

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

Lopez, Andres<sup>1</sup>; St. Aude, Isabella<sup>1</sup>; Alderete, David<sup>1</sup>; Alvarez, David<sup>1</sup>; Aultman, Hannah<sup>1</sup>; Busch, Dominique<sup>1</sup>; Bustamante, Rogelio<sup>1</sup>; Cirks, Leah<sup>1</sup>; Lopez, Martin<sup>1</sup>; Moncada, Adriana<sup>1</sup>; Ortega, Elizabeth<sup>1</sup>; Verdugo<sup>1</sup>, Carlos<sup>1</sup>; Gay, Robert J <sup>2\*</sup>.

<sup>1</sup>Mission Heights Preparatory High School, 1376 E. Cottonwood Ln., Casa Grande, Arizona 85122

<sup>2</sup>The University of Arizona, 1064 E. Lowell St., Tucson, AZ 85721

\*paleorob@gmail.com 928-660-9711

#### **Abstract:**

An unusual tetrapod tooth was discovered in the Upper Triassic Chinle Formation of southeastern Utah. In this paper, we compare MNA V10668 to other known fossil tooth crowns from the Chinle Formation and assign the tooth to the least inclusive clade currently available, Archosauriformes, based on the presence of mesial and distal serrations, a distal keel, and a conical mesiodistal profile. 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, including a teardrop-shaped labiolingual profile, but possesses a unique combination of characteristics not found in other archosauromorph teeth thus observed. This increases the known diversity of archosauromorphs from the Chinle Formation and represents the first tooth of this morphotype to be found from Utah in the Late Triassic.



#### **Introduction:**

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2 The recovery of vertebrate life from the Permian-Triassic transition resulted in a diverse 3 array of new body forms as life filled ecological voids (MacLeod et al., 2000; Benton et al., 4 2004; Retallack et al, 2007). This is especially noticeable in the archosauromorphs. Many 5 archosauromorph, archosauriform, and archosaurian reptile-groups radiated across the globe, 6 filling numerous niches with novel body forms (Nesbitt et al., 2010) and dietary specializations 7 (Heckert, 2004; Parker et al., 2005; Barrett et al., 2011). The ecological revolution of the Triassic 8 Period laid the groundwork for dinosaurs (including modern birds), crocodiles, and mammals to 9 dominate terrestrial vertebrate assemblages for the next 200 million years. 10 It is perhaps somewhat surprising then that the terrestrial record of the Upper Triassic 11 Period from Utah, USA has not reflected the global disparity of tetrapod clades. While 12 paleontologists were making collections in Utah since at least the late 1800s (e.g., Cope, 1875) 13 most of the collection effort has gone towards finding vertebrate fossils in younger rocks. In 14 addition, greater attention that Late Triassic deposits in neighboring Arizona and New Mexico 15 have received (e.g., Long and Murry, 1995; Heckert et al., 2005; Parker, 2005; Parker et al., 16 2006). Until recently (Fraser et al., 2005; Heckert et al., 2006; Gibson, 2013; Martz et al., 2014) 17 the Triassic vertebrate record published from Utah has mainly consisted of the ubiquitous phytosaurs (Morales and Ash, 1993). This has especially been the case when looking only at 18 19 body fossils. Even with this recent work, Utah's Triassic tetrapod record is lower in diversity 20 compared to adjoining states, with the majority of specimens being identified as either 21 phytosaurs or aetosaurs (Martz et al., 2014).



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In May of 2014 a paleontological expedition to Comb Ridge in southeastern Utah was conducted by Mission Heights Preparatory High School (Figure 1). During the expedition a new, very rich (>300 specimens collected representing 15 taxa in two field seasons) microsite they dubbed "The Hills Have Teeth" (Museum of Northern Arizona Locality 1724), approximately five meters south of a locality that was previously discovered (MNA Loc. 1721). Both at "The Hills Have Teeth" and area immediately adjacent to the west of the hill a dozen partial and complete tetrapod teeth were collected. Most of these teeth belonged to phytosaurs (e.g. MNA V10658, MNA V10659, etc.) and temnospondyls (e.g. MNA V10655, MNA V10656). Two teeth were notably different from these two taxa that dominate the locality in number of specimens. One, referred to *Crosbysaurus sp.*, is described elsewhere (Gay and St. Aude, 2015). The other collected is the subject of this contribution. 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 madagaskarensis (Flynn et al., 2010), Mesosuchus browni (Dilkes, 1998), and Teraterpeton hrynewichorum (Sues, 2003), several nonarchosaurian archosauriforms including *Crosbysaurus harrisae* (Heckert, 2004), Krzyzanowskisaurus hunti (Heckert, 2005), Lucianosaurus wildi (Hunt and Lucas, 1995), Protecovasaurus lucasi (Heckert, 2004), Revueltosaurus callenderi (Hunt, 1989), Tecovasaurus murryi (Hunt and Lucas, 1994), unnamed archosauriform teeth (Heckert, 2004), and various other archosaurs (e.g., 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, including brushes, dental tools, and other small hand tools. Specimens were wrapped in toilet paper and placed in plastic zip-seal bags for transport back to the



