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**Faunal Composition and Significance of High Diversity, Mixed Bonebeds Containing
Agujaceratops mariscalensis and other Dinosaurs, Aguja Formation (Upper Cretaceous),
Big Bend, Texas**

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RH: Bonebeds and *Agujaceratops* in Big Bend

Abstract

New sedimentologic and paleontologic information are presented from multiple, closely associated mixed bonebeds in the Aguja Formation (Campanian) from the Big Bend area of Texas. These bonebeds appear to have been deposited as component parts of channel lags during major flooding events. One of these bonebeds yields the most complete skull of *Agujaceratops mariscalensis*. Correlation of paleosols in the bonebed sections with those from the well studied Dawson Creek section (Big Bend), provides a critical stratigraphic context for *A. mariscalensis* and these bonebeds.

Cumulatively, all the sites yield a rich assemblage of plants, invertebrates and other vertebrates. The combined vertebrate assemblage provides a means of assessing local terrestrial-community composition in the Late Cretaceous in Big Bend, and for comparing Late Cretaceous southern faunas with those of comparable age from Montana and Alberta.

Introduction

Big Bend National Park, Texas, is the southernmost area in the United States that yields Upper Cretaceous macrofossil dinosaur remains, as well as rich and diverse vertebrate microfossil assemblages. Although this area contains unique vertebrate assemblages, much less is known about them than those of similar age from regions farther north in Montana and Alberta. The most-complete skull of the ceratopsian *Agujaceratops mariscalensis* (originally *Chasmosaurus mariscalensis* [Lehman 1989]) was collected from a mixed bonebed in the late Campanian upper Aguja Formation at Rattlesnake Mountain in Big Bend. However, to date, only a few associated fossils have been described from this site, and no sedimentological and taphonomic information have been presented. Since discovery of the skull, hundreds of dinosaur teeth, bones, and

eggshell pieces have been collected from this site and another mixed bonebed that overlies the site. These sites and their assemblages are described here, with special emphasis on the dinosaurs. The dinosaur component is particularly rich and is emphasized here because of the biogeographic and biostratigraphic utility of comparing these large terrestrial vertebrates within North America (see Sampson and Loewen this volume). Most notably, these dinosaur assemblages include: 1) teeth and bones from hatchling dinosaurs (abundant hadrosaurs and less common ceratopsians and ankylosaurs); 2) postcranial bones and teeth from tyrannosaurids, dromaeosaurids, and ornithomimids; and 3) more than 300 dinosaur eggshell fragments from six different eggshell morphotypes.

In combination, all of these data provide a glimpse of the paleoenvironment and paleocommunity of which *Agujaceratops mariscalensis* was a part, and provide opportunities for comparisons with other Late Cretaceous fossil assemblages.

Background

Big Bend National Park, Texas

Shoreline, coastal plain, and alluvial sediments were deposited in the Tornillo Basin of west Texas during the Late Cretaceous - Paleocene (Figs. X.1, X.2). These deposits are now exposed in Big Bend National Park. This is a unique terrestrial record because it contains the southern most Late Cretaceous (latest Campanian) through Paleocene terrestrial deposits with vertebrates from the U.S.A. (Lehman 1985; Standhardt 1986, 1989; Schiebout et al. 1987; Sankey 1998, 2006, 2008; Nordt et al. 2003; Sankey et al. 2007a, b).

Previous investigations of the latest Campanian through Paleocene alluvial deposits and their paleosols exposed at Dawson Creek in Big Bend have resulted in the development of a

high-resolution stratigraphic and paleoclimatic framework that includes temperature and rainfall estimates (Fig. X.2; Nordt et al. 2003; Atchley et al. 2004). The *A. mariscalensis* “mixed bonebed” at Rattlesnake Mt. is correlated to the Dawson Creek section in this paper. Importantly, the Dawson Creek section is currently the only terrestrial section known that records *both* the middle and late Maastrichtian greenhouse episodes (Nordt et al. 2003). Additionally, the Tornillo Basin contains an excellent record of the effects of the Western Interior Seaway’s sea level fluctuations on alluvial deposits. The distance between the shoreline and the Tornillo Basin fluctuated from 100 to 500 km during the latest Campanian through early Paleocene, and was less than 100 km away during deposition of the Rattlesnake Mt. bonebeds during the late Campanian (Atchley et al. 2004).

< FIGURES 1 and 2 HERE >

Big Bend Dinosaurs

Lehman (1997) recognized differences among the late Campanian dinosaur faunas within the Western Interior of North America and named the southern biogeographic province the “*Kritosaurus* fauna.” Sullivan and Lucas (2006) argued that this apparent provincialism might be a result of comparing northern and southern faunas of slightly different ages, and they assigned the upper Aguja Formation vertebrate assemblages to the recently named Kirtlandian Land Vertebrate Age (LVA), which spans the time between the Judithian and Edmontonian LVA. However, the age of the Aguja is not well enough constrained to test Sullivan and Lucas’s idea (2006) (see Lehman et al. 2006 for a detailed discussion about the age of the Aguja and Javelina Formations).

In terms of numbers and completeness of specimens and diversity of taxa, much less is known about the dinosaurs from the “*Kritosaurus* fauna” compared to its northern counterpart,

the “*Corythosaurus* fauna,” from Alberta, Montana, Wyoming, and northern Colorado. It is of considerable interest then that the Big Bend fossil assemblages contain some of the southernmost dinosaurs of the “*Kritosaurus* fauna.”

Based on the presence of abundant soil nodules, this area had dry seasons at least as early as the late Campanian, with more intense and frequent dry seasons in the Maastrichtian. During the Late Cretaceous, Big Bend vertebrates were probably better adapted to dry paleoenvironments than their northern counterparts (Sankey 1998, 2001).

One of the dinosaur taxa unique to Big Bend is the ceratopsian, *Agujaceratops mariscalensis* (Lucas et al. 2006). In Big Bend, it is common in the late Campanian Aguja Formation, and is often associated with coastal floodplain sedimentary deposits. In fact, all but one specimen have been found from coastal plain deposits in the lower part of the upper shale member of the Aguja, and *A. mariscalensis* may have preferred densely vegetated marshy areas (Lehman 2007). Associated skeletons and isolated bones of *A. mariscalensis*, the hadrosaur *Kritosaurus*, ankylosaurs, and tyrannosaurids have been collected from bonebeds in the upper Aguja near Talley Mountain. These bonebeds may have formed during droughts when the dinosaurs accumulated at watering holes, the skeletons were exposed and trampled, and then were transported and buried during subsequent floods (Lehman 1982, 1989; Davies and Lehman, 1989).

Microvertebrate Sites

Although the large dinosaurs from Big Bend, such as *A. mariscalensis* and *Kritosaurus*, have been described based on material from the Talley Mountain bonebeds, considerably less is known about the rarer dinosaurs in the assemblage, such as the theropods, especially compared

to the northern fauna. Additionally, little is known about baby dinosaurs and nesting sites in Big Bend. However, in Big Bend, screening and surface collection of microsites has yielded numerous teeth from baby dinosaurs and from theropods. These sites have also produced thousands of teeth and/or small bones of other vertebrates, such as sharks and rays, amphibians, lizards, turtles, crocodylians, pterosaurs, and mammals (Standhardt 1986; Rowe et al. 1992; Cifelli 1995; Schiebout 1997; Sankey 1998, 2001, 2005, 2006, 2008; Schiebout et al. 1998; Sankey and Gose 2001; Sankey et al. 2005b; Welsh 2005; Nydam et al. 2007; Welsh and Sankey 2008).

For example, microvertebrate sites associated with the Talley Mountain bonebeds have produced more than 3,000 specimens from 38 vertebrate taxa, and clarified the age and paleoecology of these deposits (Sankey 1998, 2005, 2008; Sankey and Gose 2001). The dinosaur teeth include those from baby hadrosaurs, ceratopsians, pachycephalosaur, and theropods (*Saurornitholestes*, *Richardoestia*, and tyrannosaurid), have been described in detail, and have been used to document that nesting sites occurred in Big Bend (Sankey 2001).

One advantage of microsites is that they can yield large samples, the size of which are important because: (1) typically rare fossils, such as mammal teeth, are present and can provide important biostratigraphic information (Sankey 1998; Sankey and Gose 2001); (2) teeth of small sharks and rays can be recovered, which can document marine influences (Sankey 1998, 2005, 2008); and (3) unusual paleoecological information can be obtained. For example, small teeth from juvenile dinosaurs and dinosaur eggshell fragments were the first evidence that dinosaurs nested in the Big Bend area (Standhardt 1986; Sankey 2001; Sankey et al. 2005b; Welsh 2005; Welsh and Sankey 2008).

