An unusual archosauromorph tooth increases known archosauromorph diversity in the lower portion of the Chinle Formation (Late Triassic) of southeastern Utah, USA

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Abstract:

An unusual tetrapod tooth was discovered in the Upper Triassic Chinle Formation of southeastern Utah. The tooth was originally hypothesized to pertain to *Revueltosaurus* but further investigations have rejected that hypothesis. In this paper, we compare MNA V10668 to other known fossil teeth found in the Chinle Formation and assign the tooth to the least inclusive clade currently available. Using data found in other publications and pictures of other teeth, we compare this specimen to other Triassic dental taxa. MNA V10668 shares some similarities with *Crosbysaurus*, *Tecovasaurus*, and several other named taxa but possesses a unique combination of characteristics not found in other archosauromorph teeth. We conclude that it is most likely an archosauromorph and possibly an archosauriform. This increases the known diversity of archosauromorph from the Chinle Formation and represents the first tooth morphotype completely unique to Utah in the Late Triassic.

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Introduction:

The recovery of vertebrate life from the Permian-Triassic transition resulted in an amazing array of new body forms as life filled ecological voids [citations]. This is especially noticeable in the archosaurosauromorphs. Many archosauromorph, archosauriform, and archosaurian reptiles adapted and radiated across the globe, filling or creating numerous resource zones with novel body forms (Nesbitt et al., 2010) and dietary specializations (Heckert, 2004; Parker et al., 2005). The ecological revolution of the Triassic Period laid the groundwork for dinosaurs (including extant birds), crocodylian, and mammals to dominate terrestrial vertebrate assemblages for the next 200 million years.

It is perhaps somewhat surprising then that the terrestrial record of the Upper Triassic from Utah, USA has not reflected the global diversification of tetrapod clades. Some of this may be attributed to the greater attention that Late Triassic deposits in neighboring Arizona and New Mexico have received (Long and Murray, 1995; Parker et al., 2006). Until recently (Heckert et al., 2006; Gibson, 2013; Martz et al., 2014) the Triassic vertebrate record published from Utah has mainly consisted of the ubiquitous phytosaurs (Morales and Ash, 1993). This is especially true when looking at body fossils only. Even with this recent work, Utah's Triassic tetrapod record is low in diversity compared to adjoining states, with the majority of specimens being identified as either phytosaurs or aetosaurs (Martz et al., 2014).

In May of 2014 a paleontological expedition was conducted by Mission Heights Preparatory High School to Comb Ridge in southeastern Utah. During the expedition two of the authors (AM and IS) discovered a new, very rich microsite they dubbed The Hills Have Teeth (Museum of Northern Arizona Locality 1724), near a locality that was previously discovered by

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the senior author (RG). Both at The Hills Have Teeth and the alluvial fan immediately adjacent to the hill, a dozen partial and complete tetrapod teeth were collected. Most of these teeth belonged to phytosaurs and temnospondyls. Two teeth were notably different from the dominant taxa. One, discovered by IS, is described elsewhere (Gay and St. Aude, 2015). The other was collected by one of the authors (AM) and is the subject of this contribution. and defied classification at the time of discovery. Since then we have had the opportunity to compare this new specimen to other identified teeth from across the Chinle and Dockum Formations. That specimen, MNA V10668, is compared here to many Triassic diapsids in order to assign it to a taxon. We compare it to the non-archosauriform archosauromorphs *Azendohsaurus* (Flynn et al., 2010), *Mesosuchus browni* (Dilkes, 1998), and *Teraterpeton hrynewichorum* (Sues, 2003), several non-archosaurian archosauriforms including *Crosbysaurus harrisae* (Heckert, 2004), *Crosbysaurus sp.* (Gay and St. Aude, 2015), *Krzyzanowskisaurus hunti* (Heckert, 2005), *Lucianosaurus wildi* (Hunt and Lucas, 1995), *Protecovasaurus lucasi* (Heckert, 2004), *Revueltosaurus callendari* (Hunt, 1989), *Tecovasaurus murrayi* (Hunt and Lucas, 1994), unidentified or unnamed archosauriform teeth (Heckert, 2004), and several archosaurs (Colbert, 1989; Dalla Veccia, 2009; Heckert, 2004).

