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6 The first occurrence of the enigmatic archosauriform *Crosbysaurus* Heckert 2004 from the  
7 Chinle Formation of southern Utah

8  
9 **ABSTRACT** - Originally identified as an ornithischian dinosaur, *Crosbysaurus harrisae* has  
10 been found in New Mexico, Arizona, and its type locality in Texas, as well as in North Carolina.  
11 The genus has been reassessed by other workers in light of reinterpretations about the  
12 postcrania of another putative Triassic ornithischian, *Revueltosaurus*. The understanding of  
13 Triassic dental faunas has become more complicated by the extreme convergence between  
14 pseudosuchian archosaurs and ornithischian dinosaur dental morphologies. We report here on  
15 a new specimen of *Crosbysaurus* (MNA V10666) from the Chinle Formation at Comb Ridge in  
16 southeastern Utah. This new specimen is assigned to *Crosbysaurus* sp. on the basis of the  
17 unique compound posterior denticles, labiolingual width, and curvature. While MNA V10666  
18 does not help resolve the affinities of *Crosbysaurus*, it does represent the extension of the  
19 geographic range of this taxon for approximately 250 kilometers. This is the first record of the  
20 genus *Crosbysaurus* in Utah and as such it represents the northernmost known record of this  
21 taxon. This indicates that *Crosbysaurus* was not limited to the southern area of the  
22 Chinle/Dockum deposition but instead was widespread across the Late Triassic paleoriver  
23 systems of western Pangea. The reported specimen was found in close association with a  
24 typical Late Triassic Chinle fauna, including phytosaurs, metoposaurs, and dinosauromorphs.

## 25 26 INTRODUCTION

27  
28 *Crosbysaurus harrisae* was first described by Heckert (2004) the assumption was that it,  
29 like the better-known *Revueltosaurus*, was an ornithischian dinosaur. Several purported  
30 ornithischian taxa were named upon the discovery of isolated teeth, leading several authors to  
31 suggest that herbivorous dinosaurs were widespread across Pangea (Hunt and Lucas, 1994;  
32 Heckert, 2002, 2004, 2005). This scenario contrasted sharply with previous views on  
33 ornithischian diversity and stood in sharp contrast with the non-dental fossil record of  
34 ornithischians outside of the southern hemisphere.

35 This interpretation isolated teeth from the fossil record was challenged by Parker et al.  
36 (2005) with the discovery of the postcrania of *Revueltosaurus* from the Petrified Forest of  
37 Arizona. Not only did this revise how *Revueltosaurus* was seen but it called into question the  
38 systematics of all purported ornithischian dinosaurs from North America (Irmis et al., 2007; see  
39 also Nesbitt et al., 2007). Without any supporting skeletal remains it was no longer  
40 unambiguous to assign “fabrosaur”-like teeth to any known dinosaur clade. While  
41 *Revueltosaurus* is now known from cranial and postcranial elements, other supposed  
42 ornithischians known from only isolated teeth, such as *Tecovasaurus murrayi* and *Crosbysaurus*  
43 *harrisae*, can only be identified as being archosauriforms of uncertain affinity. While some  
44 authors have suggested that ornithischians were present in the Late Triassic of North America

1 (Heckert 2005) virtually all authors are in agreement that *Crosbysaurus* cannot be diagnosed  
2 beyond an indeterminate archosauriform and new data suggest that it may be instead an non-  
3 archosauriform archosauromorph based on similar dental features found in the  
4 archosauromorph *Azendohsaurus* (Flynn et al., 2010). While this new record does not clarify the  
5 systematic affiliations of *Crosbysaurus* it does significantly extend its range. Previous reports of  
6 *Crosbysaurus* in the southwestern United States have been limited to Texas (the type locality),  
7 New Mexico, and Arizona (Heckert 2004). Comb Ridge in southeastern Utah is approximately  
8 245 kilometers away from the closest reported *Crosbysaurus* remains in the Chinle Formation of  
9 Arizona.

10 In May of 2014 ten students from Mission Heights Preparatory High School traveled to  
11 southeastern Utah. Students prospected the Chinle Formation exposed at Comb Ridge and  
12 opened a test pit at a possible metoposaurid temnospondyl site discovered by the first author in  
13 March of the same year. The second author, accompanied by another student, discovered a  
14 rich locality to the south of the metoposaur site. The second author and another student named  
15 this rich microsite "The Hills Have Teeth." While combing the ground near the base of The Hills  
16 Have Teeth locality (MNA Locality 1724) the second author discovered an unusual partial tooth,  
17 MNA V10666, to the west-southwest of the main outcrop. This second locality has been  
18 designated MNA Locality 1725. The students brought this tooth to the attention of the first  
19 author and it is described here.

## 22 MATERIALS AND METHODS

24 **Abbreviations** - Mission Heights Preparatory High School, Casa Grande, Arizona  
25 (MHPRO); Museum of Northern Arizona, Flagstaff, Arizona (MNA), New Mexico Museum of  
26 Natural History, Albuquerque, New Mexico (NMMNH)

28 **Materials** - Standard paleontological hand tools were used to collect MNA V10666.  
29 Geographic locality data were recorded via BackCountry Navigator Android Application running  
30 on a Samsung Galaxy S4. All specimens were collected under Bureau of Land Management  
31 paleontology permit UT14-001S issued to the first author and are curated at the MNA. The  
32 stratigraphic section was measured using a standard 1.8 meter Jacob Staff and a Brunton  
33 transit. Figures and line drawings were produced using GIMP 2.8.4. Photos used for figures  
34 were obtained using an Olympus E-500 DSLR camera. Specimen measurements were obtained  
35 using Crafsman (model 40257) metal sliding calipers with a precision of 0.05 mm.

