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The first occurrence of the enigmatic archosaur *Crosbysaurus* (Heckert 2004) from the Chinle Formation of Southern southern Utah

ABSTRACT - Originally identified as an ornithisichian dinosaur, *Crosbysaurus* has been found in New Mexico, Arizona, and the its type locality in Texas. The genus has been reassessed by other workers in light of revelations reinterpretations about the postcrania of another putative Triassic ornithischian, *Revueltosaurus*. The understanding of Triassic dental faunas has become more complicated by the extreme convergence between pseudosuchian archosaurus and ornithichian dinosaur dental morphologies. We report here on a new specimen of *Crosbysaurus* from the Petrified Forest Member of the Chinle Formation at Comb Ridge in southeastern Utah. This new specimen is assigned to *Crosbysaurus* on the basis of the unique compound posterior denticles, mediolateral labiolingual width, and curvature. While this specimen, MNA V10666, does not help resolve the affinities of *Crosbysaurus* it does represent an approximately 250 kilometer extension of the geographic range of this taxon. This is the first record of this taxon in Utah and as such it represents the northernmost known record of *Crosbysaurus*. This indicates that *Crosbysaurus* was not limited to the southern area of Chinle/Dockum deposition but instead was widespread across the paleoriver systems of the Late Triassic in western Pangea. The specimen we report on here was found in close association with a typical Late Triassic Chinle fauna, including phytosaurs, metoposaurs, and dinosauromorphs.

INTRODUCTION

When *Crosbysaurus* was first described by Heckert (in 2004) the assumption was that it, like the better-known *Revueltosaurus*, was an ornithischian dinosaur. Several purported ornithischian tooth taxa were named, leading several authors to suggest that herbivorous dinosaurs were widespread across Pangea (Hunt and Lucas, 1984; Heckert 2002, 2004, 2005). This contrasted sharply with the previous views on ornithischian diversity and stood in sharp contrast with the non-dental fossil record of ornithischian diversity outside of the southern hemisphere.

This interpretation of the fossil record was challenged by Parker et al. (2005) with the discovery of the postcrania of *Revueltosaurus* from the Petrified Forest of Arizona. Not only did this revise how *Revueltosaurus* was seen but it called into question the systematics of all of North America's supposed Triassic ornithischian dinosaurs from the Triassic Period North America (Irmis et al. 20062007). Without any supporting skeletal remains it was no longer parsimonious unambiguous to assign "fabrosaur" type like teeth to any known dinosaur clade. While *Revueltosaurus* is now known from postcrania, other supposed ornithischians known from only teeth, such as like *Tecovasaurus* and *Crosbysaurus*, can only be identified as being either archosaurs or archosauriforms of uncertain affinity. While some authors have suggested that

Comment [M1]: The correct year of publications is 2007: http://www.tandfonline.com/doi/abs/10.1080/08912960600719988#preview

Comment [M2]: Irmis et al. (2007) reinterpret them as archosauriforms.

ornithischians were present in the Late Triassic of North America (Heckert 2005), virtually all authors are in agreement that *Crosbysaurus* cannot be diagnosed beyond an indeterminate ~~does not represent a dinosaur and instead is an~~ archosauriform (Irmis et al. 2007). While this new record does not add any clarity to the ~~taxonomic~~ systematic affiliations of *Crosbysaurus* it does significantly extend its range. Previous reports of *Crosbysaurus* have been limited to Texas (the type locality), New Mexico, and Arizona (Heckert 2004). Comb Ridge in southeastern Utah is approximately 245 kilometers away from the closest reported *Crosbysaurus* remains in the Chinle Formation of Arizona.

In May of 2014, ~~10~~ ten students from Mission Heights Preparatory High School went to southeastern Utah. Despite temperatures over 100˚F (ca. 38ºC) the students were able to prospect the Chinle Formation exposed at Comb Ridge, Utah as well as open a test pit at a possible metoposaur site located by the first author in March. The second author, accompanied by another student, discovered a rich locality to the south of the metoposaur site. The second author and another student named this rich microsite "The Hills Have Teeth." While combing the ground near the base of The Hills Have Teeth locality (MNA Locality 1724) the second author discovered an~~d~~ unusual partial tooth, MNA V10666, to the west-southwest of the main outcrop. This second locality has been designated MNA Locality 1725. The students brought this tooth to the attention of the first author~~'s attention~~ and ~~. I~~it is ~~this specimen that we~~ describe~~d~~ here.

MATERIALS AND METHODS

Abbreviations - Mission Heights Preparatory High School, Casa Grande, Arizona (MHPRO); Museum of Northern Arizona, Flagstaff, Arizona (MNA).

