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TURTLES OF THE UPPER AGUJA FORMATION (LATE CAMPANIAN), BIG BEND NATIONAL PARK, TEXAS

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Abstract—The Late Cretaceous vertebrates from Big Bend National Park, Texas are some of the southern most vertebrates from the Western Interior of North America. These fossils provide important information on the distinctiveness of the southern vertebrates. Turtle fossils (388 specimens) were collected from 13 sites in the upper shale member of the Aguja Formation (late Campanian) of Big Bend. Turtles include: Baenidae indet., cf. *Hoplochelys*, *Adocus*, *Basilemys*, trionychids, and cf. *Helopanoplia.* The most abundant turtles are the trionychids (81%), with all others less than 10%; *Adocus* (6%), *Basilemys* (6%), baenid (5%) and kinosternoid (1%). The Aguja turtle assemblage is similar, but possibly more diverse, than that of the contemporaneous Fruitland and Kirtland turtle fauna of New Mexico. Turtles are sensitive proxies to paleoclimatic change; higher turtle diversity has been shown to correspond to warmer climates. This trend continues in the Big Bend turtle record, and detailed paleoclimatic reconstructions were compared with turtle diversity. The highest turtle diversity occurred in the late Campanian and the lowest diversity in the Maastrichtian.

INTRODUCTION

Objectives of Study

This study documents and describes the turtles from the upper Aguja Formation of Big Bend, a new late Campanian turtle assemblage from this extreme southern part of North America (Fig. 1 and 2). The turtles provide a "snapshot" of late Campanian life in this area, immediately before climatic and environmental changes that occurred at the Campanian/Maastrichtian boundary. This late Campanian turtle assemblage is compared to the Maastrichtian turtle assemblages to determine how turtle diversity changed in this area during the climatic changes of the latest Cretaceous.

Aguja Formation

The Aguja Formation is a widespread sedimentary unit in Big Bend. It is an eastward thinning deposit composed of 135 to 285 meters of sandstones interbedded with shale and lignite. Environments of deposition vary from marine, paralic, to inland floodplain (Lehman, 1985). The upper shale member represents the last of the pre-Laramide tectonic sedimentation in the area (Lehman, 1991), and records the final marine regression of the Western Interior Sea from west Texas (Regression 8 of Kauffman, 1977). The lower part of this member contains carbonaceous mudstones, thin beds of lignite, and large siderite ironstone concretions representing distributary channels, levees, crevasse splays, and poorly drained interdistributary marshes and bays. The upper part of this member, with variegated mudstones and sandstones containing conglomeratic lags of paleo-caliche nodules, represents fluvial environments within a deltaic coastal floodplain and inland floodplain. A variety of well-developed paleosols formed on the inland floodplain of the upper Aguja and overlying Javelina Formations, and their stage of development has been linked to sea level fluctuations in the nearby Western Interior Seaway (Atchley et al., 2004)

Typical large vertebrates from the lower part of the upper Aguja are the giant crocodilian *Deinosuchus riograndensis* and the horned dinosaur *Chasmosaurus mariscalensis*; the hadrosaur *Kritosaurus* sp. is more abundant higher in the upper Aguja (Lehman, 1985). All are known from quarries with associated skeletons.

Turtles are more common in the marginal marine, brackish, and freshwater floodplain deposits than in the other facies of the Aguja or from the more inland fluvial floodplain deposits of the Javelina Formation. They are most common in the upper shale member. Most of the turtles are from freshwater groups. Trionychids are the most abundant and baenids are second in abundance. Neither *Adocus* nor *Basilemys* are common (Tomlinson, 1997).

The age of the upper Aguja is late Campanian to early Maastrichtian (Lehman, 1985, 1987, 1989, 1990; Sankey, 1998; Sankey and Gose, 2001; Standhardt, 1986).

Rattlesnake Mountain Microsites

Turtle shell fragments were collected from the surface of microsites from the upper Aguja Formation (late Campanian) at Rattlesnake Mountain. The most productive and intensely collected sites are the "Purple Hill" microsites. These microsites are located approximately ten meters below the first well-developed paleosol (i.e., purple in "Purple Hill") in the inland floodplain facies of the upper shale member of the Aguja in the Rattlesnake Mountain area. The microsites are in grey, organic-rich silty mudstones. Sediments have abundant tiny fragments of carbonized plants, large pieces of burned wood, large isolated bones of dinosaurs, and small bones and/or teeth of fish, frog, salamander, lizard, turtle, crocodilian, dinosaur, birds, and mammals.

The following taxa have been identified from the "Purple Hill" microsites. Rays are present, but rare; rays are known from brackish to freshwater deposits from the Western Interior. Large gar scales and vertebrae are present; gars are common in fresh and brackish water deposits. Frogs and salamanders are present. Eight types of turtles are represented, including baenid, kinosternoid, adocid, nanhsiuhgchelyid, and trionychid. Trionychids are the most diverse and abundant. Teeth and scutes from crocodilians are abundant. However, no *Deinosuchus* fossils have been found. *Deinosuchus* is more common in the coastal floodplain deposits, which are stratigraphically lower in the section. Teeth and bones of dinosaurs are present. Several isolated hadrosaur bones are present. Tiny teeth of hatchling and juvenile hadrosaurs are the most abundant vertebrate fossil at the site. Two teeth of juvenile or hatchling ankylosaur were collected, in addition to ankylosaur scutes. Teeth of a tyrannosaurid, and of the small theropods, *Richardoestesia*, and *Saurornitholestes,* are present. Unguals and metacarpals of ornithomimids have been found. Eggshell fragments from both carnivorous and herbivorous dinosaurs are present (Welsh, 2005). One partial metacarpal from a possible bird is present. One multituberculate mammal incisor was recovered (Sankey, 2005 a, b, c, in press).

