

THE FIRST RECORD OF THE HOLOCEPHALAN *CRASSIDONTA STUCKENBERGI* BRANSON, 1916 (CHONDRICHTHYES, HOLOCEPHALI, COCHLIODONTIFORMES) FROM THE LOWER-MIDDLE PERMIAN KAIBAB FORMATION, GRAND CANYON NATIONAL PARK, ARIZONA

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Abstract—A new record of the cochlodont holocephalan *Crassidonta stuckenbergi* is described from the lower-middle Permian Kaibab Formation. The fossil was identified during the 2019 National Park Service Paleontological Resource Inventory of the North Rim of the Grand Canyon National Park. A new model for the dental tooth plate arrangement is proposed for *C. stuckenbergi*. This record of *Crassidonta* adds new information to the distribution of this holocephalan along the western coastline of the lower-middle Permian Laurentian continent.

INTRODUCTION

Although best known for its invertebrate assemblages (McKee, 1938; Miller and Unklesbay, 1942; Nicol, 1944; Brezinski, 1991), the lower-middle Permian Kaibab Formation is known to have a unique marine vertebrate assemblage found both in Flagstaff and at Grand Canyon National Park, Arizona (McKee, 1938; Hussakof, 1943; David, 1944; Gass, 1963; Ossian, 1976; Johnson and Zidek, 1981; Hodnett et al. 2012, 2013; Elliott and Hodnett, 2013). The earliest report of a vertebrate fossil from the Kaibab Formation at Grand Canyon National Park was by McKee (1938) who briefly mentioned and illustrated the lower mandibular tooth plate to the holocephalan chondrichthyan *Deltodus mercurii* from the South Rim of the park. David (1944) assigned the holotype to *Megactenopetalus kaibabianus*, a giant pristodont petalodontimorph chondrichthyan that was purportedly collected near Point Sublime of the North Rim. In addition to the *Megactenopetalus* specimen, a large holocephalan tooth plate was also collected from the same vicinity which was later described briefly by Gass (1963) and referred by him to *Psephodus* sp. However, the survey work discussed below demonstrated Point Sublime did not have fossiliferous limestones at that site. Large to small tooth plates of platysomid actinopterygian fishes were collected along the Bright Angel Trail and described by Johnson and Zidek (1981). Thompson (1995) collected a sample of microvertebrate fossils from the type section of the Fossil Mountain Member at the South Rim, which included the teeth and denticles of ctenacanth, xenacanth, hybodonts, euselachians, petalodonts, holocephalans, and actinopterygians.

Of interest here, field work during the 2019 National Park Service (NPS) Paleontological Resource Inventory identified a new vertebrate-rich fossil locality within Grand Canyon National Park, in which the tooth plate of the holocephalan *Crassidonta stuckenbergi* was collected. *C. stuckenbergi* was first described by Branson (1916) from the Permian Embar Formation at Bull Lake Creek and Landers, which is now considered to be the Phosphoria Formation (McKelvey et al., 1959). Wyoming as well as material originally described from Russia by Stuckenberg (1905). Another species of *Crassidonta*, *C. subcrenulata*, was described by Teichert (1943) from the lower Permian of Western Australia. Teichert (1943) suggested that *Crassidonta* was a member of the Psammodontiformes, while Stahl (1999) suggested this genus belonged in the family Cochlodontidae in the Cochlodontiformes. Below we present the new Kaibab Formation record of *C. stuckenbergi* collected

from Grand Canyon National Park, Arizona.

GEOLOGIC SETTING

The Kaibab Formation crops out throughout much of northern Arizona, southern Utah, and southeastern Nevada (McKee, 1938; Cheevers, 1980; Hopkins and Thompson, 2003). This marine unit was deposited during the eastward transgression of a shallow sea that extended northward into Canada and southward into Mexico (Fig. 1), and thins towards the east as the paleo-coastline is approached (McKee, 1938; Norton, 1990; Hopkins and Thompson, 2003). The Kaibab Formation was initially divided into three members: the alpha, beta, and gamma (McKee, 1938). These were later reorganized into the Harrisburg Member (alpha) and the Fossil Mountain Member (beta and gamma) (Sorauf, 1962; Clark, 2021).

