

A NEW EUCHONDROCEPHALAN CHONDRICHTHYAN (CHONDRICHTHYES, EUCHONDROCEPHALI) FROM THE MIDDLE MISSISSIPPIAN (VISÉAN) JOPPA MEMBER OF THE STE. GENEVIEVE FORMATION AT MAMMOTH CAVE NATIONAL PARK, KENTUCKY, USA AND A REASSESSMENT OF THE LOWER MISSISSIPPIAN (TOURNAISIAN-VISÉAN) “*HELODUS*” *COXANUS* NEWBERRY, 1897

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Abstract—A new euchondrocephalan chondrichthyan, *Macadens olsoni* gen. et sp. nov., is identified from the Middle Mississippian (Viséan) Joppa Member, Ste. Genevieve Formation from Mammoth Cave National Park, Kentucky. *Macadens olsoni* shares various morphological traits with the enigmatic taxon “*Helodus*” *coxanus* Newberry 1897, from the Lower-Middle Mississippian (Tournaisian) Keokuk Limestone of Iowa. These morphological traits of a lower symphyseal on a narrow mesiodistally elongated base with rounded and blunt cusps are not seen in *Helodus* and we create a new genus name and combination, *Rotuladens* gen. nov. *coxanus* Newberry 1897. *Macadens* and *Rotuladens* are proposed as members of unnamed clade with a sister-group relationship with Eugeneodontiformes.

INTRODUCTION

The subclass Euchondrocephali, is a diverse group of cartilaginous fishes with an extensive fossil record dating back to the Devonian to the Recent that includes extant holocephalans (Lund and Grogan, 1997; Stahl, 1999; Ginter et al., 2010). The greatest diversification of euchondrocephalans occurred during the Mississippian subperiod of the Carboniferous, which saw numerous genera filling a large assortment of ecological niches around the world (Lund and Grogan, 1997; Lund et al., 2015; Schnetz et al., 2024). Most of what we know of the Mississippian euchondrocephalans had historically been based on isolated teeth and dermal elements collected and described in the mid to late 1800’s (Newberry and Worthen, 1870; St. John and Worthen, 1875, 1883; Davis, 1883; Newberry, 1897). Additional more complete samples of euchondrocephalans consisting of partial to complete skeletons have come to light more recently, allowing for better resolution of the anatomy and relationships of these cartilaginous fishes (i.e. Lund and Grogan, 1997; Lund et al., 2015).

Of interest here is the recent discovery of a diverse chondrichthyan assemblage from the Middle Mississippian Joppa Member of the Ste. Genevieve Formation exposed in the world’s longest cave system, Mammoth Cave National Park in Kentucky, which has produced a large sample of teeth and dermal elements of euchondrocephalan chondrichthyans (Hodnett et al., 2024a). Recently, one of us (KT) collected a unique tooth whorl from one of the cave passages within Mammoth Cave that shares similar morphological traits with an enigmatic taxon “*Helodus*” *coxanus* Newberry, 1897 from the Lower-Middle Mississippian (Tournaisian-Viséan) Keokuk Limestone, Keokuk, Iowa. Here we present a revaluation of the type specimen of “*Helodus*” *coxanus* and its taxonomic position along with a description of a new related taxon from Mammoth Cave.

“*Helodus*” *coxanus* Newberry, 1897—The euchondrocephalan known as “*Helodus*” *coxanus* was first described by Newberry (1897) from a single tooth whorl (USNM V 3518) from the Keokuk Limestone and was named for its discoverer, L. A. Cox (Fig. 1). The Keokuk Limestone is dated as Early-Middle Mississippian (Osagean, Tournaisian-Viséan). Newberry (1897) interpreted “*Helodus*” *coxanus* as a

type of cochliodont holocephalan median tooth. Eastman (1902) relied written communication from Orestes St. John, in 1871 in that St. John commented that this tooth type represents the symphyseal series of *Cochliodus leidy* (Stahl, 1999). Itano and Lambert (2018) provided a brief overview of “*Helodus*” *coxanus* and concluded that its inclusion in the genus *Helodus* was not warranted based on its morphology. We agree with Itano and Lambert (2018) and assign a new genus, *Rotuladens* for this taxon and provide a new hypothesis on its relationship within Euchondrocephali and with the new taxon from Mammoth Cave National Park described below.