Based on the sedimentology and paleontology of the sediments from the microsites, the sediments are interpreted to have formed in a crevasse splay deposit that overflowed the banks of a river. The large size of some of the gar scales and the fragments of large trionychid shells indicate that this

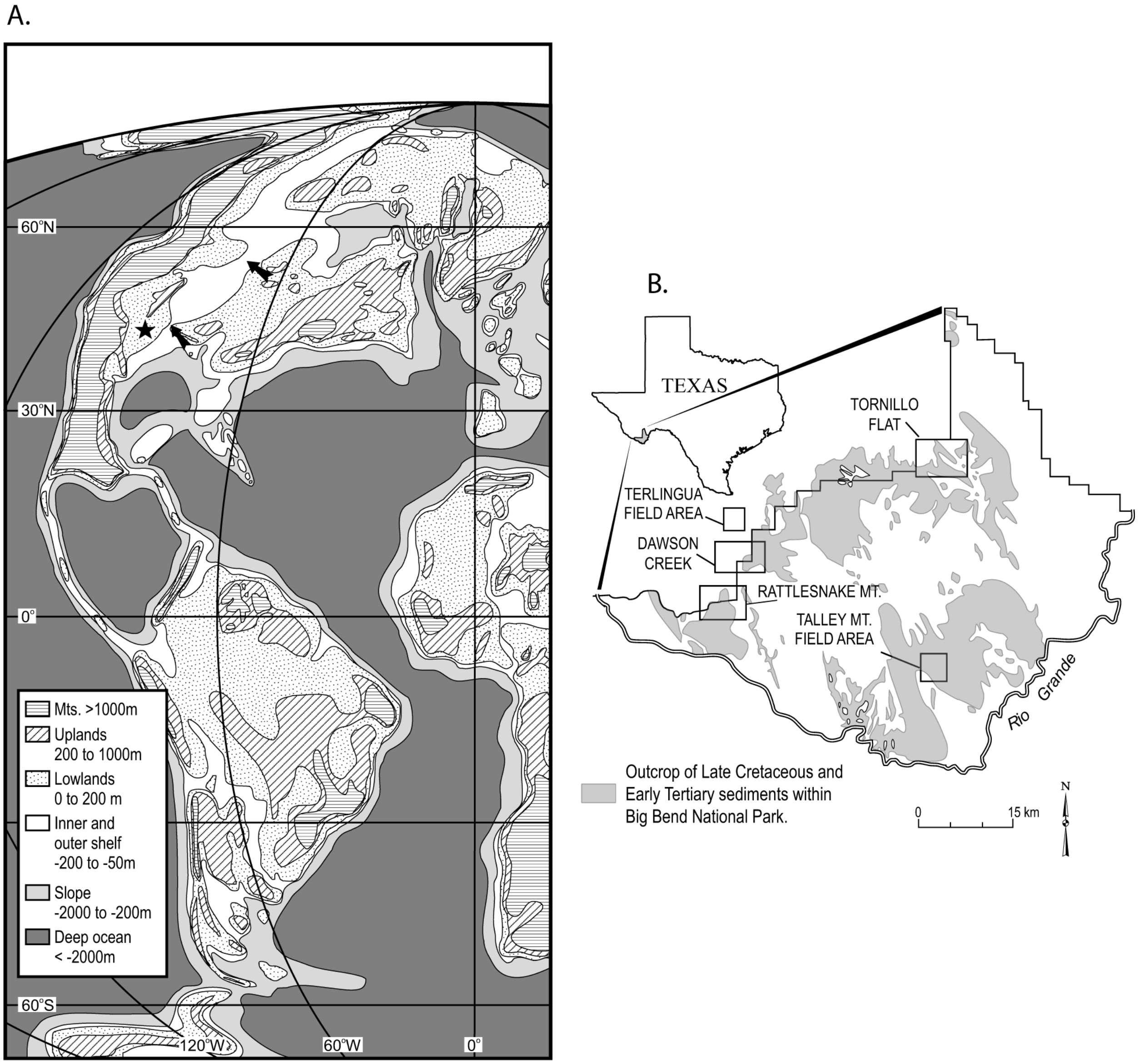

FIGURE 1. Late Cretaceous (Maastrichtian) paleogeographic reconstruction (**A**) of North and South America (redrawn from Ziegler and Rowley 1998); Big Bend National Park (**B**), west Texas with Aguja Formation outcrops stippled. Fossil sites from Rattlesnake Mountain, Talley Mountain, Terlingua, and Dawson Creek are shown by arrows.

was a fairly large river. The deposit has abundant small (2 mm in length) carbonized (burned) plant fragments, which indicate tumbling and transport within a stream. Several large (2 meter long) pieces of burned wood were found; all are poorly fossilized and with a thick coating of calcite. The burned log and the burned plant fragments are evidence that a fire occurred in this area, and that they were transported and deposited at this site soon after this occurred.

Stratigraphy of Microsites

The purple paleosol overlies the microsites by approximately ten meters. The purple bed is useful for correlating the deposits exposed in the southeastern flank of Rattlesnake Mountain because it is widespread and easy to recognize from a distance. Above the purple paleosols in the Rattlesnake Mountain area are approximately 100 meters of predominately tan to brown sandstones within the upper shale member of the Aguja Formation; they extend to the first igneous rocks in the cliffs of Rattlesnake Mountain (Sankey, pers. observation, 1999).

METHODS AND MATERIALS

Fossil Collection and Curation

Fossils were surface collected from microsites from the upper shale member of the Aguja Formation at Rattlesnake Mountain. Most of the microsites were surface collected only. This was done by carefully crawling over the surface on hands and knees, with prospectors having their eyes almost literally to the ground. All fossils are curated in the Louisiana State University Museum of Natural Science (LSUMNS) Geology Collections in Baton Rouge. Locality numbers are indicated by the letters, VL (vertebrate locality). Specimen numbers are indicated by the letter V (vertebrate fossil). A complete LSUMNS catalog number has the VL and V numbers separated by a colon. Specimen and locality information will be available to qualified researchers by written request to Sankey.

