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PERMIAN VERTEBRATES OF ARIZONA

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Abstract—Arizona has significant ichnofaunas from Permian nonmarine strata and a sparse record of Permian marine selachian teeth. The ichnofaunas include the first extensive Paleozoic ichnofaunas to have been described from North America, the largest sample sizes of trace fossils from eolianites and significant Leonardian tetrapod ichnofaunas. Two Leonardian eolianites (Coconino Sandstone and DeChelly Sandstone) have similar ichnofaunas, including a low diversity tetrapod ichnofauna formed almost exclusively of *Chelichnus* spp. Two redbed units (Hermit Formation and Schnebly Hill Formation) also produce ichnofossils. The Wolfcampian Hermit Formation has a diverse tetrapod ichnofauna that includes *Batrachichnus delicatulus*, *Parabaropus coloradensis*, *Hyloidichnus bifurcatus*, *Gilmoreichnus hermitanus*, *Limnopus* sp. and *Ichniotherium* sp. The Coconino Sandstone and DeChelly Sandstone belong to the *Chelichnus* biotaxonichnofacies, and the Hermit Formation and the Schnebly Hill Formation pertain to the *Batrachichnus* biotaxonichnofacies. The selachian records are of a few teeth from the Kaibab Limestone along the north rim of the Grand Canyon.

Keywords: Permian, Arizona, tracks, Wolfcampian, Leonardian, eolian, Grand Canyon, selachian

INTRODUCTION

Undoubtedly one of the most significant collections of Permian vertebrate and invertebrate tracks in North America came from the Grand Canyon of Arizona (Fig. 1) and was collected and described by Charles Gilmore of the United States National Museum (Smithsonian) in a series of classic works (Gilmore, 1926b, 1927b, 1928a). Arizona has also produced other significant Permian ichnofaunas, and a few records of Permian selachian teeth and other vertebrates (Fig. 1). The purpose of this paper is to review the Permian vertebrate fossil record of Arizona. USNM refers to the United States National Museum (Smithsonian) in Washington; MNA refers to the Museum of Northern Arizona in Flagstaff.

TETRAPOD TRACKS

History of Study

Grand Canyon

Schuchert (1918) first mentioned tetrapod tracks in Paleozoic strata on the South Rim of the Grand Canyon (Fig. 1). Previously, Charles D. Walcott had collected a specimen that was not noted until 1928 (Gilmore, 1928a). Lull (1918) utilized Schuchert's collection from the Permian Coconino Sandstone in the first scientific description of Paleozoic tetrapod tracks from Arizona. In 1924, the National Park Service invited Charles Gilmore to visit Schuchert's locality and to prepare an *in situ* exhibit on the now abandoned Hermit Trail (Spamer, 1984). Gilmore (1926b) described this new Coconino collection and was later funded by the Marsh Fund Committee of the National Academy of Sciences (1926) and the Grand Canyon Exhibit Committee of the National Academy of Sciences (1927) to make additional collections and exhibits (Spamer, 1984). These new collections came from the Hermit Shale (Permian) and the Wescogame Formation of the Supai Group (Pennsylvanian) as well as the Coconino and were described by Gilmore in additional monographs (Gilmore, 1927b, 1928a) and a short paper on the first tracks from the north rim (Gilmore and Sturdevant, 1928). Gilmore also wrote three more popular papers describing his collecting efforts (Gilmore, 1926a, 1927a, 1928b).

For the next 70 years there was little reevaluation of Gilmore's work except by Donald Baird of Princeton (Baird, 1952; Baird in Spamer, 1984). A renaissance of Paleozoic track studies took place in the mid 1990s. The Rosetta Stone for a new re-evaluation of Permian tracks was provided by studies of the extensive ichnofaunas from the redbeds of southern New Mexico (Haubold et al., 1995a; Hunt et al., 1995). The New Mexico tracksites provided large sample sizes of all the most significant Permian ichnotaxa and included a broad range of preservational variants. These samples provided a new perspective on the plethora of ichnotaxonomic

