

LATE CAMPANIAN SOUTHERN DINOSAURS, AGUJA FORMATION, BIG BEND, TEXAS

JULIA T. SANKEY

Royal Tyrrell Museum of Paleontology, P.O. Box 7500 Drumheller, Alberta T0J 0Y0 Canada

ABSTRACT—One of the southernmost North American late Campanian microvertebrate assemblages was collected from the upper Aguja Formation, Big Bend National Park, Texas. The dinosaurs provide additional evidence that distinct southern and northern terrestrial vertebrate provinces occurred contemporaneously during this time due to latitudinal differences in temperature and rainfall. Southern areas, such as west Texas, were warm dry, with non-seasonal climates, and with open-canopy woodlands; they appear to be less fossil-rich and less diverse than northern areas. Nine dinosaurs are present, based on isolated teeth: pachycephalosaurid; hadrosaurid; ceratopsian; tyrannosaurid; *Sauromitholestes* cf. *langstoni* (Sues, 1978); *Richardoestesia* cf. *gilmorei* (Currie et al., 1990); a new species of *Richardoestesia*, which is named here; and an undetermined theropod unlike any previously described. Previous reports of *Troodon* sp. from the Talley Mt. and Terlingua microsites are mistaken; they are a pachycephalosaurid. Many of the dinosaur teeth are small, and are probably from juveniles or younger individuals, evidence that dinosaurs nested in the area. Paleocologically, the upper Aguja was probably more similar to the lower and more inland faunas of the Scollard Formation (~66 Ma) of Alberta than to contemporaneous northern faunas: both had drier, open environments and lower dinosaur abundance. This connection between climate and dinosaur abundance suggests that climatic factors were important in the Late Cretaceous dinosaur extinctions.

INTRODUCTION

DURING THE late Campanian and early Maastrichtian, distinct southern and northern terrestrial vertebrate provinces occurred in the Western Interior of North America. Lehman (1997) named two late Campanian provinces based on taxonomic differences: the northern “*Corythosaurus*” fauna (Wyoming and north) and the southern “*Kritosaurus*” fauna. The southern province is characterized by the *Normapolles* palynoflora, and had a warm, dry, non-seasonal climate with open-canopy woodlands. The northern province is characterized by the *Aquillapollenites* palynoflora, and had a temperate and more humid climate, with a more closed-canopy forest. North–south temperature and rainfall differences were the main factors that produced this pattern (Lehman, 1997).

The Aguja Formation, west Texas, contains some of the southernmost late Campanian to Maastrichtian terrestrial vertebrates in North America (Lehman, 1985; Standhardt, 1986; Rowe et al., 1992; Sankey, 1998). The Aguja is less fossil-rich than contemporaneous northern faunas, so less is known about it. However, before this present work, a direct comparison between the Aguja and contemporaneous northern faunas had not been made. In this paper I: 1) describe the dinosaur teeth from a new late Campanian Aguja fauna from Big Bend National Park, Texas (Table 1); 2) compare them to those from Albertan Campanian through Maastrichtian deposits (Table 2); and 3) discuss the paleoecological and biogeographic implications.

Aguja Formation.—The Late Cretaceous Aguja Formation (Figs. 1 and 2) is widespread in the Big Bend area of west Texas. It is an eastward thinning unit of 135 to 285 m of paralic and marine sandstones interbedded with shale and lignite (Lehman, 1985). The upper shale member of the Aguja represents the last of the pre-Laramide tectonic sedimentation in the area (Lehman, 1991). In the lower part are 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, with variegated mudstones and sandstones with conglomeratic lags of paleo-caliche nodules, represents fluvial environments in a deltaic coastal plain and inland floodplain (Lehman, 1985).

Talley Mountain fossil sites, Big Bend, Texas.—Previous to this work, the lower part of the upper shale member of the Aguja in the Talley Mountain (Mt.) area produced the type giant crocodylian *Deinosuchus riograndensis* (Colbert and Bird, 1954) and bonebeds (WPA quarries) of the horned dinosaur *Chasmosaurus mariscalensis* and the hadrosaur, *Kritosaurus* sp. Deposits become more terrestrial upsection, from interdistributary marsh-bay facies at the base to inland floodplain facies at the top (Lehman, 1982, 1985).