Abbreviations

The following abbreviations are used: LSUMG (Louisiana State University Museum of Natural Science Geology Collections, Baton Rouge); RTMP (Royal Tyrrell Museum of Paleontology, Drumheller, Alberta); TMM

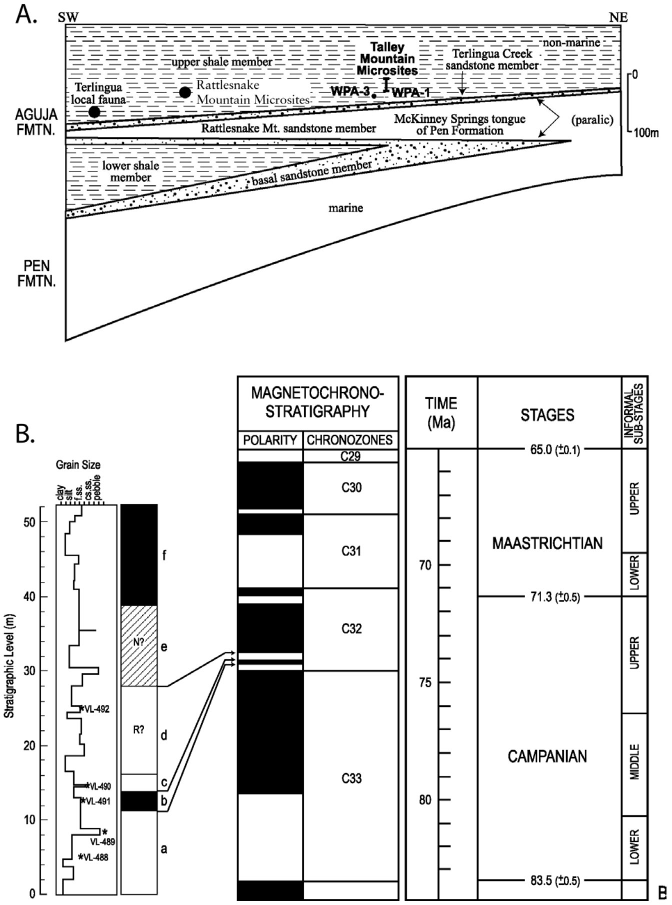

FIGURE 2—Stratigraphy of the Aguja Formation (**A**), Big Bend National Park, Texas. Lithostratigraphy of the Aguja Formation modified from Rowe et al. (1992), showing positions of the Rattlesnake Mountain sites (this paper), Talley Mountain sites (Sankey 1998; 2001; Sankey and Gose, 2001), and Terlingua site (Rowe et al. 1992). Stratigraphic position of the Talley Mt. microsites and WPA dinosaur quarries 1 and 2 (Work Progress Administration) from Lehman (1985; Plate III and written comm., 1998). Formal members of the Aguja Formation are capitalized; informal members are not. Magnetostratigraphic correlations (**B**) of upper Aguja Formation from Talley Mountain area to the geomagnetic polarity of Gradstein et al. (1995) (from Sankey and Gose, 2001).

(Texas Memorial Museum, University of Texas, Austin).

Images

Fossils were coated with vaporized ammonium chloride and photographed with a digital camera under a dissecting microscope by Sankey (2005) in Brinkman's lab at the Tyrrell Museum of Paleontology.

SYSTEMATIC PALEONTOLOGY

Order Testudines Batsch, 1788

Suborder Eucryptodira Gaffney, 1975

Family Baenidae Cope, 1882

Fig. 3

Referred specimens - Shell fragments (VL-746:17617, 17711; 834:8325; 726:17715, 17602, 6208, 17712, 17733; 841:8303). Fig. 3A-D. Morphotype A (Fig. 3B, C, and D). Morphotype B (Fig. 3A and E).

Description - Shell fragments can be grouped into two morphotypes. Morphotype A are 5 mm thick, have smooth shells, and subtle sulci (Fig. 3 B, C, and D). Morphotype B are large, 6 to 7 mm thick, have a distinctive "lumpy" surface, and a few, large, shallow pits. The 'lumps' are approximately 1 to 2 mm high and up to 13 mm in greatest diameter (Fig. 3A and E).

Discussion - Shell fragments are easily referable to baenids because of the following characteristics: shells are heavily built, smooth, with no shell sculpture, and shallow sulci (Peng et al., 2001). Tomlinson (1997) referred specimens from the Aguja Formation to "*Baena*" cf. *B. nodosa* Gilmore 1916 and "*Baena*" sp. She described these specimens as having a rough shell sculpture, with nodular bumps and ridges. Some of the specimens described here under Morphotype B, such as V-8303, have the same "lumpy" appearance as parts of the carapace illustrated in Tomlinson (1997, p. 37) and which is referred to as "*Baena*" cf. *Baena ornata*. Other Campanian baenids from New Mexico with similarly ornate shell sculpture include *Boremys, Thescelus hemisphericus,* "*Baena*" *nodosa* and "*Baena*" *ornata* (Gilmore, 1935; Mateer, 1981).

The Aguja baenids differ from those in Alberta in having a more knobby sculpture on their shell (Brinkman, pers. comm., 2005); most of the Alberta baenid specimens are *Neurankylus*. No baenids have been found from the Cerro del Pueblo Formation (Late Cretaceous) of Coahuilla, Mexico (Rodriquez de la Rosa and Cevallos-Ferriz, 1998).

Kinosternoidea Gaffney and Meylan, 1988

cf. *Hoplochelys* Hay, 1908a

Fig. 4

Referred specimens - 841:8304; 746: 17608, 17757. Fig. 4 A-C.

Description - Shell fragments are thin, with deep sulci, prominent ridges, and "tents" on neurals.