GEOLOGIC SETTING

The Mississippian strata found at Mammoth Cave National Park in central Kentucky (Fig. 2A) represent one of the southeasternmost portions of the ancient marine Illinois Basin (Fig. 2B) (Palmer, 1981). The euchondrocephalan

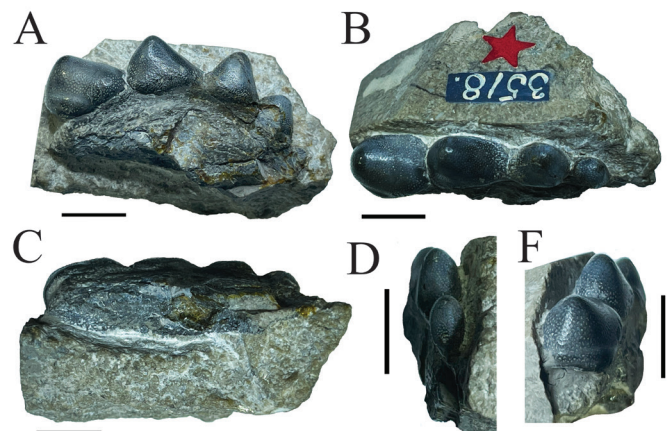


FIGURE 1. USNM V 3518, holotype of *Rotuladens* gen. nov. *coxanus* (Newberry, 1897), a lower symphyseal tooth from the Lower Mississippian (Tournaisian) Keokuk Limestone, Keokuk, Iowa. A) right distal view, B) oral view, C) aboral view, D) labial view, E) lingual view. Scale equals 10 mm.

