GEOLOGY OF THE INTERMOUNTAIN WEST
an open-access journal of the Utah Geological Association
ISSN 2380-7601
Volume 5 *2018*

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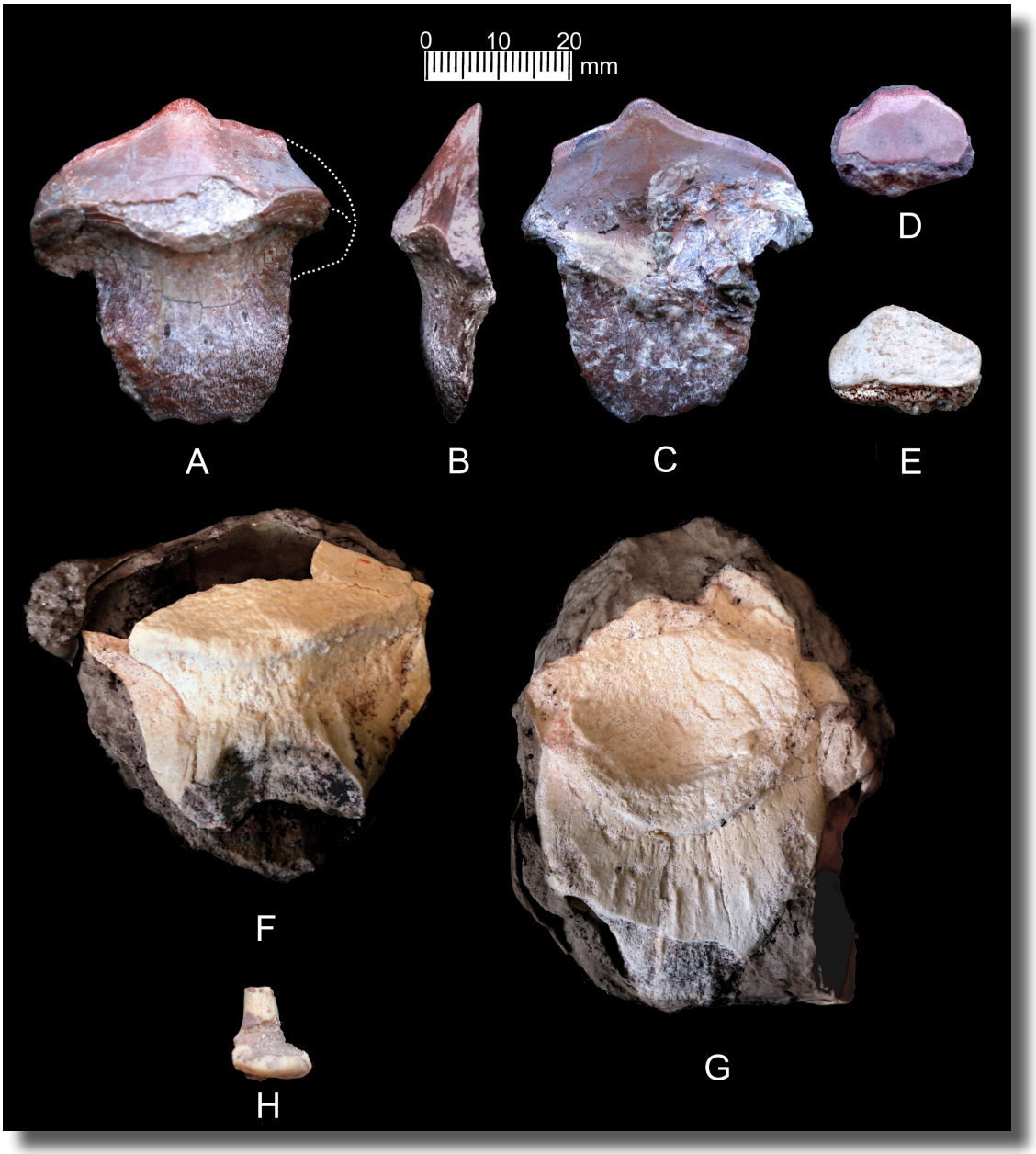
Kenneth Carpenter and Lin Ottinger



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Cover
Shark teeth from the lower Cutler beds, Shafer Basin from near Moab, Utah

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Permo-Pennsylvanian Shark Teeth from the Lower Cutler Beds Near Moab, Utah

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ABSTRACT

Several shark teeth have been collected from limestones in the marine-nonmarine transitional zone of the lower Cutler beds in the Shafer Basin near Moab, Utah. The shark teeth include the Pennsylvanian petalodontiform *Petalodus ohioensis*, which is the first described from the state, and the Permo-Carboniferous cladodontomorph *Cladodus* sp. The *Petalodus* specimens are compared with the holotype *P. hastingsae* Owen, *P. acuminatus* (Agassiz), *P. ohioensis* (Shafer), and *P. alleghaniensis* (Leidy). Several of these key taxa are illustrated with photographs for the first time.

INTRODUCTION

The late Paleozoic shark record from Utah is poorly known, but what is known was summarized by Sumida and others (1999). They report teeth of the freshwater xenacanth *Orthacanthus* from the Lower Permian Halgaito Shale (Cutler Group) and an unnamed partial chondrichthyean tooth from the nonmarine Lower Permian Organ Rock Formation (Cutler Group). In addition, Miller (1981) reported on occurrences of the form genus *Cladodus* sp. from the Mississippian Great Blue Limestone and the Manning Canyon Shale in north central Utah. One of us (Ottinger) amassed a small collection of marine shark teeth during the 1970s from the area between the potash mine and evaporation ponds in the Shafer Basin southwest of Moab, Utah. This is the same general area that Lohman (1974) reported the cochliodont shark *Deltodus* sp. and the petalodont shark *Petalodus*. Lohman's specimens have not been figured or described and their current location are unknown. Owing to the importance of documenting the new collection, we describe and illustrate the material below. Original specimens or casts of specimens are curated at the Prehistoric Museum, Utah State University Eastern, Price, Utah. Exact locality information for each specimen is no longer known.

