# THE HOLOCEPHALANS (CHONDRICHTHYES) OF THE MISSISSIPPIAN (VISEAN) REDWALL LIMESTONE, GRAND CANYON NATIONAL PARK, ARIZONA

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**Abstract—**Two species of holocephalan chondrichthyans are identified and described from the Mooney Falls Member of the early Late Mississippian Redwall Limestone at the Grand Canyon National Park. A specimen previously referred to "*Helodus* sp." from the South Kaibab Trail is re-diagnosed as *Psephodus* sp. A new specimen of *Helodus* sp. is identified from the Surprise Canyon region of the Grand Canyon. Based on the current fossil and stratigraphic data, these two holocephalans are considered to be of Visean (early Late Mississippian) age.

## INTRODUCTION

The Grand Canyon National Park (GRCA) in northern Arizona is a time capsule of Precambrian and Paleozoic rocks, representing a half billion years of life in what is now the Colorado Plateau region. Of interest here is the vertebrate history of the upper Paleozoic formations at GRCA, which, until recently, has been dominated by research on the rich assemblages of vertebrate ichnofossils from the Pennsylvanian-lower Permian Supai Group and Coconino Sandstone (e. g., Lull, 1918; Gilmore, 1926, 1927, 1928; McKee, 1982; Spamer, 1984; Elliott and Blakey, 2005a and 2005b; Hunt et al., 2005; Francischini et al., 2019). Vertebrate body fossils are known from the upper Paleozoic rocks of GRCA, but are mostly based on isolated fish remains. McKee (1938) mentioned and illustrated the first upper Paleozoic vertebrate fossil from GRCA, a holocephalan chondrichthyan tooth plate of *Deltodus mercurii* from the lower Permian Kaibab Formation. This was followed by the description of *Megactenopetalus kaibabanus*, a large petalodont chondrichthyan from the Kaibab Formation (David, 1944). McKee (1982) also mentioned the presence of chondrichthyan fossils from the Wescogame Formation (Supai Group) and the Pakoon Limestone in the western Grand Canyon. Recently, Hodnett and Elliott (2018) described a rich chondrichthyan assemblage from multiple localities within the latest Mississippian Surprise Canyon Formation and the lower part of the Early Pennsylvanian Watahgomigi Formation of the Supai Group.

McKee and Gutschick (1969) provided the first reports of vertebrate fossils from the Redwall Limestone at GRCA, but most of these specimens were never described in detail or figured. These include *Helodus* sp. from the South Kaibab Trail (see new diagnosis below) and indeterminate fish remains from the Bright Angel Trail. The indeterminate fish specimen could not be located and thus is not included in this study. All vertebrate fossils mentioned by McKee and Gutschick (1969) were identified as coming from the Mooney Falls Member of the Redwall Limestone. New information is presented here on the holocephalan chondrichthyans from the Mooney Falls Member, including a new specimen from Surprise Canyon at GRCA (Fig. 1).

## MARINE VERTEBRATES FROM THE REDWALL LIMESTONE OUTSIDE OF GRCA

McKee and Gutschick (1969) worked with David Dunkle on the identification of the vertebrate remains they encountered in the Redwall Limestone in northern and central Arizona, which consisted primarily of durophagous holocephalan chondrichthyan dental elements and a dermal spine. The following taxa were identified from outside of GRCA: the euchondrocephalan *Orodus major* (Salt River, U.S. 60) and the holocephalans *Psephodus* sp. (Drake Quarry, Mount Elden, and Sycamore Canyon) *Deltodus* sp., and *Psammodus* sp. (Bridge Canyon and Sycamore Canyon), and a single dorsal spine of *Physonemus* was also identified from Sycamore Canyon (McKee and Gutschick 1969). Just outside of Grand Canyon, from the top of a mesa between Rock and Blye canyons, in Peach Springs Arizona, a dolostone nodule was collected that preserved the external mold and some bony debris of a large gyracanthid acanthodian pectoral spine (USNM 409810, Babcock and Feldmann 1986). Babcock and Feldmann (1986) identified this specimen as *Oracanthus* sp.

Dunkle noted that much of the Redwall fish fauna was similar to taxa found in the Early Mississippian Burlington Limestone of Iowa (St. John and Worthen, 1875; McKee and Gutschick, 1969). Elliott and Blakey (2005a and 2005b) observed that the Redwall Limestone is approximately contemporaneous with the Escabrosa Limestone in southern Arizona, which has a rich but poorly studied fish assemblage (Gass, 1963). The assemblage of fishes from the Escabrosa Limestone at the Dos Cabezas locality includes chondrichthyans (xenacanthids, ctenacanthids, eugenodonts, indeterminate euchondrocephalans, petalodonts, and holocephalans), an acanthodian, and indeterminate

