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Cover

Two views of a cast of the long-lost holotype of **Petalodus ohioensis** Safford, 1853 and hypothetic restoration of the shark. The cast resolves the long historical debate about the validity of this ancient shark tooth species.



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Taxonomic Validity of *Petalodus ohioensis* (Chondrichthyes, Petalodontidae) Based on a Cast of the Lost Holotype

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ABSTRACT

Only a crude line drawing of the holotype tooth of the shark *Petalodus ohioensis* Safford, 1853 has ever been published, and the location of that specimen has long been unknown. The discovery of a cast of the holotype in the collections of the Yale Peabody Museum of Natural History demonstrates that *P. alleghaniensis* Leidy, 1856, is a junior subjective synonym of *P. ohioensis*, thus resolving a long-standing dispute.

INTRODUCTION

The discovery of teeth from the Late Paleozoic shark, Petalodus, from the near the top of the Permian "lower Cutler beds" of the Cutler Group in southeastern Utah, led to a brief description and illustration of many important holotypes and referred specimens in order to determine the taxon to which the lower Cutler teeth belonged (Carpenter and Ottinger, 2018). Several important and key specimens were illustrated by photographs for the first time, including the holotypes of P. hastingsii Owen, 1840, P. acuminatus (Agassiz, 1838), P. rhombus (M'Coy, 1854), and P. alleghaniensis Leidy, 1856. One crucial specimen that could not be located for photographic inclusion was the holotype of P. ohioensis Safford, 1853 from the Cambridge Limestone of the Conemaugh Formation in Ohio. Specimens have been referred to this species (e.g., Hay, 1895; Lucas and others, 2011; Carpenter and Ottinger, 2018) based on the crude illustration by Safford (1853) (see figures 1A and 1B). This specimen is crucial for resolving the issue of whether P. alleghaniensis (figures 1E and 1F) is

a separate taxon from *P. ohioensis* or a junior subjective synonym of *P. ohioensis* (e.g., Hay, 1895; Zidek and Kietzke, 1993, 1996; Brusatte, 2007; Ivanov and others, 2009; Ginter and others, 2010; Carpenter and Ottinger, 2018). The discovery of a cast (figures 1C and 1D) of the holotype of *P. ohioensis* finally resolves the issue.

INSTITUTIONAL ABBREVIATIONS

ANSP-Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; MCZ-Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; NHMUK-Natural History Museum, United Kingdom, London, England; USNM-United States National Museum (National Museum of Natural History), Washington, D.C.; YPM-Yale Peabody Museum of Natural History, New Haven, Connecticut.

HISTORY OF THE PROBLEM

The morphological tooth genus *Petalodus* was named by Richard Owen (1840–1845), as *Petalodus*

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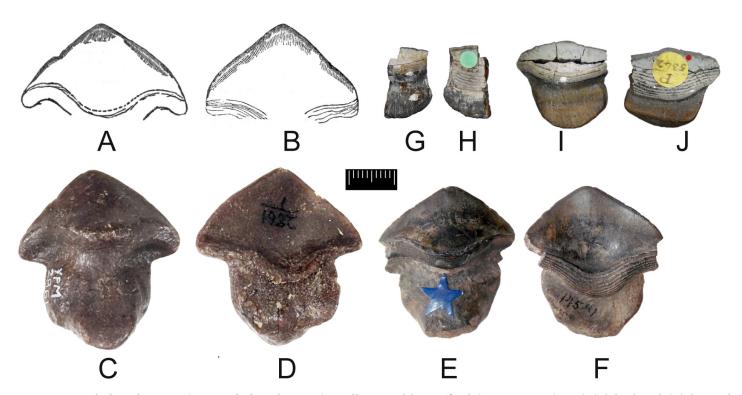


Figure 1. *Petalodus ohioensis* (as *Getalodus ohioensis*) as illustrated by Safford (1853, p. 142) in (A) labial and (B) lingual views, compared to a cast (YPM 2861) purported to be of the specimen in (C) labial and (D) lingual views. Holotype of *Petalodus alleghaniensis* (ANSP 14541) in (E) labial and (F) lingual views. Holotype of *Petalodus hastingsii* (NHMUK PV P.613) in (G) labial and (H) lingual views. Proposed neotype (NHMUK PV P.75414, formerly part of P.5342; Carpenter and Itano, 2018) in (I) labial and (J) lingual views. The origin of the green dot on specimen H is uncertain but may have been the code used by Woodward (1889) or Owen (1840–1845) to denote it was a holotype. The red dot on specimen J is a blob of wax used by Woodward (1889) to denote that he included the specimen in his catalog of fossil fishes. The blue star on specimen E is the old symbol used to denote a holotype. Scale in mm.