GEOLOGICAL SETTING

The specimens were collected in the Shafer Basin, which is located between Cane Creek and Shafer anticlines, southwest of Moab Utah (figure 1). Here, the Permian strata are well exposed along the Colorado River below the cliffs of Dead Horse Point State Park (figure 2A). Matrix adhering to the teeth show that all but one came from the Shafer limestone bed, an informal name applied to a prominent limestone in the Shafer Basin. This limestone caps a 90 m interval (figure 2B) of alternating marine limestones and muddy sandstones containing invertebrate fossils and burrows (fig-

Citation for this article.
Carpenter, K., and Ottinger, L., 2018, Permo-Pennsylvanian shark teeth from the Lower Cutler beds near Moab, Utah: Geology of the Intermountain West, v. 5, p. 105–116.

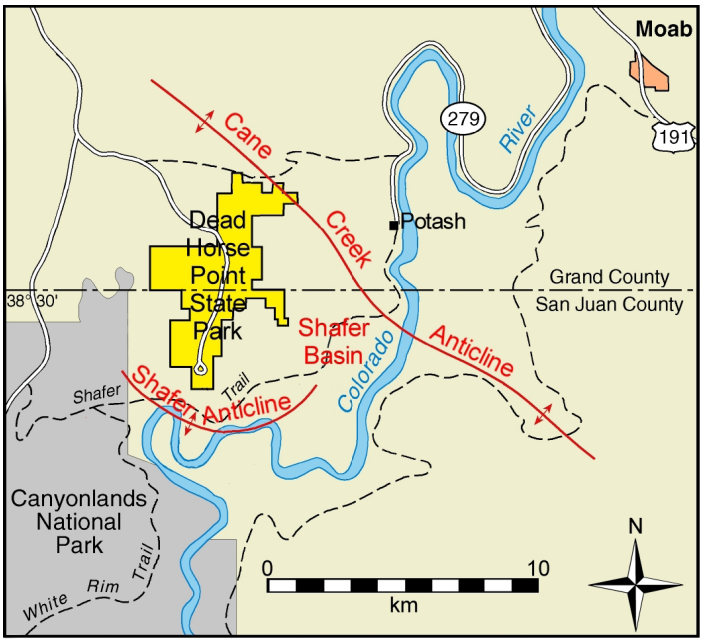

Figure 1. Map showing the location of Shafer Basin southwest of Moab, Utah, where the shark teeth were found. Adapted from Doelling and Chidsey (2004).

ure 2C), and nonmarine arkosic sandstones and aeolian sandstones containing rhizoliths (figure 2D), including a possible lycopod root (figure 2E).

These strata have been variously called or mapped in this basin as the Rico Formation (Prommel, 1923; Baker and others, 1927; McKnight, 1974; Hinrichs and others, 1967; Loope, 1984), Rico transition facies (Wengerd and Matheny, 1958), Elephant Canyon Formation (Terrell, 1972; Campbell, 1987), the lower Cutler beds (Condon, 1997; Doelling and others, 1994; Doelling and Chidsey, 2009; Dubiel and others, 2009), lower Cutler Group (Doelling, 2004), or simply considered as part of the Cutler Formation undifferentiated (Mattox and Brand, 1974; Huntoon and others, 2002). We refer these marine-continental transition strata as the "lower Cutler beds" as used by Loope and others (1990), with the Shafer limestone as the top of this unit.

Specimen abbreviations: CEUM – College of Eastern Utah Museum (now Prehistoric Museum, Utah State University Eastern), Price, Utah. MHNN – Muséum d'histoire naturelle de Neuchâtel, Neuchâtel, Switzerland; NHMUK – Natural History Museum, United Kingdom, London, England.

SYSTEMATIC PALEONTOLOGY

Class Chondrichthyes Huxley 1880
Order Petalodontiformes Zangerl 1981
Family Petalodontidae Newberry and Worthen 1866
Genus *Petalodus* Owen 1840–1845
Species *Petalodus ohioensis* (Safford 1853)
Material CEUM 81502, 81503, 81504 teeth
CEUM 81643 cast, CEUM 81644 cast
Figures 3A to 3G

Petalodus is a distinctive form genus characterized by a labio-lingually compressed, vertically short, broad-based, triangular crown that is convex anteriorly and concave posteriorly. The base of the crown is bordered by a band or cingulum composed of imbricated ridges that are especially well developed on the lingual side (Leidy, 1856, first referred to the structure as a cingulum and is followed here; Robb, 2003 refers to it as the "distal crown tongue"). The crown is situated on a long, tapering root (base). The five teeth vary in size and in the height and width of the crowns; their measurements are given in table 1. Part of these differences may be ontogenetic; wear and location in the jaws as has long been recognized (e.g., Newberry and Worthen, 1866; Eastman, 1896). The specimens are assigned to the species *P. ohioenesis* because of the vertically narrow cingulum around the crowns; the cingulum is much wider in *P. acuminatus*. Hansen (1985) notes that *P. ohioenesis* is the only species in the Pennsylvanian and Lower Permian of the United States.

