

First reported actinopterygian from the Navajo Sandstone (Lower Jurassic, Glen Canyon Group) of southern Utah, USA

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Abstract.—We report the first occurrence of an actinopterygian fish from the Lower Jurassic Navajo Sandstone, discovered in the Grand Staircase-Escalante National Monument in southern Utah, U.S.A. The site contains multiple individuals, preserved within an interdune deposit, possessing the elongate modified dorsal scales usually characterizing semionotiform fishes. The presence of moderately sized fish provides further evidence that interdune oases were occasionally persistent environmental habitats within the greater Navajo dune system, and that the paleobiota is still woefully undersampled. Additionally, this site could help fill a gap in the actinopterygian fossil record between the patchy Lower Jurassic and better-known Middle Jurassic documentation of western North America.

Introduction

Late Triassic and Early Jurassic fish assemblages from western North America are, in part, very diverse. Assemblages in the Chinle Formation and the “Lake Dixie fauna” of the Whitmore Point Member of the Moenave Formation document an ichthyofaunal transition across the Triassic-Jurassic boundary (Milner et al., 2006), but the remainder of the known Early Jurassic fish record in the West is rather sparse. This stands in contrast to the rich and well-documented coeval faunas from the Eastern Seaboard. Here, large lacustrine deposits have been discovered (e.g., the Newark Supergroup) with morphologically diverse assemblages of fish, chiefly composed of semionotiform taxa (Olsen et al., 1982; McCune, 1987).

Worldwide, semionotiforms were dominant and ubiquitous in aquatic ecosystems by the Late Triassic (Padian and Clemens, 1985; Cavin, 2010), and this certainly characterizes the group in the Early Jurassic “Lake Dixie fauna” (Milner and Kirkland, 2006). However, the ichthyofauna from the overlying Kayenta Formation and Navajo Sandstone range from depauperate to unknown, respectively, despite the wealth of fossil tetrapods described from the Kayenta (see Sues et al., 1994; Tykoski et al., 2002 and references therein). Whether this biased record is a result of unequal sampling (Milner et al., 2006) or a result of preservational or paleoenvironmental factors (Curtis and Padian, 1999) is debatable. Regardless, their relative rarity makes the discovery of any new fish-bearing sites in the Early Jurassic of the American West noteworthy. Here we report a new locality that has produced several semionotiform specimens from the Lower Jurassic Navajo Sandstone of Utah, representing the first known actinopterygian fossils from the entire unit. Additionally, the

presence of moderately sized fish within the expansive Navajo erg system bolsters the case for persistent, deep interdune lakes (e.g., Eisenberg, 2003; Parrish and Falcon-Lang, 2007) and highlights the importance of targeting interdune deposits for future field study, which will likely increase the diversity of the Navajo paleobiota (Winkler et al., 1991).

Repository and institutional abbreviation.—OMNH, Oklahoma Museum of Natural History, Norman, Oklahoma, USA.

Geologic setting

The Navajo Sandstone records an expansive Early Jurassic (Pliensbachian–Toarcian) dune system, covering much of what is now the Colorado Plateau (Fig. 1). The unit is the youngest component of the Glen Canyon Group; at its base, the Navajo intertongues with the dominantly fluvial Kayenta Formation, while the top of the unit is truncated by the J-1 unconformity where it meets the overlying Temple Cap or Carmel formations (e.g., Blakey et al., 1988; see reinterpretation of this transition by Doelling et al., 2013). Lithologically, the Navajo is predominantly composed of eolian sands stacked in thick sets of high-angle crossbeds. Interdune deposits are represented by localized limestones or relatively thin, horizontally bedded clastics. Periodic and occasionally prolonged shifts to a wetter climate stabilized portions of the Navajo erg and have been implicated in the formation of some of these deposits (Loope and Rowe, 2003), with some interdunes remaining wet enough for long enough to preserve large fossil trees (Parrish and Falcon-Lang, 2007) and even giant stromatolites (Eisenberg, 2003). Similar paleontological and sedimentological indicators of wet episodes have been recorded in the laterally equivalent Nugget Sandstone in northeastern Utah (e.g., Good and Ekdale, 2014).

