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

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Originally identified as an ornithischian dinosaur, *Crosbysaurus harrisae* has been found in New Mexico, Arizona, and its type locality in Texas, as well as in North Carolina. The genus has been reassessed by other workers in light of 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 archosaurs and ornithischian dinosaur dental morphologies. We report here on a new specimen of *Crosbysaurus* (MNA V10666) from the Chinle Formation at Comb Ridge in southeastern Utah. This new specimen is assigned to *Crosbysaurus* sp. on the basis of the unique compound posterior denticles, labiolingual width, and curvature. While MNA V10666 does not help resolve the affinities of *Crosbysaurus,* it does represent the extension of the geographic range of this taxon for approximately 250 kilometers. This is the first record of the genus *Crosbysaurus* in Utah and as such it represents the northernmost known record of this taxon. This indicates that *Crosbysaurus* was not limited to the southern area of the Chinle/Dockum deposition but instead was widespread across the Late Triassic paleoriver systems of western Pangea. The reported specimen was found in close association with a typical Late Triassic Chinle fauna, including phytosaurs, metoposaurs, and dinosauromorphs .

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ABSTRACT - Originally identified as an ornithischian dinosaur, *Crosbysaurus harrisae* has been found in New Mexico, Arizona, and its type locality in Texas, as well as in North Carolina. The genus has been reassessed by other workers in light of 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 archosaurs and ornithischian dinosaur dental morphologies. We report here on a new specimen of *Crosbysaurus* (MNA V10666) from the Chinle Formation at Comb Ridge in southeastern Utah. This new specimen is assigned to *Crosbysaurus* sp. on the basis of the unique compound posterior denticles, labiolingual width, and curvature. While MNA V10666 does not help resolve the affinities of *Crosbysaurus,* it does represent the extension of the geographic range of this taxon for approximately 250 kilometers. This is the first record of the genus *Crosbysaurus* in Utah and as such it represents the northernmost known record of this taxon. This indicates that *Crosbysaurus* was not limited to the southern area of the Chinle/Dockum deposition but instead was widespread across the Late Triassic paleoriver systems of western Pangea. The reported specimen was found in close association with a typical Late Triassic Chinle fauna, including phytosaurs, metoposaurs, and dinosauromorphs.

INTRODUCTION

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

This interpretation based on isolated teeth was challenged by Parker et al. (2005) with the discovery of the postcrania of *Revueltosaurus* from the Petrified Forest of Arizona. This contribution, not only shed light on how *Revueltosaurus* was seen but it called into question the systematics of all purported ornithischian dinosaurs from North America (Irmis et al., 2007; see also Nesbitt et al., 2007). Without any supporting of skeletal remains it was no longer unambiguous to assign "fabrosaur"-like teeth to any known dinosaur clade. While *Revueltosaurus* is now known from cranial and postcranial elements, other supposed ornithischians known from only isolated teeth, such as *Tecovasaurus murrayi* and *Crosbysaurus harrisae,* can only be identified as being archosauriforms of uncertain affinity. While some authors have suggested that 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 archosauriform and new data suggest that it may be instead an non-archosauriform archosauromorph based on similar dental features found in the archosauromorph

46   *Azendohsaurus* (Flynn et al., 2010). While this new record does not clarify the systematic affiliations of
47   *Crosbysaurus* it does significantly extend its range. Previous reports of *Crosbysaurus* in the
48   southwestern United States have been limited to Texas (the type locality), New Mexico, and Arizona
49   (Heckert 2004). Comb Ridge in southeastern Utah is approximately 245 kilometers away from the
50   closest reported *Crosbysaurus* remains in the Chinle Formation of Arizona.
51   In May of 2014 ten students from Mission Heights Preparatory High School traveled to
52   southeastern Utah. Students prospected the Chinle Formation exposed at Comb Ridge and opened a
53   test pit at a possible metoposaurid temnospondyl site discovered by the first author in March of the
54   same year. The second author, accompanied by another student, discovered a rich locality to the
55   south of the metoposaur site. The second author and another student named this rich microsite "The
56   Hills Have Teeth." While combing the ground near the base of The Hills Have Teeth locality (MNA
57   Locality 1724) the second author discovered an unusual partial tooth, MNA V10666, to the west-
58   southwest of the main outcrop. This second locality has been designated MNA Locality 1725. The
59   students brought this tooth to the attention of the first author and it is described here.
60
61   **Abbreviations** - Mission Heights Preparatory High School, Casa Grande, Arizona (MHPRO);
62   Museum of Northern Arizona, Flagstaff, Arizona (MNA), New Mexico Museum of Natural History,
63   Albuquerque, New Mexico (NMMNH)
64
65   **Materials and Methods** - Standard paleontological hand tools (ice picks, dental tools, natural-
66   bristle brushes, plastic bags) were used to collect MNA V10666. Geographic locality data were
67   recorded via BackCountry Navigator Android Application running on a Samsung Galaxy S4. MNA
68   V10666 was collected under Bureau of Land Management paleontology permit UT14-001S issued to
69   the first author and are curated at the MNA. The stratigraphic section was measured using a standard
70   1.8 meter Jacob Staff and a Brunton Pocket Transit. Figures and line drawings were produced using
71   GIMP 2.8.4. Photos used for figures were obtained using an Olympus E-500 DSLR camera. Specimen
72   measurements were obtained using Crafstman (model 40257) metal sliding calipers with a precision
73   of 0.05 mm.
74   **Systematic paleontology**
75
76   Diapsida Osborn 1903
77   Archosauromorpha Huene 1946
78   ?Archosauriformes Gauthier 1986
79   *Crosbysaurus* Heckert 2004
80
81   **Type Material**
82   The type material of *Crosbysaurus* comes from Crosby County, Texas, and consists of a single tooth
83   (NMMNH P-34200). Several other teeth were collected from the same locality and are paratype
84   specimens: NMMNH P-34201, NMMNH P-34319, NMMNH P-34320, NMMNH P-34260, NMMNH P-
85   34261, NMMNH P-34262, NMMNH P-34393, NMMNH P-34394, and NMMNH P-34397 (Heckert
86   2004). All teeth illustrated by Heckert (2004; figures 51-54) are labiolingually compressed with
87   compound denticles on the distal edge. In labial view the holotype and paratypes possess a conical
88   and short outline. The figured teeth have a slight labial bulge but are otherwise symmetrical in occlusal
89   view.