CEUM 81502 (figures 3A to 3C)

The most complete tooth in the collection, it has a crown that is convex on the labial surface and concave on the lingual side just above the root. The concavity may accommodate the convex surface of the succeeding replacement tooth (figure 4A) in a manner similar to those reported by Davis (1883) for the petalodontiforms *Petalorhynchus* and *Glossodus*. Lucas and others (2011) suggested that the concavity accommodated the crown apex of the opposing tooth (figure 4B). In profile view, the root and crown are slightly angled relative to one another. The cutting edges of the crown terminate in a

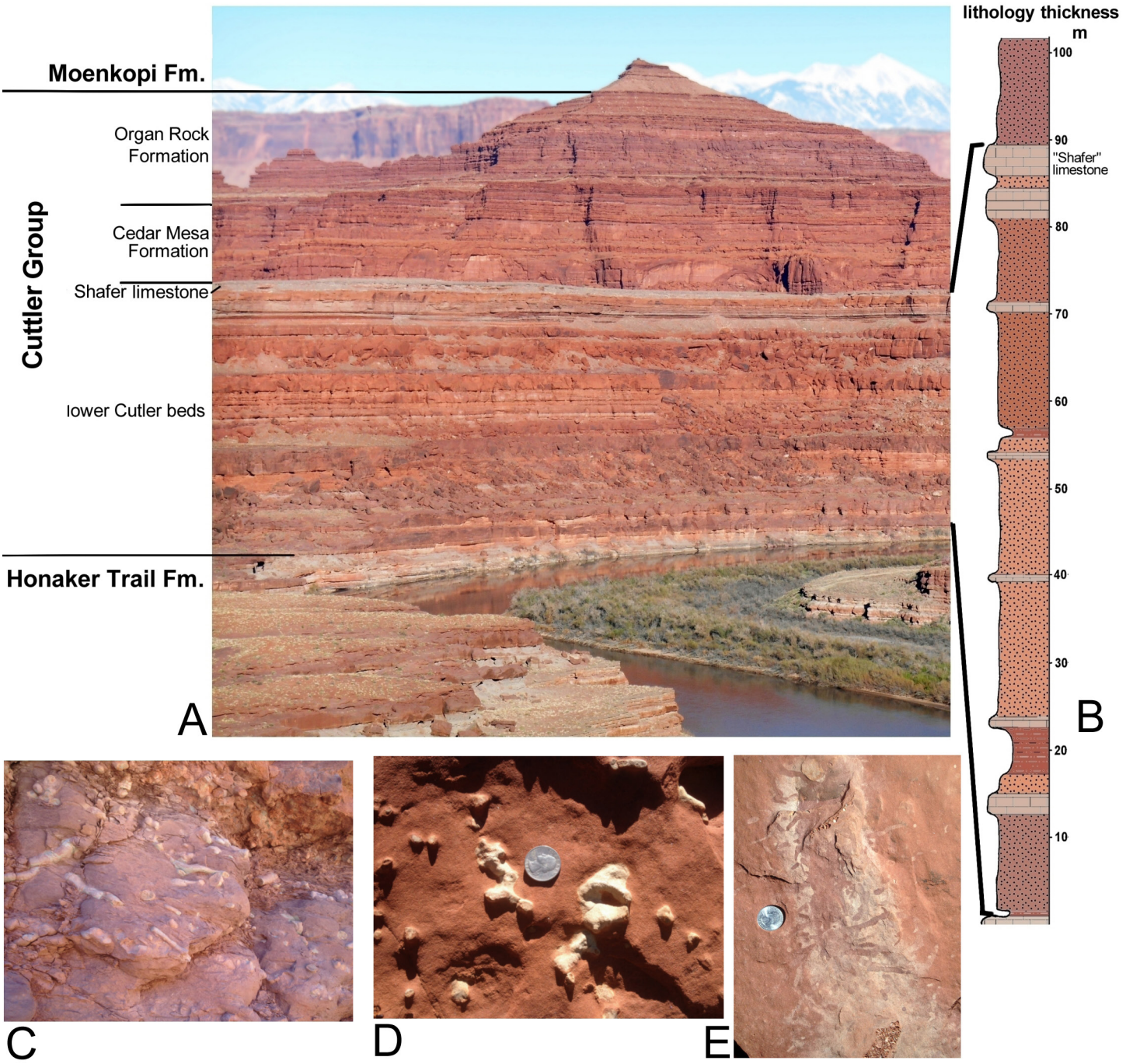

Figure 2. (A) Complete section of the Cutler Group at Pyramid Butte, south end of Shafer Basin; Colorado River in foreground and Shafer anticline to immediate left out of frame. (B) Stratigraphic column based on a measured section of the Shafer Basin given by Terrell (1972, appendix 1) extending northwest from the J.L. Eddy boat ramp (38°30'19.97"N, 109°39'33.75"W). (C) burrows in the marine facies of the lower Cutler beds, Shafer anticline (38°27'57.41"N, 109°43'12.23"W). (D) rhizoliths in an eolian facies (note uniform grain size) of the lower Cutler beds, Shafer anticline (38°27'53.99"N, 109°43'9.65"W). (E) Unusual occurrence of a lepidodendrale(?) root and rootlets in aeolian facies of the lower Cutler beds, Shafer anticline (approximately 38°27'52.63"N, 109°43'11.44"W).

Table 1. Tooth crown measurements (in mm) of Petalodus sp., CEUM 81644 too damaged to be included.

Catalog Number	Width	Height
CEUM 81502	40.5	22.5
CEUM 81503	17.8	11.1
CEUM 81504	21.2	13.75
CEUM 81643*	50.75	25.2

*measured from impression on matrix

slightly acuminate asymmetrical apex. A narrow band on each side of the edges shows tiny parallel dentine tubules. The labial band shows irregular wear, which extends onto the crown and exposes the underlying tangled-fibered enameloid as described and illustrated by Lund (1989, figure 16). A broad, slightly developed medial ridge extends from the apex towards the base were it merges. The labial side of the crown base is sigmoid and shows faint traces of ridges where the enameloid is preserved. In profile, the crown overhangs the root, which becomes thicker distally. The root is D-shaped in horizontal cross-section, with the lingual side flat. The acuminate and slight asymmetry of the crown indicate this is an anteromedial tooth (Robb, 2003).

CEUM 81503 (figure 3D)

The smallest of the teeth, it is also the most worn. Much of the upper part of the crown reveals the enameloid on the surface well below the parallel dentine tubule band on the labial side. The apex is worn to a notch and the medial ridge is absent. The low, elongate crown indicate that it is a lateral tooth (Robb, 2003).

