book shall be got up in a style that you will not be ashamed of. Sixty days will see the completion of it." (Morton to Mantell, Philadelphia, 31 May 1834, ATL, MS-Papers-0083-072).

While Morton's book had just been printed, Mantell was visited by Louis Agassiz (Fig. 1D) who came to Brighton to study his collection of fossil fish from October 29 to November 2, 1834. At that time, Agassiz was preparing his "Recherches sur les poissons fossiles" and only the three first Livraisons

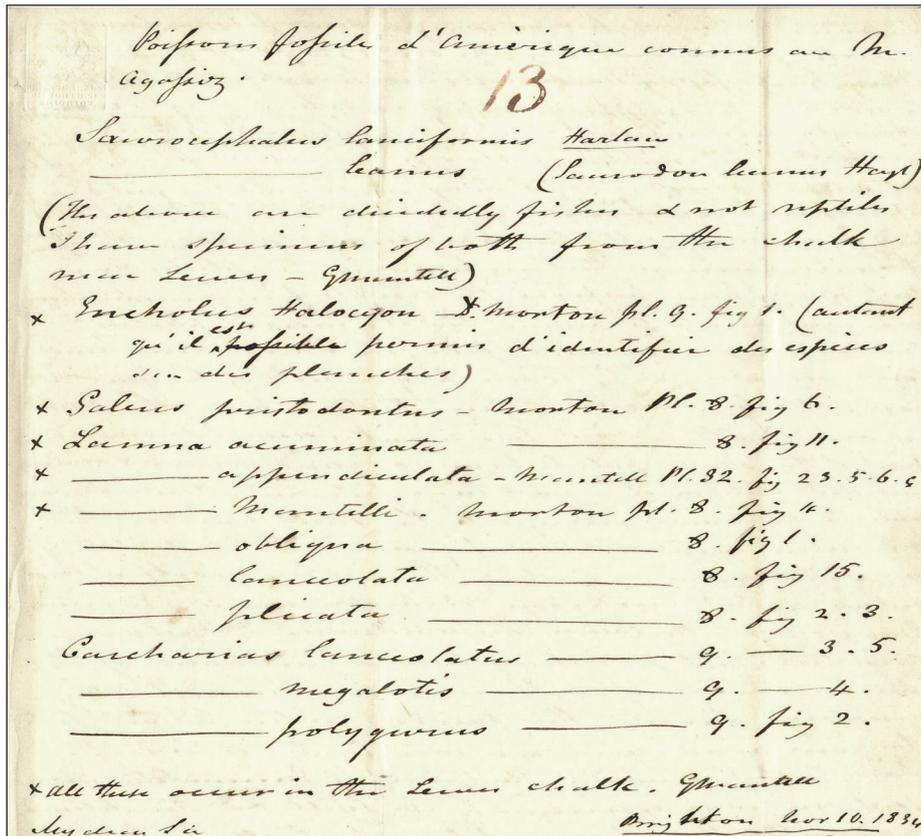


Fig. 4 - Note written by Mantell to Morton in November 1834 transcribing Agassiz's identifications of the fossil fish teeth depicted in the two plates shown in Fig. 2 (American Philosophical Society, Mss.B.M843, Samuel George Morton Papers, Series I, letters from Mantell to Morton, Brighton, 10 November 1834).

had been published. Since August 1834, he had been traveling in Great Britain to study the fossil fishes kept in British collections. His trip ended with a visit to the Mantell's museum in Brighton, particularly rich in specimens from the English Chalk (Dean 1999: 143; Brignon 2019a: 54, 99). The Swiss naturalist was accompanied by William Buckland (1784-1856) and Charles Lyell (1797-1875) and was soon joined by Robert Bakewell (1767-1843) and Michael Faraday (1791-1867). Taking advantage of Agassiz's visit, Mantell asked him to identify the teeth illustrated on the proof version of the plates (Fig. 2) that Morton had sent him two years before, in September 1832. Mantell hastened to write to his American correspondent:

"I now write to you [...] to communicate some remarks on your fossil fishes' teeth which M. Agassiz of Neuchatel, whose work on Ichthyolites is now in progress (& which if you have not I would strongly recommend you to purchase - two livraisons are out) has enabled me to offer you. M. Agassiz, Dr. Buckland, M. Lyell, Bakewell, and Faraday (an eminent chemist) were at my house last week: Agassiz come to inspect my fishes and I availed myself of the opportunity to obtain his opinion of your specimens that are figured in the plates you sent me." (Mantell to Morton, Brighton, 10 November 1834, APS, Mss.B.M843, Samuel George Morton Papers, Series I).

Mantell attached to his letter to Morton a note transcribing Agassiz's identifications and comments in French to which he added his own remarks signed "G Mantell" (Fig. 4):

"Poissons fossiles d'Amérique connus au [sic] M. Agassiz [Fossil fishes from America known to Mr. Agassiz]
Saurocephalus lanciformis Harlan
 [*Saurocephalus*] *leanus* (*Saurodon leanus* Hays)
 (The above are decidedly fishes & not reptiles, I have specimens of both from the chalk near Lewes - G Mantell)
 **Enchodus halocyon* - Morton pl. 9. fig. 1 (autant qu'il est permis d'identifier des espèces sur des planches) [as far as it is possible to identify species from plates]
 **Galeus pristodontus* - Morton Pl. 8. fig. 6.
 **Lamna acuminata* - [pl.] 8. fig. 11.
 **[Lamna] appendiculata* - Mantell Pl. 32. fig. 2 3 5 6 9
 **[Lamna] Mantelli* - Morton pl. 8. fig. 4.
 [*Lamna*] *obliqua* - [pl.] 8. fig. 1.
 [*Lamna*] *lanceolata* [pl.] 8. fig. 15.
 [*Lamna*] *plicata* [pl.] 8. fig. 2. 3.
Carcharias lanceolatus [pl.] 9. [fig.] 3. 5.
 [*Carcharias*] *megalotis* [pl.] 9. [fig.] 4.
 [*Carcharias*] *polygurus* [pl.] 9. fig. 2.
 * All these occur in the Lewes chalk, G Mantell"

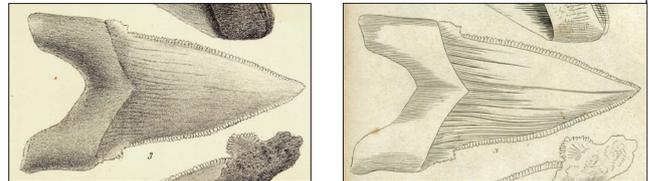
Note that the proof version of the plates are misnumbered 8 and 9 and correspond to the plates

Tab. 1 - The two issues of Morton's "Synopsis" (Morton 1834, 1835a). The two figures (excerpts of plate XII) exemplify the different engraving techniques in these two issues.

(*) Some copies bear the mention "From the Appendix to Dr. S. G. Morton's Synopsis of the Organic Remains of the Cretaceous Group of the United States." at the top of the first page of this Catalogue.

(**) In bound copies of the 2nd issue of the "Synopsis", the "Additional observations" section is sometimes placed before the "Catalogue of the fossil shells".

Edition	1 st issue	2 nd issue
Date of publication	1834 (between August and November 1834)	1835 (in or after June 1835, but before 10 October 1835)
Title page	Dated 1834	Dated with the wrong year 1834 (same title page as for the 1 st issue)
Text block	i-vi + 7-88	i-vi + 7-88 Same text as the 1 st issue
"Catalogue of the fossil shells of the Tertiary formations of the United States"	[1]-8	[1]-8 Same text as the 1 st issue (*)
"Additional observations" (June 1835)	Not present	[1]-[4] (**)
Explanation of the plates and Index	[1]-[8]	[1]-[8] Same text as the 1 st issue
Plates	Plates I to XIX Plates XI and XII in 1 st state (stone engraving)	Plates I to XIX Plates XI and XII in 2 nd state (copper engraving) Plates I to X and XIII to XIX are the same as in the 1 st issue



11 and 12, or more precisely XI and XII, in the published issues of the "Synopsis". Morton received the letter and the note from Mantell only around January 10, 1835. He had already sent his English correspondent in mid-fall 1834 a copy of his "Synopsis". By the end of December 1834, the publishers Key and Biddle had also sent 50 copies to Obadiah Rich, bookseller in London, in charge for distributing the book in Great Britain:

"I wrote to you May 25 immediately on my return from the West Indies and about the middle of the past autumn sent you a copy of my Synopsis. [...] About a month ago 50 copies of my work were sent to Mr Rich, London, by the publishers. [...] About three weeks ago I received your letter of Nov. 10 with the notes of M. Agassiz, which I do assure you, are in the highest degree interesting & instructive. I may, however, remark that the fig. on plate XII which he supposes to be a tooth of *Enchodus halyon* has proved on examination here to have belonged to a species of *Sphyræna*, as you will see by reference to the Synopsis. The other teeth are no doubt identical with those of the European strata as he has indicated. But in order to make this matter more tangible I design having casts made of all the teeth figures in the Synopsis - and also to have them re-drawn on stone in order to their better illustration." (Morton to Mantell, Philadelphia, 31 January 1835, ATL, MS-Papers-0083-072).

The first issue of the "Synopsis" was published in 1834 (Morton 1834), thereby it did not

contain the fossil shark names proposed by Agassiz. Morton was not satisfied with the two plates 11 and 12, showing the fossil teeth of fishes and reptiles. In January 1835, Morton was considering having them redrawn. A second issue of the "Synopsis" was published in or after June 1835 (Morton 1835a), with these two plates being made from copper (rather than stone) engravings (Fig. 5; Tab. 1). A four-page Appendix dated June 1835 was also added to this second issue (Fig. 6; Tab. 1). This Appendix is of the utmost importance as it includes the names proposed by Agassiz, some of them being introduced for the first time herein. Referring to the figures shown in Morton's plates 11 and 12, these names meet the requirements of Articles 11 and 12.2.7 of the International Code of Zoological Nomenclature (ICZN 1999; hereafter referred to as "the Code") for names published before 1931. It should be noted that the publication date of Agassiz's names in Morton's "Synopsis" is June 1835 and not 1834 as the title page of the book might suggest. In order that his readers who had purchased the first issue of his "Synopsis" could benefit from the information contained in this Appendix, and in particular of the names proposed by Agassiz for the shark teeth, Morton also published them in July 1835 in the American Journal of Science and Arts (Morton 1835b). On October 10, 1835, Morton announced to Mantell that he was going to send him two co-