The Kaibab Formation is composed of yellow to gray calcareous limestones, yellow to orange sandy limestones, calcareous sandstones, and red chert beds (McKee, 1938; Clark, 2021). Sand in the limestone units is derived from coastal deserts along the western shore of the continent to the east (McKee, 1938; Hopkins, 1986; Norton, 1990; Hopkins and Thompson, 2003). The Fossil Mountain Member is divided into eastern and western regions (Cheevers, 1980; Hopkins and Thompson, 2003). In the east is a predominately dolomitic unit with the percentage of sand increasing easterly, and in the west are resistant fossiliferous limestones with scattered sandstone and dolomite units and abundant chert nodules (Hopkins and Thompson, 2003). The Harrisburg Member includes a basal gypsum unit followed by red siltstone ledges and resistant limestones with chert nodules, interspersed with beds of gypsum. Both members thicken to the west (Cheevers, 1980; Hopkins and Thompson, 2003).

The Fossil Mountain Member represents a shallow, open-marine environment to the west, while to the east there was a shift to restricted, near-shore, and increasingly saline environments (Hopkins and Thompson, 2003). In the Harrisburg Member, the restricted environments became common as the sea retreated to the west and the faunas changed from brachiopods and other open-marine species to bivalves and gastropods (Cheevers, 1980; Hopkins and Thompson, 2003; Clark, 2021).

The age of the Kaibab Formation had been considered Leonardian based on comparison of brachiopod faunas and distribution of the siliceous sponge *Actinocoelia maeandrina* (McKee, 1938; Hopkins and Thompson, 2003; Clark, 2021). This has been further supported by conodont studies that confirm a late Leonardian age and help to establish correlation

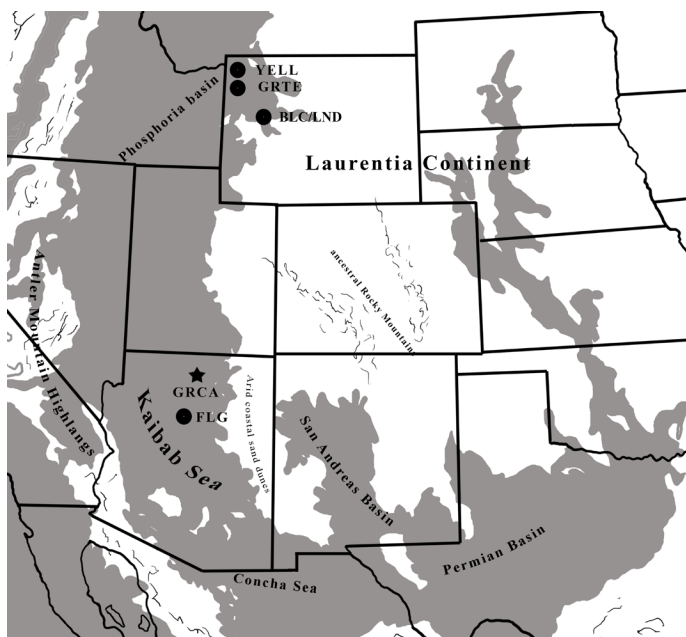


FIGURE 1. Paleogeographic map of the lower-middle Permian (Kungurian/Roadian) of western North America. Abbreviations: BLC/LND, Bull Lake Creek and Lander, Wyoming; FLG, Flagstaff region, Arizona; GRCA, Grand Canyon National Park, Arizona; GRTE, Grand Teton National Park, Wyoming; YELL, Yellowstone National Park, Wyoming.

with other Permian sequences (Thompson, 1995; Hopkins and Thompson, 2003; Clark, 2021). However, conodont and brachiopod data support a Roadian age for the upper part of the Fossil Mountain Member (Hopkins and Thompson, 2003), and a correlation between the San Andres Formation of New Mexico, which ranges from the Leonardian to the Capitanian in age, and the Kaibab Formation has been proposed (Brezinski, 1991; Sonnenfeld, 1993). It therefore seems probable that the upper part of the Fossil Mountain Member and all of the Harrisburg Member are early Guadalupian in age.

