

## Article

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# Obruchevodid petalodonts (Chondrichthyes, Petalodontiformes, Obruchevodidae) from the Middle Mississippian (Viséan) Joppa Member of the Ste. Genevieve Formation at Mammoth Cave National Park, Kentucky U.S.A.

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## Abstract

Obruchevodid petalodonts are rare small chondrichthyans known from nearly complete to partial skeletons from the Upper Mississippian (Serpukhovian) Bear Gulch Limestone of central Montana and isolated teeth from the Upper Mississippian Bangor Limestone of northern Alabama. New records of obruchevodid petalodonts are presented here from the Middle Mississippian (Viséan) Joppa Member of the Ste. Genevieve Formation at Mammoth Cave National Park, Kentucky. Obruchevodids are here represented by multiple teeth of a new taxon, *Clavusodens mcginnisi* n. gen. n. sp., and a single tooth referred to ?*Netsepoye* sp. *Clavusodens mcginnisi* n. gen. n. sp. is characterized by teeth with pointed mesiodistal and lingual margins and more robust chisel-like cusps on the anterolateral and distolateral teeth. The suggestion that obruchevodid petalodonts evolved to inhabit complex reef-like environments and other nearshore habitats with a feeding ecology analogous to extant triggerfish is explored and discussed.

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## Non-technical Summary

New records of two species of obruchevodid petalodont chondrichthyans are described from the Middle Mississippian Joppa Member of the Ste. Genevieve Formation from Mammoth Cave National Park, Kentucky. The two species are *Clavusodens mcginnisi* new genus new species, which had more robust crushing-type teeth for its kind, and ?*Netsepoye* sp., which is based on a partial tooth. These two records represent the oldest known obruchevodid petalodonts, which previously were known from younger Mississippian-age rocks in Montana and Alabama. Obruchevodid petalodonts were among the most specialized cartilaginous fishes during the Mississippian, potentially adapted to live in complex reef and reef-like habitats.

## Introduction

The Carboniferous–Permian chondrichthyan order Petalodontiformes, or “petal-toothed sharks,” was a globally distributed and diverse group of cartilaginous fishes. Most early work on petalodonts was restricted to isolated or partial associated dentitions (Newberry and Worthen, 1866; St. John and Worthen, 1875; Davis, 1883; Hansen, 1985; Ginter et al., 2010). More complete skeletal materials of the Late Mississippian petalodonts *Belantsea montana* Lund, 1989, *Netsepoye hawesi* Lund, 1989, and *Siksika ottae*, and the Permian petalodont *Janassa bituminosa* (Schlotheim, 1820) added better resolution on the diversity of body forms within Petalodontiformes (Jaekel, 1899; Schaumberg, 1979; Lund, 1989). Early work on petalodonts proposed that this order had close relationship ties with either elasmobranchs or holocephalans (Patterson, 1965; Zangerl, 1981; Hansen, 1985; Lund, 1989; Ginter et al., 2010). Recent work on more complete skeletal specimens suggested petalodonts may have had a sister relationship with crown holocephalans, united under the larger Euchondrocephali with eugonodonts, orodonts, and paraselachians (Grogan et al., 2014; Lund et al., 2014).

According to Lund et al. (2014) the Petalodontiformes is divided into two distinct groups characterized by either homodont dentitions or heterodont dentitions. The homodont petalodonts include two families, Belantseidae (*Belantsea*) and Petalodontidae (*Petalodus* and

*Polyrhizodus*), which have more simplified triangular-shaped crowns that only vary in size based on tooth-family position (Lund, 1983, 1989; Lund *et al.*, 2014). The heterodont petalodonts are currently known from three families: Janassidae (*Janassa*, *Strigilodus*, *Cholodus*, *Cypripediodens*, and *Cavusodus*), Petalorhynchidae (*Petalorhynchus*), and Obruchevididae (Lund *et al.*, 2014; Hodnett *et al.*, 2023). The obruchevidid petalodonts are of interest here, as they are considered to be the most heterodont petalodonts currently known.

**Mississippian obruchevidid petalodonts.** Obruchevididae was recognized by Lund *et al.* (2014) as a unique group of small dignathic heterodont petalodonts that included the taxa *Obruchevodus griffithi* Grogan, Lund, and Fath, 2014, *Netsepoye hawesi*, and *Fissodopsis robustus* Lund, Grogan, and Fath, 2014 (Fig. 1). These taxa share dentitions with a bifid *Fissodus*-like lower symphyseal tooth, a single-cusped upper symphyseal tooth, *Ctenoptychius*-like anterolateral teeth, and *Janassa*-like posterolateral teeth (Grogan *et al.*, 2014; Lund *et al.*, 2014; Fig. 1.3, 1.7). Both *Netsepoye* and *Obruchevodus* are represented by nearly complete body fossils showing they had relatively dorsoventrally deep and laterally compressed bodies, triangular heads with anteroventral mouths, males with large barbed denticles on the labial cartilage, enlarged pectoral fins with anterior barbed denticles, small dorsal fins, and males with relatively small pelvic fins with elongate claspers (Lund, 1989; Grogan *et al.*, 2014; Fig. 1.1, 1.4). All three taxa were initially only known from the Late Mississippian (Serpukhovian) Bear Gulch Limestone of the Heath Formation in central Montana. However, recently *N. hawesi* (Fig. 1.2) and *F. robustus* (Fig. 1.5, 1.6) have been identified from isolated symphyseal teeth from the Late Mississippian Bangor Limestone in northern Alabama (Egli *et al.*, 2024). Here we report a new record of Middle Mississippian (Viséan) obruchevidid petalodonts from Mammoth Cave National Park, Kentucky found during National Park Service paleontological resource inventory work.

### Geologic setting

The Mississippian strata found at Mammoth Cave National Park in central Kentucky (Fig. 2.1) represent one of the southeasternmost portions of the ancient marine Illinois Basin (Fig. 2.2) (Palmer, 1981). The Illinois Basin is historically significant to early American paleoichthyology because a large number of middle to late Paleozoic fish fossils were collected and described from this basin in states such as Missouri, Illinois, Iowa, and Indiana (Newberry and Worthen, 1866, 1870; St. John and Worthen, 1875, 1883). At the time, these early collections were widely compared with similar fossils from Europe, which formed the basis for modern Paleozoic chondrichthyan paleoichthyology. The petalodont fossils presented here were collected from passageways within Mammoth Cave National Park, Kentucky that cut through the Middle Mississippian Joppa Member of the Ste. Genevieve Formation.