Fossils were collected from five horizons spanning 20 m in the lower portion of this section, and record environmental change. Within this section, the chondrichthyans, actinopterygians, and salamanders decrease in abundance upsection due to increased aridity partly resulting from the continued marine regression from the area. Evidence that the area was arid comes from the abundant carbonate-cemented sandstone conglomerates that contain pedogenic nodules. The source for the carbonate was probably caliche-rich soils in the area, which develop in arid environments. The conglomerates are lag deposits of large stream channels that may represent major down-cutting events in the area related to the marine regression and its consequent drop in base level. Moreover, they may represent sudden flooding events, possibly related to droughts and subsequent flash floods (Sankey, 1998).

The five microvertebrate horizons collected are from these carbonate-cemented, pedogenic-nodule, sandstone conglomerate channel lag deposits. A large sample of the conglomerates were collected (1,753 kg), and broken down in a 25 percent solution of acetic acid. The resulting residue was washed through fine-meshed screens and the concentrate picked for small fossils. Thirty eight taxa of fish, amphibians, turtles, squamates, crocodylians, dinosaurs, and mammals were identified from small teeth and bones from these microsites. All fossils have been catalogued within the LSUMNS (Louisiana State University Museum of Natural Science), and detailed locality descriptions are on file there (Sankey, 1998). Locality information on the WPA quarries, 1 and 3, is on file in the Vertebrate Paleontology Laboratory, Texas Memorial Museum, University of Texas at Austin.

The dinosaur teeth in this sample are mostly small and fragmentary because of taphonomic and fossil preparation factors. However, because there are few records of the theropod dinosaurs from the Aguja, this sample is an important contribution. Identifications of dinosaur teeth were based on tooth and denticle size, overall shape, and cross-sectional shape; on comparison to extensive and well-studied collections of dinosaur teeth at the RTMP

¹ Present address: South Dakota School of Mines and Technology, Museum of Geology and Department of Geology and Geological Engineering, 501 E. Saint Joseph St., Rapid City 57701 <Julia.Sankey@sdsmt.edu>

TABLE 1.—Dinosaurs from the Talley Mountain microsities (VL-488 to VL-492) and the Terlingua (Terl.) local fauna (Rowe et al., 1992). *Pachycephalosaur teeth from both the Talley Mt. microsities (Sankey, 1998) and the Terlingua local fauna (Rowe et al., 1992) were originally identified as cf. *Troodon*. Teeth were referred to *Dromaeosaurus* in Sankey (1998) and Rowe et al. (1992); however, they do not have a twisted anterior carina, characteristic of this taxon (Currie et al., 1990) and are referred to here as family and genus undetermined.

Taxa	VL-488	VL-489/140	VL-491	VL-490	VL-492	Terl.
ORNITHISCHIA						
Ankylosauridae Osborn	—	—	—	—	—	x
Hadrosauridae Cope	—	x	x	x	—	x
Ceratopsidae Marsh	x	—	—	—	x	x
Pachycephalosauridae Sternberg	—	x*	—	—	—	x*
Ornithischia-indet.	—	x	—	—	x	x
SAURISCHIA						
Tyrannosauridae Osborn	—	x	—	—	—	x
<i>Sauromitholestes</i> Sues cf. <i>langstoni</i>	—	x	x	—	x	x
<i>Richardoestesia</i> Currie, Rigby, and Sloan cf. <i>gilmorei</i>	—	x	—	—	—	x
<i>Richardoestesia isosceles</i> n. sp.	—	x	—	—	x	—
Family and genus undetermined	x	x	—	—	—	—
Theropoda-indet.	x	x	x	—	—	x

(Royal Tyrrell Museum of Paleontology); and on the literature, especially Currie et al. (1990) and Baszio (1997b).

The Terlingua was the first late Campanian microvertebrate fauna reported for the Aguja (Rowe et al., 1992; Weil, 1992; Cifelli, 1995). Taxonomically, the Talley Mt. and Terlingua microsite assemblages are similar, confirming the uniqueness of the Aguja fauna. However, there are paleoenvironmental and taphonomic differences between the two. The Terlingua microsite was deposited in an estuarine environment and has more fossils and higher taxonomic diversity. Both faunas are late Campanian. Because both are from the lower part of the upper shale member of the Aguja and contain similar mammals they are probably similar in age (Sankey, 1998).