Materials - Standard paleontological hand tools were used to collect MNA V10666. Geographic locality data were recorded via BackCountry Navigator Android Application running on a Samsung Galaxy S4. All specimens were collected under Bureau of Land Management paleontology permit UT14-001S issued to the first author and are curated at the Museum of Northern Arizona. Figures and line drawings were produced using GIMP 2.8.4. Photos used for figures were obtained using an Olympus E-500 DSLR camera. Specimen measurements were obtained using metal sliding calipers.

RESULTS

Systematic paleontology

Reptilia Laurenti 1768

Archosauromorpha ~~von~~ Huene 1946

Archosauriformes Gauthier 1986

~~?Archosauria Cope 1869~~

Crosbysaurus Heckert 2004

Referred material

Comment [M3]: Please, provide minimum deviation of the calipers.

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Comment [M5]: I think that Crosbysaurus, and other taxa based on isolated, serrated crowns, cannot be referred unambiguously to Archosauriformes anymore because the non-archosauriform archosauromorph Azendohsaurus possess denticles. See reviewer letter and comments below.

Comment [M6]: See Irmis et al. (2007); they reinterpret Crosbysaurus as an indeterminate archosauriform.

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MNA V10666, a single shed tooth crown.

Locality and horizon

MNA 1725 in San Juan County, Utah (Figure 1). The exact coordinates remain on file at the Museum of Northern Arizona. This locality, named The Hills Have Teeth, produced numerous partial and complete phytosaur and metoposaur teeth along with several dinosaur or dinosauromorph teeth. MNA V10666 was found approximately 4 meters west-southwest of The Hills Have Teeth as surface float and very likely ~~. We presume it to~~ ha~~s~~ve originated at The Hills Have Teeth. This is corroborated by the presence of phytosaur tooth fragments found close to MNA V10666, which the second author was able to connect with fragments collected at the main deposit at The Hills Have Teeth.

This area has not been mapped in detail but this portion of the Chinle Formation has been reported to ~~be or~~ correlate to the Petrified Forest Member (Bennett, 1955). Further work by the authors and others is ongoing and the relationships between the beds at Comb Ridge and other exposures of the Chinle Formation ~~will~~ would be clarified in the near future. None~~-~~the~~-~~less, it is clear that MNA V10666 originally was deposited near the base of the Chinle Formation as part of the earliest fauna recorded in the Comb Ridge area (Figure 2).

The precise fossil-bearing horizon ~~where~~ of MNA V10666 has not been identified but the nearby outcrop consists of fine white to grey mudstones and siltstones interpreted by us as floodplain deposits. Based on the fossil deposits nearby it is likely that MNA V10666 originated from these floodplain deposits as well.

Description - MNA V10666 is a single, nearly complete shed tooth crown. Since *Crosbysaurus* is known only from dental material it is not possible to confidently assign a tooth row position to MNA V10666~~the tooth~~. Heckert (pers. comm., 2014) suggested to the first author that this tooth may be from the premaxilla based on the relative robustness. The tooth itself is ~~laterally~~ labiolingually compressed and ~~anterio-posteriorally expanded at the base tapering~~ tapers mesiodistally towards the apex. There is an obvious resorption pit at the base of the tooth and the tip is taphonomically worn down ~~and broken~~ (Figure 3). These data suggest that MNA V10666 is a shed tooth crown.

The ~~tooth~~ crown is 3.7mm from the base to the apically-most preserved point and 3mm ~~anterio-posteriorally~~mesiodistally at its base. ~~Mediolaterally~~ Labiolingually the tooth measures 1 mm (Figure 3). The enamel is a light tan to mottled brown color, typical of many of the teeth from The Hills Have Teeth locality. The preserved ~~posterior~~ distal edge of the tooth is curved posteriorly and has six equally spaced denticles. The basalmost denticle is approximately 0.3 mm in ~~basal-apical~~apicobasal height, while the apical-most denticle is 0.2 mm in height. Above the apical-most denticle there is a thin ridge of enamel. Since the tooth has been worn and was shed during life additional denticles may have been present further up the posterior side. This is not possible to evaluate at this time due to the premortem and postmortem wear of the tooth. The preserved posterior denticles ~~that are present appear to have~~ possess~~ed~~ smaller accessory ~~denticles~~serrations. Most of these are worn but one denticle preserves four accessory denticles on the basal edge and three on the apical edge (Figure 4).

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Comment [M9]: The Hills Have Teeth locality? Please, provide the name of this outcrop.

