A REVUELTOSAUR-LIKE TOOTH FROM THE PETRIFIED FOREST FORMATION (UPPER TRIASSIC: REVUELTIAN), ZION NATIONAL PARK

ANDREW B. HECKERT[1], SPENCER G. LUCAS[2], DONALD D. DEBLIEUX[3] AND JAMES I. KIRKLAND[3]

[1]Department of Geology, Appalachian State University, ASU Box 32067, Boone, NC 28608-2067;
[2]New Mexico Museum of Natural History, 1801 Mountain Road NW, Albuquerque, NM 87104;
[3]Utah Geological Survey, 1594 West North Temple, Suite 3110, P.O. Box 146100, Salt Lake City UT 84114-6100

Abstract—We describe an isolated archosauriform tooth from the Upper Triassic Painted Desert Member of the Petrified Forest Formation in Zion National Park in southwestern Utah. This tooth is relatively low (mesio-distally as long as baso-apically tall), bulbous and asymmetrical in occlusal view, and has denticles that are oblique to the tooth crown. The base of the tooth is also slightly expanded relative to the root. Among Triassic archosaurs, this tooth most closely resembles maxillary/dentary teeth of *Revueltosaurus callenderi* Hunt, although the Utah specimen is somewhat smaller and bears finer denticles than typical *R. callenderi* teeth. Although most archosaurs have somewhat generalized teeth, there are distinctive morphotypes, and these have been shown to reliably document taxa that are rarer than the usual phytosaurs, aetosaurs, and metoposaurs the dominate most Chinle faunas.

INTRODUCTION

In 2003, while participating in a comprehensive inventory of paleontological resources in Zion National Park conducted by National Park Service interns and the Utah Geological Survey, one of us (DD) discovered an isolated reptile tooth in Upper Triassic outcrops in Zion National Park (Fig. 1). This tooth was weathering out as float in the upper red-bed mudstone slopes of the Petrified Forest Formation, a stratigraphic unit that is commonly undivided throughout southern Utah (Stewart et al., 1972; Lucas, 1993). In this paper we describe and illustrate this fossil (Fig. 2) and briefly comment on its significance.

STRATIGRAPHY AND AGE

The Petrified Forest Formation is part of the Upper Triassic Chinle Group (*sensu* Lucas, 1993) and is of Late Triassic age throughout its outcrop belt (e.g., Stewart et al., 1972; Lucas, 1993, 1997). In the vicinity of Zion National Park, the unit is seldom, if ever, subdivided into constituent members, the Blue Mesa, Sonsela, and Painted Desert (in ascending order), as commonly recognized to the south in Arizona and New Mexico. Instead, the Chinle above the Shinarump has been mapped as the Petrified Forest Member undifferentiated (e.g., Gregory, 1950; Cook, 1960; Doelling and Davis, 1989; Biek et al., 2000, 2003; see insert in Fig. 1). However, in Zion National Park, we (ABH and SGL) can readily recognize the Blue Mesa, Sonsela and Painted Desert members of the Petrified Forest Formation, as well as the overlying Owl Rock Formation (Fig. 1).

The site is one of many new Chinle localities found during a recent paleontological inventory (DeBlieux et al., 2003). This locality, termed 42Ws223v, is located in the southwestern portion of Zion National Park south of Cougar Mountain. Other fossils found at the site include indeterminate bone fragments, phytosaur teeth, small coprolites, and some fragments of petrified wood. The tooth itself was recovered from a slope-forming interval stratigraphically high in what we recognize as the Petrified Forest Formation. The tooth locality is in a 0.6-m-thick bed of green siltstone that is approximately 12 m below the contact of the Petrified Forest Formation (Painted Desert Member) with the overlying Owl Rock Formation (Fig. 1). Strata of the Painted Desert Member are variegated red, green and purple, slope-forming mudstone and siltstone with sparse calcrete nodules. The overlying Owl Rock Formation is ~12 m thick locally and consists of purple mudstone with numerous calcrete nodules. A sharp unconformity (Tr-5 unconformity of Lucas, 1993) separates the Owl Rock Formation from the overlying Moenave Formation (Fig. 1), as it does in northwestern Arizona (Lucas et al., 2005).