The 2019 NPS Paleontological Resource Inventory of Grand Canyon National Park identified a new vertebrate-rich horizon within the Kaibab Formation on the Kaibab Plateau just north of the North Rim visitor center (Fig. 2). This site, informally dubbed “shark ridge”, consists of a limestone to sandstone outcrop with orange limestones near the base of the outcrop, that graded into sandy to dolomitic orange tan limestones, then to a gray sandy limestone, a tan sandstone, and a capping coarse gray sandstone (Figs. 3 and 4). Observed vertebrate fossils consisted primarily of small phyllodont-grade actinopterygian teeth, which have been found elsewhere in the Kaibab Formation (Johnson and Zidek, 1981). Shark teeth and spines (Figs. 4C-D) were primarily concentrated in the capping gray sandy limestone, but a euselachian grade dorsal fin spine was identified from the lower sandy to dolomitic orange tan limestone (Fig 4B).

MATERIALS AND METHODS

The fossil featured here was discovered by one of us (JMB) on September 23, 2019 during a field paleontological resource survey just north of the North Rim visitor center at Grand Canyon National Park, Arizona. Fossil samples were collected from the surface and prepared with an electric Dremel engraving tool with a carbide needle point. Imagery was created with an Apple iPhone 12 pro and edited with Adobe Illustrator and Photoshop.

Institutional Abbreviation— GRCA, Grand Canyon National Park Museum, Arizona

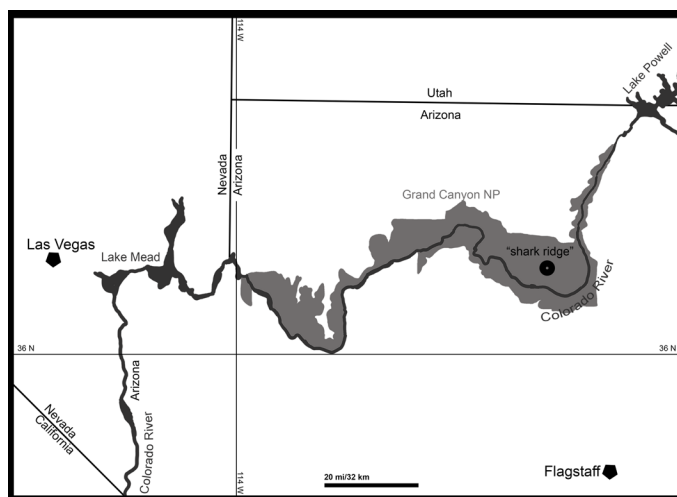


FIGURE 2. Park boundary of Grand Canyon National Park, Arizona with the approximate location of the “shark ridge” locality.

SYSTEMATIC PALEONTOLOGY

CLASS Chondrichthyes Huxley, 1880

SUBCLASS Euchondrocephali Lund and Grogan, 1997b

INFRACLASS Holocephali Bonaparte, 1832

ORDER Cochlodontiformes Obruchev, 1953

FAMILY Cochlodontidae Owen, 1867

***Crassidonta stuckenbergi* Branson, 1916**

Occurrence— North Rim, Grand Canyon National Park, Arizona, lower-middle Permian (Roadian-Kungurian) Kaibab Formation.

Material— GRCA 122709, complete ?anterior tooth plate (Fig. 5).

Description— Probable anterior tooth plate that has a labiolingual length of 25 millimeters and a mesiodistal width of 21 millimeters. Medial ridge tall and mesiodistally wide and thick. Mesial flange rectangular and approximately two thirds the length of the crown. The distal flange is triangular and about one half the length of the crown. The aboral surface of the base is slightly concave.

Comparison and Remarks— GRCA 122709 compares

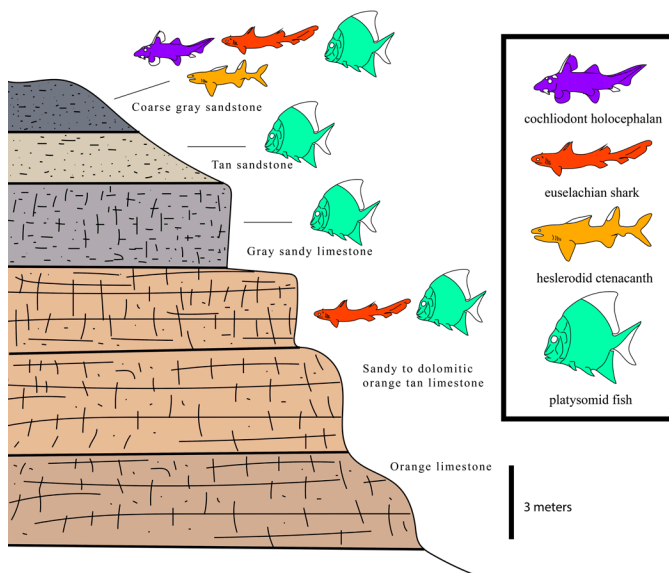


FIGURE 3. Stratigraphy of the Kaibab Formation at the “shark ridge” locality and distribution of vertebrate taxa encountered during the 2019 GRCA Paleontological Resource Inventory.