## 37 RESULTS

### 39 Systematic paleontology

41 Diapsida Osborn 1903  
42 Archosauromorpha Huene 1946  
43 ?Archosauriformes Gauthier 1986  
44 *Crosbysaurus* Heckert 2004

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## Type Material

The type material of *Crosbysaurus* comes from Crosby County, Texas, and consists of a single tooth (NMMNH P-34200). Several other teeth were collected from the same locality and are paratype specimens: NMMNH P-34201, NMMNH P-34319, NMMNH P-34320, NMMNH P-34260, NMMNH P-34261, NMMNH P-34262, NMMNH P-34393, NMMNH P-34394, and NMMNH P-34397 (Heckert 2004). All teeth illustrated by Heckert (2004; figures 51-54) are labiolingually compressed with compound denticles on the distal edge. In labial view the holotype and paratypes possess a conical and short outline. The figured teeth have a slight labial bulge but are otherwise symmetrical in occlusal view.

## Referred material

MNA V10666, a single shed tooth crown.

## Locality and horizon

MNA 1725 is located 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 four meters west-southwest of The Hills Have Teeth as surface float, six meters above the Moenkopi Formation and very likely has originated at The Hills Have Teeth (Figure 2). This is corroborated by the presence of phytosaur tooth fragments found close (within 10 cm) 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 the upper portion of the Chinle Formation have been reported to correlate to the Petrified Forest Member by Bennett (1955), the Rock Point Member (Lucas et al., 1997), the Owl Rock Member (Molina-Garza et al., 2003), and the Church Rock Member (Martz et al., 2014). 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 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.

The precise fossil-bearing horizon of MNA V10666 has not been identified but the nearby Hills Have Teeth outcrop consists of fine white to grey mudstones and siltstones here interpreted as floodplain deposits. The uppermost horizon at The Hills Have Teeth is nine meters above the Moenkopi Formation, giving an upper limit to the stratigraphic position of MNA V10666. Based on the fossil deposits nearby it is likely that MNA V10666 originated from these floodplain deposits as well.

In order to test this stratigraphic hypothesis, the first author measured a stratigraphic section through The Hills Have Teeth (Figure 3). The Chinle Formation exposed at Comb Ridge at this location has an exposed thickness of 76.8 meters with an estimated 77 meters of section covered by colluvium up to the contact with the Wingate Formation. The strike and dip of the Chinle Formation at this section is 024°/114° E. This remained consistent throughout the section

1 measured at The Hills Have Teeth. The lower member has a thickness of 24.2 meters and  
2 contains multiple horizons of bentonite clays. The lower portion of the section is fossiliferous  
3 with abundant petrified wood. Silicified wood remains become rare up the section with no wood  
4 present above the 21 meter level. Significant vertebrate remains are so far constrained to the  
5 lower nine meters of the formation, though indeterminate vertebrate fragments were found as  
6 high as 12 meters above the Moenkopi Formation. The vast majority of vertebrate remains  
7 (>95%) in this section come from light grey bentonitic mud-grading-to-shale forming The Hills  
8 Have Teeth outcrop. No *in situ* fossil remains have been found below The Hills Have Teeth. The  
9 unionid bivalve found three meters from the base of the Chinle Formation, below MNA Locality  
10 1725, was recovered on the surface (Figure 4). Similarly the phytosaur and temnospondyl teeth  
11 recovered from the alluvial fan below The Hills Have Teeth outcrop alongside MNA V10666  
12 were collected as float.

13 In general the lower member of the Chinle Formation appears grey to dark blue on the  
14 surface. Bentonite is common throughout the member. Paleosols are rare. Caliche development  
15 is common with seven distinct zones of caliche present between the base of the Chinle  
16 Formation and the contact with the Church Rock Member. A limey sand, possibly representing a  
17 short period of standing water, is present as a discontinuous bench at the base of The Hills  
18 Have Teeth outcrop, 12.6 cm thick.

19 The contact between the lower member and the Church Rock Member of the Chinle  
20 Formation occurs at a caliche-rich reddish-brown silt. Generally the Church Rock appears more  
21 reddish or pinkish on the surface. More of the Church Rock is covered by colluvial and alluvial  
22 deposits in this section so the stratigraphy is less well defined above the contact with the lower  
23 member. The Church Rock appears more homogeneous than the lower member. Most of the  
24 exposure consists of weak red mottled white mudstones through the majority of the section.  
25 This mottling may indicate reduction mottling and becomes more common towards the top of  
26 the measured section. Six distinct caliche beds were measured in the section, including the  
27 caliche present in the contact with the lower member. The remainder of the caliches occur in the  
28 upper 20 meters of the measured section. In contrast with the lower member, the Church Rock  
29 appears to lack bentonite in this locality, in line with other exposures of the Church Rock in Utah  
30 and across the Colorado Plateau (Martz et al., 2014). No conglomerate beds exist in the  
31 measured section in contrast to those seen further northeast (Martz et al., 2014) though  
32 conglomeritic lenses occur further north at Comb Ridge. While both vertebrate and plant fossils  
33 are common in the Church Rock Member in Lisbon Valley to the northwest (Martz et al., 2014),  
34 no fossil remains were recovered above the lower member in this section of Comb Ridge.  
35 Indeed few fossils have yet been found in the Church Rock Member at Comb Ridge. While this  
36 may reflect actual the actual preservation of fossil material in the Church Rock it is also likely  
37 influenced by the amount of colluvial cover from the more recent Wingate Sandstone.