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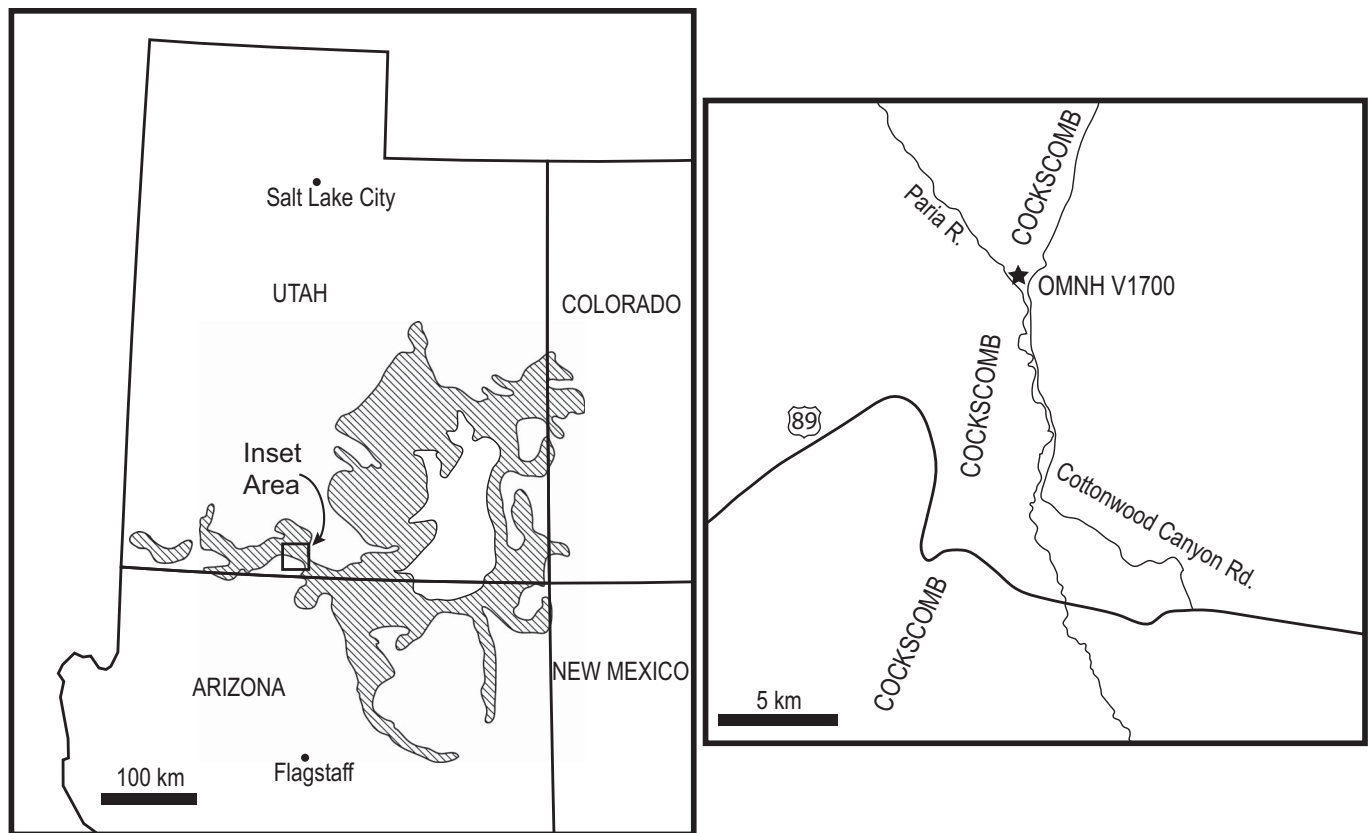


Figure 1. Map showing extent of Navajo Sandstone exposures in southwestern USA; inset shows location of OMNH V1700. Modified from Winkler et al. (1991).

