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To cite this article: John-Paul M. Hodnett, Rickard Toomey, H. Chase Egli, Gabe Ward, John R. Wood, Rickard Olson, Kelli Tolleson, Justin S. Tweet & Vincent L. Santucci (01 Feb 2024): New ctenacanth sharks (Chondrichthyes; Elasmobranchii; Ctenacanthiformes) from the Middle to Late Mississippian of Kentucky and Alabama, *Journal of Vertebrate Paleontology*, DOI: [10.1080/02724634.2023.2292599](https://doi.org/10.1080/02724634.2023.2292599)

To link to this article: <https://doi.org/10.1080/02724634.2023.2292599>



Published online: 01 Feb 2024.



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NEW CTENACANTH SHARKS (CHONDRICHTHYES; ELASMOBRANCHII; CTENACANTHIFORMES) FROM THE MIDDLE TO LATE MISSISSIPPIAN OF KENTUCKY AND ALABAMA

JOHN-PAUL M. HODNETT,^{1,2*} RICKARD TOOMEY,³ H. CHASE EGLI,⁴ GABE WARD,⁴ JOHN R. WOOD,²
RICKARD OLSON,³ KELLI TOLLESON,³ JUSTIN S. TWEET,² and VINCENT L. SANTUCCI²

¹Archaeology Office, Maryland–National Capitol Parks and Planning Commission, Upper Marlboro, Maryland, U.S.A. 20772; jp.hodnett@pgparks.com;

²Paleontology Program, Geological Resource Division, National Park Service, Washington, D.C., U.S.A. 20240; jack_wood@nps.gov, justin_tweet@nps.gov, vincent_santucci@nps.gov;

³Mammoth Cave National Park, National Park Service, Kentucky, U.S.A. 42259; rick_toomey@nps.gov, rickardolson16@gmail.com, kelli_tolleson@nps.gov;

⁴Department of Geological Sciences, University of Alabama, Tuscaloosa, Alabama, U.S.A. 35487; hcegli@crimson.ua.edu; gward@mays.tamu.edu

ABSTRACT—Two new ctenacanthiform sharks representing two families, Ctenacanthidae and Heslerodidae, have been identified from the Middle to Late Mississippian marine sediments from Mammoth Cave National Park, Kentucky, and two Late Mississippian marine horizons in northern Alabama. The ctenacanthid, *Troglocladodus trimblei*, gen. et sp. nov., is known from isolated teeth from the Middle Mississippian St. Louis Formation and Ste. Genevieve Formation of Mammoth Cave and the Late Mississippian Bangor Limestone of northern Alabama. *Troglocladodus* gen. nov. is characterized by broad median cusps, pronounced longitudinal cristae, multiple intermediate cusps, and labiolingually shortened tooth bases. The heslerodid, *Glikmanius careforum* sp. nov., is known from isolated teeth and visceral arches from the Middle Mississippian St. Louis Formation and Ste. Genevieve Formation and the Late Mississippian Haney Formation, a Hartselle Sandstone-equivalent shale interval, and Bangor Limestone. *Glikmanius careforum* sp. nov. has proportionately distinct teeth among species of *Glikmanius*, with more robust and shorter cusps. The palatoquadrate of *G. careforum* has a short palatine ramus, otic process that is dorsoventrally deep and less expanded antero-posteriorly similar to *Heslerodus* and *Dracopristis*, and an elongated quadrate process like *Heslerodus*. The Meckel's cartilage is less dorsoventrally deep than *Dracopristis*. These two new ctenacanth taxa add important information on the diversity of Ctenacanthiformes suggesting three major lineages within the order. Ctenacanthids have a rich fossil history from the Late Devonian to the Middle Permian evolving a variety of tooth types and small to large body sizes.

<http://zoobank.org/urn:lsid:zoobank.org:pub:5B580862-0A90-4255-9EEA-57A240A7028D>

Citation for this article: Hodnett, J-P. M., Toomey, R., Egli, H.C., Ward, G., Wood, J. R., Olson, R., Tolleson, K., Tweet, J. S., & Santucci, V. L. (2024) New ctenacanth sharks (Chondrichthyes; Elasmobranchii; Ctenacanthiformes) from the Middle to Late Mississippian of Kentucky and Alabama. *Journal of Vertebrate Paleontology*. <https://doi.org/10.1080/02724634.2023.2292599>

Submitted: October 3, 2023

Revisions received: November 20, 2023

Accepted: December 5, 2023

INTRODUCTION

The chondrichthyan order Ctenacanthiformes is a group of early phalacanthous (fin-spine bearing) elasmobranch sharks that originated during the early Late Devonian and persisted into the Permian (Ginter et al., 2010; Hodnett et al., 2021a; Maisey, 1981). Ctenacanthids were first recognized and defined by their “comb-like” dorsal fin spines (Agassiz, 1837; Maisey, 1981, 1982, 1984), with more complete skeletal material later described that placed tooth-based taxa within Ctenacanthiformes (Dean, 1909; Ginter et al., 2010; Hodnett et al., 2021a; Moy-Thomas, 1936; Traquair, 1884). Though ctenacanthids originated during the early Late Devonian, their greatest diversification occurred during the Middle to

Late Mississippian (Viséan to Serpukhovian stages of the Carboniferous), where a number of species evolved and often co-occurred in shallow sea deposits, just prior to the formation of Pangea (Feichtinger et al., 2021). The majority of these ctenacanth taxa are based on isolated teeth and spines found nearly worldwide. The usefulness of isolated dorsal fin spines in taxonomic determination is debatable as a single spine type can be found in multiple taxa with differing dentitions and skeletal morphologies (Hodnett et al., 2021a). Here we will concentrate on tooth-based taxa from the Middle to Late Mississippian.

Middle to Late Mississippian Ctenacanthiforms

Presently, two families of ctenacanthiform sharks are recognized during the Middle to Late Mississippian: Ctenacanthidae Dean 1909 and Heslerodidae Maisey 2010. Ctenacanthidae includes the genera *Ctenacanthus* (known primarily from isolated spines in the Mississippian; Maisey, 1981), *Cladodus*

*Corresponding author.

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(teeth and skeletal elements; Duffin & Ginter, 2006; Ginter & Maisey, 2007; Ginter et al., 2010), and *Goodrichthys* (teeth and nearly complete skeleton; Ginter, 2009; Moy-Thomas, 1936). The dentition of ctenacanthids shares the general characters of having a single ridge-like orolingual and basolabial projection, and a shallow basolabial depression (Duffin & Ginter, 2006; Ginter et al., 2010). *Cladodus* is known from at least six species from the Middle to Late Mississippian. *Cladodus mirabilis*, *Cl. elegans*, and *Cl. gailensis* have a generalized “cladodont” dentition of five or more prominent, though mesiodistally narrow, cusps bearing fine longitudinal cristae (Duffin & Ginter, 2006; Feichtinger et al., 2021; Ginter et al., 2010). The other three species of *Cladodus*, *Cl. bellifer*, *Cl. marginatus*, and *Cl. vanhornei*, are more specialized in having five or fewer cusps that are often broader mesiodistally, with fewer or no fine longitudinal cristae (Duffin & Ginter, 2006). Teeth of *Goodrichthys* are similar to most species of *Cladodus* in bearing the “cladodont” five or more cusps but differ in having more pronounced longitudinal cristae, the tooth base being less labiolingually wide, and the presence of multiple small foramina in the basolabial depression (Ginter, 2009).

Heslerodidae was established by Maisey (2010) based on dorsal fin spine traits seen in three taxa, Pennsylvanian to Permian *Heslerodus*, and the Middle to Late Mississippian *Bythiacanthus* and *Avonacanthus*, respectively. However, recently tooth-based taxa have been recognized as belonging to this family based on the shared dental traits seen in *Heslerodus*, which are the presence of two separate button-like orolingual and basolabial projections and a moderate to deep basolabial depression (Feichtinger et al., 2021; Ginter, 2002; Hodnett et al., 2012, 2021a; Ivanov, 2022). At present, only two genera from the Heslerodidae are known from the Middle to Late Mississippian, *Glencartius* and *Glikmanius*. *Glencartius* is known from both partial to near complete skeletons from the Middle Mississippian of Scotland and isolated teeth and scales from Europe and North America (Ginter & Skompski, 2019; Moy-Thomas, 1936; JP Hodnett, pers. obs.). A Middle Mississippian record of *Glikmanius*, a taxon previously known primarily from the Pennsylvanian to Permian, was first noted by Lebedev (1996) on a single tooth (originally referred to as “*Symmorium*” *occidentalis*) from the Upper Viséan of the Mikhailov Horizon, at Polotnyany Zavod Quarry, Kaluga region of Russia. Ginter et al. (2005) would later identify *Glikmanius* sp. from the Late Mississippian Heath Formation of central Montana based on teeth previously attributed to *Stethacanthus* and *Cladodus* (Lund, 1985).

A third yet-to-be formally defined family group of ctenacanth is present in the Middle to Late Mississippian, which includes the genus *Saivodus*. *Saivodus* teeth are known at many Middle to Late Mississippian North American and European localities (Duffin & Ginter, 2006) and also are known from the Permian of North America (Hodnett et al., 2012). Hodnett et al. (2012, 2021a) proposed this group of ctenacanth that have dentitions with multiple intermediate cusps between the median and lateral cusps, divided orolingual projections, and a ridge or boss-like single basolabial projection. Recently, a partial cranium of *Saivodus* with a 60 cm jaw has been identified from Mammoth Cave National Park, Kentucky, suggesting *Saivodus* could have reached large body sizes of 4–5 meters in length or more (Hodnett et al., 2020). This *Saivodus* skeletal material will be described elsewhere and will help define this third family group of ctenacanth.