38  
39 **Description** - MNA V10666 (Fig. 5-7) is a single, nearly complete shed tooth crown.  
40 Since *Crosbysaurus* is known only from isolated dental material it is not possible to confidently  
41 assign a tooth row position to the MNA V10666. Heckert (pers. comm. 2014) suggested to the  
42 first author that this tooth may be from the premaxilla based on the relative robustness. Given  
43 that *Crosbysaurus* cranial material is unknown, this is not currently testable. The tooth itself is  
44 labiolingually compressed and tapers mesiodistally towards the apex. There is an obvious

1 resorption pit at the base of the tooth and the tip is taphonomically worn down (Figure 5). These  
2 data suggest that MNA V10666 is a shed tooth crown. A reconstructed outline of the tooth is  
3 shown in Figure 6.

4 The crown height is 3.7mm from the base to the apically-most preserved point and 3mm  
5 wide mesiodistally at the base. It is curved along the mesial margin and acute along the distal  
6 margin at the base of the crown. Labiolingually the tooth measures 1 mm (Figure 5). The  
7 enamel color is a light tan to mottled brown, typical of many of the teeth from The Hills Have  
8 Teeth locality. The preserved distal edge of the tooth is straight and has six equally spaced  
9 denticles. The basalmost denticle is approximately 0.3 mm in apicobasal height. The apical-  
10 most denticle is 0.2 mm in height. Above the apical-most denticle there is a thin ridge of enamel.  
11 Since the tooth has been worn and was shed during life there is damage to the mesial and distal  
12 surfaces near the apex. This precludes determining if additional denticles may have been  
13 present higher on the distal side. This is not possible to evaluate at this time due to the  
14 premortem and postmortem wear of the tooth. The preserved posterior denticles possess  
15 smaller accessory serrations. Most of these are worn but one denticle preserves four accessory  
16 denticles on the basal edge and three on the apical edge (see Figure 7).

17 The figured mesial edge of the tooth possesses a ridge that is expanded 2 mm from the  
18 base of the crown, approximately even with the level of the last distal denticle. Very fine (<0.1  
19 mm) denticles cover the mesial edge of this ridge that extends for 1 mm. Below this ridge the  
20 crown's enamel is intact and does not possess denticles, indicating this is the natural  
21 termination of this ridge. The mesial denticles do not appear to possess accessory denticles,  
22 unlike what has been reported from other specimens of *Crosbysaurus* (Heckert 2004).

## 23 DISCUSSION

### 24 Taxonomic Affinities

25  
26  
27  
28 MNA V10666 differs from most described herbivorous Triassic teeth with subdivided  
29 denticles in several features. It differs from the teeth of *Revueletosaurus*, the most commonly  
30 reported leaf-shaped-tooth in the Late Triassic of North America (Hunt, 1989; Heckert, 2002;  
31 Parker et al., 2005), by being labiolingually narrower. The teeth of *Revueletosaurus* are also  
32 mesiodistally broader compared to their apical-basal height. *Revueletosaurus* is now known  
33 from non-dental remains (Parker et al. 2005) and the tooth variation documented in the  
34 premaxilla, maxilla, and dentary do not match any teeth reported as *Crosbysaurus* (Irmis et al.,  
35 2007). This holds true for MNA V10666 as well; there appears to be no place in the dentition of  
36 *Revueletosaurus* for a tooth with the morphology of the described specimen.

37 *Krzyzanowskisaurus hunti* (Heckert, 2005) was originally named as a species of  
38 *Revueletosaurus* by Heckert (2002) based mainly on the presence of a cingulum on the tooth  
39 crown, separating it from the congeneric *R. callenderi*. After it was recognized that *R. callenderi*  
40 is in fact a pseudosuchian (Parker et al., 2005; Irmis et al., 2007), Heckert (2005) erected a new  
41 genus. Specimens formerly assigned to *R. hunti* were placed in this new genus,  
42 *Krzyzanowskisaurus*. At the time the change was done it was thought that *K. hunti*, represented  
43 a possible ornithischian (Heckert, 2005) but work by other authors (Irmis et al., 2007)  
44 challenged both its validity and its assignment to dinosauria. It is outside the scope of this paper

1 to analyze the validity or affiliations of other Triassic tooth-based taxa. Regardless of the  
2 affinities of *K. hunti* it is clear that MNA V10666 does not possess a cingulum (Figure 3). As  
3 such MNA V10666 cannot be referred to *Krzyzanowskisaurus*.