Materials and Methods:

Standard paleontological field materials and methods were used to collect all specimens from MNA locality 1725, as described in Gay and St. Aude (2015). GPS coordinates of???? MNA V10668 was recorded using Backcountry Navigator Pro running on an Android OS smartphone. It was collected in a zip-seal collection bag after being removed from the surface exposure by hand. Measurements of MNA V10668 were obtained using a set of Craftsman metal calipers (model 40257) with 0.05mm precision. Figures were created using GIMP 2.8.4. Photos

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were captured taken with an Olympus E-500 DSLR and PC USB digital microscope. MNA V10668 was collected under Bureau of Land Management permit UT14-001S and is permanently housed at the Museum of Northern Arizona (MNA) along with exact locality information.

Geologic Setting:

MNA V10668 was found on the surface of Lower Member of the Chinle Formation at Comb Ridge, Utah (Figure 1), roughly 6 meters from the base of the Lower Member along with teeth of phytosaurs, temnospondyls, and *Crosbysaurus* (Gay & St. Aude 2015) at MNA Locality 1725. As with earlier work, we hold that fossil material from locality 1725 has washed down slope from The Hills Have Teeth outcrop, MNA locality 1724. In May of 2015 the precise fossil-bearing horizon was located at The Hills Have Teeth. The horizon is a light grey mudstone with interspersed carbonaceous clasts and numerous teeth (Figure 2). This mudstone is 13 cm below the red brown mudstone-grading-to-shale, 8.75 meters above the base of the Chinle Formation (Gay and St. Aude, 2015; figure 4). The fossil-bearing Hills Have Teeth bed is exposed locally for about half a kilometer in the Rainbow Garden area and appears be present where the base of the Chinle Formation is exposed all along the western face of Comb Ridge.

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Description:

MNA V10668 is a single tooth crown that is flattened labiolingually and concical in profile. It measures 5 mm apicobasally and 3 mm mesiodistally. The distal side of the tooth has a continuous serrated edge from the base to the apex. These distal serrations are 0.1 mm in length. There are eight serrations per millimeter with an estimated thirty serrations along the entirety of the distal keel. The serrations show increasing wear apically with the apex itself completely worn away. These serrations are stacked and do not stagger as they progress to the apex of the

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specimen. The mesial side is missing most of its enamel so identification of features is difficult. Nonetheless the dentine does preserve traces of several apical serrations but there is no evidence of a pronounced keel mesially. There is no root preserved and a small resorbtion pit is present on the base, suggesting this is a shed tooth crown. The tooth has a small chip on its base, distal to the midline (Figure 3, 4).

Differential Diagnosis:

MNA V10668 differs from most described Triassic teeth with serrations on only one side. Because this morphology may be due to taphonomic processes, we compare MNA V10668 to other diapsids with thecodont or sub-thecodont dentition with both mesial and distal serrations as well as those only possessing distal serrations.

Azendohsaurus is an archosauromorph from Madagascar known from reasonably complete remains (Flynn et al., 2010). Its dentition is well documented and illustrated, allowing comparisons to be made easily. *Azendohsaurus* teeth are slightly recurved with a basal constriction while MNA V10668 appears to be conical with no mesiodistal constriction apical to the base. The teeth of *Azendohsaurus* do not possess significant wear facets or worn denticles, as MNA V10668 does. The denticles that exist on the teeth of *Azendohsaurus* are apically directed. In MNA V10668 the preserved distal denticles appear perpendicular to the long axis of the tooth. The denticles of *Azendohsaurus* are also much larger and fewer in number than those of MNA V10668. MNA V10668 clearly does not represent a specimen of *Azendohsaurus*.