Discussion - Shell fragments are tentatively referred to the kinosternoid turtle *Hoplochelys* because of the following characteristics: thin shell, deep sulci, and prominent ridges on the carapace, making the shell structure appear 'wormy'. V-8304 is a neural, and compares well to the strong neurals of *Hoplochelys* (Brinkman, pers. comm., 2005). V-17608 is a costal and V-17757 is a plastron element; both have well developed sutures and the shell sculpture patterns resemble that of *Hoplochelys* figured in Hutchison and Holroyd, 2003, Fig. 7D).

Family Adocidae Cope, 1870

Genus *Adocus* Cope, 1868

Adocus sp.

Fig. 5

Referred specimens - 842:8299; 841:17600, 8299; 833: 17702; 834:17606, 17705; 837:17694; 840:17697; 746:17730, 17695; 747:17700; 726:17709, 17707. Fig. 5A-C.

Description - Shell fragments have a fine ornamentation of faint, shallow, and small pits. Pits are approximately 1 mm in diameter and there are five pits/cm. Pits are arranged in lines.

Discussion - Shell fragments were referred to *Adocus* based on the diagnostic delicate punctate sculpturing (Holroyd, pers. comm., 2005). In *Adocus* there are five plus pits per cm (Estes et al., 1969). In comparison, shell fragments of *Basilemys* are similar, but are thicker and bigger with deeper and larger pits of three to four pits per cm (Estes et al., 1969).

Tomlinson (1997) referred four specimens from the lower part of the upper shale member of the Aguja Formation to *Adocus* sp. She describes the specimens as having minute, densely patterned tubercles and pits arranged in rows. This description matches the specimens reported here. No specimens of *Adocus* have been reported from the Cerro del Pueblo Formation of Coahuilla, Mexico (Rodriquez de la Rosa and Cevallos-Ferriz, 1998).

Adocus and *Basilemys* are two primitive trionychoids. The osteology of *Adocus* is well documented based on an almost complete specimen from the Hell Creek Formation of Montana (Meylan and Gaffney, 1989). *Adocus* was common in the Late Cretaceous of North America. It was a large, aquatic turtle. It is also known from the Campanian upper Milk River, Foremost and Oldman, and Dinosaur Park Formations of Alberta (Brinkman, 1990) and the Fruitland and Kirtland Formations of New

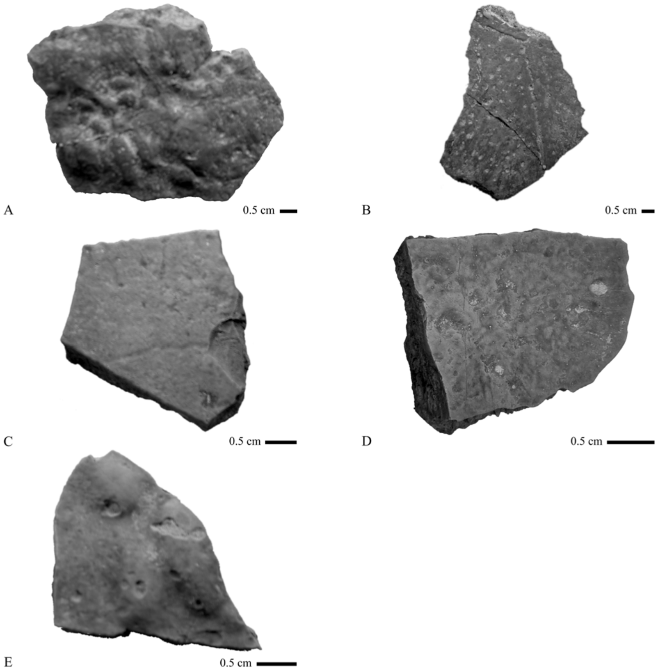

FIGURE 3. Baenidae Morph B, 841:8803 (**A**); 726:17715 (**E**). Morph A, 746:17610 (**B**); 746:17617 (**C**); 726:17712 (**D**).

Mexico (Gilmore, 1916).

Family Nanhsiungchelyidae Yeh, 1966

Genus *Basilemys* Hay, 1902

Basilemys sp.

Fig. 6

Referred specimens - 841:8356-1st costal; 8302; 842:8300, 8302; 833:17701; 834:17704, 17706, 17607; 726:17699; 17710; 17708; 746:17610, 17618, 17696, 17698. Fig. 6A-C.

Description - Shell fragments have deep pits of about 1 mm in depth. Pits are large, 4 mm in greatest diameter, with 4 pits/cm. Pit shape varies from oval to crescentic. In unworn specimens, there are bulbous-shaped points and ridges between pits. One of the most characteristic features of these shell fragments is the geometrically arranged pits; they are aligned in rows. Shells are 0.5 to 1.0 cm thick. None of the shell fragments have sutures or sulci, indicating that none represent complete elements. One specimen (V-8356) is particularly large (9 cm in maximum diameter) and is covered by calcite cement.

Discussion - Shell fragments were referred to *Basilemys* based on the following characteristics: very thick shells and coarse shell sculpture, with three to four pits per cm; pits are chevron-shaped in unworn specimens; sculpture of pits arranged in rows and similar to *Adocus*, but with considerably larger and deeper pits (Sahni, 1972; Peng et al., 2001).

Tomlinson (1997) referred specimens from the upper shale member of the Aguja Formation and from the Javelina Formation to *Basilemys*. Although she did not illustrate these specimens, her descriptions match the specimens reported here in having thick shells and with shell surfaces with distinctive rows of pits. *Basilemys* is widespread in the Cretaceous of the Rocky Mountain Interior (e.g., Langston, 1956; Brinkman and Nicholls, 1993; Holroyd and Hutchison, 2002). Rodriquez de la Rosa and Cevallos-Ferriz, 1998) did not have any *Basilemys* specimens from the Coahuilla sites.