Study of the vertebrate paleobiota of the Navajo Sandstone has understandably been focused on its ichnofauna. Vertebrate trackways are diverse and locally abundant (see summary in Irmis, 2005; Milàn et al., 2008), and complex burrows potentially made by small mammaliaforms have also been found (Riese et al., 2011). However, some body fossils are known from the Navajo; while incomplete, most are articulated and very well preserved. Though most specimens are indeterminate below family or order, the assemblage is clearly taxonomically diverse (Irmis, 2005). Some specimens (at least two sauropodomorphs) were discovered in eolian sandstones: a partial skeleton first reported by Brady (1935, 1936) and described later by Galton (1971); and the sauropodomorph *Seitaad* (Sertich and Loewen, 2010), which was preserved in a dune-collapse deposit. The majority of body fossils, however, have been recovered from interdune deposits. These represent paleoenvironments with better preservational potential than the surrounding dunes, and likely served as beacons to concentrate animals (Winkler et al., 1991; Irmis, 2005). Despite the inferred persistence and scale of some Navajo interdunes (from plant and invertebrate remains, e.g., Eisenberg, 2003; Parrish and Falcon-Lang, 2007), aquatic taxa such as fish have not been described, and the known record of vertebrates is limited to tetrapods (crocodylomorphs, dinosaurs, and tritylodontids, though turtles are also yet unknown). It is unclear if this reflects a lack of suitable distribution routes between Navajo interdunes and larger surrounding bodies of water or, more likely, poor sampling.

In 2013, an OMNH field party discovered small patches of articulated fish scales in an interdune deposit within the Navajo

Sandstone along the Paria River in Grand Staircase-Escalante National Monument, southern Utah (OMNH locality V1700, Fig. 1). These exposures are within the Cockscomb, a portion of the East Kaibab monocline (see Doelling et al., 2010). The entire section is heavily tilted and folded such that the Navajo partly overlies the stratigraphically higher Carmel Formation at their contact. The interdune deposit is positioned towards the top of the Navajo, but the contact with the Carmel has been deformed so its precise position in the section is difficult to determine. The deposit is ~5–8 m thick, and begins with a lower, structureless, dark-reddish sandstone that weathers into large, angular boulders. This is followed by a thinly laminated (5 mm beds), well-cemented purple siltstone that transitions upwards to a pale yellow, indurated but still laminated siltstone. A blocky, yellow, tabular sandstone with ~30 cm beds caps the sequence. Typical eolian sandstone beds are present above and below the interdune deposit, with fairly sharp contacts. The specimens described in this paper were recovered from the purple siltstone beds. Precise locality information is on file at the OMNH, and is available to qualified investigators upon request.

Systematic paleontology

Class Actinopterygii Klein, 1885
 Subclass Neopterygii Regan, 1923
 Order Semionotiformes Arambourg and Bertin, 1958 sensu
 Olsen and McCune, 1991
 Family indeterminate

Materials.—At least two partially articulated individuals composed of scales, scale impressions, and possible teeth and fin rays (OMNH 77069–77072). Isolated scales were also recovered from the same site, within a few meters laterally of the more complete material.

Occurrence.—OMNH V1700, Navajo Sandstone (Lower Jurassic), ~38 km southeast of Cannonville, Kane County, Utah, USA.

Description.—The material described here represents several individuals belonging to one or more indeterminate, medium-sized semionotiform species. Although we cannot exclude the possibility that these specimens represent different taxa, no obvious features (other than size) serve to differentiate them; thus, we will herein refer to them under a single moniker as the Navajo fish. Both partially articulated specimens possess an incomplete squamation composed of rhomboidal ganoid scales (Fig. 2.1–2.4). Preserved scales vary from relatively long and caudally pointed in apparent dorsal ridge scales (Fig. 2.5, 2.6), to taller than long and more rectangular in the scales of the mid-body. Isolated scales indicate that this specimen lacks a large peg and socket articulation, although a small dorsal projection and corresponding medial groove can be seen on one scale impression (Fig. 2.7, 2.8). In addition, some isolated scales possess both the rostral and rostroventral projection used by Cavin et al. (2009) to diagnose isolated semionotid scales from Thailand. The rostroventral projection is nearly a third the size of the rostradorsal process in this specimen (OMNH 69349), but other scales appear to lack this feature altogether (Fig. 2.9, 2.10). Given the lack of comprehensive scale studies for semionotid fishes, we tentatively attribute these differences to intraspecific variation between scales from varying parts of the body.