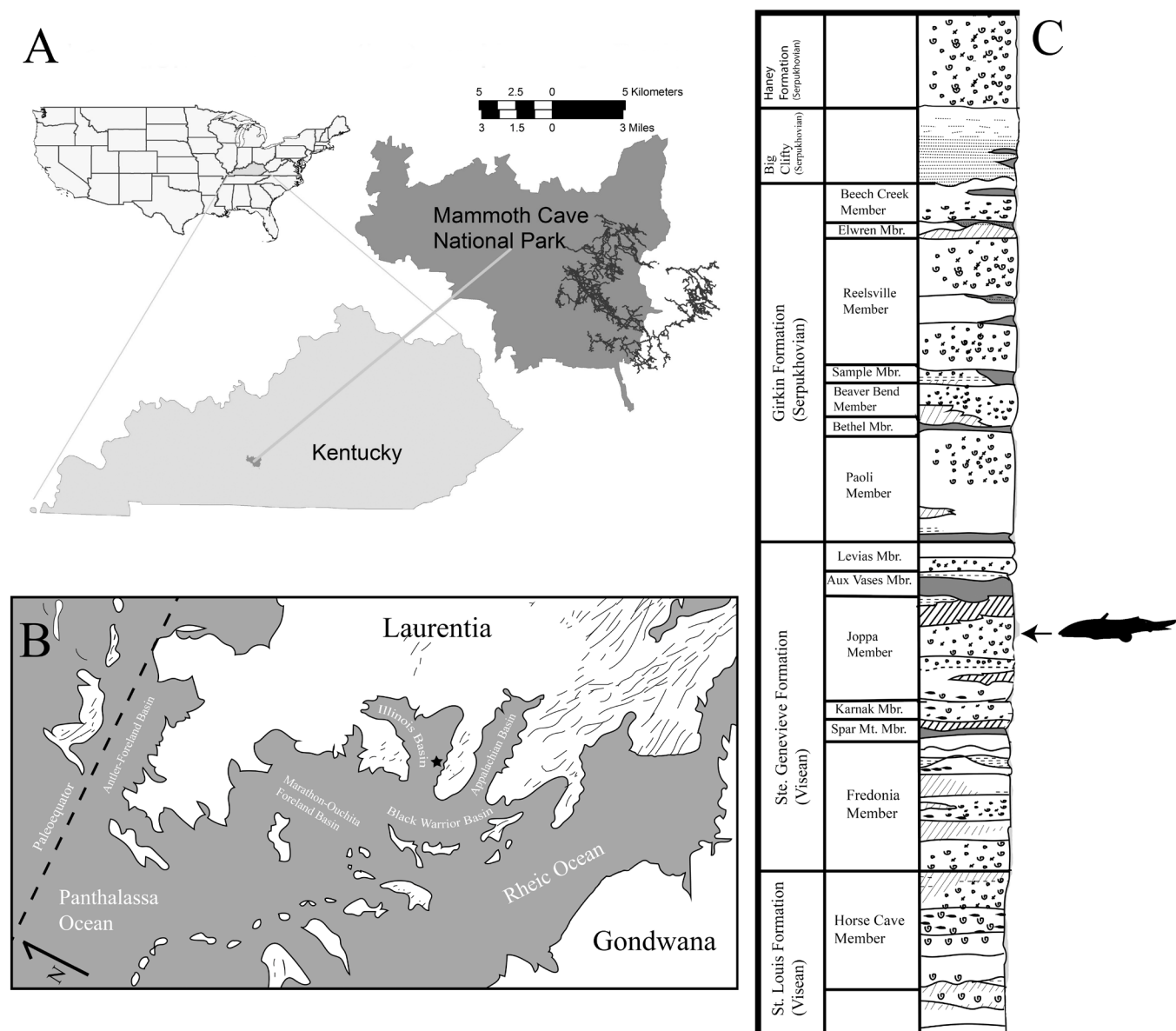


FIGURE 2. Location and stratigraphy of Mammoth Cave National Park, Kentucky. **A)** location of Mammoth Cave National Park in Kentucky. **B)** The relative paleogeographic position of Mammoth Cave National Park in the Illinois Marine Basin during the Middle Mississippian (Viséan) of Laurentia. **C)** The stratigraphic position of the obruchevoidid petalodonts from the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave National Park, Kentucky.

fossils presented here were collected from passageways within Mammoth Cave National Park, Kentucky that cut through the Middle Mississippian Joppa Member (J2 bed) 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 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 (Fig. 2C). At present, more than 70 taxa of fish have been identified

from this geologic horizon (Hodnett et al. 2024a), including the type specimens of the ctenacanth *Troglodactylus trimblei* and *Glikmanius careforum*, and the janassid petalodont *Strigilodus tollesonae* (Hodnett et al. 2023, 2024b).

MATERIALS AND METHODS

Specimens collected from Mammoth Cave National Park were part of a National Park Service Paleontological Resource Inventory between 2019-2022 from the cave walls and ceiling (Fig. 3). Fossils were extracted from the cave walls or ceilings with a dental pick. Screenwashing of loose cave floor sediments from some cave passages was accomplished with graded sieves. 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. Photography of the fossils presented here were captured with an AmScope camera mounted



FIGURE 3. Photo of holotype to *Macadens olsoni* gen. et sp. nov., in situ at Mammoth Cave National Park, Kentucky, of the upper Joppa Member grainstone consisting of primarily of invertebrate debris, such as the crinoid stem fragments seen above the tooth. Scale in mm.

on a stereoscope microscope with a metric scale bar. Figures were created with Adobe Illustrator 2023 and Photoshop 2023.

Institutional Abbreviations—MACA, Mammoth Cave National Park, Kentucky; USNM, Smithsonian National Museum of Natural History, Vertebrate Paleontology Collections, Washington D.C.

SYSTEMATIC PALEONTOLOGY
CLASS Chondrichthyes Huxley, 1880
SUBCLASS Euchondrocephali Lund and Grogan, 1997
FAMILY Indeterminate
Rotuladens gen. nov.

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Type species—*Helodus coxanus* Newberry, 1897.

Included species—Only the type species.

Type specimen—USNM V 3518, a lower symphyseal tooth whorl.

Distribution—Lower-Middle Mississippian (Tournaisian-Viséan) Keokuk Limestone, Keokuk, Iowa.

Etymology—Latin rotula, little wheel, and, Latin, dens, tooth; in reference to the recurved tooth whorl morphology.

Diagnosis—Small holocephalimorph chondrichthyan with symphyseal tooth whorl bearing five symmetric cusps, the largest positioned lingually and the smallest positioned labially, on a long mesiodistally thin base that is positioned directly under the crowns. The tooth base of the symphyseal tooth recurves labially.

Comments—See below for discussion of the anatomical differences between *Rotuladens* and *Macadens* and *Helodus*.

***Macadens* gen. nov.**

urn:lsid: zoobank.org:pub:24DD62EE-6E0E-4D12-BD72-E2F2FDF61318

Type species—By monotypy.

Diagnosis—As for type species by monotypy.

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

Etymology—MACA, the National Park Service acronym for Mammoth Cave National Park, Kentucky and, Latin, *dens* (tooth); in recognition of this unique tooth taxon found in the world's longest cave system.

Remarks—See Comparison and remarks, below.

***Macadens olsoni* sp. nov.**

Holotype—MACA 62366, a complete lower symphyseal tooth.