Basilemys is the sole North American representative of the family Nanhsiungchelyidae although additional general are present in Asia (Joyce and Norell, 2005). They were large, terrestrial, and herbivorous turtles, with armored limbs, and were ecologically similar to tortoises (Hutchison and Archibald, 1986). *Basilemys* was one of two taxa of turtles that went extinct at the K/T.

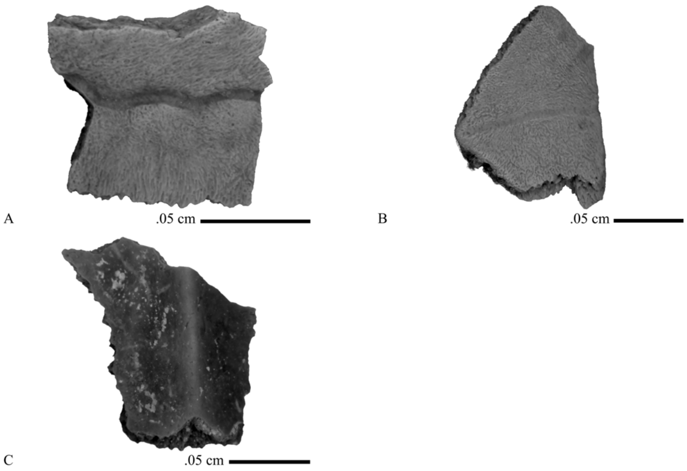

FIGURE 4. Kinosternoid cf. *Hoplochelys* costal 746:17608 **(A)**; right xiphiplastron, 746:17757 **(B)**; 841:8308 **(C)**.

Family Trionychidae

Gray, 1825

cf. *Helopanoplia* Hay, 1908a

Fig. 7

Referred specimens - 834:8324, 17605; 837:17717; 841:8306; 726: 17716; 746:17718. Fig. 7A-D.

Description - Shell fragments are all approximately 0.5 cm thick. Shells have a distinctive punctate sculpture made up of tubercles. In most specimens the tubercles are coalesced into short tube like structures of about 4 mm long and 0.5 mm wide that are branching and anastomizing, making a "wormy" sculpture pattern (see V-8306, figure 7A).

Discussion - Shell fragments are referred to *Helopanoplia* based on their characteristic pustulate shell sculpture (Holroyd, pers. comm., 2005). They match specimens referred by Hutchison and Holroyd (2003; Fig. 7E) to *Helopanoplia* cf. *H. distincta*, which are described as having a distinctive pedicellate surface sculpture. They also closely match Big Bend specimens identified as ?*Helopanoplia* by Tomlinson (1997)

Tomlinson (1997) referred specimens from the upper shale member of the Aguja Formation and lowermost Javelina Formation to *Helopanoplia* sp. because of similarity to those described by Hay (1908). Tomlinson (1997) described the shells small, thin, and with tiny (pin-head size) tubercles. No *Helopanoplia* have been reported from the Coahuilla sites (Rodriquez de la Rosa and Cevallos-Ferriz, 1998).

Helopanoplia is a large trionychid; it is known from the Lancian of Wyoming, Montana, North Dakota, and Colorado (Holroyd and Hutchison, 2002), and the Campanian of Arizona (Heckert et al., 2003), but not as far north as Alberta (Brinkman, pers. comm., 2005). Although the Big Bend specimens resemble *Helopanoplia* from Lancian sites, they are different enough in plastron shape to be from a different species (Holroyd, pers. comm., 2006 and Holroyd and Hutchison, 2002). However, the *Helopanoplia* specimens from Big Bend significantly extend the geographic range of this genus to the south.

Trionychids are common in Late Cretaceous deposits in the Western Interior; they occur in 70 and 90 % of all localities. However, they are only present in 27% of Cretaceous localities in the Denver Formation (Hutchison and Holroyd (2003).

Genus et sp. indet.

Figs. 8 and 9

Referred specimens - 833:17726, 17664, 17729; 834:8338, 8260,

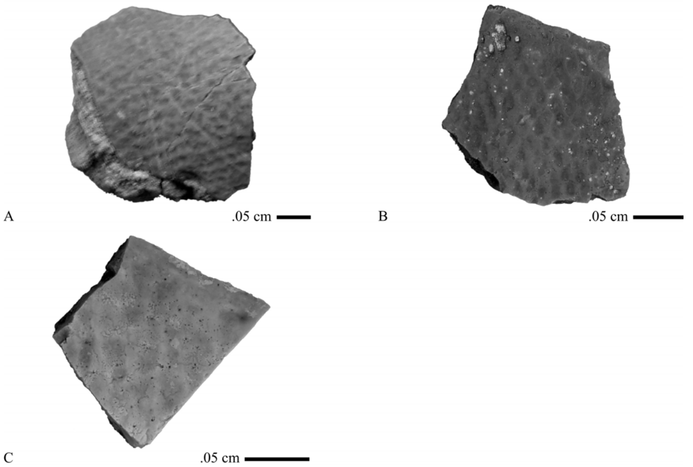

FIGURE 5. *Adocus*, 837:17694 **(A)**; 834:17606 **(B)**; 746:17730 **(C)**.

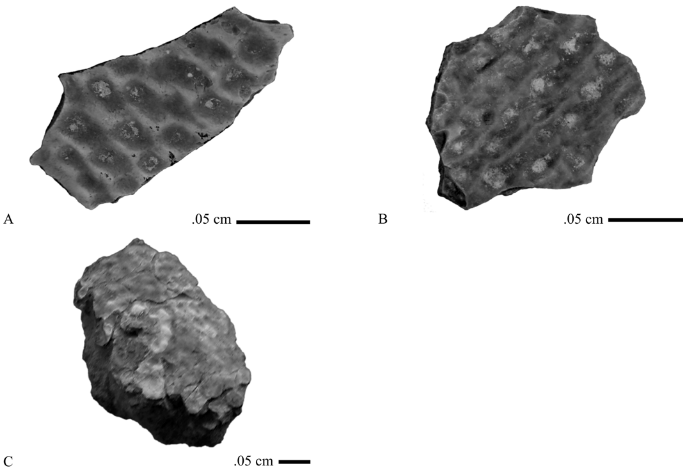

FIGURE 6. *Basilemys*, 834:17706 **(A)**; 746:17618 **(B)**; 834:17704 **(C)**.