Additionally, unlike rarer macrofossil bonebed sites, the abundance of microsites in Big Bend allows them to be sampled from numerous different stratigraphic intervals. Comparison and stratigraphic analyses of Big Bend microsite assemblages and their associated facies also provide detailed information about how Late Cretaceous paleoenvironments and paleocommunities changed through time (Brinkman 1990; Sankey et al. 2005b; Brinkman et al. 2007). For example, stratigraphic analyses of five microsite horizons in the upper Aguja near Talley Mountain and from a sample of 3,349 specimens, show that up section, sharks and rays decrease in abundance, thus reflecting the eustatic drop in sea level that occurred at the Campanian/Maastrichtian boundary (Sankey 1998, 2008).

Another advantage of microsites is that large sample sizes can be compared between geographically separate areas in order to determine biogeographic differences (Brinkman et al. 2007). For example, theropod teeth recovered from the Talley Mountain microsites are distinct from northern faunas, at least at the species level, and theropods in Big Bend were possibly less diverse (Sankey 2001).

The *A. mariscalensis* skull from Rattlesnake Mountain was collected from a “mixed bonebed” (defined by Eberth et al. 2007 as containing vertebrate microfossils and macrofossils). Hundreds of small teeth and bones from dinosaurs were collected from this site and those closely associated with it. The dinosaurs are described here, which is important because: 1) the dinosaurs associated with *Agujaceratops mariscalensis* are not well known, and 2) from this large sample, rare specimens were found such as eggshells, bones and teeth from hatchlings, and rare dinosaurs such as ankylosaurs and theropods. These data fill an important gap in our knowledge about the dinosaurs in Big Bend in general and the dinosaurs associated with *Agujaceratops mariscalensis*

in particular. Together these data represent an important baseline for future biogeographic and comparative stratigraphic studies.

Materials and Methods

The measured section was trenched to unweathered rocks (approximately 0.5 meters). Beds were measured using a hand level and a Jacob's Staff marked with centimeter gradations. Rock and paleosol color designations were assessed using a GSA rock color chart (GSA 1991). Most fossils were surface collected. Some fossils were collected in situ. A sample of sediment from the bonebeds was wet screened and picked for small fossils, using a microscope. All fossils are curated in the Louisiana State University Museum of Natural Science (LSUMNS) Geology Collections in Baton Rouge. Locality data are also on file at that institution. A complete LSUMNS catalog number contains the locality and specimen numbers, separated by a colon (e.g. 834:17621). Most fossils were coated with vaporized ammonium chloride and photographed using a Nikon E995 with a Nikkor lens, attached to a Wild Leitz MSC microscope.

Results

Rattlesnake Mountain Microsites

In 1991, the most complete skull of an *Agujaceratops mariscalensis* was collected from the upper Aguja at Rattlesnake Mountain (Texas Memorial Museum 43098-1; Forster et al. 1993). Forster et al. (1993) described the skull as appearing to be from a mature individual based on the level of ossification of the cranial sutures. Lehman (2007) noted that the skull was from stream channel deposits, which agrees with the interpretations presented in Sankey et al. (2007a,

b) and here. Interestingly, the skull is the only specimen of an *Agujaceratops* that has been found from deposits other than coastal marsh and swamp deposits (Lehman 2007).

From 2002 to 2007, intensive surface collection from the microvertebrate sites preserved in the same deposits that contained the skull yielded thousands of vertebrate and other fossils, and is now one of the largest collections of fossils from the upper Aguja Formation in terms of numbers of specimens and diversity of taxa (Table X.1). Fossils include snails, vertebrate coprolites, fish (gar), salamander, lizard, turtle, crocodylian, pterosaur, dinosaur, bird, and mammal (Sankey 2005, 2006; Gasaway et al. 2007). Study of the salamander, lizard, and crocodylians are in progress. However, the turtle and dinosaur eggshell specimens have been studied and described in detail, including counts of specimens, and those findings are summarized below.

Turtle shell fragments are the most common fossils, and hundreds of specimens have been collected. Taxa include Baenidae indet., cf. *Hoplochelys*, *Adocus*, *Basilemys*, and cf. *Helopanoplia* and other trionychids. From a study of 388 turtle specimens collected primarily from these microsites, trionychids are the most abundant (81%), with other taxa considerably less common: *Adocus* (6%), *Basilemys* (6%), baenids (5%), and kinosternoids (1%; Sankey 2006). Compared to the turtle diversity in the overlying, more inland, Maastrichtian-aged Javelina Formation (Tomlinson 1997), turtles were more diverse in the Aguja Formation, probably reflecting a warmer and wetter climate (Sankey 2006).

In 2002, Ed Welsh recognized and collected dinosaur eggshell fragments from the microsites (Welsh 2005). During 2005 and 2006 we increased this sample to over 300 dinosaur eggshell fragments; all are described by Welsh and Sankey (2008). Six different eggshell morphotypes are present, including those from ornithischian and theropod dinosaurs. The six

morphotypes include dinosauroid spherulitic, dinosauroid prismatic, cf. ornithoid prismatic, ornithoid ratite, and two types tentatively referred to the oogenera *Continuoolithus* and *Porituberoolithus* (Welsh 2005; Welsh and Sankey 2008). Many of the eggshells have spherulitic shell units, typical of hadrosaur eggs and some eggshells have a mammillary layer and continuous layer, typical of theropods. Many of the eggshells have the angusticaniculate type of pore canal system, common in eggs from arid environments (Mikhailov 1997; Carpenter 1999). Importantly, the eggshells do not closely match any eggshell types from contemporaneous northern faunas (Zelenitsky et al. 1996), further supporting one of these conclusions proposed here and previously on the basis of teeth that Big Bend dinosaurs were distinct, at least at the species level, from those in northern faunas (Sankey 2001; Sankey et al 2005b). Based on the variety of eggshell morphotypes in the microsites, it seems reasonable to conclude that a variety of dinosaurs either nested together or that their nesting sites were in close proximity (Welsh 2005; Welsh and Sankey 2008).

Sankey et al. (2005b) described the theropod teeth made during the initial (2002) surface collection of these microsites, in addition to the theropod teeth collected from the Maastrichtian-aged uppermost Aguja and Javelina formations (Standhardt 1986), and noted differences between the Campanian and Maastrichtian theropods in Big Bend. However, since this initial report, hundreds of additional dinosaur teeth have been collected, including numerous teeth from embryonic and hatchling hadrosaurs, and lesser amounts from hatchling ceratopsians, ankylosaurs, and theropods. These are described here. Dinosaur teeth are difficult to age, so the term hatchling is used here to refer to teeth less than 15% adult size; these are assumed to be from individuals that are less than two years old, following Lehman (2007).

< TABLE 1 HERE >

Sedimentology and Stratigraphy. The Rattlesnake Mountain microsites are hosted by grey, organic-rich silty mudstones. Sediments have abundant tiny fragments of coalified plants, large pieces of burned wood, and large and small isolated bones. The microsites are located approximately ten meters below the first moderately-developed paleosol in the inland floodplain facies of the upper shale member of the Aguja in the Rattlesnake Mountain area (Sankey et al. 2007a, b, in prep). The microsites were correlated to the base of the Dawson Creek section, 7 km to the north of Rattlesnake Mt., using paleosols. We were able to correlate the paleosols directly above the Rattlesnake Mt. microsites to paleosols #42 and #43 at the base of the well studied Dawson Creek section (Nordt et al. 2003). Our correlations were based on similarities in paleosol morphology, and carbon and oxygen isotope values (Sankey et al. 2007a, b, in prep). In addition to similarities in paleosol morphology and color, the carbon and oxygen ratios from the carbonate soil nodules in the Rattlesnake Mt. paleosols are similar to those from the Dawson Creek paleosols #42 and #43 (Sankey et al. 2007a, b, in prep.).