The Ste. Genevieve Formation stratigraphically overlies the St. Louis Formation and is recognized as Viséan/lower Chesterian (Thompson, 2001). The Ste. Genevieve Formation is locally 360–394 m thick and the majority of the passages of the Mammoth Cave System are developed in this formation (Palmer, 1981). This horizon consists primarily of light gray limestones and dolomitic limestones, with alternating thin dark, silty, granular limestones in the upper beds (Palmer, 1981). The large

number of cave passages cutting through the Ste. Genevieve Formation has led to well-exposed fossils and fossil-bearing beds containing a prolific fossil record.

The Joppa Member of the Ste. Genevieve Formation at Mammoth Cave contains several biostrome beds rich with corals, bryozoans, brachiopods, and echinoderms (mainly crinoids and blastoids), separated by somewhat less fossiliferous zones (Fig. 2.3). These biostrome deposits are interpreted as a crinoidal “forest” that would have supported trophic feeding niches for a variety of Middle Mississippian fishes (Hodnett *et al.*, 2024a). Isolated chondrichthyan teeth, dermal spines, and denticles are common within multiple horizons of the Joppa Member at Mammoth Cave and isolated to partially articulated skeletal cartilage occurs as well. At present, more than 70 fish taxa have been identified from this geologic horizon (Hodnett *et al.*, 2024a), including the type specimens of the ctenacanth *Troglocladodus trimblei* Hodnett *et al.*, 2024b, and *Glikmanius careforum* Hodnett *et al.*, 2024b, and the janassid petalodont *Strigilodus tollersonae* Hodnett *et al.*, 2023.

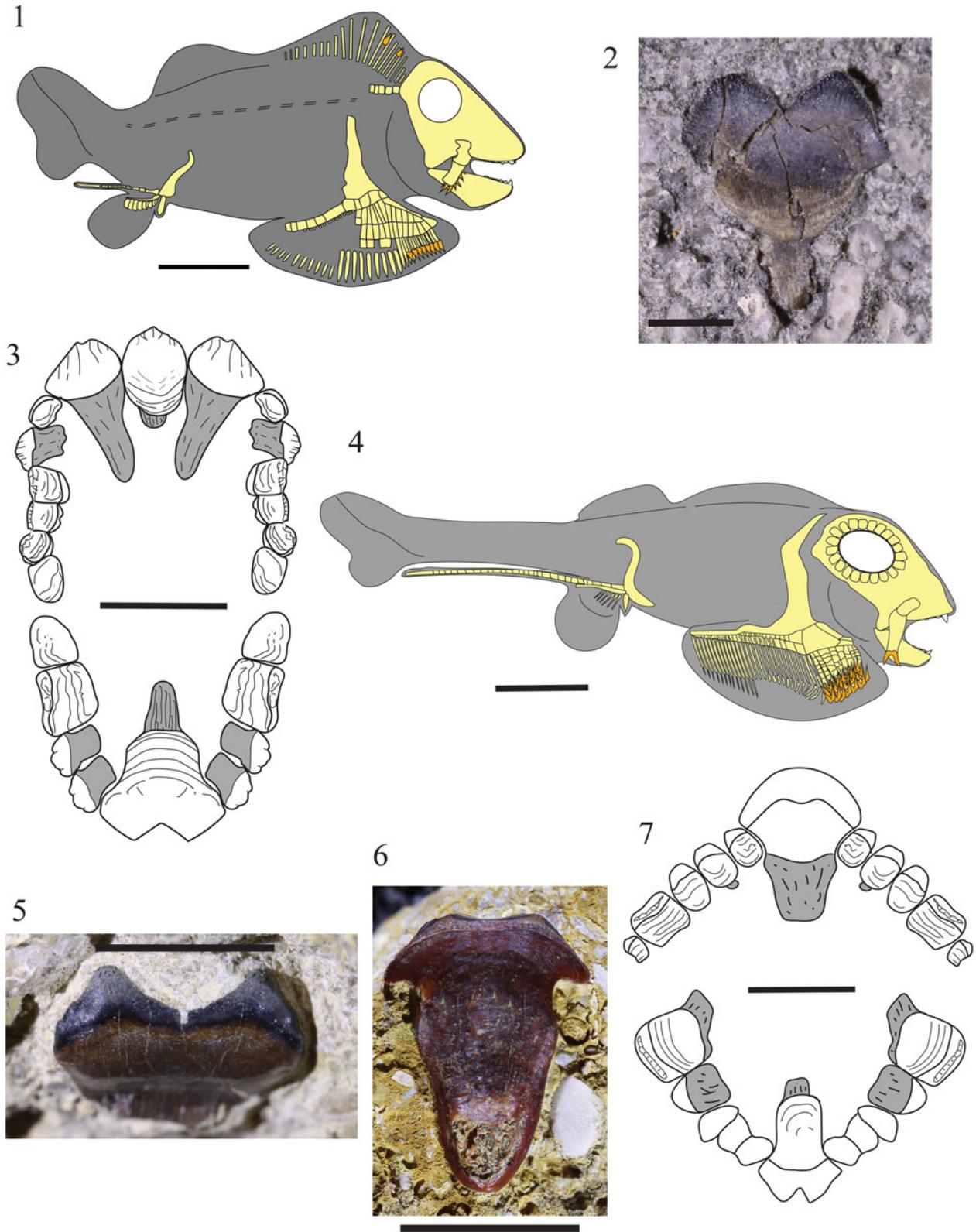
### Materials and methods

Field work for the Mammoth Cave National Park Paleontological Resource Inventory (PRI) commenced in November 2019. At present, more than 25 caves and cave passages have been surveyed fully or in part as part of a concentrated effort to document, collect, and identify Mississippian vertebrate fossils. Space in field packs limits the amount of collecting gear to what can be safely carried through cave passages. That limitation and cave passage size and shape make collecting a challenge in some passages. Some sites require a rock saw or hammer and chisel to remove specimens while limiting breakage; in other passages, specimens can easily be teased out of the cave surfaces with a pointed tool such as a dental pick. Many of these sites have low ceilings requiring crawling for long distances on hands and knees, and at times belly crawling. The fish fossils are frequently encountered in the cave ceilings or walls.

