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A new species of *Palaeohypotodus* Glückman, 1964 (Chondrichthyes, Lamniformes) from the lower Paleocene (Danian) Porters Creek Formation, Wilcox County, Alabama, USA

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Abstract

The historic collection of the Geological Survey of Alabama includes several fossil shark specimens that were recovered from the lower Paleocene Porters Creek Formation in southwestern Alabama, USA. Among these specimens are 17 teeth that we herein recognize as a new species within the extinct Paleogene genus, *Palaeohypotodus*. Detailed examination of these individual teeth, coupled with analyses of the dentitions of various extant lamniform sharks, allowed us to confirm monognathic and dignathic heterodonty within *Palaeohypotodus*. We identified upper and lower anterior and lateral tooth files that can be differentiated from one another by minor variations in morphology. Additionally, numerous isolated teeth from other Danian exposures in Alabama and Arkansas, USA, enhance our understanding of the composition of the dentition and ontogenetic heterodonty of both the new species and the genus as a whole.

Key Words

Elasmobranchii, Galeomorphi, Gulf Coastal Plain, Paleocene, Shark, Teeth

Introduction

Palaeohypotodus Glückman, 1964 is an extinct lamniform shark genus that has a purported temporal range extending from the Late Cretaceous (Maastrichtian) to the late Eocene (Priabonian), and isolated teeth have been reported from widely disparate localities from around the world (Cappetta 2012; Kriwet et al. 2016). Three species are herein recognized within the genus, including the Cretaceous *Palaeohypotodus bronni* (Agassiz, 1843), and the Paleogene *P. volgensis* Zhelezko in Zhelezko & Kozlov, 1999 and *P. rutoti* (Winkler, 1874). These species are characterized by robust teeth having a combination of erect to strongly distally hooked crown, smooth cutting edges, one or more pairs of lateral cusplets, and distinctive plications along the labial crown foot. *Palaeohypotodus* is known primarily by isolated teeth, but at least one partially associated skeleton has been reported (Casier 1942). Herein we describe several teeth belonging to a new species of *Palaeohypotodus* that was recently discovered in the historical collections of the Geological Survey of Alabama (Tuscaloosa). These 17 teeth, cataloged under the number GSA–V447, were derived from the lower Paleocene (Danian) Porters Creek Formation of Wilcox County, Alabama, USA. The purpose of this report is to describe and interpret the teeth and dentition of this extinct shark through comparisons with extant lamniform shark jaw sets. Further insights regarding ontogenetic heterodonty and intraspecific variation within the new species were drawn through an analysis of isolated teeth that were recovered from contemporaneous deposits in Alabama and Arkansas. We also comment on the taxonomic history of the genus and the paleobiogeographic distribution of the new species.

Geological setting

A search through the historical collections at the Geological Survey of Alabama (GSA) in Tuscaloosa by two of the authors (JAE and TLH) resulted in the discovery of 17 teeth belonging to the extinct lamniform shark, *Palaeohypotodus*. The original label associated with these teeth (which were all cataloged together under the number GSA–V447) stated that they were collected from the lower Paleocene (Danian) Porters Creek Formation on the McConnico Plantation near Prairie Creek in Wilcox County, Alabama, USA (Fig. 1). Although the date when the specimens were collected was not recorded, the associated label is of a style used by the GSA during the late 1800s to early 1900s. The exact location of the McConnico Plantation, a historical collecting site located north-northwest of the town of Oak Hill, was rediscovered by examining a property map of Wilcox County that is housed in the GSA archives (Fig. 2a). When this map was overlain on a geologic map of Wilcox County (Fig. 2b), the position of the McConnico Plantation shows that the only area on the property underlain by the Porters Creek Formation is in NW1/4, Sec. 32, T12N, R10E (U.S. Public Land Survey System). As several of the teeth exhibit evidence of sun bleaching and root etching (indicating a prolonged period of surface exposure), we believe that the specimens were collected from an erosional gulley in a field rather than a gravel bar in the nearby Prairie Creek. This gulley, now evidently filled, exposed strata of the Porters Creek Formation, a Paleocene (Danian/Selandian) unit occurring between the subjacent Clayton Formation and suprajacent Naheola Formation (Fig. 3). In Alabama, the Porters Creek Formation is divided into a lower unnamed member and the overlying Matthews Landing Marl Member. Although we cannot ascertain which member the specimens were derived from, we believe they originated from the unnamed member because 1) the geologic map indicates that the site lies close to the contact with the Clayton Formation, and 2) the Matthews Landing Marl has not been mapped in the immediate vicinity of the McConnico locality. The Porters Creek Formation in Wilcox County, AL consists of approximately 37 m (120 feet) of various fine-grained siliciclastic facies, but a prominent limestone bed occurs in the middle of the unit and carbonate content increases to the east (Raymond et al. 1988). The siliciclastic facies have been described as consisting of micaceous silty sand, massive calcareous clay, and massive black clay, with the Matthews Landing Marl comprised of fossiliferous calcareous clay and glauconitic sandstone (LaMoreaux and Toulmin 1959). Mancini and Tew (1993) reported that the Porters Creek Formation of south-central Alabama attained a thickness of 46 m (150 feet), and they further subdivided the unnamed member into "lower," "middle," and "upper" portions. The lower and middle portions were described as consisting of marlstone, limestone, and calcareous silty claystone, whereas the upper portion consists of bioturbated siltstone and marlstone. The overlying Matthews Landing Marl Member includes fossiliferous, glauconitic sandstone and marlstone (Mancini and Tew 1993), and the unit attains a thickness of 6 m (20 feet) in Wilcox County (Raymond et al. 1988). The geologic formations in Wilcox County dip gently to the south-southwest.

A rather diverse fossil mollusk assemblage from the McConnico Plantation (GSA collection, Table 1) supports an early-to-middle Paleocene age for the Porters Creek Formation. This age is further corroborated biostratigraphically, as the basal portion of the unit in Wilcox County lies within the uppermost P1 (P1c) *Subbotina triloculinoides* (Plummer, 1927) planktonic foraminifera interval zone (formerly *Subbotina trinidadensis* (Bolli, 1957) = *Praemurica inconstans* (Subbotina, 1953) interval zone) and the basal portion of the NP4 *Ellipsolithus macellus* (Bramlette & Sullivan, 1961) nannoplankton zone (Mancini 1984; Fluegeman et al. 1990; Mancini and Tew 1993). Zone NP4 was subsequently extended downward into Zone P1 (see Ogg et al. 2016) after Mancini and Tew's (1993) publication.

Table 1. List of historically collected fossil invertebrate taxa in the Geological Survey of Alabama collection that were derived from the Porters Creek Formation at the McConnico Plantation in Wilcox County, AL, USA.

Gastropods
Eoancilla mediavia (Harris, 1896)
Natica reversa Whitfield, 1865
Caricella leana Dall, 1890
Coronia mediavia (Harris, 1896)
Exilia pergracilis Conrad, 1860
Euspira perspecta (Whitfield, 1865)
Mesalia alabamiensis (Whitfield, 1865)
Mesalia allentonensis (Aldrich, 1894)
Orthosurcula longipersa (Harris, 1896)
Turritella alabamiensis Whitfield, 1865
Turritella humerosa Conrad, 1835
Turritella levicunea (Harris, 1896)
Volutocorbis rugatus (Conrad, 1860)
Bivalves
Crassatella aquiana Clark, 1895
Cucullaea macrodonta Whitfield, 1865
Nucula mediavia Harris, 1896
Ostrea sp. indet. Linnaeus, 1758
Venericardia wilcoxensis Dall, 1903
Scaphopods
Dentalium mediaviense Harris, 1896

Material and methods

The 17 teeth that are the focus of this report are reposited in the collection of the Geological Survey of Alabama in Tuscaloosa and are curated under catalog number GSA–V447. Of these 17 teeth, nine are complete, with the remaining eight consisting of either the main cusp lacking some or all of the root, or complete root with partial main cusp. We herein note the possibility that all 17 teeth cataloged under the number GSA–V447 represent a single individual, in which case the specimens

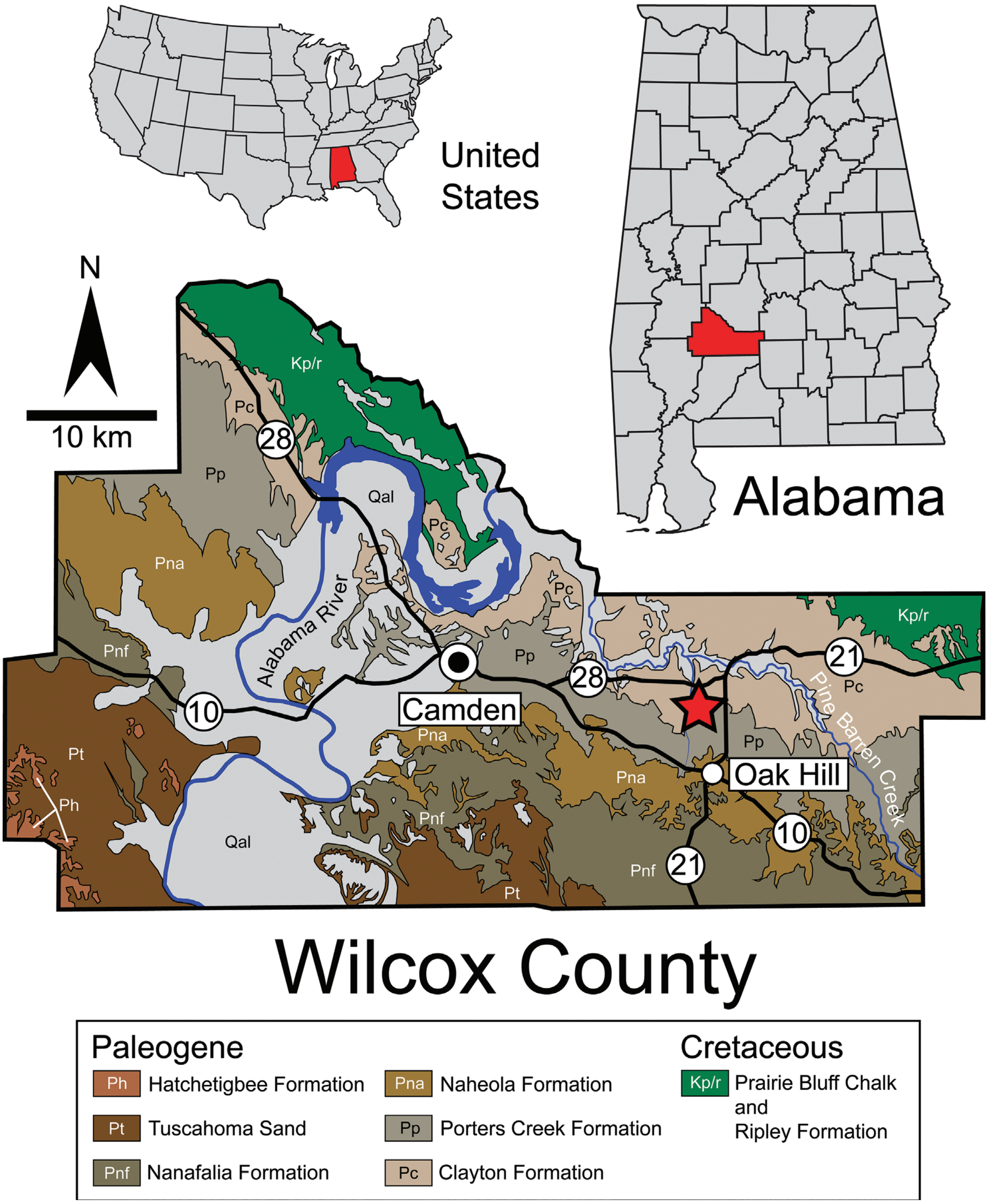

Figure 1. Geologic map of Wilcox County showing the approximate location of the McConnico Plantion (indicated by red star). Scale bar applies to Wilcox County map.

represent an associated dentition. However, the lack of unequivocal replacement teeth and associated vertebral centra within the lot perhaps indicates that the 17 teeth are not associated. The consistent preservation amongst the teeth, combined with the relative paucity and low density of vertebrate remains within the Porters Creek Formation (JAE, pers. observation), suggests that these teeth are associated (although this may also be an indication that this taxon is abundant within this particular lithostratigraphic unit). Nevertheless, as GSA–V447 was historically collected and no field notes are available that indicate or contradict the direct association of these 17 teeth, we herein treat them as isolated finds and use the specimens as an artificial tooth set. For the purposes of this report, we herein retain all of the teeth within the original catalog number GSA–V447 but refer to them individually by the use of sub-numbers (i.e., GSA–V447.1–.17).