CEUM 81504 (figure 3E)

Unlike the other teeth, this one was recovered from a white to light grey, arkosic, coarse sandstone, which Terrell (1972) states only occurs in the middle of the upper limestone (unit 20) in Shafer Basin. The tooth is white, rather than gray to reddish colored. The medial crown ridge is absent. The enameloid surface is etched and in places has remnants of pink feldspar and white quartz embedded. The parallel dentine tubules are accentuated from wear. The root is missing, but the low, elongate crown shows that it is a lateral tooth (Robb, 2003).

CEUM 81643 cast (figure 3F)

Much of the crown is damaged, either lacking enameloid or missing exposing the inner core. The impression shows that the apex was not acuminate, possible due to wear. A trace of the medial ridge is present. The root is incomplete, but enough remains to show that it was expanded distally in profile. The low, elongate crown, with low apex suggests it was lateral to the medial teeth, but not far posterolaterally in the jaw.

CEUM 81644 cast (figure 3G)

The crown is also damaged, with all of the enameloid eroded exposing the inner core. The lingual side of the tooth is exposed. The distal end of the root is damaged, but enough remains to suggest it curved labially much like one of the specimens figured by Lucas and others (2011; figure 3D). The high crown suggests this was an anteromedial tooth.

Superorder Cladodontomorphi Ginter, Hampe and Duffin 2010
Order CTENACANTHIFORMES Glikman 1964
Family CTENACANTHIDAE Dean 1909
Genus *Cladodus* Agassiz 1843
Species *Cladodus* sp.

CEUM 81505 tooth (figure 5H)

The tooth is heavily damaged, having an incomplete mid-crown and a base of one side crown attached to an incomplete base. It is assigned to the form genus on the basis of the large median cusp that is convex on the lingual side, flat on the labial side, and the broken base of a smaller, rounded in cross section lateral cusp. This specimen is the youngest occurrence of *Cladodus* in Utah. The two others reported by Miller (1981) are from the Mississippian Great Blue Limestone and from the Manning Canyon Shale. Adhering matrix is a dull, reddish-brown, fine, micaceous sandstone.

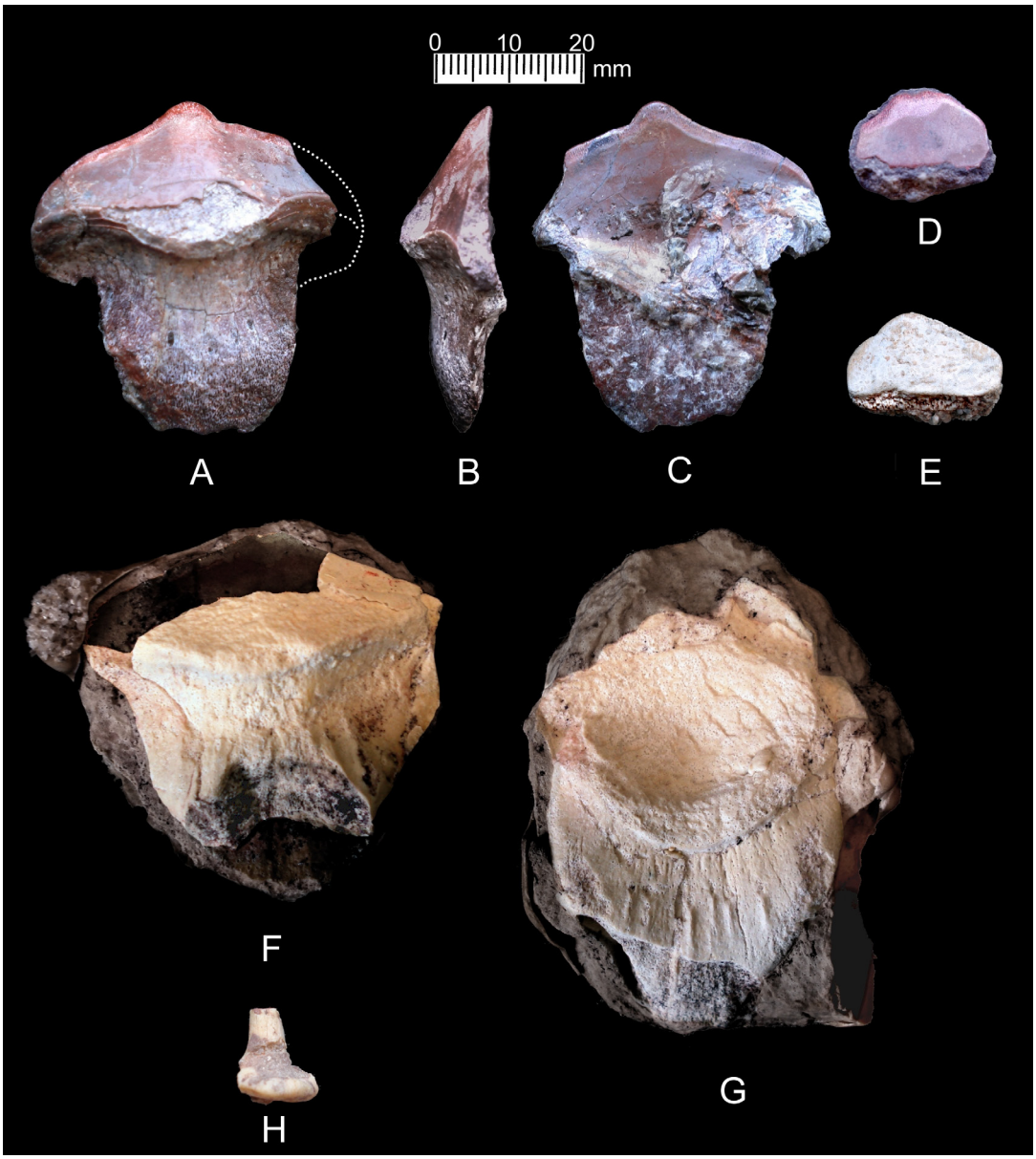

Figure 3. Shark teeth from the lower Cutler beds, Shafer Basin. *Petalodus ohioensis*. CEUM 81502 in (A) labial, (B) profile, and (C) lingual views. CEUM 81503 in (D) labi al view. CEUM 81504 in (E) labial view. CEUM 81643 cast in (F) labial view. CEUM 81644 cast in (G) lingual view. *Cladodus* sp. CEUM 81505 in (H) labial view. Scale in mm.