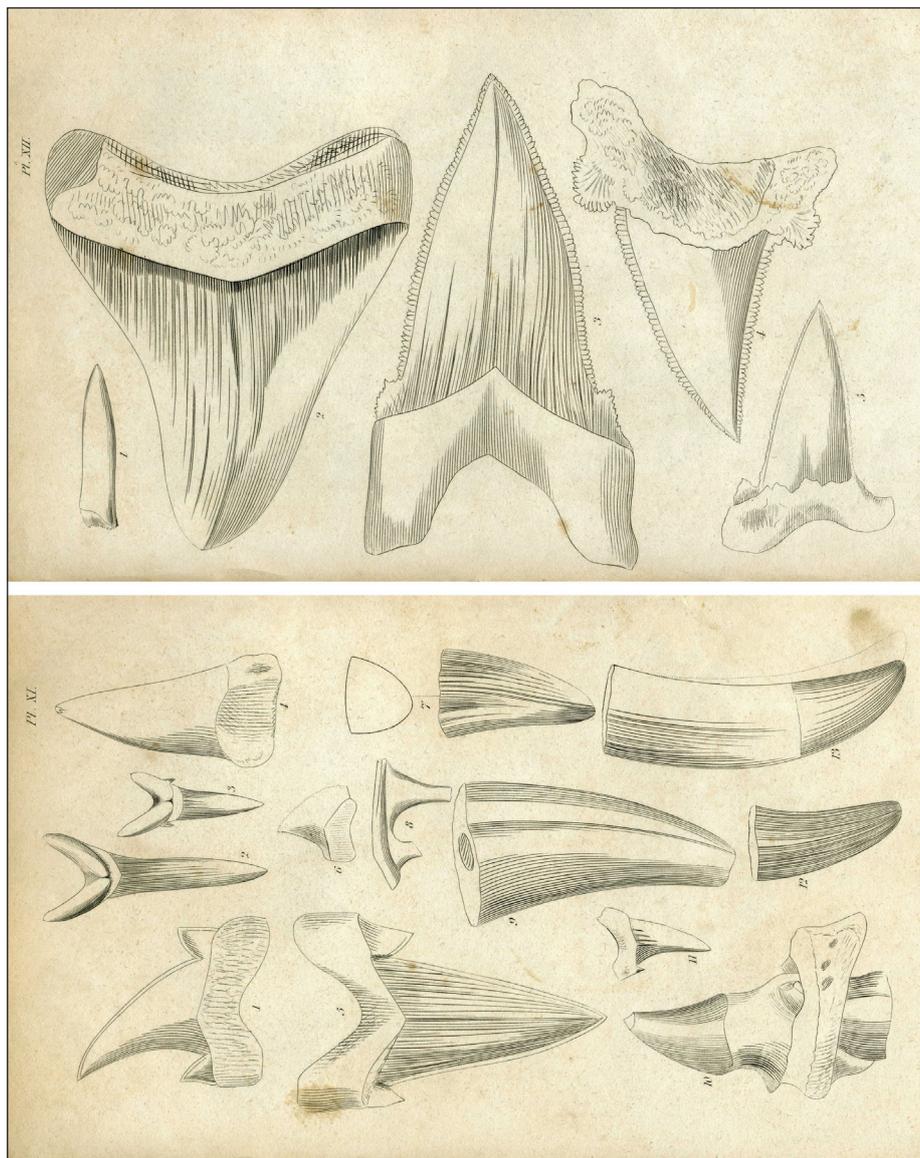


Fig. 5 - The two plates (second state, copper engraving) of the second issue of Morton's "Synopsis" representing fossil vertebrate teeth (Elasmobranchii, Actinopterygii, Squamata) (Morton 1835a: pl. 11, 12).

pies of the second issue of his "Synopsis" with the additional Appendix and plates 11 and 12 in their second state:

"I will [...] send you two more copies of my synopsis, to which I have lately added a short Appendix. I have also had plates XI & XII done on copper, so that the figures shew much better than they did on stone. This work has been extensively circulated in this country, and appears to give general satisfaction." (Morton to Mantell, Philadelphia, 10 October 1835, ATL, MS-Papers-0083-072).

Few weeks later, Morton confirmed to Mantell that a copy of his "Synopsis" and a collection of fossils from Alabama were being mailed on the first ship to England. Note that a fossil shark tooth, later named *Ptychodus mortoni* by Mantell in 1836, was included in this collection (Everhart 2013; Ikejiri &

Everhart 2015; Brignon 2019a: 72-73). On his side, Mantell sent a collection of fossil fish teeth from England identified according to Agassiz's nomenclature:

"I put you up accordingly some Eocene fossils from Alabama [...] and another copy of my synopsis, in which pl. XI and XII are engraved on copper, & much better done than the original lithograph. [...] You speak of having sent me a box by way of Liverpool containing some fishes teeth marked accordingly to Agassiz. Nothing could be more acceptable than such a present; & when you get my models together with some teeth I have put aside for you, our means of comparison will be complete. There is one additional favour I may perhaps ask - viz - to send me a few more remains of fishes from the Chalk with their names, in order that I can the better identify those in the Academy's collection & my own." (Morton to Mantell, Philadelphia, 28 October 1835, ATL, MS-Papers-0083-072).

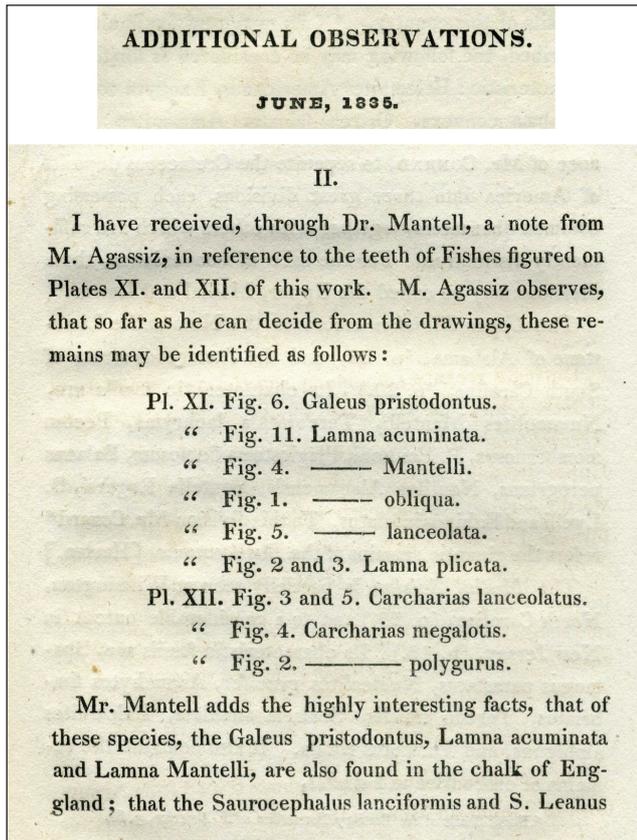


Fig. 6 - Appendix added in the second issue of Morton's (1835a) "Synopsis". Title (top) and explanation of plates 11 and 12 (bottom).

Morton had wax casts made of the five largest shark teeth illustrated in his "Synopsis", namely those shown on plate 11, fig. 5 and plate 12, fig. 2-5. He sent them to Mantell so that the latter could in turn communicate them to Agassiz:

"I have been very much disappointed in not getting good casts made from the sharks teeth, so often promised you; & even now, after having the specimens for eight months with an artist, I can only send you the casts of one species: but in order to compensate in some measure for the depriving, I send you some real teeth, which you will readily identify in my synopsis by comparing them. The others are now in competent hands, & I trust, & indeed believe, will be ready to send you on the 20th of next month, when a friend of mine will take charge of them as far as Liverpool. Please give M. Agassiz any information that may suit him in this respect, as I shall not attempt to communicate with him". (Morton to Mantell, Philadelphia, 28 April 1836, ATL, MS-Papers-0083-072).

"I send [...] this little package, containing casts in wax of the five large sharks' teeth figured in my synopsis. Please communi-

cate with M. Agassiz on this subject if any thing interesting occurs to you. I had intended to write to that gentleman, but not having been able, for want of time, to have a second set of casts made, I have deferred it for the present." (Morton to Mantell, Philadelphia, 18 August 1836, ATL, MS-Papers-0083-072).

In his journal, Mantell acknowledged receipt of a "packet of models of shark's teeth from Dr Morton of Philadelphia" on November 4, 1836 (Cooper 2010: 66). As shown hereafter, some of these casts are still preserved in the Natural History Museum, London, the former British Museum (Natural History) (White 1956: 126), where the Mantell collection eventually found its way in 1839 (Woodward 1904: 205). However, none of these casts has been found in the Agassiz collection kept in the Muséum d'Histoire Naturelle de Neuchâtel, Switzerland.

NOMENCLATURE IMPLICATIONS OF THE NAMES INTRODUCED IN MORTON'S "SYNOPSIS"

Some of the names given for shark teeth in the second issue of Morton's (1835a) "Synopsis" published in or after June 1835 were already introduced by Agassiz in January 1835 in the 4th Livraison of his "Recherches" (Agassiz 1835a: feuilletton additionnel, 54). Those include *Galeus pristodontus* Agassiz, 1835a, *Lamna acuminata* Agassiz, 1835a, and *Lamna mantelli* Agassiz, 1835a, now respectively known under the combinations *Squalicorax pristodontus*, *Acrolamna acuminata*, and *Cretoxyrhina mantelli*. Interestingly, in the first publication introducing these three species, published just after his visit to Mantell's museum in Brighton, Agassiz (1835a: feuilletton additionnel, 54) mentions their presence in "Amérique septentr. [septentrionale]" [northern America]. There is no doubt that he was referring to Morton's figures that Mantell had just shown him during his visit. The specimens illustrated by Morton (1834, 1835a: pl. 11, fig. 6, 11, 4) are therefore part of the syntypes of these species according to Article 72.1.1 of the Code. On the other hand, four of the five names given in the second issue of Morton's (1835a) "Synopsis" for otodontid teeth (*Lamna obliqua*, *Lamna lanceolata*, *Carcharias lanceolatus*, *Carcharias polygurus*) were introduced for the first time in this work and are deemed as available in light of the requirements of the Code. The nomenclature

questions that the introduction of these names in Morton's work raises deserve to be analyzed since they concern some well-known and ubiquitous otodontid species such as *Otodus obliquus*, and the iconic *Otodus megalodon*.

According to Morton (1834, 1835a: 30), all the fossil shark teeth illustrated in plates 11 and 12 of his "Synopsis" came from the Cretaceous of New Jersey. However, the otodontid teeth designated as *Lamna obliqua*, *Lamna lanceolata*, *Carcharias lanceolatus*, *Carcharias megalotis* and *Carcharias polygurus* were obviously found in Cenozoic formations. Geological strata that yield fossil shark teeth in New Jersey include the Vincentown and Hornerstown Formations (Paleocene), the Manasquan Formation (Early Eocene), the Shark River Formation (Middle and Late Eocene) and the Kirkwood Formation (Early and Middle Miocene) (Fowler 1911; Case 1996; Gallagher 2003; Maisch et al. 2015). The specimens presented by Morton were kept in the collection of his friend John Price Wetherill. As mentioned before, the collection was eventually deposited in the Museum of the Academy of Natural Sciences of Philadelphia. In 1911, Fowler published a monograph on the fossil fishes of New Jersey in which five of the six otodontid teeth in the Wetherill collection figured by Morton are illustrated again (Fowler 1911: fig. 23.1, 23.7, 26.1, 26.6, 27.2). Another otodontid tooth from this collection, not figured by Morton, was also illustrated by Fowler (1911: fig. 23.6). Thanks to the inventory made by Dana Ehret (New Jersey State Museum) in the ANSP collection, most of the otodontid teeth figured by Fowler have been identified. Those include six specimens from the Wetherill collection. The following subsections review the nomenclatural status of the names that are listed in the second issue of the "Synopsis" (Morton 1835a).

***Lamna obliqua* Agassiz in Morton, 1835a**

The cosmopolitan species *Otodus obliquus* is rather common in the Paleocene and Early Eocene (Ypresian) of Europe, North America, northern and western Africa, and Asia (Cappetta 2012; Guinot et al. 2020). For nearly two hundred years, it was believed that this species had been introduced in Agassiz's "Recherches". In this book, the name appears for the first time in the legend accompanying the plate 31 of volume 3 published in November 1838 with the 11th Livraison. However, the name

Lamna obliqua associated with the illustration pl. 11, fig. 1 (Fig. 7A) in the second issue of Morton's "Synopsis" fulfills the requirement of Articles 11 and 12.2.7 of the Code (ICZN 1999). This name is thus available with the publication date of June 1835 (Article 21.2 of the Code) and the authorship of Agassiz in Morton (1835a) (Article 50.1.1 of the Code) (Tab. 2). The tooth illustrated by Morton was also figured by Fowler (1911, fig. 23.1) under the name "*Otodus lanceolatus* Morton" (Fig. 7B) and is now kept in the vertebrate paleontology collection of the ANSP (Fig. 7C, D). According to the accompanying label, it was found in Burlington County, New Jersey, but precise locality and stratigraphic whereabouts are unknown.