Here we present two new ctenacanthiform taxa, one ctenacanthid and one heslerodid, from the Middle to Late Mississippian sediments from Mammoth Cave National Park, Kentucky and from northern Alabama that adds to the diversity of ctenacanth sharks during the Mississippian period.

GEOLOGIC SETTING

Mammoth Cave National Park, Kentucky

The Mississippian strata found at Mammoth Cave National Park in central Kentucky represent one of the southeasternmost portions of the ancient marine Illinois Basin (Palmer, 1981) (Fig. 1A). The Illinois Basin is historically significant to early American palaeoichthyology because a large number of Middle to Late Paleozoic fish fossils were collected and described from within this basin in states such as Missouri, Illinois, Iowa, and Indiana (Newberry & Worthen, 1870; St. John & 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 palaeoichthyology. The new ctenacanth fossils presented here was captured from three geologic formations within Mammoth Cave National Park, Kentucky which are the Middle Mississippian St. Louis Formation and Ste. Genevieve Formation, and the Late Mississippian Haney Formation.

The St. Louis Formation is an extensive geologic formation in the central U.S.A. with a historical contribution to the early research on Paleozoic fish in North America. The St. Louis Formation is typically characterized by micritic to lutitic carbonate limestone beds, dark shales, and grayish green shales (Sable & Dever, 1990). Chert nodules and invertebrate fossils are common (Butts, 1917; Palmer, 1981). Locally, the St. Louis Formation is only encountered within the deepest passages of the cave system at Mammoth Cave National Park, and is not mapped surficially on the USGS geological quadrangles within park boundaries. Within the cave system, the St. Louis Formation is approximately 60 meters thick, and only in the upper sections of the Horse Cave Member at the top of the formation are there cave passages in the park where marine vertebrate fossils have been encountered. Presently, 24 taxa of chondrichthyans are known from the Horse Cave Member of the St. Louis Formation at Mammoth Cave National Park (Hodnett et al., 2021b).

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 (110–120 feet) 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 documenting 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. Chondrichthyan teeth, dermal spines, and denticles are common within multiple horizons within the Joppa Member at Mammoth Cave and isolated to partially articulated skeletal cartilage also occurs. Presently, 60 taxa of cartilaginous fishes have been identified from the Joppa Member (Hodnett et al., 2020).

The Late Mississippian Haney Formation consists primarily of biomicritic limestones as well as skeletal limestones and micritic dolomite. Some shales can also occur within this formation. The Haney Formation overlies the Big Clifty Formation and is overlain by the Hardinsburg Formation. The age of the Haney Formation is considered to be Late Chesterian/Serpukhovian. Chondrichthyan fossils are rare within the Haney Formation and presently only five taxa (a eugenodontiform, a petalodontiform, a cochliodontiform holocephalan, and two ctenacanthiforms; *Saivodus striatus* and the new heslerodid species presented below) have been found in small spring-fed caves within Mammoth Cave National Park.

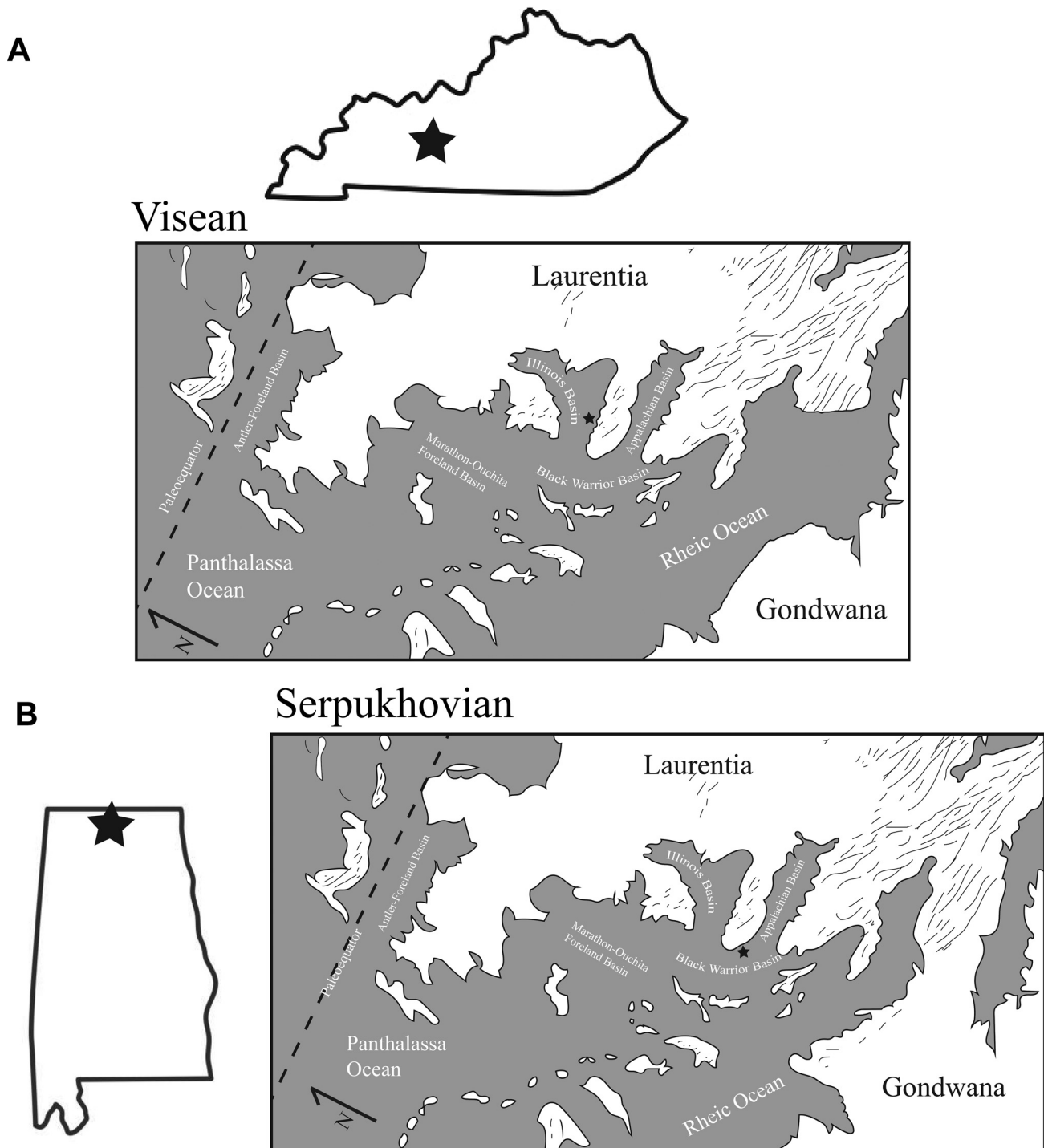


FIGURE 1. Localities and paleogeographic position of the ctenacanthifform sites. **A**, the approximate position of Mammoth Cave National Park, Kentucky and the Laurentia paleogeography of the Viséan stage. **B**, the approximate position of the Alabama fossil sites and the southeastern Laurentia paleogeography of the Serpukhovian.

Late Mississippian of Alabama

There are three physiographic regions of Alabama where Mississippian subperiod strata crop out (Fig. 1B): Valley and Ridge, Highland Rim, and Cumberland Plateau. The outcropping Mississippian strata represent marine to marginal-marine depositional environments and uncommonly contain chondrichthyan fossils (Algeo & Rich, 1992; Ciampaglio et al., 2011; Itano,

2023; Itano & Lambert, 2018; Stapor & Cleaves, 1992; Thomas, 1972, 1979). Nine formally described strata represent the Mississippian subperiod in Alabama (Kopaska-Merkel et al., 2020; Thomas, 1972, 1979). The new ctenacanth taxa described here have been found within an informal Hartselle Sandstone-equivalent shale unit (Kopaska-Merkel et al., 2020) and the Bangor Limestone. The two strata are both dated to the Early Serpukhovian ICS Stage and the Middle Chesterian North American Stage

(Itano & Lambert, 2018; Kopsaka-Merkel et al., 2020). Three Alabama sites are represented in this study.

An unnamed shaly unit that overlies the Upper Monteagle Limestone and is stratigraphically equivalent with the Hartselle Sandstone is present at multiple sites in Jackson and Madison counties of north central Alabama (Kopsaka-Merkel et al., 2020). This interval is described from an outcrop along U.S. Route 72 in southeastern Jackson County within Thomas Cove near Woodville and is noted for having a carbonate mound with abundant associated mound-building biota, with numerous invertebrate and vertebrate taxa (Haywick et al., 2016; Kopsaka-Merkel et al., 2020). The mound and highly fossiliferous shale at the Woodville outcrop sit roughly halfway up the unit, with the shale bed being the largest local shale facies in the unit and other minor lithologies include fossiliferous limestones and calcareous sandstones (Kopsaka-Merkel et al., 2020).

This interval is also present within the southeastern wall of a roadcut along Cecil Ashburn Boulevard in the city of Huntsville in central Madison County. Though the Huntsville occurrence is stratigraphically thinner than the Woodville outcrop, both the Woodville and Huntsville sites exhibit a similar gray-gray brown shale, which are underlain by limestone, and have similar assemblages of taxa (G. Ward, pers. obs.). The Cecil Ashburn roadcut, however, does not exhibit any minor lithologies. At the Woodville outcrop, the shale interval is overlain by the typical Bangor Limestone lithology (Kopsaka-Merkel et al., 2020). At the Cecil Ashburn roadcut, the shale interval is overlain by a massive, grain-supported limestone (formation assignment uncertain by the authors). This shale interval could also be the calcareous-to-sandy Pride Mountain Formation shales described in Thomas (1972, 1979) as overlying the Monteagle Limestone after the northeastern extent of the typical Hartselle Sandstone lithology. Calcareous sandstone lenses within this shale unit could also represent the Upper Hartselle Sandstone as both the lenses and the Upper Hartselle Sandstone.