The two most complete specimens are composed of articulated scales preserved mostly as impressions with inconsistent, small occurrences of heavily mineralized scale or bone. The first specimen (OMNH 77070, Fig. 2.1, 2.2) consists of dorsal and rostral scales abutted to impressions that compare favorably to the triangular posttemporal and rounded supraclithrum of other semionotids (Olsen and McCune, 1991, fig. 4A). As preserved, this specimen is at least seven scales long rostrocaudally, measuring ~30 mm in length. The dorsal margin is also preserved in this specimen, typified by scales with a highly modified elongate and caudally directed spine. Moving ventrally, the scales become more poorly preserved, but appear to elongate closer to the hypothesized midline of the fish. The second specimen (OMNH 77069) is larger, with an unbroken series at least eight scales tall by seven scales long, ~50 mm in total length as preserved (Fig. 2.3, 2.4). This specimen is composed largely of tall mid-ventral scales, as well as remnants of one of the ventral fins (likely the pelvic fin). Multiple scales on the underside of the block containing this specimen belong to an additional individual. Of interest are two scales preserved with their elongate caudal processes aligned into a single ridge, representing an additional specimen bearing the characteristic semionotid dorsal ridge crest (Fig. 2.5, 2.6). The scales of all of the specimens are relatively smooth, lacking obvious large tubercles. A third block preserves what appear to be cross-sections of small, circular teeth packed in close proximity to one

another. They appear to be of a crushing-style tooth morphology, which McCune (1986) attributed mostly to *Lepidotes* species, but acknowledged that this is likely size-related and exceptions do occur. The Navajo fish does not have the large humped back seen in *Lophionotus sanjuanensis* Gibson, 2013a, nor is its body greatly thickened dorsoventrally as in many other semionotiform species (e.g., Jain, 1984; McCune, 1986; Wenz, 2003). In life, this species would have been a medium-sized semionotiform, eclipsed by some of the Late Jurassic and Cretaceous species (e.g., Jain, 1984), but substantially larger than the diminutive *Lophionotus kanabensis* Schaeffer and Dunkle, 1950 (Gibson, 2013b), one of the few described species of semionotids from the Western United States, which is not known to exceed 74 mm in length.

Remarks.—The Navajo fish material is decidedly similar to other North American Jurassic fish, mainly of the genera *Lepidotes* and *Semionotus* (the latter of which likely represents two genera, including *Lophionotus* of Gibson, 2013a, 2013b, but which will be treated here as single genus for historical context); however, difficulties differentiating these genera are well documented (Schaeffer, 1967; McCune, 1986). Precise determination of the Navajo fish species is hindered in part by the state of preservation of the few known specimens. No skull was recovered with any of the specimens, making genus- and species-level identification impossible. Nonetheless, the elongate dorsal ridge scales and scale morphology provide enough comparative material to confidently assign the order Semionotiformes. Further, given the numeric abundance of *Semionotus* and *Lepidotes* during the Early to Middle Jurassic, it would be reasonable to hypothesize that this material represents one of these taxa. Olsen and McCune (1991, p. 270) condensed both genera into a restricted definition of the family Semionotidae, based on two synapomorphies: the presence of dorsal ridge scales; and a large, posteriorly directed “epiotic.” More recent phylogenetic analyses of semionotiform relationships, however, demonstrated that even this reduction is paraphyletic. Cavin (2010) recovered *Lepidotes* and *Semionotus* as consecutive branches on an unnamed node nested within a monophyletic Semionotiformes. Like previous analyses, Semionotiformes has been recovered as a monophyletic group, containing Macrosemiidae, Semionotidae, and Lepisosteidae (Olsen and McCune, 1991; Brito, 1997; Cavin et al., 2003). Cavin’s (2010) phylogeny further recovers an unnamed clade within Semionotiformes to the exception of the Macrosemiidae, which can be diagnosed in part by the presence of dorsal ridge scales. This character, which is unambiguously present on the Navajo material, is highly conspicuous in most *Semionotus* species, but often more discreet in *Lepidotes* (McCune, 1986). However, a more recent phylogenetic analysis by López-Arbarello (2012; corroborated by Gibson, 2013a, 2013b, 2016) brings into question the close relationship between *Semionotus* and *Lepidotes*. In this analysis, *Lepidotes* was recovered in a separate clade (order Lepisosteiformes) more similar to the modern gar (*Lepisosteus* Lacepède, 1803 and *Atractosteus* Rafinesque, 1820) than to *Semionotus*. *Semionotus* was found to be monophyletic (Semionotidae), nested within a broader order Semionotiformes. The large, conspicuous dorsal ridge, used by previous authors to diagnose semionotids, was recovered in this