Comment [M10]: I think that this statement is very unsupported based on the unknown cranial morphology of Crosbysaurus and should be removed from the text.

Comment [M11]: Please, for tooth description use labial (instead of lateral), lingual (medial), mesial (anterior) and distal (posterior). This is the common dental anatomical terminology.

Comment [M12]: You should describe that the mesial margin is convex and the distal one acute at the base of the crown.

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The ~~anterior~~ mesial edge of the tooth possesses a ridge that is expanded 2 mm from the base of the ~~tooth~~crown. This basalmost portion of this ridge is~~,~~ approximately even with the level of the last ~~posterior~~ distal denticle. Very fine (<0.1 mm) denticles cover the ~~anterior~~ mesial edge of this ridge ~~which~~ that extends for 1 mm.

DISCUSSION

~~Differential Diagnosis~~Taxonomic affinities

MNA10666 differs from most described Triassic tooth taxa in several ~~important ways~~features. It differs from the teeth of *Revueltosaurus*, the most commonly reported tooth taxon in the Late Triassic of North America, by being ~~mediolaterally~~ labiolingually narrower than all published specimens of *Revueltosaurus* (Hunt, 1989; Parker et al., 2005). The teeth of *Revueltosaurus* are also ~~anteriorposteriorally~~ mesiodistally broader compared to their apical-basal height. *Reveueltosaurus* is now known from non-dental remains (Parker et al. 2005) and the tooth variation documented in the premaxilla, maxilla, and dentary do not match any teeth reported from *Crosbysaurus* (Irmis et al., 2006). This holds true for MNA V10666 as well; there appears to be no place in the dentition of *Revueltosaurus* for a tooth with the morphology of this specimen.

MNA V10666 differs from ~~the putative Triassic ornithischian,~~ *Tecovasaurus* ~~(Hunt and Lucas, 1994),~~ in several ways. The teeth of *Tecovocsaurus* tend to be much shorter and broader (Hunt and Lucas, 1994) as compared to this specimen specifically, as well as *Crosbysaurus* generally. ~~Anterior~~ Mesial denticles in *Tecovosaurus* tend to be large and coarse, while being more numerous than those on the ~~posterior~~ distal edge of the tooth (Heckert 2004). In contrast, i~~I~~n MNA V10666 the posterior denticles are much coarser than the anterior denticles (Figure 3).

~~The possible Triassic ornithischian~~ *Protecovasaurus lucasi* (Heckert 2004) differs from MNA V10666 because in the former~~, T~~ the ~~anterior~~ mesial and ~~posterior~~ distal denticles are roughly equivalent in size and number. ~~. In MNA the posterior denticles are both larger and more numerous than those on the anterior edge (Figure 3).~~ Indeed, ~~N~~no teeth reported for *Protecovasaurus* match the morphology seen in MNA V10666. Since non-dental fossils are not known for this or other of the previously ~~possible~~ supposed ornithischians from the Triassic of North America it does not rule out positional or ontonogenic variation accounting for the morphological distance between MNA V10666 and these taxa. Given the homodonty present in most basal archosaurs and archosauriformes it is unlikely that any other teeth taxa published from the Late Triassic of North America are represented by MNA V10666.

MNA V10666 closely matches the published illustrations and descriptions of *Crosbysaurus harrisae* (Heckert, 2004). The complex ~~posterior~~ distal denticles, with multiple accessory serrations, ~~coupled with the recurved nature of the tooth itself are~~ are an autapomorphy ~~diagnostic to the genus~~ of *Crosbysaurus* (Heckert, 2004: 67, 68) and, as a result, we assign MNA V10666 to this taxon. None~~-~~the~~-~~less, several differences exist between MNA V10666 and all other published specimens ~~which~~ that warrant some discussion.

Comment [M14]: It is not 0.2mm?

Comment [M15]: You should provide more information about the mesial margin of the crown. For example, does the portion of the margin basal to the ridge completely lack denticles? Do the preserved denticles possess accessory serrations?

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Teeth referred to *Crosbysaurus* by other workers fall into two morphotypes: ~~laterally~~ labiolingually compressed and highly recurved, or basally wide and moderately recurved (see Heckert, 2004 for examples). MNA V10666 falls into neither category. While the tooth is moderately recurved it is also ~~laterally~~ labiolingually compressed, especially compared to other *Crosbysaurus* teeth in the literature. The ~~posterior~~ distal denticles bear fewer accessory denticles than any other *Crosbysaurus* teeth in the literature. The ~~anterior~~ mesial denticles are much smaller, not compound, and are not found along the complete length of the ~~anterior~~ mesial surface of the tooth.