Diagnosis—Small holocephalimorph chondrichthyan with teeth bearing blunt low crowns consisting of tritorial dentine and with thin tooth bases of trabecular and lamellar dentine. Symphyseal tooth whorl bearing three labiolingually symmetrical cusps, the largest positioned lingually and the smallest positioned labially, on a long thin base that is positioned directly under the crowns. The tooth base of the symphyseal tooth is recurve labially. Anterior tooth with a large, low and blunt median cusp and a blunt minute distal cusp with expanded lingual surface with a rounded mesial ridge and a thin lingual ridge, on a thin triangular tooth base. Mediolateral tooth with three blunt cusps, the medial cusp being the tallest, all cusp bearing a singular labial vertical ridge, a small ridge present on lingual margin, crown resting on a thin tooth base.

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

Description—The holotype (MACA 62366; Fig. 4) is a symphyseal tooth that is 10 mm long, with the first labial cusp 2 mm in length, the medial cusp 4 mm in length, and the lingual cusp 3 mm in length. The labial cusp is triangular in outline with the longest side on the lingual margin, relatively laterally compressed and bears a relatively blunt apical point. The median cusp bears a blunt apical point, is more labiolingually expanded and triangular with relatively evenly lengthen labial and lingual margins, though more expanded on the distal margins on the lingual side in oral view (Fig. 4D). The lingual cusp, though not as elongated as the median cusp, is greatly expanded with flaring distal margins, a concave labial margin and a convex lingual margin, with a robust and blunt apical point. The tooth base is recurved, originating towards the labial margin of the lingual cusp and extending beyond the labial cusp. Viewed aborally (Fig. 4F), the tooth base is thin with the lingual margin expanded distally and narrows to a point labially. A thin shallow trough is present on the aboral surface, punctuated with numerous small, circular to narrow ovate vascular openings. Similar narrow ovate vascular openings also occur along the distal margins of the tooth base. A large number of circular vascular openings are present on the lingual aboral side of the lingual cusp.

We also refer two additional teeth from the same stratigraphic horizon from Mammoth Cave National Park to *Macadens olsoni* due to their similarity in dental tissue anatomy and cusp and tooth base morphologies. MACA 62070 (Fig. 5) is 3 mm in length and is approximately 2.5 mm tall and is interpreted as anterolateral tooth. The crown has a low blunt median cusp and a small minute mesial cusp. The lingual margin is more vertically expanded compared to the labial margin and bares a thin lingual ridge above the tooth base. The tooth base is lingually directed and has a thin triangular aboral ridge that is slightly recurved mesiodistally. The labial and lingual surfaces of the base had numerous vascular openings.

MACA 62357 (Fig. 6) is 5 mm long and approximately 3.5 mm tall and is interpreted as a mediolateral tooth. The crown has three blunt cusps that bear a single labial vertical ridge. The median cusp is relatively tall and has a blunt apical point.