This informal shale unit is considered Serpukhovian in age by the authors as it overlies the Lower Serpukhovian-Upper Monteagle Limestone in northeastern Alabama (Kopsaka-Merkel et al., 2020). It is likely that these facies changes represent sudden clastic deposition in deeper water off the barrier island complex in the Hartselle Sandstone and Pride Mountain Formation and subsequent return to the shallow carbonate shelf environments present in both the underlying Monteagle and overlying Bangor Limestones (Thomas, 1972, 1979). Although this interval occurs between the uppermost Monteagle and lowermost Bangor limestone, current stratigraphic nomenclature is vague regarding the assignment of this interval. Further study is necessary to definitively determine the depositional environment and paleo-water depth. We will herein refer to these intervals as a Hartselle-equivalent shale unit in line with the nascent literature regarding this horizon (Haywick et al., 2016; Kopsaka-Merkel et al., 2020).

The Bangor Limestone fossil site is located in north central Franklin County, west of the city of Russellville. The Franklin County site is dominated by oolitic wacke-packstones; however, numerous interbeds and lenses of minor lithologies occur locally (Thomas, 1972, 1979). These minor lithologies include bioclastic grainstones, shales, and mudstones. Typical Hartselle Sandstone lithology described in Thomas (1972, 1979) crops out to the east of the Franklin County site and underlies the Bangor Limestone. Within the section, this site sits in the Lower Bangor Limestone. The depositional environment of the Lower Bangor Limestone at the Franklin County site represents a shallow carbonate shelf (Algeo & Rich, 1992; Thomas, 1972, 1979). This carbonate shelf often exhibited varying bioherms and local oolitic mound structures (Haywick et al., 2009; Kopsaka-Merkel & Haywick, 2001, 2014; Kopsaka-Merkel et al., 2020). The Lower Bangor Limestone has been

both chronostratigraphically and biostratigraphically dated to be Early Serpukhovian in age, however the stratum is younger than the underlying Hartselle Sandstone-equivalent shale interval (Itano & Lambert, 2018; Kopsaka-Merkel et al., 2020).

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 commonly 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. Our primary method is to remove all but one cotton ball, carefully tease the fossil from the cave surface (often from the cave ceiling) into the tube, place a cotton ball on top, and continue on 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.

Specimens from Alabama were surface-collected by the University of Alabama, between 2013 and 2022. These specimens are deposited in the Alabama Museum of Natural History (ALMNH) in Tuscaloosa, Alabama. Specimens were collected primarily from loose rock originating from the outcrops at the sites. Exact locality information is on file at ALMNH.

Photography 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.

Institutional Abbreviations—ALMNH:Paleo, Alabama Museum of Natural History, Tuscaloosa, Alabama, U.S.A.; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, U.S.A.; MACA, Mammoth Cave National Park, Kentucky, U.S.A.

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
 Subclass ELASMOBRANCHII Bonaparte, 1838
 Order CTENACANTHIFORMES Glikman, 1964
 Family CTENACANTHIDAE Dean, 1909
TROGLOCLADODUS TRIMBLEI, gen. et sp. nov.
 (Fig. 2)

Holotype—MACA 62062, complete mediolateral tooth from the Ste. Genevieve Formation.

Referred Material—St. Louis Formation; MACA 62133, medial tooth, MACA 62132, mediolateral tooth. Ste. Genevieve Formation; MACA 64343, anterolateral tooth, MACA 64340, juvenile anterolateral tooth, MACA 64341, juvenile ?distolateral tooth. Bangor Limestone; ALMNH:Paleo: 9793, mediolateral tooth.

Etymology—the generic name derived from the Greek words ‘trogle’ (hole dwelling), ‘klados’ (branching) and ‘odous’ (tooth); species name in honor of Mammoth Cave National Park superintendent Barclay Trimble, who discovered the holotype specimen.

Type Locality and Horizon—Mammoth Cave National Park, Kentucky, Middle Mississippian (Upper Visean) Joppa Member, Ste. Genevieve Formation.

Additional Localities and Horizons—Mammoth Cave National Park, Kentucky, Middle Mississippian (Lower Visean) Horse Cave Member, St. Louis Formation; north Central Franklin County, Alabama, Late Mississippian (Serpukhovian) Bangor Limestone.

Diagnosis—Small- to medium-sized teeth measuring between 7–23 mm mesiodistally. Median cusp biconvex and relatively broad and triangular with 12–15 cristae on labiolingual margins, more erect in anterior positioned teeth and recurved posteriorly in mediolaterally positioned teeth. Lateral cusps flare from the base with 5–6 cristae, approximately a quarter the height of the median cusp, and bulbous at the base. Intermediate cusps vary in size and number with 1–4 cusps between the median and lateral cusp that can be half as tall or as tall as the lateral cusp. Tooth base trapezoidal, slightly concave labially, with a weakly developed lingual torus. Orolingual projection a thin rectangular ridge. Basolabial projection a thin ridge along the basolabial margin. Basolabial depression moderately developed and triangular in shape. Numerous nutrient foramina present on the labial margin between basolabial rim and crown.

Description—Juvenile to adult teeth range from 7–23 mm mesiodistally (Fig. 2). The median cusp is biconvex, triangular, recurved lingually, and relatively broad at the base and narrowing to a point at the apex. A non-serrated carina is present on the mesial and distal margins of the cusp. Both the labial and lingual surfaces of the median cusp are ornamented with 12–15 pronounced longitudinal cristae, which may be continuous from the apex to the base of the crown, occasionally bifurcate towards the crown base, or originate from the base and stop a quarter up the length of the cusp. The median cusp orientation varies from more erect on anterior position teeth (Fig. 2A) and inclined distally on mediolaterally positioned teeth (Fig. 2E). The lateral cusps are approximately a quarter of the height of the median cusp and flare from the base. The base of the lateral cusps is bulbous in shape, narrowing to a cone-like apex and the labial and lingual surfaces are ornamented with 5–6 prominent longitudinal cristae. There are 1–4 intermediate cusps. Height is also variable, with some intermediate cusps being approximately half the height of the lateral cusp or as tall as the lateral cusp. All intermediate cusps are ornamented with 4–5 prominent cristae on the labial surface, and can be either smooth or have 1–3 cristae on the lingual surface. Both lateral and intermediate cusps recurve lingually. A moderately developed broad triangular basolabial depression is present, and has a number of well-developed foramina between the labial rim and the base of the crown. The tooth base is approximately a narrow trapezoidal shape, being mesiodistally longer than labiolingually wide. A slight labial depression is present on the labial margin, giving the tooth base a slightly u-shaped appearance when viewed orally or aborally. The lingual torus is convex, weakly developed compared with other ctenacanthiforms, and rounded on the mesiodistal margins. The basolabial projection is a thin rectangular ridge that forms part of the basolabial rim. The orolingual projection is a rectangular ridge that is wider than the median cusp and positioned just between the lingual base of the median cusp and the lingual rim. A number of well-developed foramina are present on the labial and lingual margins of the orolingual projection. On the aboral surface of the tooth base, a shallow depression is present between the basolabial projection and the lingual rim, which also has a number of

foramina within the depression. The aboral surface of the tooth base is recurved mesiodistally.

Comparison and Remarks—*Troglocladodus trimblei* is a ctenacanthiform based on the dental characteristics of enameloid connecting the cusps, presence of a basolabial depression beneath the median cusp, basolabial and orolingual projections of the dentition wider than the median cusps, and a well-developed lingually extended tooth base (Duffin & Ginter, 2006; Ginter et al., 2010; Hodnett et al., 2021a). The latter characteristic is one of the more distinguishing traits for *Troglocladodus* in that the lingual torus of the tooth base is proportionately shorter labiolingually compared with the contemporaneous *Cladodus*, *Saivodus*, and *Glikmanius*. The reduced width of the lingual torus is similar in proportion to those illustrated by Ginter (2009:fig. 3a–j) and referred to *Goodrichthys eskdalensis*. The rectangular ridge-like basolabial and orolingual projection seen in *Troglocladodus* is similar to that seen in *Ctenacanthus*, *Cladodus*, and *Goodrichthys*, and not divided into two separate button-like structures as seen in *Glikmanius* or *Glencartius* (Duffin & Ginter, 2006; Ginter, 2009, 2010; Ginter & Skompski, 2019; Ginter et al., 2005; Hodnett et al., 2012, 2021a). *Troglocladodus* is also distinct from *Cladodus*, *Saivodus*, *Glikmanius*, and *Glencartius* in having a number of small labial foramina present between the labial rim and the base of the crown. Ginter (2009) noted similar features in teeth referred to *Goodrichthys* but suggested they were trabecular dentine canals exposed through chemical or mechanical preparation.

The crown of *Troglocladodus* also differs from other contemporaneous ctenacanthiforms. The median cusp of *Troglocladodus* differs from several species of *Cladodus* (*C. mirabilis*, *C. bellifer*, and *C. elegans*; vide Duffin & Ginter, 2006) in being proportionately broader at the base and not narrowly elongated. However, *Cladodus marginatus*, *C. vanhornei*, and *C. gailensis* do have broad triangular median cusps (Duffin & Ginter, 2006; Feichtinger et al., 2021). In *Glikmanius* and *Saivodus*, the median cusp is proportionately narrow and elongated (Duffin & Ginter, 2006; Ginter et al., 2005; Hodnett et al., 2012, 2021a). The labial and lingual margins of the median cusp in *Troglocladodus* are biconvex, similar to *Saivodus* and *Goodrichthys* (Duffin & Ginter, 2006; Ginter, 2009), while *Cladodus*, *Glikmanius*, and *Glencartius* have a flattened labial margin and convex lingual margin (Duffin & Ginter, 2006; Ginter & Skompski, 2019). The short lateral cusps of *Cladodus* and *Glikmanius* tend to be prominent, ranging from approximately half to a third the height of the median cusp (Duffin & Ginter, 2006; Ginter et al., 2005). Like *Troglocladodus*, the lateral cusps of *Saivodus* and teeth referred to *Goodrichthys* are less prominent in being about a quarter or less the height of the median cusp (Duffin & Ginter, 2006; Ginter 2009).