The cusp is triangular and bent distally. The lingual face is smooth and convex. The lingual collar is well developed and chevron-shaped, with a marked median angle. The cutting edges are smooth. There is a pair of triangular, broad, divergent lateral cusplets. The root is robust, with a well-marked lingual protuberance and rounded root lobes. These characteristics are consistent with a left upper lateral tooth of *Otodus obliquus*, a valid combination introduced by Agassiz in 1838 along with the genus *Otodus* Agassiz, 1838. A second left upper lateral tooth of *Otodus obliquus* from the Wetherill collection is illustrated by Fowler (Fig. 7E) and is kept in the ANSP collection (Fig. 7F, G). This tooth also comes from Burlington County, New Jersey. It is about twice as large as the previous one. A small mesial secondary cusplet is present. In New Jersey, this species is commonly found in the Manasquan Formation (Early Eocene). In some publications on vertebrate fossils from New Jersey (Fowler 1911; Miller 1955), this taxon has been erroneously reported (as "*Otodus lanceolatus* Morton" or "*Isurus lanceolatus* Morton") from the Shiloh Marl Member, or more generally, from the Kirkwood formation (Early and Middle Miocene). In his "Check list of the fossil fishes of New Jersey", Rapp (1946) reports the species only from the Eocene. It has also been recorded in the Middle Hornerstown Formation (Paleocene) by Gallagher (2003).

In the original Morton's publication (Morton 1835a), no type specimens are explicitly indicated. It would be unwise for nomenclatural stability to declare that the tooth illustrated by Morton (ANSP 6833) is the only type specimen (holotype by monotypy), as its provenance is hypothetical. In-



Fig. 7 - *Otodus obliquus* (Agassiz in Morton, 1835a), Burlington County, New Jersey, probably Manasquan Formation (Early Eocene), Wheterill collection. A-D) syntype, upper left lateral tooth; A) figure from Morton (1835a: pl. 11, fig. 1), labial view; B) figure from Fowler (1911: fig. 23.1), lingual view; C-D) ANSP 6833 in labial (C) and lingual (D) views. E-G) *Otodus obliquus*, upper left lateral tooth; E) figure from Fowler (1911: fig. 23.6), lingual view; F-G) ANSP 6832 in labial (F) and lingual (G) views. H-K) holotype of *Otodus lanceolatus* (Agassiz in Morton, 1835a), subjective junior synonym of *Otodus obliquus*; H) figure from Morton (1835a: pl. 11, fig. 5), labial view; I) figure from Fowler (1911: fig. 23.7), lingual view; J-K) ANSP 6831 in labial (J) and lingual (K) views. Scales: 20 mm. Photograph credit for (C, D, F, G, J, K): D. Ehret.

deed, Agassiz knew this species well before 1835. In 1834, while visiting British collections, he already used the name *Lamna obliqua* to designate teeth of the same taxon from the Ypresian-aged London Clay Formation of the Isle of Sheppey (Egerton 1836: 369; 1837: [6]). Agassiz (1843a: vol. 3, 269) even specified that this species was one of the first species of fossil sharks he had studied in the early

1830s. As stated by article 72.4.1.1, “for a nominal species or subspecies established before 2000, any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series”. Under the authority of this article, it is legitimate to retain in the type series of “*Lamna*” *obliqua* all the specimens from the Ypresian of Sheppey that Agassiz knew before the fall

Blainville 1818			<i>Squalus auriculatus</i> Blainville, 1818					
Agassiz 1835b			<i>Carcharias auriculatus</i>	<i>Carcharias megalotis</i> Agassiz, 1835		<i>Carcharias angustidens</i> Agassiz, 1835		<i>Carcharias megalodon</i> Agassiz, 1835
Morton 1835a	<i>Lamna obliqua</i> Agassiz in Morton, 1835	<i>Lamna lanceolata</i> Agassiz in Morton, 1835			<i>Carcharias lanceolatus</i> Agassiz in Morton, 1835		<i>Carcharias polygurus</i> Agassiz in Morton, 1835	
Agassiz 1838	<i>Otodus obliquus</i> (Agassiz in Morton, 1835)							
Agassiz 1843a		<i>Otodus lanceolatus</i>	<i>Carcharodon auriculatus</i>	<i>Carcharodon megalotis</i>	<i>Carcharodon lanceolatus</i>	<i>Carcharodon angustidens</i>	<i>Carcharodon polygurus</i>	<i>Carcharodon megalodon</i>
Jordan 1923			<i>Carcharocles auriculatus</i>					
Glickman 1964			<i>Otodus auriculatus</i>			<i>Otodus angustidens</i>		<i>Megaloselachus megalodon</i>
Cappetta 2012								<i>Otodus megalodon</i>
This work	<i>Otodus obliquus</i> (Agassiz in Morton, 1835)	<i>Otodus lanceolatus</i> (Agassiz in Morton, 1835)	<i>Otodus auriculatus</i> (Blainville, 1818)	<i>Otodus megalotis</i> (Agassiz, 1835)	Belongs to genus <i>Otodus</i> Agassiz, 1838	<i>Otodus angustidens</i> (Agassiz, 1835)	<i>Otodus polygurus</i> (Agassiz in Morton, 1835)	<i>Otodus megalodon</i> (Agassiz, 1835)
Status	Valid	Invalid Subjective junior synonym of <i>Otodus obliquus</i> (Agassiz in Morton, 1835)	Valid	Invalid Subjective junior synonym of <i>Otodus auriculatus</i> (Blainville, 1818)	Invalid Junior secondary homonym of <i>Otodus lanceolatus</i> (Agassiz in Morton, 1835)	Valid	Invalid Subjective junior synonym of <i>Otodus megalodon</i> (Agassiz, 1835)	Valid

Tab. 2 - Nomenclatural status of the otodontid species introduced in the second issue of Morton's (1835a) "Synopsis", and of the main otodontid species introduced in Agassiz's "Recherches sur les poissons fossiles" and Blainville's article on "Poissons fossiles".

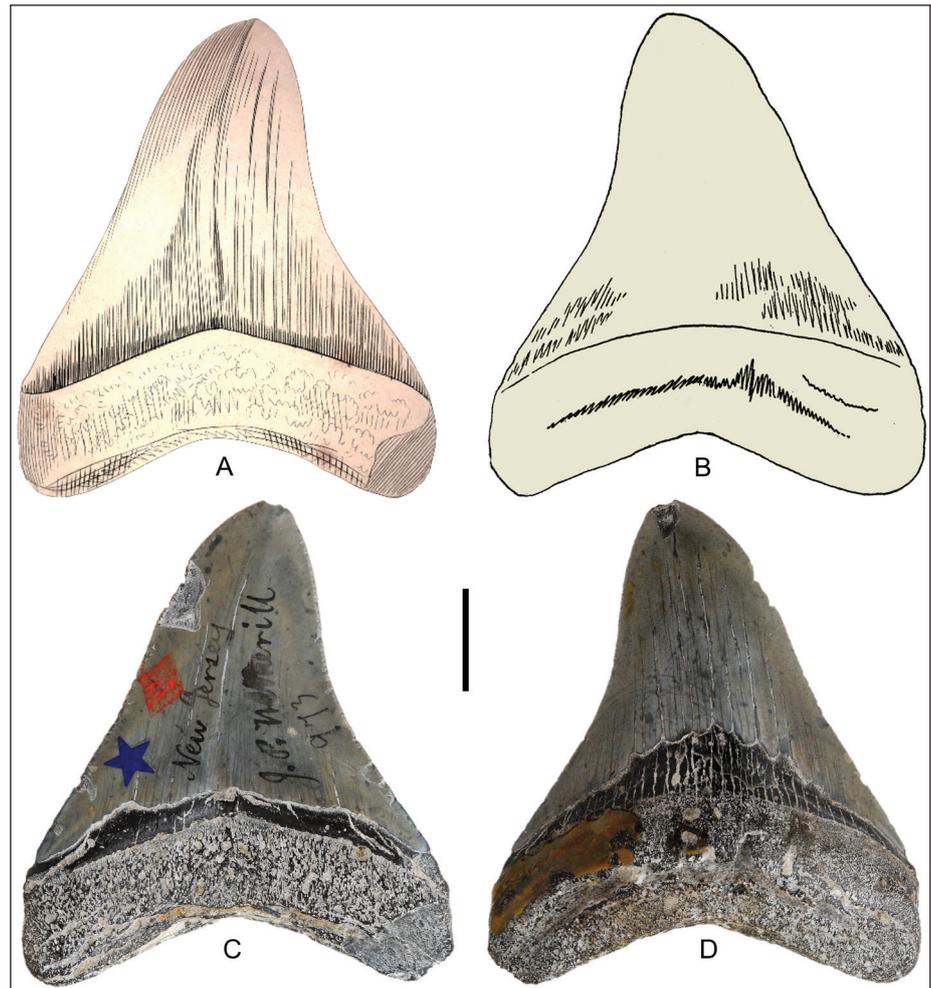
of 1834 when he named the fossil shark teeth depicted in Morton's plates. Some of these specimens were illustrated on plate 31 of volume 3 published in 1838 in the 11th Livraison of his "Recherches". In the legend of this plate, the new combination *Otodus obliquus* and the genus *Otodus* Agassiz, 1838 are validly introduced according to the Article 12.2.7 of the Code. The specimens known to Agassiz prior to 1834 that are shown on this plate can therefore be considered as syntypes of *Lamna obliqua*, in addition to the New Jersey tooth in the Wetherill collection, ANSP 6833. Those are the teeth that Agassiz had studied in France at the Strasbourg and Paris Museums and that are illustrated in plate 31, figures 1, 2, 10-14 (Agassiz 1838: vol. 3). Indeed, Agassiz and Joseph Dinkel (1806-1891), the artist he had hired to draw the fossil fish specimens, stayed in Strasbourg in the fall of 1831 and in Paris from December 1831 to the summer of 1832 (Agassiz 1885; Appel 1997). On the other hand, there is no evidence that the teeth of *Otodus obliquus* he received from reverend Frederick William Hope (1797-1862) (Moore et al. 1991: 102) and illustrated on pl. 31, fig. 3-9 (Agassiz 1838: vol. 3) and pl. 36, fig. 22-27

(Agassiz 1843b: vol. 3) were known to him before 1835. Pending discovery of additional evidence, the teeth in the Hope collection are therefore excluded from the type series of *Otodus obliquus*.