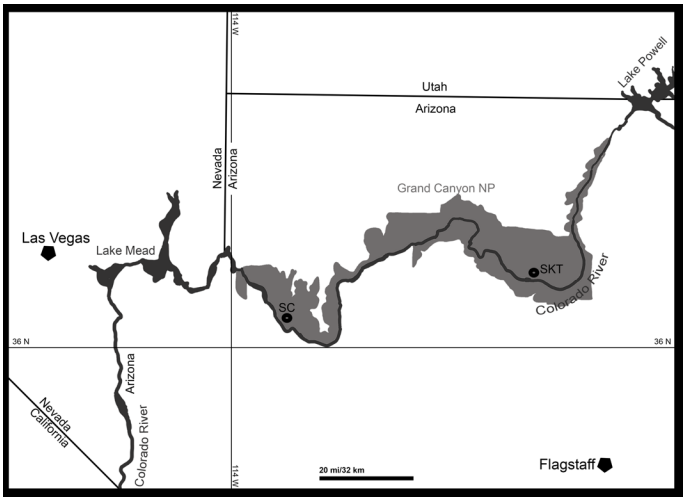


FIGURE 1. Map of the Grand Canyon National Park and the approximate locations of the Surprise Canyon (SC) and the South Kaibab Trail (SKT) localities.

actinopterygian fishes (Gass, 1963).

**Institutional abbreviation**—**GRCA**, Grand Canyon National Park Museum Collection, Grand Canyon Village, Arizona.

## GEOLOGIC SETTING

The Redwall Limestone is a cliff-forming unit of Early to early Late Mississippian-age marine sediments, and consists primarily of light-olive-gray to light gray (the characteristic red surface is due to staining from the overlying Supai Group), thin- to thick-bedded cherty limestones, interbedded crystalline dolomites, and limestone layers with chert lenses (Beus, 2003). It is divided into four lithologic units starting with the Whitmore Wash Member at the base, and ascending through the Thunder Springs Member, Mooney Falls Member, and Horseshoe Mesa Member (McKee and Gutschick, 1969). The Redwall Limestone was formed during two marine transgression and regression events from a seaway to the west (McKee and Gutschick, 1969). The Whitmore Wash Member represents the first transgression event, and the Thunder Springs Member represents the first regression event, followed by the second transgression event of the Mooney Falls Member, and the final regression of the Horseshoe Mesa Member (McKee and Gutschick, 1969). The Redwall Limestone has an upper unconformable contact with the Surprise Canyon Formation; the unconformity represents a time of uplift and the development of karstic paleovalleys cutting into the Redwall Limestone (Beus, 2003).

The Mooney Falls Member is thickly bedded, reaching 106 meters total thickness in some sections, and is the most fossiliferous unit in the Redwall Limestone, although most fossils are neither conspicuous nor well preserved (McKee and Gutschick, 1969). The invertebrate fauna includes endothyrid foraminifers, solitary and colonial corals, bryozoans, brachiopods (spiriferids, productoids, orthotetids, and other forms), gastropods, ostracodes, crinoids, and blastoids (McKee and Gutschick, 1969). Orthotetid brachiopods are noted as being common in the coarse crystalline limestone about one-third the distance above the base of the member (McKee and Gutschick, 1969). Diagnostic foraminifers (Skipp, 1969; Mamet and Skipp, 1970) and conodonts (Racey, 1974; Ritter, 1983) indicate a late Osagean-Meramecian age, which correlates to the Visean.

## SYSTEMATIC PALEONTOLOGY

### CLASS Chondrichthyes Huxley, 1880
### SUPERORDER Holocephali Bonaparte, 1832–1841
### ORDER Helodontiformes Patterson, 1965
### FAMILY Helodontidae Patterson, 1965
### GENUS *Helodus* Agassiz, 1838
### *Helodus* sp.

**Occurrence**—Redwall Limestone, Mooney Falls Member, Late Mississippian (Visean); Surprise Canyon, Grand Canyon National Park.

**Material**—GRCA 121976, anterior tooth whorl with two teeth (Fig. 2).

**Description**—A partial tooth whorl with two teeth (Fig. 2); the preserved dimensions of the labial tooth are mesiodistal length of 21.5 mm and labiolingual width of 9.2 mm; the preserved dimensions of the lingual tooth are mesiodistal length 18.1 mm and labiolingual width 10.9 mm. The labially positioned tooth is the more complete of the two, although the lingual tooth is slightly more robust labiolingually. The median crown is low, labiolingually expanded and has a rounded labial edge and straight lingual edge. The distal margin of the crown narrows to a rounded point. Both teeth are connected by a thin bony plate.