Mesosuchus browni is a basal rhynchosaur, deeply nested within archosauromorpha, (Dilkes, 1998) known from multiple specimens. The dentition of *Mesosuchus* is rounded in cross-section and conical in profile. The tooth-jaw junction is not well preserved enough to say

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whether the teeth had thecodont implantation. Dilkes (1998) noted an unusual wear facet on the teeth of *Mesosuchus*, which is why it is included here. Despite MNA V10668 and *Mesosuchus* both having erosional surfaces, those on *Mesosuchus* are mesiolabially directed wheres in MNA V10668 the wear is mesiobasal. Coupled with the differences in cross-sectional profile, MNA V10668 does not represent a specimen of *Mesosuchus* or any rhynchosaur by extension.

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The unusual archosauromorph *Teraterpeton hrynewichorum* from the Triassic of Nova Scotia was first described by Sues (2003). The teeth are round to oval in cross-section, with the posterior-most teeth being much broader labiolingually than mesiodistally. The teeth have a distal triangular cusp and a flattened area mesially on each occlusal surface. The narrow, conical profile and labiolingually compressed cross-section of MNA V10668 strongly differs from the teeth of *Teraterpeton* in all these aspects, excluding it as the animal that possessed MNA V10668 during the Triassic.

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Crosbysaurus (Heckert, 2004) is an archosauriform that has serrations on both mesial and distal sides of the tooth, with the distal serrations being much larger than those on the mesial keel. These denticles are subdivided and on the distal keel they point apically. *Crosbysaurus harrisae* and MNA V10668 have a similar shape and size. Both MNA V10668 and *Crosbysaurus* teeth are similar in size apicobasally and have the same triangular shape in labial and lingual views. *Crosbysaurus* teeth are distally curved on the apicomesial keel, a condition not present in MNA V10668.

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MNA V10668 and MNA V10666, referred to *Crosbysaurus sp.* by Gay and St. Aude (2015), were both found at the same locality. Because of the close association between these two specimens we paid special attention to MNA V10666 when considering the affinities of this new specimen. MNA V10666 does lack serrations on the mesiobasal keel, as does MNA V10668.

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That is where the similarities end. The tooth referred to as *Crosbysaurus sp.* by Gay and St. Aude (2015) has clear mesial denticles towards the apex. The distal denticles are much larger and subdivided, as in all other *Crosbysaurus* teeth. Whereas MNA V10668 is labiolingually compressed like MNA V10666 and other known *Crosbysaurus* teeth, it is not as mesiodistally narrow. Considering that *Crosbysaurus* serrations are larger, present on the mesial side, apically directed, and the teeth tend to be mesiodistally narrower it is doubtful that MNA V10668 is a *Crosbysaurus* tooth.

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Krzyzanowskisaurus hunti (Heckert 2005) is a (presumably) small herbivorous pseudusuchian known only from dental remains. It superficially resembles *Revueltosaurus* but can be diagnosed by the presence of a cingulum on the base of the tooth. Since MNA V10668 does not have a cingulum it is obvious that it cannot be a specimen of *Krzyzanowskisaurus*.

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Lucianosaurus wildi (Hunt and Lucas, 1995) is similar to other isolated Triassic teeth described in the literature by having enlarged denticles and a squat shape with convex mesial and distal edges, being mesiodistally broad while apicobasally short. MNA V10668 is taller than it is long and has relatively small denticles. MNA V10668 does not represent *Lucianosaurus*.

Protecovasaurus lucasi (Heckert, 2004) is diagnosed by having a recurved mesial surface where the apex is even with or overhangs the distal margin. The denticles on both the mesial and distal keels are apically directed. In all these features the teeth of *Protecovasaurus* do not match the features seen in MNA V10668.