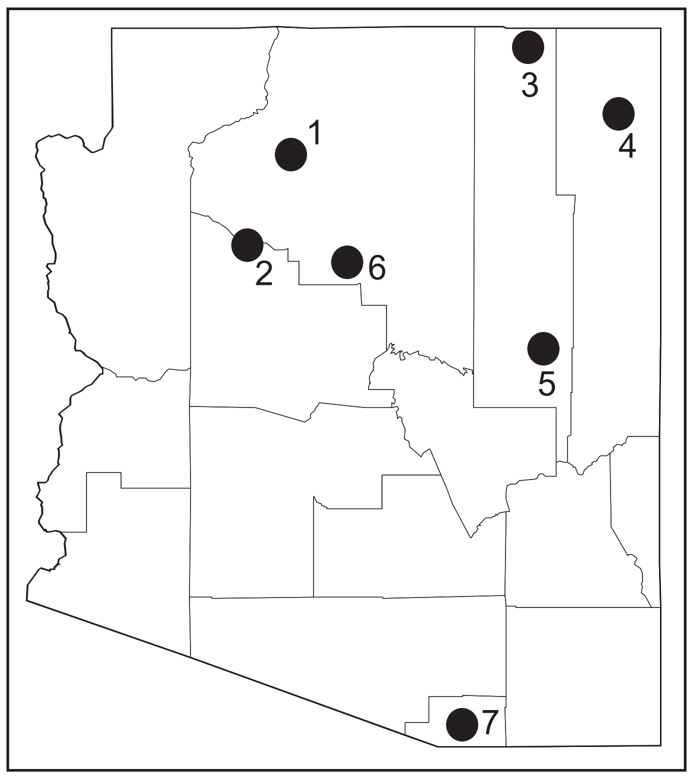

FIGURE 1. Map of Arizona showing distribution of Permian vertebrate fossil localities. 1 = Grand Canyon; 2 = Seligman; 3 = Monument Valley; 4 = Canyon DeChelly; 5 = Show Low; 6 = Flagstaff; 7 = Santa Cruz County.

names of tetrapod tracks from Permian redbeds, most of which had been described on the basis of small sample sizes (Haubold et al., 1995a; Hunt et al., 1995; Haubold, 1996, 2000). During the same timeframe there was a major reevaluation of the equally confused ichnotaxonomy of tetrapod tracks from Permian eolianites (Morales and Haubold, 1995; Haubold et al., 1995b; McKeever and Haubold, 1996). Also, Hunt and Santucci (1998a, b, 2001) reviewed the Grand Canyon tracks and recognized a new morphotype.

Other Areas

Edwin D. McKee started his distinguished career as Park Naturalist at Grand Canyon National Park in the 1920s (Morales and Haubold, 1995). He found tracks in the DeChelly Sandstone near Canyon DeChelly in Apache County, northeastern Arizona near the New Mexico border (Fig. 1) that were very similar to those from the Coconino Sandstone (McKee, 1934). The ichnotaxa included *Dolichopodus*, *Laoporus* and *Baropezia* (currently all considered to be *Chelichnus*). Subsequently, Lionel F. Brady briefly mentioned DeChelly tracks and later made some collections of tetrapod tracks (Brady, 1947; Morales and Haubold, 1995). Vaughn (1963) published an account of a track trending down a dune face near Monument Valley, Navajo County in northeastern Arizona near the Utah border (Fig. 1). Sadler (1993) described invertebrate tracks from the DeChelly Sandstone.

The area around Monument Valley was investigated in the early 1990s by Martin Lockley and APH and yielded large numbers of tetrapod and invertebrate traces (Lockley et al., 1995). Morales and Haubold (1995) described the MNA collections, which included the specimens collected by Brady in this area. Haubold et al. (1995b) described an unusual specimen discovered by Lockley as *Dromopus* cf. *D. agilis*, an unusual occurrence of a lacertoid track in a Permian eolianite.

There is an area outside Grand Canyon National Park that yields extensive ichnofaunas from the Coconino Sandstone. This area is south of the Grand Canyon and north of Interstate 40 near Seligman in Yavapai County (Fig. 1). Brady and others from MNA collected in this area, and in the 1990 crews from the Potomac Museum Group collected abundant large specimens. These specimens include those described by Kramer et al. (1995) as well as the large slabs illustrated by Lockley and Hunt (1995, figs. 2.9, 2.11, 2.12, 2.14, 2.15). One spectacular specimen preserves multiple, parallel tracks of *Chelichnus* (Lockley and Hunt, 1995, fig. 2.11).

