1. Abstract

The Late Cretaceous vertebrates from Big Bend National Park, Texas are some of the southernmost from the Western Interior of North America. Considerably less is known about these southern vertebrates compared to those from northern areas like Alberta and Montana. Numerous vertebrate fossils were collected from microsites in the Aguja Formation (late Campanian), adding new information about the distinct southern Late Cretaceous ecosystems. Many vertebrates common in Big Bend are rare or absent from northern areas, reflecting paleoclimatic and paleoenvironmental differences, with periodic aridity occurring earlier in Big Bend than in northern areas.
Aguja, Cretaceous, Campanian, Big Bend National Park, Texas, vertebrates, dinosaurs, mammals, paleoclimate, magnetostratigraphy.

2. Introduction

2.1. Southern Biogeographic Province

During the late Campanian to early Maastrichtian, Big Bend was part of a southern dinosaur biogeographic province, the “Kritosaurus” fauna (Lehman 1997), within the Western Interior of North America (Fig. 1). The southern province, from southern Colorado to the south, was characterized by the Normapolles palynoflora, and had a warm climate with open-canopy woodlands (Wheeler & Lehman 2000; Lehman & Wheeler 2001). 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 & 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 & Lucas 2003.) Big Bend in the late Campanian to mid-Maastrichtian was at ~35 degrees N paleo-latitude (Robinson-Roberts & Kirschbaum 1995), and the Western Interior Seaway was nearby (Atchley et al. 2004).

(!!(Figure 1 near here!!))

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 Formation that formed during periodic droughts severe enough to cause marshes to dry up (Davies & 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 is 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 & 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. Additionally, although Alberta also experienced periodically dry conditions, it was not until the late Maastrichtian. The Maastrichtian is known for having the coolest and most variable climates of the Cretaceous (Barrera 1994), with the exception of two short Greenhouse events in the mid and late Maastrichtian (Nordt et al. 2003).

2.2. Importance of Microsites

Big Bend is a good example of how important microsite studies can be for areas that do not have abundant fossils. Information about the Late Cretaceous vertebrate faunas from
southern North America and from west Texas in particular would be missing a great deal of information without the fossils recovered from microsites. In Big Bend, large fossil fragments and bones are easily seen, so turtles, crocodylians, and large dinosaurs are well documented from this area. However, almost no information about Late Cretaceous mammals would be known from Big Bend without the collection of microsites, especially by screenwashing (Rowe et al. 1992; Sankey & Gose 2001). Collection of microsites in Big Bend has also produced important records of Late Cretaceous lizards, and these lizards are considerably different to northern ones (Rowe et al. 1992; Miller 1997; Nydam et al. in press). Additionally, most of our knowledge about Big Bend theropod dinosaurs (tyrannosaurids and small theropods), including dinosaur eggshells and juveniles, comes from microsites (Sankey 2001; 2005; Welsh 2004; 2005; Welsh & Sankey this volume).

Collection of microsites is also important because large sample sizes are produced which allow detailed paleoecological analyses. For example, from Late Cretaceous microsites in Alberta, paleocommunities changed as a response to changes in paleoenvironments (Brinkman 1990; Peng et al. 2001; Sankey et al. 2005a). Collection of Late Cretaceous microsites in Big Bend contributes important paleoecological information and allows similar paleoecological analyses to be done for this southern area.

2.3. Aguja Formation

The Aguja Formation is a widespread sedimentary unit in Big Bend (Fig. 2). 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 Formation are the giant crocodilian *Deinosuchus riograndensis* and the horned dinosaur *Chasmosaurus mariscalensis*; the hadrosaur *Kritosaurus* sp. is more abundant higher in the upper Aguja Formation (Lehman 1985). All are known from quarries yielding associated skeletons. The age of the microsites reported here was constrained by paleomagnetic analysis of the fine-grained sedimentary rocks. Magnetostratigraphic correlations to the base of chronozone 32 (Fig. 2), constrain the microsites to approximately 71 to 75 Ma (late Campanian to early Maastrichtian (Sankey 1998; Sankey & Gose 2001). Similar work constrains the upper Aguja Formation to the early Maastrichtian (Lehman 1985, 1989, 1990; Standhardt 1986).

2.4. Objectives of Study

The purpose of this study was to significantly increase our knowledge of this southern fauna by collecting large samples of vertebrates from microsites from the upper Aguja Formation.
in the Talley Mountain area. In particular, the goals were to: 1) determine the abundance of each vertebrate group within each microsite; 2) determine the paleoecological trends through the sampled section; and 3) provide a more detailed paleoecological reconstruction of the upper Aguja Formation.