***Lamna lanceolata* Agassiz in Morton, 1835a**

In reference to the tooth illustrated in figure 5, plate 11 of Morton's "Synopsis" (Fig. 7H), the second available otodontid name introduced by Agassiz in Morton's (1835a) work is *Lamna lanceolata*. This specimen was also figured by Fowler (1911: fig. 23.1) (Fig. 7I) and is still kept in the vertebrate paleontological collection of the ANSP, although one of the cusplets is now missing (Fig. 7J, K). In the 15th and 16th Livraisons of his "Recherches", Agassiz (1843a: vol. 3, 269-270) redescribed this species under the new combination *Otodus lanceolatus*. His description was based on specimens from the base of the "ferruginous sandstone" of Kressenberg in Bavaria, Germany (probably Kressenberg Formation, uppermost Paleocene - Ypresian; see Rasser & Piller 1999) and were illustrated in the 17th Livraison of his book (Agassiz 1843b: vol. 3, pl. 37, fig. 19-23). All these specimens were kept in the collection

Fig 8 - Lectotype of *Otodus polygurus* (Agassiz in Morton, 1835a), subjective junior synonym of *Otodus megalodon* (Agassiz, 1835b), upper right lateral tooth, New Jersey, Wheterill collection; A) figure from Morton (1835a: pl. 12, fig. 2), labial view; B) figure from Fowler (1911: fig. 27.2), lingual view; C-D) ANSP 973 in labial (C) and lingual (D) views. Scale: 20 mm. Photograph credit for (C, D): Academy of Natural Sciences of Drexel University.



of the German paleontologist Georg zu Münster (1776-1844) in Bayreuth. Most of the original drawings and paintings for Agassiz's "Recherches" are now kept in the Archives of the Geological Society of London (Brignon 2015b: 51; 2019a: 55-56). The two original watercolor paintings (GSL LDGSL/613/4/73/5 and LDGSL/613/4/73/6) of the teeth figured in plate 37, fig. 19-23, were made respectively in 1837 and 1838 by the artist G. A. H. Köppel. Thus, it is not obvious that the teeth from Kressenberg were known by Agassiz when *Lamna lanceolata* Agassiz in Morton, 1835a, was introduced. The only eligible name-bearing specimen for this species is consequently specimen ANSP 6831 (Fig. 7J, K), the holotype by monotypy according to Article 73.1.2 of the Code.

The main cusp of this specimen is high, triangular and straight, with a strongly convex lingual face and a moderately convex labial face. The cutting edges are well developed and smooth. The lingual collar is high and chevron-shaped. The preserved cusplet is triangular, large, diverging and well

separated from the main cusp by a notch. The lingual root face bears a strong lingual protuberance. Root lobes are well developed and separated by a broad and deep concavity of the basal edge of the root. The tooth is indistinguishable from anterior teeth of *Otodus obliquus*. Agassiz (1843a: vol. 3) acknowledged that *Otodus lanceolatus* was possibly synonymous with *O. obliquus* but differed in having larger cusplets and a less marked lingual bulge of the crown (Guinot et al. 2020). However, it appears that these variations fit the intraspecific variability seen in *O. obliquus*, so that *O. lanceolatus* is a subjective synonym of *O. obliquus* (Tab. 2). Since both species were introduced in the same work in June 1835, there is no obstacle to follow the current usage (Woodward 1889: 404) giving priority to *Otodus obliquus*, contrary to the evaluations by Fowler (1911) on the same issue.

Carcharias polygurus Agassiz in Morton, 1835a

The name *Carcharias polygurus* associated with the illustration shown in plate 12, figure 2 (Fig. 8A)

in the second issue of Morton's "Synopsis" fulfills the requirements of Articles 11 and 12.2.7 of the Code (ICZN 1999). This name is thus available with the publication date of June 1835 (Article 21.2 of the Code) and the authorship of Agassiz in Morton (1835a) (Article 50.1.1 of the Code). The same tooth, was illustrated by Fowler (1911: fig. 23.1) (Fig. 8B) and is now kept in the ANSP collection, under number ANSP 973 (Gillette & Shapiro 1978: 121; Spamer et al. 1995: 99) (Fig. 8C, D). The tooth is massive with a wide, triangular cusp. The cutting edges are slightly concave except towards the apex where they become ogival. Small and uniform serrations are visible on some parts of the edges but are sometimes faded due to their condition of preservation. The lingual face of the cusp is convex and shows a very well-marked collar at its base. The crown bends distally so that the concavity of the distal cutting edge is more pronounced than that of the mesial one. The root is thick, with a lingual protuberance. The lateral margins of the root are vertical and straight. The labial face of the root is flat and symmetric. The morphology of this tooth is identical to that of upper right lateral teeth (probably L3 or L4) of *Otodus megalodon* (see Leriche 1926: pl. 35; Cappetta 2012; Perez et al. 2021: fig. 1B). The tooth was from the John Price Wetherill collection and was found in New Jersey. Its age was believed by Morton to be Cretaceous but was given to be Cenozoic by Fowler (1911).

In Morton's (1835a) work, no type specimen is designated. In this condition, any evidence may be taken into account to determine what specimens constitute the type series under the authority of Article 72.4.1.1 of the Code. Specimen ANSP 973 is clearly part of the type series of *Carcharias polygyrus*. When naming this specimen as *Carcharias polygyrus*, based on Morton's illustration that Mantell had presented to him in the fall of 1834, Agassiz knew other specimens that he had informally named as such. Prior to his visit to Mantell's museum, he had seen a tooth from New Bern, North Carolina, that he assigned to this species. This specimen was kept in the collection of William Willoughby Cole (1807-1886), later 3rd Earl of Enniskillen. It is listed in the catalog of this collection (Egerton 1836: 367; 1837: [6]) and in the catalog of fossil fishes in the British Museum (Natural History) where the tooth is preserved today as NHMUK PV P 2383a (Woodward 1889: 418). In 1838, Agassiz published the plate 30 of

volume 3 of his "Recherches" in which four teeth are depicted under the name *Carcharias polygyrus* [sic], an incorrect subsequent spelling (Article 33.3 of the Code). They all came from the Swiss Molasse which encompasses deposits ranging from the Early Oligocene to the Middle Miocene. According to the original drawings of Agassiz's "Recherches" preserved at the Geological Society of London, three of these teeth (Agassiz 1838: vol. 3, pl. 30, fig. 9, 10 and 12) were drawn by Jacques Bourkhardt (ca.1808-1867), an artist who worked for Agassiz from 1835 (GSL, LDGSL/613/4/68/5, 6 and 7). There is no evidence that these specimens were known to Agassiz when *Carcharias polygyrus* Agassiz in Morton, 1835a, was established. The fourth specimen (Agassiz 1838: vol. 3, pl. 30, fig. 11) was certainly drawn before 1835 in the Karlsruhe Museum by his wife Cécile Agassiz (1810-1848), née Braun (GSL, LDGSL/613/4/68/8). This specimen can therefore reasonably be considered as part of the type series of this species. Later, Agassiz (1843a: vol. 3, 253) attached this species to the genus *Carcharodon* Smith in Müller & Henle, 1838. In 1978, the tooth ANSP 973 was designated as the "holotype" of *Carcharodon polygyrus*. According to article 74.6 of the Code, "if it is considered subsequently that the original description was based on more than one specimen, the first author to have published before 2000 the assumption that the species-group taxon was based upon a single type specimen is deemed to have designated that specimen as the lectotype". Thus, ANSP 973 is the lectotype of *Carcharodon polygyrus* (Agassiz in Morton, 1835a) by the designation of Gillette & Shapiro (1978).

Based on the morphology of its lectotype (ANSP 973), "*Carcharodon*" *polygyrus* is conspecific with *Otodus megalodon*. The question about the date of publication and authorship of *Otodus megalodon* has been discussed in previous works (Purdy et al. 2001; Cahuzac et al. 2007). This species name with the combination *Carcharias megalodon* first appears in few works published between 1832 and 1834 (Lingg 1832; Schübler & Lingg 1833; Agassiz 1834). However, without any adequate description or indication, these first designations fail to meet the requirements of availability and must be declared *nomina nuda*. In the 5th Livraison of the "Recherches", Agassiz published the plate 29 of volume 3, in which seven teeth are illustrated (Fig. 9D) with a legend designating them as *Carcharias megalodon*.

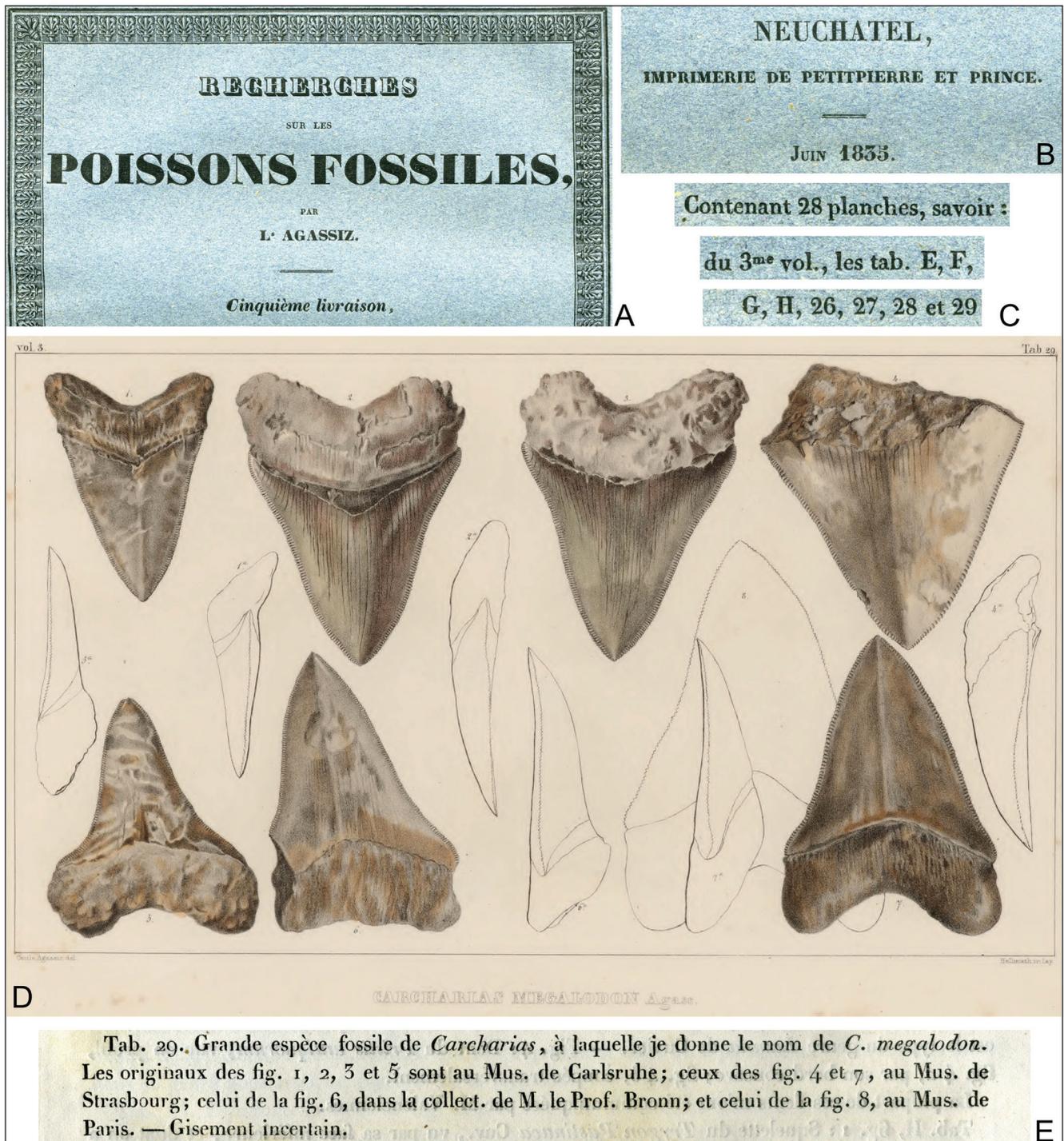


Fig. 9 - *Carcharias megalodon* Agassiz, 1835b [now referred to as *Otodus megalodon* (Agassiz, 1835b)] introduced as a valid name in the 5th Livraison of Agassiz's (1835b) "Recherches sur les poissons fossiles". A-C) parts of the original front wrappers of the 5th Livraison published in June 1835; A) title; B) printer name, place, and date "Juin 1835" [June 1835]; C) list of the plates of the third volume contained in the 5th Livraison including plate 29. D) plate 29 with caption "*Carcharias megalodon*". E) caption of plate 29 printed on page 72 of the "Feuilleton additional" inserted in the 5th Livraison.