The “Purple Hill” section is 11.4 meters thick (Fig. X.3) and begins at the base of the southern tip of the small hill (locality VL-842). The lower one meter contains light olive grey (5Y 5/2), poorly sorted, moderately well indurated, muddy sandstone with abundant clay balls, pedogenic carbonate nodules, small plant fragments, snails, and small and large vertebrate bones (Bonebed #1; Fig. X.3). The deposits fine and lighten in color upwards, with less plant and bone material in the uppermost 0.9 meters. The section continues at the southern base of “Purple Hill” (locality VL-747). Between the 2.5 and 4.5 meter level are medium-dark grey (N4), muddy sandstones, with abundant clay balls, pedogenic carbonate nodules, small plant fragments, snails, and small and large vertebrate bones (Bonebed #2; Figs. X.3, X.4A). Between the 4.5 and 6 meter level are coarser and lighter-colored sands (10 YR 6/6), with common gypsum casts of

large wood and bones (Fig. X.4B, C). From the 6 to 7.7 meter level are yellowish grey (5Y 7/2), moderately well cemented, muddy, fine-grained sandstones. Plant fragments, vertebrate fossils, and clayballs are absent. From the 7.7 to 10.2 meter level are mudstones, with moderately-developed paleosols. The lowest paleosol (Paleosol #1) is 1.5 meters thick, and grayish red (5R 4/2) with small areas of green staining. This is the purple stratum referred to in the name “Purple Hill,” and is easily recognized and useful for local stratigraphic correlation (Fig. X.3). Paleosol #2 (Fig. X.3) is one meter thick, brownish grey (5YR 4/1) with small areas of green staining (i.e. iron depletion due to episodic anaerobiosis). This paleosol is erosionally overlain by 1.2 meters of moderately sorted, moderately indurated, yellowish grey (SY 7/2) sandstone with rip-up clasts of the underlying green mudstone.

Most of the fossils were collected from the surface, and some were collected in situ (Fig. X.4B) from the two deposits of poorly-sorted, muddy sandstone (Bonebeds #1, #2). The *A. mariscalensis* skull site is in Bonebed #1.

< FIGURES 3 AND 4 HERE >

Depositional Environments. The “Purple Hill” stratigraphic section is interpreted as a succession of interbedded channel and over-bank deposits (Fig. X.3). The two main bone-producing deposits (Bonebeds #1, #2) are muddy sandstones at the base of their own fining upward successions, and are interpreted as fluvial channel deposits that were deposited during upper flow-regime flow. The overlying upward-fining successions of finer sandstone were probably deposited during lower energy flows.

Eberth (1990) described two main sedimentary facies in which vertebrate microfossil sites accumulated in the late Campanian beds of the Oldman and Dinosaur Park formations at Dinosaur Provincial Park, Alberta: 1) mudstone pebble intraclast deposits that formed during

high energy, in-channel flow and 2) tabular or sheet-like, interbedded siltstone/sandstones that were deposited as overbank splays. Based on the more limited sedimentary data available here, the Rattlesnake Mt. bonebeds appear to match Eberth's high energy, in-channel flow facies.

The 1.9 meter thick interval comprising stacked mudstone beds near the top of the section is interpreted as an overbank floodplain setting in which muds episodically settled out from suspension. The absence of erosional contacts and the presence of numerous moderately-developed paleosols through the interval indicate that an alluvial plain paleoenvironment was established for a considerable time in this area. However, the top paleosol is truncated by a disconformity overlain by a paleosol/mudstone-intraclast-rich sandstone. This stratigraphic arrangement indicates the start of a major channel incision perhaps due to channel avulsion into this area, or, possibly, a regional drop in relative sea level.

Systematic Paleontology

Ankylosauria Osborn 1923

Nodosauridae Marsh 1890a

cf. *Edmontonia* Sternberg 1928

(Figs. X.5, X.6)

Referred Specimens. 834:17621 and 746:17849 (osteoderms); 834:17859 (ossicle); 834:17749, 746:6271, and 746: 8439 (teeth).

Description. 8439 is a small tooth (6 mm anterior to posterior dimension and 6 mm top to base). The anterior denticles are large (1 mm in width). The surface is rugose, with coarse wrinkles. Both the lingual and labial sides have a shelf or cingulum. The anterior surface of the tooth, from tip to base, shows evidence of tooth wear. 6271 is a small, unworn tooth (8 mm from tip to base; 6 mm greatest FABL; Fig. X.6B, C). Denticles are large and pointed (4 on posterior

side and 5 on anterior side). Specimen 17749 is an extremely worn, probably digested, tooth. No denticles are present, but the typical shape of an ankylosaur tooth remains.

Specimen 17849 is a small, complete osteoderm (Fig. X.5H, I). It is oval in outline. The exterior side has a single conical point, but no keel, and the interior side is flat to slightly concave. The surface is pitted, grooved, and rugose. The edges are scalloped shaped. Specimen 17621 is a fragment of a larger osteoderm. It is 5.5 cm in diameter. The surface has deep grooves and pits. The edge is fluted and rugose. Specimen 17859 is a dermal ossicle. It is oval in outline. The surface is pitted.

Discussion. The teeth are clearly ankylosaur based on their distinctive morphology, specifically the conical shape in lateral outline; the enlarged, bulbous base; the large, pointed denticles (i.e. cusps), with the apical cusp the largest; and the teeth are slightly labially-lingually compressed. In the nodosaurids, teeth are generally bigger and often have a shelf (cingulum) at the base of the tooth crown instead of a swollen base of the crown in ankylosaurids (Carpenter 1997). Ankylosaurid teeth have smoother, less wrinkled surfaces (Carpenter 1982). (See Coombs 1990 and Carpenter 1997 for descriptions of ankylosaur teeth).

Both of the two unworn Big Bend teeth have a cingulum, although it is larger in specimen 8439, and both have surfaces that are wrinkled and rugose. The teeth more closely resemble those of nodosaurids than of ankylosaurids.

The scutes of ankylosaurs are typically flat or keeled in the neck and shoulder regions and over the back and tail, scutes are smaller and keeled (Carpenter 1997). Located between the areas with large scutes are abundant small, irregular ossicles, which gave the animals flexibility (Carpenter 1997). The small (pebble-sized) dermal ossicle (17859) is similar to those illustrated for *Edmontonia* (Carpenter 1997: fig. 21.4). The small, oval, complete osteoderm (17849) with

the conical point, but no keel, matches the small skull dermal ossicles illustrated in Coombs (1978).

In a recent review of ankylosaurs, Vickaryous et al. (2004) list the nodosaurids *Edmontonia* sp. and *Edmontonia rugosidens* (= *Panoplosaurus rugosidens* Gilmore 1930) as present in the Aguja of Big Bend. The latter species is known from a skull without lower jaws and from other isolated bones from Big Bend (Coombs 1978). *Edmontonia* occurs from Texas to Alberta (Vickaryous et al. 2004). There are few other published reports on ankylosaurs from Big Bend, and most are brief, without detailed descriptions or illustrations. Lehman (1985: 263) mentioned the presence of ankylosaur osteoderms, limb bones, and vertebrae in the upper Aguja, and referred them to the nodosaurs based on the “flattened bases of the osteoderms, a condition present in Nodosaurinae.” Standhardt (1986) referred a small ankylosaur tooth (LSUMNS 1305) from the upper Aguja of Dawson Creek (site LSUMNS 113) to the ankylosaurid cf. *Euoplocephalus*, based on its resemblance to *E. tutus* (Lambe 1902: 57, 152), in particular the “leaf-shaped crown with large serrations and the small size of the crown relative to the root.” The specimen was mentioned in Standhardt (1989) and photographed in Schiebout (1997). This tooth resembles those described in this paper, which are tentatively identified as *Edmontonia*. Rowe et al. (1992) also mentioned ankylosaur osteoderms from the Terlingua microsite in the upper Aguja Formation. Based on these reports of isolated and fragmentary fossils, ankylosaurs were rare in Big Bend, and most are referred to the nodosaurids.

Importantly, the three small ankylosaur teeth described here are similar in size to teeth of baby ankylosaurs (i.e. embryonic or hatchling) from the Hell Creek Formation (Carpenter 1982: 128), documenting that ankylosaurs nested in Big Bend. Similar to the Hell Creek site, these two Big Bend teeth are unworn, indicating little abrasion during transport prior to burial. Horner and

Currie (1994) showed that some embryonic dinosaur teeth have wear on their tips, possibly from grinding their teeth while still in the egg. This is seen in hadrosaurs, sauropods, and *Psittacosaurus*. The other small tooth is a digested tooth; possibly evidence for predation. The baby dinosaur teeth and the abundance of eggshell material in the Rattlesnake Mt. bonebeds indicate that nesting sites were nearby. Also similar to the Hell Creek site, the Rattlesnake Mt. bonebeds contains baby dinosaur teeth from a variety of taxa. However, what is not discussed in Carpenter (1982) is how and why a variety of baby dinosaur fossils are preserved together in the Hell Creek site. Were multiple nesting sites eroded and transported or did nesting sites include different species of dinosaurs?