A REVIEW OF SOME KEY SPECIMENS OF *PETALODUS*

The five teeth of *Petalodus* from Utah are the first described and illustrated from the state. At least 21 species of *Petalodus* have been named (Hansen, 1985), the majority during the 1800s when the range of variation of tooth shape was less well known. The consensus today is that the majority of the species either belong to other genera or are morphological variants based on position within the jaws (e.g., Hansen, 1985; Lucas and others, 2011; Ginter and others, 2015). Unfortunately, there is no agreement as to whether there is only a single species (Lucas and others, 2011) or two species that are chronostratigraphical distributed (Hansen, 1985). As a result, it was necessary for us to look closely at several key species and specimens in order to determine the correct species name for the Utah specimens.

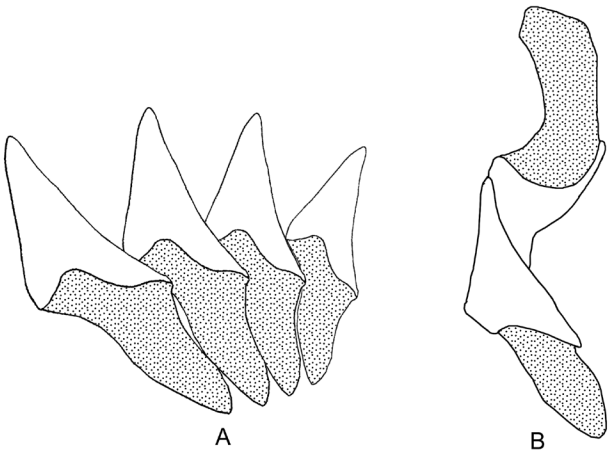

Figure 4. Possible serial stacking of replacement teeth in lateral view (A) of *Petalodus* to explain the convexo-concave crown (A, lower teeth only), versus the dental occlusion (B, lower and upper teeth) advocated by Lucas and others (2011) for the same convexo-concave feature. The serial stacking is more in keeping with the serial replacement of teeth seen in sharks.

The genus was proposed by Richard Owen (1840–1845 as *Petalodus hastingsii*, p. 61; also given as *P. hastingsae*, figure caption). However, there is a problem regarding this specimen that apparently has not been discussed before in the literature. Namely, that the description and figures of type tooth do not remotely look anything like the teeth traditionally referred to *Petalodus*. Owen (1840–1845: p. 3) described the tooth as "A thin lamella, slightly concave like a finger-nail …which I have, on that account, named *Petalodus*" (Greek *petalon* leaf, and *odus* tooth). His more detailed description (p. 61–62) refers to the tooth being "lamelliform," i.e., thin plate form, plate-like or scale-like. The tooth (NHMUK PV P613) was illustrated as more complete than it actually is (figures 5A to 5C vs 5D to 5G). Woodward (1889) referred to the specimen as a fragment, so was probably not more complete when described by Owen. It is most likely that the tooth was reconstructed by mirroring the fragment to give the impression of how an entire tooth would look (E. Barnard, Natural History Museum, London, England, written communication, 2017). Such a technique was used, for example, by Yale paleontologist O.C. Marsh (e.g., 1896, pl. 21, *Brontosaurus excelsus* dorsal). Despite Owen misleading reconstruction, Louis Agassiz correctly referred a nearly complete tooth from his collection to the genus *Petalodus*, thus establishing the sub-rhomboidal or subtriangular morphology by which it is known.

This version of *Petalodus*, rather than the rectangular shape given by Owen, was established in Agassiz's multi-year (1833–1845), 10 volume, limited edition "Recherches sur les Poissons Fossiles." The multi-year publication was due to his constant revisions (18 non-consecutive revised printings of the 10 volumes, Jeannet 1928). In text volume 3, he named a new genus, *Chomatodus*, and three species for several fossil fish teeth he states are from the Bristol Museum, England (but also stated as received from Roderick Murchison, p. 108). One of these teeth was named (text: Agassiz, 1833–1845a, p. 108–109) and figured (atlas: Agassiz, 1833-1845b, plate 19, figures 11 to 13) as *Chomatodus acuminatus* (figures 5S and 5T), which Woodward (1889) states were published in 1838 and confirmed by Brown (1890) and Jeannet (1928, p. 120). Later (revised text: Agassiz, 1833–1845a, p. 159), Agassiz writes that the tooth differs too much from the other two species of *Chomatodus* "since it is a tooth with a cutting blade…It is in the new genus *Petalodus*, by Mr. Owen." He reiterates this in a footnote (p. 174), which Woodward gives as published in 1843 and confirmed by Brown (1890) and Jeannet (1928, p. 122). The "cutting blade" is apparently the only justification that Agassiz gives as his reason for considering *Chomatodus acuminatus* as belonging to the genus *Petalodus*. The specimen was damaged (figure 5U) sometime between 1838 and 1927 as first reported by Jeannet (1927, p. 109) "Exemplaire mutilé depuis qu'il a été figuré" ("Specimen mutilated since it was figured"). Agassiz had a second tooth (figure 5V) also acquired from the Bristol Museum that he never discussed or figured.