This act fulfills the requirements of Articles 11 and 12.2.7 of the Code; consequently, this name was made available in 1835. Even if the detailed description of this plate was published in 1843 (Agassiz 1843a: vol. 3, 247-249) with the new combination *Carcharodon megalodon*, the publication year that must

be retained is 1835 and not 1843 under the authority of Article 21.5 concerning "dates of work issued in parts". As indicated in the original front wrapper of the 5th Livraison (Fig. 9A), the date of publication written in French is "juin 1835" [June 1835 in English] (Fig. 9B). The exact days of publication of

the second issue of Morton's (1835a) "Synopsis" and Agassiz's (1835b) 5th Livraison being unknown, the date to be adopted is the last day of the month, i.e., 30 June 1835 in both cases, according to Article 21.3.1 of the Code. In consequence, the names *Carcharias polygurus* Agassiz in Morton, 1835a and *Carcharias megalodon* Agassiz, 1835b have been published simultaneously. However, several authors have misstated the dates of publication of these names (Hay 1902: 308; Fowler 1911; Gillette & Shapiro 1978: 121; Spamer et al. 1995: 99), leading some of them to consider "*Carcharodon*" *polygurus* to have priority over "*Carcharodon*" *megalodon* (Fowler 1911; Rapp 1946). Since the names *Carcharias megalodon* Agassiz, 1835b and *Carcharias polygurus* Agassiz in Morton, 1835a were published simultaneously, there is no obstacle to follow the prevailing usage and order of precedence proposed by Woodward (1889: 415) even though the latter was wrong about the actual publication date of *Carcharias polygurus*. *Otodus polygurus* (nov. comb.) is therefore a subjective junior synonym of *Otodus megalodon* (Tab. 2). This species appears in the middle Miocene (Perez et al. 2019). If the tooth from the Wetherill collection truly came from New Jersey, it could have been found probably in the upper part of the Kirkwood Formation, which is dated to the middle Miocene (Andrews 1987; Sugarman & Miller 1997).

Note that *Otodus megalodon* was assigned by Agassiz (1843a) to the genus *Carcharodon*, under the assumption that it was related to the extant great white shark *Carcharodon carcharias* (Lamnidae). Until quite recently, this view was followed by several authors (Applegate & Espinosa-Arrubarrena 1996; Gottfried et al. 1996; Purdy 1996; Purdy et al. 2001). Another scenario suggests that *Otodus megalodon* evolved as a lineage derived from *Otodus obliquus* within the Otodontidae family (Casier 1960; Glickman 1964; Zhelezko & Kozlov 1999; Ward & Bonavia 2001; Cappetta 2012; Shimada et al. 2017; Perez et al. 2019, 2021). Alternative generic names have been proposed for species with serrated teeth within this lineage, including *Carcharocles* Jordan & Hannibal in Jordan, 1923, and its junior synonym *Procarcharodon* Casier, 1960 (Cappetta, 1987; Kent 2018). Glickman (1964, 1980) and Zhelezko & Kozlov (1999) proposed to widen the content of *Otodus* to some species with serrated cutting edges, while assigning *Otodus megalodon* to the genus *Megaselachus* Glickman, 1964. Cappetta (2012) further extended

the use of *Otodus* for the entire megatoothed shark lineage, given that their fossil record suggests anagenetic-type evolution where most of them represent different chronospecies (Shimada et al. 2017). This hypothesis is now shared by many researchers (Bor et al. 2012; Andrianavalona et al. 2015; Trif et al. 2016; Boessenecker et al. 2019; Jambura et al. 2019; Shimada 2019; Cooper et al. 2020; Herraiz et al. 2020; Maisch et al. 2020; Ballell & Ferrón 2021; Perez et al. 2021).

***Carcharias megalotis* Agassiz, 1835b**

The name *Carcharias megalotis* appears simultaneously in the 5th Livraison of Agassiz's "Recherches" and in the second issue of Morton's (1835a) "Synopsis". As shown above, the publication date of these two works is 30 June 1835 (Article 21.3.1 of the Code). In both cases, the name *Carcharias megalotis* is associated with an illustration (Agassiz 1835b: vol. 3, pl. 28, fig. 8-10; Morton 1835a: pl. 12, fig. 4). The two works meet the requirements of Articles 11 and 12.2.7 of the Code to make the name *Carcharias megalotis* available. In order to follow the prevailing usage considering that the name was introduced in Agassiz's "Recherches" (Woodward 1889: 412), priority is given to this act. No type specimen was designated by Agassiz. In this case, any evidence may be taken into account to determine what specimens constitute the type series as stated by the Article 72.4.1.1 of the Code. It makes sense to consider the two specimens figured in the works of Agassiz (1835b) and Morton (1835a) as part of the type series of *Carcharias megalotis* Agassiz, 1835b. In addition, two specimens assigned by Agassiz (1843a: vol. 3, 259) to this species and known by him before 1835 can be also considered as part of the type series. Those include a specimen kept in the Museum of natural history of Caen (Normandy, France) and a specimen in the collection of William Willoughby Cole, later 3rd Earl of Enniskillen. Agassiz visited the Museum of Caen in March 1832 (Brignon 2015b: 46) and studied the specimens of the Cole collection for the first time in 1834 (Agassiz 1835a: feuilletton additionnel, 45). No information is known about the specimen kept in the Museum of Caen, whose collections were destroyed during World War II (Bigot 1945). The specimen kept in the Cole collection came from the Cenozoic of Maryland and was listed in Egerton's (1836, 1837) catalogues. Agassiz (1843a: vol. 3, 259) also mentions

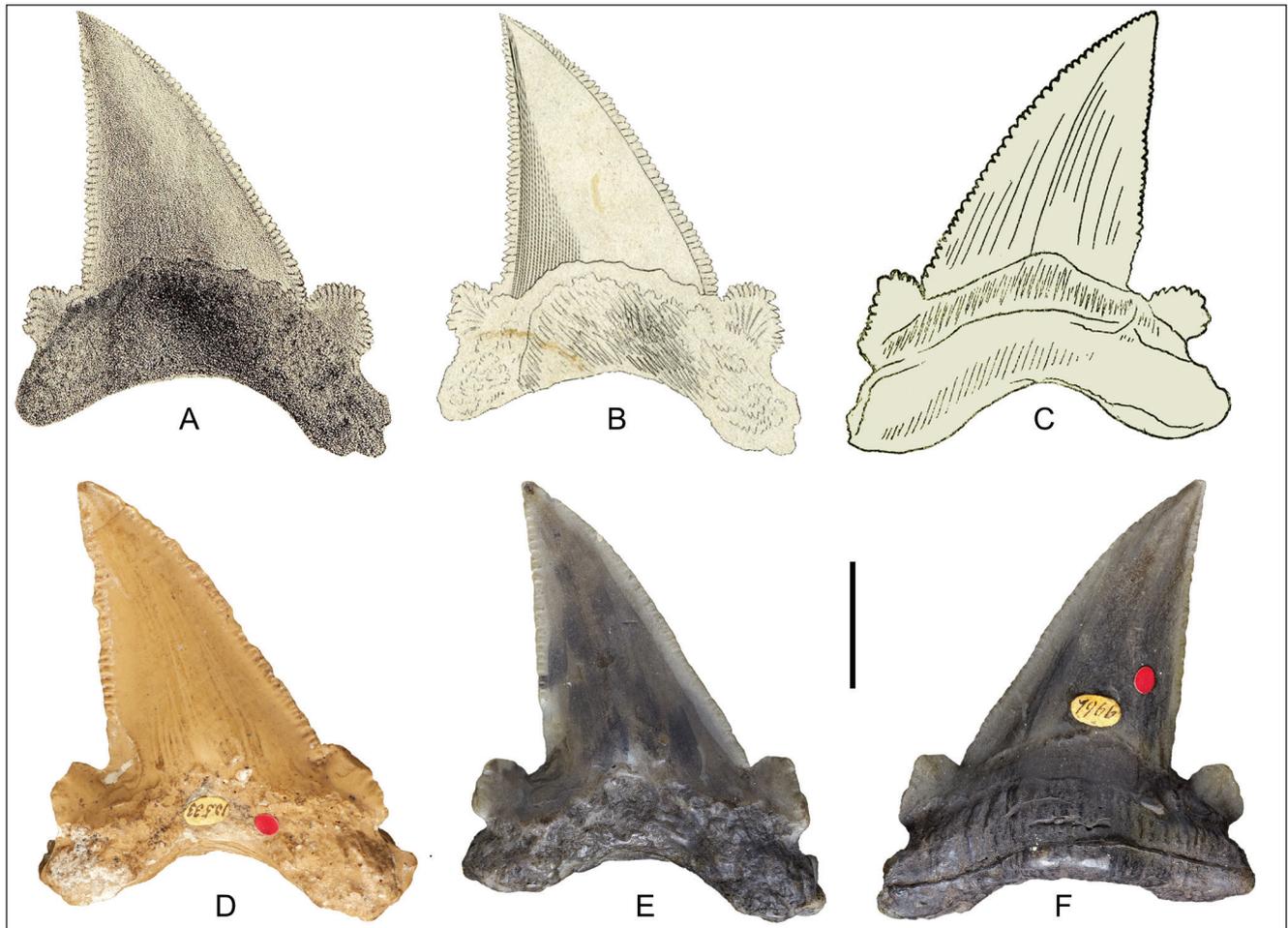


Fig. 10 - *Otodus* sp., upper left lateral tooth, New Jersey, probably Shark River Formation (Lutetian to Priabonian, Middle to Late Eocene), Wheterill collection; A) figure from Morton (1834: pl. 12, fig. 4), labial view; B) figure from Morton (1835a: pl. 12, fig. 4), labial view; C) figure from Fowler (1911: fig. 26.6), lingual view. D-F) casts in wax received by Mantell from Morton in November 1836; D) NHMUK PV OR 10533, labial view; E-F) NHMUK PV OR 7966 in labial (E) and lingual (F) views. Scale: 20 mm. Photograph credit for (D-F): The Trustees of the Natural History Museum, London.

another specimen that was communicated by Jakob Kaup (1803-1873) after the publication of the 5th Livraison of the “Recherches” (Agassiz 1836: feuilleton additionnel, 84). This specimen is therefore rejected from the type series as it was probably not known to Agassiz when the species name was introduced. Note that Morton later referred to *Carcharias myalotis*, which is an incorrect subsequent spelling of *Carcharias megalotis* (Morton 1842: 220).

The specimen illustrated in Morton’s (1834, 1835a) “Synopsis” (Fig. 10A, B) was also figured by Fowler (1911) (Fig. 10C). The original tooth has not been found in the ANSP (D. Ehret, pers. comm.). Nonetheless, two unpainted (NHMUK PV OR 10532 and NHMUK PV OR 10533) (Fig. 10D) and one painted (NHMUK PV OR 7966) casts in wax of this tooth sent to Mantell by Morton in 1836 are preserved in the Natural History Museum, London

(Fig. 10E, F). According to the drawings and the casts, the specimen is stretched mesio-distally, with the crown slanting distally as typical of upper left lateral teeth of *Otodus*. The mesial cutting edge is slightly convex and the distal one is straight. The lateral cusplets are prominent. As far as it can be inferred from the drawings and the casts, the serrations of the cutting edges and cusplets are well-marked. The basal edge of the root is slightly concave. *Carcharias megalotis* Agassiz, 1835b with the combination *Carcharodon megalotis* (Agassiz, 1835b) was synonymized by some authors with *Carcharodon angustidens* (Agassiz, 1835b) (Gibbes 1848: 145) or *Carcharodon auriculatus* (Blainville, 1818) (Woodward 1889: 412; Fowler 1911), both species being now assigned to the genus *Otodus* Agassiz, 1838 (Glickman 1964; Zhelezko & Kozlov 1999; Cappetta 2012; Shimada et al. 2017).