With some exceptions, most North American ankylosaur fossils are typically isolated elements or fragmentary skeletons (Vickaryous et al. 2004). In general, ankylosaurs were rare, a minor component of Late Cretaceous dinosaur faunas (Carpenter 1990). This is also true for Big Bend, where isolated ankylosaur bones and osteoderms are usually a minor component in bonebeds of hadrosaurs and ceratopsians in the upper Aguja. Several quarries were collected by the WPA (Works Progress Administration) crews in the 1930s near Talley Mt., and in one example (Quarry #3), ankylosaurs make up 29% out of 82 prepared specimens (Lehman 1982; Davies and Lehman 1989). Lehman (1997) estimates that ankylosaurs were only 8% of the dinosaur fauna in Big Bend. However, based on extensive collection of the productive Rattlesnake Mt. bonebed, where only three teeth (all juveniles) and three osteoderms have been found, ankylosaurs are may have been an even rarer component, at least in this particular paleoenvironmental setting. Based on North American localities of ankylosaur tracksites (McCrea et al. 2001) and the presence of aquatic vertebrates associated with ankylosaur bone and teeth, ankylosaurs probably preferred wet environments (Vickaryous et al. 2004). However,

many Asian ankylosaurs lived in arid or semi-arid environments (Carpenter 1997) and their rarity in Big Bend and other coastal and floodplain settings may indicate that they were more common in more inland areas that are not well documented in the North American fossil record.

Ornithopoda Marsh 1881b

Hadrosauridae Cope 1869

(Figs. X.5, X.6)

Referred Specimens. Hundreds of isolated small teeth and several small bones from hatchlings.

Description. These teeth are clearly from hadrosaurs because they have the diagnostic ridge on the outer surface of the tooth (Carpenter 1999). Hundreds of small hadrosaur teeth are the most abundant dinosaur fossils in the bonebeds (Fig. X.6A). Tooth size matches those of hatchling dinosaurs. Bones from hadrosaur hatchlings are also present, such as three small vertebral centrae with the notochordal pit present (Fig. X.5A-G). This is a characteristic of baby (i.e. embryonic or hatchling) hadrosaurs; the pit usually disappears after the hatchling stage (Weishampel and Horner 1990).

Discussion. Hadrosaurs are the most common embryonic dinosaurs found, and are associated with *Spheroolithus* eggs in Alberta, Montana, and Mongolia (Carpenter 1999). In the Aguja, hadrosaur specimens are more common than ceratopsians by about 60% (Lehman 2007). Hadrosaur hatchling teeth are the most abundant teeth in the bonebeds; many of these teeth are small and unworn. The most abundant eggshell type in the bonebeds match those of hadrosaurs (Welsh and Sankey 2008).

Ceratopsia Marsh 1890a

cf. *Agujaceratops mariscalensis* Sullivan and Lucas 2006

(=*Chasmosaurus mariscalensis* Lehman 1989)

Referred Specimens. Uncounted, fragmentary and shed teeth.

Description. Teeth match those referred to as ceratopsian teeth in the Judith River Group of Alberta (Baszio 1997; Peng et al. 2001).

Discussion. Isolated shed ceratopsian teeth are present, but they are rare compared to the common hadrosaur teeth. An epioccipital process was also collected (identified by Sampson, pers. comm. 2007).

<FIGURES 5 AND 6 HERE>

Theropoda Marsh 1881a

Family Tyrannosauridae Osborn 1905

Tyrannosauridae indeterminate

(Figs. X.5, X.6)

Referred Specimens. LSUMNS 726:17896, 6219, 8236, 6209, 6201, 6220, 6221; 842:8375; 746:17803, 6272, 6274, 8368, 8291, 6262, 6227, 8252; 834:8416, 8332, 8243, 8323; (tooth fragments); 842:17876 (complete tooth); 746:6282 (fragment of premaxillary tooth); 746:8371; 726:6218, (complete premaxillary teeth); 746:8374, 8414 (4 specimens), 6247; 834:8211; 726:8217, (complete teeth); 746:8440 (1 manual phalanx).

Description. Most specimens are fragments of teeth, but are easily identified as tyrannosaurid based on distinctive tooth and denticle shape and size. Nine complete and nearly complete teeth range in size, from small (8 mm in length) to large (40 mm), with an average of 24 mm. Lengths were measured along a straight line between tip and base of tooth, where the

enamel ends. Widths vary from 6 to 18 mm, with an average of 13 mm. Width refers to the size of the tooth, mesially-distally, and was measured at the base of the tooth. Lateral teeth (i.e. non-premaxillary) vary in cross-sectional shape from oval to flattened oval. Degree of recurvature ranges from strongly to slightly recurved. Denticles are present on both the anterior and posterior carinae (carinae are the serrated ridges that extend along the anterior and posterior edges of theropod teeth). Denticles are approximately equal in size on both carinae, although slightly larger on the posterior. Denticle size is approximately uniform from tooth base to tooth tip, although slightly smaller near the tooth base and tip. In most teeth, denticles are broad and wide, with bulbous tips. On unworn denticles, tips are also slightly pointed. In some teeth, denticles are longer, narrower, and tightly packed (i.e. smaller interdenticle spaces). Denticles/mm on posterior carinae range from 2 to 3/mm. (All denticle measurements were made from the complete teeth only, and from the largest denticles present on the posterior carinae). In premaxillary teeth, both carinae are on the anterior surface, teeth have little recurvature, are round in cross-section, and denticles are quite small. Two complete and nearly complete premaxillary teeth are 6 and 16 mm in length.

Additionally, there is one tyrannosaurid manual phalanx (Fig. X.5U-X; Longrich pers. comm. 2007).

Discussion. Sankey et al. (2005b) described and measured 13 tyrannosaurid teeth and teeth fragments collected from the Rattlesnake Mt. bonebeds (LSUMNS localities: 726, 746, 747, 834) from the initial field work in 2002, in addition to those from other sites in the Aguja and from the Javelina Formations. The subsequent years collecting from the Rattlesnake Mountain bonebed sites has increased the sample by 32 specimens, including nine complete teeth. These are described here.

Tyrannosaurid teeth are easily identifiable based on characteristics of their distinctive tooth and denticle size and shape. Tyrannosaurid teeth are described in detail in Currie et al. (1990), Abler (1997), Baszio (1997), Sankey et al. (2002), and Samman et al. (2005), and these characteristics are summarized here. Typically, the teeth are rounder in cross-section (i.e. less flattened, labial-lingually) than from other theropods such as the dromaeosaurids. Both carinae have similar-sized denticles and their size is consistent from base to tip of tooth. This is different from dromaeosaurid teeth, which have considerably larger denticles on the posterior carinae and less uniformly-sized denticles along the carina. Denticle shape and size is also distinctive in tyrannosaurids. Denticles usually occur 3/mm (Currie et al. 1990), with clear interdenticle spaces. Denticle tips are bulbous, and slightly pointed if unworn.

Sankey (2001: figs. 3.6-3.7, 3.13-3.14) referred two incomplete teeth from the Talley Mt. microsites to theropod indet., based partly on their long, narrow, closely-spaced denticles that did not closely resemble those from tyrannosaurids or from small theropods. However, among the Rattlesnake Mt. sample are additional teeth with similar denticles. Some are complete teeth, such as 746:8374, which is clearly a tyrannosaurid. Juvenile tyrannosaur teeth may contain denticles that are slightly different from those of adult teeth, and this may be the reason for the variation seen here.

Some of the teeth from the Rattlesnake Mt. bonebeds are clearly from juveniles. For example, 746:8371 is a small, complete premaxillary tooth (6 mm in length) and 842:17876 is a small, complete tooth (8 mm in length). Even fragmentary teeth can be referred to small teeth, especially if it is a tooth tip or if two sides of the tooth remain, giving a sense of tooth size. Many other Rattlesnake Mt. teeth fragments are from small teeth, and probably also from juveniles. Some of the complete teeth are labial-lingually flattened and recurved, and this may be due to

variation of tooth shape along the tooth row (Samman et al. 2005). Additionally, juvenile tyrannosaurid lateral teeth are more bladelike (i.e. flattened labial-lingually) than in adults, where teeth are broader and can be almost as thick (labial-lingually) as wide (mesial-distally) (Holtz 2004). So, these bladelike teeth may be from juveniles. Many of the tyrannosaurid teeth from the Rattlesnake Mt. bonebeds are from juveniles, and a few are from quite small individuals; possibly from hatchlings. Finding juvenile tyrannosaurid teeth along with small theropod and other dinosaur teeth is common from other Late Cretaceous deposits (Currie et al. 1990).