FIGURE 4. Field photos from the “shark ridge” locality at Grand Canyon National Park, Arizona. **A)** Limestone outcrop of Kaibab Formation, **B)** cross-section of a euselachian dorsal fin spine, **C)** small heslerodid ctenacanth tooth, **D)** the tooth plate of *Crassidonta stuckenbergi* (GRCA 122709) as found.

well with the type material that Branson (1916) figured in his description of the Phosphoria Formation specimens along with images of the Russian fossils of *Crassidonta stuckenbergi* (in Branson, 1916; plate 1, figs 17-21, 25-27 for the Phosphoria (Embar) specimens from Bull Lake Creek and Lander, Wyoming, and figs 22-24 for the Russian Moscowian specimens). The Kaibab, Phosphoria, and Moscowian specimens bear a tall, thick and mesiodistally wide median labiolingual ridge with mesial and distal wing-like extensions that are either rectangular or triangular in shape. There is variability in the labiolingual length in these mesial and distal wing-like extensions as well as the lingual marginal width for the tooth plates of *C. stuckenbergi*, which may reflect tooth position. Neither Branson (1916) nor Stahl (1999) have attempted to place the variable dental plate morphs for *C. stuckenbergi* into dental family position.

We propose here that the larger tooth plates with the labiolingual elongated mesial and distal extensions may have been posteriorly positioned like other posterior tooth plates in Holocephali (Stahl, 1999). Both the upper and lower posterior tooth plates of holocephalans tend to be larger than the medial (if present) and anterior tooth plates (Stahl, 1999). The more triangular and small tooth plates of *Crassidonta stuckenbergi* most likely represent either medial or anterior tooth plates. The number of pre-posterior tooth plates tends to be variable in Cochlodontiformes, which can have either one to two in either the upper or lower jaw (Patterson, 1965, 1992; Lund and Grogan, 1997a; Stahl, 1999). We present here a tentative model arrangement of the dental plates based on the known

figured material from Russia, Wyoming, and Arizona, with two upper and lower tooth plate families (Fig. 6). Our model tentatively suggests that *C. stuckenbergi* had a cochlodont-like arrangement with an upper posterior tooth plate that was similar in morphology to the lower posterior tooth plate. This arrangement is similar to that seen in *Deltodus angularis* and *D. mercurii* (Branson, 1916; Stahl, 1999; Stahl and Hansen, 2004), whereas taxa like *Cochliodus*, *Deltoptychius*, and *Traquairius* had elongated and labiolingually narrowed upper posterior tooth plates (Patterson, 1992; Lund and Grogan, 1997a, 1997b; Stahl, 1999). The proposed anterior teeth of *C. stuckenbergi* are more triangular in shape with the potential upper anterior tooth having wider mesiodistal extensions compared than the posterior tooth plates, and with the lower anterior tooth plates bearing narrower mesiodistal extensions. This arrangement of the lower anterior tooth plate is also seen in *D. angularis* where the lower anterior tooth plate has a less developed distal margin (Stahl and Hansen, 2004).

DISCUSSION AND CONCLUSIONS

GRCA 122709, collected from the North Rim of Grand Canyon National Park, Arizona, is the first record of *Crassidonta stuckenbergi* from the lower-middle Permian Kaibab Formation. This record extends the known distribution of *C. stuckenbergi* within the western marine waters of Laurentia, previously known only from the northern Phosphoria Formation in Wyoming (Branson, 1916; Yochelson and Van Sickle, 1968; Stahl, 1999). Its occurrence in the southern Kaibab fish assemblage suggests that at least larger fish taxa were more mobile along