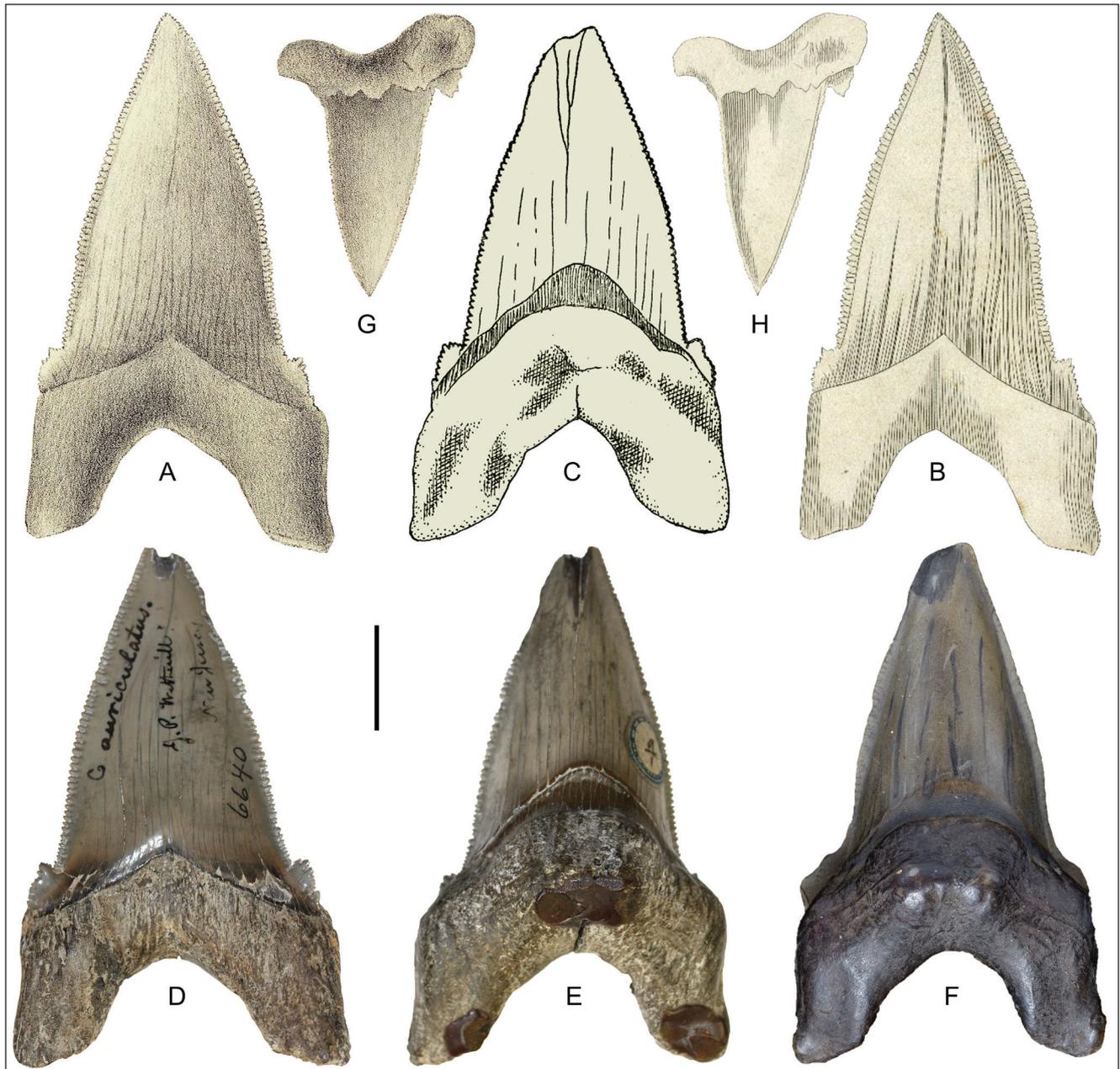


Fig. 11 - Syntypes of “*Carcharias*” *lanceolatus* Agassiz in Morton, 1835a, junior secondary homonym of *Otodus lanceolatus* (Agassiz in Morton, 1835a), New Jersey, probably Shark River Formation, Wheterill collection. A-F) *Otodus* sp., anterior tooth; A) figure from Morton (1834: pl. 12, fig. 3), labial view; B) figure from Morton (1835a: pl. 12, fig. 3), labial view; C) figure from Fowler (1911: fig. 26.1), lingual view; D-E) ANSP 6640 in labial (D) and lingual (E) views; F) painted cast in wax received by Mantell from Morton in November 1836, NHMUK PV OR 7964, lingual view. G-H) *Otodus* cf. *auriculatus* (Blainville, 1818), anterior tooth, labial view; G) figure from Morton (1834: pl. 12, fig. 5); H) figure from Morton (1835a: pl. 12, fig. 5). Scale: 20 mm. Photograph credit: D. Ehret (D-E), and The Trustees of the Natural History Museum, London (F).

Zhelezko & Kozlov (1999) proposed a detailed subspecies lineage scenario based on the fossil record from Urals and central Asia. At the species level, the succession introduced by these authors for fully serrated forms includes *Otodus auriculatus* (Lutetian, Middle Eocene), *Otodus poseidoni* Zhelezko in Zhelezko & Kozlov, 1999 (Bartonian, upper Middle Eocene), *Otodus sokolovi* Jaekel, 1895

(Priabonian, Late Eocene), and *Otodus angustidens* (Oligocene). In passing, it is worth noting that *Otodus* “*sokolovi*”, which is sometimes in use in recent literature (Zhelezko & Kozlov 1999; Diedrich 2013; Shimada et al. 2017; Ebersole et al. 2019), is an incorrect subsequent spelling of *Otodus sokolovi*, according to Article 33.3 of the Code. Based on the North American fossil record, Applegate & Espi-

nosa-Arrubarrena (1996) proposed a quite similar succession of species even if they placed them in the genus *Carcharodon* as part of the lineage of the great white shark, a vision that is now largely abandoned (Cappetta 1992; Shimada et al. 2017). Part of the sequence proposed by Applegate & Espinosa-Arrubarrena (1996) includes “*Carcharodon*” *auriculatus*, “*Carcharodon*” sp., “*Carcharodon*” *sokolowi* and “*Carcharodon*” *angustidens*. Interestingly, the description of “*Carcharodon*” sp. from the middle and late Eocene given by these authors matches the tooth morphology of *Otodus poseidoni*, which is characterized by lower teeth being large and massive, with elongated root lobes having very deep interspaces (Applegate & Espinosa-Arrubarrena 1996: 29; Zhelezko & Kozlov 1999). In more recent studies, *Otodus poseidoni* has been often removed from the *Otodus* chronospecific lineage, *Otodus auriculatus* (Lutetian, middle Eocene) passing directly into *Otodus sokolowi* (Bartonian-Priabonian, middle and late Eocene), and eventually *Otodus angustidens* (Oligocene) (Trif et al. 2016; Lebrun & Canevet 2016). The morphology of *Otodus auriculatus* from the Lutetian is characterized by cutting edges of the cusp with a strong and irregular serrations. The cusplets are well-developed and widely united to the base of the cusp in labial view (Storms 1901; Case & Cappetta 1990; Van den Eeckhout & De Schutter 2009; Cappetta 2012: fig. 209; Cappetta & Case 2016). Upper middle Eocene and late Eocene (Bartonian-Priabonian) forms assigned to *Otodus sokolowi* have much larger size, well-marked and regular serrations along the cutting edges, and a pair of lateral cusplets; the latter are not very high and often divergent in lateral teeth, whereas they are less developed in anterior teeth (Case & Cappetta 1990; Adnet et al. 2010; Underwood et al. 2011; Zalmout et al. 2012; Kriwet et al. 2016; Zalat et al. 2017; Zouhri et al. 2021). Ehret & Ebersole (2014) noted that, when looking at small time intervals, species distinctions are difficult to discern. They consequently opted for a simplified view by assigning all the serrated otodontid forms from the Middle and Late Eocene (Lutetian to Priabonian) of Alabama to the single species *Otodus auriculatus*. Similarly, Ebersole et al. (2019) noted the large variability in tooth morphology for specimens sampled in the Middle Eocene (lower Lutetian to middle Bartonian) Claiborne Group in Alabama and advised against making specific determinations.

The specimen figured by Morton (Fig. 10) corresponds to a serrated Eocene *Otodus* species, and as such, it undoubtedly comes from the Shark River Formation, whose geological age spans from the Lutetian to the Priabonian. Since the precise stratigraphic whereabouts of this find are unknown, its affinity with other species is difficult to assess. The only specimen illustrated in Agassiz’s (1835b: vol. 3, pl. 28, fig. 8-10) “Recherches” was kept in the Karlsruhe Museum, but its locality and stratigraphic position remain unknown. However, its morphology is similar to that of the typical forms of *Otodus auriculatus* from the Lutetian. In order to avoid further confusion into the nomenclature of Otodontidae, we here explicitly designate the specimen figured by Agassiz (1835b: vol. 3, pl. 28, fig. 8-10) as the lectotype of *Otodus megalotis*. In consequence, *Otodus megalotis* (Agassiz, 1835) can be considered a subjective junior synonym of *Otodus auriculatus* (Blainville, 1818) (Tab. 2). All the other specimens from the type series of *Otodus megalotis*, including the one from the Wetherill collection (Fig. 10), become paralectotypes, so that their name-bearing function is withdrawn (Article 73.2.2 of the Code). Furthermore, it is here proposed to identify Wetherill’s specimen in open nomenclature, as belonging to *Otodus* sp.

***Carcharias lanceolatus* Agassiz in Morton, 1835a**

The name *Carcharias lanceolatus* associated with the illustration of two teeth shown in plate 12, figures 3 and 5 (Fig. 11B, H) in the second issue of Morton’s “Synopsis” fulfills the requirements of Articles 11 and 12.2.7 of the Code (ICZN 1999). This name is thus available with the publication date of June 1835 (Article 21.2) and the authorship of Agassiz (Article 50.1.1) in Morton (1835a). No type specimen is designated in the original publication, so that the type series can be determined by taking into account any evidence in or outside this publication as stated by Article 72.4.1.1 of the Code. It can be inferred that the two specimens figured by Morton are part of the type series. In the 11th Livraison of the “Recherches” published in November 1838, Agassiz illustrated two other incomplete teeth accompanied by a caption indicating “*Carcharias lanceolatus* Agass. Du terrain tertiaire de Westphalie; de la collection du comte de Münster” [From the Tertiary formation of Westphalia, in the collection of count zu Münster (1776-1844)] (Agassiz 1838:

vol. 3, pl. 30, fig. 1, 3; feuilletton additionnel, 114). Agassiz also noted that “*Depuis la publication de la dernière livraison, j’ai reçu différens envois relatifs aux Poissons Fossiles, qui m’ont été fort utiles. M. le comte de Münster, avec l’obligeance qu’il a toujours mise à me tenir au courant des découvertes ichthyologiques qu’il fait continuellement, m’a encore adressé cette année un grand nombre de planches d’espèces nouvelles, accompagnées de descriptions très-exactes et de figures détaillées de toutes les espèces de sa collection, qui me manquaient encore*” [Since the publication of the last livraison (i.e., the 8th and 9th livraisons published in September 1837 knowing that the 10th Livraison was published after the 11th Livraison, see Brignon 2014), I have received various shipments relating to fossil fishes, which have been very useful to me. Mr the count zu Münster, with the obligingness that he has always put in keeping me informed of the ichthyological discoveries that he continually makes, has again this year sent me a large number of plates of new species, accompanied by very exact descriptions and detailed figures of all the species in his collection, which I still lacked]. This excerpt clearly shows that Agassiz did not know the specimens depicted in the plate 30, volume 3, of his “Recherches” when *Carcharias lanceolatus* was introduced in Morton’s “Synopsis”. Therefore, these specimens cannot be part of the type series of this species. The type series is thus limited to the two syntypes figured by Morton (Fig. 11A, B, G, H). In 1843, Agassiz (1843a: vol. 3, 257) published a description of this species under the new combination *Carcharodon lanceolatus*. He designated one of the teeth figured in the plate 30, volume 3, as the type of the species. However, this act cannot be regarded as a valid lectotype designation since this tooth is not a syntype (Article 74.2 of the Code).