A single specimen of a *Dimetropus* pedal impression was found in a roadcut of the Schnebly Hill Formation in east-central Arizona near Show Low (Fig. 1) in Navajo County (Haubold et al., 1995a). One of us (SGL) visited this locality in east-central Arizona and failed to find additional specimens, as the outcrop from which it came appears to have been altered or destroyed by highway construction.

Ichnotaxonomy

Coconino Sandstone (Leonardian)

The first Permian fossil footprints to be described came from Permian eolianites in Scotland (Grierson, 1828). Subsequently, important ichnofaunas were described from eolian strata of Germany (Cornberger Sandstein), Colorado (Lyons Sandstone) and Arizona (Coconino Sandstone, DeChelly Sandstone) as well as additional specimens from Scotland (Hopeman, Corncockle and Locharbriggs Sandstone formations). A large literature described many ichnotaxa from these formations (Haubold, 1971). However, recent work spearheaded by Hartmut Haubold has demonstrated that virtually all tetrapod tracks from Permian eolianites represent three ichnospecies of one ichnogenus, with only the rarest exceptions (Haubold et al., 1995b; Haubold, 1996; McKeever and Haubold, 1996). Certainly, all the Coconino tracks fall within three species of *Chelichnus* (McKeever and Haubold, 1996) (Table 1). *Chelichnus* is characterized by rounded manual and pedal impressions that are of nearly equal size and that exhibit five short, rounded toe impressions (though less than five are often preserved) (Fig. 2). Trackways have a pace angulation of about 90°, and the manual and pedal impressions are close together (McKeever and Haubold, 1996). The three valid species of *Chelichnus* are distinguished on the basis of size alone, and they are presumed to be the tracks of a caseid-like animal (e.g. Haubold, 1971). *Chelichnus bucklandi* has pedal impression lengths of 10-25 mm, *C. duncani* 25-75 mm and *C. gigas* 75-125 mm (McKeever and Haubold, 1996). Thus, all Gilmore's (and Lull's) named ichnotaxa from the Coconino Sandstone of the Grand Canyon can be placed in one of these three species. Gilmore (1927b) was aware of the similarity of some of his specimens from the Grand Canyon to those from Scotland, but he persisted with his (and Lull's) distinct ichnotaxonomy (e.g., Gilmore, 1928a). Tracks from near Seligman pertain to *C. bucklandi* and *C. duncani*.

TABLE 1 Tetrapod ichnofauna of the Coconino Sandstone (McKeever and Haubold, 1996; Hunt and Santucci, 1998).

Chelichnus duncani (Owen, 1842) (= *Baropezia arizonae, Allopus? arizonae, Baropezia eakini*, *Agostopus matheri*, *Agostopus medius*, *Palaeopus regularis*, *Barypodus tridactylus*, *Barypodus metszeri*, *Nanopus maximus, Laoporus noblei* in part of Gilmore, 1926b)
Chelichnus gigas Jardine, 1850 (=*Barypodus palmatus*, *Amblyopus pachypodus, Baropus coconinoensis*)
Chelichnus bucklandi (Jardine, 1850) (=*Dolichopodus tetradactylus*, *Laoporus schucherti*, *Laoporus coloradensis*, *Nanopus merriami*, *Laoporus noblei* of Lull, 1918)

Size by itself is not the ideal criterion to distinguish between ichnospecies, but the ichnotaxonomy presented here represents the current consensus. The low ichnotaxonomic diversity in Table 1 is in keeping with the low animal diversity that would be expected in a dunefield.

DeChelly Sandstone (Leonardian)

The ichnofauna of the eolian DeChelly Sandstone is broadly similar to that of the Coconino Sandstone in being dominated by *Chelichnus* (Lockley et al., 1995; Morales and Haubold, 1995). The specimens described by Lockley et al. (1995) and Morales and Haubold (1995) can be assigned to *C. bucklandi* and *C. duncani*. The DeChelly is unusual among Permian eolianites in yielding a specimen of the lacertoid track *Dromopus* cf. *D. agilis* (Haubold et al., 1995b).