**Remarks**—At this time we assign the Surprise Canyon specimen only to *Helodus* sp., although its overall morphology is similar to *Helodus didymus* from the Mississippian (Visean) of Armagh, Ireland (Agassiz, 1843; McCoy, 1855; Stahl, 1999). Woodward (1889) suggested that *H. didymus* in fact represents the anterior tooth whorls of several related forms and is not indicative of a distinct species of *Helodus*. Stahl (1999) suggested *Helodus* is only represented by a single species, the type *H. simplex*, which is known from several partial to complete specimens from England. It is clear that the taxonomic diversity of *Helodus* needs a serious review and revision in terms of the morphological variation seen in the fossil record, which would help place the Surprise Canyon *Helodus* in its appropriate species. This specimen marks the oldest record of *Helodus* at GRCA, the youngest being an isolated tooth from the overlying latest Mississippian (Serpukhovian) Surprise Canyon Formation (Hodnett and Elliott, 2018).

FIGURE 2. GRCA 121976, an anterior tooth whorl of *Helodus* sp. from the Mooney Falls Member, Redwall Limestone, Surprise Canyon locality, Grand Canyon National Park. Scale equals 1 cm.

### ORDER Cochliodontiformes Obruchev, 1953
### FAMILY Psephodontidae Zangerl, 1981
### GENUS *Psephodus* Morris & Roberts, 1862
### *Psephodus* sp.

**Occurrence**—Redwall Limestone, Mooney Falls Member, early Late Mississippian (Visean); South Kaibab Trail, Grand Canyon National Park.

**Material**—GRCA 20037, isolated tooth plate in matrix (Fig. 3).

**Description**—The tooth plate (Fig. 3) has a mesiodistal length of 12.1 mm and a labiolingual width of 8.8 mm. About half of the oral surface of the tooth plate was weathered, and the rest of the tooth plate has been prepared. The tooth plate is relatively thick dorsoventrally and labiolingually recurved. The oral surface has very faint longitudinal imbrications. The lingual border is relatively broad and rounded. The labial border is slightly square-shaped. The mesial border is longer than the distal border.

**Remarks**—As noted above, this specimen was previously mentioned by McKee and Gutschick (1969) and was identified, but not described or illustrated, as a specimen of *Helodus* sp. This diagnosis was carried on by Elliott and Blakey (2005a, b). However, this specimen lacks the tall median ridge seen in the tooth plates of *Helodus*, nor do the ends narrow mesiodistally like those of individual teeth of *Helodus* (Moy-Thomas, 1936; Stahl, 1999). The tooth plate also lacks the distal "wing" typical of the tooth plates of *Deltodus*, another taxon present in the Redwall Limestone (McKee and Gutschick, 1969; Stahl, 1999). The lower tooth plates of *Psephodus* overall tend to be quadrangular in shape, convex orally, longer mesially than distally, and occasionally have faint growth lines or longitudinal


FIGURE 3. GRCA 20037, a posterior tooth plate of *Psephodus* sp. from the Mooney Falls Member, Redwall Limestone, South Kaibab Trail locality, Grand Canyon National Park. **A**, Specimen in matrix. **B**, Tooth plate enlarged. Scale equals 1 cm.

imbrications (Stahl, 1999). These traits are seen in GRCA 20037. *Psephodus* is another cochlidont taxon with multiple taxonomic names based on isolated tooth plates (Stahl, 1999). We identify the South Kaibab Trail specimen at the generic level until a more critical taxonomic review of *Psephodus* is carried out.

## DISCUSSION AND CONCLUSIONS

The previous identifications of chondrichthyan remains from the Mooney Falls Member of the Redwall Limestone in north-central Arizona demonstrate that this particular horizon has the potential to yield more information on the marine vertebrates from the Redwall Limestone. McKee and Gutschick (1969) have indicated that the temporal range of the Redwall Limestone starts in the Early Mississippian, with the basal beds being of the Kinderhookian (Tournaisian) age, and extends into the Late Mississippian with the youngest rocks of the Horseshoe Mesa Member which are Late Mississippian, Chesterian (late Visean to early Serpukhovian), in age. The *Helodus* tooth-whorl from Surprise Canyon at GRCA resembles very closely *Helodus didymus*, which is a tooth taxon from the Visean of Ireland, and it is possible that the Mooney Falls Member of the Redwall Limestone could be Visean in age. McKee and Gutschick (1969) suggested the upper western Redwall Limestone members were of middle Meramecian (late Visean) age, based on the invertebrate fossil data (foraminifers and brachiopods).

In conclusion, the *Helodus* sp. specimen from the Redwall Limestone of the South Kaibab Trail (GRCA 20037), mentioned in McKee and Gutschick (1969), has been reviewed and re-identified as the holocephalan cochliodontiform genus *Psephodus*. *Helodus* sp. (GRCA 121976) is represented by an anterior tooth whorl from GRCA from the Surprise Canyon region of the park. Based on the invertebrate fossil record of the Mooney Falls Member (McKee and Gutschick, 1969) and the similarity of the Surprise Canyon *Helodus* to the *H. didymus* tooth taxon (Woodward, 1889; Stahl, 1999), the Mooney Falls Member represents a Visean (early Late Mississippian) assemblage.

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