90
91 **Referred material**
92
93 MNA V10666, a single shed tooth crown.
94
95 **Locality and horizon**
96
97 MNA 1725 is located in San Juan County, Utah (Figure 1). The exact coordinates remain on file at the
98 Museum of Northern Arizona. This locality, named The Hills Have Teeth, produced numerous partial
99 and complete phytosaur and metoposaur teeth along with several dinosaur or dinosauromorph teeth.
100 MNA V10666 was found approximately four meters west-southwest of The Hills Have Teeth outcrop
101 as surface float, six meters above the Moenkopi Formation and very likely has originated at The Hills
102 Have Teeth (Figure 2). This is corroborated by the presence of phytosaur tooth fragments found close
103 (within 10 cm) to MNA V10666 which the second author was able to connect with fragments collected
104 at the main deposit at The Hills Have Teeth. The lack of recent damage to the fine mesial denticles
105 further supports the hypothesis that MNA V10666 was not transported post-exposure very far from
106 where it was discovered.
107 This area has not been mapped in detail but the upper portion of the Chinle Formation have
108 been reported to correlate to the Petrified Forest Member by Bennett (1955), the Rock Point Member
109 (Lucas et al., 1997), the Owl Rock Member (Molina-Garza et al., 2003), and the Church Rock Member
110 (Martz et al., 2014). Further work by the authors and others is ongoing and the relationships between
111 the beds at Comb Ridge and other exposures of the Chinle Formation will be clarified in the near
112 future. None-the-less, it is clear that MNA V10666 was originally deposited near the base of the Chinle
113 Formation as part of the earliest fauna recorded in the Comb Ridge area.
114 The precise fossil-bearing horizon of MNA V10666 has not been identified but the nearby Hills
115 Have Teeth outcrop consists of fine white to grey mudstones and siltstones here interpreted as
116 floodplain deposits. The uppermost horizon at The Hills Have Teeth is nine meters above the
117 Moenkopi Formation, giving an upper limit to the stratigraphic position of MNA V10666. Based on the
118 nearby fossil deposits, it is likely that MNA V10666 originated from these floodplain deposits as well.
119 In order to test this stratigraphic hypothesis, the first author measured a stratigraphic section
120 through The Hills Have Teeth section (Figure 3). The Chinle Formation exposed at Comb Ridge has a
121 thickness of 76.8 meters with an estimated 77 meters of section covered by colluvium up to the
122 contact with the Wingate Formation. The strike and dip of the Chinle Formation at this section is
123 024º/114º E. This remained consistent throughout the section measured at The Hills Have Teeth. The
124 lower member has a thickness of 24.2 meters and contains multiple horizons of bentonite clays. The
125 lower portion of the section is fossiliferous with abundant petrified wood. Silicified wood remains
126 become rare at the upper part of the section with no wood present above the 21 meters level.
127 Significant vertebrate remains are so far constrained to the lower nine meters of the formation, though
128 indeterminate vertebrate fragments were found as high as 12 meters above the Moenkopi Formation.
129 The vast majority of vertebrate remains (>95%) in this section come from light grey bentonitic mud-
130 grading-to-shale, forming The Hills Have Teeth outcrop. No *in situ* fossil remains have been found
131 below The Hills Have Teeth section. The unionid bivalve found three meters from the base of the
132 Chinle Formation, below MNA Locality 1725, was recovered on the surface (Figure 4). Similarly the

133 phytosaur and temnospondyl teeth recovered from the alluvial fan below The Hills Have Teeth
134 outcrop, alongside MNA V10666 were collected as float.
135   In general the lower member of the Chinle Formation appears grey to dark blue on the surface.
136 Bentonite is common throughout the member. Paleosols are rare. Caliche development is common
137 with seven distinct zones of caliche present between the base of the Chinle Formation and the contact
138 with the Church Rock Member. A limey sand, possibly representing a short period of standing water,
139 is present as a discontinuous bench at the base of The Hills Have Teeth outcrop, 12.6 cm thick.
140   The contact between the lower member and the Church Rock Member of the Chinle Formation
141 occurs at caliche-rich reddish-brown silt. Generally the Church Rock Member appears more reddish or
142 pinkish on the surface. More of this member is covered by colluvial and alluvial deposits in this
143 section, so the stratigraphy is less well defined above the contact with the lower member. The Church
144 Rock Member appears more homogeneous than the lower member. Most of the exposure consists of
145 weak red mottled white mudstones through the majority of the section. This mottling may indicate
146 reduction mottling and becomes more common towards the top of the measured section. Six distinct
147 caliche beds were measured in the section, including the caliche present in the contact with the lower
148 member. Other caliches occur in the upper 20 meters of the measured section. In contrast with the
149 lower member, the Church Rock appears to lack bentonite in this locality, in line with other exposures
150 of the Church Rock in Utah and across the Colorado Plateau (Martz et al., 2014). No conglomerate
151 beds exist in the measured section in contrast to those seen further northeast (Martz et al., 2014)
152 though conglomeritic lenses occur further north at Comb Ridge. While both vertebrate and plant
153 fossils are common in the Church Rock Member in Lisbon Valley and to the northwest (Martz et al.,
154 2014), no fossil remains were recovered above the lower member in this section of Comb Ridge.
155 Indeed few fossils have yet been found in the Church Rock Member at Comb Ridge. While this may
156 reflect the actual preservation of fossil material in the Church Rock it is also likely influenced by the
157 amount of colluvial cover from the more recent Wingate Sandstone and the steep angle of the
158 exposures, resulting in rapid transport of any material exposed on the surface.
159
160   **Description** - MNA V10666 (Figs. 5-8) is a single, nearly complete shed tooth crown. Since
161 *Crosbysaurus* is known only from isolated dental material it is not possible to confidently assign a
162 tooth row position to the MNA V10666. Heckert (pers. comm. 2014) suggested to the first author that
163 this tooth may be from the premaxilla based on the relative robustness. Given that *Crosbysaurus*
164 cranial material is unknown, this is not currently testable. The tooth itself is labiolingually compressed
165 and tapers mesiodistally towards the apex. There is an obvious resorption pit at the base of the tooth
166 and the tip is taphonomically worn down (Figure 5). These data suggest that MNA V10666 is a shed
167 tooth crown. A reconstructed outline of the tooth is shown in Figure 6.
168   The crown height is 3.7mm from the base to the apically-most preserved point and 3mm wide
169 mesiodistally at the base. It is curved along the mesial margin and acute along the distal margin at the
170 base of the crown. Labiolingually the tooth measures 1 mm (Figure 5). The enamel color is a light tan
171 to mottled brown, typical of many of the teeth from The Hills Have Teeth locality. The preserved distal
172 edge of the tooth is straight and has six equally spaced denticles. The basalmost denticle is
173 approximately 0.3 mm in apicobasal height. The apical-most denticle is 0.2 mm in height. Above the
174 apical-most denticle there is a thin ridge of enamel. Since the tooth has been worn and was shed
175 during life, it is damaged at the mesial and distal surfaces near the apex. This precludes determining if
176 additional denticles may have been present higher on the distal side. This is not possible to evaluate