Hermit Formation (Wolfcampian)

The Hermit Formation (Shale) tetrapod tracks occur in redbeds, in contrast to the eolian strata of the Coconino Sandstone. Recent work has indicated that Permian redbed ichnofaunas are of low diversity and cosmopolitan in distribution (Haubold et al., 1995a; Haubold, 1996; Hunt and Lucas, 1998b). A reevaluation of Gilmore's ichnotaxonomy indicates that he had overestimated the diversity of the Hermit Formation ichnofauna. Gilmore, in common with all pre-1990s ichnologists, was not sufficiently aware of the variable traces that could made by a single trackmaker given variations in substrate conditions and gait. Thus, Gilmore assumed that all differences in footprint morphology or trackway pattern reflected the presence of different trackmakers. A reevaluation of the tetrapod ichnotaxa from the Hermit Formation of the Grand Canyon thus reveals a lower ichnodiversity (Table 2).

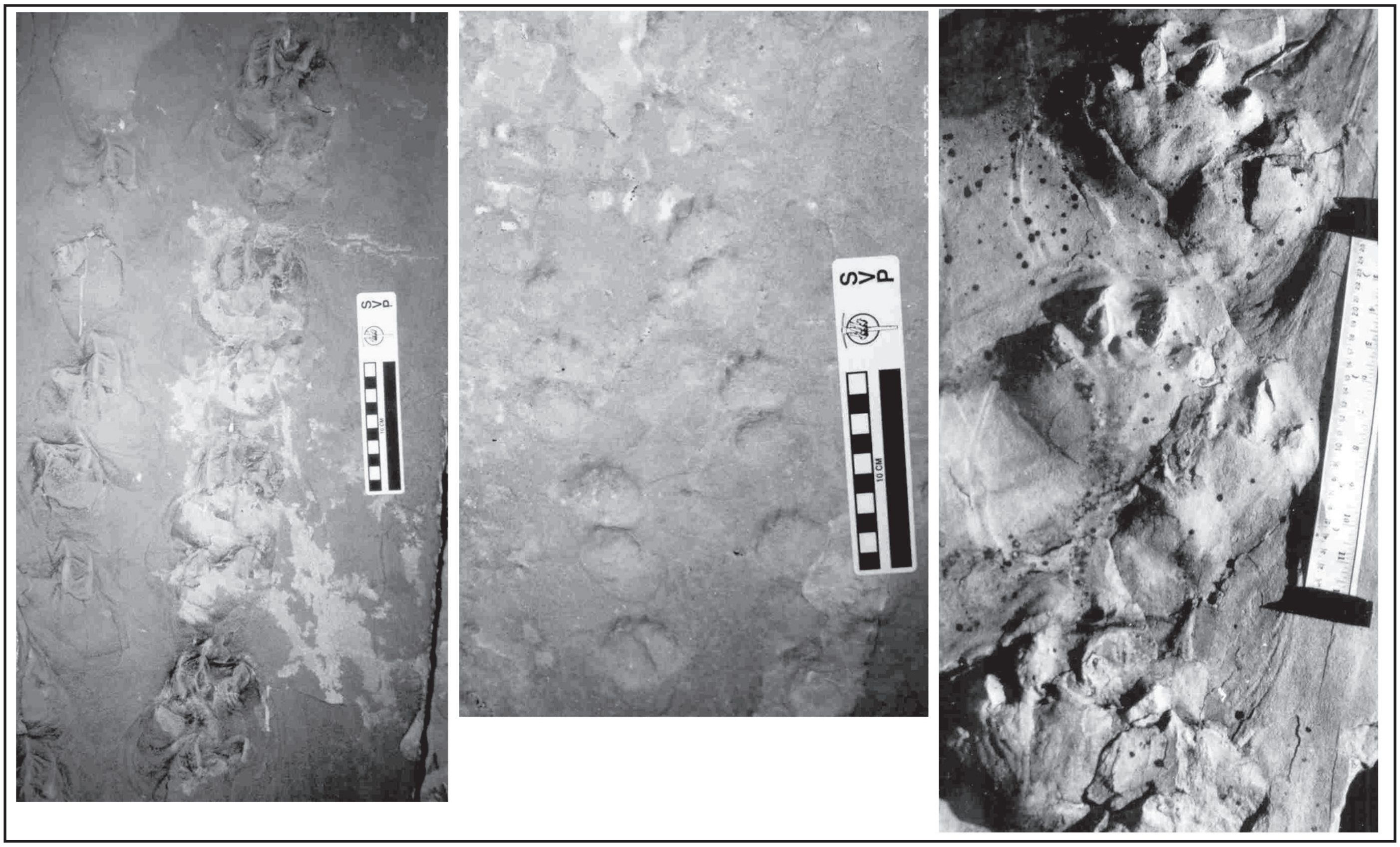

FIGURE 2. Selected trackways of *Chelichnus* in the Coconino Sandstone in the Grand Canyon National Park. **A**, *C. gigas*; **B**, *C. duncani*; **C**, *C. gigas*.