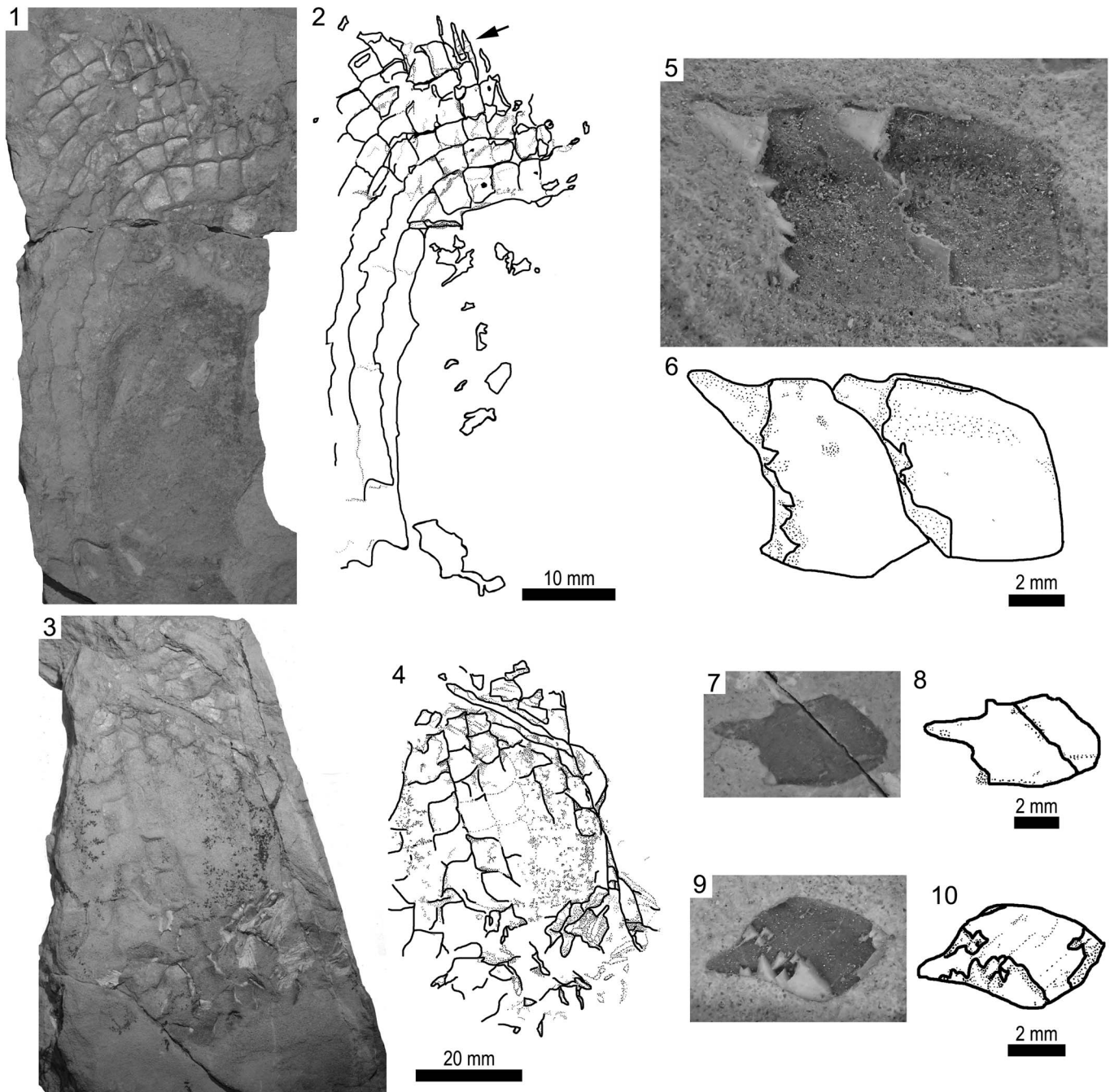


Figure 2. Semionotiform specimens recovered from OMNH V1700. (1, 2) OMNH 77070, a specimen preserving the rostradorsal squamation, including the characteristic dorsal ridge scales (black arrow); (3, 4) OMNH 77069, mid-ventral scale pattern and possible pelvic fin rays; (5, 6) OMNH 77069, dorsal ridge scales likely from a second individual on the same slab as Figure 2.3, 2.4; (7, 8) OMNH 69349, isolated ganoid scale preserving the peg and socket joint; (9, 10) OMNH 69350, isolated ganoid scale without the peg and socket joint.