3. Methods

3.1. Fossil Collection and Preparation

From the Talley Mountain Area, fossils were collected from five horizons of carbonate-cemented sandstone conglomerates containing numerous clasts of clay, pedogenic nodules, small bones and teeth, and large fragments of wood and bones. Collected rocks (1753 kg) were disaggregated by soaking in a 10-25% solution of acetic acid and screened through fine-mesh screens with 1 mm maximum openings (methods described in SANKEY 1998). Matrix was sorted with a dissecting microscope, and all identifiable fossils, even small fragments of teeth, were counted (Table 1) and percentages were calculated (Fig. 4).

3.2. Curation

All fossils are curated in the LSU Museum of Natural Science Vertebrate Paleontology Collections. VL, refers to vertebrate locality and V, refers to the particular vertebrate fossil specimen number. A complete LSUMG catalog number for a vertebrate fossil includes both of these numbers, separated by a colon; for example, 488:5566. Often only the second number is used. Additionally, all specimens have been collected within Big Bend National Park, and have been assigned NPS catalog numbers. Specimen and locality information will be available to qualified researchers by written request to the author.
3.3. Fossil Identifications

Fossil identifications were made in part by comparisons to collections at Louisiana State University Museum of Natural Science Vertebrate Paleontology Collections, Baton Rouge; Royal Tyrrell Museum of Paleontology, Drumheller, Alberta; University of Alberta Laboratory for Vertebrate Paleontology, Edmonton; University of California Museum of Paleontology, Berkeley; University of Texas, Texas Memorial Museum’s Vertebrate Paleontology Laboratory, Austin; University of Oklahoma, Oklahoma Museum of Natural History, Norman; and Weber State University, Department of Geosciences, Ogden, Utah. Literature used to identify the fossils were: ESTES 1964, BRYANT 1989, and WELTON & FARISH 1993 for fish; ESTES 1964, ESTES 1981, STANDHARDT 1986, BRYANT 1989, GAO & FOX 1996, MILLER 1997, and TOMLINSON 1997 for amphibians and reptiles; CURRIE et al. 1990, BASZIO 1997, and SANKEY et al. 2002 for dinosaurs; and ROWE et al. 1992 and WEIL 1992 for mammals.

3.4. 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); UALVP (University of Alberta, Lab for Vertebrate Paleontology, Edmonton).

4. Results

4.1. Microsites
Five microsites spanning 20 meters of stratigraphic section were collected from the Talley Mountain area. These microsites are stream channel deposits of carbonate-cemented sandstone conglomerates containing numerous clasts of clay, pedogenic nodules, small bones and teeth, and large fragments of wood and bones. Large samples of vertebrates (3,349 identifiable specimens) were collected. 38 taxa were identified, including fish (68%), sharks and rays (14%), crocodylomorphs (11%), dinosaurs (3%), amphibians (2%), turtles (not counted), squamates (1%), and mammals (1%) (figs. 3 & 4). The stratigraphically lowest microsite is adjacent to the AMNH quarry yielding the giant crocodylian Deinosuchus riograndonensis (COLBERT & BIRD 1954) and to the bonebeds of the horned dinosaur Chasmosaurus mariscalensis and the hadrosaur Kritosaurus sp. (LEHMAN 1982). Deposits become more terrestrial up section, from interdistributary marsh-bay facies at the base to inland floodplain facies at the top, and aquatic vertebrates (fish, sharks, and rays) decrease in abundance upsection, while terrestrial vertebrates (dinosaurs and mammals) increase in abundance.