Revueltosaurus (Hunt, 1989; Heckert, 2002; Parker et al., 2005) has serrations on both the mesial and labial sides. Its serrations are proportionally larger and closer together. The teeth of *Revueltosaurus* are broader mesiodistally compared to their apicobasal height. In general, *Revueltosaurus* teeth have more serrations on the distal keel of the tooth than at the mesial side

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of the tooth. Furthermore, *Revueltosaurus* has been distinguished by more than it's teeth (Parker et al., 2005). MNA V10668 is labiolingually narrower than the teeth of *Revueltosaurus.* These differences rule out the possibility that MNA V10668 is *Revueltosaurus.*

Heckert (2004) described some tetrapod teeth found from other localities across the Chinle Formation. Some of these teeth are from phytosaurs (Heckert, 2004, figure 43). NMMNH P-30806 for example is roughly conical in outline and somewhat labiolingually compressed. The serrations are oriented perpendicular to the long axis of the tooth. In these regards, young phytosaur teeth are similar to MNA V10668. Unlike MNA V10668, however, these teeth are moderately curved and have serrations on their mesial surface. In addition the serrations on phytosaur teeth, like the ones figured in Heckert (2004), are more dense per millimeter compared to MNA V10668. Phytosaur teeth in general, especially the teeth from segments of the jaw posterior to the premaxillary rosette, tend to be more robust than MNA V10668. Although phytosaurs are the most common taxa represented at The Hills Have Teeth it not likely MNA V106668 is a phytosaur tooth.

Heckert described another specimen, NMMNH P-34013 (Heckert, 2004, figure 20), that is roughly the same size as MNA V10668. Both have a resorption pit at the base. However the serrations on NMMNH P-34013 are smaller than MNA V10668, and has a slight curve unlike MNA V10668. Heckert described this tooth as belonging to an indeterminate archosauriform. Despite their differences this tooth, NMMNH P-34013, is the closest in morphology to the tooth of MNA V10668 yet identified.

Based on the examination of a skull cast of *Coelophysis bauri* at Mission Heights Preparatory High School and from the literature (Colbert, 1989), it can be seen that *Coelophysis* and MNA V10668 have a similar tooth shape and size. This is especially true for teeth from the

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mid-posterior region of the maxilla of *Coelophysis*. Both teeth are 5 mm tall from the apex to the base. When they are looked at closely many things stand out as to why they are different. *Coelophysis* teeth are naturally recurved, at least slightly, whereas MNA V10668 does not have a noticeable curve to it. *Coelophysis* teeth have small serrations along the mesial and distal sides. *Coelophysis* teeth tend to be even more mesiodistally compressed and the serrations at the distal side are completely different. *Coelophysis* tooth serrations are smaller and are closer together to each other. We can conclude that MNA V10668 cannot be a *Coelophysis* tooth.

Austriadactylus teeth (Dalla Veccia, 2009) and MNA V10668 are completely different in shape and size. *Austriadactylus* teeth are smaller and sharper; also they have serrations at the mesial and labial sides of the tooth. The serrations are completely different because they are larger and possess more distinct tips. *Austriadactylus* has a few different types of teeth. Most teeth are small, have three cusps, and a slight curve to them. Other teeth have only one distinct cusp and have a slight curve to them. They have very few and large serrations. MNA V10668 differs from all of the *Austriadactylus* teeth as it has no visible curve, and serrations along the mesial side. Seeing this, MNA V10668 does not represent *Austriadactylus*.

Reported Chinle early sauropodomorph teeth, such as those figured in Heckert (2004, figures 45, 83, 84) are extremely mesiolaterally compressed. They also exhibit serrations on the mesial and labial sides of the tooth. Its serrations are relatively larger, closer together, and are apically directed. Also early sauropodomorph teeth have a distinctly "pointy" apex with no wear facets. Its shape is completely different because this MNA V10668 is relatively wider labiolingually and apicobasally smaller than the reported early sauropodomorph specimens. There is no possibility that the specimen is a early sauropodomorph. It should also be noted that

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the extreme convergence seen in *Azendohsaurus* (Flynn et al., 2010) makes the identification of early sauropodomorph from the Chinle Formation tentative at best.