DESCRIPTION

The specimen (ZION 15675; reposited in the Natural History collections of Zion National Park), is a microvertebrate fossil preserved as a shed(?) tooth crown lacking any root but possessing a resorbtion cavity (Fig. 2). As preserved, the tooth is approximately 3.2 mm tall (basal-apical height), 3.6 mm long (mesial-distal length), and 2.3 mm wide (labial-lingual thickness). In occlusal view, the labial margin is bulbous relative to the lingual margin, so that the tooth is asymmetric from this perspective (Fig. 2D). The crown of ZION 15675 is slightly expanded relative to the resorbtion cavity at the base where the crown attached to the root. Both the mesial and distal margins bear fine (8-12/mm) denticles that are oblique to the tooth margin. The apical surface is incomplete, presumably as a result of wear. Because the resorbtion cavity is preserved intact at the base of the tooth crown, and most of the denticles basal to the apical surface are relatively well-preserved, we interpret this as pre-mortem wear, presumably the result of relatively precise tooth occlusion. Indeed, comparison of much of the worn surface with the small fractures and breaks in the enamel across the labial face of the tooth (e.g., Fig. 2E-F) shows that most wear is relatively even, and that post-mortem fracturing is a minor component of the damage to the tooth. The general pattern of wear on ZION 15675 mimics that documented for *Revueltosaurus callenderi* by Heckert (2002) in that the tooth is worn down more or less perpendicular to its height, and the worn surface is not offset either mesio-distally or labio-lingually. Additionally, the dentine is exposed along the worn tips of the denticles, another feature documented by Heckert (2002) in *R. callenderi*. This is distinct from, for example, tooth wear observed in *Krzyzanowskisaurus hunti* (Heckert, 2002, 2005).

COMPARISONS

Several of the preserved features of ZION 15675 have historically been considered synapomorphies of the Ornithischia (Sereno, 1991, Hunt and Lucas, 1994). These include a base that is expanded relative to the root, a low profile (ratio of height:length < 1), denticles that are oblique to the tooth margin, and an asymmetrical shape in occlusal (apical) view due to a prominent labial bulge. We use "expanded tooth crown" (as opposed to "constricted near root") to note the importance of the evolutionary transition to wider teeth that presages the more advanced dental