The teeth of GSA–V447 are believed to represent various tooth positions within the dentition of one taxon, and a standard set of linear measurements (Fig. 4), ratios, and morphological observations were recorded for each tooth to assist with the reconstruction and interpretation of the dentition of this shark. These measurements and observations are as follows:

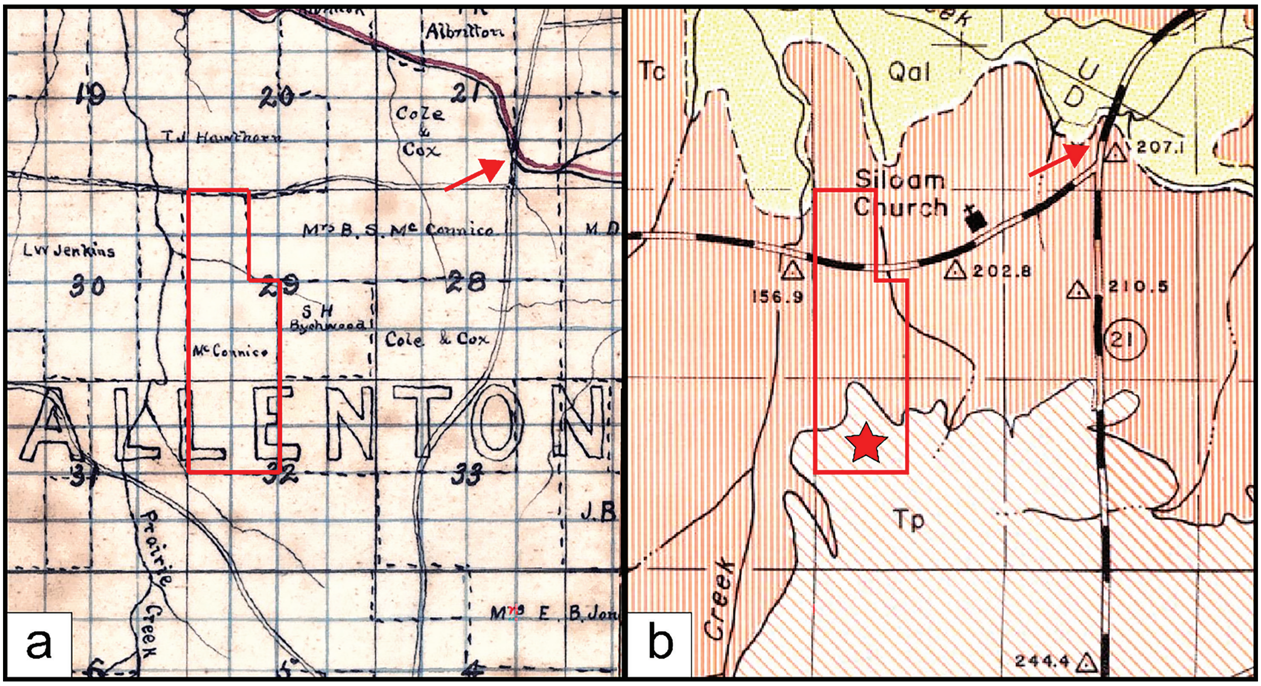

Figure 2. Location of McConnico Plantation in Wilcox County, AL, USA; **a.** Portion of a historical property map of Wilcox County, AL (Crump 1870) showing the location of the McConnico Plantation (red polygon). **b.** Portion of a geologic map of Wilcox County, AL (LaMoreaux and Toulmin 1959) showing the location of the McConnico Plantation (red polygon) and the area where GSA–V447 was likely recovered (red star). Arrows indicate the location of Smith's Bridge which is a landmark for orientation. **Qal** = Quaternary alluvium, **Tc** = Clayton Formation, **Tp** = Porters Creek Formation.

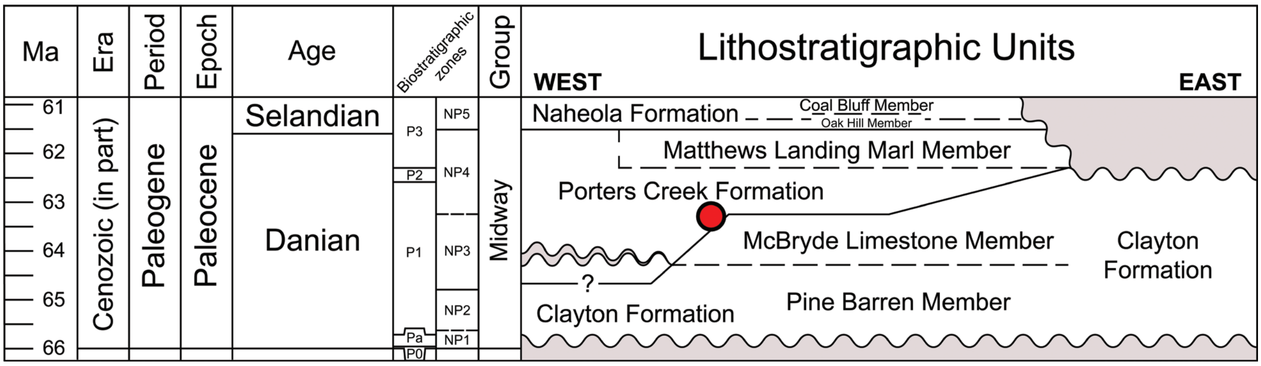

Figure 3. Stratigraphic column of early-to-middle Paleocene strata of Alabama. Red dot indicates the likely horizon of GSA–V447. Column is based on Raymond et al. (1988) and modified with data from Gibson et al. (1982), Mancini et al. (1989), Mancini and Tew (1993), and Ogg et al. (2016).

Total height (TH). On a complete tooth, this is the maximum apico-basal height measured from the apex of the main cusp to the base of the root lobes (with the tooth positioned so the basal extent of the mesial and distal root lobes are equal).

Root width (RW). With the tooth positioned so the basal extent of the mesial and distal root lobes are equal, this is the maximum mesio-distal width measured from the mesial and distal-most extent of the root lobes.

Main cusp height (MCH). The maximum apico-basal height of the main cusp measured on the labial face from the medial portion of the crown base to the apex of the main cusp.

Root height (RH). Calculated by subtracting the main cusp height from the total height (i.e., TH – MCH).

Main cusp width (MCW). Measured on the labial face, the distance between the distal and mesial-most points of the main cusp.

Main cusp thickness (MCT). Measured from the medial portion of the lingual crown base to the corresponding point at the labial crown base, inclusive of the neck (aka chevron or dental band), if present.

Depth of the interlobe area (DIA). Measured from the apical extent of the interlobe area to the base of the root lobes, with the base of the lobes being equal.

Root thickness (RT). The labio-lingual thickness of the root measured from the highest point on the lingual protuberance to the corresponding labial face of the tooth.

Number of mesial cusplets (#MC). The total number of mesial cusplets.

Number of distal cusplets (#DC). The total number of distal cusplets.

Labial ornamentation present? (LOP). A brief description of any ornamentation present along the labial crown foot.

For the nine complete teeth associated with GSA–V447, the standard measurements were used to calculate the three following ratios:

Ratio of main cusp height to total tooth height (%MCH). Calculated by dividing the main cusp height by the total height (i.e., MCH ÷ TH).

Ratio of root height to total tooth height (%RH). Calculated by dividing the root height by the total height (i.e., MCH ÷ TH).

Ratio of the depth of the interlobe area to total tooth height (%DIA). Calculated by dividing the depth of the interlobe area by the total height (i.e., DIA ÷ TH).

An additional 17 isolated teeth of the new *Palaeohypotodus* species were identified in the collections of McWane Science Center (MSC) in Birmingham, AL, USA, and the Mississippi Museum of Natural Science (MMNS) in Jackson, USA (see Referred specimens list below). These specimens were collected from four counties in Alabama (Dallas, Butler, Lowndes, and Wilcox) and one county in Arkansas, USA (Hot Spring County). One of these specimens (MSC 49452) was derived from the type stratum of GSA–V447 (Porters Creek Formation), albeit from Butler County in Alabama. The remaining 16 teeth were recovered from the lower Paleocene (Danian) Clayton Formation (including the Pine Barren Member), a lithostratigraphic unit that is largely temporally equivalent to the lower unnamed member of the Porters Creek Formation (see Fig. 3). Ten of these teeth are complete and were incorporated into our morphological dataset so they could be directly compared with the teeth of GSA–V447. The remaining seven specimens were excluded from our analyses because they are incompletely preserved.

To assist with the dental reconstruction of the *Palaeohypotodus* species, we directly examined the jaws of numerous recent lamniform sharks in the collections of MSC and the South Carolina State Museum in Columbia (SC). These specimens included *Alopias superciliosus* Lowe, 1841 (SC2020.53.12) and *A. pelagicus* Nakamura, 1935 (SC2020.53.19), two *Carcharodon carcharias* (Linnaeus, 1758) (MSC 42596 and SC86.62.1), juvenile and adult *Isurus oxyrinchus* Rafinesque, 1810 (MSC 42606 and SC2020.53.15, respectively), juvenile and adult *I. paucus* Guitart-Manday, 1966 (SC2020.53.22 and SC2020.53.27, respectively), and two *Carcharias taurus* Rafinesque, 1810 (SC86.62.2 and SC2000.120.6). Additionally, we examined a *Lamna nasus* (Bonnaterre, 1788) jaw set from the Gordon Hubbell collection (unnumbered specimen) in Gainesville, FL, USA. Finally, published images of the dentitions of *A. vulpinus* (Bonnaterre, 1788), *Odontaspis ferox* (Risso, 1810), *O. noronhai* (Maul, 1955), and *Mitsukurina owstoni* Jordan, 1898 were utilized (i.e., Ebert and Dando 2021). The dentitions of the filter-feeding lamniforms, *Cetorhinus* and *Megachasma*, were excluded from our study due to their atypical dentitions.

The terminology used for identifying the jaw position of isolated teeth of elasmobranch fishes has varied greatly in the literature (see Leriche 1905; Applegate 1965; Cappetta 1987, 2012; Cunningham 2000; Shimada 2001, 2002a, b, c, 2004), but herein we follow a combination of Siverson (1999) and Cicimurri et al. (2020) by utilizing the terms anterior, intermediate, lateral, and posterior to identify jaw position in lamniform sharks. Herein, anterior teeth refer to those that develop within the anterior dental hollow in the Meckel's cartilage or palatoquadrate, whereas lateral teeth are those occurring within the upper or lower lateral hollows. Teeth referred to as intermediate are those that occur at the extreme distal end of the anterior hollow or on a cartilage bar located between the upper anterior and lateral dental hollows. These teeth are conspicuously smaller than the preceding anterior and succeeding lateral tooth and may also be strongly distally hooked and/or inclined (more so than in lateral files), which is reflective of the limited space available for tooth development. Posterior teeth are those that comprise files located at the far distal ends of the upper and lower lateral dental hollows and are positioned closest to the jaw commissure. These teeth are significantly smaller and morphologically different from lateral teeth, often mesiodistally as wide as tall (ratio of 1:1) and, in some cases, their width exceeds the overall tooth height (see Cicimurri et al. 2020). The morphological changes across the upper and lower lateral tooth rows are gradational within most lamniform shark dentitions (see Ebert and Dando 2021), and herein we utilize the terms anterolateral and posterolateral to refer to lateral teeth that are located near the anterior or posterior half, respectively, of the lateral dental hollow.

All of the teeth we illustrate were photographed with a Nikon D80 camera and Tamron macro lens. To account for depth of field, specimens were photographed from several focal lengths and the resulting photographs were merged in Adobe Photoshop v. 22.5.9 utilizing the software's auto-align and auto-blend functions. We constructed the figures using the same software.

Institutional abbreviations

GIK: State Darwin Museum, Moscow, Russia. **GSA**: Geological Survey of Alabama, Tuscaloosa, USA. **IRSNB**: Royal Belgian Institute of Natural Sciences, Brussels, Belgium. **MMNS**: Mississippi Museum of Natural Science, Jackson, USA **MSC**: McWane Science Center, Birmingham, Alabama, USA. **SC**: South Carolina State Museum, Columbia, USA.

Systematic Paleontology

Class Chondrichthyes Huxley, 1880
Subclass Euselachii Hay, 1902
Infraclass Elasmobranchii Bonaparte, 1838
Division Selachii Cope, 1871
Superorder Galeomorphi Compagno, 1973
Order Lamniformes Berg, 1958
Family Jaekelotodontidae Glückman, 1964

Genus *Palaeohypotodus* Glückman, 1964

Type species. *Otodus rutoti* Winkler, 1874, Orp Member of the Heers Formation, Orp-le-Grand (Maret), Belgium.

Emended generic diagnosis. Lamniform shark with teeth consisting of a triangular main cusp and one to three pairs of lateral cusplets. Enameloid plications occur along the labial crown foot on unworn teeth, and these may coalesce to form transversely oriented ridge-like structures on posterior teeth. Cutting edges are complete on all upper teeth but are incomplete on lower teeth. Although the main cusp is tall and relatively narrow in anterior files, it becomes progressively lower and broader the closer a file is located with respect to the commissure. Upper lateral teeth have a wide triangular and distally hooked main cusp, whereas lower lateral teeth have a narrower and more erect main cusp. Upper third anterior teeth have a basally extended mesial root lobe, the distal cutting edge is more convex than the mesial edge, and the crown appears to be mesially recurved. Teeth have a robust lingual root protuberance that bears a nutritive groove. The root lobes are long and the interlobe area is deep and U-shaped. Upper anterior teeth have shorter and slightly more divergent root lobes compared to those in the lower anterior files.

***Palaeohypotodus bizzocoi* sp. nov.**

https://zoobank.org/9E51D855-B537-4088-95BE-8F20C549BF6F

Figs 4–7

Etymology. The species is named for the late Bruce D. Bizzoco in honor of his dedicated volunteer service to MSC and his lifelong commitments to education and the preservation of local history in Alabama, USA.

Hypodigm. GSA–V447.1 (holotype), upper left anterior tooth (Fig. 5a–d); GSA–V447.2 (paratype), upper right lateral tooth (Fig. 5y–bb); GSA–V447.3 (paratype), upper right lateral tooth (Fig. 5cc–ff); GSA–V447.4 (paratype), lower right anterior tooth (Fig. 6a–d); GSA–V447.5 (paratype), lower left lateral tooth (Fig. 6q–t).

Referred specimens. N = 29: GSA–V447.6, upper left anterior tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.7, upper left anterior tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.8, upper left lateral tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.9, upper right lateral tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.10, upper left lateral tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.11, upper anterior tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.12, lower left anterior tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.13, lower left anterior tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.14, lower right lateral tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.15, lower left lateral tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.16, lower left lateral tooth, Porters Creek Formation, Wilcox County, AL; GSA–V447.17, lower left lateral tooth, Porters Creek Formation, Wilcox County, AL; MMNS VP–7292.2, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MMNS VP–7292.3, upper left lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MMNS VP–7292.4, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MMNS VP–7295.4, upper right posterior tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MMNS VP–7311, lower right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MMNS VP–8578, upper right lateral tooth, basal Clayton Formation, Hot Spring County, AR; MSC 3020, lower left anterior tooth, lower Clayton Formation, Wilcox County, AL; MSC 42727, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MSC 42733, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MSC 42741.4, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MSC 42741.5, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MSC 42742.1, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MSC 42742.2, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MSC 42742.3, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; MSC 49451, upper left lateral tooth, lower Clayton Formation, Wilcox County, AL; MSC 49452, upper left 3rd anterior tooth, Porters Creek Formation, Butler County, AL; MSC 49454, upper left lateral tooth, lower Clayton Formation, Wilcox County, AL.

Type stratum and age. Basal unnamed member, Porters Creek Formation, Paleocene, Danian Stage, zones NP3–4 (Fig. 3).