4 MNA V10666 differs from the Triassic tooth-based taxon *Tecovasaurus* in several ways.  
5 The teeth of *Tecovasaurus* tend to be much shorter and broader (Hunt and Lucas, 1994) as  
6 compared to MNA V10666 specifically, as well as to *Crosbysaurus* generally. Mesial denticles in  
7 *Tecovasaurus* tend to be large and coarse while being more numerous than those on the distal  
8 edge of the tooth (Heckert 2004). In contrast, in MNA V10666 the preserved distal denticles are  
9 much coarser than those along the mesial edge (Figure 6).

10 *Lucianosaurus wildi* (Hunt and Lucas, 1994) is another Late Triassic tooth-based taxon.  
11 Irmis et al. (2007) suggest it is an archosauriform though it was originally described as an  
12 ornithischian dinosaur. The holotype and referred specimen of *L. wildi* are dissimilar to MNA  
13 V10666 in that they possess finer denticles on both their mesial and distal edges. In addition,  
14 the tooth crowns of *L. wildi* are mesiodistally deeper than what is seen in MNA V10666. MNA  
15 V10666 is further differentiated by the steep mesial and distal edges that are nearly straight,  
16 compared to the low-angle convex edges of *L. wildi*.

17 The teeth of an unnamed taxon from the Owl Rock Member of the Chinle Formation of  
18 Arizona was described and figured by Butler et al. (2006). MNA V10666 differs from this  
19 unnamed taxon in several ways. The distal denticles of MNA V10666 are subdivided into  
20 multiple accessory denticles, unlike the simple cleft of the unnamed taxon. The mesial denticle  
21 of MNA V10666 are much smaller, not subdivided, and do not run to the base of the crown. The  
22 unnamed taxon is also much more symmetrical mesiodistally than MNA V10666.

23 *Protecovasaurus lucasi* (Heckert 2004) differs from MNA V10666 because in the former  
24 the mesial and distal denticles are roughly equivalent in size and number. Indeed, no teeth  
25 reported for *Protecovasaurus* match the morphology seen in MNA V10666. Since non-dental  
26 fossils are not known for this or any other of the previously supposed ornithischians from the  
27 Triassic of North America it is not possible to rule out positional or ontogenetic variation  
28 accounting for the morphological distance between MNA V10666 and these taxa. Given the  
29 homodonty present in most basal archosaurs and archosauriformes it is unlikely that any of  
30 these tooth-based taxa published from the Late Triassic of North America are represented by  
31 MNA V10666.

32 MNA V10666 closely matches the published illustrations and descriptions of  
33 *Crosbysaurus harrisae* (Heckert, 2004). The complex distal denticles with multiple accessory  
34 serrations, are an autapomorphy of *Crosbysaurus* (Heckert, 2004: 67, 68). None-the-less,  
35 several differences exist between MNA V10666 and all other published specimens that warrant  
36 some discussion.

37 Teeth referred to *Crosbysaurus* by other workers fall into two morphotypes: labiolingually  
38 compressed and highly recurved or basally wide and moderately recurved (see Heckert, 2004:  
39 67, 68). MNA V10666 falls into neither category. It is labiolingually compressed, especially  
40 compared to other *Crosbysaurus* teeth in the literature, but without being recurved. The distal  
41 denticles bear fewer accessory denticles than any other teeth referred to *Crosbysaurus* in the  
42 literature. The mesial denticles are much smaller, not compound, and are not found along the  
43 complete length of the anterior surface of the tooth.

1 It is tempting to think that these differences may be systematically significant. However,  
2 we refrain from using these differences to taxonomically segregate MNA V10666 from other  
3 *Crosbysaurus* specimens for several reasons. The sample size from Utah is low (n=1) and  
4 individual variation within this taxon has not been quantified. In addition we lack any other body  
5 fossil remains from *Crosbysaurus* and it is currently unknown the dental variation along the  
6 tooth row, if present. Coupled with the taxonomic and systematic problems associated with  
7 *Revueltosaurus* (Hunt, 1989; Hunt and Lucas, 1994; Heckert, 2002; Parker et al., 2005;  
8 Heckert, 2005; Irmis et al., 2007; Heckert et al., 2012), a taxon whose relationships have been  
9 radically altered by the discovery of body fossils, we refrain from adding to the confusing  
10 plethora of tooth taxa known from the Late Triassic of North America.

11 Previous authors have suggested that *Crosbysaurus* is useful as a biostratigraphic index  
12 taxon of the St. Johnian division of the Adamanian Land Vertebrate Faunachron assemblage  
13 (late Carnian-early Norian in age) (Heckert and Lucas, 2006). If these previous workers are  
14 correct MNA V10666 may provide an important lower limit on the age of the Chinle Formation at  
15 Comb Ridge, an area that has received little paleontological or stratigraphic work in the past.

## 17 CONCLUSIONS

18  
19 The discovery of *Crosbysaurus* from the Chinle Formation of southeastern Utah extends the  
20 geographic range of this taxon northward by approximately 250 kilometers. *Crosbysaurus* was  
21 apparently a rare, but widespread taxon during the Chinle Formation deposition times. The  
22 single tooth crown recovered from Utah (MNA V10666) bears unique morphological  
23 characteristics that separate it from other published specimens of *Crosbysaurus*, as well as from  
24 other contemporaneous herbivorous archosaurs such as *Revueltosaurus callendari*. These  
25 characters may represent various tooth positions within the jaw of *Crosbysaurus*, variation  
26 between individuals, or taxonomic differences. The sample size and preservation of known  
27 specimens of *Crosbysaurus* does not allow us to discriminate between these sources of  
28 variation at this time so we refrain from making any statements about what the primary cause is.  
29 It is hoped that future work by Mission Heights' field crews can help to better clarify the  
30 stratigraphic and taxonomic relationships of this enigmatic archosauriform.

