TAXONOMIC VALIDITY OF *PETALODUS OHIOENSIS* (CHONDRICHTHYES, PETAŁODONTIDAE) BASED ON A CAST OF THE LOST HOLOTYPE

Kenneth Carpenter and Wayne M. Itano
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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**


**HISTORY OF THE PROBLEM**

The morphological tooth genus *Petalodus* was named by Richard Owen (1840–1845), as *Petalodus*
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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 emigrated 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 *Petalodus 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 *Petalodus 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 emigrated 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 *Petalodus 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 Oku- ra, 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 Leidy 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.

<table>
<thead>
<tr>
<th>Taxon (catalog number)</th>
<th>Crown side</th>
<th>Maximum tooth height (mm)</th>
<th>Maximum crown width (mm)</th>
<th>Maximum mid-crown height to top of cingulum (mm)</th>
<th>Maximum cingulum mid-height (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. ohioensis</em> (YPM 2861) (H)</td>
<td></td>
<td>39.3</td>
<td>35.3</td>
<td>15.5</td>
<td>3.4</td>
</tr>
<tr>
<td></td>
<td>Labial</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lingual</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. alleghaniensis</em> (ANSP 14541) (H)</td>
<td></td>
<td>34.5 (35.3 e)</td>
<td>30.2 (30.6 e)</td>
<td>15.6</td>
<td>3.7</td>
</tr>
<tr>
<td></td>
<td>Labial</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lingual</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>P. acuminatus</em> (MHNN-FOS 171) (H)</td>
<td></td>
<td>NA</td>
<td>34.6 (e)</td>
<td>16.6</td>
<td>3.3</td>
</tr>
<tr>
<td></td>
<td>Lingual</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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 alleghaniensis* 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).

**ACKNOWLEDGMENTS**

Don Brinkman (Yale Peabody Museum of Natural History, New Haven, Connecticut) gave W. Itano access to collections, which led to the discovery of the cast YPM 2861 and provided collection data. Jessica Cundiff (Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts) searched for the original of *Petalodus ohioensis* and provided information on the *Petalodus* specimens under her care. Ned Gilmore (Academy of Natural Sciences, Drexel University, Philadelphia, Pennsylvania) provided images of the holotype of *Petalodus alleghaniensis*. Emma Bernard (Natural History Museum, London, England) provided W. Itano access to collections and assigned a new specimen number for a specimen selected as the neotype of *Petalodus hastingsii*. We thank Mike Hansen (retired, Ohio Geological Survey, The Ohio State University, Columbus, Ohio), Jim Kirkland (Utah Geological Survey), and Spencer Lucas (New Mexico Museum of Natural History and Science) for their reviews.
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