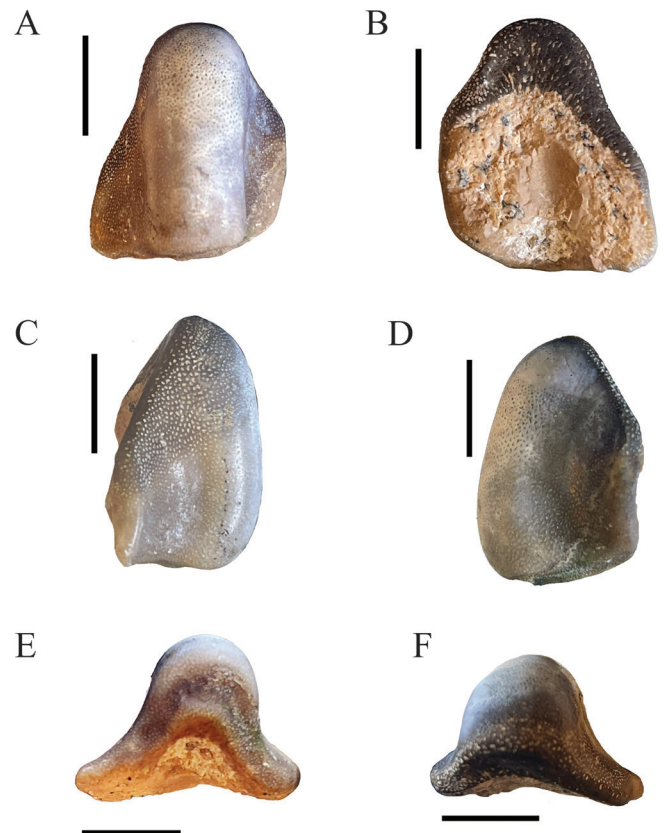


FIGURE 5. GRCA 122709, the tooth plate of *Crassidonta stuckenbergi* from the Kaibab Formation from North Rim of the Grand Canyon National Park, Arizona. **A)** Oral view, **B)** aboral view, **C)** distal view, **D)** mesial/symphyseal view, **E)** labial view, **F)** lingual view. Scale equals 1 cm.

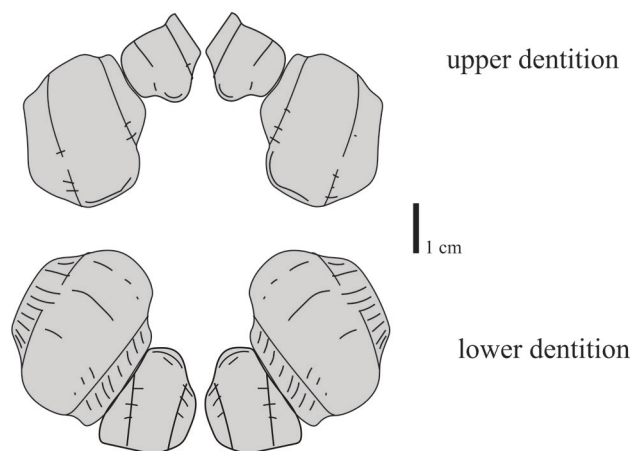


FIGURE 6. Proposed dental plate arrangements for *Crassidonta stuckenbergi*. GRCA 122709 is proposed to be a lower anterior tooth plate.

the western coastline of Laurentia during the Permian and these fish assemblages may have been less endemic in terms of their diversity than suspected. More field sampling and museum collection assessment from both the Kaibab and Phosphoria Formations is needed to better understand the dynamics of these fish assemblages.

The cochlodont holocephalan, *Crassidonta stuckenbergi*, is found in the lower-middle Permian of both the Phosphoria and Kaibab formations, which both geologically represent a western coastline of Laurentia (McKee, 1938; Sheldon, 1963; Yochelson and Van Sickel, 1968). The dental plate arrangement, for *Cr. stuckenbergi* is modeled in a cochlodont-like arrangement with enlarged tooth plates with labiolingual-elongated mesiodistal extensions representing the posterior tooth plates within the upper and lower jaws, and smaller triangular shaped tooth plates representing the upper and lower anterior tooth plates. Lastly, the discovery of this new record of *Crassidonta* was made possible through rigorous field inventories of fossil resources within Grand Canyon National Park. Such inventories are vital to both understanding and interpreting the types of paleontological resources that occur within our public lands as well as permitting the discovery of new data and records of ancient life previously unknown to science.

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