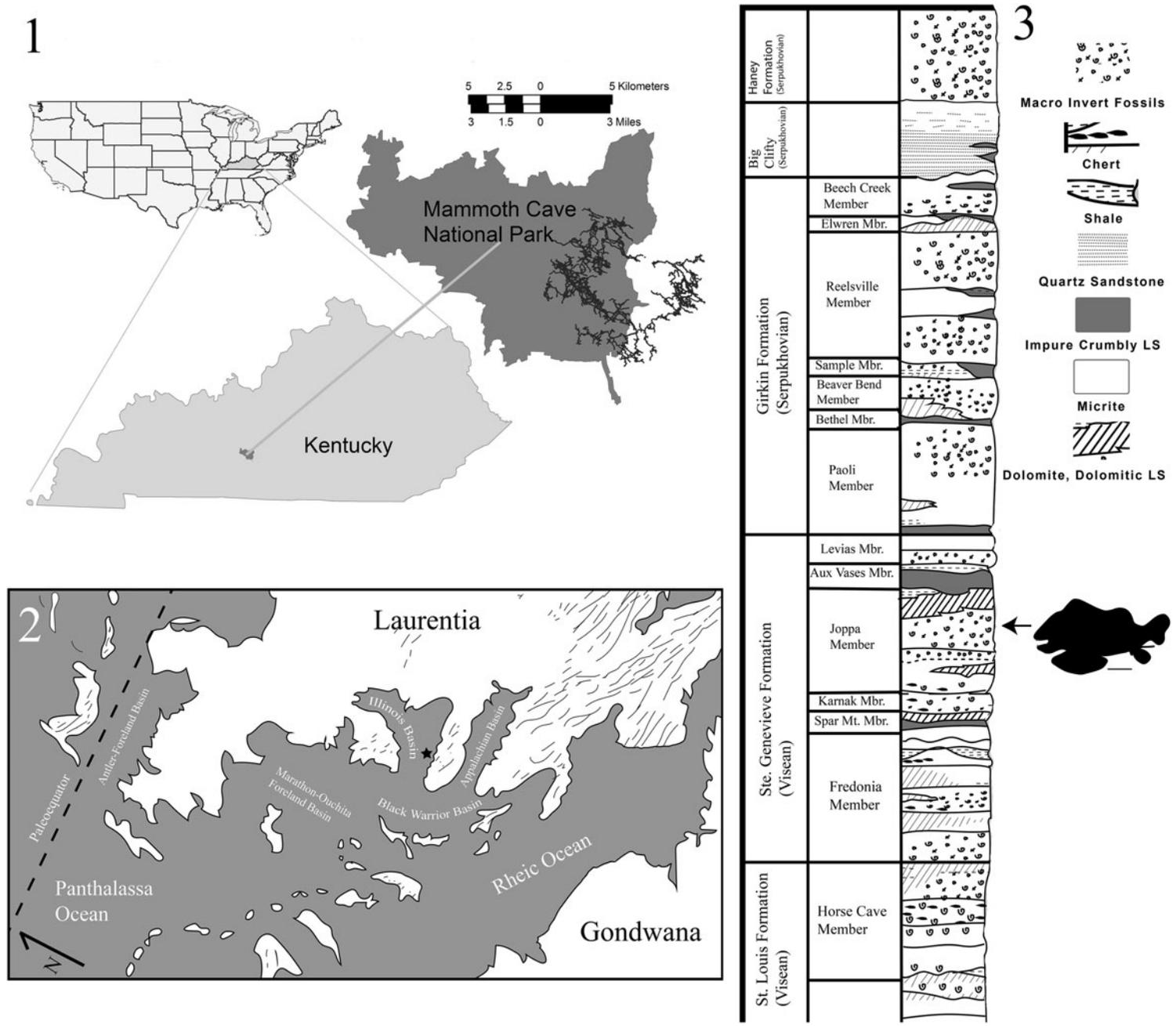
To protect the fossils for transport to the surface, each fossil is wrapped either in paper towel or toilet paper and placed in a hard-sided container. Screw-capped sampling tubes lined with cotton balls are used for collecting smaller fossil teeth. The primary method is to remove all but one cotton ball, carefully tease the fossil from the cave surface (often the cave ceiling) into the tube, place a cotton ball on top, and continue to the next specimen. This is repeated until the tube is full, and locality information is recorded on the tube. This method is extremely useful in areas where there is a high concentration of vertebrate fossils in a small area. All Mammoth Cave specimens are housed in the Mammoth Cave National Park Museum Collections.

Scanning electron microscopy was conducted at the Western Kentucky University Biology Department Electron Microscopy lab using a JEOL6510 LV scanning electron microscope. Photographs of the fossils presented here were captured with an AmScope camera mounted on a stereoscope microscope with a metric scale bar. Figures were created with Adobe Illustrator 2023 and Photoshop 2023.

**Repositories and institutional abbreviations.** ALMNH: Paleo: Alabama Museum of Natural History, Tuscaloosa, Alabama; CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MACA: Mammoth Cave National Park, Kentucky.



**Figure 1.** Late Mississippian obruchevodid petalodonts. (1–3) *Netsepoye hawesi*; (1) Reconstruction of the skeleton of *Netsepoye hawesi* based on holotype CM 46092 from the Heath Formation of Montana; (2) ALMNH:Paleo:20553, a lower symphyseal tooth of *N. hawesi* from the Bangor Limestone of northern Alabama; (3) revised reconstruction of the upper and lower dentition of *N. hawesi*. (4) Reconstruction of *Obruchevodus griffithi*, based on holotype CM 48833 from the Heath Formation of Montana. (5–7) *Fissodopsis robustus*: (5) ALMNH:Paleo:20556, upper symphyseal tooth; (6) ALMNH:Paleo:9774, partial lower symphyseal tooth; (7) revised reconstruction of the upper and lower dentition of *F. robustus* based on holotype CM 62710 from the Heath Formation of Montana. Scale bars: (1, 4) = 10 mm; (2, 5, 6) = 5 mm; (3) = 4 mm; (7) = 20 mm.