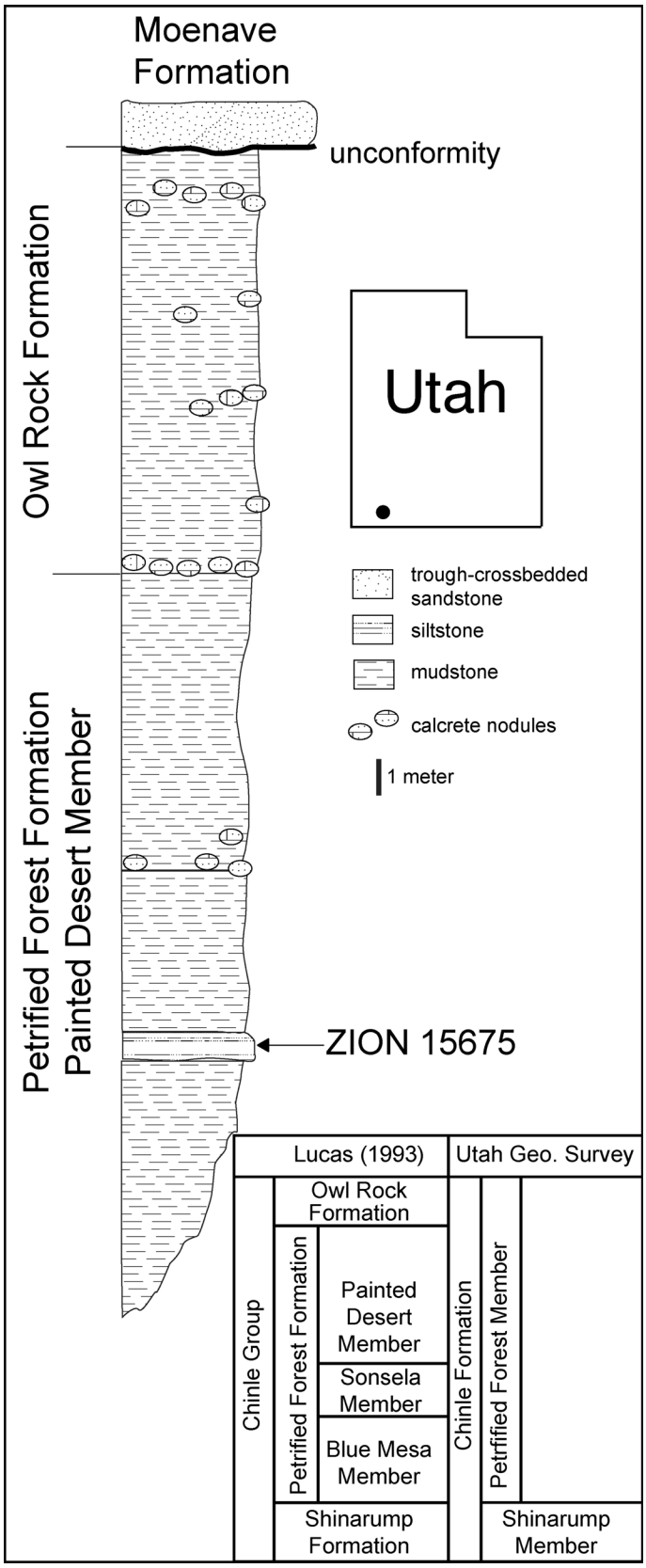

FIGURE 1. Index map and generalized stratigraphic column showing the location of the tooth described here. Inset chart compares the lithostratigraphy used here by Lucas and Heckert to traditional Utah Geological Survey usage in Zion National Park.

batteries of derived ornithischians. Indeed, the only ornithischian synapomorphy that the Zion tooth lacks is a prominent cingulum involved in tooth occlusion, a synapomorphy that is actually absent in many teeth of basal ornithischians (e.g., Sereno, 1991; Thulborn, 1992; Hunt and Lucas, 1994; Heckert, 2002, 2005; Hunt et al., 2005). These features led Hunt (1989) and most subsequent workers to consider *Revueltosaurus callenderi* an ornithischian dinosaur, an hypothesis that was only recently falsified when Parker et al. (2005) demonstrated that teeth of *R. callenderi*, while diagnostic to genus and species, occur in the jaws of a crurotarsan archosaur. Thus, the only unambiguous synapomorphy Parker et al. (2005) recognize uniting all ornithischians is the presence of a well-developed cingulum, a feature lacking in ZION 15675.

As in *R. callenderi*, the denticles extend equally far down the tooth on both the mesial and distal carinae. The most basal denticles are badly damaged, but appear to be somewhat finer than the more apical denticles. The apical denticles are worn away, and the tooth itself is worn flat (perpendicular to tooth height). The denticles are offset lingually, and indeed are more readily visible in lingual than labial view (Fig. 2). However, the denticles themselves are much finer (8-12/mm) than the 1.5-3.7/mm reported for *R. callenderi* (Heckert, 2002). This may, in part, be an artifact of the small size of the tooth. However, even if the denticles scale evenly with the height of the crown, then a 7-10 mm tall tooth of the same size as ZION 15675 would have 3-6 denticles/mm. The crown wear, however, is identical to that observed on maxillary/dentary teeth of *R. callenderi*, where the tooth is worn down perpendicular to crown height, forming a surface that is relatively flat (i.e., not inclined either labio-lingually or mesial-distally) (Heckert, 2002).