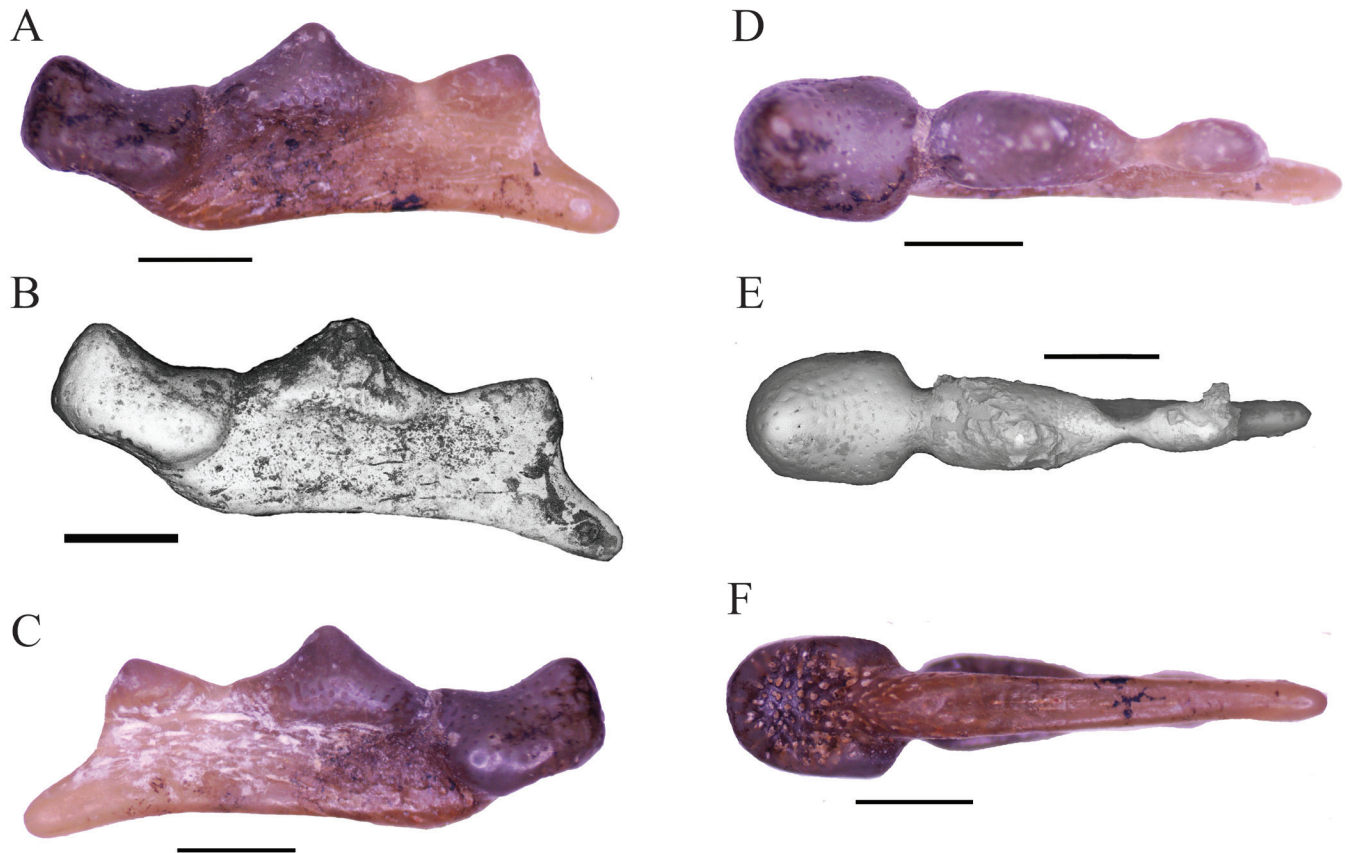


FIGURE 4. MACA 62366, holotype to *Macadens olsoni* gen. et sp. nov, lower symphyseal tooth. **A)** left distal view, **B)** SEM image of left distal view, **C)** right distal view, **D)** oral view, **E)** SEM image of oral view; note sediment presence prior to additional preparation, **F)** aboral view. Scale equals 2 mm.

The mesial and distal cusps are approximately two-thirds the height of the median cusp and are robust and bluntly pointed, the distal cusp being slightly more enlarged than the mesial cusp. The lingual margin above the tooth base bears a small ridge. The tooth base is lingually directed and labiolingually thin with numerous vascular openings on both sides.

Etymology—In honor of retired National Park Service ecologist and cave scientist Rickard Olson, who served at Mammoth Cave National Park for 27 years, mapping, exploring, and studying the geological and biological resources in the world's longest cave system and other NPS park cave sites.

Additional Material—MACA 62070, anterolateral tooth; MACA 62357, mediolateral tooth (Figs. 5 and 6).

Comparison and remarks—We tentatively consider *Macadens olsoni* as an euchondrocephalan chondrichthyan because the cusps consist of tritorial dentine on thin bases of trabecular and lamellar dentine. This dental tissue anatomy is consistent with other euchondrocephalans taxa such as the enigmatic *Harpacanthus fimbriatus* and members of the superorder Holocephali (Stahl 1999; Lund and Grogan 2004a).

The holotype symphyseal tooth of *Macadens olsoni* shares several traits with *Rotuladens coxanus* (Newberry 1897; USNM 3518, Fig. 7), that include anteriorly rounded to bluntly triangular shaped posterior crowns on a labiolingually narrow base. *M. olsoni* differs from *R. coxanus* in having an oral-aborally shorter tooth base with a mesially extended process, reduced number of crowns on the whorl, and relatively mesiodistally wider posterior crown with a more posteriorly positioned apex. The cusps of the symphyseal whorls of *Macadens* and *Rotuladens* have a superficial appearance to the teeth of *Helodus*; they lack

the mesiodistal narrow bar-like processes of the crown that is typical of the teeth referred to the genus nor do any of the tooth whorls of *Helodus* have narrow mesiodistally elongated bases (Stahl, 1999; Coates et al. 2021; Johanson et al. 2021). The teeth of *Helodus* have low, mesiodistally wide and labiolingually narrow bases that are aborally convex, with numerous vascular openings (Stahl, 1999; Coates et al. 2021; Johanson et al. 2021).