The number of intermediate cusps typically seen in species of *Cladodus* varies from absent (*C. vanhornei*), singular (*C. marginatus* and *C. gailensis*), to two or more (*C. mirabilis* and *C. elegans*) (Duffin & Ginter, 2006; Feichtinger et al., 2021). *Glikmanius* is also variable, with some species having one intermediate cusp (*G. occidentalis* and *G. culmenis*) and *G. yachkovensis*, having either one or two intermediate cusps (Ginter et al., 2005; Hodnett et al., 2012; Koot et al., 2013). Teeth referred to *Goodrichthys* tend to have one intermediate cusp (Ginter, 2009). Both *Saivodus* and *Glencartius*, like *Troglocladodus*, can have multiple intermediate cusps with *Glencartius* having up to three prominent intermediate cusps (Ginter & Skompski, 2019) and *Saivodus* having three or more less prominent intermediate cusps (Duffin & Ginter, 2006). *Saivodus* also differs from other contemporaneous ctenacanthiforms in having additional labial accessory cusplets (Duffin & Ginter, 2006).

The ornamentation on the cusps differs between most *Cladodus* species and *Troglocladodus*. In *Troglocladodus* the longitudinal labial and lingual cristae are more prominent, whereas

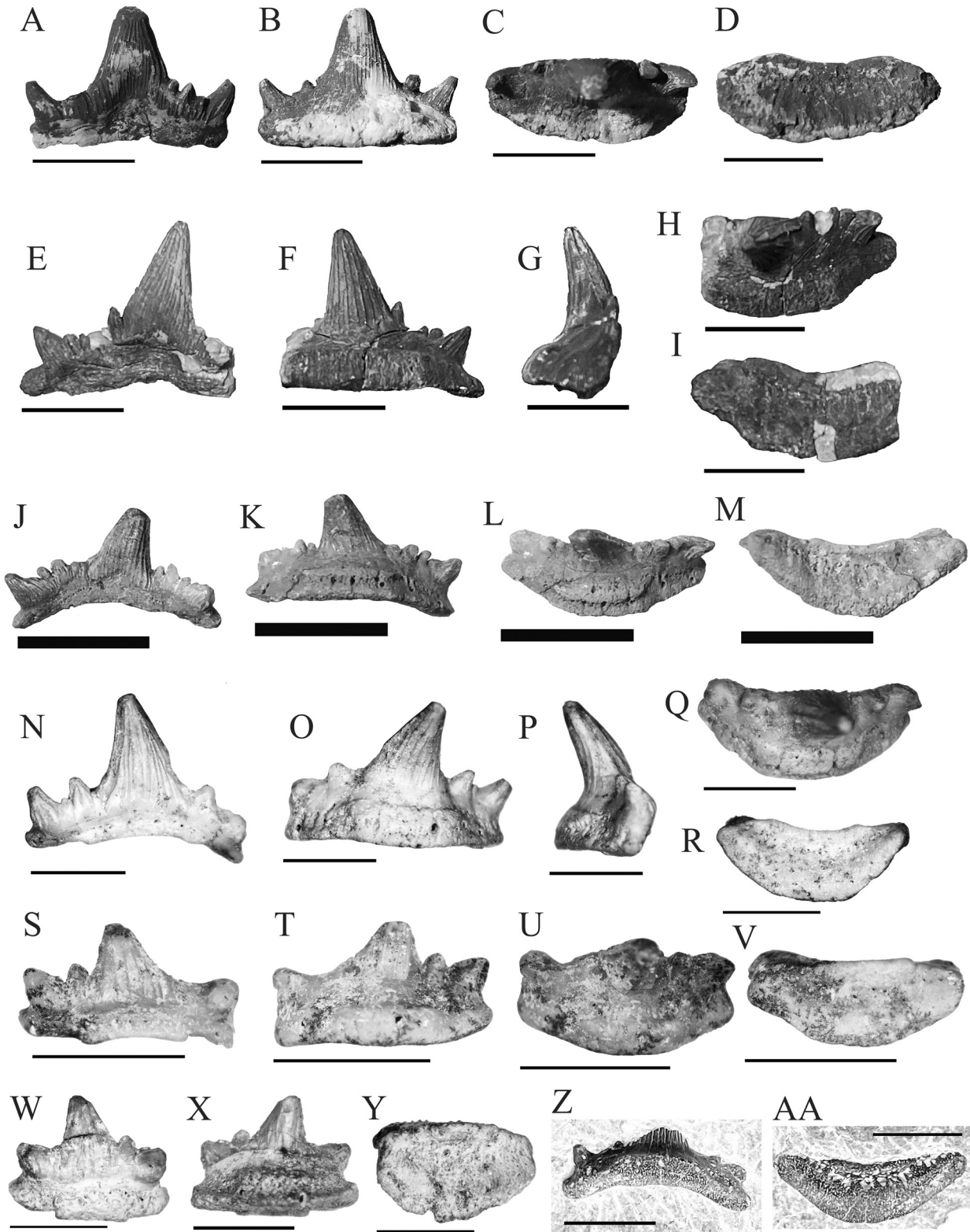


FIGURE 2. Teeth of *Troglodadodus trimblei*. **A–I**, teeth from the Horse Cave Member of the St. Louis Formation of Mammoth Cave National Park, Kentucky. **A–D**, MACA 62133; medial tooth in **A**, labial; **B**, lingual; **C**, oral; and **D**, aboral views. **E–I**, MACA 62132, mediolateral tooth in **E**, labial; **F**, lingual; **G**, mesial; **H**, oral; **I**, aboral views. **J–Y**, teeth from the Joppa Member of the Ste. Genevieve Formation of Mammoth Cave National Park, Kentucky. **J–M**, MACA 62062 (holotype), mediolateral tooth in **J**, labial; **K**, lingual; **L**, oral; **M**, aboral view. **N–R**, MACA 64343, anterolateral tooth in **N**, labial; **O**, lingual; **P**, distal; **Q**, oral; **R**, aboral views. **S–V**, MACA 64340, juvenile anterolateral tooth in **S**, labial; **T**, lingual; **U**, oral; **V**, aboral views. **W–Y**, MACA 64341, juvenile? distolateral tooth in **W**, labial; **X**, lingual; **Y**, aboral view. **Z–AA**, ALMNH:Paleo: 9793, mediolateral tooth from the Bangor Limestone, Alabama in **Z**, lingual; **AA**, aboral views. Scales **A–M** and **Z–AA** equal 10 mm; **N–Y** equal 5 mm.

Cladodus may have fine narrow longitudinal cristae (*C. mirabilis*, *C. marginatus*, *C. bellifer*, and *C. elegans*) or a smooth surface lacking cristae (*C. vanhornei*) (Duffin & Ginter, 2006). The exception is *Cladodus gailensis*, which does have relatively prominent cristae (Feichtinger et al., 2021). Fine thin labial and lingual cristae are also found in *Glikmanius* and *Saivodus*, while *Glencartius* has prominent cristae (Duffin & Ginter, 2006; Ginter & Skompski, 2019; Ginter et al., 2005).

Family HESLERODIDAE Maisey, 2010

Revised Diagnosis—Ctenacanthiform chondrichthyans with dentitions including two button-like basolabial and orolingual projections on the tooth base. Palatoquadrates with the otic process dorsoventrally taller than craniocaudally long, with relatively shorter palatine ramus. Dorsal fin spine morphology variable potentially at subfamily to genus level.

Included Genera—*Avonacanthus* Maisey 2010; *Bythiacanthus* St. John and Worthen 1875; *Dracopristis* Hodnett et al. 2021a; *Glencartius* Ginter and Skompski 2019; *Glikmanius* Ginter et al. 2005; *Heslerodus* Ginter 2002; *Heslerodoides* Ivanov 2022; *Kaibabvenator* Hodnett et al. 2012; *Nanoskalme* Hodnett et al. 2012.

Remarks—Maisey (2010) created a new family of “phalacanthous sharks” to include *Heslerodus divergens*, a chondrichthyan known from partial skeletons with dorsal fin spines and isolated teeth from the Early Pennsylvanian to Middle Permian (Ginter, 2002; Ginter et al., 2005, 2010; Hodnett et al., 2012; Stahl, 1988; Williams, 1985) as well as the isolated spine taxa *Bythiacanthus* and *Avonacanthus* from the Mississippian. These three taxa were united by Maisey (2010) based on their shared morphology of the dorsal fin spines: a stout rhombic profile, posterior wall convex apically, longitudinal rows of large rounded tubercles with radial striations, lack of posterior denticle rows, and extremely short exposed spine in comparison to its insertion. It is doubtful that workers on ctenacanthiform dentitions noted the strong similarities of the dental characters of *Heslerodus*, particularly the presence of two basolabial and orolingual button-like projections on the tooth base, which are also shared with taxa such as *Heslerodoides*, *Glikmanius*, *Glencartius*, *Kaibabvenator*, and *Nanoskalme*, and must have had a shared family relationship (Ginter & Skompski, 2019; Ginter et al., 2005; Hodnett et al., 2012; Ivanov, 2022). Some recent work has gone as far as including ctenacanth teeth with two button-like basolabial and orolingual projections into the Heslerodidae, though dorsal spine data were lacking (Feichtinger et al., 2021; Ivanov, 2022). Complicating the diagnosis of inclusion into the Heslerodidae either by dentition or by dorsal spines was the description of the complete skeleton of the Late Pennsylvanian *Dracopristis*, which is a ctenacanthiform with *Heslerodus*-like teeth and *Ctenacanthus*-like dorsal spines (Hodnett et al., 2021a). It is proposed here that a broader family diagnosis, as described above, that is not restricted to dorsal spine morphology is necessary for the inclusion of ctenacanth taxa with shared dental traits with *Heslerodus*. However, at this time we follow Maisey (2010) in keeping the spine-based taxa *Bythiacanthus* and *Avonacanthus* within the Heslerodidae until additional information comes to light.