The most common vertebrate remains from the Chinle Formation are phytosaur teeth. Despite the small size of MNA V10668 it is possible that this specimen pertains to a juvenile phytosaur. To test this hypothesis, two juvenile phytosaur snouts were examined at the Museum of Northern Arizona. One of these, PEFO 13890/MNA V1789 was collected by Billingsly in 1979 from the Upper Petrified Forest Member of the Chinle Formation in Petrified Forest National Park (PEFO). It represents articulated paired premaxillae with 15 preserved alveoli on the right and 14 on the left, all of which save one are empty. The total preserved length of this specimen is 9.3 cm. While identified in collections as *Pseudopalatus zunii* there are no preserved autapomorphies to support this assignment.

The second specimen, MNA V3601, is a partial right dentary from the Blue Mesa Member of the Chinle Formation (Ramezani et al., 2014) *Placerias* Quarry, near St. Johns, Arizona identified as *Leptosuchus sp.* (Long and Murray, 1995). MNA V3601 is 4.95 cm in length, preserving the anterior tip and eight alveoli. In this specimen several of the tooth crowns are present and show wear whereas others are broken off at the gum line or inside the alvelolus.

In both specimens the juvenile phytosaurs exhibit remarkable homodonty, especially considering the heterodonty present in more mature phytosaurs (Heckert, 2004). Whereas MNA V10668 is roughly the right size of tooth to have come from a juvenile phytosaur similar in ontogenetic age to PEFO13890/MNA V1789 or MNA V3601, the basal structure of the tooth is unlike any preserved juvenile phytosaur teeth or alveoli. Both undisputed juvenile phytosaur specimens have round alveoli with serrated or unserrated conical teeth preserved (Figure 5). In addition, all preserved teeth in MNA V3601 do not show any lingual curvature as seen in MNA

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V10668. While adult phytosaurs have triangular, lingually curved teeth in their dentition, especially as one moves posteriorally (Long and Murray, 1995; Heckert, 2004), these seem to be absent in juveniles from the specimens we have on hand. The lingually curved teeth of adult phytosaurs are also much more robust, with labiolingually wide basal and mid-crown section, unlike the laterally compressed and teardrop-shaped base of MNA V10668. It may be that phytosaur dentition changed during ontogeny to adapt to a changing diet. Even considering this we do not think that MNA V10668 can be assigned to the Phytosauria due to the marked differences between it and all other known phytosaur teeth.

Conclusions:

MNA V10668 cannot identified as any previously described Triassic taxon as it does not have any distinguishing autapomorphies preserved. However, this tooth can be identified at least as Archosauriformes *incertae sedis*. MNA V10668 has many character states that match up with other archosauriforms. Another indeterminate tooth, NMMNH P-34013, is the closest tooth to MNA V10668. Despite their similarities it is obvious that MNA V10668 is morphologically distinct from NMMNH P-34013. Although isolated teeth have been described before from Utah (Heckert et al., 2006; Gay and St. Aude, 2015) this is the first tooth morphotype described from Utah to not be assigned to an existing genus of Triassic tetrapod. As such it may represent an animal endemic to what is now Utah.

These findings are important because they demonstrate the existence of a previously unrecognized clade of diapsids from the Chinle Formation in Utah. In addition, most of the tetrapod record from Utah's Chinle Formation has come from the Church Rock Member (Martz et al., 2014; RG pers. obs.) This specimen, coming from the Lower Member of the Chinle

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Formation, demonstrates increased diversity in an older part of the formation that has not been studied until recently (Gay and St. Aude, 2015).

Work is ongoing at Comb Ridge by crews from Mission Heights Preparatory High School. The tetrapod diversity of Chinle Formation at Comb Ridge will continue to increase as new discoveries come to light. It is hoped that additional taxa can be added to the growing faunal assemblage with additional fieldwork in the near future.

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Acknowledgements:

The authors would like to thank Jason Durivage, Gary Shepler, Steven Hall, and Deborah Avey for their assistance with fieldwork while MNA V10668 was collected. We would also like to thank David and Janet Gillette for their assistance with collections and access to specimens. We would also like to thank ReBecca Hunt-Foster for her assistance with our permit.

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