**Figure 2.** Location and stratigraphy of Mammoth Cave National Park, Kentucky. (1) Location of Mammoth Cave National Park in Kentucky; (2) relative paleogeographic position of Mammoth Cave National Park in the Illinois Marine Basin during the Middle Mississippian (Viséan) of Laurentia; (3) stratigraphic position of the obruchevodid petalodonts from the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave National Park, Kentucky.

## Systematic paleontology

Class **Chondrichthyes** Huxley, 1880

Subclass **Euchondrocephali** Lund and Grogan, 1997

Order **Petalodontiformes** Patterson, 1965

Family **Obruchevodidae** Lund, Grogan, and Fath, 2014

Genus **Clavusodens** new genus

*Type species.* *Clavusodens mcginnisi* n. gen. n. sp., this work.

*Diagnosis.* As for type species by monotypy.

*Occurrence.* Mammoth Cave National Park, Kentucky, Middle Mississippian (upper Viséan) Joppa Member, Ste. Genevieve Formation.

*Etymology.* Latin, *clavus* (nail), and *dents* (tooth); in recognition of the nail-like shape of the distal lateral teeth.

*Life Science Identifier.* [urn:lsid:zoobank.org:act:2A61340B-A18A-4422-9919-823A6FA98BA2](https://zoobank.org/act:2A61340B-A18A-4422-9919-823A6FA98BA2).

*Remarks.* See Comparison and remarks for *Clavusodens mcginnisi* n. gen. n. sp., below.

***Clavusodens mcginnisi* new species**

Figures 3, 4

*Holotype.* MACA 62284, a complete distolateral tooth (Fig. 3).

*Diagnosis.* Small obruchevodid petalodont shark with heterodont dentition bearing pointed mesiodistal and lingual margins on the crown. The upper symphyseal tooth is relatively tall, with rounded chisel-like cusp, lingual side with two minor lower lingual plications, and tooth base flat labiolingually and wide mesiodistally. The lower symphyseal tooth is relatively tall, the trenchant crown bifid with narrow pointed mesiodistal margins, the lingual surface with two slight mesiodistal basins between the crown and the lingual heel, the lingual heel bearing four slight shallowly u-shaped and well-spaced plications, and the tooth base long and narrow. Anterolateral teeth wider mesiodistally than tall, with relatively rounded shallow chisel-like cusps and lingual surface with two to six plications. Distolateral teeth wider mesiodistally than tall, crown bearing two short cusps or a single notched cusp, a small labial ridge present, lingual surface relatively flat with three to four lingual plications, and tooth base long and narrow.

*Occurrence.* Mammoth Cave National Park, Kentucky, Middle Mississippian (upper Viséan) Joppa Member, Ste. Genevieve Formation.

*Description.* Teeth range in labiolingual crown height from 6 to 7 millimeters. All teeth share relatively pointed mesiodistal and lingual margins of the crown over a tooth base that originates labially and is positioned above the lingual heel.

The upper symphyseal tooth (MACA 62285; Fig. 4.1–4.3) has a broad rhomboidal crown and an almost chisel-like cusp with a rounded carina. The lingual surface does not bear any evidence of a basin and has two slight plications near the lingual margin. The tooth base of the upper symphyseal tooth is flattened labiolingually and relatively broad mesiodistally with a number of small foramina on the labial and lingual surfaces.

The relatively sigmoidal lower symphyseal tooth (MACA 62339; Fig. 4.4–4.6) has a relatively tall crown with a trenchant bifid cusp. The small notch between the two short cusps is u-shaped. The lateral margins of the cusp are steeply angled and expanded mesiodistally. Two small lingual basins are present on the distal margins between the cusp and beginnings of the lingual heel. The lingual surface bears four slightly pronounced shallowly u-shaped plications that end at the pointed lingual heel. The long and narrow tooth base originates on the lower labial side of the tooth, positioned above the lingual heel.

The anterolateral teeth (MACA 62018 and 62264; Fig. 4.7–4.11) are mesiolaterally wider than tall and have a less expanded lingual heel. The crown is relatively ovate in shape and has a mesiodistally broad chisel-like cusp. Both samples show the lingual surface of the crown was relatively flat between the cusp and the lingual margin. We propose that MACA 62018 was most likely positioned closer to the symphyseal tooth position due to its higher cusp height and two lingual plications, compared to MACA 62264, which has a lower crown and six lingual plications.

The crowns of the distolateral teeth, MACA 62284 (holotype, Fig. 3) and MACA 62763 (Fig. 4.12–4.14), are generally ovate in shape, with a pointed lingual margin. There are two low cusps or a single low cusp with a distinct notch, with the mesial side being longer and more prominent than the distal side. A distinct labial ridge is present just below the cusp. The lingual surface is relatively flat between the cusp and three to four u-shaped plications. The peg-like tooth base is long and narrow, with a number of small foramina present on all sides of the base.

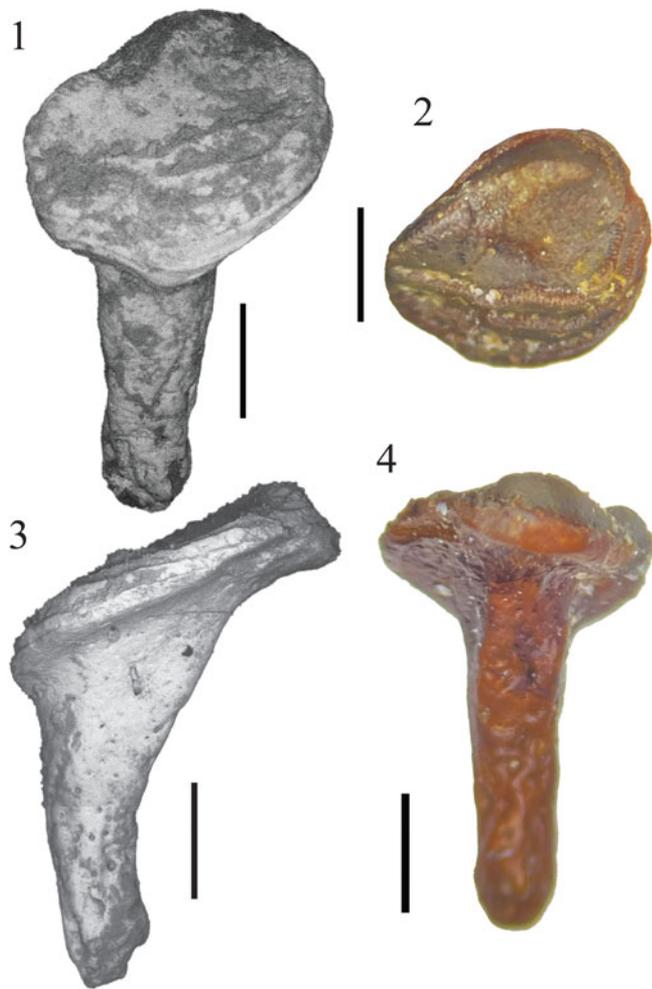
*Etymology.* In honor of retired National Park Service superintendent and naturalist David McGinnis for his leadership in paleontological resource stewardship during his 39-year career beginning at Mammoth Cave National Park.