Genus *GLIKMANIUS* Ginter, Ivanov, & Lebedev, 2005
GLIKMANIUS CAREFORUM, sp. nov.
 (Fig. 3)

Holotype—MACA 64335, complete anterolateral tooth from the Ste. Genevieve Formation.

Referred Material—St. Louis Formation; MACA 64338, partial anterolateral tooth. Ste. Genevieve Formation; MACA 64336, distolateral tooth, MACA 64337, partial anterolateral tooth, MACA 64342, right palatoquadrate, Meckel’s cartilage, associated dentition, hyomandibula, and gill arches preserved

in a cave passage ceiling. Haney Formation; MACA 64339, partial anterolateral tooth. Hartselle Sandstone-equivalent shale interval; ALMNH:Paleo: 9775, partial mediolateral tooth, ALMNH:Paleo: 9831, partial anterolateral tooth, ALMNH:Paleo: 9835, partial anterolateral tooth; ALMNH:Paleo: 9808, partial anterolateral tooth, ALMNH:Paleo: 9839, partial anterolateral tooth. Bangor Limestone; ALMNH:Paleo: 9810, distolateral tooth, ALMNH:Paleo: 8919, distolateral tooth.

Etymology—In honor of the Cave Research Foundation and its members, which supports research and conservation at Mammoth Cave National Park, Kentucky that discovered the first jaws with dentition of *Glikmanius* within the cave. Species name is constructed by the first two letters of Cave Research Foundation.

Type Locality and Horizon—Mammoth Cave National Park, Kentucky, Middle Mississippian (Upper Viséan) Joppa Member, Ste. Genevieve Formation.

Additional Localities and Horizons—Mammoth Cave National Park, Kentucky, Middle Mississippian (Lower Viséan) Horse Cave Member, St. Louis Formation; Woodville, Alabama, Hartselle Sandstone-equivalent shale unit, Huntsville, Alabama, Hartselle Sandstone-equivalent shale unit North Central Franklin County, Alabama, Bangor Limestone.

Diagnosis—Small- to medium-sized teeth measuring between 5–21 mm mesiodistally. Median cusp flat labially and convex lingually, as broad as tall and triangular with 18–25 cristae on labiolingual margins, with anterior positioned teeth more erect and mediolaterally positioned teeth recurved posteriorly. Lateral cusps flare from the base with 7–8 cristae, approximately half the height of the median cusp, and broad at the base. Single intermediate cusp between the median and lateral cusp approximately three-quarters as tall as the lateral cusp. Tooth base is reniform in shape, slightly concave labially, with a well-developed lingual torus. Orolingual projections consisting of two well-developed, relatively robust, elliptical pads positioned between the median cusp and the lingual rim of the tooth base. Basolabial projections of two well-developed, relatively robust, elliptical pads. Basolabial depression moderately developed and triangular in shape.

Palatoquadrate otic process is dorsoventrally deep and less expanded craniocaudally. Articular process of the quadrate directed ventroposteriorly. Palatine ramus short and deep. Meckel’s cartilage dorsally concave and ventrally convex with a well-developed mandibular knob and short retroarticular process. Hyomandibula strap-like, with shallow anterior depression and triangular posterior facet.

Description—Dentition: juvenile to adult teeth ranging from 5–21 mm (Fig. 3). The median cusp is flattened on the labial surface and lingually convex. The overall shape of the median cusp is triangular and recurved lingually. The base of the median cusp is about as mesiodistally broad as it is tall. A non-serrated carina is present on the mesial and distal margins of the cusp. Both the labial and lingual surfaces of the median cusp are ornamented with 18–25 fine longitudinal cristae, which either are continuous from the apex to the base of the crown, or originate from the base and stop halfway up the length of the cusp. The median cusp orientation varies, with the anterior positioned tooth being more vertically erect (Fig. 3F) and the mediolaterally positioned teeth having the median cusp inclined distally (Fig. 3J). The lateral cusps are approximately half of the height of the median cusp and flare from the base. The base of the lateral cusps is broad and narrowing to a cone-like apex, and the labial and lingual surfaces are ornamented with 7–8 fine longitudinal cristae. A single intermediate cusp is present between the median and lateral cusps, and is approximately three-quarters the height of the lateral cusp. Intermediate cusps are ornamented with eight fine cristae on the labial and lingual surfaces. A moderately developed broad triangular-shaped

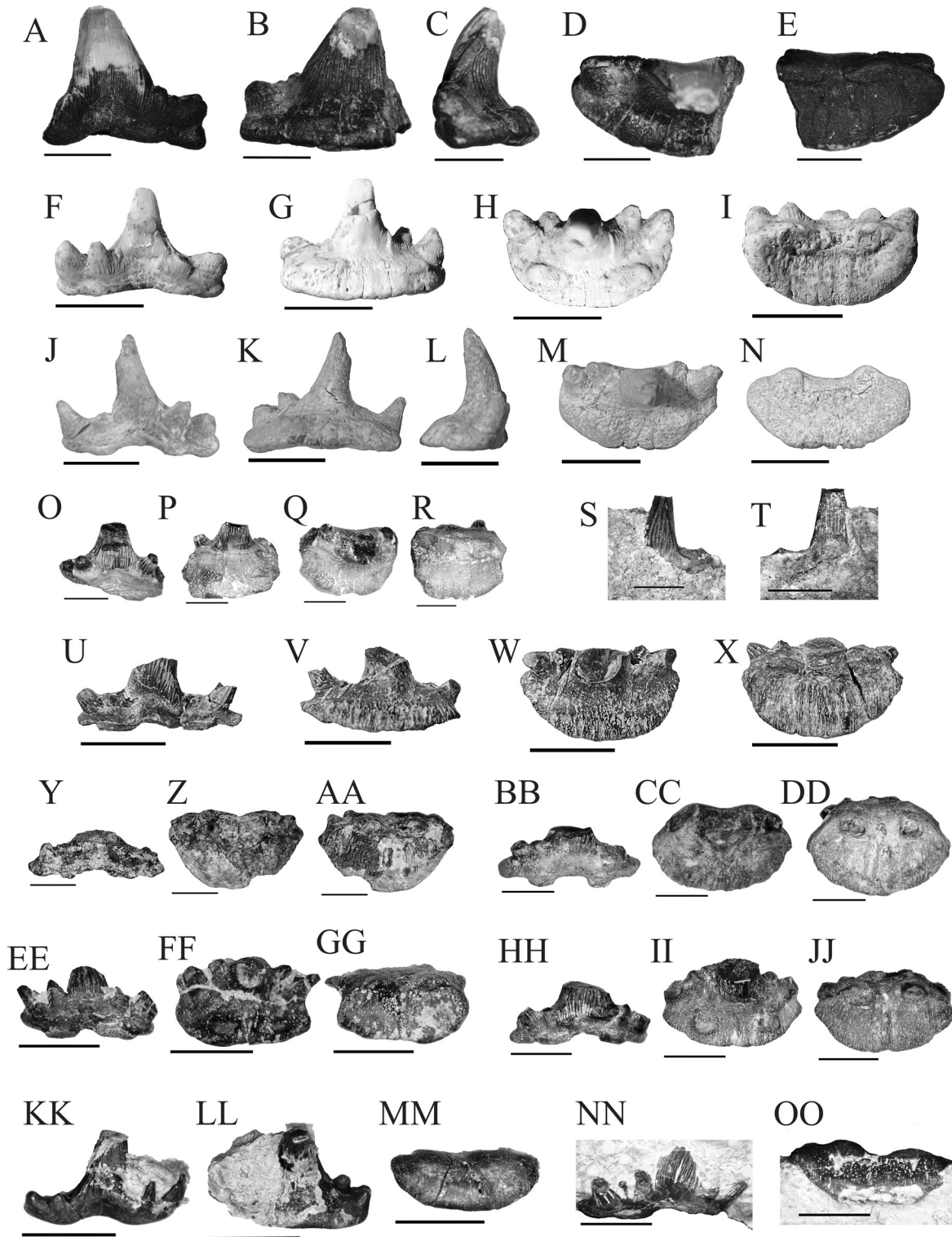


FIGURE 3. Teeth of *Glikmanius careforum*. **A–E**, MACA 64338, partial anterolateral tooth from the Horse Cave Member of the St. Louis Formation of Mammoth Cave National Park, Kentucky in **A**, labial; **B**, lingual; **C**, mesial; **D**, oral; and **E**, aboral views. **F–R**, teeth from the Joppa Member of the Ste. Genevieve Formation of Mammoth Cave National Park, Kentucky. **F–I**, MACA 64335 (holotype), anterolateral tooth in **F**, labial; **G**, lingual; **H**, oral; and **I**, aboral views. **J–N**, MACA 64336, distolateral tooth in **J**, labial; **K**, lingual; **L**, distal; **M**, oral; and **N**, aboral views. **O–R**, MACA 64337, partial anterolateral tooth in **O**, labial; **P**, lingual; **Q**, oral; and **R**, aboral views. **S–T**, MACA 64339, partial anterolateral tooth from the Haney Formation of Mammoth Cave National Park, Kentucky in **S**, labial; **T**, lingual views. **U–X**, teeth from the Hartselle Sandstone-equivalent shale interval. **U–X**, ALMNH:Paleo: 9775, partial mediolateral tooth in **U**, labial; **V**, lingual; **W**, oral; and **X**, aboral views. **Y–AA**, ALMNH:Paleo: 9831, partial anterolateral tooth in **Y**, labial; **Z**, lingual; and **AA**, aboral views. **BB–DD**, ALMNH:Paleo: 9835, partial anterolateral tooth in **BB**, labial; **CC**, oral; and **DD**, aboral views. **EE–GG**, ALMNH:Paleo: 9808, partial anterolateral tooth in **EE**, labial; **FF**, oral; and **GG**, aboral views. **HH–JJ**, ALMNH:Paleo: 9839, partial anterolateral tooth in **HH**, labial; **II**, oral; and **JJ**, aboral views. **KK–OO**, teeth from the Bangor Limestone, Alabama. **KK–MM**, ALMNH:Paleo: 9810, distolateral tooth in **KK**, labial; **LL**, lingual; and **MM**, aboral views. **NN–OO**, ALMNH:Paleo: 8919, distolateral tooth in **NN**, labial and **OO**, aboral views. Scales **A–E**, **O–T**, and **Y–OO** equal 5 mm; **F–N** and **U–X** equal 10 mm.