Another taxon that ZION 15675 resembles is the putative ornithischian *Pekinosaurus olseni* Hunt and Lucas. Like the holotype and referred maxillary/dentary teeth of *Pekinosaurus*, ZION 15675 is mesiodistally longer than baso-apically tall (FABL of Farlow et al. [1991] exceeds crown height). Similarly, both *Pekinosaurus* and ZION 15675 exhibit numerous relatively fine denticles that are offset (subperpendicular) to the tooth margin. ZION 15675 is too worn to determine if it bore vertical denticles akin to the most apical denticles of *Pekinosaurus*. The Zion tooth is somewhat smaller than the type and referred specimens of *Pekinosaurus olseni*. The denticles of ZION 15675 are also less prominent (a qualitative observation) and finer (8-12 denticles/mm versus 2-3 denticles/mm in the holotype of *Pekinosaurus olseni*). Again, even if the different size of the teeth is taken into account, the Zion tooth is still much more finely denticulate. It is also not as markedly asymmetric in occlusal view as the holotype of *P. olseni*, although it does compare favorably with the referred *Pekinosaurus* maxillary/dentary tooth illustrated by Hunt and Lucas (1994, fig. 12.5a-b).

We envision two hypotheses for the taxonomic placement of ZION 15675. The first of these is that the differences between the Zion tooth and *R. callenderi* are a result of the ontogenetic age of the former; thus, perhaps it represents a juvenile of *R. callenderi*. A second possibility is that it pertains to another taxon entirely, perhaps *Pekinosaurus* or a similar taxon. In support of the first hypothesis are (1) the small size of the specimen, especially given that scaling it up matches *R. callenderi* denticle counts more precisely; and (2) the fact that the wear corresponds to that observed in *R. callenderi* teeth. In support of the latter hypothesis is the fact that there are several significant differences between the teeth of *R. callenderi* and ZION 15675, and that not all of these are readily explained as due to ontogeny. Recently we have been made aware of work that suggests that *Pekinosaurus* is congeneric with *Revueltosaurus* (S. Nesbitt and W. Parker, personal commun.), and that it may come from strata younger than Otischalkian (P. Olsen, personal commun.). We consider this data evidence in support of our hypothesis that this tooth represents a "revueltosaur."

It may therefore be instructive to consider what ZION 15675 is not. It is clearly not the tooth of a phytosaur because even the blade or