Type locality. Historic McConnico Plantation near Prairie Creek in Wilcox County, Alabama, USA, NW1/4, Sec. 32, T12N, R10E (U.S. Public Land Survey System) (Figs 1, 2).

Description. Specimen GSA–V447 consists of 17 teeth that are herein assigned to anterior and lateral files of the upper and lower jaws. This assortment of teeth includes nine from the palatoquadrate (upper jaw) and eight from the Meckel's cartilage (lower jaw). Teeth from both the left and right sides of the upper and lower

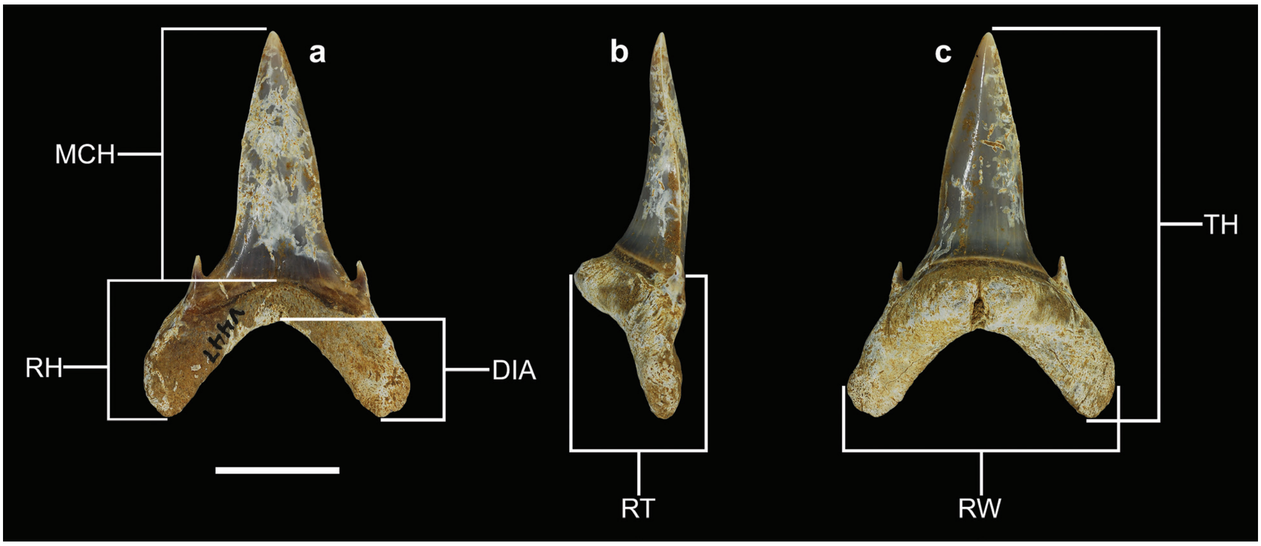

Figure 4. Standard tooth measurements. **a–c.** GSA–V447.6, *Palaeohypotodus bizzocoi* sp. nov. upper anterior tooth; **a.** Labial view; **b.** Mesial view; **c.** Lingual view; **DIA** – Depth of the interlobe area; **MCH** – Main cusp height; **RH** – Root height; **RT** – root thickness; **RW** – Root width; **TH** – Total height; Scale bar: 1 cm.

jaws are represented, and it is possible that at least two of the teeth were derived from the same tooth file. Unfortunately, the limited number of teeth included with specimen GSA–V447 did not allow us to determine exactly how many anterior or lateral files were present within the dentition of this taxon, or how many posterior files occurred. However, based on the jaw sets of several extant lamniform sharks like *Carcharodon carcharias*, *Isurus* spp., *Lamna nasus*, and *Odontaspis ferox* (see Materials and Methods), we believe that upper and lower teeth are preserved, and both anterior and lateral tooth files are represented. Tooth morphologies we identified in GSA–V447 include:

***Upper anterior teeth* (GSA–V447.1, .6–.7, .11, Fig. 5a–p).** We identified four teeth within this tooth group, including three complete specimens and one with an incomplete main cusp. Unlike the lateral teeth (see below), the sequential position within the jaw of *P. bizzocoi* sp. nov. is unknown because the total tooth height and root width of the upper anterior teeth is extremely variable within the extant lamniform jaws examined. The three complete teeth have a total height (TH) ranging between 28.87 and 29.16 mm and a root width (TW) that ranges from 18.84 to 19.99 mm. The height/width (H/W) ratios vary from 1.44 to 1.55 (Table 2).

The three complete teeth (GSA–V447.1, .6–.7; Fig. 5a–k) have a tall and triangular main cusp. In labial view the main cusp is nearly symmetrical, but the mesial edge is slightly more convex than the distal edge, and this feature allows us to determine if they were derived from the left or right palatoquadrate. The labial face of the main cusp is slightly convex, whereas the lingual face is strongly convex. The mesial and distal cutting edges are complete and extend to the base of the main cusp. The crown enameloid is smooth except for faint plications occurring along the labial crown foot. The main cusp is slightly sinuous in profile view. The teeth have a single pair of diminutive lateral cusplets that are both medially and lingually hooked. Both lateral cusplets have mesial and distal cutting edges that do not connect to those on the main cusp. The root is bilobate, with lobes being divergent and of nearly equal length and width. The interlobe area is deep, wide, and U-shaped. The teeth have a robust lingual protuberance that is bisected by a deep nutritive groove. The height of the root represents approximately 30% of the total tooth height. Specimen GSA–V447.11 (Fig. 5m–p), the tooth with broken main cusp, is assigned to the upper anterior tooth group because it has a deeper interlobe area (8.44 mm) than any of the upper lateral teeth (see Table 2), the root lobes are shorter and more divergent than those on the lower teeth, and the interlobe area is wider and U-shaped compared to the lower anterior teeth (see additional discussion below).

At least two upper anterior files are represented within GSA–V447 based on the slightly different dimensions and gross morphologies of teeth GSA–V447.6 and GSA–V447.7 (see Table 2). Both teeth have a narrow, triangular main cusp with cutting edges that are sub-parallel except near the apex, where they are biconvex. Tooth GSA–V447.7 (Fig. 5i–l) has a slightly narrower main cusp that is very slightly distally inclined compared to GSA–V447.6 (Fig. 5a–d), and it also has slightly longer root lobes. Teeth GSA–V447.1 and GSA–V447.6 have nearly identical dimensions (see Table 2), suggesting they belong to the same anterior file. Additionally, tooth GSA–V447.11 has a nearly identical root width to that of GSA–V447.7 (Fig. 5i–l), suggesting that these two teeth also represent the same anterior file.

***Upper lateral teeth* (GSA–V447.2–.3, .8–.10, Fig. 5q–ii).** Five upper lateral teeth are preserved with GSA–V447, four of which are complete. The basal margins of the root lobes of tooth GSA–V447.9 are not preserved. The crowns of these teeth range in height from 17.64 to 11.4 mm, and the overall height of the complete teeth

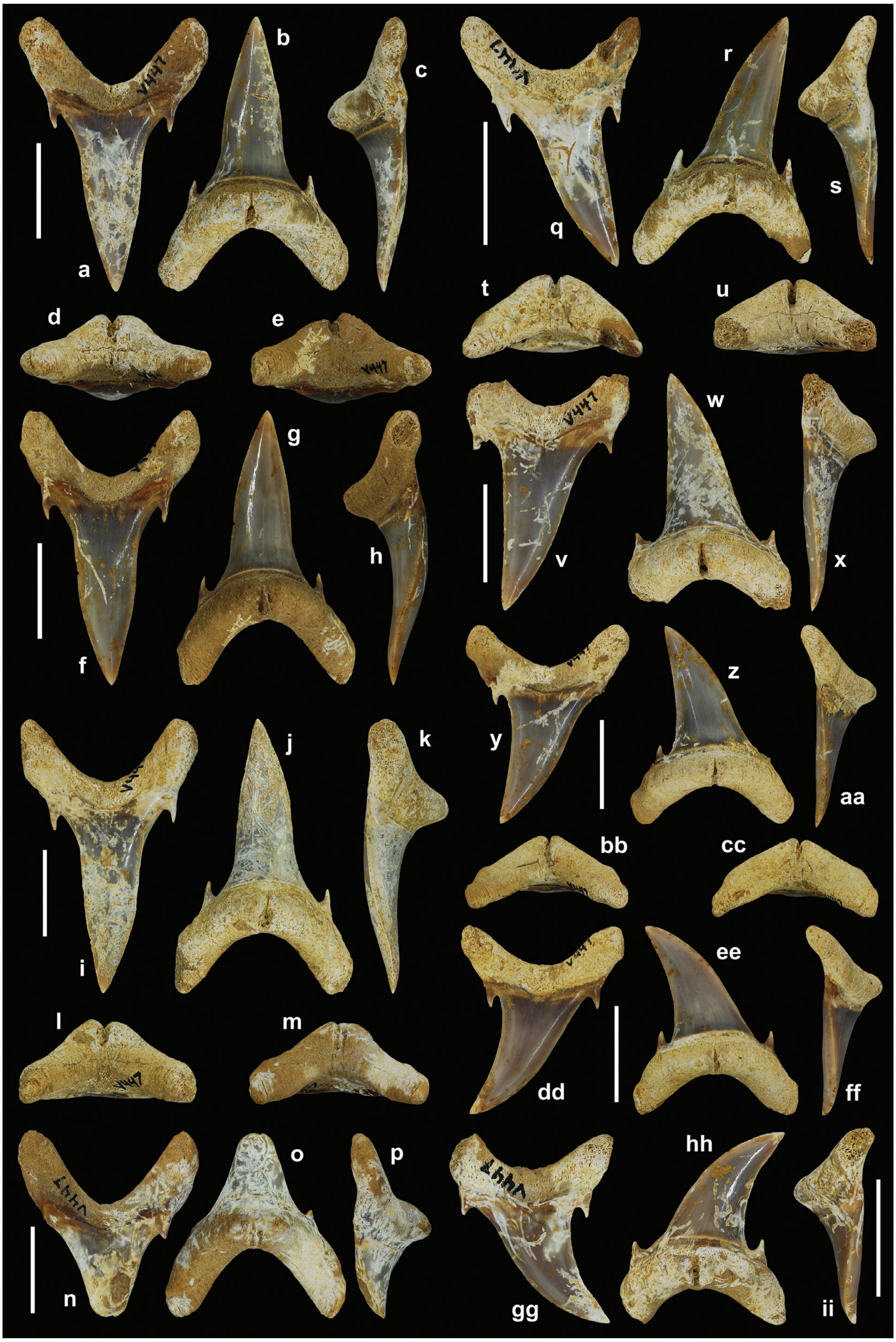

Figure 5. (a–ii) *Palaeohypotodus bizzocoi* sp. nov. upper teeth. **a–d.** GSA–V447.6, upper left anterior tooth; **a.** Labial view; **b.** Lingual view; **c.** Mesial view; **d.** Basal view. **e–h.** GSA–V447.1 (holotype), upper left anterior tooth; **e.** Basal view; **f.** Labial view; **g.** Lingual view; **h.** Mesial view. **i–l.** GSA–V447.7, upper right anterior tooth; **i.** Labial view; **j.** Lingual view; **k.** Mesial view; **l.** Basal view. **m–p.** GSA–V447.11, upper anterior tooth; **m.** Basal view; **n.** Labial view; **o.** Lingual view; **p.** Profile view. **q–t.** GSA–V447.8, upper left intermediate or lateral tooth; **q.** Labial view; **r.** Lingual view; **s.** Mesial view; **t.** Basal view. **u–x.** GSA–V447.9, upper right lateral tooth; **u.** Basal view; **v.** Labial view; **w.** Lingual view; **x.** Mesial view. **y–bb.** GSA–V447.2 (paratype), upper right lateral tooth; **y.** Labial view; **z.** Lingual view; **aa.** Mesial view; **bb.** Basal view. **cc–ff.** GSA–V447.3 (paratype), upper right lateral tooth; **cc.** Basal view; **dd.** Labial view; **ee.** Lingual view; **ff.** Mesial view. **gg–ii.** GSA–V447.10, upper left lateral tooth; **gg.** Labial view; **hh.** Lingual view; **ii.** Mesial view. Scale bars: 1 cm.

Table 2. Measurements, ratios, and observations on the *Palaeohypotodus bizzocoi* sp. nov. teeth associated with GSA–V447. **Abbreviations: #DC.** Number of distal cusplets. **DIA.** Depth of the interlobe area. **H/W Rat**. Height/width ratio; **LOP.** Labial ornamentation present and the nature of the ornamentation; **#MC.** Number of mesial cusplets; **MCH.** Main cusp height; **%MCH.** The percentage of the main cusp height in relation to the total tooth height; **MCT.** Main cusp thickness; **MCW.** Main cusp width; **RH.** Root height; **%RH.** The percentage of the root height in relation to the total tooth height; **RT.** Maximum root thickness; **RW.** Root width; **TH.** Total height. **N/A.** Measurement, ratio, or observation could not be taken due to the incomplete preservation of the tooth.