It is tempting to think that these differences may be systematically significant. However, ~~We~~ we refrain from using these differences to taxonomically segregate MNA V10666 from other *Crosbysaurus* specimens~~, however,~~ for several reasons. The sample size from Utah is low (n=1) and individual variation within this taxon has not been quantified. In addition, we lack any other body fossil remains from *Crosbysaurus* and it is currently ~~so it is~~ unknown the dental variation along the tooth row, if present. ~~what role tooth position has in tooth morphology.~~ Coupled with the taxonomic and systematic problems associated with *Revueltosaurus* (Hunt, 1989; Hunt and Lucas, 1994; Heckert, 2002; Parker et al., 2005; Heckert, 2005, Irmis et al., 2006, Heckert et al., 2012), a taxon whose relationship and taxonomy has been radically altered by the discovery of body fossils, we refrain from adding to the confusing plethora of tooth taxa known from the Late Triassic of North America.

Previous authors have suggested that *Crosbysaurus* is useful as a biostratigraphic index taxon of the St. Johnsian division of the Adamanian Land Vertebrate Faunachron (LVF) assemblage (late Carnian-early Norian in age) (Heckert and Lucas, 2006). If these previous workers are correct, MNA V10666 may provide an important lower limit on the age of the Chinle Formation at Comb Ridge, an area that has received little paleontological or stratigraphic work. However, ~~S~~such correlations should be treated as highly tentative, ~~however,~~ pending further stratigraphic work at Comb Ridge ~~by the authors and others~~. Considering the different morphology found in MNA V10666 and other specimens of *Crosbysaurus* it is possible that this taxon may not be as useful as an index fossil as originally suggested. This view is bolstered by the discovery of a single isolated tooth of *Reticulodus synergus* (MNA V10652) at a similar stratigraphic level north of The Hills Have Teeth locality by the first author. Interestingly, *Reticulodus*~~*R.*~~ *synergus* has been regarded as an index taxon for the Norian-aged Revueltian LVF (Heckert and Lucas, 2006). While detailed stratigraphic work remains to be done, the data available at this time suggest that MNA V10666 is Norian in age. The occurrence of two index taxa from different LVFs in the same stratigraphic range would reduce or eliminate the utility of those taxa to high resolution biostratigraphy. It is hoped that additional remains of both taxa will be recovered at Comb Ridge by future workers to provide additional data to test these conclusions.

CONCLUSIONS

The discovery of *Crosbysaurus* from the Chinle Formation of southeastern Utah extends the geographic range of this taxon by approximately 250 kilometers. *Crosbysaurus* was apparently a rare, but widespread species during Chinle deposition times. The single tooth crown recovered, MNA V10666, bears unique morphological characteristics that separate from other

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published specimens of *Crosbysaurus*, as well as other contemporaneous herbivorous archosaurs, such as *Revueltosaurus*. These characters may ~~represent~~ reflect different ~~various~~ tooth positions within the jaw of *Crosbysaurus*, variation between individuals, or taxonomic differences. The sample size and preservation of known specimens of *Crosbysaurus* does not allow us to discriminate between these sources of variation at this time so we refrain from making any statements about what the primary cause is. The near co-occurrence of *Reticulodus synergus* and *Crosbysaurus* may have implications for the utility of these taxa as biostratigraphic index fossils. The Chinle Formation at Comb Ridge has been mapped as the Petrified Forest Member (Bennett, 1955). If further investigations support this, then MNA V10666 represents the youngest occurrence of *Crosbysaurus* and extends its stratigraphic range into the Norian. It is hoped that future work by Mission Heights' field crews can help better clarify the stratigraphic and taxonomic relationships of this enigmatic archosauriform.

Comment [M21]: Irmis et al. (2007) interpreted Crosbysaurus as an indeterminate archosauriform, because the presence of denticles was supposed to be an archosauriform diagnostic feature. However, the recent description of Azendohsaurus as a non-archosauriform archosauromorph has proved the presence of denticles among more basal archosauromorphs. As a result, I think that Crosbysaurus cannot be diagnosed currently beyond Archosauromorpha indet. The authors should explore this possibility.

Acknowledgements

The authors would like to thank Dave and Janet Gillette at the Museum of Northern Arizona for their help with curation, cataloging, and guidance on this project, as well as Andrew Heckert for his helpful comments on the identification of MNA V10666 and providing materials to assist in the preparation of this manuscript. The authors would like to also thank ReBecca Hunt-Foster for helping with the permitting process, as well as Matthew Chesney and Patrick Brown for helping get Mission Heights Paleontology fieldwork started.

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