177   at this time due to the premortem and postmortem wear of the tooth. The preserved posterior
178   denticles possess smaller accessory serrations. Most of these are worn but one denticle preserves
179   four accessory denticles on the basal edge and three on the apical edge (see Figure 7).
180   The figured mesial edge of the tooth possesses a ridge that is expanded 2 mm from the base
181   of the crown, approximately to the level of the last distal denticle. Very fine (<0.1 mm) denticles cover
182   the mesial edge of this ridge that extends for 1 mm. Below this ridge the crown's enamel is intact and
183   does not possess denticles, indicating this is the natural termination of this ridge (Figure 8). The
184   mesial denticles do not appear to possess accessory denticles, unlike what has been reported from
185   other specimens of *Crosbysaurus* (Heckert 2004).
186
187   **DISCUSSION**
188
189   **Taxonomic Affinities**
190
191   MNA V10666 differs from most described Triassic teeth with subdivided denticles assigned to
192   herbivorous taxa in several features. It differs from the teeth of *Revueltosaurus*, the most commonly
193   reported leaf-shaped-tooth in the Late Triassic of North America (Hunt, 1989; Heckert, 2002; Parker et
194   al., 2005), by being labiolingually narrower. The teeth of *Revueltosaurus* are also mesiodistally
195   broader compared to their apical-basal height. *Revueltosaurus* is now known from non-dental remains
196   (Parker et al. 2005) and the tooth variation documented in the premaxilla, maxilla, and dentary do not
197   match any teeth reported as *Crosbysaurus* (Irmis et al., 2007). This holds true for MNA V10666 as
198   well; there appears to be no place in the dentition of *Revueltosaurus* for a tooth with the morphology of
199   the described specimen.
200   *Krzyzanowskisaurus hunti* (Heckert, 2005) was originally named as a species of
201   *Revueltosaurus* by Heckert (2002) based mainly on the presence of a cingulum on the tooth crown,
202   separating it from the congeneric *R. callenderi*. After it was recognized that *R. callenderi* is in fact a
203   pseudosuchian (Parker et al., 2005; Irmis et al., 2007), Heckert (2005) erected a new genus.
204   Specimens formerly assigned to *R. hunti* were placed in this new genus, *Krzyzanowskisaurus*. At the
205   time the change was done it was thought that *K. hunti,* represented a possible ornithischian (Heckert,
206   2005) but work by other authors (Irmis et al., 2007) challenged both its validity and its assignment to
207   dinosauria. It is outside the scope of this paper to analyze the validity or affiliations of other Triassic
208   tooth-based taxa. Regardless of the affinities of *K. hunti* it is clear that MNA V10666 does not possess
209   a cingulum (Figure 3). As such MNA V10666 cannot be referred to *Krzyzanowskisaurus*.
210   MNA V10666 differs from the Triassic tooth-based taxon *Tecovasaurus* in several ways. The
211   teeth of *Tecovasaurus* tend to be much shorter and broader (Hunt and Lucas, 1994) as compared to
212   MNA V10666 specifically, as well as to *Crosbysaurus* generally. Mesial denticles in *Tecovasaurus*
213   tend to be large and coarse while being more numerous than those on the distal edge of the tooth
214   (Heckert 2004). In contrast, in MNA V10666 the preserved distal denticles are much coarser than
215   those along the mesial edge (Figure 6).
216   *Lucianosaurus wildi* (Hunt and Lucas, 1994) is another Late Triassic tooth-based taxon. Irmis
217   et al. (2007) suggest it is an archosauriform though it was originally described as an ornithischian
218   dinosaur. The holotype and referred specimen of *L. wildi* are dissimilar to MNA V10666 in that they
219   possess finer denticles on both their mesial and distal edges. In addition, the tooth crowns of *L. wildi*
220   are mesiodistally deeper than what is seen in MNA V10666. MNA V10666 is further differentiated by

221   the steep mesial and distal edges that are nearly straight, compared to the low-angle convex edges of
222   *L. wildi*.
223   The teeth of an unnamed taxon from the Owl Rock Member of the Chinle Formation of Arizona
224   was described and figured by Butler et al. (2006). MNA V10666 differs from this unnamed taxon in
225   several ways. The distal denticles of MNA V10666 are subdivided into multiple accessory denticles,
226   unlike the simple cleft of the unnamed taxon. The mesial denticles of MNA V10666 are much smaller,
227   not subdivided, and do not run to the base of the crown. The unnamed taxon is also much more
228   symmetrical mesiodistally than MNA V10666.
229   *Protecovasaurus lucasi* (Heckert 2004) differs from MNA V10666 because in the former the
230   mesial and distal denticles are roughly equivalent in size and number. Indeed, no teeth reported for
231   *Protecovasaurus* match the morphology seen in MNA V10666. Since non-dental fossils are not known
232   for this or any other of the previously supposed ornithischians from the Triassic of North America it is
233   not possible to rule out positional or ontonogenic variation accounting for the morphological distance
234   between MNA V10666 and these taxa. Given the homodonty present in most basal archosaurs and
235   archosauriformes it is unlikely that MNA V10666 represents any of the tooth-based taxa reported from
236   the Late Triassic of North America.
237   MNA V10666 closely matches the published illustrations and descriptions of *Crosbysaurus*
238   *harrisae* (Heckert, 2004). The complex distal denticles with multiple accessory serrations, are an
239   autapomorphy of *Crosbysaurus* (Heckert, 2004: 67, 68). None-the-less, several differences exist
240   between MNA V10666 and all other described specimens that warrant some discussion.
241   Teeth referred to *Crosbysaurus* by other workers fall into two morphotypes: labiolingually
242   compressed and highly recurved or basally wide and moderately recurved (see Heckert, 2004: 67,
243   68). MNA V10666 falls into neither category. It is labiolingually compressed, especially compared to
244   other *Crosbysaurus* teeth in the literature, but without being recurved. This tooth lacks the labial bulge
245   found in other specimens referred to *Crosbysaurus.* The distal denticles bear fewer accessory
246   serrations than any other teeth referred to *Crosbysaurus*. The mesial denticles are much smaller, not
247   compound, and are not found along the complete length of this tooth.
248   It is tempting to think that these differences may be systematically significant. However, we
249   refrain from using these differences to taxonomically segregate MNA V10666 from other
250   *Crosbysaurus* specimens for several reasons. The sample size from Utah is low (n=1) and individual
251   variation within this taxon has not been quantified. In addition we lack any other body fossil remains
252   from *Crosbysaurus* and it is currently unknown the dental variation along the tooth row, if present.
253   Coupled with the taxonomic and systematic problems associated with *Revueltosaurus* (Hunt, 1989;
254   Hunt and Lucas, 1994; Heckert, 2002; Parker et al., 2005; Heckert, 2005; Irmis et al., 2007; Heckert et
255   al., 2012), a taxon whose relationships have been radically altered by the discovery of body fossils, we
256   refrain from adding to the confusing plethora of tooth taxa known from the Late Triassic of North
257   America.
258   Previous authors have suggested that *Crosbysaurus* is useful as a biostratigraphic index taxon
259   of the St. Johnsian division of the Adamanian Land Vertebrate Faunachron assemblage (late Carnian-
260   early Norian in age) (Heckert and Lucas, 2006). If these previous workers are correct MNA V10666
261   may provide an important lower limit on the age of the Chinle Formation at Comb Ridge, an area that
262   has received almost no paleontological and very little stratigraphic work in the past.
263
264   **CONCLUSIONS**