The morphology of the symphyseal tooth whorls of *Macadens* and *Rotuladens* with symmetrical cusps on a labiolingually directed narrow tooth base is superficially like that seen in eugeneodontiform chondrichthyans (Nielsen, 1932, 1952; Zangerl, 1981; Tapanila et al. 2020). However, the crowns of most eugeneodont lower symphyseal tooth whorls have paired anterior directed processes and a deep aboral labiolingual directed groove (Ginter et al. 2010; Tapanila et al. 2020). *Macadens* and *Rotuladens* lack the paired anterior processes on the crowns and only have a faint or shallow aboral aboral groove on the base. *Macadens* and *Rotuladens* also lack root scars, like those on the symphyseal teeth of *Edestus*, that also lacks an aboral groove on the base (Tapanila and Pruitt, 2019). This lack of root scars suggests that *Macadens* and *Rotuladens* did not have shedding crowns for the symphyseal tooth whorl, which is seen in younger *Helodus* samples and *Edestus* which shed their teeth (Tapanila and Pruitt, 2019; Johanson et al. 2021). However, with the currently available data, we cannot suggest that *Macadens* and *Rotuladens* had a continuously growing symphyseal tooth whorl like that seen in other eugeneodontiforms (Tapanila et al. 2020).

The two lateral teeth referred to *Macadens olsoni* (MACA 62070 and MACA 62357) share the same dental anatomy of

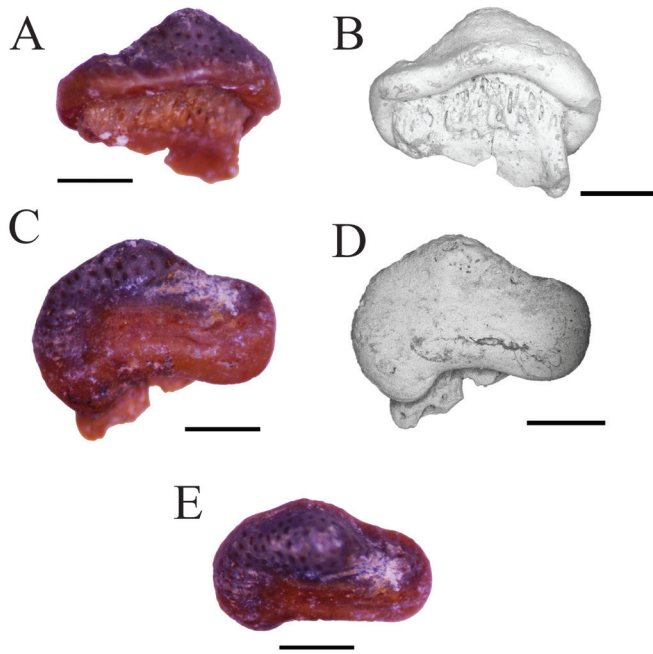


FIGURE 5. MACA 62070, specimen referred to *Macadens olsoni* gen. et sp. nov, anterolateral tooth. **A)** labial view, **B)** SEM image of labial view, **C)** lingual view, **D)** SEM image of lingual view, **E)** oral view. Scale equals 1 mm.

the cusps to the holotype symphyseal tooth whorl consisting of tritorial dentine on thin bases of trabecular and lamellar dentine and bear a superficial resemblance to the cusps of *Helodus*. The anterior tooth (MACA 62070) differs from *Helodus* in that crown is asymmetrical with the mesial end bearing a small cusplet. This tooth also has a lingual ridge, which is absent in typical teeth referred to *Helodus* (Stahl, 1999). The base of the anterior tooth is highly anaulacorhize (sponge-like) on both the lingual and labial margins, with the aboral surface of the base having an elongated tear-drop-like shape. This aboral surface in *Helodus* tends to be rectangular (Stahl, 1999). The crown of the mediolateral tooth (MACA 62357) differs from *Helodus* in having a much more prominent and narrower median cusp and prominent apices on the mesial and distal arms of the crown. The crown also differs from *Helodus* in having a well-defined vertical crest on the labial surface of the mesial, median, and distal cusps, and a lingual ridge. Unfortunately, the tooth base of this specimen is partially worn but bears a similar anaulacorhize morphology seen in *Helodus* (Stahl, 1999; Coates et al., 2021; Johanson et al., 2021). The mediolateral tooth has a superficial appearance to those seen in the palatoquadrate and Meckel's cartilages of an enigmatic paraselachian euglenodontiform, "L2SP", known from complete skeletons from the Late Mississippian Bear Gulch Fauna of the Heath Formation in Central Montana (Grogan and Lund, 2000; Lund and Grogan, 2004b; Andermann, 2011). The "L2SP" taxon has tricuspid teeth for the four lateral tooth families in the palatoquadrate and Meckel's cartilages (Andermann, 2011). However, the teeth have a confluent glossy hard tissue, with no indication of tritorial dentine as seen in the referred lateral teeth for *M. olsoni* (Andermann, 2011).