Abbreviations cited.—The following abbreviations are used: WPA, Work Progress Administration; RTMP (Royal Tyrrell Museum of Paleontology, Drumheller, Alberta); UALVP (University of Alberta, Lab for Vertebrate Palaeontology, Edmonton); LSUMG, Louisiana State University Museum of Geoscience (a division of the LSU Museum of Natural Science), Baton Rouge, Louisiana; VL, vertebrate locality; and V, vertebrate fossil specimen. 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. All measurements are given in millimeters (mm): AP, anteroposterior length; W, greatest width; and FABL, fore-aft basal length.

SELECTED SYSTEMATIC PALEONTOLOGY

Order ORNITHISCHIA Seeley, 1888

Family PACHYCEPHALOSAURIDAE Sternberg, 1945

PACHYCEPHALOSAURIDAE indeterminate

Figure 3.4,3.5

Description.—V-6117 is a complete crown of a tooth; the root is missing. It is 3.7 mm tall (proximal-distal), 2.9 mm wide (labial-lingual), with a FABL (fore-aft basal tooth length) of 3.8 mm. The tooth is triangular in lateral outline and convex. The crown is constricted at the base, and a large cingulum is present. Large, worn serrations are present on both the anterior and posterior edges of the crown.

Material Examined.—LSUMG 140:6117.

Discussion.—The shape and size of the tooth closely resemble pachycephalosaurid teeth in the RTMP collections, in Baszio (1997b), and in Sues and Galton (1987). Baszio (1997b) discussed the differences between pachycephalosaur and ankylosaur teeth, and also pointed out that pachycephalosaur teeth were misidentified as *Troodon* in Rowe et al. (1992). Sankey (1998) also originally misidentified LSUMG 140:6117 as *Troodon*. With these corrections, no *Troodon* has been found in the Aguja Formation.

Order ORNITHOPODA Marsh, 1881

Family HADROSAURIDAE Cope, 1869

HADROSAURIDAE indeterminate

Figure 3.1

Description.—The tooth crowns and tooth crown fragments are small. Two complete tooth crowns (V-5700 and V-5538) are 2 and 4 mm in diameter, respectively and have a star-shaped occlusal outline.

Material examined.—LSUMG 140:5562, 5578; 489:5538, 5700; 491:5544; 490:5570.

Discussion.—Hadrosaur skulls and mandibles contained rows of many, densely packed, interlocking teeth that formed tooth batteries. Although hadrosaur identifications are mainly based on skull characteristics (Weishampel and Horner, 1990), Horner (1990) did include dental characteristics to distinguish the hadrosaurinae and the lambeosaurinae. In the former's dentary teeth, the angle between the crown and root is less than 130 degrees and the teeth are diamond shaped (Horner, 1990).

Because no teeth with roots were recovered from the conglomerates, identifications to the subfamily level are not possible. However, the most common hadrosaur in the Aguja is *Kritosaurus* cf. *navajovius*, and it is likely that these teeth are from this taxon. The other fragmentary teeth are also referred to hadrosauridae based on their shape and on the absence of the rugose external surface present in ceratopsian teeth. Based on the small sizes, all of these teeth (including tooth fragments) are probably from juveniles or hatchlings.

Hadrosaurid teeth, including some from very young individuals, were the most common dinosaur teeth found from the Terlingua local fauna (Rowe et al., 1992). Hadrosaur teeth were also recovered from the uppermost Aguja in the Dawson Creek area (VL-113), and the small teeth (probably from juveniles) are the most common dinosaur fossil from this locality (Standhardt, 1986).

Kritosaurus sp., *K.* cf. *navajovius*, and an unidentified lambeosaurine have been found elsewhere in the Aguja. *Kritosaurus* sp. bones were found in the WPA 1 and 3 quarries and in other localities in the Talley Mt. field area (Lehman, 1982; Davies, 1983; Davies and Lehman, 1989). Within the WPA quarries, the hadrosaur bones were associated with ceratopsian, crocodylian, ankylosaur, and a small number of tyrannosaur, small theropod, fish, and turtle fossils. WPA #3 had the largest percentage of hadrosaur bones (66 percent; Davies and Lehman, 1989). The *Kritosaurus* faunal assemblage in the Aguja, dominated by bones of this dinosaur, accumulated in coastal marshes and swamps and is found in carbonaceous claystones associated with crevasse sand sheets (Lehman, 1985).