265

266 The discovery of *Crosbysaurus* from the Chinle Formation of southeastern Utah extends the
267 geographic range of this taxon northward by approximately 250 kilometers. *Crosbysaurus* was
268 apparently a rare, but widespread taxon during the Chinle Formation deposition times. The single
269 tooth crown recovered from Utah (MNA V10666) bears unique morphological characteristics that
270 separate it from other described specimens of *Crosbysaurus,* as well as from other contemporaneous
271 herbivorous archosaurs such as *Revueltosaurus callenderi*. These characters may represent various
272 tooth positions within the jaw of *Crosbysaurus*, variation between individuals, or taxonomic
273 differences. The sample size and preservation of known specimens of *Crosbysaurus* does not allow
274 us to discriminate between these sources of variation at this time so we refrain from making any
275 statements about what the primary cause is. It is hoped that future work by Mission Heights' field
276 crews can help to better clarify the stratigraphic and taxonomic relationships of this enigmatic
277 archosauriform.

278

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280

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290

291 **REFERENCES**

292

293 Bennett HS. 1955. *Photogeologic map of the Elk Ridge-15 [Hotel Rock] quadrangle, San Juan*
294 *County, Utah.* Geologic Map, Salt Lake City: Utah Geological Survey.

295

296 Butler RJ, Porro LB, Heckert AB. 2006. A supposed heterodontosaurid tooth from the Rhaetian of
297 Switzerland and a reassessment of the European Late Triassic record of Ornithischia
298 (Dinosauria). *Neues Jahrbuch für Geologie und Paläontologie: Monatshefte* **10**:613-633.

299

300 Flynn JJ, Nesbitt SJ, Parrish JM, Ranivoharimanana L, Wyss AR. 2010. A new species of
301 Azendohsaurus (Diapsida: Archosauromorpha) from the Triassic Isalo Group of southwestern
302 Madagascar: cranium and mandible. *Palaeontology* **53**(3):669-688

303

304 Gauthier JA. (1986). "Saurischian monophyly and the origin of birds." In *The Origin of Birds and the*
305 *Evolution of Flight*, edited by Padian, K.*,* 1-55 *Memoirs of the California Academy of Sciences 8* San
306 Francisco, California: California Academy of Sciences.

307

Heckert AB. 2002. *A revision of the Upper Triassic ornithischian dinosaur Revueltosaurus, with a description of a new species.* Vol. 21, in *Upper Triassic Stratigraphy and Paleontology*, edited by A. B. Heckert and S. G. Lucas, 253-268. Albuquerque, New Mexico: New Mexico Museum of Natural History and Science.

—. 2004. *Late Triassic microvertebrates from the lower Chinle (Otischalkian-Adamanian:Carnian), southwestern U.S.A.* Vol. 27. Albuquerque, New Mexico: New Mexico Museum of Natural History and Science.

—. 2005. *Krzyzanowskisaurus, a new name for a probable ornithischian dinosaur from the Upper Triassic Chinle Group, Arizona and New Mexico, USA.* Vol. 29, in *Vertebrate Paleontology in Arizona*, edited by A. B. Heckert and S. G. Lucas, 77-83. Albuquerque: New Mexico Museum of Natural History and Science.

Heckert AB, Lucas SG. 2006. *Micro- and small vertebrate biostratigraphy and biochronology of the Upper Triassic Chinle Group, southwestern USA.* Vol. 37, in *The Triassic-Jurassic Terrestrial Transition*, edited by J. D. Harris, S. G. Lucas, J. A. Spielmann, M. G. Lockley, A. R.C. Milner and J. I. Kirkland, 94-104. Albuquerque, New Mexico: New Mexico Museum of Natural History and Science.

Heckert AB, Mitchell JS, Schneider VP, Olsen PE. 2012. Diverse new microvertebrate assemblage from the Upper Triassic Cumnock Formation, Sanford Subbasin, North Carolina, USA. *Journal of Vertebrate Paleontology* **86**(2):368-390.

von Huene F. 1946. Die grossen Stamme der Tetrapoden in den geologischen Zeiten. *Biologisches Zentralblatt.* **65**(7/12):266-275

Hunt AP. 1989. "A new ?ornithischian dinosaur from the Bull Canyon Formation (Upper Triassic) of east-central New Mexico." In *Dawn of the age of dinosaurs in the American Southwest*, edited by S. G. Lucas and A. P. Hunt, 355-358. Albuquerque, New Mexico: New Mexico Museum of Nature and Science.

Hunt AP Lucas SG. 1994. "Ornithisichian dinosaurs from the Upper Triassic of the United States." In *In the shadow of the dinosaurs: Early Mesozoic tetrapods*, edited by H. -D. Sues and N. C. Fraser, 227-241. Cambridge, Massachusetts: Cambridge University Press.

Irmis RB. Parker WG, Nesbitt SJ, Liu J. 2007. "Early ornithischian dinosaurs: the Triassic record." *Historical Biology* **19**(1):3-22.