8422, 17625, 8364, 8418, 8364, 17737; 835:17665, 17724; 836:17652; 837:17668; 838:17660; 839:17656; 17723; 726:17644, 17639, 8287, 6203, 17627, 8431, 17601, 17721; 746:17673, 17689, 8442, 17713, 17676, 17631, 17735, 17612, 17613, 17758, 8294, 8292, 8429, 8423; 747:6284; 842:8432, 17736; 840: 17722, 17723; 841:8319, 17622. Fig. 8A-D and 9A-G.

Description - Most specimens have the following characteristics: large, thick shells (2 to 4 mm thick) and pits deep (1 mm), round to oval in shape, large (1-2 mm in greatest diameter), and occur 4 pits/cm. Fewer specimens have thinner shells and smaller pits.

Discussion - Trionychids are aquatic and carnivorous soft shelled turtles. In the Late Cretaceous of North America, they are the most common turtles. Their fossils are easily recognized by their distinctive shell sculpture patterns of numerous pits of various shapes and sizes surrounded by ridges and/or grooves surrounded by ridges (Peng et al., 2001). Tomlinson (1997) recognized four morphotypes of *Aspideretoides* based on differences in ornamentation, shell thickness, and size. However, small-scale features of sculpture ornamentation are not significant at lower taxonomic levels (Estes, 1964; Nicholls, 1972; Gaffney, 1979; Gardner and Russell, 1994), and only more complete elements that demonstrate overall patterns of sculpturing and shape can be ascribed to species (Gardner et al., 1995). A variety of trionychid taxa have been reported from Late Cretaceous deposits of the western U.S. (e.g., Gardner et al. 1995; Brinkman, 2005; Mateer, 1981; Gilmore, 1916, 1938; Hay, 1908a) and many of the specimens referred here may be assignable to the most common genus, *Aspideretoides*. However, none of these specimens are sufficiently well-preserved to assign with confidence.

DISCUSSION

Southern Biogeography

Within the Western Interior of North America during the late Campanian to early Maastrichtian, Big Bend was part of a southern dinosaur biogeographic province, the "*Kritosaurus*" fauna (Lehman, 1997). The southern province, from southern Colorado to the south, was characterized by the *Normapolles* palynoflora, and had a warm climate with open-canopy woodlands (Lehman and Wheeler, 2001; Wheeler and Lehman, 2000). In contrast, the northern province, from southern Colorado to the north, was characterized by the *Aquillapollenites* palynoflora, and had a temperate and more humid climate, with a more closed-canopy forest (Nichols and Sweet, 1993). Rainfall and temperature differences were the main factors that produced these north-south biogeographic patterns (Baghai, 1996; Lehman, 1997). (For a differing opinion on Late Cretaceous provinces, see Sullivan and Lucas, 2003.) Big Bend in the late Campanian to mid-Maastrichtian was at ~35 degrees N paleo-latitude (Robinson-Roberts and Kirschbaum, 1995), and the Western Interior Seaway was nearby (Atchley et al., 2004).

Considerably less is known about the southern biogeographic province compared to the long-studied northern areas. Big Bend is critical in understanding the southern province because it contains some of the southernmost Late Cretaceous vertebrate fossils in North America. There are some important differences between the two. First, because Big Bend was relatively distant from uplands in the late Campanian, the area had slower sedimentation rates compared to northern areas, resulting in condensed stratigraphic and faunal records in Big Bend (Lehman, 1991). Second, increased aridity, due to retreat of the Western Interior Seaway and uplift of western mountains, occurred in Big Bend earlier (late Campanian) than in the north and was an important influence on its paleocommunities. Evidence for aridity in Big Bend comes from dinosaur bonebeds from the upper Aguja that formed during periodic droughts severe enough to cause marshes to dry up (Davies and Lehman, 1989). Further evidence is from the numerous carbonate-cemented and pedogenic nodule rich conglomeratic channel lag deposits in the upper Aguja and Javelina formations (Sankey, 1998; Schiebout et al., 1997).

This paleoenvironmental and paleoecological picture for Big Bend during the late Campanian differs from contemporaneous northern areas such as Alberta. For example, the mid to late Campanian-aged Dinosaur Park formation of Alberta was an extremely fossil-rich unit that was deposited under high rates of sedimentation and fossil burial by a high-sinuosity fluvial system within an extensive mesic coastal lowland and under high subsidence rates in the Alberta foreland basin (Eberth and Hamblin, 1993). In contrast, the Aguja formation is considerably less fossil-rich and had considerably slower rates of sedimentation and fossil burial due to lower rates of subsidence within the Tornillo Basin.

Another major difference between these two areas was the influence of periodic aridity in Big Bend. For example, both the dinosaur bonebeds and paleocaliche in the soils were influenced by periods of aridity in Big Bend (Sankey, 1998; Sankey and Gose, 2001). Although Alberta also experienced periodically dry conditions, it was not until the late Maastrichtian, which is known for having the coolest and most variable climates of the Cretaceous (Barrera, 1994), with the exception of two Greenhouse events in the mid and late Maastrichtian (Nordt et al., 2003).