Number	Tooth Position	TH	RW	H/W Rat	MCH	%MCH	RH	%RH	MCW	MCT	DIA	RT	#MC	#DC	LOP
GSA–V447.6	Upper anterior	29.16	18.84	1.55	20.39	69.9	8.77	30.1	10.53	5.14	6.7	8.63	1	1	Faint across base
GSA–V447.1	Upper anterior	29.11	19.08	1.52	19.98	68.6	9.13	31.4	11.19	5.24	7.18	8.9	1	1	Faint across base
GSA–V447.7	Upper anterior	28.87	19.97	1.44	19.63	67.9	9.24	32.1	11.18	5.28	6.28	8.12	1	1	Faint across base
GSA–V447.11	Upper anterior	N/A	19.99	N/A	N/A	N/A	N/A	N/A	10.26	5.23	8.53	8.44	1	N/A	Faint across base
GSA–V447.8	Upper lateral	20.09	14.54	1.01	14.6	72.6	5.49	27.4	7.34	3.95	5.02	6.1	2	2	Faint across base
GSA–V447.9	Upper lateral	N/A	N/A	N/A	17.64	N/A	N/A	N/A	10.85	4.39	N/A	6.98	1	1	Faint across base
GSA–V447.2	Upper lateral	23.93	19.81	1.21	17.03	71.1	6.9	28.9	11.29	4.64	5.35	6.91	2	2	Faint across base
GSA–V447.3	Upper lateral	19.51	16.94	1.15	14.39	73.7	5.12	26.3	9.52	4.05	4.97	5.91	2	2	Faint across base
GSA–V447.10	Upper lateral	15.59	13.33	1.17	11.4	73.1	4.19	26.9	8.6	3.58	3.78	4.88	1	1	Faint across base
GSA–V447.4	Lower anterior	32.63	17.28	1.89	19.9	60.9	12.73	39.1	9.51	5.48	10.48	9.14	1	1	Faint across base
GSA–V447.12	Lower anterior	N/A	N/A	N/A	18.59	N/A	N/A	N/A	8.8	4.97	N/A	8.16	N/A	N/A	Faint across base
GSA–V447.13	Lower anterior	N/A	N/A	N/A	18.09	N/A	N/A	N/A	10.09	4.79	N/A	N/A	N/A	N/A	Faint across base
GSA–V447.14	Lower lateral	N/A	N/A	N/A	17.53	N/A	N/A	N/A	8.24	4.7	N/A	7.67	1	2	Faint across base
GSA–V447.5	Lower lateral	27.06	15.53	1.74	17.23	63.6	9.83	36.4	8.51	4.59	7.2	7.28	1	1	Faint across base
GSA–V447.15	Lower lateral	N/A	N/A	N/A	14.88	N/A	N/A	N/A	8.49	4.45	N/A	7.06	1	1	Faint across base
GSA–V447.16	Lower lateral	N/A	N/A	N/A	NA	N/A	N/A	N/A	7.96	4.25	N/A	N/A	N/A	1	N/A
GSA–V447.17	Lower lateral	N/A	N/A	N/A	8.74	N/A	N/A	N/A	4.06	2.34	N/A	3.13	N/A	1	Faint across base

ranges from 23.93 to 15.59 mm. The H/W ratios range from 1.01 to 1.21 (Table 2). All the teeth have a triangular main cusp that is distally inclined in the anterolateral positions, but the cusp becomes shorter and more distally hooked the closer a tooth is positioned to the commissure. The labial and lingual faces of the main cusp are almost equally convex. In mesial or distal views, the main cusp is straight except for a slight labial bend at the apex. The crown enameloid is smooth except for very faint plications (visible under magnification) along the labial crown foot. There are one to two pairs of lateral cusplets, and when two pairs are present the larger pair is always positioned medially, and the lateral pair is much reduced in size. The larger pair of cusplets are distinctively hooked both medially and lingually. The main cusp cutting edges are complete and extend to the base of the main cusp. The cutting edges extend across the apical half of the lateral cusplets. A pair of minute mesial and distal denticulations occur between the main cusp and lateral cusplets on specimen GSA–V447.9 (Fig. 5u–x), but such denticles are absent on all other teeth associated with GSA–V447. The bilobate root has short and thin (labio-lingually) lobes that are divergent and rounded at their extremities. The interlobe area is wide and U-shaped. The pronounced lingual protuberance is bisected by a deep nutritive groove.

Teeth GSA–V447.2 and GSA–V447.9 (Fig. 5u–bb) differ somewhat with respect to the degree of distal inclination of the main cusp, with GSA–V447.2 being slightly more inclined. These lateral teeth could be from succeeding lateral files, as for example GSA–V447.9 could be from the second lateral file and GSA–V447.2 the third lateral file. Tooth GSA–V447.3 (Fig. 5cc–ff) is slightly smaller in overall size and has a more distally inclined and curved crown compared to the other teeth assigned to this group, indicating that it is from a more distally located lateral file. Based on its small size and strongly distally hooked crown, tooth GSA–V447.10 (Fig. 5gg–ii) was likely part of a posterolateral file located closer to the jaw commissure, where the dental hollow is tapered and space for developing teeth is rather limited.

One tooth, GSA–V447.8 (Fig. 5q–t), is believed to be from the upper dentition due to the distal inclination of the crown, and the short length of the root lobes and wide interlobe area. However, it exhibits an unusual morphology as it is significantly smaller than the anterior teeth and it is also conspicuously distally inclined. Additionally, the tooth is smaller than and/or lacks the distal crown curvature exhibited by the lateral teeth. Furthermore, the crown is mesio-distally thinner than all the other upper teeth. Specimen GSA–V447.8 conforms to our observations of the intermediate teeth of the extant lamniform shark dentitions we examined, although we cannot definitively rule out the possibility that it represents a lateral file.

Lower anterior teeth **(GSA–V447.4, Fig. 6a–d).** GSA–V447.4 is the only definitive lower anterior tooth associated with GSA–V447. This tooth measures 32.63 mm in total height and 17.28 mm in root width and has a H/W ratio of 1.89 (Table 2). The main cusp is tall and nearly symmetrical. Its labial face is slightly convex, whereas the lingual face is strongly convex. The crown enameloid is smooth save for faint plications occurring at the labial crown foot. The crown is weakly sigmoidal in mesial and distal views. There is a single pair of short lateral cusplets that are slightly lingually inclined. The mesial and distal cutting edges are incomplete and do

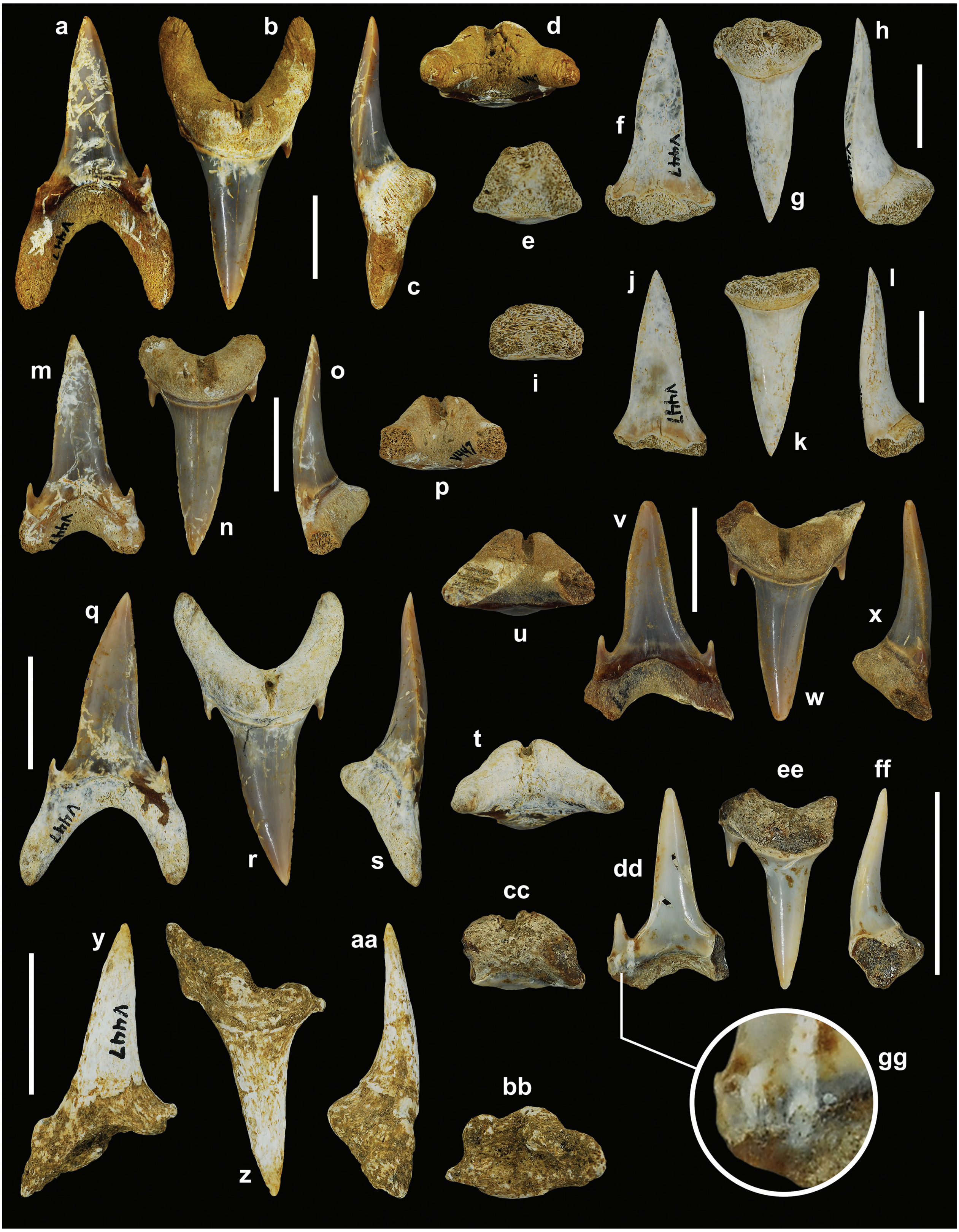

Figure 6. a–gg. *Palaeohypotodus bizzocoi* sp. nov. lower teeth. **a–d.** GSA–V447.4 (paratype), lower right anterior tooth; **a.** Labial view; **b.** Lingual view; **c.** Mesial view; **d.** Basal view. **e–h.** GSA–V447.12, lower right anterior tooth; **e.** Basal view; **f.** Labial view; **g.** Lingual view; **h.** Mesial view. **i–l.** GSA–V447.13, lower right anterior tooth; **i.** Basal view; **j.** Labial view; **k.** Lingual view; **l.** Mesial view. **m–p.** GSA–V447.14, lower right lateral tooth; **m.** Labial view; **n.** Lingual view; **o.** Mesial view; **p.** Basal view. **q–t.** GSA–V447.5 (paratype), lower left lateral tooth; **q.** Labial view; **r.** Lingual view; **s.** Mesial view; **t.** Basal view. **u–x.** GSA–V447.15, lower left lateral tooth; **u.** Basal view; **v.** Labial view; **w.** Lingual view; **x.** Mesial view. **y–bb.** GSA–V447.16, lower left lateral tooth; **y.** Labial view; **z.** Lingual view; **aa.** Mesial view; **bb.** Basal view. **cc–gg.** GSA–V447.17, lower right lateral tooth; **cc.** Basal view; **dd.** Labial view; **ee.** Lingual view; **ff.** Mesial view; **gg.** Close-up of labial crown ornamentation. Scale bars: 1 cm.

not extend to the base of the main cusp. Smooth cutting edges extend across the lateral cusplets. The bilobate root has elongated, thin, and rounded lobes that are slightly divergent. The interlobe area is deep and U-shaped. The pronounced lingual protuberance is bisected by a deep nutritive groove. The crown height measures 19.9 mm, and this portion of the tooth comprises approximately 61% of the total height (Table 2).

Two additional teeth associated with GSA–V447, GSA–V447.12–.13 (Fig. 6e–l), consist only of the main cusp and a portion of the root. These teeth are attributed to the lower dentition because the main cusp is not as sigmoidal as that of upper anterior teeth, the labial face is less convex compared to upper lateral teeth, and they have incomplete cutting edges. We believe these teeth represent lower anterior files because they have a more symmetrical main cusp compared to lower lateral teeth included with GSA–V447 (see below). Additionally, the main cusp height of these two teeth (18.59 and 18.09 mm, respectively) is greater than that of any lower lateral tooth (17.53 to 8.74 mm) (Table 2).

***Lower lateral teeth* (GSA–V447.5, 14–17, Fig. 6m–gg).** Although five lower lateral teeth are part of GSA–V447, only one is complete (GSA–V447.5, Fig. 6q–t). The other four teeth have a complete main cusp but are missing one or both root lobes. These five teeth have a tall and narrow main cusp that has a very slight distal inclination. The slight distal inclination is most evident on the mesial side of the main cusp because the mesial edge is more convex than the distal edge near the apex. This morphology allowed us to determine if the tooth was from the right or left Meckel's cartilage. The labial face of the main cusp is slightly convex, whereas the lingual face is strongly convex. The crown enameloid is smooth except for very faint plications (seen under magnification) along the labial crown foot. In mesial and distal views, the main cusp has a slight lingual inclination. The teeth generally have a single pair of lateral cusplets, but GSA–V447.1 (Fig. 6m–p) has a second diminutive distal cusplet that is united to the base of the much larger, more medially located cusplet. The lateral cusplets have a slight medial curve and are also lingually inclined. The mesial and distal cutting edges of the main cusp are incomplete, and the cutting edges that extend across the lateral cusplets do not meet the base of the main cusp. The bilobate root has lobes that are narrow, elongated, and slightly divergent. The interlobe area is deep and U-shaped. A robust lingual protuberance is bisected by a deep nutritive groove. The H/W ratio of GSA–V447.2 (complete tooth) is 1.74 (Table 2), and main cusp height on the five teeth ranges from 17.53 to 8.74 mm, indicating that overall tooth size decreased towards the commissure. Tooth GSA–V447.17 (Fig. 6cc–gg) has the shortest main cusp height of any tooth associated with GSA–V447 (Table 2), and this interesting tooth is regarded as a lower posterolateral tooth due to its small size but overall similarity to the other four teeth attributed to the lower lateral tooth group.

Remarks. Our analysis of the 17 teeth included with GSA–V447 indicates that monognathic and dignathic heterodonty were developed within the dentition of *Palaeohypotodus bizzocoi* sp. nov. Our examination of 17 isolated teeth from temporally equivalent strata also indicate a degree of ontogenetic heterodonty within this taxon.

Monognathic heterodonty. Some of the variation observed amongst the teeth within GSA–V447 reflects the presence of anterior and lateral tooth files in the palatoquadrate and Meckel's cartilage of *P. bizzocoi* sp. nov. (Fig. 7). Upper anterior teeth differ from upper lateral teeth by having a taller and mesiodistally narrower main cusp, and the H/W ratios of anterior teeth range from 1.44–1.55 but those of lateral teeth are much lower at 1.01–1.21 (Table 2). The main cusp of anterior teeth is also more erect, more symmetrical, and labiolingually thicker compared to the inclined to strongly distally hooked crown of lateral teeth. Additionally, the anterior teeth have longer and less divergent root lobes and a deeper interlobe area than lateral teeth. The root height is therefore lower on lateral teeth (between 26.3 to 28.9% the height of the tooth) than on anterior teeth (between 30.1 and 32.1%) because of the shorter root lobes. Furthermore, the lateral teeth can have up to two pairs of lateral cusplets but there is only one pair on the anterior teeth. Lastly, although the teeth of the Meckel's cartilage are similar to one another, the lateral teeth are characterized by the slight distal inclination of the main cusp (Fig. 6). Additionally, the root of GSA–V447.5 shows that lobes are more widely separated compared to the complete anterior tooth (GSA–V447.4).