One of the two syntypes was illustrated by Fowler (1911, fig. 26.1) (Fig. 11C) and is now kept in the ANSP collection, with number ANSP 6640 (Fig. 11D, E). A painted cast in wax of the same tooth sent to Mantell by Morton in 1836 is also preserved in the Natural History Museum, London (Fig. 11F). The second syntype (Fig. 11G, H) seems to be lost. The general morphology of both syntypes indicates Middle to Late Eocene serrated forms of the *Otodus* lineage. They most probably come from the Shark River Formation of New Jersey (Lutetian to Priabonian). Since these tooth belong to the genus *Otodus*, the species-group name

in “*Carcharias*” *lanceolatus* Agassiz in Morton, 1835a becomes a junior secondary homonym of *Otodus lanceolatus* (Agassiz in Morton, 1835a) discussed above (Fig. 7H-K). According to Article 60 of the Code, the species-group name in “*Carcharias*” *lanceolatus* Agassiz in Morton, 1835 is invalid and “must be replaced either by an available and potentially valid synonym or, for lack of such a name, by a new substitute name”.

According to the drawings given by Morton, the lost syntype of “*Carcharias*” *lanceolatus* is an anterior tooth with an elongated and straight cusp (Fig. 11G, H). As far as the drawings are trustable, the cusplet (one of which is missing) is triangular and slightly diverging, and it seems to bear irregular serrations (Fig. 11G, H). The root lobes are rounded at their extremities. The general morphology of this specimen is close to that of anterior teeth of *Otodus auriculatus* (see Cappetta & Case 2016: pl. 6, fig. 9). The second syntype (ANSP 6640) is a much massive tooth with an overall height exceeding 10 cm. The elongated and straight cusp indicates that it is an anterior tooth. The tooth shows a broad crown narrowing rapidly in its apical region. The labial face is rather flat and the lingual one is convex. The lingual collar is well developed and v-shaped. The cutting edges of the cusp have strong and rather regular serrations. There is a pair of small lateral cusplets. Their serrations are irregular and more stronger than those of the main cusp. One of the cusplet has a secondary accessory (right side in Fig. 11D). The root is remarkably high, with two long and narrow lobes having sharp extremities and forming a very deep concavity at the basal edge of the root. The lateral margins of the root are straight, almost vertical and slightly diverging. The lingual protuberance is very salient. The morphology of this tooth suggests some affinities with *Otodus poseidoni* from the Bartonian of Kazakhstan (Zhelezko & Kozlov 1999: pl. 19-21), although in the anterior teeth of the latter species the root lobes are more divergent, the crown slightly less broad at its base, and the cusplets more clearly separated from the main cusp. ANSP 6640 is quite similar to teeth figured by Glickman (1964: 149, fig. 56b; 1980: pl. 9, fig. 2) under the name *Otodus angustidens* (Agassiz, 1835). One of those (Glickman 1964: fig. 56b) was assigned to *Otodus poseidoni* by Zhelezko & Kozlov (1999: 147). The shape of the cusp of ANSP 6640 is also reminiscent of a tooth from the Late Eocene

Tab. 3 - Status of the otodontid sharks in the John Price Wetherill collection.

Reference to Morton's (1834, 1835a) figures	Reference to Fowler's (1911) figures	Original specimens in ANSP	Casts in NHMUK	Status (this work)
pl. 11, fig. 1	fig. 23.1	ANSP 6833		<i>Otodus obliquus</i> (Agassiz in Morton, 1835a) Syntype (Fig. 7A-D)
Not figured	fig. 23.6	ANSP 6832		<i>Otodus obliquus</i> (Agassiz in Morton, 1835a) Non-type (Fig. 7E-G)
pl. 11, fig. 5	fig. 23.7	ANSP 6831		<i>Otodus obliquus</i> (Agassiz in Morton, 1835a) Holotype of <i>Otodus lanceolatus</i> (Agassiz in Morton, 1835a), junior synonym of <i>O. obliquus</i> (Fig. 7H-K)
pl. 12, fig. 4	fig. 26.6	Lost?	NHMUK PV OR 7966, 10532, 10533	<i>Otodus</i> sp. Paralectotype of <i>Otodus megalotis</i> (Agassiz, 1835), junior synonym of <i>Otodus auriculatus</i> (Blainville, 1818) (Fig. 10)
pl. 12, fig. 3	fig. 26.1	ANSP 6640	NHMUK PV OR 7964	<i>Otodus</i> sp. Syntype of “ <i>Carcharias</i> ” <i>lanceolatus</i> (Agassiz in Morton, 1835a), junior secondary homonym of <i>Otodus lanceolatus</i> (Agassiz in Morton, 1835a) (Fig. 11A-F)
pl. 12, fig. 5	Not figured	Lost?		<i>Otodus</i> cf. <i>auriculatus</i> (Blainville, 1818) Syntype of “ <i>Carcharias</i> ” <i>lanceolatus</i> (Agassiz in Morton, 1835a), junior secondary homonym of <i>Otodus lanceolatus</i> (Agassiz in Morton, 1835a) (Fig. 11G-H)
pl. 12, fig. 2	fig. 27.2	ANSP 973		<i>Otodus megalodon</i> (Agassiz, 1835b) Lectotype of <i>Otodus polygurus</i> (Agassiz in Morton, 1835a), junior synonym of <i>Otodus megalodon</i> (Fig. 8)

of Egypt figured under the name *Otodus* cf. *sokolovi* by Case & Cappetta (1990: 7, pl. 1, fig. 9-10), who suggested that it might belong to a new species. ANSP 6640 could also have some affinities with the large Eocene form described as *Carcharodon* sp. by Applegate & Espinosa-Arrubarrena (1996: 29). Finally, whether the two teeth referred to as “*Carcharias*” *lanceolatus* in Morton’s “Synopsis” (Fig. 11) belong to one or two species cannot be ascertained. In any case, it would be useless to designate a lectotype, and to replace this species-group name by a substitute name, which would add confusion into otodontid nomenclature.

SYSTEMATIC PALEONTOLOGY

The aim of this section is to provide an amended synonymy list of valid otodontid species, including the names introduced in Morton’s (1835a) “Synopsis”. Diagnoses are intentionally omitted, being available elsewhere (Casier 1966; Cappetta 2012; Cappetta & Case 2016). The nomenclatural status of the otodontid sharks in the John Price Wetherill collection is summarized in Tab. 3.

Subclass **ELASMOBRANCHII** Bonaparte, 1838

Cohort **EUSELACHII** Hay, 1902

Subcohort **NEOSELACHII** Compagno, 1977

Order **Lamniformes** Berg, 1937

Family Otodontidae Glickman, 1964

Genus *Otodus* Agassiz, 1838

Type species: *Lamna obliqua* Agassiz in Morton, 1835a

Otodus obliquus (Agassiz in Morton, 1835a)

- 1699 *Gracirrhynchus* - Lhuyd, p. 64, pl. 15, n°1260, 1265.
 1769 *Glossopetra* - Knorr & Walch, p. 235, pl. H.1.a, fig. 3.
 1811 Fossil tooth resembling those of *Squalus cinereus* - Parkinson, p. 256, pl. 19, fig. 5.
 1834 Shark teeth - Morton, p. 31, pl. 11, fig. 1, 5.
 †1835a *Lamna obliqua* Agassiz in Morton - Morton, additional observations, p. [2], pl. 11, fig. 1.
 1835a *Lamna lanceolata* Agassiz in Morton - Morton, additional observations, p. [2], pl. 11, fig. 5.
 1835b *Lamna lanceolata* - Morton, p. 277.
 1836 *Lamna obliqua* - Egerton, p. 369 (name only).
 1837 *Lamna obliqua* - Egerton, p. [6] (name only).
 1838 *Otodus obliquus* - Agassiz, vol. 3, pl. 31, fig. 1-14.
 1842 *Lamna obliqua* - Morton, p. 219.
 1842 *Lamna lanceolata* - Morton, p. 220.
 1843a *Otodus obliquus* - Agassiz, vol. 3, p. 267-269.
 1843a *Otodus lanceolatus* - Agassiz, vol. 3, p. 269-270.
 1843b *Otodus obliquus* - Agassiz, vol. 3 pl. 36, fig. 22-26, fig. 27?
 1843b *Otodus lanceolatus* - Agassiz, vol. 3, pl. 37, fig. 19-23.

- 1849 *Otodus obliquus* - Gibbes, p. 199, pl. 26, fig. 131-137.
 1885 *Carcharodon obliquus* (Agassiz) - Noetling, p. 84-88, pl. 6, fig. 4-6.
 1889 *Lamna* (?) *obliqua* (Agassiz) - Woodward, p. 404-407.
 1911 *Otodus lanceolatus* (Morton) - Fowler, p. 57.
 1952 *Lamna obliqua* (Agassiz) - Arambourg & Signeux, p. 106-108, pl. 18.
 1966 *Lamna obliqua* (Agassiz) - Casier, p. 76-79, pl. 6, 7.
 1999 *Otodus obliquus* Agassiz, 1843 - Kent, p. 22, pl. 2.2, fig. L, M.
 1999 *Otodus obliquus* Agassiz, 1843 - Zhelezko & Kozlov, p. 142-144, pl. 14, fig. 5; pl. 16, fig. 5; pl. 17, fig. 1; pl. 43.
 2012 *Otodus* (*Otodus*) *obliquus* Agassiz, 1838 - Cappetta, p. 224, fig. 208A-E.
 2014 *Otodus obliquus* (Agassiz, 1838) - Ehret & Ebersole, p. 7.
 2020 *Otodus* (*Otodus*) *obliquus* Agassiz, 1838 - Guinot et al., p. 21-23, fig. 4.

Syntypes: ANSP 6833 and the seven specimens figured by Agassiz (1838: vol. 3) in plate 31, fig. 1, 2, 10-14 (see previous section for the details on identification of the syntypes). Since all the syntypes are conspecific, there is no need to designate a lectotype.

Type localities: Sheppey Island, UK, London Clay Formation, Ypresian (Early Eocene); Burlington County, New Jersey (unknown precise locality); unknown formation, probably Manasquan Formation (Early Eocene).

