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

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Abstract:

An unusual tetrapod tooth was discovered in the Late Triassic Chinle Formation of southeastern Utah. The tooth was originally ~~thought to belong~~referred to *Revueltosaurus*, but further investigations have rejected that hypothesis. In this paper we compare MNA V10668 to other known fossil teeth ~~found in~~ from the Chinle Formation and ~~identify~~ assign it to the least inclusive clade ~~it may belongs to~~possible. ~~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 unique characteristics not found in other diapsid teeth. We conclude that it is most likely an archosauromorph and probably an archosauriform. This increases the known diversity of tetrapods from the Chinle Formation and represents the first tooth morphotype completely unique to Utah in the Late Triassic ~~Period~~Epoch.

Comment [Anon1]: You need to put the name of the clade in the abstract as it is a result.

Comment [Anon2]: Similarities or characters. You are looking for synapomorphy.

Comment [Anon3]: You need to be more clear. You can only assign it to the least inclusive clade based on preserved characters.

Comment [Anon4]: So you are claiming it is autapomorphic?

Introduction:

The recovery of vertebrate life from the Permian-Triassic transition resulted in an ~~amazing~~ diverse array of new body forms as life filled ecological voids. This is especially noticeable in the ~~archosaur~~Archosauromorpha~~ line diapsids~~. Many archosauromorph, archosauriform, and archosaurian ~~reptiles~~ reptile-groups adapted and radiated across the globe, filling ~~or creating~~ numerous niches with novel body forms (e.g., 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 modern birds), crocodiles, 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 Late Triassic Period from Utah 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 (e.g., Long and Murr~~a~~y, 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 to Comb Ridge in southeastern Utah 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), was

Comment [Anon5]: What do you mean by this?

Comment [Anon6]: There are more appropriate papers to cite here such as Barrett et al., 2011 (The roles of herbivory and omnivory in early dinosaur evolution).

Comment [Anon7]: Don't birds and mammals still dominate. You are mainly referring to non-avian dinosaurs when you provide this age range.

Comment [Anon8]: You mean disparity?

Comment [Anon9]: Poor Phil Murry, almost everyone misspells his last name.

Comment [Anon10]: I would cite Heckert et al 2005 (Triassic Fossil Vertebrates in Arizona) instead and Parker (2005) as well as Irmis (2005) who also had reviews of the Chinle Formation fauna.

Comment [Anon11]: Yes, but this is a sampling problem.

discovered~~near a locality that was previously discovered by the senior author (RG)~~. Both at ~~The Hills Have Teeth~~ MNA 1724and in ~~the~~ an alluvial ~~fan~~ deposit immediately adjacent to the hill, a dozen partial and complete tetrapod teeth were collected. Most of these teeth belong~~ed~~ to ~~phytosaurs~~ phytosaurian archosauriforms and temnospondyl amphibians. 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~~ 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 Formation and Dockum ~~Formations~~Group. That ~~speciemen~~specimen, MNA V10668, is compared here to many Triassic diapsids to ~~help classify it~~determine its taxonomic assignment. We compare it to the non-archosauriform archosauromorphs *Azendohsaurus* (Flynn et al., 2010), *Mesosuchus browni* (Dilkes, 1998), and *Terraterpeton 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*~~ *callenderi* (Hunt, 1989), *Tecovasaurus murr~~a~~yi* (Hunt and Lucas, 1994), unidentified or unnamed archosauriform teeth (Heckert, 2004), and several archosaurs (Colbert, 1989; Dalla Veccia, 2009; Heckert, 2004).

Comment [Anon12]: This other locality is irrelevant unless discussed further.

Comment [Anon13]: This would not really be an 'alluvial fan'

Comment [Anon14]: Include species name.

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). Geospatial data for MNA V10668 was recorded using Backcountry Navigator Pro running on an Android OS smartphone. ~~It~~ The tooth was ~~collected~~ stored in a zip-seal collection bag after being removed from the surface exposure by a hand. Measurements of MNA V10668 were obtained using a set of

Comment [Anon15]: Redescribe it here.

Craftsman metal calipers (model 40257) with 0.05mm precision. Figures were created using GIMP 2.8.4. Photos 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).

Comment [Anon16]: What about the technique used to assign the specimen to the least inclusive clade?

Geologic Setting:

MNA V10668 was found at MNA Locality 1725 on the surface ~~of~~ in the ~~Lower~~ lower ~~Member~~ portion of the Chinle Formation at Comb Ridge, Utah (Figure 1), roughly 6 meters from the base of the ~~Lower Member~~unit along with teeth of phytosaurs, temnospondyls, and *Crosbysaurus* sp.. (Gay & St. Aude 2015)~~ at MNA Locality 1725~~. ~~As with earlier work, we hold that~~ The 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~~MNA 1724. The horizon is a Fossiliferous light grey mudstone with interspersed carbonaceous clasts ~~and numerous teeth~~ (Figure 2). This mudstone is 13 cm below ~~the~~ a 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.

Comment [Anon17]: Is this a formal geological member?