Dignathic heterodonty. The teeth included with GSA–V447 also demonstrate morphological variation between the teeth of the palatoquadrate and Meckel's cartilage of *P. bizzocoi* sp. nov. (Figs 5, 6). Overall, the upper teeth differ from the lower teeth by having a wider U-shaped interlobe area, as the root lobes on the upper teeth are shorter and more divergent. This is reflected in the H/W ratios among the teeth, which are much higher for lower teeth (1.74 to 1.89) than for the uppers (1.01 to 1.55) (Table 2). In addition, the height of the root constitutes between 26–32% of total tooth height of upper teeth and between 36–39% of lower teeth.

Upper anterior teeth (i.e., GSA–V447.1, 6–7, Fig. 5a–p) are distinguished by their complete cutting edges, whereas those of lower anterior teeth (i.e., GSA–V447.4, Fig. 6a–d) do not reach the main cusp base. In profile view, the upper anterior teeth have a more sigmoidal main cusp compared to the lower anterior files. Additionally, the lateral cusplets on upper anterior teeth are lingually curved but those on the lower anterior teeth have a slight distal inclination. With respect to the tooth root, that of the upper anterior teeth has shorter and more divergent lobes compared to lower anterior teeth, and the interlobe area is resultantly more widely U-shaped on the upper anterior teeth. Furthermore, the root comprises 30–32% of the total height of upper anterior teeth but is close to 40% on the lower anterior tooth GSA–V447.4 (Table 2).

The lower lateral teeth are easily differentiated from upper lateral teeth by their narrower and nearly vertical main cusp with relatively flat labial face. In contrast, the

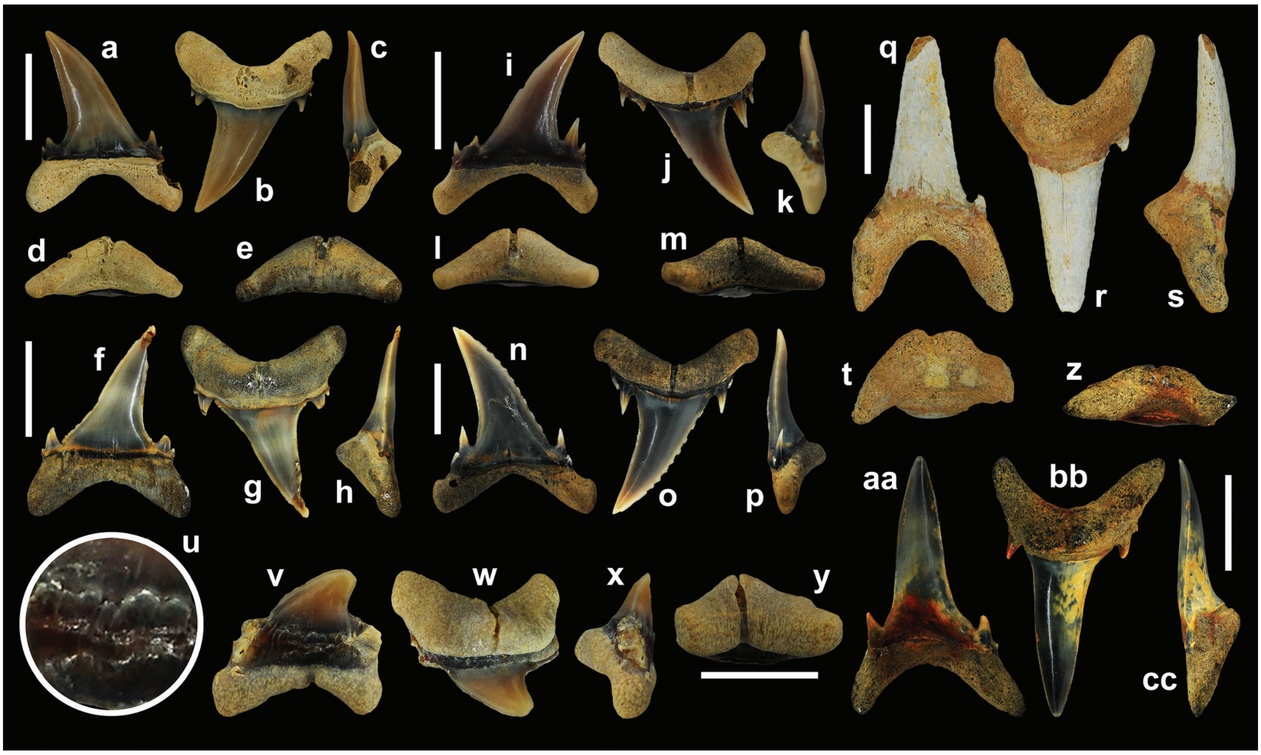

Figure 7. *Palaeohypotodus bizzocoi* sp. nov. referred specimens. **a–d.** MSC 49451, upper left lateral tooth, lower Clayton Formation, Wilcox County, AL; **a.** Labial view; **b.** Lingual view; **c.** Mesial view; **d.** Basal view. **e–h.** MMNS VP–8578, upper right lateral tooth, basal Clayton Formation, Hot Spring County, AR; **e.** Basal view; **f.** Labial view; **g.** Lingual view; **h.** Mesial view. **i–l.** MMNS VP–7292.3, upper right lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; **i.** Labial view; **j.** Lingual view; **k.** Mesial view; **l.** Basal view. **m–p.** MSC 42733, upper left lateral tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; **m.** Basal view; **n.** Labial view; **o.** Lingual view; **p.** Mesial view. **q–t.** MSC 3020, lower left anterior tooth, lower Clayton Formation, Wilcox County, AL; **q.** Labial view; **r.** Lingual view; **s.** Mesial view; **t.** Basal view. **u–y.** MMNS VP–7295.3, upper right posterior tooth, Pine Barren Member of the Clayton Formation, Lowndes County, AL; **u.** Close-up of labial crown ornamentation; **v.** Labial view; **w.** Lingual view; **x.** Mesial view; **y.** Basal view. **z–cc.** MSC 49452, upper left 3rd anterior tooth, Porters Creek Formation, Butler County, AL; **z.** Basal view; **aa.** Labial view; **bb.** Lingual view; **cc.** Mesial view. Scale bars: 1 cm (**a–h, q–t, z–cc**); 5 mm (**i–p, v–y**).

upper lateral teeth are conspicuously distally inclined to strongly distally hooked, and the labial crown face is more convex. In addition, the mesial and distal cutting edges of the main cusp on lower lateral teeth are incomplete, whereas they extend to the lateral cusplets on the upper lateral teeth. The main cusp of lower lateral teeth is also slightly curved lingually near the apex, whereas upper lateral teeth have a straighter lingual crown face. Furthermore, the lateral cusplets of lower lateral teeth have a slight distal inclination, whereas those of the upper teeth are distally curved. Moreover, the lateral teeth have a deeper interlobe area due to more elongated but less divergent root lobes compared to the upper lateral teeth. Lastly, the root height of the only complete lower lateral tooth in our sample (GSA–V447.5) constitutes 36.4% of the total tooth height, which far exceeds that on any of the upper lateral teeth (only 26.9% to 28.9%; see Table 2).

Ontogenetic heterodonty. The 17 teeth included with GSA–V447 were derived from the Danian Porters Creek Formation in Wilcox County, AL. No additional *P. bizzocoi* sp. nov. specimens are known from the type locality, but the collections at MSC and the MMNS include 17 isolated teeth collected from Alabama and Arkansas, USA (see Referred specimens above) that we associate with this new species. One of these teeth (MSC 49452) was collected from the type stratum (albeit from a different locality), whereas the other 16 teeth were derived from lithostratigraphic units that are temporally equivalent to the Porters Creek Formation. Two specimens in particular, MSC 49451 and MMNS VP–8578, are morphologically, qualitatively, and quantitatively comparable to teeth within GSA–V447. Specifically, MSC 49451 (Fig. 7a–d) is an upper left lateral tooth that is nearly indistinguishable from the *P. bizzocoi* sp. nov. paratype tooth GSA–V447.3 (Fig. 5cc–ff) in terms of size and gross morphology (see Tables 2, 3). In addition, specimen MMNS VP–8578 (Fig. 7e–h), an upper right lateral tooth, is nearly identical in all respects to *P. bizzocoi* sp. nov. paratype tooth GSA–V447.2 (Fig. 5y–bb). The morphological similarity of the 17 isolated teeth to those included with GSA–V447 leads us to conclude that they represent *P. bizzocoi* sp. nov. and that they reflect intraspecific (ontogenetic) variation within the species.

Ten of the additional 17 isolated teeth referred to *P. bizzocoi* sp. nov. are complete and could be described in their entirety and measured, allowing us to directly

Table 3. Measurements, ratios, and observations of *Palaeohypotodus bizzocoi* sp. nov. teeth. Teeth are organized by tooth group and increasing TH. **Column abbreviations: #DC.** Number of distal cusplets. **DIA.** Depth of the interlobe area. **H/W Rat**. Height/width ratio; **LOP.** Labial ornamentation present and the nature of the ornamentation; **#MC.** Number of mesial cusplets; **MCH.** Main cusp height; **%MCH.** The percentage of the main cusp height in relation to the total tooth height; **MCT.** Main cusp thickness; **MCW.** Main cusp width; **RH.** Root height; **%RH.** The percentage of the root height in relation to the total tooth height; **RT.** Maximum root thickness; **RW.** Root width; **TH.** Total height. **N/A.** Measurement, ratio, or observation could not be taken due to the incomplete preservation of the tooth.

	TH	TW	H/W Rat	MCH	%MCH	RH	%RH	MCW	MCT	DIA	RT	#MC	#DC	LOP
Upper anterior teeth														
MSC 49452	23.79	15.87	1.5	18.29	76.9	5.5	23.1	8.34	4.57	4.91	5.54	2	2	Faint across base
MSC 42738	24.55	13.79	1.78	18.13	73.8	6.42	26.2	8.39	5.29	5.99	6.86	1	N/A	Faint across base
GSA–V447.7	28.87	19.97	1.44	19.63	67.9	9.24	32.1	11.18	5.28	6.28	8.12	1	1	Faint across base
GSA–V447.1 (holotype)	29.11	19.08	1.52	19.98	68.6	9.13	31.4	11.19	5.24	7.18	8.9	1	1	Faint across base
GSA–V447.6	29.16	18.84	1.55	20.39	69.9	8.77	30.1	10.53	5.14	6.7	8.63	1	1	Faint across base
Upper lateral teeth														
MMNS VP–7292.3	10.06	9.02	1.12	7.89	78.4	2.17	21.6	3.86	1.88	2.7	3.01	3	3	Faint across base
MMNS VP–7292.4	10.67	9.25	1.15	8.29	77.7	2.38	22.3	4.61	1.91	2.76	3.02	3	3	Faint across base
MSC 42733	12.75	11.21	1.13	10.39	81.5	2.36	18.5	4.98	2.49	3.33	3.66	2	2	Faint across base
MMNS VP–7292.2	12.76	10.42	1.22	9.43	73.9	3.33	26.1	4.78	2.49	4.06	3.78	3	3	Faint across base
GSA–V447.10	15.59	13.33	1.17	11.4	73.1	4.19	26.9	8.6	3.58	3.78	4.88	1	1	Faint across base
GSA–V447.3 (paratype)	19.51	16.94	1.15	14.39	73.7	5.12	26.3	9.52	4.05	4.97	5.91	2	2	Faint across base
MSC 49451	20.5	17.82	1.15	15.38	75	5.12	25	9.77	4.32	5.57	5.99	2	2	Faint across base
GSA–V447.8	20.09	14.54	1.01	14.6	72.6	5.49	27.4	7.34	3.95	5.02	6.1	2	2	Faint across base
MMNS VP–8578	22.01	18.89	1.17	16.16	73.4	5.84	26.6	10.23	4.01	6.24	7.09	2	2	Faint across base
GSA–V447.2 (paratype)	23.93	19.81	1.21	17.03	71.1	6.9	28.9	11.29	4.64	5.35	6.91	2	2	Faint across base
Lower anterior teeth														
GSA–V447.4 (paratype)	32.63	17.28	1.89	18.86	60.9	12.73	39.1	9.67	5.08	10.48	8.65	1	1	N/A
MSC 3020	37.67	22.01	1.71	24.74	65.7	12.93	34.3	11.92	7.29	11.16	10.65	1	1	Faint across base
Lower lateral teeth														
MMNS VP–7311	21.24	14.53	1.46	14.81	69.7	6.43	30.3	9.01	5.06	5.28	6.36	1	2	Faint across base
GSA-VP447.5 (paratype)	27.06	15.53	1.74	14.6	63.6	9.83	36.4	7.45	4.07	7.2	6.29	1	2	N/A

compare them to the teeth of GSA–V447. One of the referred specimens was identified as a posterior tooth (see below) and was excluded from our quantitative analysis due to its atypical morphology.

Our quantitative evaluation of the total tooth sample of *P. bizzocoi* sp. nov. revealed several morphological trends that we interpret to represent ontogenetic heterodonty within the species. Table 3 lists all the complete teeth according to tooth group (i.e., upper and lower anterior and upper and lower lateral) and are presented by ascending order of total tooth height (TH). Our data shows that the teeth associated with GSA–V447 are among the largest in our sample, indicating these specimens likely represent adult individuals (or a single adult individual). Interestingly, specimen MSC 3020 (Fig. 7q–t), a lower anterior tooth, has a TH over 5 mm greater than the largest lower anterior tooth associated with GSA–V447 (paratype tooth GSA–V447.4), indicating that this species could achieve even larger sizes than indicated by the type specimens.