hastingsii, for a fragment of a tooth from the Ticknall Limestone (upper Viséan = upper Middle Mississippian) in South Derbyshire, England (the fragment, figures 1G and 1H, is not diagnostic and a proposal has been submitted by us to the International Commission on Zoological Nomenclature to make the more complete NHMUK PV P.75414, figures 1I and 1J, from the same locality, the neotype for the taxon; Carpenter and Itano, 2018).

In 1850, Professor James Safford, geologist at Cumberland University in Lebanon, Tennessee, collected a tooth having a triangular crown from the Cambridge Limestone of the Conemaugh Formation (middle to upper Missourian = lower Upper Pennsylvanian) near the town of Cambridge in Guernsey County, southeastern Ohio. Fortuitously for him, Louis Agassiz had emi-

grated to the United States in 1847 and was at the 1851 American Association for the Advancement of Science meeting, where Safford showed him the tooth. Before emigrating, Agassiz had published his multi-year (1833-1845a, 1833-1845b), ten volume "Recherches sur les Poissons Fossiles" ["Research on Fossil Fish"] and was quite familiar with the kind of tooth Safford showed him. Agassiz, who was then at Harvard University, "pronounced it at once a new species of Getalodus" (Safford, 1853, p. 142). Shortly thereafter, Safford was successful in removing the specimen from the matrix and published a brief paragraph (Safford, 1853) naming the taxon Getalodus ohioensis and provided two views of the tooth (reproduced here as figures 1A and 1B), which Hay (1895) reports were woodcuts. Safford's publication was overlooked in subsequent descriptions

of specimens of *Petalodus* from the United States (Leidy, 1855, 1856, 1873; Newberry and Worthen, 1866; St. John, 1870; Newberry, 1875), until its "rediscovery" by Hay (1895). Hay (1895, 1902) commented that the generic name "*Getalodus*" was a typographical error for *Petalodus*, either due to misinterpretation of Safford's handwritten manuscript by the typesetter, or Safford's misunderstanding of Louis Agassiz' heavy Swiss French accent during their conversations.

Two years after Safford named Petalodus ohioensis, Leidy (1855) named Sicarius extinctus for a tooth that was loaned to him, and noted, that it resembled a pangolin scale. Leidy (1855) thought it was fish but did not rule out reptile. The specimen was found in the Glenshaw Formation (Missourian = lower Upper Pennsylvanian) at Bens Creek Station in what is now the Allegheny Portage Railroad National Historic Site near Cresson, Pennsylvania (Koch and Santucci, 2004). The following year, Leidy (1856) renamed the tooth Petalodus alleghaniensis (note original spelling, sometimes subsequently misspelled allegheniensis [Goto and Okura, 2004; Monson, 2010]), described it in detail and illustrated it. The specimen is currently in the collections of The Academy of Natural Sciences of Philadelphia (ANSP 14541, figures 1E and 1F). The name change from Sicarius to Petalodus is understandable once Leidv learned what Petalodus teeth were like. What is not clear is why he also changed the species name; no reason was given.

Hay (1895) raised the possibility that *P. ohioensis* had priority over *P. alleghaniensis*, as well as *P. destructor* named by Newberry and Worthen (1866) and his own *P. securiger*. However, because he did not think Safford's drawings were wholly accurate and because the whereabouts of Safford's specimen was unknown for comparison, he only synonymized *P. destructor* with *P. ohioensis* based on similarities of the crowns and sizes. Eastman (1896) considered *P. ohioensis* a nomen dubium because Safford's description was insufficient and the drawing probably inaccurate. This position, however, has not been followed (e.g., Hay, 1902; Hansen, 1985, 1996; Dalla Vecchia, 1988; Zidek and Kietzke, 1993; Brusatte, 2007; Ginter and others, 2010; Carpenter and Ottinger, 2018).