Description:

MNA V10668 is a single tooth crown that is labiolingually flattened ~~labiolingually~~ and con~~e~~ic al in profile. It measures 5 mm apicobasally and 3mm mesiodistally. The distal side of the tooth crown 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

Comment [Anon18]: What direction?

itself completely worn away. These serrations are stacked and do not stagger as they progress to the apex of the specimen. The mesial side of the tooth is missing most of its enamel so identification of features is difficult. None~~-~~the~~-~~less the dentine does preserve the traces of several apical serrations, but there is no evidence of a pronounced keel mesially. ~~There is no~~The root ~~preserved~~ is broken away and a small resorbtion pit ~~is~~ present on the base~~, suggesting~~ suggests this is a shed tooth crown. The tooth has a small chip on its base, distal to the midline (Figures 3, 4).

Comment [Anon19]: I don't understand what you mean here.

Comment [Anon20]: Ditto, cite figure.

~~Differential Diagnosis~~Comparisons:

Comment [Anon21]: You don't provide a diagnosis.

MNA V10668 differs from most described Triassic teeth with serrations ~~on~~ only along one ~~side~~edge. 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.

Comment [Anon22]: You mean that the tooth is incomplete?

Azendohsaurus is an archosauromorph reptile from Madagascar known from reasonably complete remains (Flynn et al., 2010). Its dentition is well documented and illustrated [cite], allowing comparisons to be made easily. *Azendohsaurus* teeth are slightly recurved with a basal constriction ~~while~~whereas 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~~cannot be assigned to *Azendohsaurus*.

Comment [Anon23]: Sp.?

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

The unusual archosauromorph *Terraterpeton hrynewichorum* from the Triassic of Nova Scotia was first described by Sues (2003). The teeth of *Terraterpeton* are as odd as the rest of its skull. 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 *Terraterpeton* in all these aspects, excluding it as the animal that possessed MNA V10668 during the Triassic..

Crosbysaurus harrisae (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 seen in MNA V10668.

Comment [Anon24]: Do they share other characters? You say this twice.

MNA V10668 and MNA V10666, referred to *Crosbysaurus sp.* by Gay and St. Aude (2015), were both found at ~~the same locality~~MNA 1724. ~~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. ~~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. While 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.

Comment [Anon25]: Try not to be colloquial.

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Krzyzanowskisaurus hunti (Heckert 2005) is a (presumably) small herbivorous ~~pseudusuchian~~ pseudosuchian 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~~referred to *Krzyzanowskisaurus*.

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 *callenderi* (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 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 orientied 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~~those 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~~MNA 1724 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~~es~~. Despite their differences this tooth, NMMNH P-34013, is the closest tooth to 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 mid-posterior region of the maxilla of *Coelophysis*. Both teeth are 5mm 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.

Comment [Anon26]: Is there a catalog number? What specimen is the cast of?

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~~ Purported Chinle prosauropod 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 prosauropod 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 prosauropod specimens. There is no possibility that the specimen is a prosauropod. It should also be noted that the extreme convergence seen in ~~*Azhendousaurus*~~ *Azhendohsaurus* (Flynn et al., 2010) makes the identification of prosauropods 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 George Billingsley 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*~~ *“Machaeroprosopus”* *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 Murr~~a~~y, 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 while others are broken off at the gum line or inside the alve~~l~~olus.

In both specimens the juvenile phytosaurs exhibit remarkable homodonty, especially considering the heterodonty seen in more mature phytosaurs (Heckert, 2004). While MNA

Comment [Anon27]: Why?

Comment [Anon28]: Also see discussion by Nesbitt et al. 2007.

Comment [Anon29]: Can this claim be supported?

Comment [Anon30]: This is not the correct anatomical term.

Comment [Anon31]: Can't say this for the first specimen as only a single tooth is preserved.

V10668 is roughly the right size of tooth to have come from a juvenile phytosaur similar in age to PEFO13890/MNA V1789 or MNA V3601, the basal structure of the tooth is unlike any preserved juvenile phytosaur teeth or ~~alveoli~~alveolus. 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 V10668. While adult phytosaurs have triangular, lingually curved teeth in their dentition, especially as one moves ~~posteriorally~~posteriorly (Long and Murr~~a~~y, 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 sections, 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~~ Phytosauria ~~due~~ because of ~~to~~ the marked differences between it and all other known phytosaur teeth.

Conclusions:

MNA V10668 cannot be 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~~ Archosauriformes *incertae sedis*. MNA V10668 has many characteristics that match up with other archosauriformes. Another taxonomically 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,

Comment [Anon32]: You should be citing Hungerbuehler here.

Comment [Anon33]: I don't think you can say this with the sample you have on hand.

Comment [Anon34]: Evidence to support this idea?

Comment [Anon35]: Then it has a unique combination of characters.

Comment [Anon36]: Based on?

Comment [Anon37]: Morphologically or positionally?

Comment [Anon38]: Tell us why it is obvious.

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.

Comment [Anon39]: This is very difficult to believe. You have not seen all of the material from Utah.

Comment [Anon40]: So it is a new form?

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

Comment [Anon41]: You can only say this if you run a phylogenetic analysis.

Comment [Anon42]: This is incorrect.

Comment [Anon43]: What is the actual name of this unit?

Comment [Anon44]: This is a stretch based on a single indeterminate archosauriform tooth.

~~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 list with additional fieldwork in the near future.~~

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Comment [Anon45]: List permit #.

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Comment [Anon46]: You need to go through this section and make sure all reference are cited properly and consistently.

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