*Additional material.* MACA 62018, anterolateral tooth; MACA 62264, anterolateral tooth; MACA 62285, upper symphyseal tooth; MACA 62339, lower symphyseal tooth; MACA 62763, distolateral tooth (Fig. 4).

*Life Science Identifier.* [urn:lsid:zoobank.org:act:A0D08023-C905-402E-8C00-1C8F0CE75FE2](https://zoobank.org/act:A0D08023-C905-402E-8C00-1C8F0CE75FE2).

*Comparison and remarks.* The teeth referred here to *Clavusodens mcginnisi* n. gen. n. sp. were found as isolated elements distributed throughout the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave National Park. However, these teeth are united as a distinct new taxon because all the teeth bear pointed mesiodistal and lingual margins on the crowns, while sharing the obruchevodid traits of a lower bifid symphyseal tooth with an elongated lingual heel, upper symphyseal tooth with a broad singular cusp, posterolateral teeth with broad crowns with low cusps, and a few u-shaped lingual plications (Lund, 1989; Grogan et al., 2014; Lund et al., 2014).

*Clavusodens* n. gen. shares a lower bifid symphyseal tooth with a relatively elongated lingual heel with obruchevodid petalodont genera such as *Netsepoye* and *Fissodopsis* (Lund, 1989; Grogan et al., 2014; Lund et al., 2014). The lower symphyseal tooth of the type specimen of *Obruchevodus griffithi* (CM 48833) is obscured by the upper symphyseal tooth and not available for comparison (Grogan et al., 2014). The lower symphyseal teeth of *Clavusodens* n. gen. and *Fissodopsis* differ from *Netsepoye* in having the crown, bifid notch, and lingual heel less expanded mesiodistally.



**Figure 3.** MACA 62284, the holotype (a complete distolateral tooth) of *Clavusodens mcginnisi* n. gen. n. sp. (1) Lingual view, (2) oral view, (3) mesial view, (4) labial view. Scale = 2 mm.

In comparison, *Clavusodens* n. gen. differs from *Fissodopsis* in having a shallow u-shaped bifid notch, more prominent pointed distal margins of the cusp, and a more expanded lingual heel with a pointed lingual margin. Other petalodonts with a bifid lower symphyseal tooth include *Siksika ottae*, “*Ctenoptychius*” (*Janassa*) *korni* (Weigelt, 1930), *Petalorhynchus beargulchensis* Lund, 1989, and *Fissodus bifidus* St. John and Worthen, 1875 (St. John and Worthen, 1875; Lund, 1989; Brandt, 1996; Lund *et al.*, 2014). *Clavusodens* n. gen. differs from *Siksika* in lacking prominent cusplets on the carina. The lower symphyseal teeth of *Petalorhynchus beargulchensis* and *Fissodus bifidus* are similar in having a more expanded upper portion to the lingual heel, forming a wedge-like shape, which is straight in this region in *Clavusodens* n. gen., *Netsepoye*, and *Fissodopsis*. In “*Ctenoptychius*” (*Janassa*) *korni*, the crown of the lower symphyseal tooth appears to be more rectangular in overall shape and bears an additional lateral cuspid with a less labiolingually expanded lingual heel (Brandt, 1996, 2009; Lund *et al.*, 2014).

The upper symphyseal tooth of *Clavusodens* n. gen. is similar to *Fissodopsis* in being more spoon-like in shape with a smooth carina, compared to the “blade-like” with cusplets morphology seen in *Netsepoye* and *Obruchevodus* (Lund, 1989; Grogan *et al.*, 2014; Lund *et al.*, 2014). However, *Fissodopsis* lacks the pointed

lingual heel seen in *Clavusodens* n. gen. The anterolateral teeth of *Clavusodens* n. gen. have more robust and thicker chisel-like carinae and lack cusplets, whereas the crowns are more blade-like and have prominent cusplets in *Netsepoye*, *Fissodopsis*, and *Obruchevodus* (Lund, 1989; Grogan *et al.*, 2014; Lund *et al.*, 2014). The posterolateral teeth of *Clavusodens* n. gen. also share broad crowns with low cusps and a few u-shaped lingual plications with *Netsepoye*, *Fissodopsis*, and *Obruchevodus* (Lund, 1989; Grogan *et al.*, 2014; Lund *et al.*, 2014). *Clavusodens* n. gen. is unique in having thicker chisel-like cusps lacking cusplets and a pointed lingual heel on the posterolateral teeth.

*Clavusodens* n. gen. and other obruchevodid petalodonts differ from members of the Petalodontidae (e.g., *Petalodus*, *Antilodus*, *Polyrhizodus*, etc.) and Belantseidae (*Belantsea*) in having heterodont dentitions consisting of a bifid lower symphyseal tooth and upper and lower molariform-like posterior teeth (Grogan *et al.*, 2014; Lund *et al.*, 2014). The lingual plications in Petalodontidae and Belantseidae tend to consist of thin closely spaced straight to u-shaped ridges, while in *Clavusodens* n. gen. and other obruchevodids the lingual plications are more widely spaced apart. Petalodontids, *Siksika*, and *Belantsea* all lack a well-defined lingual heel on the dentition, unlike what is seen in obruchevodids, janassids, and petalorhynchids, in which the lingual heel is prominent (Lund *et al.*, 2014). Janassid and petalorhynchid petalodonts have elongated lingual heels, with janassids having more numerous and closely spaced lingual plications and petalorhynchids having fewer and more widely spaced plications (Hodnett *et al.*, 2023). *Clavusodens* n. gen. and other obruchevodids have less elongate lingual heels and a smaller number of lingual plications.