The Hermit Formation ichnofauna includes the nearly ubiquitous Permian temnospondyl track *Batrachichnus delicatulus*. Reptile tracks include *Parabaropus coloradensis* and *Hyloidichnus bifurcatus* (seymouriamorph or diadectid tracks) and the small pelycosaur track *Gilmoreichnus hermitanus*. Two other more problematic ichnotaxa are present in the Hermit Shale collections. Haubold (1971) named *Ichniotherium gilmorei* for a specimen (USNM 11707) originally described by Gilmore (1928a, pl. 1). Unfortunately, the holotype of this specimen is now lost (Haubold et al., 1995a). *Ichniotherium* is common in Europe but very rare in North America (Haubold et al., 1995a; Hunt et al., 1995; Hunt and Lucas, 1998b). A second problematic specimen is USNM 11598, a specimen that Gilmore (1927b, pl. 17, no. 1; Haubold et al., 1995a, fig. 24b) assigned to *Parabaropus coloradensis*. Haubold et al. (1995a) noted that this specimen is different from *P. coloradensis* in possessing distinct plantigrade impressions, elongate pedal imprints and less diverging digit impressions. They concluded that this trackway represents undertracks of either a *Dimetropus* specimen that preserves prominent pads and reduced digit impressions or a large *Limnopus* specimen (e. g., *Limnopus zeilleri*). We prefer the second interpretation because of the large manual pad impressions and because the long axis of the manual imprints is inclined at a high angle to the direction of travel.

Schnebly Hill Formation (Leonardian)

The Schnebly Hill Formation has yielded a single pedal impression of *Dimetropus* sp. (MNA V 3392) (Haubold et al., 1995a).

Ichnofacies

History of Study

Gilmore was aware that the Coconino Sandstone and Hermit Shale were deposited in different sedimentary environments, but Baird (1965) first emphasized that the differences between the Permian ichnofaunas of the redbeds of the American West and those of eolianites might be a result of facies differences. There has been a long tradition of recognizing ichnofacies in invertebrate traces, but the concept has only recently been applied to vertebrate tracks (Lockley et al., 1994). Tetrapod ichnofacies have been defined as "multiple ichnocoenoses that are similar in ichnotaxonomic composition and show recurrent association in particular environments" (Lockley et al., 1994, p. 242). Several subsequent workers have discussed Permian tetrapod ichnofacies (Lockley et al., 1994; Hunt et al., 1995, Haubold, 1996; Hunt and Lucas, 1998a). Hunt and Lucas (2005) reviewed Paleozoic tetrapod ichnofacies and recognized two nonmarine tetrapod biotaxonichnofacies, *Batrachichnus* for aqueous environments and *Chelichnus* for eolian ichnofaunas.

TABLE 2. Tetrapod ichnofauna of the Hermit Shale (Haubold et al., 1995; Hunt and Santucci, 1998).

Batrachichnus delicatulus (Lull, 1918) (= *Exocampe (?) delicatula, Batrachichnus delicatula, Batrachichnus obscurus, Dromillopus parvus*)
Parabaropus coloradensis (Lull, 1918)(= *Megapezia* (?) *coloradensis*)
Hyloidichnus bifurcatus Gilmore, 1927b (= *Hyloidichnus whitei*)
Gilmoreichnus hermitanus (Gilmore, 1927b)(= *Palaeosauropus hermitanus*, *Hylopus hermitanus*, *Collettosaurus pentadactylus, Cursipes* sp.)
Limnopus sp. (= *Parabaropus coloradensis* of Gilmore, 1927b in part)
Ichniotherium sp. (= *Parabaropus coloradensis* of Gilmore 1928a in part)

Coconino Sandstone and DeChelly Sandstone

The low diversity tetrapod ichnofauna of the Coconono and Chelly Sandstones clearly represents the *Chelichnus* biotaxonichnofacies (= *Laoporus* ichnofacies of Lockley et al., 1994) that is known from the DeChelly and Coconino Sandstone of Arizona, the Lyons Sandstone of Colorado, the Hopeman, Corncockle and Locharbriggs Sandstone formations of Scotland, the Cornberger Sandstein of Germany and the Los Reyunos Formation of Argentina (Hunt and Lucas, 1998a,b, 2005).