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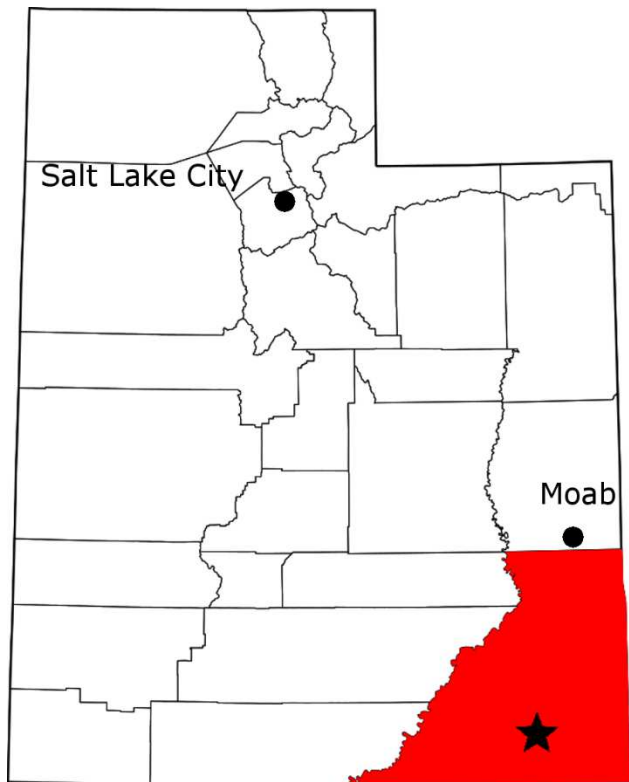
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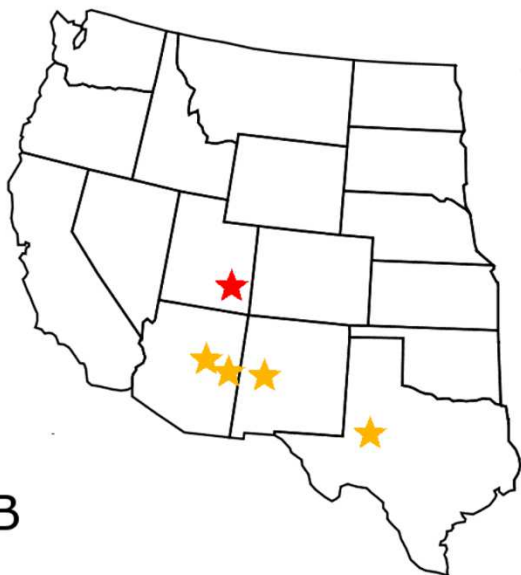
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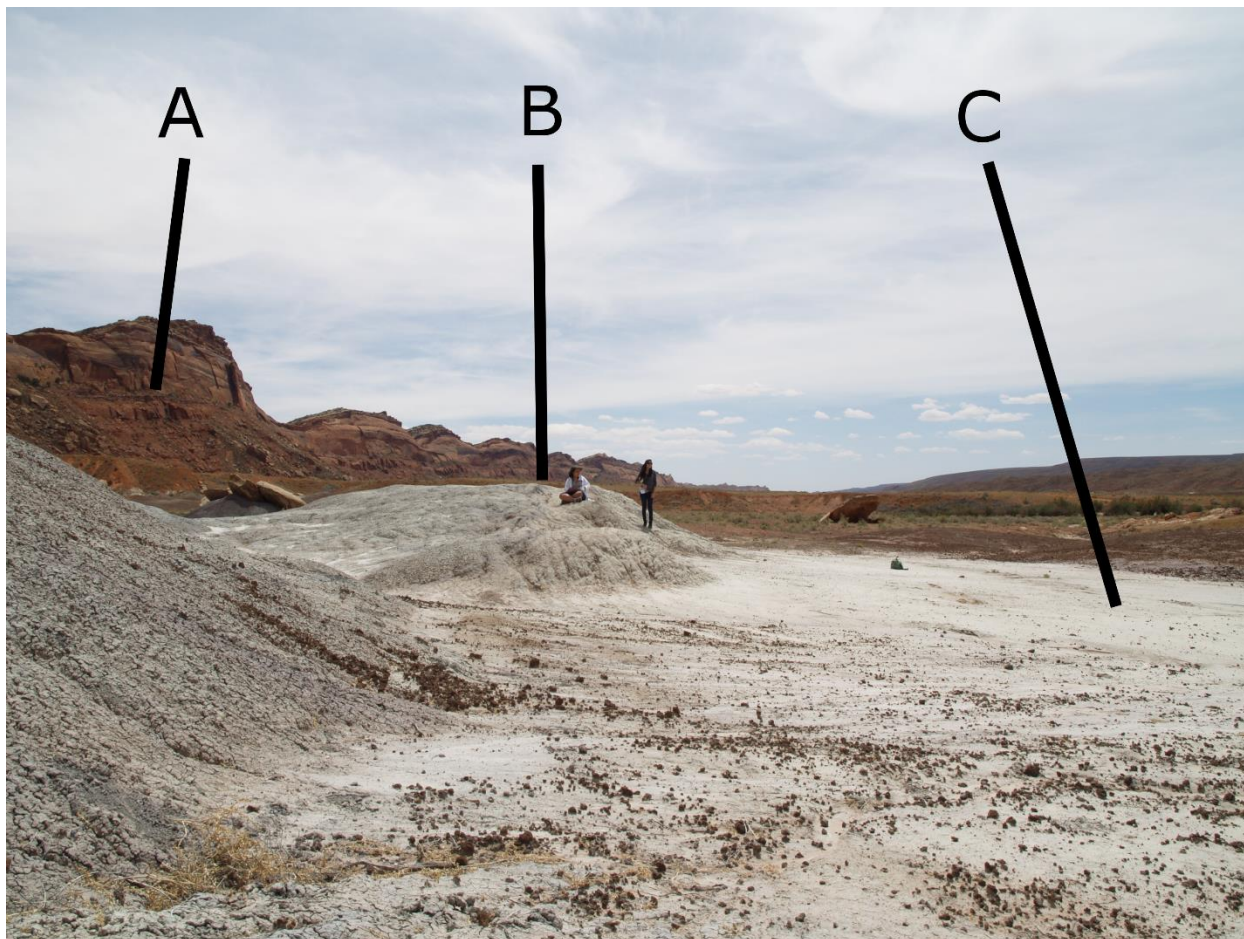