One morphological trend that is evident in Table 3 is the ontogenetic reduction in the number of lateral cusplets on upper teeth. Of the upper anterior teeth in our sample, all the specimens with a TH less than 24 mm have two pairs of lateral cusplets, whereas those with a TH greater than 24 mm only have a single pair. Additionally, the number of lateral cusplets on the upper lateral teeth ranges from one to three pairs, but the occurrence of three pairs is limited to teeth with a TH of 13 mm or less. In contrast, all upper lateral teeth that exceed 15 mm in TH have a maximum of two lateral cusplet pairs. Similarly, the number of lateral cusplets on each side of the main cusp on lower anterior and lateral teeth also does not exceed two, with most specimens having a single pair regardless of tooth size. We observed that the mesial and distal cusplets on teeth of both the palatoquadrate and Meckel's cartilage can be unequal in number (Tables 2, 3), particularly on lateral teeth.

Our data shows a general trend across all tooth groups of both the palatoquadrate and Meckel's cartilage that, as the TH of a tooth increases, the total width (TW), main cusp height (MCH), main cusp width (MCW), root height (RT), root thickness (RT), and depth of the interlobe area (DIA) also increases (see Table 3). These trends reflect ontogenetic change from small and gracile teeth in juvenile stages to large and robust teeth into adulthood. Interestingly, when the ratio of the root to overall tooth height is calculated (%RH) and then compared to that of the main cusp (%MCH), these values show an inverse relationship through ontogeny. As the shark matures the %RH increases and the %MCH decreases, which is a result of an increase in the length of the mesial and distal root lobes through ontogeny. This is also reflected in the DIA (i.e., depth of the interlobe area), which increases (deepens) as the root lobes become elongated (Table 3). Although subtle changes are evident across ontogeny based on the aforementioned values, the height/width ratios (H/W) remain relatively constant. This indicates that juvenile teeth, at least in terms of H/W ratios, are essentially smaller versions of the larger teeth, with any differences in the values likely being a result of different tooth files within a particular tooth group (for example, a lower second versus lower third anterior).

Additional tooth files. In addition to elucidating ontogenetic heterodonty, the sample of 17 isolated *P. bizzocoi* sp. nov. teeth increases our understanding of monognathic and dignathic heterodonty within the species. Included in the sample are two tooth positions that are not represented amongst the teeth associated with GSA–V447. One of these teeth, MSC 49452 (Fig. 7z–cc), has a tall and triangular main cusp, two pairs of lingually curved lateral cusplets, complete mesial and distal cutting edges, plications along the labial crown base, a pronounced lingual root protuberance with nutritive groove, and a deep U-shaped interlobe area, which are all characteristics of *P. bizzocoi* sp. nov. anterior teeth. However, this tooth also has an elongated and mesially extended mesial root lobe, and the distal edge of the main cusp is more convex than the mesial edge, giving the main cusp a slight mesial curve (as opposed to distally inclined or hooked). Of the extant lamniform dentitions we examined, these unique characteristics are remarkably similar to those of the upper third anterior teeth of *Carcharias taurus* and *Mitsukurina owstoni*.

Specimen MMNS VP–7295.4 is herein regarded as an upper posterior tooth of *P. bizzocoi* sp. nov. (Fig. 7u–y). This tooth is very small and measures 5.4 mm in TH and 6.4 mm in RW. The tooth has a short and distally hooked main cusp and although the lateral cusplets are not preserved on this tooth, it appears to have had at least one pair. The mesial and distal cutting edges are complete and extend to the base of the lateral cusplets. The root is robust and, in lingual view, the height of the root (3.8 mm) is more than twice the height of the crown (1.6 mm). The root lobes are short, rounded, divergent, and form a wide and U-shaped interlobe area. The lingual face of the root is bisected by a deep nutritive groove. Perhaps the most conspicuous feature of this tooth is the extensive ornamentation along the labial crown foot, where enameloid plications coalesce into spine-like structures. Similar ornamentation has been reported on posterolateral and posterior teeth of *Palaeohypotodus rutoti* (see Herman 1972, pl. 2, figs 1–3, 5; Herman 1977, pl. 10, fig. 3e; Cappetta 2012, fig. 192h–j), and this specific characteristic was noted by Leriche (1902, 1906) and Herman (1972, 1977). This phenomenon indicates a degree of dental homology and stasis between the temporally younger *P. rutoti* and the Danian *P. bizzocoi* sp. nov.

Discussion

Generic assignment of GSA–V447

Palaeohypotodus was previously comprised of three valid species, including Cretaceous *P. bronni* (Agassiz, 1843) and Paleogene *P. rutoti* (Winkler, 1874) and *P. volgensis* Zhelezko & Kozlov, 1999. Multiple other species have been named, like *Palaeohypotodus houzeaui* (Woodward, 1891) and *P. lerichei* Glückman, 1964, but these (and some other) taxa were subsequently synonymized with *P. rutoti* (Cappetta & Nolf, 2005). Still other species, including *P. speyeri* (Darteville & Casier, 1943) and *P. striatula* (Dalinkevicius, 1935), have been referred to other genera (see Cappetta 2012). Several morphological features have been utilized to identify teeth of *Palaeohypotodus*, including; the variable occurrence of one to three pairs of lateral cusplets; upper lateral teeth having a strongly distally inclined to hooked main cusp; upper and lower anterior teeth with tall, triangular and generally symmetrical main cusp; lower lateral teeth with a tall and relatively erect main cusp; upper teeth with complete mesial and distal cutting edges; lower teeth with incomplete cutting edges; a pronounced lingual root protuberance with nutritive groove; and a U-shaped interlobe area. Although many of these features are present on teeth of other taxa, like *Jaekelotodus* Glückman, 1964 and *Odontaspis winkleri* Leriche, 1905, all teeth assigned to *Palaeohypotodus* bear plications across the labial crown foot (particularly on lateral and posterior teeth). Additionally, upper and lower anterior teeth of *Jaekelotodus* have complete cutting edges, and all those of *O. winkleri* have incomplete edges. The teeth included with GSA–V447 all exhibit these characteristics, and their assignment to *Palaeohypotodus* is appropriate.

Of the recognized species, *Palaeohypotodus rutoti* (Winkler, 1874) is the one most often reported in the literature. This species would seem to have a rather long temporal distribution, being variously reported from Danian to Priabonian (late Eocene) strata, as well as an extensive geographic distribution (see Cappetta 2012; Kriwet et al. 2016). Although *P. bronni* (Agassiz, 1843) is predominantly known from the Maastrichtian (Late Cretaceous) of Europe, at least two reports suggest this species may have survived the K/Pg extinction event into the Paleocene (see Leriche 1906; Adolfssen and Ward 2015). To our knowledge, *P. volgensis* has not been identified beyond the type discussion (Zhelezko and Kozlov 1999). Many of the identifications to these species appear to be tentative at best and we believe that these occurrences need further evaluation. Although such a thorough reassessment of *Palaeohypotodus* is beyond the scope of this paper, we present a limited discussion of the morphological criteria that have been used to identify these species so they can be adequately compared to *P. bizzocoi* sp. nov.

Palaeohypotodus bronni (Agassiz, 1843)

This taxon was originally named by Agassiz (1843) based on two teeth collected from Upper Cretaceous (Maastrichtian) deposits in the Mount St. Peter area in Maastricht, Netherlands (pl. 37, figs 8–9), and a third tooth from an unspecified unit in Delaware, USA (fig. 10). Only the outline of the Delaware specimen was provided, and it is difficult to evaluate due to the lack of details. Also, considering that the tooth was collected from a different continent and the age of the source stratum is unknown, we suggest it be excluded from Agassiz's (1843) *P. bronni* type suite. Based on our interpretation of the dentition of *P. bizzocoi* sp. nov., the two teeth from Maastricht appear to be from the lower dentition, with that shown in Agassiz's (1843) figure 8 representing a lower lateral tooth and the one in figure 9 likely being a lower anterior tooth. Agassiz's (1843) brief description of these teeth stated that they have a symmetrical main cusp, two pairs of lateral cusplets, and plications along the labial crown foot. Unfortunately, these two teeth are embedded in limestone and only the labial face is visible.

Fortunately, additional *P. bronni* specimens from the vicinity of the type locality were subsequently reported by Preim (1897, pl. 1, figs 11–14), Van de Geyn (1937, figs 117–123), Herman (1977, pl. 10, fig. 2a–f), and Cappetta and Corral (1999, fig. 4). Additionally, we examined three teeth from Maastrichtian deposits exposed at the ENCI Quarry in Limburg, Netherlands (MMNS VP–9616, MMNS VP–10577.1–2). This assortment of teeth allows us to gain a better understanding of the dental variation within this species, as it includes anterior and lateral tooth groups from both the palatoquadrate and Meckel's cartilage (see Table 4). Critical examination of these teeth demonstrated that they are morphologically similar to one another by their having a triangular main cusp that is erect in the anterior and lower lateral files but distally hooked in the upper lateral files, labial plications occur along the crown foot, one to two pairs of lateral cusplets (with the larger pair being positioned closer to the main cusp), a robust root with a pronounced lingual protuberance and nutritive groove, and a relatively deep and U-shaped interlobe area.

Table 4. Comparison of the DIA% between *Palaeohypotodus bizzocoi* sp. nov., *P. bronni*, and *P. rutoti*. **DIA%.** Ratio of the depth of the interlobe area in relation to the overall height of the tooth.

***Palaeohypotodus bizzocoi* sp. nov.**		
Source	**Tooth Position**	**DIA%**
MSC 49452	Upper 3rd anterior tooth	0.21
MSC 43738	Upper anterior tooth	0.24
MMNS VP–7311	Lower right lateral tooth	0.25
MMNS VP–7292.3	Upper left lateral tooth	0.25
MMNS VP–7292.4	Upper right lateral tooth	0.26
MSC 42733	Upper right lateral tooth	0.26
MSC 49451	Upper left lateral tooth	0.27
MMNS VP–8578	Upper right lateral tooth	0.28
MSC 3020	Lower left anterior tooth	0.3
GSA-VP447.2 (paratype)	Upper lateral tooth	0.31
GSA-VP447.7	Upper anterior tooth	0.32
MMNS VP–7292.2	Upper right lateral tooth	0.32
GSA-VP447.10	Upper lateral tooth	0.33
GSA-VP447.6	Upper anterior tooth	0.33
GSA-VP447.8	Upper lateral tooth	0.34
GSA-VP447.3 (paratype)	Upper lateral tooth	0.35
GSA-VP447.1 (holotype)	Upper anterior tooth	0.36
GSA-VP447.5 (paratype)	Lower lateral tooth	0.42
GSA-VP447.4 (paratype)	Lower anterior tooth	0.53
	Mean	**0.31**
Palaeohypotodus bronni		
Source	**Tooth Position**	**DIA%**
MMNS VP–10557.1	Upper lateral tooth	0.16
Van de Geyn (1937) fig. 118	Upper 3rd anterior tooth	0.17
Van de Geyn (1937) fig. 121	Upper anterior tooth	0.17
Herman 1977, pl. 10, fig. 2a	Upper anterior tooth	0.18
Van de Geyn (1937) fig. 120	Lower anterior tooth	0.18
Herman 1977, pl. 10, fig. 2d	Upper lateral tooth	0.19
Agassiz 1843, pl. 37, fig. 8	Lower lateral tooth	0.19
Herman 1977, pl. 10, fig. 2f	Lower lateral tooth	0.19
Preim 1897 pl. 1, fig. 13	Upper anterior tooth	0.19
Preim 1897 pl. 1, fig. 11	Upper lateral tooth	0.2
Agassiz 1843, pl. 37, fig. 9	Upper anterior tooth	0.21
Cappetta and Corral 1999, fig. 4	Upper anterior tooth	0.21
Preim 1897 pl. 1, fig. 14	Upper anterior tooth	0.21
Herman 1977, pl. 10, fig. 2c	Upper anterior tooth	0.21
Van de Geyn (1937) fig. 123	Upper anterior tooth	0.21
MMNS VP–9616	Upper lateral tooth	0.22
Van de Geyn (1937) fig. 117	Lower anterior tooth	0.22
Van de Geyn (1937) fig. 119	Upper lateral tooth	0.23
Herman 1977, pl. 10, fig. 2b	Lower anterior tooth	0.24
Herman 1977, pl. 10, fig. 2e	Upper lateral tooth	0.27
	Mean	**0.2**
Palaeohypotodus rutoti		
Source	**Tooth Position**	**DIA%**
Casier 1942, pl. 1, fig. 6	Upper lateral tooth	0.14
Casier 1942, pl. 1, fig. 5	Upper lateral tooth	0.17
Leriche 1951, pl. 42, fig. 8	Upper anterior tooth	0.18
Leriche 1951, pl. 42, fig. 10	Lower anterior tooth	0.19
Leriche 1951, pl. 42, fig. 9	Lower 1st anterior? Tooth	0.2
Herman 1977 pl. 10, fig. 3a	Upper anterior tooth	0.21
Herman 1977 pl. 10, fig. 3d	Upper posterolateral tooth	0.21
Vincent 1876, pl. 6, fig. 1c	Lower anterior tooth	0.21
Casier 1942, pl. 1, fig. 2	Upper 3rd anterior tooth	0.21
Casier 1942, pl. 1, fig. 1	Upper anterior tooth	0.24
Casier 1942, pl. 1, fig. 9	Lower anterior tooth	0.24
Herman 1972, pl. 2, fig. 5	Upper posterolateral	0.24
Herman 1977 pl. 10, fig. 3c	Upper lateral tooth	0.25
Herman 1977 pl. 10, fig. 3e	Upper posterolateral tooth	0.25
Casier 1942, pl. 1, fig. 11	Lower lateral tooth	0.25
Leriche 1951, pl. 42, fig. 11	Lower lateral tooth	0.26
Casier 1942, pl. 1, fig. 12	Lower lateral tooth	0.26
Leriche 1902, pl. 1, fig. 37	Upper anterior tooth	0.26
Leriche 1902, pl. 1, fig. 38	Lower anterior tooth	0.26
Cappetta 2012, fig. 192e	Upper 3rd anterior tooth	0.26
Herman 1977 pl. 10, fig. 3b	Lower anterior tooth	0.28
Vincent 1876, pl. 6, fig. 1d	Upper anterior tooth	0.28
Casier 1942, pl. 1, fig. 10	Lower anterior tooth	0.28
Leriche 1902, pl. 1, fig. 39	Upper lateral tooth	0.28
Vincent 1876, pl. 6, fig. 1a	Upper anterior tooth	0.29
Casier 1950, pl. 2, fig. 1	Lower anterior tooth	0.3
Vincent 1876, pl. 6, fig. 1b	Upper anterolateral tooth	0.34
	Mean	**0.24**

The historical descriptions of *P. bronni* teeth support our observations. For example, Giebel (1848) reiterated that the teeth had one or two pairs of lateral cusplets. Sauvage (1898) also noted the presence of two lateral cusplets on *P. bronni* teeth and he mentioned that Cretaceous specimens from Portugal have conspicuous plications at the labial crown foot. Leriche (1902) described the teeth as having two pairs of lateral cusplets, with the second pair smaller, and noted that labial folds were small and obsolete on Paleocene specimens he examined (suggesting these latter specimens need to be reevaluated as they may not belong to this genus). From these descriptions, it seems clear that Late Cretaceous teeth from Europe assigned to *P. bronni* have two pairs of lateral cusplets, with the second pair being smaller than the first. Adolfssen and Ward (2015) tentatively reported a Danian record of this taxon, but they specifically noted that the material lacked labial ornamentation and only had a single pair of lateral cusplets. These differences indicate that Paleogene records of *P. bronni* need to be reevaluated, as they may not belong to this genus.