DISCUSSION AND CONCLUSIONS

Macadens olsoni is the latest addition to the diverse assemblage of Middle Mississippian chondrichthyans identified from the Joppa Member of the Ste. Genevieve Formation at Mammoth Cave National Park (Hodnett et al., 2023, 2024a, 2024b). The symphyseal tooth of *M. olsoni* shares with the

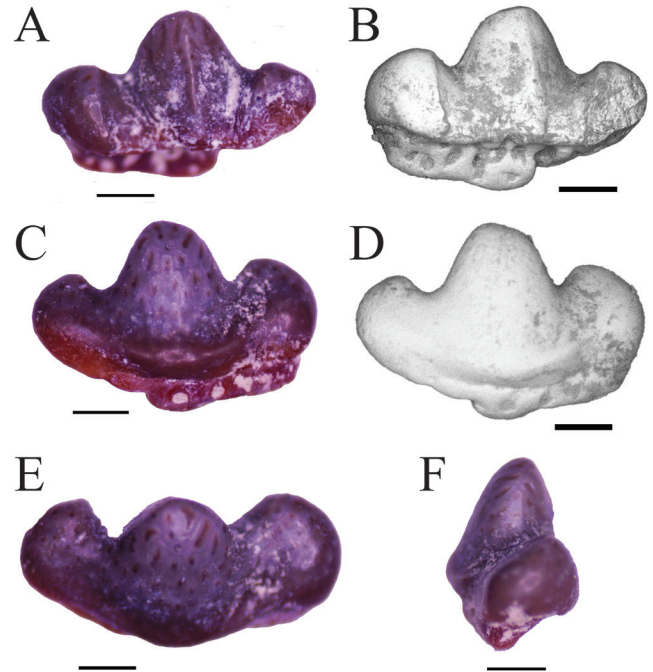


FIGURE 6. MACA 62357, specimen referred to *Macadens olsoni* gen. et sp. nov, mediolateral tooth. **A)** labial view, **B)** SEM image of labial view, **C)** lingual view, **D)** SEM image of lingual view, **E)** oral view, **F)** distal view. Scale equals 1 mm.

holotype of the Lower Mississippian *Rotuladens coxanus* Newberry, 1897 3-5 blunt and rounded *Helodus*-like crowns on a euglenodont-like mesiodistally elongated base, suggesting a close evolutionary relationship between the two taxa. This unique combination of morphological features and new information on the dental and cranial anatomy of *Helodus* (Coates et al., 2021; Johanson et al., 2021) indicates that neither *Rotuladens* nor *Macadens* is related to *Helodus sensu stricto* and the Helodontiformes *sensu lato* (as defined by Stahl [1999]), as suggested by Itano and Lambert (2018). It is unlikely that *Rotuladens* and *Macadens* represent members of the paraselachian euglenodontiform group as defined by Grogan and Lund (2000) or Lund and Grogan (2004b). The constituent taxa of the Gregoriidae (*Gregorius rexi*, *Bealbonn rogaire*, and *Srianta spp.*) have wide symphyseal tooth whorls or wide crown tooth families on symphyseal cartilages between the Meckel's cartilages along with lateral teeth with glossy enameloid and with multiple cusps with vertical crests and elongated tooth bases (Lund and Grogan, 2004b). However, the referred lateral teeth of *Macadens* do have basal lingual mesiodistal ridges on the crown but lack labial basal ridges as seen in the gregoriids (Lund and Grogan, 2004b). The Debeeriidae (*Heteropetalus elegantulus* and *Deeberius ellefseni*) have relatively short glossy enameloid crowns with few to no cusplets on an elongated base and lack symphyseal tooth whorls (Lund, 1977; Grogan and Lund, 2000). The enigmatic "L2SP" taxon has been placed phylogenetically as either a member of the paraselachians (Grogan and Lund, 2000; Andermann, 2011) or as a sister group to Euglenodontiformes (Lund and Grogan, 2004a). As mentioned above, there is a superficial resemblance of the mediolateral tooth referred to *Macadens* to those seen in the "L2SP" taxon but both taxa differ in the gross anatomy of the dental tissues with "L2SP" having glossy enameloid on the crown and *Macadens* having tritorial tissues on the crown.