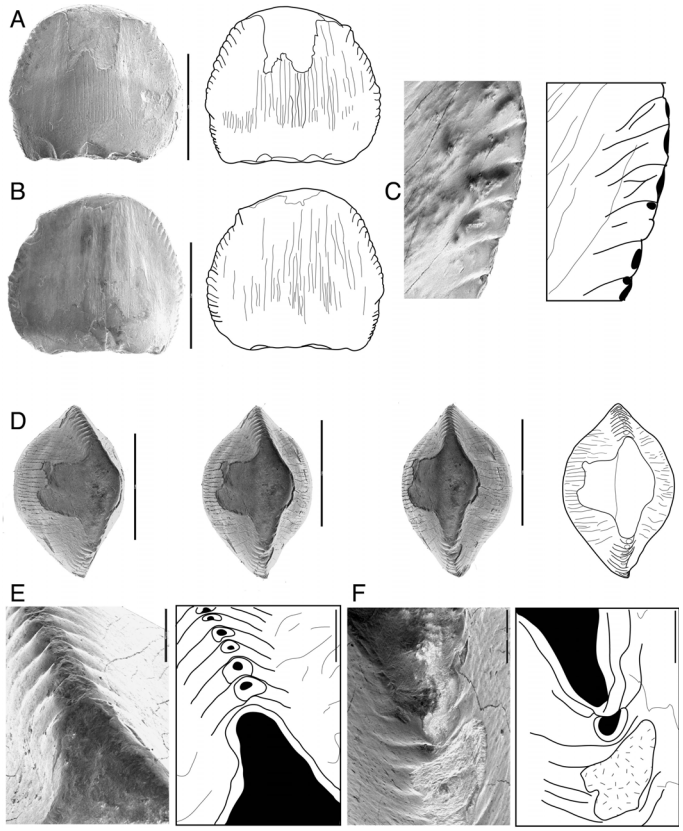

FIGURE 2. Archosauriform tooth (ZION 15675) from the Petrified Forest Formation, Zion National Park, scanning electron micrographs and interpretative sketches in **A**, labial, **B**, lingual, **C**, close-up of lower right labial side, **D**, stereo occlusal views. **E-F**, close-up of mesial and distal denticles adjacent to crown. Scale bars = 2 mm (**A-B**, **D**) and 500 microns (**C**, **E-F**).

distal teeth of phytosaurs lack both offset denticles and any indication of precise wear (e.g., Hunt, 1994; Hungerbühler, 2000). Godefroit and Cuny (1997, pl. 1d-e) illustrated a broadly similar tooth from the Upper Triassic of Saint-Nicolas-de-Port (northeastern France) that they ascribed to a phytosaur. ZION 15675 is grossly similar to that tooth, but is somewhat more coarsely denticulated (8-12 denticles/mm compared to 11-15 denticles/mm for the French tooth) has denticles that are less perpendicular to the tooth margin, and appears more asymmetrical in occlusal view than the French tooth, which may or may not represent the blade tooth of a phytosaur and is probably best considered Archosauriformes indet. Interestingly, the French tooth shows some indication of wear on the denticles, but the apical portion of the tooth is broken, not obviously worn, so we cannot ascertain whether it is worn in a fashion similar to that seen in ZION 15675 and *Revueltosaurus callenderi* (Heckert, 2002).

Similarly, ZION 15675 does not resemble any known aetosaur teeth, as aetosaurs typically lack denticles (e.g., Walker, 1961; Small, 2002). Clearly, it is not a prosauropod, all of which possess taller teeth, nor is it a prosauropod-like form (e.g., *Azendohsaurus* or the broadly similar Malagasy Triassic taxa [Gauffre, 1993; Flynn et al., 1999]). Indeed, all putative Late Triassic prosauropods have taller, more laterally compressed teeth than ZION 15675 (e.g., Benton et al., 2000; Harris et al., 2002). Nor does it appear at all similar to the putatively ornithischian-like teeth of *Silesaurus* (Dzik, 2003). Finally, ZION 15675 differs markedly in size, shape, and denticulation from most upper Triassic tooth taxa, including *Tecovasaurus*, *Galtonia*, *Crosbysaurus*, *Protecovasaurus*, *Lucianosaurus*, and *Krzyzanowskisaurus* (Hunt and Lucas, 1994; Heckert, 2001, 2004, 2005).

SIGNIFICANCE

Utah lacks the rich body fossil record of Upper Triassic vertebrates that typifies nearby Arizona, New Mexico, and Texas (e.g., Hunt and Lucas, 1993; Lucas et al., 1994; Long and Murry, 1995; Heckert et al., 2005), although this is almost certainly due to the lack of concentrated exploration of these strata. Still, the sheer volume of exposed outcrop, particularly in Utah's many national parks, should facilitate future discoveries. Prior to this study, there were no known published vertebrates from Triassic strata in Zion National Park, although the Zion Natural History Collections include indeterminate metoposaurid fossils identified by E.H. Colbert. Incidentally, the body fossils of the semionotid fish *Semionotus* sp. reported by Hesse (1935; see also Schaeffer and Dunkle, 1950) were actually derived from the Lower Jurassic Whitmore Point Member of the Moenave Formation (Biek et al., 2000, 2003). Accordingly, this record is one of the more diagnostic Triassic vertebrate fossils from Zion National Park, and demonstrates the presence of a revueltosaur-like animal, if not *Revueltosaurus* itself, in the Upper Triassic of Utah for the first time.

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