#### Genus *Netsepoye* Lund, 1989

**Type species.** CM 46092 (holotype), *Netsepoye hawesi*, small nearly complete individual preserving jaws, body, and fins, in part and counterpart from the Upper Mississippian (Serpukhovian) Bear Gulch Limestone Member of the Heath Formation, Big Snowy Group, south of Becket, Fergus County, Montana (Lund, 1989).

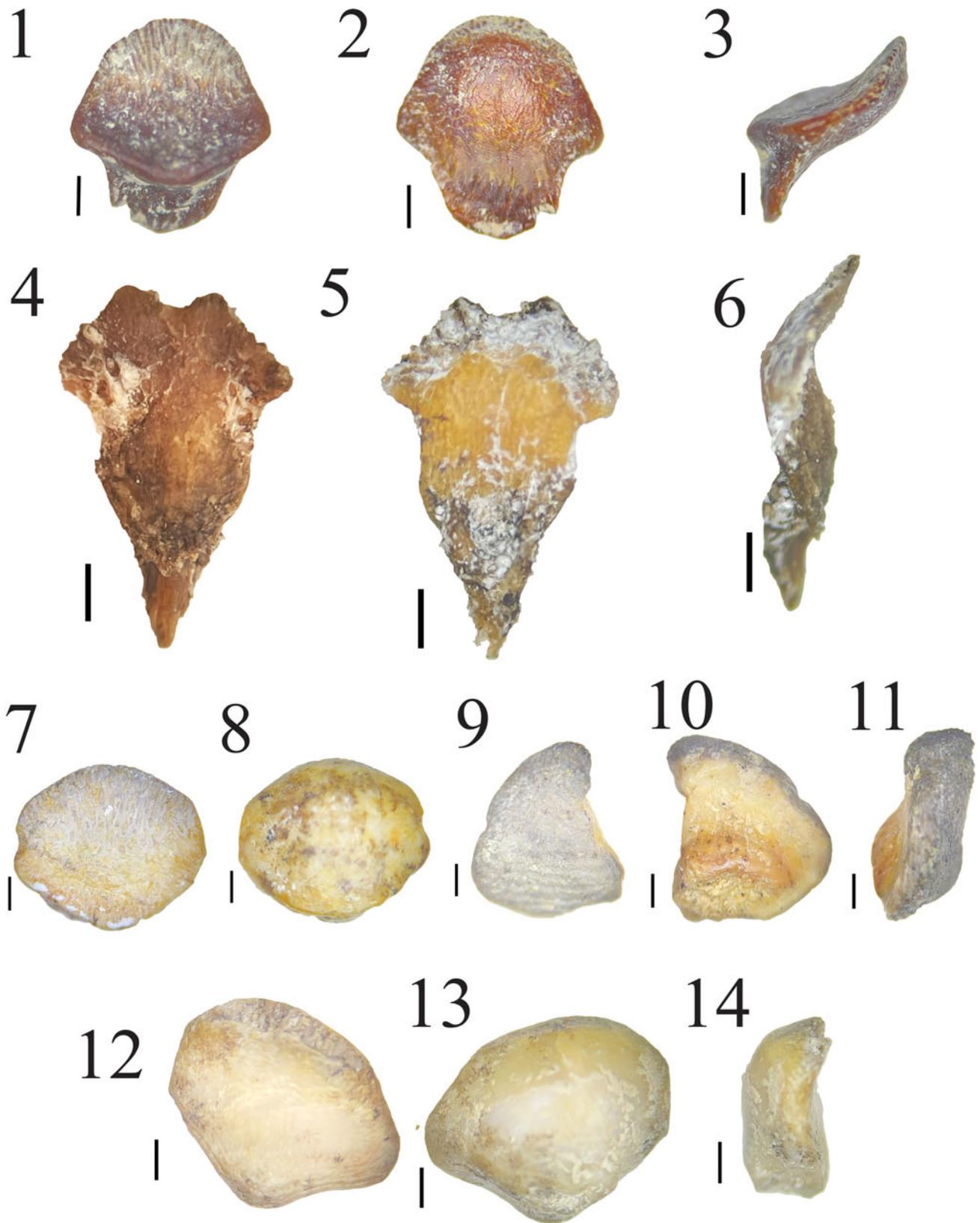
#### ?*Netsepoye* sp.

##### Figure 5

**Description.** A partial bifid lower symphyseal tooth missing the lingual shelf and tooth base, measuring approximately 5 mm mesiodistally wide and 3 mm tall as preserved (Fig. 5.). The two cuspid are low, divided by a relatively deep u-shape notch. The distal margins have small cusplets that extend up from the widest point of the crown to the cuspid point. The labial margin is recurved, and the lingual surface is convex.

**Materials.** MACA 65110, a partial lower symphyseal tooth.

**Remarks.** *Netsepoye hawesi* is based on a nearly complete skeleton with a damaged cranium, dentition, and much of the body and fins (Lund, 1989; Grogan *et al.*, 2014; Fig. 1.1). The lower symphyseal tooth of *N. hawesi* has a mesiodistally broad bifid cusp with a deep v-shaped notch between two triangular cuspid, and the lingual shelf is relatively broad with four to five u-shaped plications. The tooth base is long and narrow (Grogan *et al.*, 2014; Lund *et al.*, 2014). A similar symphyseal tooth (ALMNH:



**Figure 4.** Referred specimens of *Clavusodens mcginnisi* n. gen. n. sp. (1–3) MACA 62285, an upper symphyseal tooth in (1) lingual, (2) labial, and (3) distal views. (4–6) MACA 62339, a lower symphyseal tooth in (4) lingual, (5) labial, and (6) distal views. (7, 8) MACA 62018, an anterolateral tooth in (7) lingual, (8) labial views. (9–11) MACA 62264, an anterolateral tooth in (9) lingual, (10) aboral, and (11) distal views. (12–14) MACA 62763, a distolateral tooth in (12) orolingual, (13) aboral, and (14) mesial views. Scale = 1 mm.



**Figure 5.** MACA 65110, the partial lower symphyseal of ?*Netsepoye* sp., in (1) lingual and (2) labial views. Scale = 1 mm.