basolabial depression is present. The tooth base is reniform in shape, being mesiodistally longer than labiolingually wide. The lingual torus is convex, about three-quarters labiolingually wide as the mesiodistal length and broadly rounded on the mesiodistal margins. The basolabial projections consist of two well-developed button-like pads. The orolingual projections consist of two well-developed button-like pads positioned between the median cusp and lingual rim. A few nutrient foramina are present along the lingual rim. On the aboral surface of the tooth base, a shallow depression is present between the basolabial projection and the lingual rim with a few nutrient foramina.

The visceral arches (MACA 64342; Fig. 4) preserved in the ceiling of a passage cutting through the Ste. Genevieve Formation at Mammoth Cave National Park contain 27 teeth of the same morphology as described above, 5–6 mm in mesiodistal length at the tooth base (Fig. 5). All visceral elements are exposed medially and are from the right side. The exposed portions of the palatoquadrate and Meckel's cartilage and the slightly raised surfaces of the jaws under the sediment suggest the jaws were approximately 100 mm long. Sediment has filled the dental portion of the palatine ramus so a count of the tooth families is unavailable. The palatine ramus is dorsoventrally deep and short craniocaudally. Though sediments cover the dorsal surfaces of the otic process, the proportions exposed suggest it was dorsoventrally deep and less expanded craniocaudally. The articular process of the quadrate is ventroposteriorly directed and relatively elongated. The Meckel's cartilage is dorsally concave and ventrally convex. The mandibular knob is well-developed and the Meckel's cartilage bears a short retroarticular flange. The medial surface of the lower jaw exposes a single dental sulcus. The hyomandibula is a strap-like cartilage with shallow grooves anteriorly and along the ventral margin. Two strap-like branchial arches are exposed on the surface of the passage and three others are indicated just under the surface of the sediments.

Comparison and Remarks—The dentition of *Glikmanius careforum* shares with other *Glikmanius* species (*G. occidentalis*, *G. myachkovensis*, and *G. culmenis*) the presence of a prominent unserrated median cusp, singular but prominent lateral and intermediate cusps, multiple fine cristae on the labial and lingual sides of the cusps, relatively well-developed deep basolabial depression, and pairs of button-like basolabial and orolingual projections (Ginter et al., 2005; Hodnett et al., 2012; Koot et al., 2013). *G. careforum* differs from the other three species of *Glikmanius* by having a proportionately shorter median cusp that is also wider at the base, robust lateral and intermediate cusps, and the basolabial depression not as deep and relatively wider compared with the other three species. *Glikmanius careforum* outwardly has a similar appearance to *Glencartius* and *Dracopristis* in having low proportionately broader cusps, but differs in having fine longitudinal cristae; in *Glencartius* and *Dracopristis*, the longitudinal cristae are prominent and less numerous (Ginter & Skompski, 2019; Hodnett et al., 2021a). The visceral arches of *Glikmanius careforum* preserved at Mammoth Cave National Park are not fully exposed but can be compared with other ctenacanthiform taxa. The palatoquadrate of *G. careforum* appears to bear a relatively craniocaudally short though dorsoventrally tall otic process, similar to that of *Dracopristis* (Hodnett et al., 2021a), although *G. careforum* has an articular process of the quadrate that is more elongated and directed ventroposteriorly, as seen in *Heslerodus* and *Ctenacanthus* (Hodnett et al., 2021a; Stahl, 1988; Williams, 1985). The palatine ramus is relatively dorsoventrally deep, similar to that seen in *Dracopristis*, and craniocaudally short like that of *Dracopristis* and *Heslerodus* (Hodnett et al., 2021a; Stahl, 1988; Williams, 1985). The posterior end of the Meckel's cartilage is curved like that seen

in *Dracopristis* (Hodnett et al., 2021a), and does not have a dorsally less recurved margin as seen in *Heslerodus* (Stahl, 1988; Williams, 1985). Overall, the lower jaw of *G. careforum* appears proportionately less dorsoventrally deep compared with either *Heslerodus* or *Dracopristis*, but still proportionately deeper compared with *Cladodus elegans* and an unnamed Late Mississippian taxon from the Bear Gulch Limestone (Ginter & Maisey, 2007; Hodnett et al., 2016, 2021a). The hyomandibula in *G. careforum* is similar to *Heslerodus* in not being dorsoventrally expanded at the proximal end (Stahl, 1988) as seen in *Dracopristis* (Hodnett et al., 2021a). From the proportions of the upper and lower jaws, we propose that *G. careforum* had a short, robust head, similar in proportion to those of *Dracopristis* and *Heslerodus* (Hodnett et al., 2021a; Stahl, 1988).

DISCUSSION AND CONCLUSIONS

Taxonomic Remarks

The new ctenacanth taxa *Troglocladodus trimblei* and *Glikmanius careforum* add to our knowledge of the diversity of ctenacanth of the Middle and Late Mississippian along Laurentia's southwestern coastline. Both taxa appeared during the Middle Mississippian (Viséan stage) and extended into the Late Mississippian (Serpukhovian stage) during the closing of the Rheic Ocean that closed off the connection to the European marine platform at the end of the Mississippian (Feichtinger et al., 2021). *Troglocladodus* may have been endemic to the southwestern waters of Laurentia, as it has not yet been identified from western North American Middle to Late Mississippian marine sites or elsewhere in Europe or Asia. The increased number of intermediate cusps on the lateral teeth and more pronounced longitudinal cristae may suggest that *Troglocladodus* was either a generalist predator or had a more specific feeding niche. The teeth of *Troglocladodus* are superficially similar to those of *Glencartius* and *Dracopristis*, as well as the early euselachian *Sphenacanthus*, featuring pronounced crown ornamentation that may have increased the ability to grasp the surfaces of hardshell prey such as arthropods or cephalopods (Compagno, 1990; Hodnett et al., 2012). From the tooth dimensions of the observed samples of both adult and juvenile teeth, *Troglocladodus* may have spent its life cycle as a juvenile to adult in the same coastal waters, possibly reaching 3 meters as an adult based on the largest tooth sampled. Based on dental morphology, it is probable that *Troglocladodus* is more closely related to *Goodrichthys* than to *Cladodus* (more pronounced longitudinal cristae, shorter lateral cusps, shorter labiolingual width of the tooth base, and a number of small labial foramen present between the labial rim and the base of the crown).

Glikmanius appears to have been more widespread, although not as abundant as taxa such as *Cladodus* or *Saivodus*, both of which are known from numerous localities in North America and Europe (Duffin & Ginter, 2006; Ginter et al., 2010; Feichtinger et al., 2021). As noted above, aside from *Glikmanius careforum*, the only other Middle to Late Mississippian *Glikmanius* records are the single Middle Mississippian tooth referred to “*Symmorium*” *occidentalis* from Russia (Lebedev, 1996) and isolated teeth from the Late Mississippian Heath Formation of Montana (Ginter et al., 2005; Lund, 1985). The tooth described by Lebedev (1996) unfortunately is only figured in oral view, not allowing for complete comparison with *G. careforum*, but from the description and figure (Lebedev, 1996:fig. 7) it is apparent that this is a different species of *Glikmanius*, although most likely not *G. occidentalis*. The isolated *Glikmanius* teeth figured by Lund (1985) and Ginter et al. (2005:fig. 1b) show that at least two morphologies of teeth occurred in the Heath Formation. CM 37524 (Lund, 1985:fig. 8c, d) has the most similarities to *G. careforum*, while CM 41063 (Lund, 1985:fig. 8a, b) and CM