museum. Locality data for MNA Locality 1725 was recorded using Backcountry Navigator Pro running on an Android OS smartphone with a spatial error of +/- 2 meters. 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 were 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 the exact locality information. Quantitative and qualitative comparisons of MNA V10668 to published photographs, drawings, and descriptions, along with direct comparison to material from the Chinle Formation are housed at the MNA were used to assign MNA V10668 to its least-inclusive clade.

## **Geologic Setting:**

MNA V10668 was found at MNA Locality 1725 as float on the surface of the Chinle Formation at Comb Ridge, Utah (Figure 1), roughly 6 meters from the base of the unit along with teeth of phytosaurs (e.g., MNA V10670, MNA V10672), temnospondyls (e.g., MNA V10669, MNA V10678), and *Crosbysaurus* sp. (MNA V10666). The fossil material found at locality 1725 originated at MNA Locality 1724 and was washed down slope. The horizon is a fossiliferous light grey mudstone with interspersed carbonaceous clasts and abundant carbonized plant fragments (Figure 2). This mudstone sits below a 13 cm thick dark grey mudstone, which itself is below a red brown mudstone-grading-to-shale. The fossiliferous horizon is 8.75 meters above the base of the Chinle Formation (Gay and St. Aude, 2015; figure 4). The fossil-bearing layer, informally referred to as, "the Hills Have Teeth bed," is exposed locally for about half a kilometer in the Rainbow Garden (MNA Locality 1721) area. Preliminary stratigraphic work done in the summer of 2015 shows that this bed lenses out. It is present where the base of the

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Chinle Formation is exposed along the western face of Comb Ridge between the Hills Have Teeth and the San Juan River. At the northern end of Comb Ridge the lower member of the Chinle Formation is dominated by at least two thick (>10 m) channel sandstones and conglomerates. At this time it is unknown if these channel deposits are laterally equivalent to the Hills Have Teeth fossil-bearing bed or whether they are incised into the lowest portions of the Chinle Formation, though further work is currently ongoing to solve this problem. Although the stratigraphy of the Chinle Formation has generally been well studied across the Colorado Plateau (e.g. Stewart et al., 1972), no detailed work has been published on the exposures at Comb Ridge. Superficial work conducted by Bennett (1955), Lucas et al. (1997), and Molina-Garza et al. (2003) suggested various correlations for the uppermost reddish member of the Chinle Formation at Comb Ridge (see Gay and St. Aude for a discussion of this history). Most recently, Martz et al. (2014) have suggested that the uppermost Chinle Formation at Comb Ridge correlates to the Church Rock Member, as in Lisbon Valley to the northeast. We have elsewhere agreed with this correlation (Gay and St. Aude, 2015). The grey bed is more difficult to correlate with other members of the Chinle Formation exposed in southwestern Utah. The studies mentioned above looked primarily at the upper units of the Chinle Formation. Current work is being conducted to assess the stratigraphic correlations of this lower unit. We can state that the fossil producing beds at The Hills Have Teeth are 15 meters below the base of the Church Rock Member at Comb Ridge. Lithologically the lower part of the Chinle Formation at Comb Ridge is dominated by grey to light grey bentonitic muds and shales with rare localized conglomerates and coarsegrained sandstones. These conglomerates tend to be calcium-cemented and are dominated by sandstone clasts, though chert clasts can occur. These resistant beds tend to be clastically



homogeneous and are rarely over 2 meters in thickness. At The Hills Have Teeth beds carbonized plant remains are common but have not been noted at other localities within the lower member where trenching has been conducted and stratigraphic sections measured whereas both the Kane Springs Member to the northeast and Monitor Butte Member to the south and west preserve abundant carbonized plant fragments and occasional well-preserved plant material (Stewart et al., 1972; Martz et al., 2014).

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#### **Description:**

MNA V10668 is a single tooth crown that is labiolingually flattened and conical 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. Based on other archosauromorph teeth examined, we interpret this to be the distal edge as it presents a more vertical profile when viewed in labial or lingual view. The distal serrations are 0.1 mm apicobasally with a density of eight serrations per millimeter. We estimate there are thirty serrations along the entirety of the distal keel, though a precise count is difficult due to wear at the apex. The serrations show increasing wear apically with the apex itself completely worn away prior to fossilization. We interpret this structure as a wear facet (Figures 3, 4). The distal serrations are stacked apicobasally and are not labiolingually staggered as they progress to the apex of the specimen. The mesial side of the crown is missing most of its enamel so identification of features is difficult. Nonetheless the dentine does preserve traces of several apical serrations. It is possible that a pronounced mesial keel existed in this region but there is no evidence of this in the preserved dentine (though this does not rule out the possibility of an enameled keel). The wear on the apex is well rounded with no jagged edges. Coupled with the