Paleo:20553; Fig. 1.2) has been uncovered from the Late Mississippian Bangor Limestone in northern Alabama, marking the first record of *N. hawesi* outside of the Bear Gulch Limestone in Montana (Egli *et al.*, 2024).

We tentatively refer MACA 65110 to the genus *Netsepoye* due to its similarly mesiodistally wide bifid cusp (Lund *et al.*, 2014). Like *Netsepoye*, this specimen also has relatively broad cusps and a broad notch between the two (Grogan *et al.*, 2014; Lund *et al.*, 2014). However, the presence of small cusplets along the distal margins of the crown and the low u-shaped form of the notch between the two cusps differ from the type specimen and the Bangor specimen, both of which lack distal cusplets and have a deep v-shaped notch between the cusps. Small cusplets are also present on the symphyseal and lateral dentition of the petalodonts *Siksika ottae*, *Belantsea montana*, *Obruchevodus griffithi*, and *Fissodopsis robustus* (Lund, 1989; Grogan *et al.*, 2014; Lund *et al.*, 2014); however, the general morphology of the crown in the Mammoth Cave specimen is most similar to *Netsepoye*.

### Discussion and conclusions

The presence of the small obruchevoidid petalodonts *Clavusodens mcginnisi* n. gen. n. sp. and ?*Netsepoye* sp. within the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave National Park, Kentucky, previously known only from the Late Mississippian (Serpukhovian) (Lund, 1989; Grogan *et al.*, 2014; Lund *et al.*, 2014; Egli *et al.*, 2024), extends the temporal record of obruchevoidid petalodonts into the Middle Mississippian (Viséan). These taxa also add to the growing chondrichthyan assemblage of the Joppa Member of the Ste. Genevieve Formation, which already shows a high degree of diversity with at least 70 taxa reported (Hodnett *et al.*, 2023, 2024a, b). At Mammoth Cave, petalodont teeth are generally common, with Hodnett *et al.* (2023, 2024a) reporting at least 11 species of petalodontiforms from the Joppa Member of the Ste. Genevieve Formation: *Petalodus hastingsii* Owen, 1840, *P. linguifer* Newberry and Worthen, 1866, “*Petalodus* sp. nov.”, “? *Petalodus* sp.”, *Antilodus* sp., “? *Lisgodus* sp.”, *Harpacodus* sp., *Strigilodus tollesonae*, *Janassa* sp., *Petalorhynchus* cf. *P. spatulatus* St. John and Worthen, 1875, and *Petalorhynchus* sp. Of these 11 petalodont taxa, *Petalodus linguifer*, “? *Lisgodus* sp.”,

*Strigilodus tollesonae*, and *Petalorhynchus* cf. *P. spatulatus* are common (10 or more specimens per passage locality) throughout the Joppa Member, with the other taxa represented by a few or a single specimen. The obruchevoidid petalodonts *Clavusodens mcginnisi* n. gen. n. sp. and *Netsepoye* sp. are rare within the Joppa Member interval in Mammoth Cave, which reflects their rarity in the Late Mississippian Bear Gulch and northern Alabama localities as well. Although there are at least three genera of obruchevoidid petalodonts, two of which (*Netsepoye* and *Obruchevodus*) are known from significant body fossils, all are known only from single specimens within the Bear Gulch Limestone (Grogan *et al.*, 2014; Lund *et al.*, 2014). This rarity is also seen in the Bangor Limestone localities in northern Alabama, where only a few isolated teeth of *Fissodopsis robustus* are known from one locality and a single *Netsepoye hawesi* tooth is known from another (Egli *et al.*, 2024).

One explanation for this rarity is that obruchevoidid petalodonts were highly specialized to live in complex environments and potentially did not have large population numbers in a given locality. Lund *et al.* (2015) noted this in their overview of chondrichthyans and osteichthyans from the Bear Gulch Limestone in which they classified fishes with compressed deep bodies and sub-terminal mouths in their E6 ecomorphotype, which includes the obruchevoidids and other petalodonts and some types of actinopterygians. These taxa had plucking--crushing dentitions interpreted as having been used to feed within the dynamic environments of tropical reefs (Sale, 1977). Lund *et al.* (2015) further suggested that obruchevoidid petalodonts had dentitions analogous to extant triggerfish (Tetradontiformes, Balistidae), which are non-gregarious actinopterygians that live in shallow waters (sea surface to 50 m depth), particularly around tropical reefs, and are known to feed on echinoderms, crustaceans, and mollusks (Wainwright and Richard, 1995; Matsuura, 2015; McCord and Westneat, 2016). Lund *et al.* (2015) noted that the environment in which the majority of petalodonts were collected from the Bear Gulch Limestone represented the lower reaches of the muddy Bear Gulch Bay. This has been interpreted as the most complex of habitats within the Bear Gulch Bay system, with a high number of E6 ecomorphotype fishes (Grogan and Lund, 2002; Lund