Southern North American Late Cretaceous vertebrate faunas are not as well known compared to northern assemblages, However, there are distinct differences between the vertebrates in the two areas. The Big Bend vertebrates were taxonomically distinct at the species level or higher from contemporaneous northern faunas such as from Alberta. These taxonomic differences are probably partly due to the distinct differences in climate between the northern and southern areas, with periodic aridity occurring earlier in Big Bend than in northern areas. Understanding the effects of

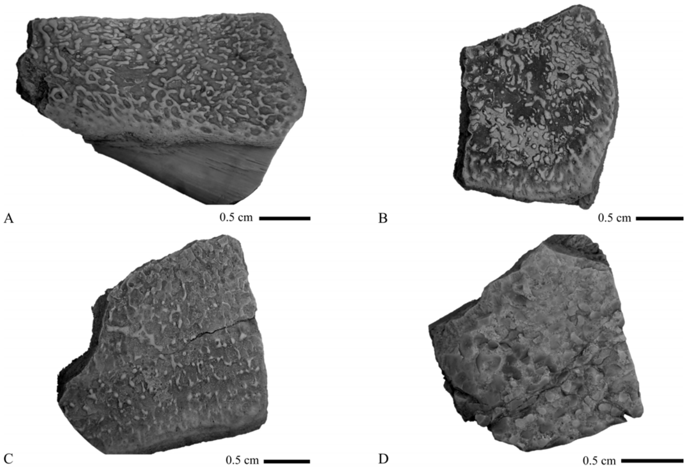

FIGURE 7. *Helopanoplia*, 841-5:8306 **(A)**; 834:17605 **(B)**; 726:17716 **(C)**; 834:8324 **(D)**.

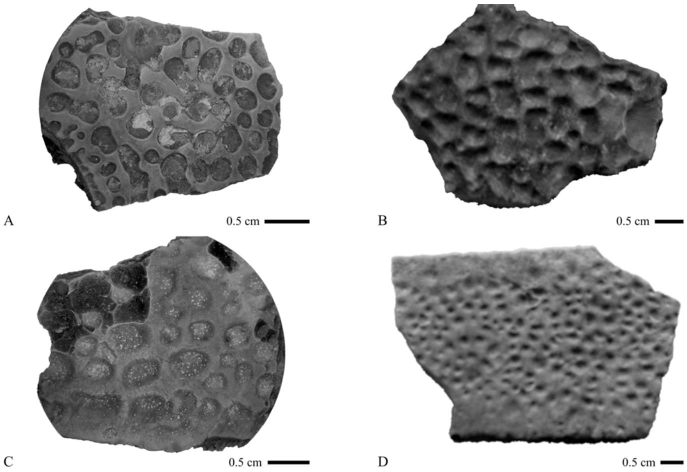

FIGURE 8. Trionychidae, 746:17676 (**A**); 841:8319 (**B**); 840:17657 (**C**); 834:8422 (**D**).

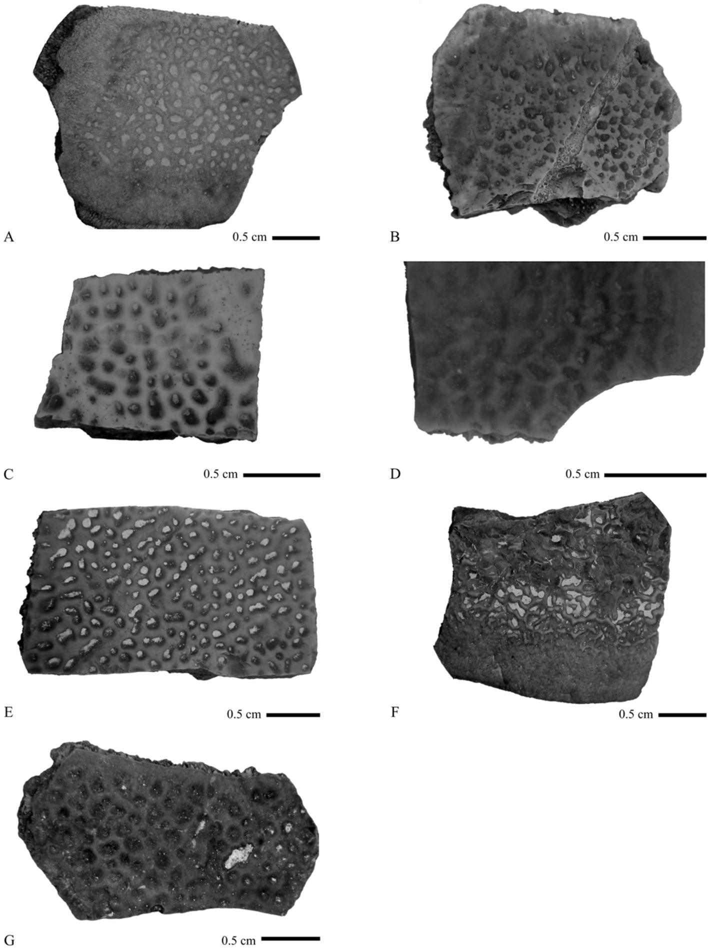

FIGURE 9. Trionychidae, 746:17612**(A)**; 746:17758**(B)**; 746:17613**(C)**; 833:17729 **(D)**; 842:17736 **(E)**; 842:17736 **(F)**; 834:17737 **(G)**.

climate change on the Late Cretaceous terrestrial ecosystems is important in order to separate the terrestrial from extraterrestrial factors involved in the Cretaceous/Tertiary extinctions.

Paleoclimate

Nordt et al. (2003) analyzed the stable isotopes of carbon and oxygen from carbonate nodules in paleosols from the uppermost Aguja, Javelina, and Black Peak Formations (late Campanian to early Paleocene, ~71 to 63.6 Ma) of Big Bend. They found two periods of atmospheric warming from 70 to 69 Ma and 65.5 to 65 Ma. These two greenhouse events, with higher atmospheric CO2 levels and temperatures, are also documented elsewhere from both oceanic and terrestrial deposits (Li and Keller, 1998a; 1998b; Barrera and Savin, 1999; Keller, 2001; Nordt et al., 2002; Olsson et al., 2001).