fact that no root is preserved and a small resorbtion pit is present on the base we suggest that MNA V10668 is a shed tooth crown. The loss of enamel from the majority of the tooth surface does not appear recent, as all the enamel edges are smooth. It is possible that this tooth was digested. Although there is no pitting observed on the preserved enamel surface the dentine shows occasional pitting. We have interpreted these pits as transport damage but the presence of both coprolites and a theropod or rauisuchian tooth (MNA V10689) showing evidence of ingestion collected in the 2015 field season do not allow us to rule out this second option. The tooth has a small chip on its base, likely a result of recent weathering and transport due to the freshness of the break, distal to the midline (Figure 3, 4).

### **Systematic Paleontology:**

- 125 Diapsida Osborn, 1903
- 126 Archosauromorpha Von Huene, 1946
- ?Archosauriformes Gauthier, 1986

# Diagnosis:

We can diagnose MNA V10668 as being an archosauriform based on the following characters from Godefroit and Cuny (1997): tooth conical in mesiodistal profile with a single cusp and possesses serrations on both the mesial and distal edges. The tooth (at least on the distal edge) possesses an enamel keel basally and is labiolingually compressed. Since MNA V10668 is a shed tooth crown we cannot assess the character of deep thecodont implantation, though Godefroit and Cuny (1997) regard this as a dubious character in any case.



# **Comparisons:**

MNA V10668 differs from most described Triassic teeth with serrations only along one edge. Because this morphology is due to taphonomic processes discussed above, we compare MNA V10668 to other archosauromorphs with the codont or sub-the codont dentition with both mesial and distal serrations as well as those only possessing distal serrations.

Azendohsaurus madagaskarensis 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 (Flynn et al., 2010). Azendohsaurus teeth are slightly recurved with a basal constriction 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 (>0.5 mm) and fewer in number than those of MNA V10668, having between four to 18 on the carinae, depending on tooth position. MNA V10668 cannot be assigned to Azendohsaurus. Flynn et al. (2010) also report that the teeth of Azendohsaurus do not possess wear facets, a feature that is seen in MNA V10668, though this is a behavioral trace and not directly tied to evolutionary trends.

*Mesosuchus browni* is a basal rhynchosaur, deeply nested within Archosauromorpha, (Dilkes, 1998), and is known from at least four 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 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 whereas in MNA V10668 the wear is mesiobasal. *Mesosuchus* dentition also lacks serrations or denticles. Indeed the mesial and distal faces, as illustrated and described by Dilkes (1998) show teeth round to square in cross section and conical in labial or lingual view. Taken all together the teeth of *Mesosuchus* are not a good match for MNA V10668 and as such does not represent a specimen of *Mesosuchus* or any rhynchosaur by extension.

The 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.

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. 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 at the apicomesial keel, a condition not present in MNA V10668.

MNA V10668 and MNA V10666, referred to *Crosbysaurus sp.* by Gay and St. Aude (2015), were both found at the same locality. MNA V10666 lacks serrations on the mesiobasal keel, as MNA V10668 appears to as well. 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 (Heckert, 2004). 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 certain that MNA V10668 is a *Crosbysaurus* tooth.

*Krzyzanowskisaurus hunti* (Heckert 2005) is a small (presumably) herbivorous archosauromorph known only from dental remains. It resembles *Revueltosaurus callenderi* but can be diagnosed by the presence of a cingulum on the base of the tooth (Heckert 2002). Since MNA V10668 does not have a cingulum it cannot presently be 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. MNA V10668 is labiolingually narrower than the teeth of *Revueltosaurus*. These differences rule out the possibility that MNA V10668 is *Revueltosaurus*.

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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 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 lingually and have serrations on their mesial surface. In addition the serrations on phytosaur teeth, like those figured in Heckert (2004), are denser (>14 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 MNA V1724 it not likely MNA V106668 is a phytosaur tooth. Heckert described another specimen, NMMNH P-34013 (Heckert, 2004, figure 20 A-C), that is roughly the same size as MNA V10668. Both have a resorption pit at the base and, seemingly unusual for predatory Triassic archosauriformes, a wear facet on the tip. This is a feature shared with MNA V10668. However the serrations on NMMNH P-34013 are smaller (<0.1 mm) 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 MNA V10668 yet identified. They differ from *Coelophysis* teeth being naturally recurved, at least slightly, whereas MNA V10668 does not have a noticeable curve to it. Coelophysis teeth (Cleveland Museum 31374; Colbert, 1989) 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 and indeed is unlikely

to be a theropod dinosaur at all. Although the enamel of MNA V10668 is not well preserved, it does not preserve any surface features such as longitudinal grooves, ridges, fluting, or undulations that are characteristic of theropod dinosaur teeth (Hendrickx et al., 2015). In addition, whereas MNA V10668 is moderately laterally compressed, Triassic theropod dinosaur teeth are compressed even more so (Colbert, 1989).