The *P. bronni* teeth we examined are morphologically very similar to those of *P. bizzocoi* sp. nov., but several distinct features distinguish the two species. Adult teeth of *P. bronni* generally have two pairs of rather wide lateral cusplets, whereas *P. bizzocoi* sp. nov. teeth typically have a single pair of relatively narrow cusplets. Overall, teeth of *P. bizzocoi* sp. nov. have one to three pairs of cusplets (adults generally with one pair and juveniles with one to three pairs) that, compared to *P. bronni*, are much shorter, narrower, more needle-like, and diminutive with respect to the size of the main cusp. In addition, the secondary cusplets (i.e., the more labial pair) on *P. bronni* teeth are much larger than those that occur on any *P. bizzocoi* sp. nov. teeth, where on the latter they are generally minute and are largely united to the larger medial cusplet (while they are more clearly separated on *P. bronni*). Furthermore, the root lobes of *P. bronni* teeth are much more robust than those of *P. bizzocoi* sp. nov. On the latter, the root lobes are thin and have consistent width across their length, whereas they widen towards the crown base on *P. bronni* teeth. Lastly, the root lobes are significantly longer on *P. bizzocoi* sp. nov. teeth, resulting in a much deeper interlobe area. This is readily apparent in Table 4, which shows the depth of the interlobe area of *P. bizzocoi* sp. nov. teeth consistently constitutes roughly 25–50% (mean = 31%) of the overall tooth height. This value rarely exceeds 23% on *P. bronni* teeth (mean = 20%). Although we identified the depth of the interlobe area as a characteristic that increases through ontogeny on *P. bizzocoi* sp. nov. teeth, many of the *P. bronni* teeth figured in the literature appear to approach and even exceed the size of the largest *P. bizzocoi* sp. nov. teeth in our sample. This indicates that the extremely elongated root lobes and deep interlobe area are characteristic of *P. bizzocoi* sp. nov. teeth.

Interestingly, Van de Geyn (1937, fig. 118) illustrated a distinct upper anterior tooth with an elongated mesial root lobe and a main cusp that has a distal cutting edge that is more convex than the mesial edge. This tooth is morphologically very similar to the upper third anterior teeth within extant lamniform taxa like *Carcharias taurus* and *Mitsukurina owstoni* and is comparable to an upper third anterior tooth of *P. bizzocoi* sp. nov. we identified in our sample (MSC 49452, Fig. 7z–cc). A comparison of these teeth clearly illustrates the morphological differences between these two species, as the *P. bronni* tooth figured by Van de Geyn (1937, fig. 118) has root lobes that are wider, the interlobe area is shallower and more V-shaped, and the lateral cusplets are wider, more triangular, and more divergent compared to *P. bizzocoi* sp. nov.

Palaeohypotodus rutoti (Winkler, 1874)

This taxon was named for two teeth (IRSNB P 123 and IRSNB P 124) derived from the Selandian (middle Paleocene) Orp Member of the Heers Formation in Orp-le-Grand (Maret), Belgium (Hovestadt and Steurbaut 2023). Winkler (1874, pl. 1, figs 3–4) illustrated only the lingual view of these two teeth, but Hovestadt and Steurbaut (2023, p. 51) provided high-resolution images of these specimens in labial, lingual, and mesial views. These images show that the type specimens have a distally hooked main cusp, which is indicative of upper lateral teeth. These teeth have two to three pairs of tall and triangular lateral cusplets that are divergent and well separated from one another and from the main cusp. Faint plications occur along the labial crown base on both teeth. Unfortunately, the roots on both type specimens are incomplete, with only the distal lobe preserved on IRSNB P 123 and both lobes are missing from IRSNB P 124. Because the *P. rutoti* type specimens represent only the upper lateral tooth morphology, we expanded our investigation into dental variation in this species by examining published descriptions and illustrations of specimens derived from, or close to, the type locality.

In his type description, Winkler (1874) noted that the teeth have a distally curved main cusp, 'creases' along the labial crown base, and two to three pairs of cusplets that decrease in size laterally and are well-delineated from one another. Leriche (1902) described Selandian *P. rutoti* (pl. 1, figs 37–40) teeth as having two or three pairs of slender, sharply pointed lateral cusplets, with the first pair being quite large, and the labial crown foot having numerous short, very closely spaced vertical plications that produced an unbroken line of sharp spines. Vincent (1876) provided a similar description of teeth with a straight to distally curved main cusp, at least one pair of lateral cusplets on anterior teeth and additional pairs on lateral teeth, and small enameloid folds along the base of the labial face. Casier (1942) provided the most thorough description of *P. rutoti* from the Selandian of Belgium based on an associated skeleton consisting of 31 teeth, 58 vertebrae, and three pieces of cartilage that were likely derived from the Meckel's cartilage or palatoquadrate. Casier (1942) described the teeth as having a slender crown with conspicuous labial folds at the crown base that were "spiniform" apically. He also noted that the teeth had two to three pairs of distinctly separated and lingually angled lateral cusplets (with most having three pairs), and a robust lingual protuberance. Casier's (1942) associated specimen included teeth from both the upper and lower jaws, with those in the lower files being described as having a straighter main cusp. The similarity of these descriptions indicates that Selandian *P. rutoti* from Belgium generally includes: 1) anterior and lower teeth with an erect main cusp; 2) upper lateral teeth with a distally hooked main cusp; 3) teeth with two to three pairs of lateral cusplets; 4) enameloid folds (and at times forming spinose ornamentation) along the labial crown base.

When the previously figured Selandian *P. rutoti* teeth from Belgium (i.e., Winkler 1874, pl. 6, figs 3–4; Vincent 1876, pl. 6, fig. 1; Leriche 1902, pl. 1, figs 37–44; Casier 1942, pl. 1, figs 1–12; Casier 1950, pl. 2, fig. 1; Leriche 1951, pl. 42, figs 8–11; Herman 1972, pl. 2, figs 1–5; Herman 1977, pl. 10, fig. 3; Cappetta 2012, fig. 192e; and Hovestadt and Steurbaut 2023, pg. 51) are compared to those of *P. bizzocoi* sp. nov., several distinct differences become apparent. First, *P. rutoti* teeth generally have two to three pairs of lateral cusplets, with most having three pairs, and at least one figured specimen appears to have four pairs (see Vincent 1876, pl. 6, fig. 1a). On *P. bizzocoi* sp. nov. teeth, the number of pairs of lateral cusplets rarely exceeds two (with three pairs occurring only on small, presumably juvenile, upper lateral teeth), with most teeth having only a single pair. Second, the more medial pair of lateral cusplets on *P. rutoti* teeth, particularly those on the type specimens (see Winkler 1974, pl. 6, figs 3–4, Hovestadt and Steurbaut 2023, pg. 51), are more robust and taller in relation to the height of the main cusp than they are on *P. bizzocoi* sp. nov. teeth. The lateral cusplets on *P. rutoti* teeth are also more widely separated from one another than they are on *P. bizzocoi* sp. nov., with the secondary pair of cusplets on the latter being more closely united to the base of the larger, more medial pair of cusplets. Lastly, the root lobes are generally longer on *P. bizzocoi* sp. nov. teeth, resulting in a deeper interlobe area than on *P. rutoti* specimens. Table 4 shows the ratio of interlobe depth to overall tooth height for *P. bizzocoi* sp. nov., *P. bronni*, and *P. rutoti* for teeth examined first-hand or published in the literature. On *P. bizzocoi* sp. nov. teeth, the depth of the interlobe area constitutes 25–50% (mean = 31%) the overall tooth height, whereas this value rarely exceeds 23% on *P. bronni* teeth (mean = 20%). Although the ratio for *P. rutoti* teeth ranges between 14–34%, which overlaps the low end of that measured on *P. bizzocoi* sp. nov. teeth, they have a significantly lower mean (mean = 24%).

Interestingly, both Casier (1942, pl. 1, fig. 2) and Cappetta (2012, fig. 192e–f) illustrated *P. rutoti* upper third anterior teeth that can be directly compared to specimen MSC 49452 (Fig. 7z–cc), which is herein referred to *P. bizzocoi* sp. nov. Although this tooth position in both taxa has two pairs of lateral cusplets, on *P. rutoti* the outer pair of cusplets is larger and more separated from the medial pair of cusplets than it is on MSC 49452. In contrast, the outer pair of cusplets on MSC 49452 is minute and mostly united to the larger medial pair of cusplets. In addition, in mesial and distal views, the lingual root protuberance on *P. rutoti* teeth is substantially more developed, although this may indicate that specimen MSC 49452 was derived from a replacement row (where the root may be incompletely developed) or the root shows some signs of erosion. Nevertheless, the labial ornamentation is extremely faint and visible only under magnification on MSC 49452. However, it is visible but inconspicuous on the tooth illustrated in Casier (1942) and is very pronounced on the specimen illustrated by Cappetta (2012).

Palaeohypotodus volgensis Zhelezko in Zhelezko & Kozlov, 1999

Existence of this taxon appears to be limited to the type description, and we are unaware of other published occurrences of this species. The type specimens were derived from the Selandian "lower Saratov beds" exposed along the Volga River near the town of Kamyshin in the Volgograd Oblast of Russia. The type suite consists of a holotype (GIK No. 8057/87) and three paratypes (GIK No. 8057/88–91) that are reposited at the State Darwin Museum in Moscow, Russia. The holotype is an upper left lateral tooth (GIK No. 8057/87; Zhelezko and Kozlov 1999, pl. 1, fig. 5), and the paratypes consist of two upper anterior teeth (pl. 1, fig. 1, 4), an upper lateral tooth (pl. 1, fig. 2), and a lower anterior tooth (pl. 1, fig. 3). Zhelezko and Kozlov (1999) also mentioned the presence of 100 additional teeth belonging to this taxon that were collected from the type locality, but unfortunately none of these specimens were figured and it is unclear whether they also reside within the State Darwin Museum collections.

In their brief description of *P. volgensis*, Zhelezko and Kozlov (1999) stated that the teeth have one to two pairs of conical lateral cusplets, a pronounced lingual root protuberance, pointed root lobes, a deep lingual nutritive groove, and a tall and triangular main cusp. An examination of their figured type specimens corroborates these remarks and also confirms that the *P. volgensis* morphology lacks enameloid plications along the labial crown foot. We considered the possibility that this characteristic was overlooked by the authors or simply not described or visible on the type specimens (pl. 1, figs 1–5), but Zhelezko and Kozlov (1999) prominently mentioned the occurrence of plications in their description of *P. rutoti*, and they are clearly visible on some of the *P. rutoti* teeth that they illustrated (pl. 36, figs 3b, 8b) alongside their *P. volgensis* specimens (pl. 36, figs 12–16). This leads us to believe that labial crown ornamentation is indeed absent on *P. volgensis* teeth, as the authors were clearly aware of this characteristic. Furthermore, the conical lateral cusplets of *P. volgensis* teeth as described by Zhelezko and Kozlov (1999) are a difficult characteristic to evaluate based on the figures they provided. However, their description, in combination with the lack of labial ornamentation, suggests that the specimens require further evaluation because they might not represent *Palaeohypotodus*.

If we consider *P. volgensis* a valid taxon, the figured type specimens are considerably different from teeth of *P. bizzocoi* sp. nov. Not only do *P. volgensis* teeth appear to lack labial plications along the crown base, but the main cusp on the upper lateral teeth has a much wider base than any of the upper lateral teeth of *P. bizzocoi* sp. nov. In addition, *P. volgensis* lateral teeth have wider and more triangular root lobes, and the root lobes are more pointed on the anterior teeth. In contrast, the root lobes on *P. bizzocoi* sp. nov. teeth are more even in width across their length, and they almost always have rounded basal extremities. Zhelezko and Kozlov (1999) also noted that the root lobes on *P. volgensis* teeth transition from rounded to flattened, whereas they are broadly rounded on all teeth of *P. bizzocoi* sp. nov. Furthermore, Zhelezko and Kozlov (1999) described the lateral cusplets on *P. volgensis* teeth as conical, which could mean that cutting edges are absent. If true, this feature provides additional evidence that *P. volgensis* and *P. bizzocoi* sp. nov. are not conspecific. Lastly, Zhelezko and Kozlov (1999, pl. 36, fig. 16e) showed an interesting characteristic on *P. volgensis* teeth where, in apical view, the crown exhibits conspicuous mesial and distal constrictions between the main cusp and lateral cusplets. This subtle characteristic is absent on all *P. bizzocoi* sp. nov. teeth.

Stratigraphic and geographic distribution of *Palaeohypotodus bizzocoi* sp. nov.

Although not exhaustive, our review of *Palaeohypotodus* has provided us with a number of morphological characteristics that can be used to differentiate the various species, as well as the means to determine the stratigraphic and paleogeographic range of *P. bizzocoi* sp. nov. The 34 *P. bizzocoi* sp. nov. teeth in our sample (i.e., 17 associated with GSA–V447 and 17 isolated teeth) were collected from four counties in Alabama (Butler, Dallas, Lowndes, and Wilcox counties) and one in Arkansas (Hot Spring County). To determine whether the range of *P. bizzocoi* sp. nov. extends beyond what our sample can elucidate, we examined the published literature for other Paleocene occurrences of *Palaeohypotodus* in Alabama, the Gulf Coastal Plain, and elsewhere in the USA.