A FINAL RESOLUTION

Recently, one of us (WMI) discovered a cast identified as of the holotype *P. ohioensis* in the collections of the YPM (YPM 2861) (figures 1C and 1D). Notes associated with the cast refer to it as the "plastotype" and that it was obtained from the MCZ. The cast was catalogued at the YPM on September 18, 1930 (Don Brinkman, YPM, written communication, June 15, 2018). However, there are no records at the MCZ of the cast or original specimen from which the cast was made (Jessica Cundiff, MCZ, written communication, June 15, 2018). This absence may explain why Eastman (1896), who was at the MCZ at the time of his article, made no mention of the specimen.

Although the quality of the cast is low, it does show that the tooth was more than just the crown. Of the crown, the cingulum of imbricated ridges at the base of the crown on both the labial and lingual sides as shown by Safford (1853) are not very distinct. Nor does the cast display the striated occlusal margin as shown by Safford. Nevertheless, the cast does confirm that the specimen has the distinctive crown of Petalodus, which is triangular, vertically short, broad-based, labio-lingually compressed, convex labially, and concave lingually. The root is complete and has the characteristic tongue-shape of Petalodus. In addition, it is D-shaped in horizontal cross section, with the lingual side flat. Measurements are given in table 1. Although larger, the tooth strongly resembles that of *P. alleghaniensis* in crown profile and presence of a notch in the lower corner of the root, which may help determine tooth position. We can find no reason for recognizing two taxa and here formally synonymize P. alleghaniensis Leidy, 1856 with P. ohioensis Safford, 1853 as first suggested by Hay (1895).

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley, 1880 Order Petalodontiformes Patterson, 1965 Petalodontida Zangerl, 1981 Family Petalodontidae Newberry and Worthen, 1866 Genus *Petalodus* Owen, 1840

Table 1. Measurements for specimens of *Petalodus* used in this study. Abbreviations: (e) – estimate; (H) – holotype; mm – millimeter; NA – not available.

Taxon (catalog number)	Crown side	Maximum tooth height (mm)	Maximum crown width (mm)	Maximum mid-crown height to top of cingulum (mm)	Maximum cingulum mid- height (mm)
P. ohioensis (YPM 2861) (H)	Labial	39.3	35.3	15.5	3.4
	Lingual			25.8	3.1
P. alleghaniensis (ANSP 14541) (H)	Labial	34.5 (35.3 e)	30.2 (30.6 e)	15.6	3.7
	Lingual			20	5.5
P. acuminatus (MHNN-FOS 171) (H)	Lingual	NA	34.6 (e)	16.6	3.3

Synonymies

Chomatodus Agassiz, 1838 (in part) Getalodus Safford, 1853 err typo Ctenopetalus Davis, 1881 Sicarius Leidy, 1855

Species Petalodus ohioensis Safford, 1853

Synonymies

Sicarius extinctus Leidy, 1855 Petalodus alleghaniensis Leidy, 1856 Petalodus allegheniensis Leidy, 1856 err typo Petalodus destructor Newberry and Worthen, 1866 Petalodus securiger Hay, 1895

CONCLUSIONS

It has been 165 years since James Safford named and illustrated Petalodus ohioensis for a tooth from the Upper Pennsylvanian of Ohio. The taxonomic validity of the name has been problematic because the holotype is missing, and the original description and illustrations are insufficient. The discovery of a cast purported to be of the holotype has resolved a decades-long debate as to the validity of the taxon and the seniority of the species name over that of P. alleghaniensis Leidy, 1856. Pending discovery of the original specimen of *P. ohioensis*, the cast (YPM 2861) may act as a representative of that specimen, but the cast itself as a three-dimensional illustration of the specimen, is not the holotype (ICZN Art. 72.5.3 with 73.1.4). The term "plastotype," which is written on a label with the cast, is a term not regulated by the International Code of Zoological Nomenclature

(ICZN) and is not used here. This cast also negates the need for a neotype (as defined by ICZN Article 75) of *P. ohioensis*, which fortunately has never been published, despite appearing on a label accompanying a cast at the NHMUK in London. That label accompanies a cast, NHMUK PV P.58463, which is a cast of USNM PAL 244454. However, ICZN Article 9 is clear that a notation written on a label is not a valid designation. Furthermore, the discovery of the cast of the holotype would set aside the neotype designation (ICZN Article 75.8).

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