Family Ornithomimidae Marsh 1890b

(Fig. X.5)

Referred Specimens. Phalanges (841:17764; 727:5913; 746:8326; 747:17769). Unguals (728:8347; 746:6260, 17755; 747:17768, 19948)

Description. The most common theropod post-cranial elements are from ornithomimids. There are three morphotypes: 1) a small ornithomimid, 2) a *Struthiomimus*-sized ornithomimid, and 3) a very large, *Ornithomimis*-sized ornithomimid (Longrich, pers. com., 2007). An example of the latter is 747:19948 (Fig. X.5M-P).

Discussion. Although Lehman (1985) reported fragmentary ornithomimid remains from Big Bend, this is the first report with illustrations.

Family Dromaeosauridae Mathew and Brown 1922

Saurornitholestes Sues 1978

Saurornitholestes indet.

(Fig. X.7)

Referred Specimens. In addition to those referred to in Sankey et al. (2005b) are the following: 726:6204; 746:6270, 6280, 6281, 8254, 8327, 8368, 8449, 17750, 17751, 17754, 17803, 17783, 17786, 747:8282; 841:17752.

Description. *Saurornitholestes* are the most abundant theropod teeth in the bonebeds (Fig. X.7). See Sankey et al. (2005b) for detailed descriptions.

Discussion. Sankey et al. (2005b) described the theropod teeth from these bonebeds in detail, and distinguished three distinct morphotypes of *Saurornitholestes*. No new taxa are present in this expanded collection, and no further descriptions are necessary.

Dromaeosauridae – indet.

(Fig. X.5)

Referred Specimens. Metacarpal I (746:17756; Fig. X.5 Y-A1). Pedal phalange (726:6212; Fig. X.5Q-T).

Description. A metacarpal and phalange are referred to the Dromaeosauridae (Longrich, pers. comm. 2007).

Discussion. Although Lehman (1985) mentions the presence of theropod postcranials in Big Bend, this is the first paper that illustrates them. Based on the abundance of *Saurornitholestes* teeth in the bonebeds, these bones may be from the same theropod.

<FIGURE 7 HERE>

Discussion

Deciphering the taphonomic history behind the Rattlesnake Mt. bonebeds is important in order to understand if the assemblage represents a local paleocommunity (i.e. animals that lived in or near

the same paleoenvironment) or a mixture from various paleocommunities. The key observations about the bonebeds are:

(1) There are no complete or associated vertebrate skeletons; all of the teeth and bones are isolated.

(2) This is a mixed assemblage, with both aquatic and terrestrial vertebrates. However, the majority of the fossils are from aquatic vertebrates, for example, gars, crocodylians, and trionychid turtles. Less common are terrestrial vertebrates such as lizards, dinosaurs, and mammals.

(3) All of the dinosaur eggshells are small fragments, less than 10 mm in diameter.

(4) Eggshells are from a variety of dinosaurs, both ornithischians and theropods.

(5) Many of the small dinosaur teeth are from hatchlings; hadrosaurs are the most abundant.

(6) The dinosaur teeth and bones are from a variety of dinosaurs, both ornithischians and theropods.

(7) All the tyrannosaurid teeth are small, shed teeth, and most are probably from juveniles.

(8) Many of the dinosaur teeth are remarkably unworn. For example the denticles on many of the *Saurornitholestes* teeth are still sharp and unabraded.

(9) Vertebrate coprolites are abundant. Their size, shape, and absence of bone material, match coprolites identified as crocodylian (Schwimmer 2006).

(10) The bonebeds are within muddy sandstones, with abundant small, carbonized plant fragments, clay balls, and snail steinkerns.

(11) All of the snail steinkerns in the bonebed are missing their shells.

(12) Several large (2 meter long) pieces of coalified wood are present; all are poorly fossilized and have a thick coating of gypsum.

The presence of isolated and fragmentary bones suggest that many were possibly exposed, reworked and/or transported before burial. The dinosaur eggshells and baby dinosaur teeth and bones indicate that bone and eggshell from at least one nesting site containing hatchlings were reworked and deposited here. The presence of complete (i.e. not fragmented) snails and the rarity of sharks and rays together indicate that the environment of deposition was fresh-water or possibly brackish. The sediments and fossils further indicate that the likely agent of reworking and transport was a fast flowing alluvial channel. However, this interpretation does not preclude the possibility that these fossils experienced other taphonomic modifications prior to final burial.

How far away were the nesting sites? Well preserved sites with dinosaur eggs, eggshells, and hatchling bones, such as nesting sites in Alberta and Montana, are usually found in paleosols within more inland and better-drained parts of floodplain (Zelenitsky et al. 1996; Carpenter 1999; Sankey, pers. obs. 1999). However, this may reflect a preservational bias in the fossil record. Soil conditions are key for eggshell preservation because acidic soils leach away the calcium carbonate of eggshells. Paleosols with high carbonate content, such as from carbonate nodules, leads to preservation of eggshells (Carpenter 1982, 1999). The carbonate from clam and gastropod shells can also provide an important buffering agent in acidic soils. For example, from the fossil-rich Dinosaur Park Formation of Alberta, only two eggshell sites have been found. However, both sites have numerous clam shell fragments, indicating that the carbonate from the clam shells buffered the acidic sediment conditions and prevented leaching of the eggshells (Brinkman 1986; Brinkman et al. 1987; Tanke and Brett-Surman 2001). Clearly, more dinosaur

eggshell sites would have been preserved under the right conditions. The abundance of carbonate soil nodules and snails in the Rattlesnake Mt. bonebeds allowed preservation of the eggshells. Interestingly, all of the snails in the bonebed are missing their shells, indicating dissolution of their shells within acidic sediment conditions.

How did the theropod teeth enter the site? Were the theropods predating or scavenging the nesting site(s)? It is interesting that all of the tyrannosaurid teeth are from juveniles. Perhaps the diet of juvenile tyrannosaurids differed from that of adult tyrannosaurids. Dietary differentiation between juveniles and adults is often seen in modern animals. Additionally, track sites composed entirely of juvenile dinosaur tracks is evidence that juvenile dinosaurs stayed together, separate from adults (Carpenter 1999).

The abundant vertebrate coprolites in the bonebeds may be a clue to predation and/or scavenging. The size and shape of the coprolites, and the absence of bone material in them, are similar to those identified as crocodylian (Schwimmer 2006).

A microvertebrate site that has been attributed to predation is from Horseshoe Canyon Formation (Maastrichtian) of Alberta (Ryan et al. 1998). The site is within over-bank deposits that formed during a flood event. In this site, 66% of the elements are hadrosaurs, with 10% from babies, 17% of the elements (teeth) are from *Troodon*, and the remaining 11% are from other theropods, ankylosaurs, and ceratopsians. The unusually high numbers of *Troodon* and hadrosaur is cited as evidence for predation by *Troodon* on eggs or babies (Ryan et al. 1998). The abundance of teeth from juvenile tyrannosaurids and hatchling hadrosaurs in the Rattlesnake Mt. microsites supports the idea that juvenile tyrannosaurids preyed on the hatchling hadrosaurs.

Eberth and Currie (2005) describe the taphonomy of the fossil assemblages in the late Campanian deposits of Dinosaur Park, Alberta. In multitaxic bonebeds, fossils are from many

different species. In one example (BB 47), the fossils include worn and rounded bones to complete turtle shells and a crocodile skull. The Rattlesnake Mt. bonebeds are similar; they contain a variety of taxa with a range of preservation quality. For example, the rounded and worn bone fragments and the unworn dinosaur teeth, indicate different taphonomic histories for various taxa.

Another taphonomic mode Eberth and Currie (2005) identify from Dinosaur Park is vertebrate microfossil assemblages, which they describe as concentrations of well-sorted, small bones and teeth. Because the fossils are typically small and resistant elements (e.g. teeth, scales, and dense bone), they suggest that some of these deposits may have had long, complex pre-burial histories (Eberth and Currie 2005), such as (1) accumulation and scattering on a floodplain or (2) concentrated within feces or (3) previously buried, before further reworking, transport, and final deposition within the microsite (Eberth 1990). However, because the taxonomic composition of the microsites changes with stratigraphic position and the sites contain easily-modified mudstone clasts, Eberth (1990) argued that they were composed of local taxa. Brinkman et al. (2005) also concluded that microfossil assemblages in Dinosaur Park are locally derived, sampling local paleocommunities. This fits my interpretation of the Rattlesnake Mt. microsites. The presence of fragile elements, such as the delicate, unworn theropod teeth and dinosaur eggshell, argues against long transport or a complex taphonomic history, at least for some of the taxa.

There are few taphonomic data currently available from the Rattlesnake Mt. bonebeds. Although the original associations, distributions and orientations of the bones cannot be reconstructed, I am confident that most if not all are disassociated and isolated elements (one exception is a partially associated partial salamander skeleton, approximately 20% complete). This preservation pattern is compatible with the interpretation of the deposits as channel lags.