Corresponding with the Late Cretaceous to early Paleocene paleoclimatic changes documented in Big Bend, Atchley et al. (2004) recorded detailed paleoenvironmental changes in the paleosols on the inland floodplain deposits of the uppermost Aguja, the Javelina, and lower Black Peaks Formations. The effects of sea level fluctuations within the Western Interior Seaway could be seen in the types of paleosols that developed on the inland floodplain. Additionally, detailed study of the paleosols by Nordt et al. (2003) document that by the mid Maastrichtian, many of the Big Bend paleosols contain vertic properties, indicating the shrinkage and swelling of clays, which is an indicator of seasonality in temperature and/or precipitation (Atchley, pers. comm., 2006).

Turtle Diversity and Paleoclimate

From the Late Cretaceous of Alberta, Brinkman (2003) demonstrated a connection between turtle diversity and paleoclimate. Lower turtle diversity corresponded with lower temperatures during the mid-Campanian to early Maastrichtian, and higher turtle diversity corresponded with higher temperatures in the late Maastrichtian. To determine whether the turtle-paleoclimate pattern documented in Alberta occurred in Big Bend, turtle diversity from the Aguja and Javelina Formations were compared to the Nordt et al. (2003) paleoclimate record in Big Bend.

In Big Bend, turtles are by far the most diverse in the upper Aguja (Tomlinson, 1997; this paper), which is late Campanian to early Maastrichtian in age. The upper Aguja was deposited during a warm dry climate (Lehman and Wheeler, 2001; Nordt et al., 2003). Turtles are rare in the Javelina (Tomlinson, 1997), which is mid to late Maastrichtian; this corresponds to a time of general climate cooling (Barrera, 1994), although there are two short episodes of warming from 70 to 69 Ma and 65.5 to 65 Ma (Nordt et al., 2003). Thus, there appears to be a connection between paleoclimate and turtle diversity in Big Bend.

Tomlinson (1997) interpreted changes in Big Bend turtle diversity to be a result of changes in the physical environment from the late Campanian through early Tertiary. For example, she argues that the highest turtle diversity, from the Aguja, was due to the abundance of favorable turtle habitats within the coastal floodplain environments of the upper Aguja. She explains the lowest turtle diversity, from the Javelina, to be a result of

TABLE 1. Turtles from the Rattlesnake Mountain microsites, upper Aguja Formation, Big Bend National Park, Texas. Sites are listed in approximate stratigraphic order, left is lowest. Numbers in each column refer to total number of fossils from each site. Because specimen numbers listed in the systematic paleontology section may include lots or groups of specimens, the numbers shown in this table are higher than the of specimen numbers listed in the text.

TAXA	VL-833	VL-836	VL-837	VL-841	VL-838	VL-842	VL-726	VL-834	VL-746	VL-839	VL-747	VL-835	VL-840	Totals
Baenidae				1			5	1	2					18
Kinosternoidea cf. *Hoplochelys*				1			1		4					
Adocidae *Adocus*	3		2	2		3	5	8	3		1		1	28
Nanhsiung chelyidae *Basilemys*	3			4		2	4	4	5					23
Plastomeninae *Helopanoplia*	1		1	1			1	2	2					7
Trionychidae Genus et sp. indet.	11		9	20	1	33	74	119	211	1	1	3	3	486

less favorable turtle habitats within the inland floodplain and that the increase in turtle diversity in the lower Black Peaks was due to the return of favorable habitats within the more coastal floodplain environments.

However, paleoclimate and paleoenvironments are closely linked. During cooler drier climates, sea level lowered, ground water tables dropped, and the inland floodplain environments contained fewer favorable turtle habitats. Change in Big Bend turtle diversity is likely a result of both paleoclimatic and paleoenvironmental changes. Highest turtle diversity, in the upper Aguja, corresponds to higher temperatures, a high stand in sea level (TE2 of Atchley et al., 2004), and to abundant favorable habitats within the coastal and near coastal inland floodplain. In contrast, the lowest turtle diversity, in the Javelina Formation, corresponds to a general trend of decreasing temperatures during the Maastrichtian, with two short spikes of higher temperatures, from 70 to 69 Ma and from 65.5 to 65 Ma (Nordt et al., 2003). This corresponds to a decrease in habitats further on the inland floodplain, during a time of lower sea levels (HFE2).

However, in addition to changes in temperatures in the Late Cretaceous of Big Bend, another important factor was aridity. Arid conditions tend to have low turtle diversity. The first evidence for periodic aridity in the terrestrial record of Big Bend starts in the late Campanian. There are several lines of evidence for this aridity. One, the dinosaur bonebeds from the upper Aguja formed during periodic droughts severe enough to cause marshes to dry up (Davies and Lehman, 1989). Second, numerous carbonate-cemented and pedogenic nodule rich conglomeratic channel lag deposits occur the upper Aguja (Sankey, 1998; Schiebout et al., 1997). Third, well-developed paleosols containing abundant carbonate nodules occur in the upper Aguja; they first appear within the inland floodplain facies. At Rattlesnake Mountain, the start of this facies occurs immediately above the "Purple Hill" microsites. However, seasonally arid conditions became more intense and frequent in the Javelina Formation, as indicated by the numerous and large paleosols carbonate nodules and by the abundant vertisols (Atchley et al., 2004).

CONCLUSIONS

This work has significantly increased the Late Cretaceous turtle record for Big Bend, one of the southernmost terrestrial records in North America. The late Campanian turtle assemblage described here represents a snapshot of the final "healthy" Big Bend vertebrate paleocommunity before climatic and environmental changes occurred in this area in the late Campanian-early Maastrichtian. Directly above the level of this assemblage, the sediments of the uppermost Aguja and the Javelina Formations change to inland floodplain deposits, with well-developed paleosols and with abundant paleocaliche nodules. This boundary marks, in this area, the start of more severe seasonal aridity, loss of favorable turtle habitat, and a decrease in turtle diversity. Both the climatic and environmental changes resulted in loss of turtle habitats for many of the typical Aguja turtles.

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