Lucas SG, Heckert AB, Estep JW, Anderson OJ. 1997. Stratigraphy of the Upper Triassic Chinle group, four corners region. *New Mexico Geological Society Guidebook* **48**:81-107.

Martz JW, Irmis RG, Milner ARC. 2014 Lithostratigraphy and biostratigraphy of the Chinle Formation (Upper Triassic) in southern Lisbon Valley, southeastern Utah. *In* UGA Publication 43 (2014)—Geology of Utah's Far South, 397-446.

352

353 Molina-Garza RS, Geissman JW, Lucas SG. 2003. Paleomagnetism and magnetostratigraphy of the
354 lower Glen Canyon and upper Chinle Groups, Jurassic-Triassic of northern Arizona and northeast
355 Utah. *Journal of Geophysical Research: Solid Earth* **108**(B4).

356

357 Nesbitt SJ, Irmis RB, Parker WG. 2007. A critical re-evaluation of the Late Triassic dinosaur taxa of
358 North America. *Journal of Systematic Paleontology* **5**(2):209-243.

359

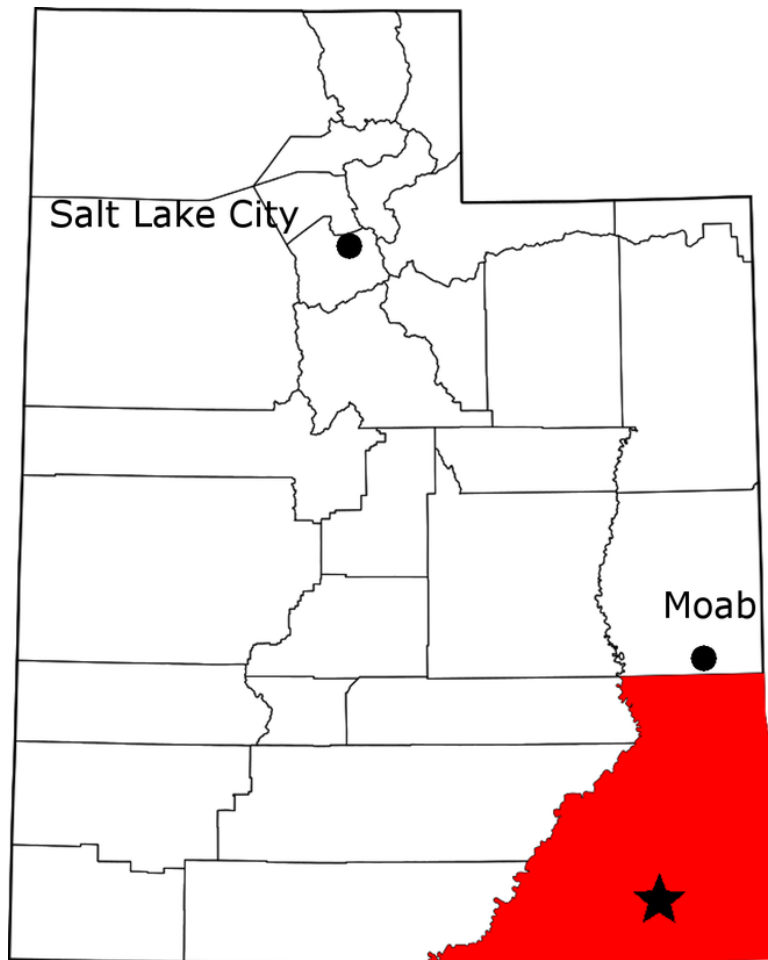
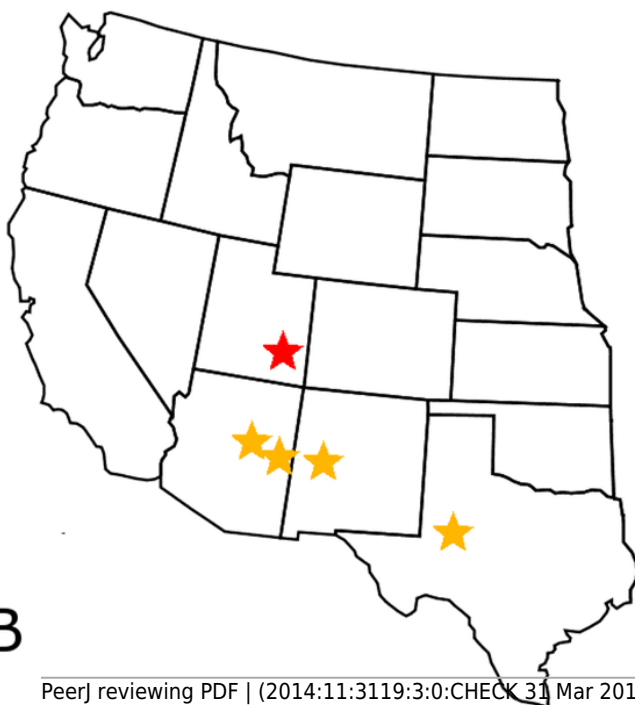
360 Osborn HF. 1903. On the primary division of the Reptilia into two sub-classes, Synapsida and
361 Diapsida. *Science* **17**(424):275-276.

362

363 Parker WG, Irmis RB, Nesbitt SJ, Martz JW, Browne LS. 2005. "The Late Triassic pseudosuchian
364 *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs."
365 *Proceedings of the Royal Society B* 272 **1566**:963-969.

1

Crosbysaurus localities in the western United States.

Figure 1: Map showing A) the location of MNA Locality 1725, The Hills Have Teeth (starred), San Juan County (highlighted), Utah, USA; B) the location of MNA locality 1725 (red) relative to previously reported *Crosbysaurus* sites (yellow) in the western United States.