analysis as an autapomorphy for the genus *Semionotus* (or a synapomorphy for Semionotidae, including both *Lophionotus* and *Semionotus* [Gibson, 2013b]). This split largely agrees with Grande's (2010) phylogeny, where Semionotiformes and Lepisosteiformes form sister groups within the broader Ginglymodii. Without a more complete dorsal series, it is nearly impossible for us to assign the Navajo specimens to either the more *Lepidotes*-like Lepisosteiformes or the *Semionotus*-like Semionotiformes using this scheme. Given that the aforementioned taxonomic issues require a more comprehensive reevaluation of

the entire clade, we hesitate to delve into this debate. Here we stick to a more classic definition of Semionotiformes (sensu Olsen and McCune, 1991), with the understanding that more complete material will require a thorough incorporation of this species into the current ginglymodian phylogeny.

Discussion

Paleoenvironmental significance.—Due to an increased risk of predation by wading predators at shallow water depths, it has

been generally observed that larger fish tend to live in deeper water systems (Werner et al., 1977; Schlosser, 1988; Harvey and Stewart, 1991). The presence of moderately sized fish in the Navajo deposits supports previous suggestions of relatively deep and possibly long-lived ponds in the Navajo dune system. Loope and Rowe (2003) conservatively estimated the wet, pluvial episodes within the Navajo Sandstone may have lasted between 4,000 and 5,000 years, during which time yearly monsoons were capable of depositing up to 170 mm of rain per storm (Loope et al., 2001). These authors note that an analogous environment existed in the mid-Holocene Selima Oasis of Sudan, where wet periods reached a precipitation rate of up to 200 mm/yr causing high stands of pluvial Lake Selima to reach depths up to 17 m (Haynes, 1987; Haynes et al., 1989; Loope and Rowe, 2003). Although it is conceivable such water depths in the Navajo could have occurred, the fish material presented here can only in the broadest sense tell us that water depth was deep enough to support a small population of moderate-sized fishes for more than a single year. Some interdune deposits in the Navajo have been interpreted as fluvial in origin (Loope and Rowe, 2003). Because these fish must have dispersed to this particular interdune lake from some larger body of water, further work on Navajo interdune deposits may reveal more about how these localized habitats were connected during wetter periods in the Early Jurassic erg.

Implications for the Early Jurassic fossil fish record.—Unlike the relatively well-documented fish assemblages of the eastern coast, Early Jurassic fishes of the western USA are incompletely known (Milner et al., 2006, and references therein). Currently, only two formations from the Jurassic west have yielded recognizable fossil fish remains. The earliest is the Hettangian “Lake Dixie fauna” from the Whitmore Point Member of the Moenave Formation of southwestern Utah and northwestern Arizona (Kirkland et al., 2014). This fauna has yielded a surprising diversity of material, including a hybodont shark, a palaeonisciform, a possible perleidiform, several semionotiforms, and at least two sarcopterygians (Milner and Kirkland, 2006; Milner et al., 2006). Semionotiforms are the numerically dominant group, with at least three known species historically recognized from the fauna (Eastman, 1917; Hesse, 1935; Schaeffer and Dunkle, 1950; see Milner and Kirkland, 2006 and Milner et al., 2006 for discussion of the validity of these taxa). The next oldest ichthyofauna is from the middle Sinemurian to early Pliensbachian Kayenta Formation, which contains two sharks and two dipnoans, as well as an undescribed coelacanth, semionotid, and palaeoniscoid (Curtis and Padian, 1999; Milner et al., 2006, 2012; Frederickson and Cifelli, 2017; personal communication, A.R.C. Milner, 2017). After these faunas, a gap in the Western Interior fossil fish record exists until the relatively diverse Middle Jurassic Sundance and Wanakah faunas (Schaeffer and Patterson, 1984; Wilson and Bruner, 2004). Schaeffer and Patterson (1984) described, but did not name, a species of *Lepidotes* among six other fish genera from the marine Sundance Formation. The Sundance *Lepidotes* is only known from a few fragmentary specimens, and is much rarer than the well known, but phylogenetically obscure, *Hulletia* and the basal teleosts *Occithrissops* and *Todiltia*. The fish occurrence described here from the Navajo Sandstone would fall into

this gap, slightly after the semionotid-dominated Early Jurassic ichthyofaunas and well before the more diverse assemblages of Middle Jurassic formations.

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