Despite glaring differences between the Owen and Agassiz illustrations and descriptions, subsequent authors were quick to accept Agassiz's synonymy. The same year that Agassiz referred *C. acuminatus* to *Petalodus*, geologist Joseph Portlock (1843) described and illustrated a tooth (figure 5W) that he referred to as "*Petalodus Hastingsii* (Agassiz)" [sic]. His reasons for this identification was never stated. Portlock was followed a few years later by Frederick M'Coy (1848), who named

Petalodus rhombus for a complete tooth, noting its more rhomboid crown as compared with *P. acuminatus* (he says nothing of *P. hastingsii*). However, in 1854, M'Coy (1854) synonymized *P. rhombus* with *P. acuminatus* and illustrated the specimen (figures 5X to 5Z). The synonymy was based on what he thought were a range of variation in several new specimens and marks the first time that morphological variation was taken into account in *Petalodus* taxonomy. Although the low profile of the crown is also seen in some *Petalodus* teeth (e.g., figures 5N and 5O), the tooth lacks the ridges along the base of the crown and cingulum that typify *Petalodus*. It is therefore possible that this tooth does not belong to that genus.

Woodward (1889) later briefly described and illustrated several teeth (NHMUK PV P5342, plate I, figures 4 to 7, here as figures 5H to 5O) that are crucial for showing what Owen's specimen would probably have looked like undamaged (figure 5E). Most importantly, these teeth are from the same locality and horizon as Owen's holotype *P. hastingsii* (Woodward, 1889). The teeth share with the holotype, NHMUK PV P613, the unique, wide (deep) ridged band that occupies the lower half or more of the crown on the lingual side (figures 5D and 5E arrow). In all other species of *Petalodus*, this ridged band occupies a narrow zone at the base of the crown, where it is angled ventroposteriorly and protrudes so that a cingulum is formed (e.g., figures 5S and 5T). In addition, the lingual side of *P. hastingsii* is only slightly concave in side view (figures 5F and 5G) compared to most other *Petalodus* (e.g., figure 5S), and the root is proportionally short compared to crown height. Other specimens referred to *Petalodus* share with NHMUK PV P5342 an acuminate apex crown that is convex and subtriangular on the labial side where a well-developed anteroventrally facing, inverted W-shaped ridged cingulum lies at the base of the crown. We therefore conclude that *P. hastingsii* is a valid species contrary to Woodward (1889). In addition, *P. hastingsii* is known from the Flechado Formation (Desmoinesian, Middle Pennsylvanian) of New Mexico (Zidek and Kietzke, 1993) (figures 5P to 5R).

Owing to the importance of the Owen and Agassiz holotype specimens to the taxon *Petalodus*, their stratigraphic position needs to be established (International Code on Zoological Nomenclature Article 76). Woodward (1889) reports that the teeth here referred to *Petalodus hastingsii* were collected from the "Upper Carboniferous Limestone" at the village of Ticknall in South Derbyshire, England. This stratum is now called the Ticknall Limestone (Monteleone, 1973; Carney and others, 2001) and was an important source of building stone. The quarries produced numerous fossils (Parsons, 1917; Monteleone, 1973), which date the strata as Brigantian (upper Visean, a.k.a. upper Middle Mississippian) (Waters and others, 2009). Ginter and others (2015) described non-petalodontiform shark teeth from these beds, which also supported a Visean age. Agassiz obtained the holotype *Petalodus acuminatus* (Agassiz), MHNN-FOS 171, from British geologist Roderick Murchison, who collected the specimen from the Carboniferous Limestone near the town of Whorlton in County Durham, England. This stratum is identified by the British Geological Survey (2017) as the Stainmore Formation (middle Carboniferous or Namurian, a.k.a. Upper Mississippian to Lower Pennsylvanian). The formation is characterized by numerous limestone beds known to have been historically quarried as building stone (King, 2012).

The *Petalodus* teeth from the lower Cutler beds better compare with *Petalodus acuminatus* than to *P. hastingsii* chiefly in lacking the wide ridged band on the lingual side. However, unlike *P. acuminatus*, the lingual cingulum is very narrow and the crown taller relative to width. They are more similar to the tooth named and illustrated as *Getalodus ohioensis* (figures 5A' and 5B') by James M. Safford (1853). The generic name is most certainly a typographical error (Hay, 1895), either due to misinterpretation of Safford's handwritten manuscript by the typesetter, or Safford's misunderstanding of Louis Agassiz' heavy Swiss French accent during conversations Safford (1853) states he had with Agassiz about the tooth at the 1851 meeting of American Association for the Advancement of Science. The tooth was subsequently referred to as the holotype of *Petalodus ohioensis* (e.g., Hay, 1895; Lucas and others, 2011; we were unable to locate this specimen to re-illustrate). Safford reports that the specimen was collected from near Cambridge, Ohio, and Condit (1912) that it came from the Cambridge Limestone, which is in the Conemaugh Forma-