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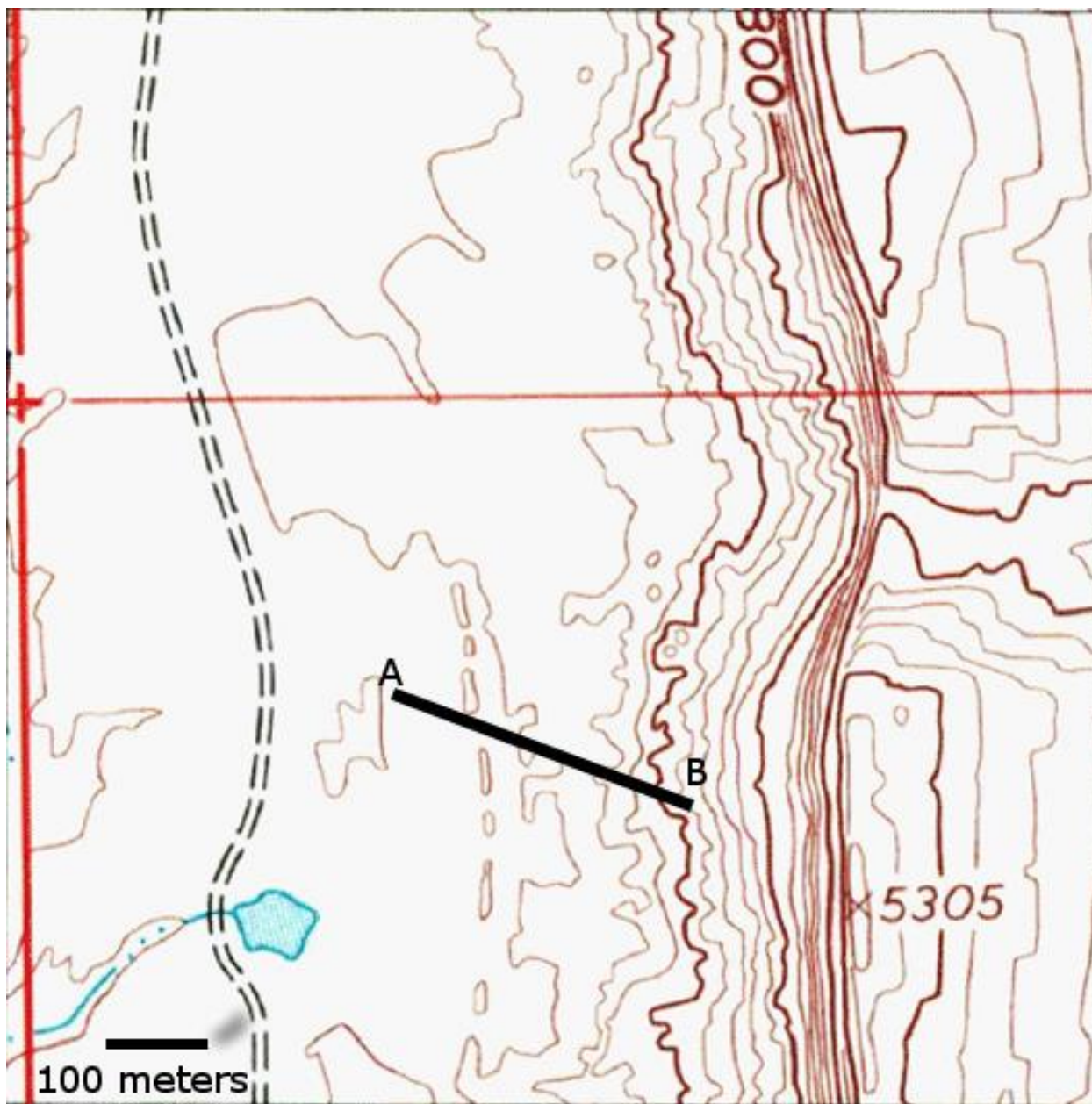