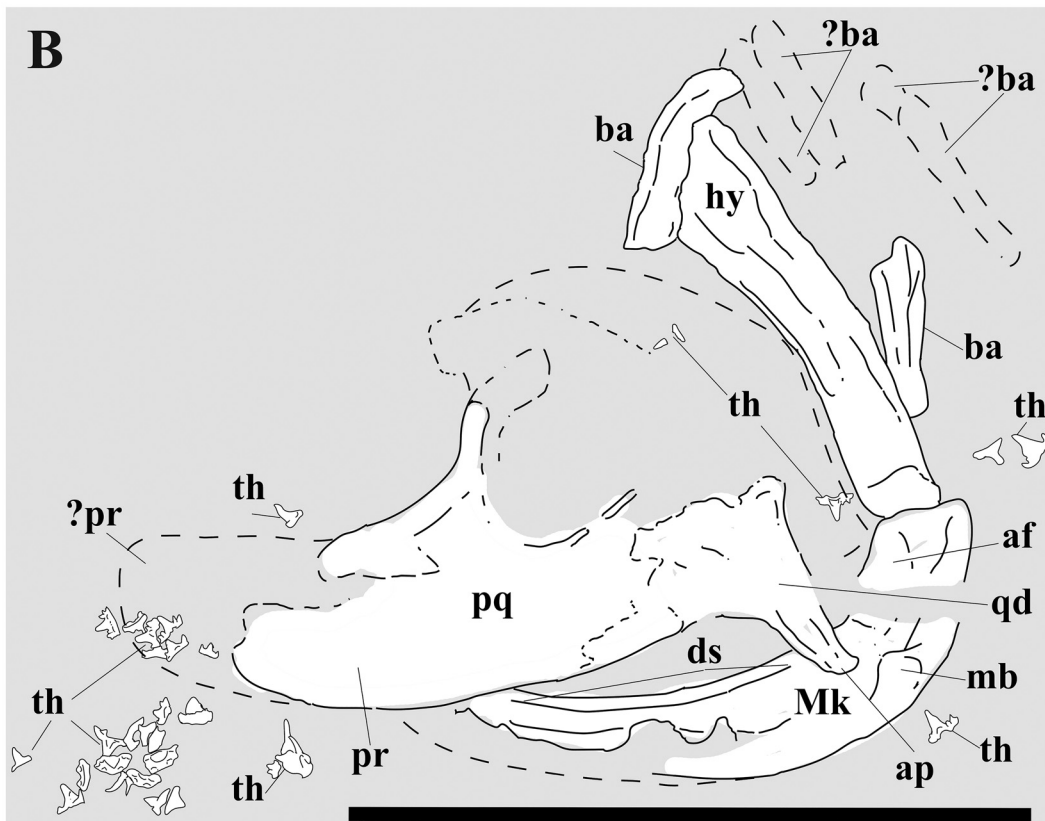
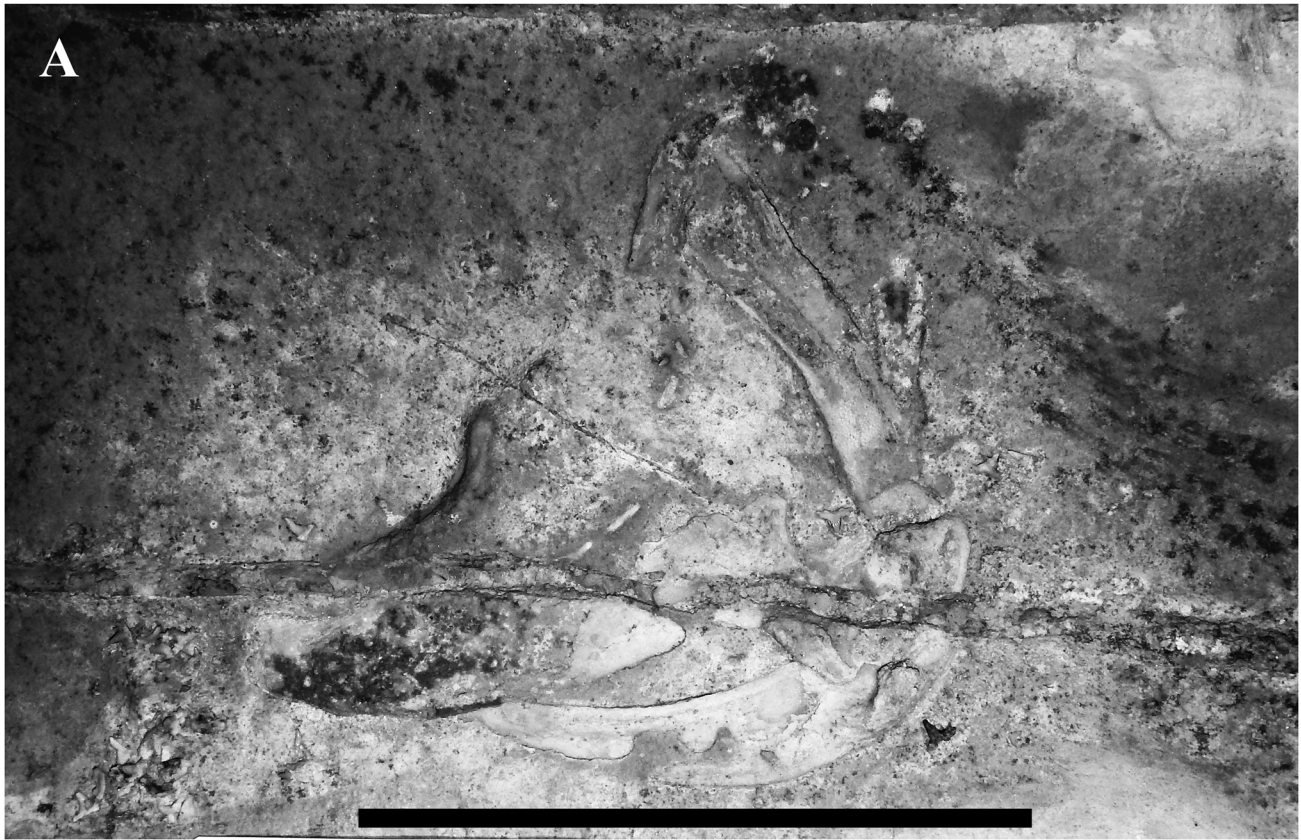


FIGURE 4. MACA 64342, the visceral cartilages and teeth of *Glikmanius careforum* in situ in the Ste. Genevieve Formation at Mammoth Cave National Park, Kentucky. **A**, photograph of the specimen. **B**, line diagram of the exposed and subsurface cartilages. **Abbreviations:** **af**, articular facet; **ap**, articular process of the palatoquadrate; **ba**, branchial arch; **ds**, dental sulcus; **hy**, hyomandibula; **mb**, mandibular knob; **Mk**, Meckel's cartilage; **pq**, palatoquadrate; **pr**, palatine ramus; **qd**, quadrate process of the palatoquadrate; and **th**, tooth or teeth. Scale bars equal 100 mm.

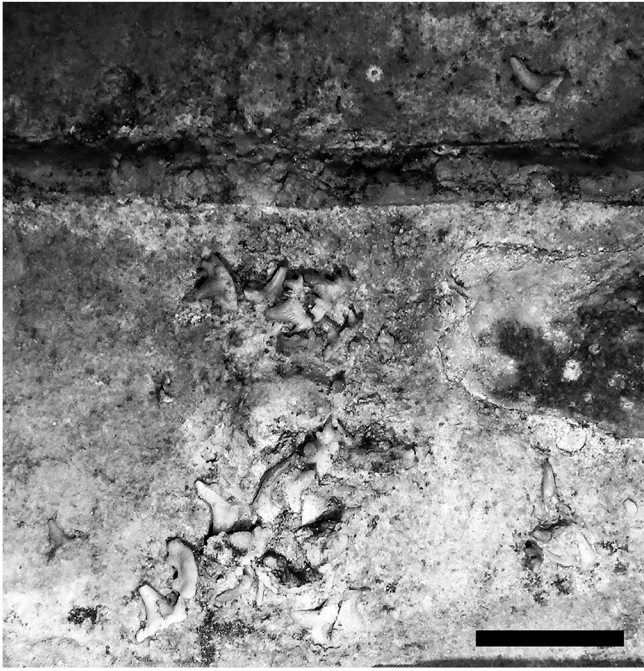


FIGURE 5. Close-up of the cluster of *Glikmanius careforum* teeth of MACA 64342. Scale equals 10 mm.

44504B (Ginter et al., 2005:fig. 1b) are unique in having two intermediate cusps between the median and lateral cusps and could represent a different species of *Glikmanius* or *Glikmanius*-like taxon. Based on the samples presented here, *G. careforum* was a generalist predator, much like its Pennsylvanian to Permian relatives (Compagno, 1990; Hodnett et al., 2012; Koot et al., 2013). From the tooth dimensions of the observed samples of adult teeth, *G. careforum* may have possibly reached 3 meters as an adult based on the largest teeth sampled.

Observations on the Diversity Trends of Ctenacanthiformes

The Ctenacanthiformes had a series of diversification events, beginning in the Late Devonian and lasting well into the Middle Permian (Fig. 6). Ctenacanth sharks first appeared in the fossil record during the Late Devonian with the appearance of *Cladodoides* during the Frasnian, which is a taxon known from both skeletal material and isolated teeth from the Late Devonian to Early Mississippian (Ginter et al., 2010; Gross, 1937, 1938; Ivanov & Plax, 2018; Jaekel, 1921; Maisey, 2005). By the Famennian, the genera *Ctenacanthus* and *Tamiobatis* had appeared and diversified into multiple species, with both partial to nearly complete skeletal information and isolated teeth (Ginter, 2010; Ginter et al., 2010; Ivanov & Plax, 2018; Williams, 1998). Isolated skeletal elements and teeth of indeterminate ctenacanthiforms demonstrate that ctenacanth were nearly worldwide by the end of the Devonian (Greif et al., 2022; Roelofs et al., 2016). Also, by the Late Devonian, ctenacanth such as *Ct. tumidus* reached large body sizes and were in competition with other apex predators of the time, such as the arthrodire placoderms (Engelman, 2023; Friedman & Sallan, 2012; Ginter, 2010). After the Hangenberg extinction event at the end of the Devonian, during the Early Mississippian (Tournaisian), chondrichthyan began a major speciation radiation (Friedman & Sallan, 2012).