Of Alabama occurrences, White (1956), who was later referenced by Thurmond and Jones (1981), reported a tooth identified as *Odontaspis* cf. *rutoti* from the Bartonian Gosport Sand in Clarke County, Alabama. White (1956, p. 148) described this tooth as resembling a lower posterolateral tooth of *Otodus rutoti* (=*Palaeohypotodus rutoti*), but his assignment to the species was tentative because the tooth appeared atypical when compared to those figured by Winkler (1874). Although White (1956) mentioned the presence of fine “puckering” along the labial crown base, he unfortunately did not figure his specimen and we therefore could not confirm its identity. However, no *Palaeohypotodus* specimens were identified by Ebersole et al. (2019) during their extensive study of lower-to-middle Eocene fishes of Alabama, which included the examination of more than 6,000 teeth derived from the Gosport Sand. This leads us to believe that the tooth reported by White (1956), and Thurmond and Jones (1981) was misidentified, and the only confirmed occurrence of *Palaeohypotodus* in Alabama is that of *P. bizzocoi* sp. nov. reported herein.

Within the Gulf Coastal Plain of the USA, Maisch et al. (2020, figs 8f–m, 12m) figured nine teeth as “*Palaeohypotodus rutori* [sic]” that were derived from the lower Clayton Formation in Hot Spring County, Arkansas. Of these teeth, the morphology of the teeth illustrated in figs 8h–i and 12m appear better aligned with *Odontaspis* rather than *Palaeohypotodus*, and those figured in fig. 8f, j–n are not well enough preserved to be properly evaluated. Furthermore, the posterior teeth figured in fig. 8j–n have wider and fewer cusplets than those illustrated for *P. rutoti* (see Herman 1972, pl. 2, figs 1–3, 5; Herman 1977, pl. 10, fig. 3e; Cappetta 2012, fig. 192h–j), and the main cusp on the anterior tooth figured in 8f is too narrow and gracile compared to the wide and robust main cusp of typical *Palaeohypotodus* teeth. It is likely these teeth belong to a genus, or genera, other than *Palaeohypotodus*. However, one tooth having a robust main cusp and two pairs of lateral cusplets was figured by these authors (fig. 8g) and morphologically it falls within the range of *P. bizzocoi* sp. nov. The small size of this tooth (1.5 cm), coupled with the extended mesial root lobe and double pair of cusplets, suggests it is an upper third anterior tooth of a juvenile *P. bizzocoi* sp. nov. individual. This tooth, along with specimen MMNS VP–8578, demonstrates the occurrence of this taxon in the Danian of Arkansas. As far as we are aware, the Alabama and Arkansas occurrences of *Palaeohypotodus* represent the only verified accounts of this genus within the entirety of the Gulf Coastal Plain of the USA.

Within Paleocene deposits from elsewhere in the USA, Ward and Wiest (1990) included *P. rutoti* in their list of elasmobranch taxa occurring in Maryland and Virgina. The authors did not figure these specimens and we could not confirm their identity. Cvancara and Hoganson (1993) reported 13 teeth derived from the Danian Cannonball Formation in North Dakota that they referred to *P. rutoti*. They noted the teeth approach nearly 3 cm in height, have two (sometimes three) pairs of large lateral cusplets, and labial plications occur at the crown foot. The cusplets were described as being “conical” but complete cutting edges were clearly visible. In their discussion of the material, Cvancara and Hoganson (1993) expressed their opinion that teeth of *P. bronni* and *P. rutoti* were indistinguishable and they therefore referred the Cannonball Formation teeth to the latter taxon. However, the tooth they illustrated (fig. 3mm–nn) which appears to be an upper lateral tooth, has large, triangular lateral cusplets and shallow interlobe area (19% the height of the tooth) that morphologically falls outside of *P. bizzocoi* sp. nov., *P. rutoti*, and *P. volgensis*. The Cannonball Formation material should be reevaluated using the criteria highlighted herein because the teeth would represent the first verified occurrence of *Palaeohypotodus* in North America and potentially a new species.

Case (1996) referred 24 teeth derived from the Danian part of the Hornerstown Formation in Monmouth County, New Jersey to *P. rutoti*. He illustrated six of these teeth (Case 1996, pl. 2, figs 1–6), all of which have extremely straight, narrow, conical, and needle-like lateral cusplets. The cusplets on some of these teeth (i.e., figs 2, 5, 6) are rather tall with respect to the height of the main cusp when compared to the teeth of *Palaeohypotodus* spp., and these particular specimens are similar to those of extant *Odontaspis* and likely belong to a Paleocene representative of this latter genus. Lastly, Purdy (1998) reported *Odontaspis rutoti* from a temporally mixed Paleocene locality in Berkley County, South Carolina. Unfortunately, the precise stratigraphic provenience of his material cannot be ascertained, as the entirety of the Williamsburg Formation (Danian to Thanetian) was exposed. However, as his figured specimens (fig. 3) possess lateral cusplets that are taller and more robust than those of *P. bizzocoi* sp. nov. and the interlobe area is shallower, referral of these teeth to *P. rutoti* appears to be appropriate.

The temporal and stratigraphic occurrences noted above establish that *P. bizzocoi* sp. nov. had a paleogeographic range that extended across the northern Gulf Coastal Plain of the USA, at least between Alabama and Arkansas. Future work may yield additional records of the taxon in other northern Gulf states, like Mississippi, Louisiana, and eastern Texas. The occurrence of *P. bizzocoi* sp. nov. is at present confined to three lithostratigraphic units that all date to the Danian Stage (zones NP2–4) of the Paleocene, including the lower Clayton Formation, Pine Barren Member of the Clayton Formation, and the Porters Creek Formation. The occurrence of this taxon within the lowermost Danian units in Alabama and Arkansas (the Pine Barren Member of the Clayton Formation and the equivalent lower beds of the Clayton Formation, respectively) establishes that this taxon was present in the Gulf Coastal Plain of the USA shortly after the K/Pg extinction event. Furthermore, the absence of the species from any Maastrichtian deposits in the region (see Ikejiri et al. 2013) indicates a first occurrence within the lower-most Paleocene. Additionally, the occurrence of *P. bizzocoi* sp. nov. within the upper Danian Porters Creek Formation demonstrates that this species persisted within this region throughout the entirety of the stage. The earliest stratigraphic occurrence of this taxon is well-defined, but its vertical stratigraphic extent is presently unknown due to the lack of systematic vertebrate paleontology work in local Selandian and Thanetian units like the Naheola Formation, Nanafalia Formation, and Tuscahoma Sand.

Familial placement of *Palaeohypotodus*

When *P. bronni* and *P. rutoti* were originally named by Agassiz (1843) and Winkler (1874), respectively, both were assigned to the genus *Otodus*. Vincent (1876) later contended that the *rutoti* morphology was similar to teeth of extant *Odontaspis* and utilized this generic name for the species. Although Daimeries (1888) followed Vincent (1876) in the use of *Odontaspis rutoti*, he also noted differences between these teeth and other species assigned to the genus at the time, namely the presence of labial vertical ridges and the greater number of lateral cusplets on the former. A review of the historical literature indicates that both the *bronni* and *rutoti* morphologies were consistently placed within *Odontaspis*, and by extension, within the family Odontaspididae, until Glückman (1964) erected the name *Palaeohypotodus* to include these species. Aside from the occasional usage of *Odontaspis* for these teeth (i.e., Purdy 1998), the *rutoti* and *bronni* morphologies were predominantly assigned to *Palaeohypotodus*, prompting Zhelezko and Kozlov (1999) to assign their *volgensis* morphology to this genus.

In addition to placing the *rutoti* and *bronni* morphologies within *Palaeohypotodus*, Glückman (1964) erected the family Jaekelotodontidae to accommodate this genus as well as *Hypotodus*, *Jaekelotodus*, and *Anotodus*. Glückman (1964) argued that a new family was warranted for these genera because they all had one to three pairs of lateral cusplets, mesiodistally expanded cusps on the upper lateral teeth, elongated root lobes, and they lacked the elongated anterior tooth morphology typical of other members of the Odontaspididae. However, due to dental similarities and the lack of lateral cusplets on *Anotodus*, this taxon was subsequently reassigned to the Alopiidae (Herman 1979; Cappetta 2012). Zhelezko (1994) later expanded the Jaekelodontidae to include *Mennerotodus*, but reconstructions of the dentition of the genus (Cicimurri et al. 2020) show that this taxon is more appropriately referred to the Carchariidae.

Although Glückman (1964) erected the family Jaekelotodontidae to include *Palaeohypotodus*, many subsequent authors continued to place the genus within Odontaspididae (i.e., Cappetta 1987; Cappetta and Nolf 2005; Iserbyt and De Schutter 2012). However, assignment of the genus to Odontaspididae has recently become problematical because of the reintroduction of the family Carchariidae by Shimada et al. (2015) and Stone and Shimada (2019). The latter authors used skeletal data to conduct a phylogenetic analysis of extant "sandtiger" sharks that ultimately corroborated paraphyly within Odontaspididae, which classically included *Odontaspis* and *Carcharias taurus*. The use of Carchariidae is supported to include extant *C. taurus*, whereas Odontaspididae contains only the genus *Odontaspis*. Unfortunately, the application of these family names to fossil species was not addressed by Stone and Shimada (2019), and determining the familial placement of an extinct species is tentative without the aid of associated skeletal material, which is largely lacking for extinct taxa. For example, the Cretaceous tooth morphology *amonensis* was variously assigned to *Odontaspis* (Cappetta & Case, 1975) and *Carcharias* (Cicimurri, 2001), but discovery of a partial skeleton allowed researchers to assign the species to a new genus and determine that it belonged to a new family, Haimrichiidae Vullo et al., 2016.

Although the familial placement of *Palaeohypotodus* has heretofore remained unresolved, it may be elucidated when the suite of teeth we herein assign to *P. bizzocoi* sp. nov., along with other *Palaeohypotodus* teeth reported elsewhere in the literature, are taken into account. For example, Van de Geyn (1937, fig. 118) and Casier (1942, pl. 1, fig. 2) figured upper third anterior teeth for *P. bronni* and *P. rutoti*, respectively, that are very similar to a tooth we assign herein to *P. bizzocoi* sp. nov. (MSC 49452, Fig. 7z–cc). All of these teeth have a distinct combination of an elongated mesial root lobe and a distal cutting edge that is more convex than the mesial edge, which compares more favorably to some teeth in dentitions of extant *C. taurus* rather than *Odontaspis ferox*, suggesting *Palaeohypotodus* is more closely allied with Carchariidae than to Odontaspididae. However, the occurrence of up to three pairs of lateral cusplets on *Palaeohypotodus* teeth is more consistent with teeth of extant *Odontaspis ferox* teeth (which can have one to three pairs), as opposed to *C. taurus* teeth that generally have only a single pair.

Our comparison of *P. bizzocoi* sp. nov., *P. bronni*, and *P. rutoti* teeth to those of extant lamniform sharks revealed similarities between the fossil taxa and both *C. taurus* and *O. ferox*. However, these extant taxa lack both the mesiodistally wide and laterally hooked upper lateral tooth morphology and enameloid plications along the labial crown base, features that have been regarded as characteristic of *Palaeohypotodus* (Herman 1977: 299). Furthermore, the distinct upper lateral tooth crown morphology of *Palaeohypotodus* is comparable to the condition of *Hypotodus* and *Jaekelotodus* (as is the dentition as a whole), suggesting that these taxa are likely closely related (as was suggested by Glückman 1964). The teeth of *Palaeohypotodus*, *Hypotodus*, and *Jaekelotodus* appear to exhibit a combination of features occurring in both Carchariidae and Odontaspididae, and there is no unequivocal modern familial analogue to assign these genera. The dentition of *Palaeohypotodus* spp. also appears to have a condition not present in extant lamniforms, where the upper teeth have complete cutting edges, whereas those in the lower files are incomplete. This characteristic, along with the evidence stated for the other genera indicates that teeth of *Palaeohypotodus*, *Hypotodus*, and *Jaekelotodus* represent an extinct type of lamniform dentition, and we find it appropriate to assign these genera to their own family and herein follow Glückman (1964) by utilizing Jaekelodontidae.

Conclusions

Our analysis of 34 shark teeth derived from lower Paleocene (Danian) deposits in Alabama and Arkansas, USA, has led to the discovery of a new species, *Palaeohypotodus bizzocoi*, sp. nov. Along with two other previously described members of this genus, *P. bronni* and *P. rutoti*, these species are united by the occurrence of teeth with one to three pairs of lateral cusplets, enameloid plications along the labial crown base, triangular and distally curved crowns on upper lateral teeth, distinct upper third lateral teeth with elongated mesial root lobe, pronounced lingual root protuberance with deep nutritive groove, and U-shaped interlobe area. A fourth species, *P. volgensis*, is known only by the type specimens. However, the lack of labial plications and the purported conical lateral cusplets on this taxon suggest that it may belong to a different genus. The tooth crowns of *Palaeohypotodus*, *Hypotodus*, and *Jaekelotodus* are similar, and their dental arrangements are comparable to one other, but also dissimilar to those of any extant lamniform sharks. Thus, we resurrect the family Jaekelodontidae Glückman 1964 to accommodate these extinct genera.

Our diagnosis of *P. bizzocoi* sp. nov. was largely based on comparisons with extant lamniform jaw sets and fossil *Palaeohypotodus* specimens derived from, or near to, the type localities for *P. bronni*, *P. rutoti*, and *P. volgensis*. However, our analysis was restricted to these particular occurrences and specimens reported from outside of the type strata/localities should be reevaluated. Our analysis has shed new light on the dental morphology of *Palaeohypotodus* and the various types of heterodonty occurring within the genus (i.e., monognathic, dignathic, ontogenetic), and future reexamination of reported specimens will allow for a better understanding of the stratigraphic and paleobiogeographic ranges of each of the species. For example, *P. rutoti* has been reported from various globally disparate localities (see Cappetta 2012) from deposits ranging in age from the lower Paleocene (Purdy 1998) to upper Eocene (Otero and Soto-Acuña 2015). It would seem unlikely that all of these occurrences represent *P. rutoti*, and our recognition of *P. bizzocoi* sp. nov. indicates a likelihood that the genus was more diverse during the Paleogene than is currently recognized.

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