Lastly, the range of fossil preservation (whole to fragmentary; pristine to worn) suggest variable taphonomic histories prior to burial.

Given the data and interpretations presented here, a likely scenario as to how the Rattlesnake Mt. bonebeds formed is:

- (1) death of the ceratopsian *A. mariscalensis* and nearby hadrosaur hatchlings;
- (2) scavenging and scattering of the ceratopsian carcass and nearby hadrosaur hatchlings by young tyrannosaurids and small theropods;
- (3) a severe flood event that washed over the floodplain, sweeping the remains of the *A. mariscalensis* skeleton(s), the theropods, and the nesting sites with hatchling hadrosaurs and eggshells into the channel of a nearby and large river;
- (4) mixing of elements in a slurry of sand, mud, snails, and small plant fragments;
- (5) deposition of this slurry as a channel lag;
- (6) subsequent deposition of the overlying finer sands during the final, receding flood stage.

Eberth and Currie (2005) proposed that the over-riding formative and preservational influences on the rich fossil deposits at Dinosaur Provincial Park were frequent and severe floods across the coastal plain. They envisioned “Bangladesh-style flooding” events for the region. Secondly, they cited predation, scavenging, and trampling as important factors that modified the carcasses and bones of vertebrates as they were about to enter the fossil record. This sort of flooding and post-mortem events are broadly similar to the scenario I envision for the Rattlesnake Mt. bonebeds.

Conclusions

This paper has provided new sedimentologic and paleontologic information from two, closely associated high diversity, mixed bonebeds in the Big Bend area. One of these sites yielded the most complete skull of *Agujaceratops mariscalensis* and, in combination, all of the sites yield a rich assemblage of plants, invertebrates and other vertebrates. This composite vertebrate assemblage provides an important glimpse of local paleocommunity structure in this region, as well as an opportunity to make comparisons with other Campanian-age vertebrate faunas within North America. Although the Big Bend Cretaceous vertebrate assemblage is less well known than vertebrate assemblages of comparable age from Montana and Alberta, it is an important southern datum.

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Table 1. Taxa present at Rattlesnake Mountain *Agujaceratops mariscalensis* bonebed (Sankey, 2006; Sankey *et al.*, 2005b; Welsh, 2005; Welsh and Sankey, 2008).

Fish

Dasyatidae

Lepisostidae

Amphibian

Albanerpeton

Turtle

Baenidae

Kinosternoidea cf. *Hoplochelys*

Adocidae - *Adocus*

Nanhsiungchelyidae - *Basilemys*

Plastomeninae - *Helopanoplia*

Trionychidae - Genus et sp. indet.

Lizard

Crocodylians

Brachychampsia

Goniophoridae

Pterosauria

Tyrannosauridae

Ornithomimidae

Dromaeosauridae - *Saurornitholestes*

Theropod - *Richardoestesia*

Aves

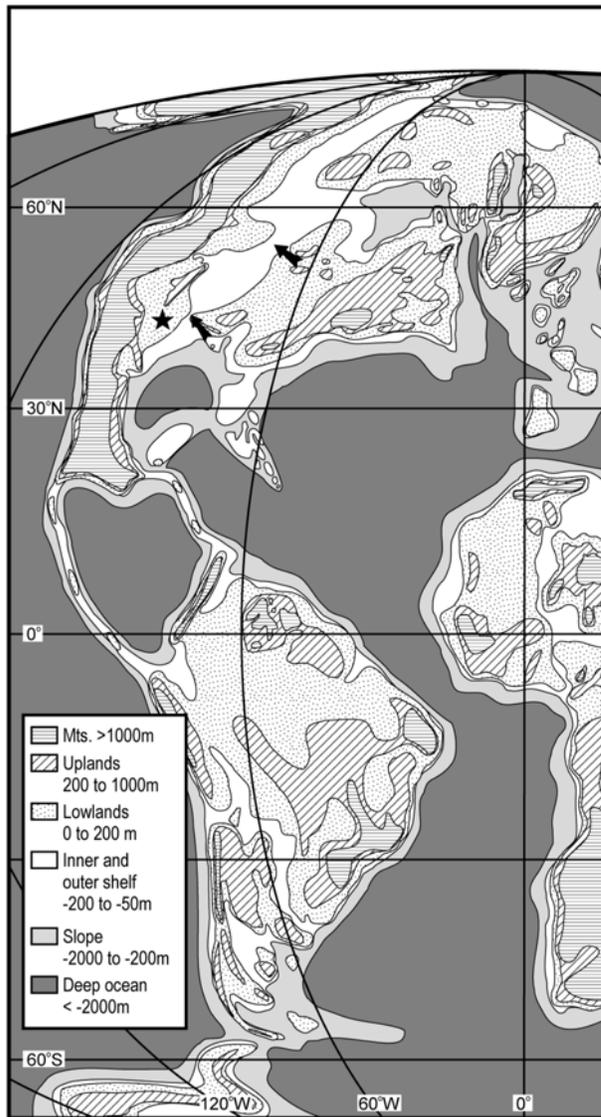
Nodosauridae cf. *Edmontonia*

Hadrosauridae

Ceratopsia cf. *Agujaceratops mariscalensis*

Mammalia, multituberculata

A.



B.

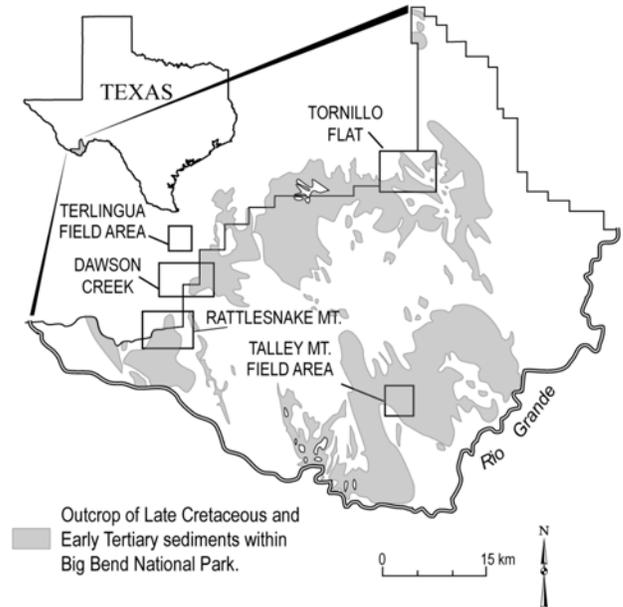


Figure X.1. (1) Late Cretaceous (Maastrichtian) paleogeographic reconstruction of North and South America (redrawn from Patzkowsky et al. 1991). (2) Late Cretaceous through Paleocene exposures of the Tornillo Basin, Big Bend National Park, Texas, with major field areas labeled.

A. Lithostratigraphy

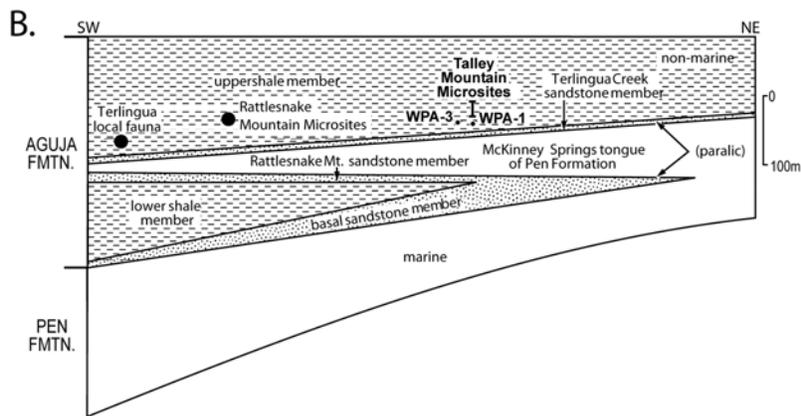
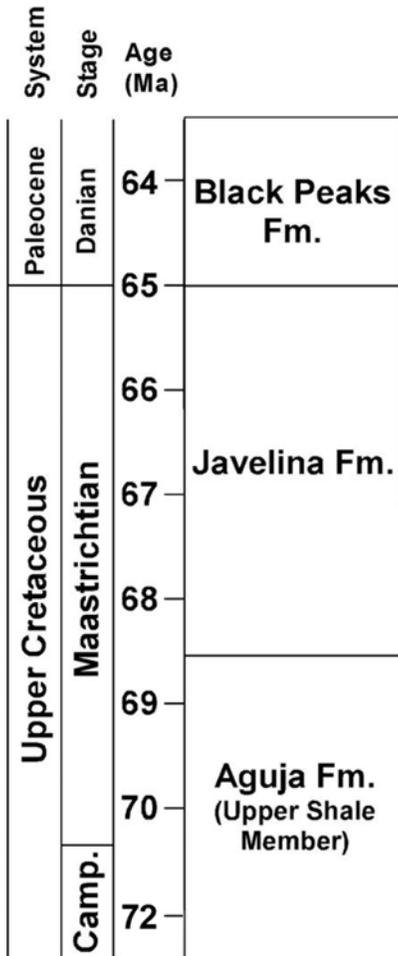


Figure X.2. (A) Late Cretaceous through Paleocene stratigraphy (redrawn from Nordt et al. 2003); (B) cross-section of Aguja Formation showing stratigraphic position of vertebrate sites (modified from Lehman 2007).