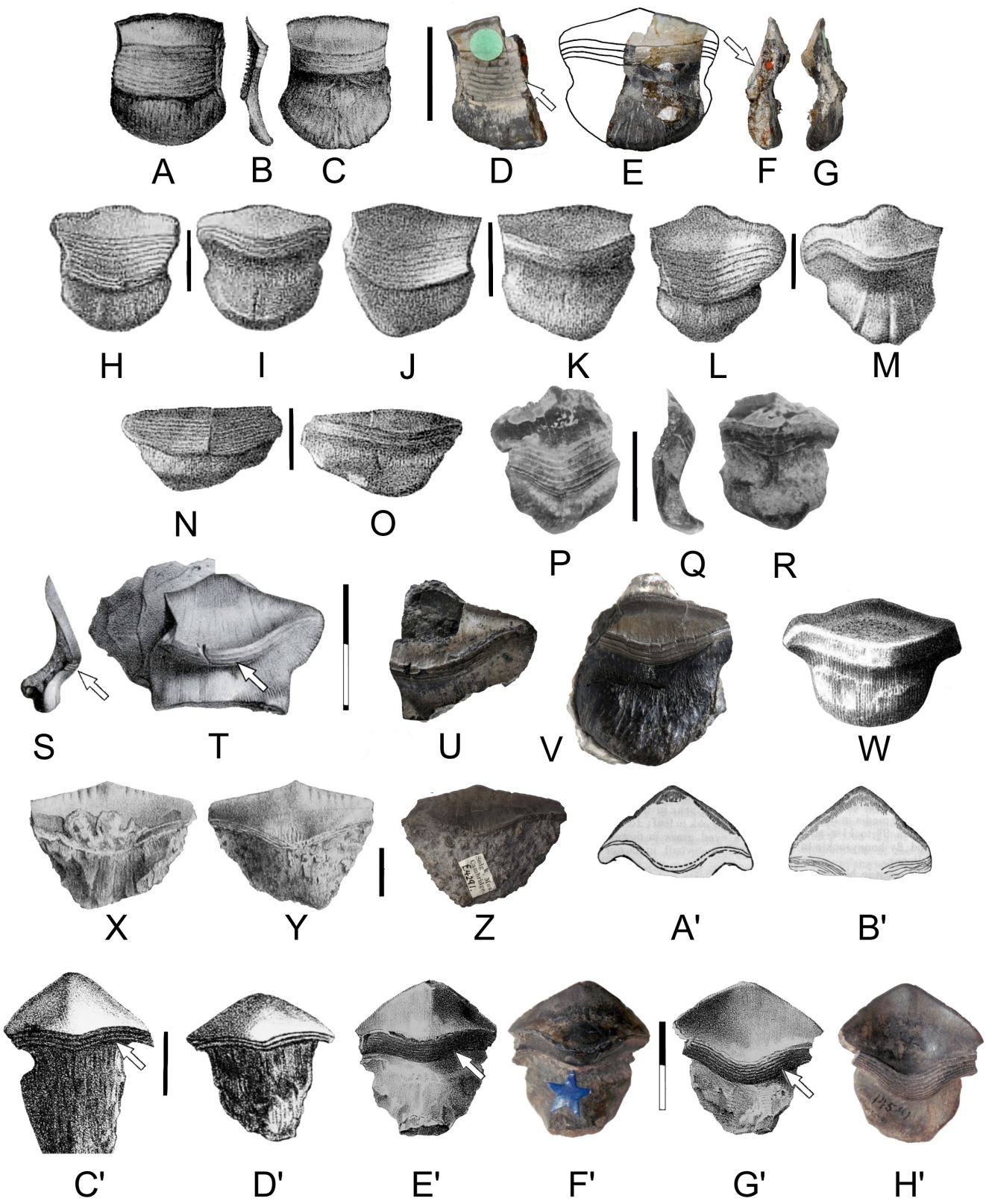

Figure 5. Caption on following page.

Figure 5 (figure on previous page). *Petalodus* as seen from original illustrations and photographs of the specimens. Holotype of *Petalodus hastingsii* as figured by Owen (1840–1845) in (A) lingual, (B) edge, and (C) labial views compared with the actual, far less complete specimen (NHMUK PV P613) in (D) lingual, (E) labial (silhouette based on more complete teeth), left broken edge (F), and right broken edge (G) views. The upper edge of the crown is heavily worn and exposes the dentine tubules. Arrows point to the distinctive ridges at the base of the enameloid crown on the lingual side. Sample of four out of 25 teeth (all NHMUK PV P5342) from the same bed and locality as the holotype and showing a range of variation in tooth form. Note the well-developed ridges at the base of the enameloid crown of the lingual side (H, J, L, and N), and on the cingulum of the labial side (I, K, M, O). Modified from Woodward 1899. *Petalodus hastingsii* (UNM 11959 – now missing), Flechado Formation, Taos County, New Mexico, in lingual (P), right broken edge view (Q) and labial (R) views (adapted from Zidek and Kietzke, 1993). Note that the ridges occur at the base of the crown on the lingual side and on the cingulum of the labial side. Holotype of *Petalodus acuminatus* (as *Chomatodus acuminatus*) as illustrated by Agassiz (1838, pl. 19, figs. 11, 13) in (S) edge and (T) labial views; and actual tooth (MHNN-FOS 171, as preserved today (U) lacking part of the crown and root (note the distinctive chip missing in the cingulum in T and in U). A second tooth of *Petalodus acuminatus* in the Agassiz collection, MHNN-FOS 174, but not mentioned by him and illustrated for the first time in (V) labial view. *Petalodus* tooth illustrated by Portlock (1843, plate 14, figure 10) a few years after Agassiz's descriptions (scale unknown) in (W) labial view. Illustrations of a tooth originally described as *Petalodus rhombus* by M'Coy (1854, plate 3g, figure 4) in (X) lingual and (Y) labial views compared to a photograph of specimen today in (Z) labial view (crown is now damaged and a corner missing from the root). Holotype of *Petalodus ohioensis* (as *Getalodus ohioensis*) in (A') labial and (B') lingual views (from Shafford 1853, p. 142); no scale given. The whereabouts of this specimen is unknown. Two specimens (C' and D') described by Newberry (1875, plate 58, figures 13 and 13a). Holotype of *Petalodus allegeniensis* as illustrated by Leidy (1856, plate 16, figures 4 and 5) compared with recent photographs: (E' and F') in labial and (G' and H') lingual views. Arrows point to the ridged basal band or cingulum. The origin of the green dot on specimen D 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 F is a blob of wax used by Woodward (1889) to denote that he include the specimen in his catalog of fossil fishes. The blue star is probably the old symbol used to denote a holotype. Scales in cm.

tion (Rice and others, 1994), or the Glenshaw Formation if the Conemaugh is raised to group (e.g., Rollins and others, 1979; Heckel and others, 2011). Conodonts demonstrate a middle to upper Missourian Stage (Middle Pennsylvanian) for the Cambridge (Heckel and others, 2011; Barrick and others, 2013). Oddly, Newberry (1875) says nothing about this specimen in his review of fossil fishes from Ohio, but does refer all *Petalodus* to *P. allegheniensis* (see below). *P. acuminatus* supposedly differs from *P. ohioensis* in the wide, ridged, lingual cingulum (Hansen, 1997).