4.2. Relative Abundance of Taxa

Fish

Two shark taxa indicate the influence of marine environments in the lowest microsites. First, the mitsukurinid shark, Scapanorhynchus texanus (Fig. 3.4-3.5) is present, but rare (less than 1%; Fig. 4; Table 1). Although modern mitsukurinids live in waters of 200 to 700 m depth, they can enter shallower water at night (CAPPETTA 1987). The second shark, Hybodus sp. (Fig. 3.1), is also present, but rare in the lowest site (less than 1%; Fig. 4; Table 1). S. texanus has been reported from the lower Aguja Formation (LEHMAN 1985), but this is the first record of Hybodus sp. for the Aguja Formation.
Several taxa indicate brackish to freshwater environments. The first, *Lissodus selachos* (Fig. 3.2-3.3) is the most abundant shark in the sites, but decreases in abundance upsection (82% from the lower site compared to 1% from the highest site; Fig. 4; Table 1). *L. selachos* is considered to be a brackish water shark, but both ESTES (1964) and CAPPETTA (1987) report that it probably also could live in fresh water. It is also common in the estuarine Terlingua fauna (ROWE et al. 1992) and is present in a freshwater deposit from the uppermost Aguja Formation (STANDHARDT 1986). The other taxa of sharks and rays from the sites are considerably less common than *L. selachos*. For example, *Squatirhina americana* (Fig. 3.9) is rare in the sites (less than 2%), but is considered a shallow marine to brackish water shark (WELTON & FARISH 1993). The sawfish *Ischyrhiza avonicola* (Fig. 3.8) is also rare (less than 1%). The paleoecology of *Ischyrhiza avonicola* was probably similar to modern sawfish (ESTES 1964), which are bottom dwellers that feed on fish and shellfish and live in near-shore areas in or around the mouths of rivers in warm to tropical seas. Although one modern Central American species of sawfish lives in fresh water (BRYANT 1989), most live in brackish and estuarine conditions (WELTON & FARISH 1993). *Onchopristis dunklei* (Fig. 3.6-3.7) is also rare (less than 3%). The paleoecology of *Onchopristis dunklei* was probably similar to modern sawfish. (These specimens extend the range of this taxon into the late Campanian). *Ptychotrygon* sp. (Fig. 3.10-3.11) is also rare (less than 1%). The paleoecology of *Ptychotrygon* sp. was also probably similar to modern sawfish. Dasyatid stingrays (Fig. 3.13) are rare (less than 4%). Stingrays are bottom dwellers; they feed on crustaceans, molluscs, and small fish and live in warm, shallow, coastal waters in the subtropics and tropics. They can enter estuaries and rivers, and some species live in freshwater (BUDKER 1971; WELTON & FARISH 1993). The gar, *Lepisosteus occidentalis* (Fig. 3.14-3.17), is the most common fossil from the microsites and from the Aguja Formation in general (LEHMAN
1985; Standhardt 1986; Rowe et al. 1992). It makes up 65% of all fossils from the lowest site, but only 29% from the highest. Its paleoecology was probably similar to the modern alligator gar, *L. spatula*, which lives in brackish to fresh water in large streams along the Gulf Coast (Wiley 1976; Bryant 1989).

(((Figure 3 near here)))

(((Table 1 near here)))

Amphibians

There are additional taxa that indicate aquatic environments, and possibly more freshwater environments. For example, two taxa of amphibians were identified. Both *Albanerpeton* (Fig. 3.22), which was considered by Estes (1964) to be primarily aquatic, and *Scapherpeton* (Fig. 3.23) are rare (5% and less; Fig. 4; Table 1). Amphibians have also been reported from the Terlingua fauna (Rowe et al. 1992) and from the uppermost Aguja Formation (Standhardt 1986).

Turtles

Other aquatic indicators are the trionychids turtles, which live in aquatic environments (Tomlinson 1997). Fragments of indeterminate trionychid turtles were recovered from the Talley Mountain microsites, but were not counted because numbers are dependent on degrees of fragmentation. The trionychid "Aspideretes" is the most common turtle from the upper shale member of the Aguja Formation (Lehman 1985; Rowe et al. 1992; Tomlinson 1997; Sankey 2006), but this level of identification was not possible with the Talley Mountain material.

Crocodylians
Crocodylians are more abundant aquatic taxa in the microsites, at 10 to 25% of the assemblage (Fig. 4; Table 1). Goniopholids (Fig. 3.32-3.33) and Brachychamps a (Fig. 3.34-3.37) are present in the microsites. Goniopholis cf. G. kirtlandicus was reported from the Terlingua fauna (Rowe et al. 1992). There are several teeth that cannot be assigned to taxa. However, they indicate a possibly more diverse crocodylian assemblage than is indicated by the taxonomic list (Table 1). The giant crocodylian, Deinosuchus (=Phobosuchus) riograndensis is present in the fauna. However, these teeth (Fig. 3.30-3.31) were surface collected from the area near the microsites and not recovered by screening the microsites. In order to keep collection methodology consistent, these specimens were not included in the specimen counts (Table 1). D. riograndensis was the largest crocodylian from the Aguja Formation and is common from the middle shale and base of the upper shale members (Lehman 1985). The type specimen of D. riograndensis was described from the Talley Mountain field area (Colbert & Bird 1954).