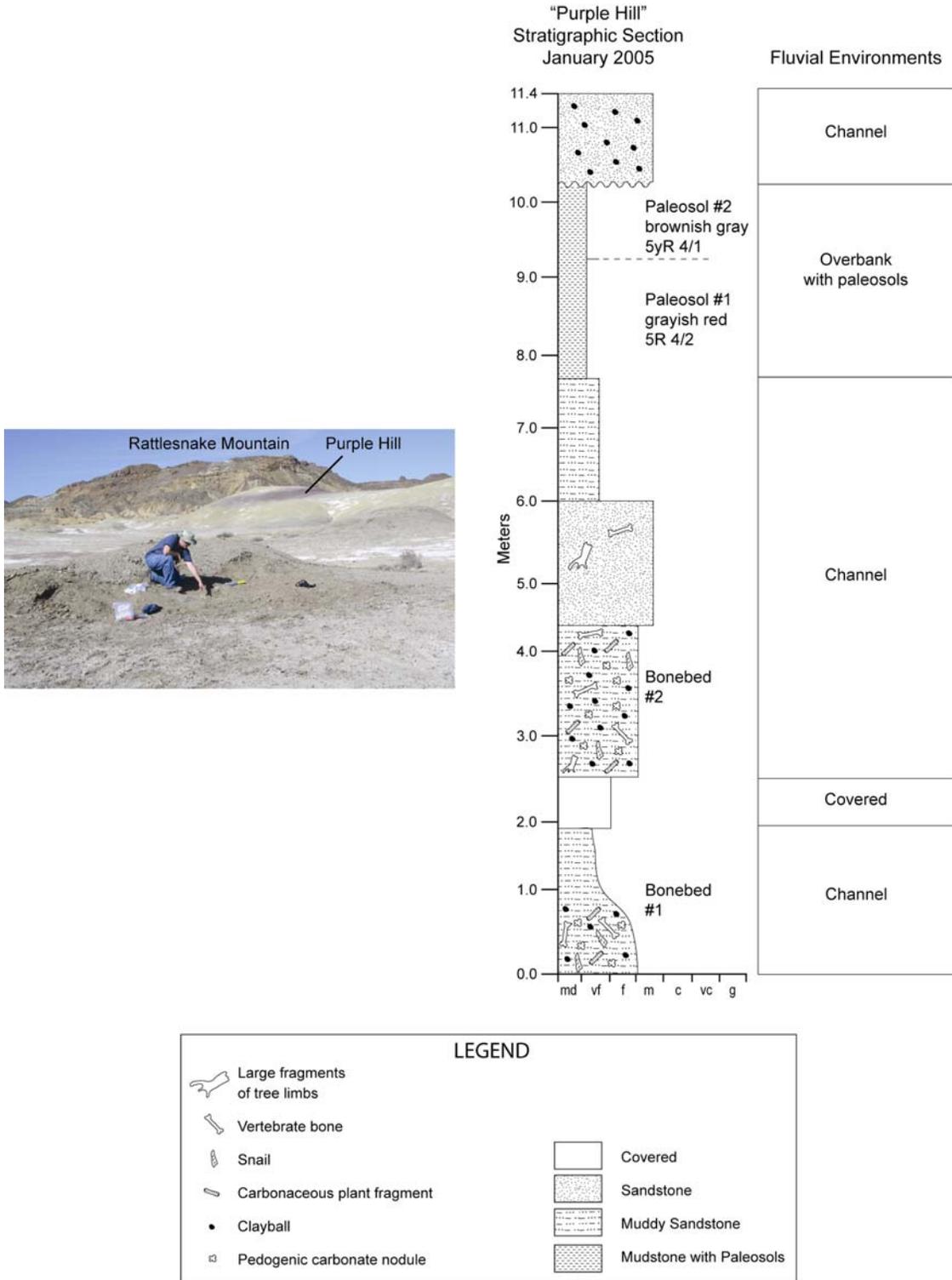


Figure X.3. "Purple Hill" stratigraphic section. Photograph shows Rattlesnake Mountain in the distance (view to the north). In the foreground is "Purple Hill," with the distinct purple paleosol near the top. Person is working at Bonebed #2. The skull of *A. mariscalensis* (TMM 43098; Forster et al. 1993) is from Bonebed #1.



Figure X.4. Sedimentary rocks and fossils from the “Purple Hill” field area. (A) Fossiliferous muddy sandstone with abundant small plant fragments from Bonebed #2; (B) in situ dinosaur vertebra from Bonebed #2; (C) coalified tree limb (~1 meter in length) from surface of Bonebed #2; (D) pedogenic carbonate nodules within sandstone overlying Bonebed #2.