Hermit Formation

Permian tetrapod ichnofaunas from redbeds are cosmopolitan in nature, but a number of ichnofacies can be recognized. Hunt and coworkers (Hunt et al., 1995; Hunt and Lucas, 1998a) have suggested that the Hermit Shale ichnofauna shows similiarities to track assemblages from "inland" environments that were not in close proximity to a marine shoreline. This hypothesis is supported by the following features of the Hermit Shale ichnofauna (Hunt et al., 1995; Hunt and Lucas, 1998a): (1) presence of *Ichniotherium* and *Parabaropus*, which are "inland" facies fossils; (2) absence of *Dromopus*, which is abundant in coastal ichnofaunas; and (3) presence of *Limnopus*, which is uncommon in coastal ichnofaunas.

The Hermit Shale ichnofauna shows several similarities with the "inland" ichnofauna of the Sangre de Cristo Formation in New Mexico (*Ichniotherium, Parabaropus*), but is distinct in lacking *Dromopus* and *Dimetropus* (Hunt et al., 1995). Hunt and Lucas (2005) proposed the *Batrachichnus* biotaxonichnofacies for Permian ichnofaunas from aqueous nonmarine environments.

SIGNIFICANCE

The Permian ichnofaunas of Arizona are therefore significant for the following reasons:

1. They include the first large Paleozoic ichnofaunas from North America to have been scientifically described.

2. They include the largest sample sizes of trace fossils from eolianites.

3. They include significant Leonardian tetrapod ichnofaunas – other notable Leonardian tracks are limited to Texas and Oklahoma (Haubold and Lucas, 2001, 2003; Lucas and Hunt, 2005).

TETRAPOD BODY FOSSILS

The only body fossils of Permian tetrapods in Arizona are from the Monument Valley area near the Utah border. There are two localities in the Wolfcampian Organ Rock Shale at Mitchell Butte and one at Mitten Buttes (Sumida et al., 1999). The Mitchell Butte localities yields *Diadectes* sp., *Ophiacodon* sp., *Dimetrodon* sp. and *Sphenacodon* cf. *S. ferocior* (Vaughn, 1964, 1966; Sumida et al., 1999). The Mitten Buttes site has only produced *Diadectes* sp. (Baker, 1936; Sumida et al., 1999).

AQUATIC VERTEBRATES

A few records of aquatic vertebrates (mostly chondrichthyan teeth) are known from Arizona (Fig. 1; Table 3). Almost no vertebrates have been reported from the Toroweap Formation, but Mullens (1967) illustrates some fragments of what may be phyllodont tooth plates together with unidentified fish teeth from the Toroweap near Ashfork.

Although vertebrates are present in the marine Kaibab Formation and its correlatives, very little has been published. Hussakof (1943) reported selachian teeth that he identified as *Deltodus mercurii*, *Psephodus* and *Janassa*, a spine of *Hybodus* and a tooth of *Lepidotus* from the Kaibab Formation, no precise locality specified. The giant petalodontid chondrichthyan *Megactenopetalus kaibabanus* (Fig. 3) was initially described (David, 1944) from an incomplete upper tooth found near Point Sublime on the north rim of Grand Canyon. A second incomplete upper tooth was found later in the same area and together with teeth from New Mexico and Texas formed part of a redescription of the species by Ossian (1976). Hansen (1978) reported on an additional specimen (lower tooth) from the Concha Limestone of Santa Cruz County, Arizona that was associated with a fin spine that is tentatively attributed to the same animal. This is a widespread taxon that has also been reported from China (Liu and Hsieh, 1965), and Iran (Golshani and Janvier, 1974).