Lizards

Although the taxa indicating terrestrial environments are in the minority, there is a diverse range of taxa represented. The lizards, according to Rowe et al. (1992) and Miller (1997), represent unique taxa compared to northern assemblages. Within the Talley Mountain microsites, lizard fossils are rare (2% or less; Fig. 4; Table 1). Chamops sp. (Fig. 3.26) is a new record for Big Bend and Peneteius sp. nov. (Fig. 3.27-3.29) is a southern range extension (Nydam et al. in press).

Dinosaurs
Small dinosaur teeth and fragments of teeth provide important information on the
dinosaur community in Big Bend. From the Talley Mountain microsites, they represent 2 to 8% of the assemblage (Fig. 4). Dinosaurs include hadrosaurid, ceratopsian, pachycephalosaurid, tyrannosaurid, *Saurornitholestes* cf. *S. langstoni*, *Richardoestesia isosceles*, and two undetermined theropod taxa (SANKEY 2001). Many of the dinosaur teeth are small and may represent hatchlings or young individuals, evidence that many of these taxa nested in the area (see WELSH & SANKEY this volume). Although pieces of eggshells have been collected from the upper Aguja Formation near Rattlesnake Mountain, no complete eggs or nests have been found in Big Bend (SANKEY et al. 2005b; WELSH 2004, 2005; WELSH & SANKEY this volume).

Mammals

Mammal fossils are another important, but small part of the fauna (1 to 5%; Fig. 3.59-3.64; Fig. 4; Table 1). They are important because certain species can provide valuable dating constraints. Mammals in the fauna include the multituberculates *Cimolomys* sp., *Mesodma* sp., cf. *Cimexomys*, cf. *Paracimexomys* and the marsupial *Alphadon* cf. *A. halleyi* and are assigned to the Judithian Land Mammal Age (SANKEY 1998; SANKEY & GOSE 2001).

5. Discussion

5.1. Significance of Big Bend Microsites

Because large samples of vertebrates were collected in the Talley Mountain area from five microsites spanning 20 meters of section, paleoenvironmental changes could be tracked during a short span of time. From this local section, deposits become more terrestrial upsection,
with interdistributary marsh-bay facies at the base and inland floodplain facies at the top. The aquatic vertebrates, such as fish (gar), which represent fresh to brackish water environments and shark and rays, which represent brackish to marine water environments, decrease in abundance upsection, from 79% from the lowest site (within the interdistributary marsh-bay facies) to 61% from the highest site (within the inland floodplain facies), while terrestrial vertebrates, such as dinosaurs and mammals, increase in abundance upsection.

Although microfossil sites provide large sample sizes and diverse taxa, two biases in the samples are observed. First, there is a bias against large fossils, such as bones from turtle, dinosaur, and large crocodylians, due to size-sorting during transport within the streams. Second, there is a bias against fragile fossils, such as from amphibians and lizards, due to destruction during transport.

Sampling and analysis of microsites from the Aguja Formation have helped flesh out the Late Cretaceous ecosystems in Big Bend, which prior to this work was primarily based on isolated finds of large vertebrates such as the crocodylian *Deinosuchus riograndensis* and dinosaurs *Chasmosaurus mariscalensis* and *Kritosaurus* sp. The vertebrate assemblage from the Talley Mountain microsites is similar to vertebrates from the Terlingua microsite, also from the lower part of the upper Aguja Formation (Rowe et al. 1992), which confirms the uniqueness of the Aguja Formation fauna.

5.2. Southern Biogeographic Province

Late Cretaceous vertebrate faunas from southern parts of North America are still poorly known compared to northern assemblages. However, their composition and change during the Late Cretaceous is important to document. Big Bend is one of the southernmost terrestrial
records for the Late Cretaceous of North America. Therefore, finding and recovering numerous Late Cretaceous vertebrates from microsites in Big Bend has contributed important information about this unique fauna.