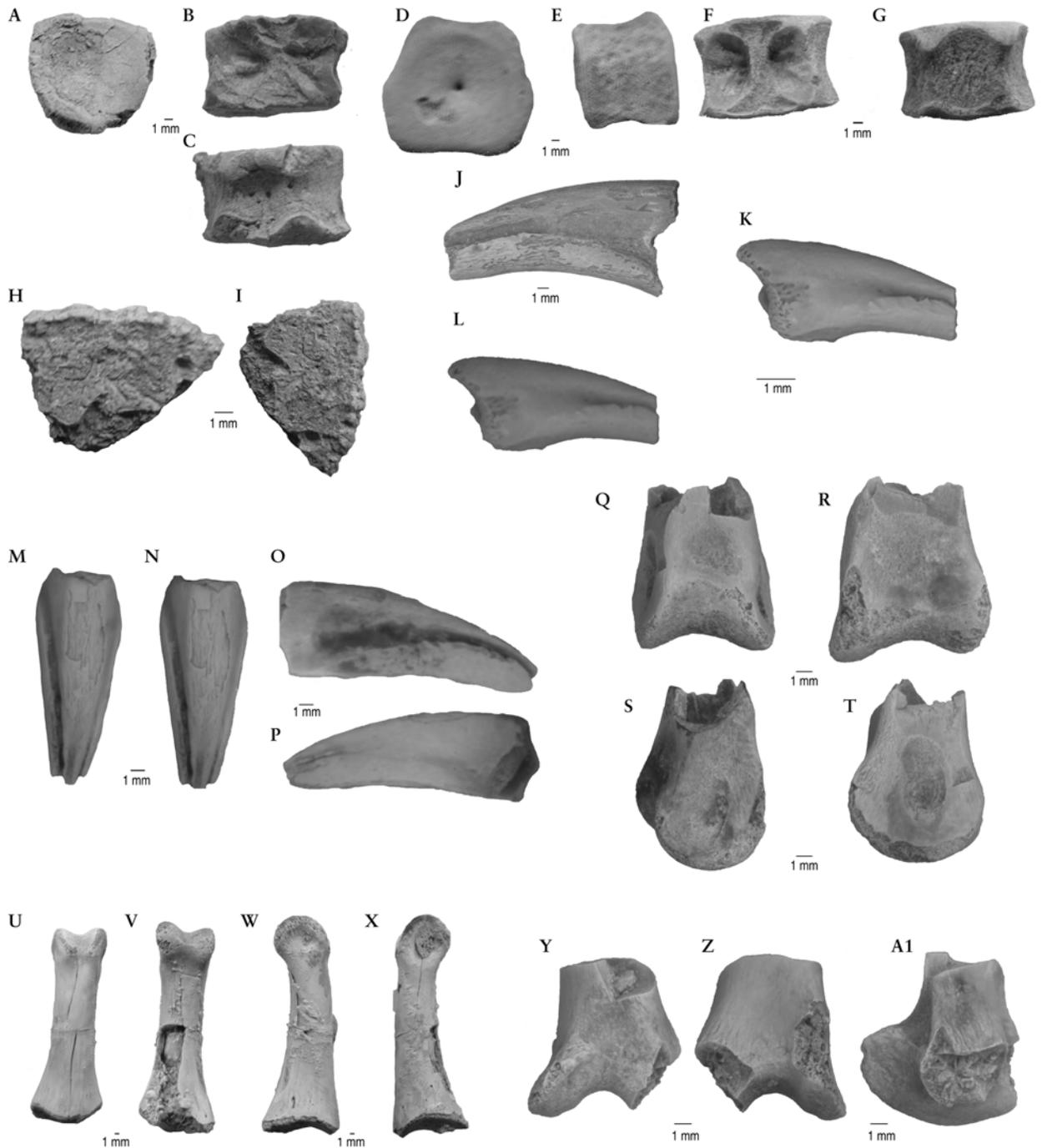


Figure X.5. Dinosaur postcranial bones from the Rattlesnake Mountain bonebeds. (A-G) Hadrosaur hatchling centra (LSUMNS 842:8397); (H-I) ankylosaur scute (LSUMNS 834:17621); (J-L) ornithomimid manual ungual (LSUMNS 726:8347); (M-P) ornithomimid ungual (LSUMNS 747:19948); (Q-T) dromaeosaurid pedal phalange (LSUMNS 726:6212); (U-X) cf. tyrannosaurid manual phalange (LSUMNS 746:8440); (Y-A1) dromaeosauridae metacarpal (LSUMNS 839:17756).

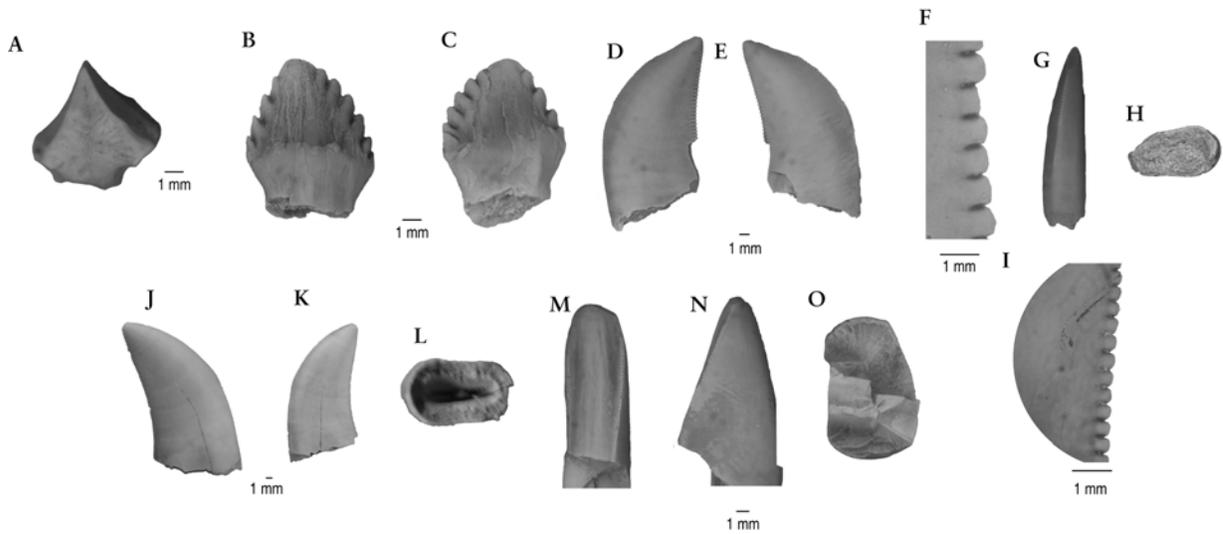


Figure X.6. Dinosaur teeth from the Rattlesnake Mountain bonebeds. (A) hadrosaur hatchling, occlusal view (LSUMNS 834:4241); (B-C) ankylosaur hatchling, side views (LSUMNS 746:6271); (D-I) tyrannosaurid juvenile (LSUMNS 746:8374); (D) labial view; (E) lingual view; (F) denticles on posterior carina; (G) anterior view; (H) basal view; (I) denticles on posterior carina; (J-L) tyrannosaurid juvenile (LSUMNS 746:8414); (J) labial view; (K) lingual view; (L) basal view; (M-O) tyrannosaurid juvenile premaxillary (LSUMNS 726:6218); (M) anterior view; (N) labial view; (O) basal view.

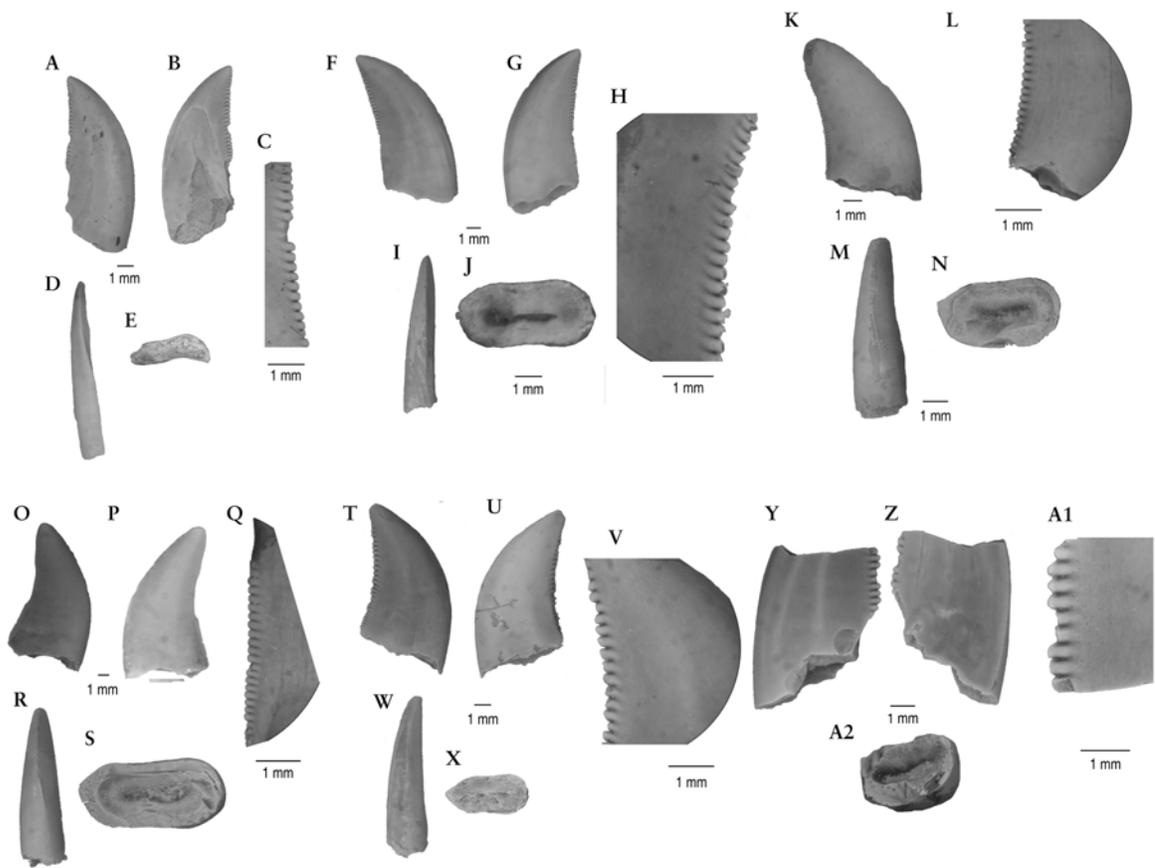


Figure X.7. Theropod teeth from the Rattlesnake Mountain bonebeds. (A-E) *Saurornitholestes* sp. (LSUMNS 726:6204); (A) labial view; (B) lingual view; (C) denticles on posterior carina; (D) anterior view; (E) basal view; (F-J) *Saurornitholestes* sp. (LSUMNS 746:8449); (F) labial view; (G) lingual view; (H) denticles on posterior carina; (I) anterior view; (J) basal view; (K-N) *Saurornitholestes* (LSUMNS 746:6281); (K) labial view; (L) lingual view; (M) anterior view; (N) basal view; (O-S) *Saurornitholestes* (LSUMNS 746:17754); (O) labial view; (P) lingual view; (Q) denticles on posterior carina; (R) anterior view; (S) basal view; (T-X) *Saurornitholestes* sp. (LSUMNS 746:8327); (T) labial view; (U) lingual view; (V) denticles on posterior carina; (W) anterior view; (X) basal view; (Y-A2) *Saurornitholestes* sp. with flat side (LSUMNS 746:8388); (Y) labial view; (Z) lingual view; (A1) denticles on posterior carina; (A2) basal view.