The specimens of Newberry are important because they appear to represent additional specimens of *P. ohioensis* and provide more accurate information about this species (attempts to locate these specimens to re-illustrate were unsuccessful). Newberry reports that the specimens are all from the Crinoidal Limestone, which Condit (1912) identifies as the Ames Limestone of the Conemaugh Formation (or the Glenshaw Formation if the Conemaugh is raised to group). Conodonts place the Ames in the lower Virgilian (Heckel and others, 2011); i.e., lower Upper Pennsylvanian, and closer in time to the *Petalodus* specimens from Utah. Two of the teeth were figured by Newberry (figures 5C' and 5D'), and one of them (figure 5D') shows a tall crown and similar crown profile to the illustration by Safford (figures 5A' and 5B'). These teeth also confirm the one feature that has been used to diagnose *P. ohioensis*, namely the vertically narrow cingulum band of ridges (e.g., Hansen, 1985; Dalla Vecchia 1988), which is about one-third to one-half that of *P. alleghaniensis* (see next).

Two years after Safford named *Petalodus ohioensis*, Leidy (1855) named *Sicarius extinctus* for a tooth he described as resembling a pangolin scale. It was renamed and figured (figures 5E' and 5G') as *Petalodus alleghaniensis* the following year (Leidy, 1856); the reason for changing the species name was not given by Leidy. *P. extinctus* was used only once, by Eastman (1896) and is considered *nomen oblitum* (ICZN Art. 23.9). The tooth described by Leidy was recovered from the Glenshaw Formation at Bens Creek Station in what is now the Allegheny Portage Railroad National Historic Site (Koch

and Santucci, 2004). Conodonts from the Glenshaw are Missourian Stage (Middle Pennsylvanian) (Heckel and others, 2011; Barrick and others, 2013) and thus, *P. alleghaniensis* is contemporaneous with *P. ohioensis*.

Hay (1895) raised the possibility that *P. alleghaniensis* might be synonymous with *P. ohioensis*, although in the end he did not accept that. The holotype of *P. alleghaniensis* does differ from the holotype of *P. ohioensis* as figured by Safford (compare figure 5A' and 5B' with 5E' to 5H') in having a vertically wider cingulum of ridges (about twice or more wider). The narrower cingulum of *P. ohioensis* was cited by Dalla Vecchia (1988), Hansen (1997) and Brusatte (2007) as diagnostic. However, the reliability of this character was questioned by Ivanov and others (2009) and Lucas and others (2011). Ginter and others (2010) and Hansen (1985) seem to accept only *P. ohioensis* as the valid taxon but do not explicitly say so. Zidek and Kietzke (1993) consider *P. alleghaniensis* synonymous with *P. ohioensis* but do not state why. Ivanov and others (2009) suggested that the width of the lingual band is so variable in *Petalodus* that it may be unreliable as a diagnostic character and that the differences may be due to position in the jaws. We agree that the utility of this character is questionable given that we can find no functional reason for a rigid dichotomy between narrow and wide bands. In addition, we note that the specimens figured by Newberry (figures 5C' and 5D') show variable cingulum width, with one (figure 5C') approaching that of *P. alleghaniensis* (figures 5E' to 5H'). We therefore conclude that *P. alleghaniensis* is synonymous with *P. ohioensis* to which we refer all of the lower Cutler bed specimens.

CONCLUSIONS

The lower Cutler beds in the Shafer Basin have produced several teeth of the petalodontiform shark *Petalodus ohioensis* and one of ctenacanthid *Cladodus*. Most of the teeth are from the Shafer limestone, an informal name applied to the widespread limestone at the top of the lower Cutler beds. The *Petalodus* teeth are the first documented occurrence of this taxon in Utah, and *Cladodus* the youngest occurrence in the state.

Among the various *Petalodus* form species, we recognize *P. hastingsii* as a valid taxon characterized by a crown with a gently concave vertical cross-section, broad band of ridges on the lingual side and a ridged, outward facing cingulum on the labial side. *P. acuminatus* as having a low crown compared to width, with a more concave vertical cross-section than in *P. hastingsii,* and imbricated ridges on the ventrally facing cingulum. *P. ohioensis* is characterized by tall crowns compared to width, having a more concave vertical cross-section than in *P. hastingsii*, and imbricated ridges on a ventrally facing cingulum. Both *P. acuminatus* and *P. ohioensis* are larger taxa than *P. hastingsii*. "*Petalodus*" *rhombus* is either a *Petalodus* species characterized by the lack of ridges on the crown, or more likely that it represents a distinct genus.

ACKNOWLEDGMENTS

We are extremely grateful to the help we had with the search for several key specimens of *Petalodus*, as well as providing photographs of key specimens: Emma Bernard, Natural History Museum, London, England; Christian Klug, Paläontologisches Institut und Museum, Zurich, Switzerland; Andreas Müller, ETH-Bibliothek, Zurich, Switzerland; Thierry Malvesy, Conservator, Muséum d'histoire naturelle de Neuchâtel, Switzerland who located the long lost tooth of *Petalodus acuminatus*, Alain Germond, Muséum d'histoire naturelle de Neuchâtel, Switzerland provided the photograph of the long lost type; Deborah Hutchinson, Bristol City Museum, Bristol, England; Matt Riley, Sedgewick Museum, Cambridge University, Cambridge, England; Ned Gilmore, Academy of Natural Sciences of Drexel University, Philadelphia, PA. Thanks also to Emma Bernard for email discussions regarding Owen's holotype, and Thierry Malvesy for discussions regarding the Agassiz specimens at the Muséum d'histoire naturelle de Neuchâtel. The teeth described from the "lower Cutler beds" are from a legacy collection made in the 1970s by Ottinger. Fianlly, review comments by James Kirkland, Grant Willis, and Doug Sprinkel are appreciated, especially in discussions on the proper name of the strata the teeth were collected from.

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