A

B

2

The Hills Have Teeth locality photo

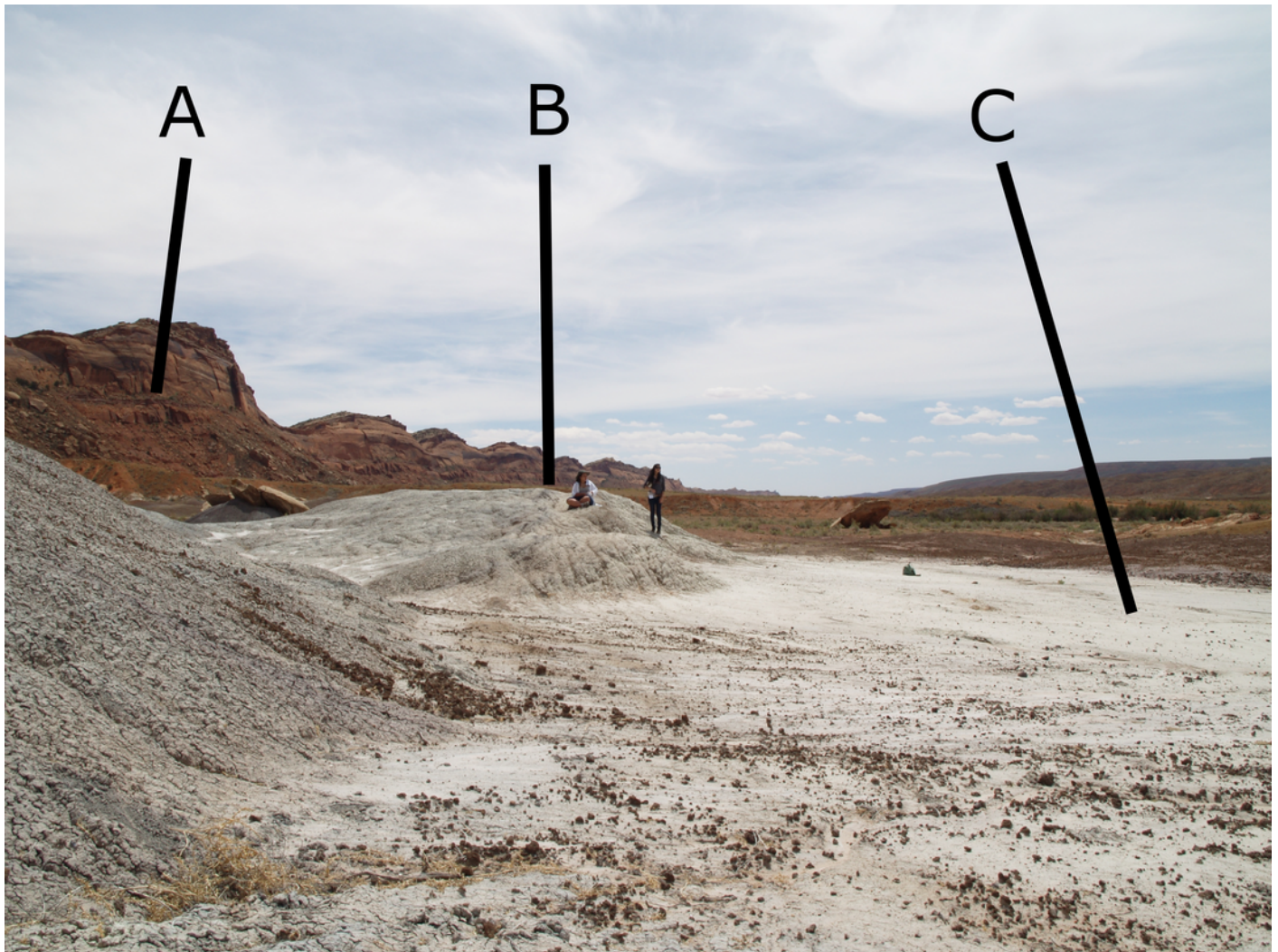
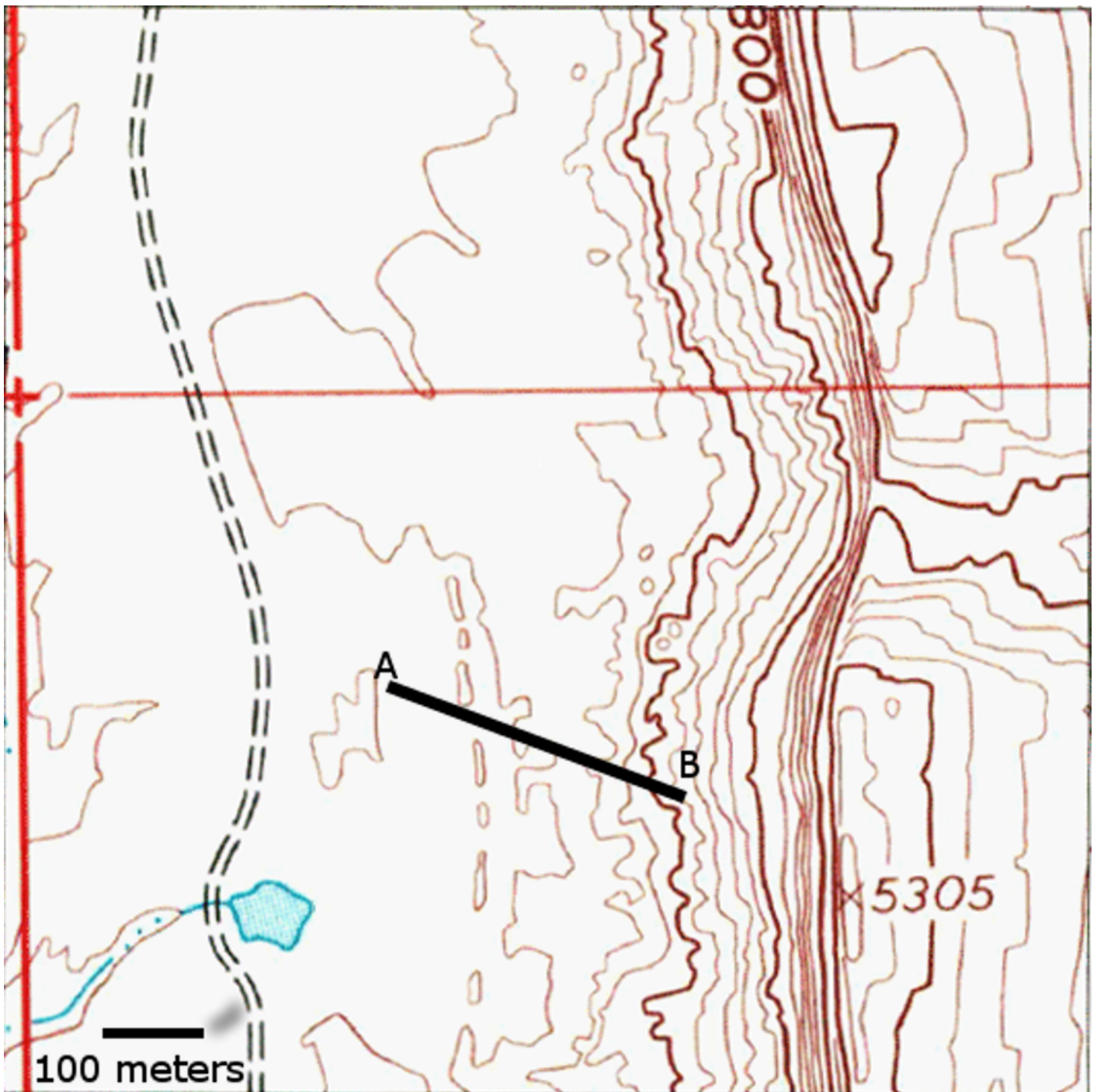
Figure 2: MNA Locality 1725, showing relative stratigraphic position of MNA V10666 to the surrounding sediments. A) Top of the Chinle Formation at Comb Ridge; B) The second author sitting at The Hills Have Teeth (MNA Locality 1724) C); location where MNA V10666 was discovered.