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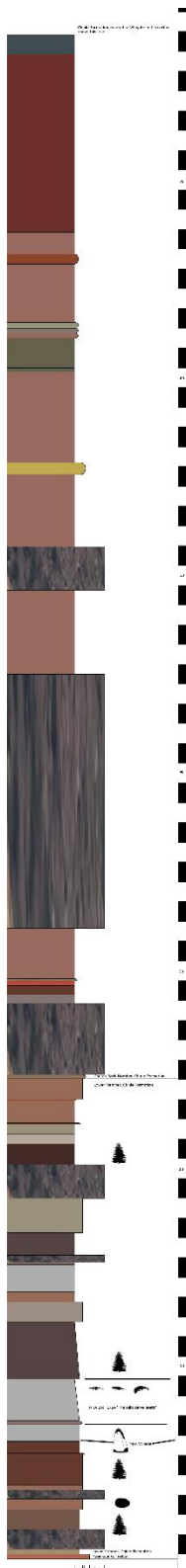
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2 Figure 1: Map showing A) the location of MNA Locality 1725, The Hills Have Teeth (starred),  
3 San Juan County (highlighted), Utah, USA; B) the location of MNA locality 1725 (red) to  
4 previously reported *Crosbysaurus* localities (yellow) in the western United States.  
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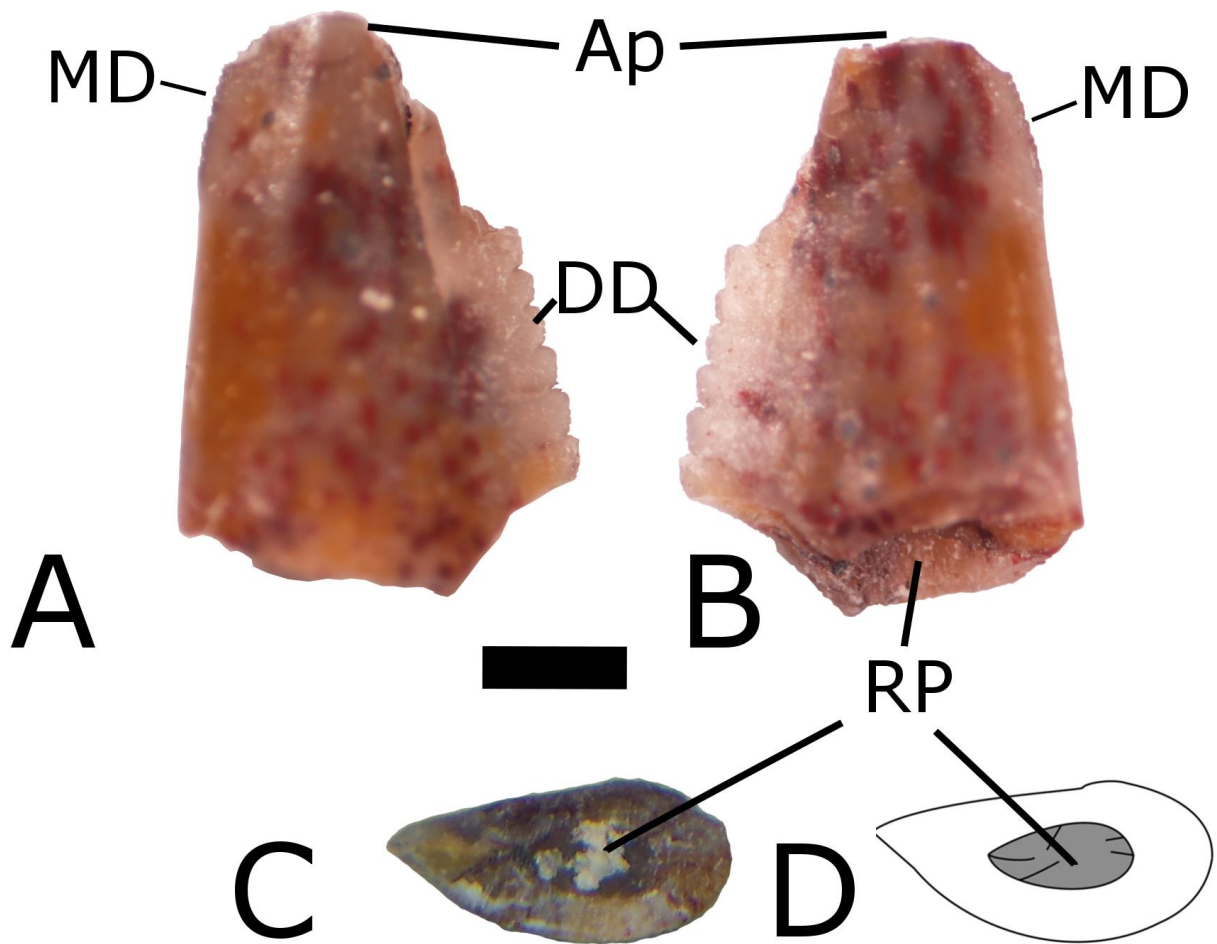
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2 Figure 2: MNA Locality 1725, showing relative stratigraphic position of MNA V10666 to the  
3 surrounding sediments. A) Top of the Chinle Formation at Comb Ridge; B) The second author  
4 sitting at The Hills Have Teeth (MNA Locality 1724) C); location where MNA V10666 was  
5 discovered.  
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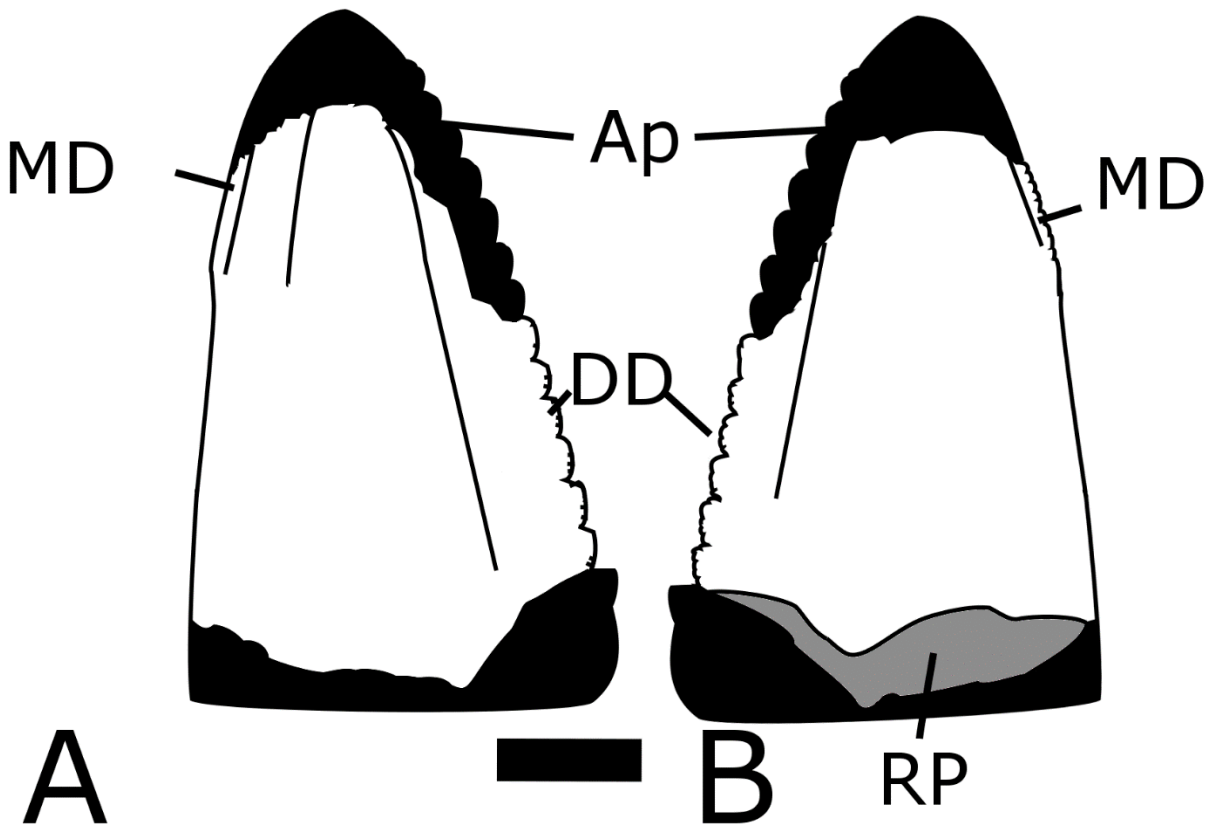
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2 Figure 3: Location of measured stratigraphic section in Figure 4. North is to the top of the figure.  
3 Scale bar = 100 meters.  
4