The fossils reported here from the Tally Mountain microsites significantly increase our knowledge for this southern area. Vertebrates from Big Bend are taxonomically distinct at the species or genus level from contemporaneous northern faunas, confirming the uniqueness of this southern fauna. Additionally, preliminary results indicate that dinosaurs in Big Bend were less diverse than contemporaneous northern areas. The late Campanian Big Bend dinosaur assemblage was more similar to the late Maastrichtian southern Alberta (Scollard Formation) dinosaur assemblage in the following ways: *Richardoestesia isosceles* was more abundant than *R. gilmorei*; *Troodon* and *Dromaeosaurus* were absent or rare; and pachycephalosaurids were present to common (Sankey 2001; Sankey et al. 2005b).

Differences between the southern and northern areas and their vertebrate faunas were primarily due to differences in climate, with periodic aridity occurring earlier in Big Bend than in northern areas. The Aguja Formation dinosaur bonebeds probably resulted from periodic droughts, severe enough to cause the marshes to dry up (Davies & Lehman 1989) and paleocaliche to form in soils. Post-drought flooding, possibly even flash floods, would have eroded and transported soil and vertebrate remains, quickly depositing them within streams, forming conglomeratic beds with an appreciable fossil content, which are microsites (Sankey 1998; Sankey & Gose 2001). This paleoenvironmental picture differs from contemporaneous northern areas such as Alberta. During the late Campanian in Alberta, the Dinosaur Park Formation was deposited within an extensive mesic coastal lowland (Eberth & Hamblin 1993), and Alberta did not experience aridity until the late Maastrichtian.
5.3. Future Focus: Late Cretaceous Climate Change

Understanding the detailed effects of 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 (Sankey 2006). Beginning in the late Campanian (~74 Ma), a cooling trend and corresponding drop in sea level and retreat of the Western Interior Seaway caused changes in paleoenvironments and paleocommunities in the Western Interior of North America. Then in the Maastrichtian, two short greenhouse events occurred, corresponding to minor extinctions before the final K/T mass extinctions (Nordt et al. 2003). What were the effects of these climatic changes on the vertebrate paleocommunities? Can we use climatically sensitive vertebrate groups, for example turtles and crocodilians, to track these changes? Future work in Big Bend will track paleocommunity changes corresponding with climatic and environmental changes through the section by making further collections from microsites and by analyzing associated paleosol carbonates. By studying the Big Bend area, we may identify a relationship between vertebrates and climate such that we can use the vertebrates to interpret climate in other areas.

6. Summary and Conclusions

Discovery and collection of microsites from the upper Aguja Formation (late Campanian) in Big Bend National Park, Texas have produced numerous vertebrate fossils, significantly improving our knowledge of the vertebrates from this extreme southern part of North America. The vertebrates differ from contemporaneous northern faunas at the species or genus level, confirming the uniqueness of the southern vertebrate fauna. Differences between the southern
and northern areas and vertebrate faunas are primarily due to differences in climate, with warmer and drier climates occurring in the south starting in the late Campanian, but not until the late Maastrichtian in the north. The southern vertebrate faunas were lower in diversity compared to contemporaneous northern assemblages due to these climatic differences. Similar results would be expected from other faunas further to the south, such as those from Mexico.

7. Acknowledgments

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FIGURE 1-- Late Cretaceous paleogeography. 1, Maastrichtian paleogeographic reconstruction of North America (redrawn from ZIEGLER & ROWLEY 1998). Star is location of Big Bend National Park, Texas. Arrows show close land connections during retreat of the Western Interior Seaway in the Maastrichtian. 2, Big Bend National Park, west Texas with Aguja Formation outcrops stippled. Locations of Talley Mountain and Terlingua field areas are shown by arrows. Both field areas have microsites that have yielded numerous vertebrates from the upper Aguja Formation (late Campanian).
FIGURE 2--Stratigraphy of the Aguja Formation, Big Bend National Park, Texas. 1, Lithostratigraphy of the Aguja Formation modified from ROWE et al. (1992), showing positions of the Talley Mountain (SANKEY 1998) and Terlingua (ROWE et al. 1992) sites. Stratigraphic position of the Talley Mountain 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. 2. Magnetostratigraphic correlations of upper Aguja Formation from Talley Mountain area (from SANKEY & GOSE 2001).
FIGURE 4—Talley Mountain stratigraphic section, with the five microsite positions shown. Vertebrate specimen counts displayed in pie charts.
TABLE 1. Taxa from Talley Mountain microsites. Microsites are listed from highest to lowest stratigraphic position, from left to right. VL-140 and 489 are the same microsite, but were collected by different groups and in different years: 140 was collected by Schiebout and Standhardt; 489 by Sankey)

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