Location of Stratigraphic Section

Figure 3: Location of measured stratigraphic section in Figure 4. North is to the top of the figure. Topographic map data from USGS. Scale bar = 100 meters.

4

Stratigraphic column of the Chinle Formation at The Hills Have Teeth

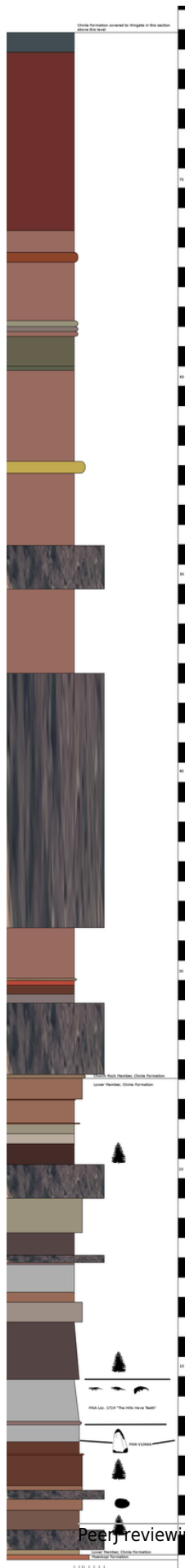
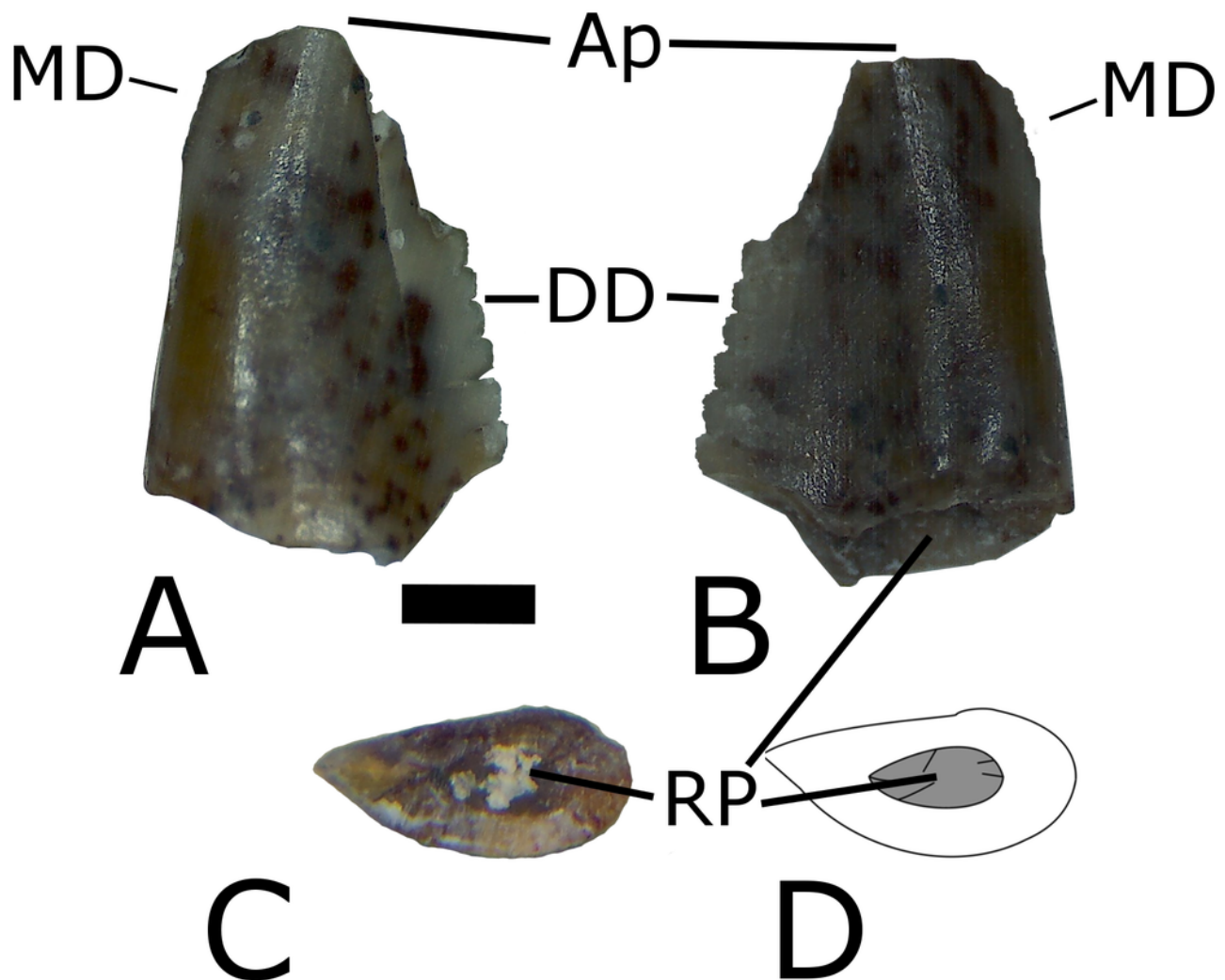
Figure 4: Measured section through the Chinle Formation exposed at The Hills Have Teeth locality. MNA V10666 is represented here by an outline diagram. Scale bar = 1 meter. Organism silhouettes from Phylopic by Dmitry Bogdanov, Nobu Tamura, Scott Hartman, and Robert Gay.

Multiple views of MNA V10666 (*Crosbysaurus* sp.)

Figure 5: MNA V10666, *Crosbysaurus* sp., from MNA Locality 1725 in A), presumed labial, B), presumed lingual and C), basal views. D) Interpretive drawing in basal view showing resorption pit. Abbreviations: Ap, apex; DD, distal denticles; MD, mesial denticles; RP, resorption pit. Scale = 1 mm.