The crowns of the tooth whorls and teeth of *Macadens* and *Rotuladens* show the presence of tritorial dentine on thin bases

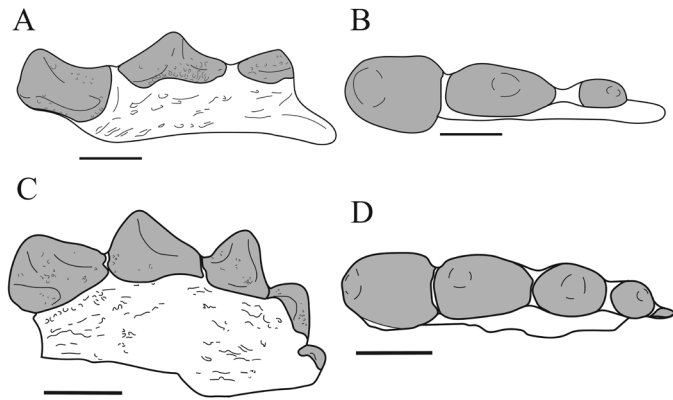


FIGURE 7. Comparative illustration of the holotypes of Middle Mississippian *Macadens olsoni* (A-B) and Lower-Middle Mississippian *Rotuladens coxanus* (C-D). *Macadens olsoni*, MACA 62366, A) distal view, B) oral view; scale 2 mm. *Rotuladens coxanus*, USNM V 3518, C) distal view, D) oral view; scales equal 10 mm.

of trabecular and lamellar dentine, a trait shared with multiple groups within the subclass Euchondrocephalii (Ginter et al. 2010) but particularly noted with the infraclass Holocephali (Stahl, 1999). Basal members of the Holocephali such as *Helodus* and the enigmatic *Harpacanthus fimbriatus* have individual teeth with tritorial tissues (Stahl, 1999; Lund and Grogan, 2004a). However, it has now been demonstrated that in *Helodus*, fusion occurs overtime with individual teeth fusing into whorls and whorls fusing into plates (Coates et al., 2021; Johanson et al., 2021). Also, new data also suggest that fusion between dental plates in some coelodontiforms can also occur (Itano and Lambert, 2018; Itano, 2022). However, holocephalans do not have symmetrical lower tooth whorls.

However, the dental anatomy of the symphyseal tooth whorls observed for *Macadens* and *Rotuladens* appears to be more similar to that of eugeneodontiforms than those observed in holocephalans. The narrow symmetrical nature of the tooth whorl base and the rounded blunt cusps for both *Macadens* and *Rotuladens* are similar to eugeneodont taxa such as *Erikodus groenlandicus* and *Fadenia crenulatus*, both of which show the presence of tritorial dental tissues (Nielsen, 1932, 1952), but *Macadens* and *Rotuladens* lack the typical eugeneodont lower symphyseal tooth whorls, in which the cusps have paired anterior directed processes on either side of the midline of the whorl (Ginter et al., 2010; Tapanila et al. 2020). The referred lateral teeth for *Macadens* also share similar base morphology with that in eugeneodontiforms in which the anaulacorhize base is as wide as the crown and usually less the height of the crown (Ginter et al., 2010). For *Macadens*, the crowns of the lateral teeth differ from eugeneodontiform lateral teeth in lacking the labial vertical ridges that are typical for this order of chondrichthyans. Due to the shared morphological traits of the tooth bases but significant differences in crown morphologies, we propose the hypothesis that *Macadens olsoni* and *Rotuladens coxanus* may represent an unrecognized sister clade to the Eugeneodontiformes.

In conclusion, the Lower-Middle Mississippian (Tournaisian-Viséan) *Rotuladens coxanus* and the Middle Mississippian (Viséan) *Macadens olsoni* were small unique euchondrocephalan chondrichthyans with durophagous tooth whorls. Dental morphologies of these two taxa suggest a closer relationship to eugeneodontiform chondrichthyans than to holocephalans or paraselachians within Euchondrocephali.

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