- 1
- 2 Measured section through the Chinle Formation exposed at The Hills Have Teeth locality. MNA
- 3 V10666 is represented here by an outline diagram. Scale bar = 1 meter. Organism silhouettes
- 4 from Phylopic by Dmitry Bogdanov, Nobu Tamura, Scott Hartman, and Robert Gay.



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 2 Figure 5: MNA V10666, *Crosbysaurus* sp., from MNA Locality 1725 in A) presumed labial B)  
 3 presumed lingual C) basal views. D) Interpretive drawing in basal view showing resorption pit.  
 4 Abbreviations: Ap, apex; DD, distal denticles; MD, mesial denticles; RP, resorption pit. Scale = 1  
 5 mm.  
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2 Figure 6: Interpretive line drawing of MNA V10666, *Crosbysaurus* sp., from MNA Locality 1725  
3 showing the outline of the tooth if complete and the surface anatomy of the preserved crown. A)  
4 presumed labial B) presumed lingual views. Abbreviations: Ap, apex; DD, distal denticles; MD,  
5 mesial denticles; RP, resorption pit. Scale = 1 mm.  
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2 Figure 7: Line drawing of posterior denticles of MNA V10666, *Crosbysaurus sp.*, from MNA  
3 Locality 1725 . Apex is to the right, the base is to the left. Scale = 1 mm.