Our knowledge of ctenacanth species during the Early Mississippian is presently limited by isolated teeth, but it is known that forms such as *Tamiobatis* and *Cladodoides* survived the

Hangenberg extinction event, with *Cladodoides* representing the Ctenacanthidae and *Tamiobatis* representing a yet-to-be formalized “*Tamiobatis/Saivodus*” family group (Ginter et al., 2010; Hodnett et al., 2012, 2021a). It is at this time we see the earliest members of the Heslerodidae, evident from an unnamed form from the Muhua Village vicinity of southern China, which shares a well-developed basolabial depression and two button-like basolabial projections (Ginter & Sun, 2007). By the Middle Viséan, the Ctenacanthidae had radiated into multiple taxa, e.g., *Cladodus*, *Goodrichthys*, and *Troglocladodus* (Duffin & Ginter, 2006; Ginter, 2009; this paper). *Cladodus*, as currently understood, evolved into multiple species during the Viséan, with medium body size (2–3 meters on average) to large size (4–5 meters) based on tooth dimensions (Duffin & Ginter, 2006). *Saivodus* also appeared during the Viséan and was one of the largest ctenacanth to have evolved by this time, with body estimates between 6–8 meters in length (Duffin & Ginter, 2006; Hodnett et al., 2020). We also see the beginning radiation of the Heslerodidae with the appearance of *Glencartius* and *Glikmanius* (Ginter et al., 2010; this paper). *Glencartius* was a small ctenacanth, under a meter in length (Ginter & Skompski, 2019) and *Glikmanius* reached approximately 3 meters in length. With the onset of the Late Mississippian (Serpukhovian), many of the Ctenacanthidae went extinct, with the exception of *Cladodus gailensis* and *Troglocladodus*. *Saivodus* continued to flourish during the Late Mississippian, retaining its large body size. A much smaller (30 cm body length) *Saivodus*-like taxon occurred at this time as well (Hodnett et al., 2016). *Glencartius* seemed to have survived into the Late Mississippian based on isolated teeth we have observed from the Bangor Limestone, but further work is needed to verify this record. *Glikmanius* also was present but not abundant during the Late Mississippian (Ginter et al., 2005).

The beginning of the Pennsylvanian saw a decline in ctenacanth shark diversity. The Ctenacanthidae appears to have gone extinct by this time; dorsal fin spines are still sometimes referred to *Ctenacanthus* (Itano et al., 2003), but *Ctenacanthus*-type or *Cladodus*-type teeth have not been identified from Pennsylvanian-age strata. The small heslerodid ctenacanth *Heslerodus* appeared during the Bashkirian and flourished well into the Permian (Ginter, 2005; Ginter et al., 2010; Hodnett et al., 2012). Though there is a short gap in its record from the end of the Mississippian to the beginning of the Pennsylvanian, *Glikmanius* was present in the Middle Pennsylvanian, with *G. occidentalis* extending into the Middle Permian (Ginter et al., 2005; Hodnett et al., 2012, 2021a). By the Late Pennsylvanian, *G. myachkovensis* had appeared and was already widespread (Ginter et al., 2005). We also see the presence of rarer forms such as *Heslerodoides* and *Dracopristis* with more specialized dentitions (Hodnett et al., 2021a; Ivanov, 2022). *Dracopristis* in particular evolved a specialized body form that was suited for a more benthic lifestyle, with enlarged dorsal fin spines to deter larger predators (Hodnett et al., 2021a). Large *G. occidentalis* teeth (approximately 4 cm wide at the tooth base) are known by the Late Pennsylvanian and have been found in the same vicinity as partial ctenacanth neurocranial fragments from the Finis Shale in Texas, representing massive sharks more than 6 meters in length (Maisey et al., 2017). If these large *Glikmanius* teeth do correspond with the large ctenacanth neurocranium fragments, it could suggest that the Late Pennsylvanian *G. occidentalis* were some of the largest predatory fish of their time (Maisey et al., 2017).

By the Middle Permian, we see the reappearance of *Saivodus* and the appearance of its relative *Neosaivodus* of the “*Saivodus* group” (Hodnett et al., 2012; Kapoor & Sahni 1971). We also see a greater diversity of heslerodid ctenacanth with *Heslerodus*, *G. occidentalis*, and *G. myachkovensis* along with new appearances of *G. culmenis*, *Kaibabvenator*, and *Nanoskalmes*

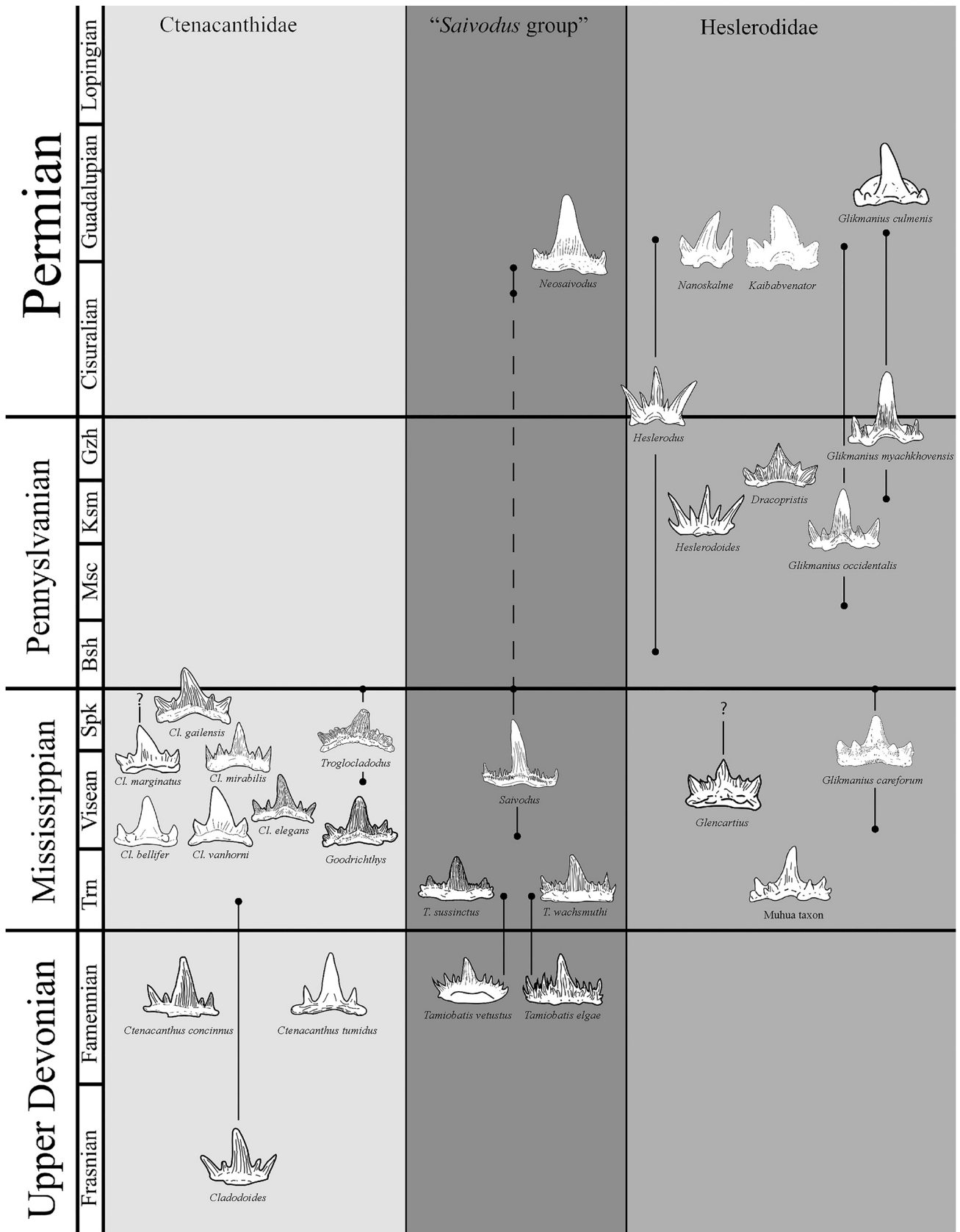


FIGURE 6. Chronological distribution of the Late Devonian to Permian Ctenacanthiformes.

(Hodnett et al., 2012; Koot et al., 2013). *Kaibabvenator* shows evidence of large body sizes, with teeth reaching 3–4 cm wide (suggesting body sizes reaching 5–6 meters in length), as well as broad cusps with the first evidence of serrations evolving in the ctenacanth lineage (Hodnett et al., 2012). At this time there is little evidence of ctenacanth sharks during the Late Permian, making their latest Paleozoic evolutionary history still enigmatic.

ACKNOWLEDGMENTS

We are greatly indebted to Mammoth Cave National Park (MACA) Superintendent Barclay Trimble and head of the MACA Science and Resource Management unit, Timothy Pinion, for their support of our paleontological resource inventory and research into the Mississippian fish assemblages. The success of our Mammoth Cave PRI project is largely in part due to a dedicated group of staff and volunteers who have helped us document new fossil localities and spot new fossils within the passages of Mammoth Cave. Park guide Rich Boldon has been instrumental in the discovery of a number of new fossil localities for this project. We also thank our fossil “spotters” K. Alessi, B. Belanger, K. Bobo, M. Cecil, M. Cleveland, J. Douglas, A. Flowers, C. Groves, M. Harris, J. Honaker, E. Jakaitis, P. Kambesis, N. Leies, M. May, K. Mikowski, M. Schorr, S. South, B. Trimble, and E. Winkler. We would like to thank A. Klompmaker of the Alabama Museum of Natural History Paleontology Collections for allowing us to reposit and study this material. We thank R. Keyes for his insights on the lithology and depositional environment of Cedar Creek Reservoir. We would also like to thank the Birmingham Paleontological Society (BPS) for their support throughout the project. Special thanks to D. Elliott for reviewing an earlier draft of the manuscript.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the author(s).

AUTHOR CONTRIBUTIONS

JPH, RT, CE, JST, and VLS designed the project, JPH drafted the manuscript, JPH, RT, CE, GW, JRW, RO, and KT gathered data, and JPH analyzed the data. All authors edited the manuscript.

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Handling Editor: Charlie Underwood.