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Line drawing of MNA V10666 (*Crosbysaurus* sp.)

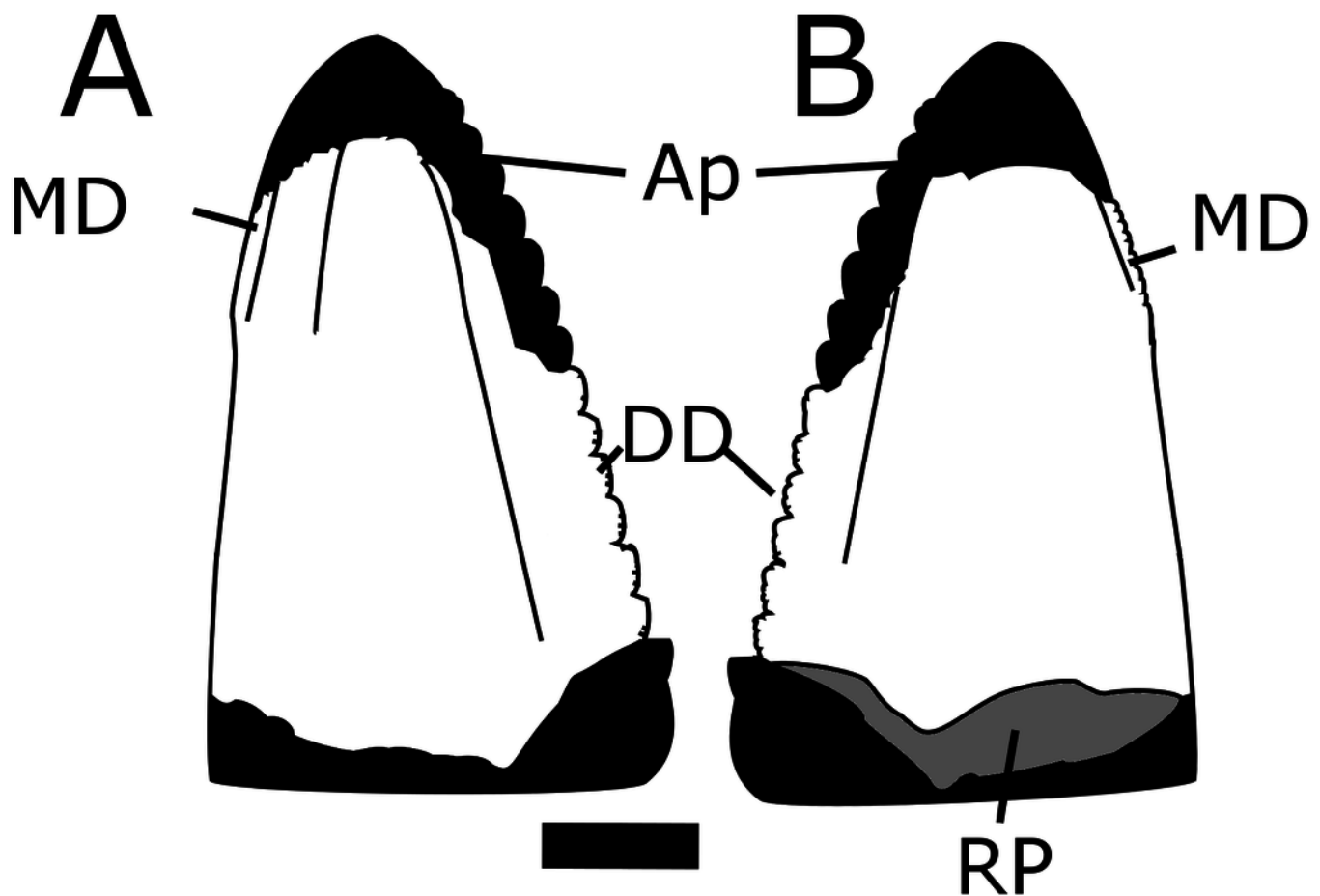
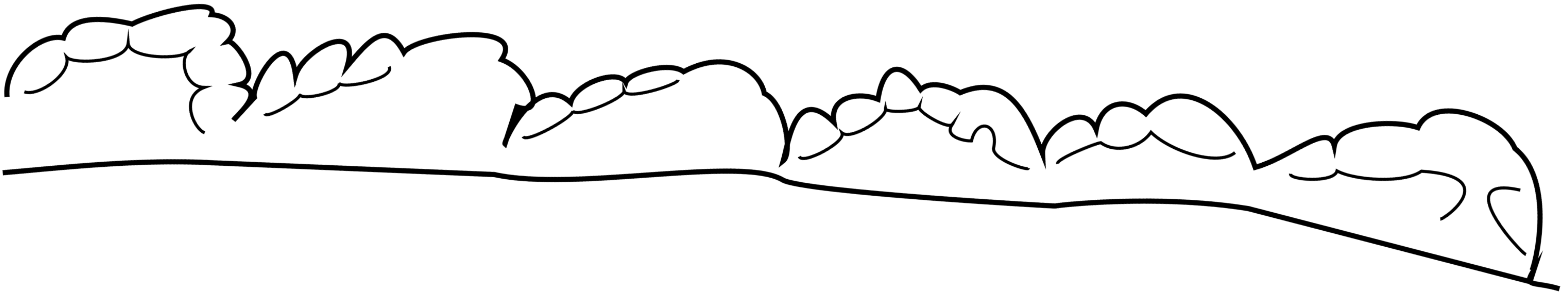
Figure 6: Interpretive line drawing of MNA V10666, *Crosbysaurus* sp., from MNA Locality 1725 showing the outline of the tooth if complete and the surface anatomy of the preserved crown. A) presumed labial B) presumed lingual views. Abbreviations: Ap, apex; DD, distal denticles; MD, mesial denticles; RP, resorption pit. Scale = 1 mm.

Line drawing of MNA V10666 (*Crosbysaurus* sp.) distal denticles.

Figure 7: Line drawing of the distal denticles of MNA V10666, Crosbysaurus sp., from MNA Locality 1725. Apex is to the right, the base is to the left. Scale = 1 mm.

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Mesial carina in mesial view of MNA V10666 (*Crosbysaurus* sp.)

Figure 8: Photograph and interpretive line drawing of the mesial carina of MNA V10666, *Crosbysaurus* sp. The apex of the tooth is at the top of the image. Scale bar = 1 mm.