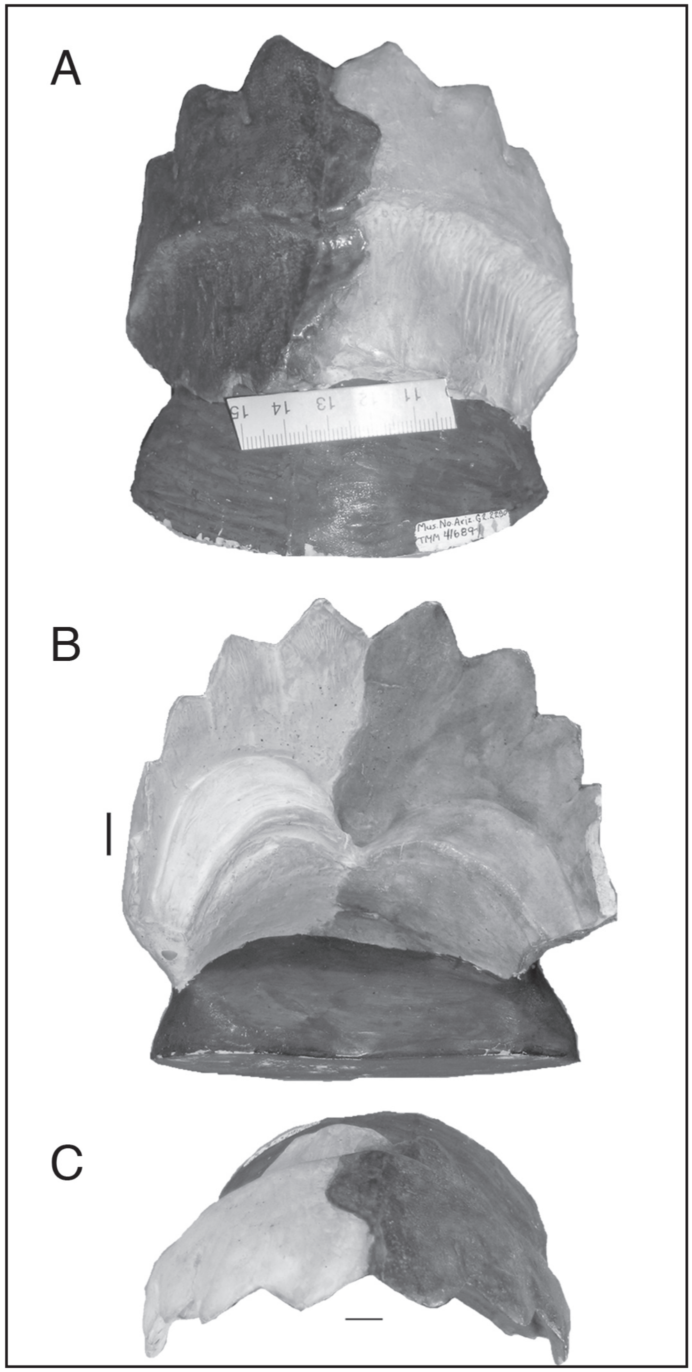

FIGURE 3. Giant petalodontid shark tooth from the Permian of Arizona, cast of MNA G 2.2280 (light-colored plaster is reconstruction), holotype of *Megactenopetalus kaibabanus* from the Kaibab Formation of the Grand Canyon, Arizona in **A**, labial, **B**, lingual, and **C**, occlusal views.

Phyllodont tooth plates were described but not named by Johnson and Zidek (1981) from localities in the Kaibab of the Grand

Canyon and Flagstaff area. Teeth of *Cladodus* sp. and *Deltodus mercurii* were reported by McKee (1982) from the Kaibab Formation in the Grand Canyon. A vertebrate microfauna has also been reported by Thompson (1995) from the Fossil Mountain Member of the Kaibab in Grand Canyon. This includes the chondrichthyan teeth *Coolyella peculiaris*, and unidentified hybodonts and the dermal denticles *Cooperella striatula*, and *Mooreyella typicalis*. It is clear, however, that an extensive vertebrate fauna awaits study.

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TABLE 3. Fish taxa reported from the Permian of Arizona.

Cladodus sp.
Coolyella peculiaris
Cooperella striatula
Deltodus mercurii
Janassa sp.
Hybodus sp.
Lepidotus sp.
Megactenopetalus kaibabanus
Mooreyella typicalis
Phyllodont tooth plates
Psephodus sp.

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