Pterosaurs are rare from the Triassic of North America and several good examples are known from Europe. Perhaps the best illustrated in terms of dentition is *Austriadactylus* (Dalla Veccia, 2009). MNA V10668 differs from *Austriadactylus* 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 tapered apex with no wear facets. Its shape is completely different; MNA V10668 is relatively wider labiolingually and apicobasally smaller than the reported early sauropodomorph specimens. There is no reason to classify this specimen is an early sauropodomorph. It should also be noted that the extreme

convergence seen in *Azendohsaurus* (Flynn et al., 2010) makes the identification of early sauropodomorphs from the Chinle Formation tentative at best (Nesbitt et al., 2007).

The most common vertebrate remains from the Chinle Formation are phytosaur teeth (Heckert, 2004; Martz et al., 2014; pers. obs.). Despite the small size of MNA V10668 it is possible that this specimen pertains to a juvenile phytosaur. To test this hypothesis two phytosaur snouts, identified as juveniles in the collections at the Museum of Northern Arizona, were examined. It should be noted that although both specimens are identified in collections data as juvenile phytosaurs no histological examinations have been conducted to assess their ontogenetic stage. 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 "Machaeroprosopus" zunii there are no preserved autapomorphies to support this assignment, so we assign it instead to Phytosauria indet.

The second specimen, MNA V3601, is a partial right dentary from the Blue Mesa Member of the Chinle Formation (Parker and Martz, 2011; Ramezani et al., 2014) *Placerias* Quarry, near St. Johns, Arizona identified in collections as *Leptosuchus sp.* (Long and Murry, 1995, though see also Stocker, 2010). 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 oral margin or inside the alveolus.

In PEFO 13890/MNA V1789 the tooth row exhibits homodonty in the alveolar cross sections (Figure 5). This tooth is lingually curved and symmetrical in mesiodistal profile. The tooth lacks any visible serrations (Figure 6).



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In MNA V3601 the erupted crown heights vary but their labiolingual and mesiodistal profiles are remarkably similar (Figure 5). This is notable considering the heterodonty present in larger phytosaurs (Heckert, 2004). We do acknowledge that not having complete juvenile skulls available limits the inferences we can make about overall tooth form, but feel that the comparisons to smaller individuals is none-the-less informative in that it allows us to directly compare similar size teeth from the Chinle Formation that are firmly associated with non-dental remains. Whereas MNA V10668 is roughly the right size of tooth to have come from a phytosaur similar in size to PEFO13890/MNA V1789 or MNA V3601, the basal structure, especially in cross section, of the tooth is unlike any of the preserved small phytosaur tooth crowns or alveoli. Both undisputed phytosaur specimens have round alveoli with serrated or unserrated conical teeth preserved (Figure 7, 8). In addition, all preserved teeth in MNA V3601 do not show any lingual curvature as seen in MNA V10668. While larger phytosaurs, presumed to be ontogenetically more mature, have triangular, lingually curved teeth in their dentition, especially as one moves posteriorly (Long and Murry, 1995; Hungerbühler, 2000; Heckert, 2004), these seem to be absent in juveniles from the preserved portions specimens observed at the MNA, though additional smaller phytosaur jaws and histological sampling would help refine our comparison. The lingually curved teeth of large phytosaurs are also much more robust, with labiolingually wide basal and mid-crown section, unlike the laterally compressed and teardropshaped base of MNA V10668. Considering this we do not think that MNA V10668 can be assigned to the Phytosauria because of the marked differences between it and all other known phytosaur teeth.

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#### **Conclusions:**



MNA V10668 cannot be identified as any previously described Triassic taxon as it does not have any distinguishing autapomorphies and preserves a unique combination of characters. However, this tooth can be identified at least as Archosauriformes. MNA V10668 has many character states that match up with other archosauriforms, including labiolingual compression and the presence of serrations on distinct carinae. Another taxonomically indeterminate tooth, NMMNH P-34013, is the closest tooth morphologically to MNA V10668 and likely belongs to Morphotype T (Sensu Heckert, 2004). Despite their similarities it is obvious that MNA V10668 is morphologically distinct from NMMNH P-34013, primarily due to the smaller serrations and slight lingual curvature found in 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 occurrence of tooth Morphotype T described from Utah. It is likely that other teeth now in collections may also represent unique morphotypes or previously described morphotypes not previously identified from Utah. It may also represent a previous identified taxon for which little or nothing is known of its dentition (e.g., *Spinosuchus*, Spielmann et al., 2009).

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