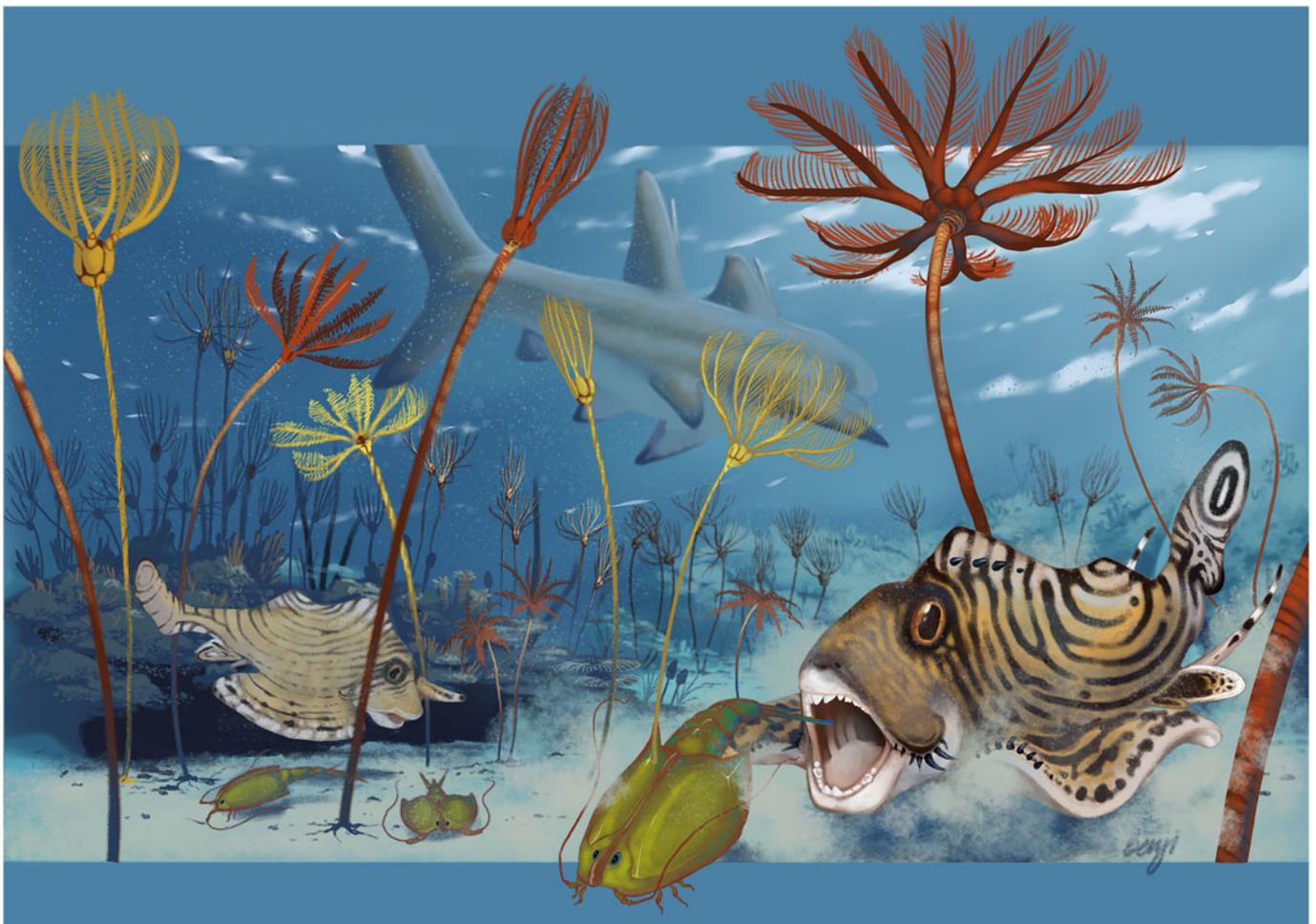
et al., 2015). Although obruchevoid petalodonts appear to be rare, the invertebrate-dominated biostrome and bioherm reef beds of the Joppa Member of the Ste. Genevieve Formation and Bangor Limestone may have been more favorable environments for obruchevoid petalodonts, based on the greater number of individual specimens collected in these geologic horizons. As noted above, the Joppa Member of the Ste. Genevieve Formation is a biostrome deposit formed from skeletal fragments derived from horn corals, tabulate corals, brachiopods, blastoids, and crinoids, contributing to the crinoidal “forest” habitat for the Joppa petalodonts.

Petalodonts are often described and depicted as feeding on hard-shelled invertebrates (Janvier, 1996; Ginter et al., 2010). Unfortunately, little work has been done on tooth biomechanics in relation to prey choice in petalodonts. Most current work on the relationship of chondrichthyan teeth to prey selection has been focused on the biomechanics of elasmobranch and elasmobranch-like shark teeth in relation to prey types (Whitenack et al., 2011; Cooper et al., 2023). The variation in the heterodont and homodont dentitions seen in obruchevoid petalodonts and *Belantsea* is most likely a result of niche partitioning to feed on specific hard- and soft-bodied invertebrate prey, algae, and larval and small fish. Similar niche partitions are also observed in extant triggerfish, which have been classified

into generalist feeders, algae/plankton eaters, and durophagous predators (McCord and Westneat, 2016). The most direct evidence of prey choice by heterodont petalodonts is seen in the type specimen of *N. hawesi*, which preserves a digestive bolus in the abdominal cavity with valves of the brachiopod *Lingula* and indeterminate crustacean fragments (Lund, 1989).

Lastly, as a comment on the potential ecomorphology of petalodonts, the obruchevoid and belantseid petalodonts appear to have had uniquely adapted body morphologies not seen in other contemporaneous or extant chondrichthyans. Compagno (1990) reviewed life-history styles within chondrichthyans in time and space and derived 27 unique ecomorphotypes for extinct and extant taxa. In this review, the only petalodont group to fit within these classifications was the janassids (typified by *Janassa bituminosa*) in the rhinobenthic habitus (Compagno, 1990). The rhinobenthic habitus includes chondrichthyans that evolved flattened bodies, enlarged paired fins, crushing dentitions, and enlarged snouts in front of the jaws to probe benthic substrates for invertebrate prey (Compagno, 1990).

In contrast, Compagno (1990) did not establish an ecomorphotype for hyperbenthic chondrichthyans that had specializations for complex environments such as reefs. The dignathic heterodont obruchevoids and the homodont *Belantsea* shared similar body traits: dorsoventrally deep and laterally compressed



**Figure 6.** Tentative reconstruction of *Clavusodens mcginnisi* n. gen. n. sp. (modeled after *Netsepoye*) feeding on phyllocarid crustaceans on the sea floor of a crinoidal forest from the Joppa Member of the Ste. Genevieve Formation, with the ctenacanth *Glikmanius careforum* swimming overhead. Art by Benji Paysnoe.

bodies with enlarged pectoral fins for maneuverability that would aid in moving through tropical crinoidal forest reefs typical of the Mississippian (Lund *et al.*, 2015).

Until further work on modeling the body and dental mechanics of petalodonts is available, we tentatively follow Lund *et al.*'s (2015) suggestion that the obruchevidid petalodonts and *Belantsea* were most likely adapted to inhabit the complex environments of reefs, crinoidal forests, and other shallow near shore habitats, with a feeding ecology analogous to extant members of the bony fish order Tetradontiformes (Fig. 6). It should be noted, however, that the petalodont body form has not yet been modeled to determine how it would perform in hydrostatic and hydrodynamic conditions, and the above suggested habitus model for obruchevidid and belantseid petalodonts is currently speculative.

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