Junior synonym (non-exhaustive list): *Otodus lanceolatus* (Agassiz in Morton, 1835); holotype: ANSP 6831 (Fig. 7J, K); Burlington County, New Jersey (unknown precise locality); unknown formation, probably Manasquan Formation (Early Eocene).

Otodus auriculatus (Blainville, 1818)

- 1784 Glossopètres - Burtin, pl. 1, fig. Q, R.
 †1818a *Squalus auriculatus* - Blainville, p. 384.
 1818b *Squalus auriculatus* - Blainville, p. 80.
 1835b *Carcharias auriculatus* - Agassiz, vol. 3, pl. 28, fig. 17-19.
 1835b *Carcharias megalotis* - Agassiz, vol. 3, pl. 28, fig. 8-10.
 1836 *Carcharias megalotis* - Egerton, p. 367 (name only).
 1837 *Carcharias megalotis* - Egerton, p. [6] (name only).
 1838 *Carcharias megalotis* - Bronn, p. 1163 (name only).
 1843a *Carcharodon auriculatus* - Agassiz, vol. 3, p. 254-255.
 1843a *Carcharodon megalotis* (Agassiz) - Agassiz, vol. 3, p. 258-259.
 1923 *Carcharocles auriculatus* - Jordan & Hannibal in Jordan, p. 99 (see Greenfield 2020).
 1960 *Procarcharodon auriculatus* (Blainville) - Casier, p. 13.
 1964 *Otodus auriculatus* (Blainville, 1818) - Glickman, p. 66, 116, fig. 49; pl. 8, fig. 1, 1a-b; pl. 16, fig. 2-4, 6-11.
 1986 *Carcharocles auriculatus* (Blainville, 1818) - Nolf, pl. 35, fig. 1-4.
 1987 *Carcharocles auriculatus* - Cappetta, p. 103.
 1999 *Otodus auriculatus* (Blainville, 1818) - Zhelezko & Kozlov, p. 145-147, pl. 17, fig. 2, 4-6; pl. 18, fig. 1-5; pl. 47; pl. 48, fig. 3-7.
 2012 *Otodus* (*Carcharocles*) *auriculatus* (Blainville, 1818) - Cappetta, p. 224, fig. 209.
 2013 *Carcharodon auriculatus* (Blainville, 1818) - Diedrich, fig. 3.
 2014 *Carcharocles auriculatus* (Blainville, 1818) - Ehret & Ebersole, fig. 3F-H, 4A-C.
 2019 *Carcharocles auriculatus* (Blainville, 1818) - Perez et al., fig. 3A.

Syntypes: One of the two teeth illustrated by Burtin (1784: pl. 1, fig. Q or R) and one tooth kept in the collection of Alexandre Brongniart (not figured).

Type localities: Brussels area, Belgium (unknown precise locality), Brussels Sand Formation or Lede Sand Formation (Lutetian, middle Eocene) (Laga et al. 2001) where the species is commonly found (Storms 1901; Van den Eeckhout & De Schutter 2009; Herman & Van den Eeckhout 2010; Cappetta 2012: fig. 209).

Junior synonyms (non-exhaustive list): *Otodus megalotis* (Agassiz, 1835b); lectotype (explicitly designated in the present work): specimen figured by Agassiz (1835b: vol. 3, pl. 28, fig. 8-10), unknown locality.

Otodus megalodon (Agassiz, 1835b)

- 1554 Langues de Malte [tongues from Malta] - Thevet, p. 204 (see Brignon 2019b, 2020 for early records of the species between the 16th and the early 19th centuries).
 1798 *Squalus carcharias* Linnaeus, 1758 - Lacépède, p. 202-208.
 1811 Shark close to the white shark *Squalus carcharias* Linnaeus, 1758 - Parkinson, p. 255, pl. 19, fig. 11.
 1818a *Squalus lamia* Blainville, 1816 [junior synonym of *Carcharodon carcharias* (Linnaeus, 1758)] - Blainville, p. 384; 1818b, p. 80.
 1818a *Carcharias verus* Cloquet, 1817 [junior synonym of *Carcharodon carcharias* (Linnaeus, 1758)] - Blainville, p. 384; 1818b, p. 80.
 1832 *Carcharias megalodon* Agassiz - Lingg, p. 16, 17 (*nomen nudum*).
 1833 *Carcharias megalodon* Agassiz - Schübler & Lingg, p. 123 (*nomen nudum*).
 1834 Shark - Morton, p. 31, pl. 12, fig. 2.
 1834 *Carcharias megalodon* Agassiz - Agassiz, p. 66 (*nomen nudum*).
 †1835b *Carcharias megalodon* Agassiz - Agassiz, vol. 3, pl. 29; feuilletton additionnel, p. 72.
 1835a *Carcharias polygyrus* Agassiz in Morton - Morton, additional observations, p. [2].
 1835b *Carcharias polygyrus* Agassiz - Morton, p. 277.
 1836 *Carcharias polygyrus* [sic] Agassiz - Egerton, p. 367 (name only, incorrect subsequent spelling).
 1836 *Carcharias megalodon* Agassiz - Charlesworth, p. 327 (name only).
 1837 *Carcharias megalodon* [sic] Agassiz - Charlesworth, p. 226.
 1837 *Carcharias polygyrus* [sic] Agassiz - Egerton, p. [6] (name only).
 1837 *Carcharias megalodon* - Bronn, p. 15, pl. 43, fig. 1.
 1838 *Carcharias polygyrus* [sic] Agassiz - Agassiz, vol. 3, pl. 30, fig. 9, 11, 12; feuilletton additionnel, p. 114.
 1838 *Carcharias productus* Agassiz - Agassiz, vol. 3, pl. 30, fig. 2, 4, 6, 7, 8.
 1838 *Charcharias* [sic] *megalodon* - Bronn, p. 1163.
 1838 *Carcharias polygyrus* [sic] - Bronn, p. 1163 (name only).
 1842 *Carcharias polygyrus* Agassiz - Morton, p. 220.
 1843a *Carcharodon megalodon* - Agassiz, vol. 3, p. 247-249.
 1843a *Carcharodon polygyrus* [sic] - Agassiz, vol. 3, p. 253.
 1911 *Carcharodon polygyrus* (Morton) - Fowler, p. 61.
 1960 *Procarcharodon megalodon* (Agassiz) - Casier, p. 13.
 1964 *Megaselachus megalodon* (Agassiz, 1843) - Glickman, p. 104.
 1986 *Carcharocles megalodon* (Agassiz, 1843) - Nolf, pl. 56, fig. 1-6.
 1987 *Carcharocles megalodon* - Cappetta, p. 103, fig. 91A-B.
 2007 *Megaselachus megalodon* (Agassiz, 1835) - Cahuzac et al., p. 18-20.
 2008 *Carcharodon megalodon* (Agassiz) - Aguilera et al., fig. 2.19, 2.20.
 2012 *Otodus* (*Megaselachus*) *megalodon* (Agassiz, 1835) - Cappetta, p. 224.
 2012 *Otodus megalodon* (Agassiz, 1835) - Bor et al., p. 37, pl. 20, fig. 1-2.
 2017 *Carcharocles megalodon* (Agassiz, 1843) - Collareta et al., fig. 2b.
 2017 *Otodus megalodon* (Agassiz) - Shimada et al., p. 712
 2019 *Carcharocles megalodon* - Perez et al., fig. 3H-I, K-L.
 2019 *Otodus megalodon* (Agassiz, 1843) - Boessenecker et al., fig. 2-8, 10.
 2021 *Otodus megalodon* (Agassiz, 1843) - Perez et al., fig. 1B, 3, 11.

Syntypes: In addition to the seven teeth illustrated by Agassiz (1835b: vol. 3, pl. 29, fig. 1-8) (Fig. 9D), the type series also includes all the teeth known by Agassiz before June 1835. These include a tooth studied by Agassiz (1834: 66; 1843a: vol. 3, 249) in the “Museum of Prague”, now the National Museum, Prague (Czech Republic), during the summer of 1833 (see Brignon 2015a). Purdy et al. (2001: 131, 133) designated as the “type specimen” or the “holotype”

one of the teeth figured by Agassiz (1835b: vol. 3, pl. 29, fig. 2, 3) of which a cast is preserved in the Staatliches Museum für Naturkunde in Karlsruhe, Germany. Since the name is based on syntypes, this designation must be rejected and cannot be considered as a valid lectotype designation as Articles 74.7.1 and 74.7.3 of the Code are not verified. Since the syntypes are conspecific, there is no need to designate a lectotype.

Type localities: According to Article 73.2.3 of the Code, “if the syntypes originated from two or more localities (including different strata), the type locality encompasses all of the places of origin”. Two teeth kept in the Museum of Strasbourg (France) are indicated as coming from Malta (Agassiz 1835b: vol. 3, pl. 29, fig. 4, 7) but Agassiz (1843a: vol. 3, 249, footnote) was not sure of this origin. At that time, the teeth of *megalodon* were often designated “Maltese tongues” in reference to older literature (Scilla 1670; Zammit Maempel 1975; Duffin, 2017; Brignon 2020). This being said, the species is common in several Miocene formations of Malta (Menesini 1974; Ward & Bonavia 2001). One tooth in the Heinrich Georg Bronn (1800-1862) collection was from Styria, southeastern Austria (Agassiz 1835b: vol. 3, pl. 29, fig. 6), where the species has been recorded in the Badenian (Langhian and early Serravallian) (Schultz 1971; Hiden 1995; Trif et al. 2016). A second tooth in the Bronn collection was from the region of Dax (Landes department, south-west France). Most of the discoveries of *O. megalodon* from this area have been found in middle Miocene deposits (Serravallian), in particular in the townships of Narrosse, Sort-en-Chalosse, Castelnau-Chalosse or Montfort-en-Chalosse (Cahuzac et al., 2007). Agassiz (1843a: vol. 3, pl. 29, fig. 8) also mentions “two very beautiful teeth” of this species in the Museum d’Histoire naturelle in Paris. According to Cahuzac et al. (2007), these two specimens could also come from the Miocene of the Landes departement.

Junior synonym (non-exhaustive list): *Carcharodon polygurus* (Agassiz in Morton, 1835a); lectotype: ANSP 973 (Fig. 8C, D), New Jersey (unknown locality), unknown formation, probably Kirkwood Formation (Early to Middle Miocene).

CONCLUSIONS

As far as paleontology is concerned, “old” scientific literature still conceals surprises and valid nomenclatural acts that have gone relatively unnoticed. The well-known names of the extinct otodontid sharks established by Louis Agassiz are no exception to this observation. In addition to the fact that the publication date of nomenclatural acts introduced in Agassiz’s “Recherches sur les poissons fossiles” are in themselves complex to disentangle, things become even more complicated when Agassiz’s names were introduced in other works prior to his (Brignon 2015a). This underscores the importance of correctly citing the exact publication date on which a new name was first introduced in compliance with the requirements of availability. Otherwise, a wrong date can lead to a misinterpretation of the precedence between two names. To give an example, the iconic species *Otodus megalodon* is still too often cited in modern scientific publications

with the wrong date of 1843, instead of 1835. It is obvious to see the nomenclatural consequences of this mistake when one knows that the long-forgotten synonym *Otodus polygurus* was introduced in 1835 in Morton’s “Synopsis”. After a detailed analysis, the nomenclatural acts introduced in the latter work fortunately do not disturb the established nomenclature of otodontid sharks, except for the date of publication of *Otodus obliquus*, which must be set in 1835. Besides these nomenclatural aspects, the fossil shark teeth of the John Price Wetherill collection still preserved in the ANSP are of great interest in the history of North American paleontology. They do represent type materials, and the first fossil shark teeth figured and named according to the binomial nomenclature in a work published in the United States.

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