TABLE 2—Dinosaur records based only on teeth recovered from microvertebrate collections from Alberta (Currie et al., 1990; Baszio, 1997a, b) and Texas (Aguja; Terlingua and Talley Mt. microsites only; Rowe et al., 1992 and Sankey, 1998). See Table 1 caption for note on the record of *Dromaeosaurus* from the Aguja. Geologic formations are listed in chronologic order across the top of the table. Milk River (MR); Oldman and Dinosaur Park (OM/DP); Aguja (AG; lower part of the upper shale member); Horseshoe Canyon (HC); and Scollard (SC).

Taxa	MR	OM/DP	AG	HC	SC
ORNITHISCHIA					
Ankylosauridae Osborn	x	x	x	—	x
Hypsilophodontidae Dollo	x	—	—	—	—
Hadrosauridae Cope	x	x	x	x	x
Pachycephalosauridae Sternberg	x	x	x	x	x
Protoceratopsidae Granger and Gregory	x	—	—	—	x
Ceratopsidae Marsh	—	x	x	x	x
SAURISCHIA					
Tyrannosauridae Osborn	x	x	x	x	x
<i>Dromaeosaurus albertensis</i> Mathew and Brown	—	x	—	x	x
<i>Saurornitholestes cf. langstoni</i> Sues	x	x	x	x	x
<i>Richardoestesia cf. gilmorei</i> Currie, Rigby, and Sloan	x	x	x	x	x
<i>Richardoestesia isosceles</i> n. sp.	x	x	x	x	x
<i>Paronychodon lacustris</i> Cope	x	x	—	x	x
<i>Troodon formosus</i> Leidy	—	x	—	x	x

Because hadrosaurs are the most common dinosaur fossils in the Aguja (Lehman, 1985), it is surprising that so few hadrosaur fossils were found in the conglomerates; the only ones were teeth from hatchlings or juveniles. These small teeth are approximately the same size as the other dinosaur teeth from the conglomerates. Obviously this is a taphonomic bias toward teeth of a particular size, and most hadrosaur teeth would have been a larger-sized clast than is typically found in the conglomerates.

Suborder CERATOPSIA Marsh, 1890
 Family CERATOPSIDAE Marsh, 1888
 CERATOPSIDAE indeterminate
 Figure 3.2

Description.—Specimens are tooth crown fragments of large teeth, probably from adults. The external surface of the single ridge has many small and round denticles.

Material examined.—LSUMG 488:6230; 492:5581.

Discussion.—The shape of the tooth fragments and the presence of the denticulate ridge closely resemble ceratopsian teeth.

They compare well to a ceratopsid tooth fragment from the uppermost Aguja (LSUMG 113:1373; Standhardt, 1986). Ceratopsian bones and teeth were also found from the Terlingua local fauna, but in lesser abundance than hadrosaurs (Rowe et al., 1992).

Ceratopsian bones are rare in the upper shale member of the Aguja, but bonebeds, for example WPA-1 in the Talley Mt. area (Lehman 1982, 1985, 1989; Davies and Lehman, 1989), of *Chasmosaurus mariscalensis* do occur, and a nearly complete skull was collected from Rattlesnake Mountain (Forster et al., 1993). Although the specimens from the conglomerates are only small tooth fragments, they were recovered near WPA-1 (V-6230; 4.5 m above the level WPA-1) and probably represent this taxon.

The WPA-1 quarry produced the largest number of ceratopsian bones of any of the WPA quarries (representing a minimum of ten individuals and 72 percent of the bones; Lehman, 1982; Davies and Lehman, 1989). This particular accumulation of ceratopsian and hadrosaurian bones is thought to represent a mass mortality event: possibly a herd was concentrated around a drying watering hole during a severe drought in the area (Davies and Lehman, 1989).

Except for unusual bonebeds like WPA-1, the general scarcity of ceratopsians in the Aguja may explain why only one partial tooth has been recovered from the conglomerates. In addition,

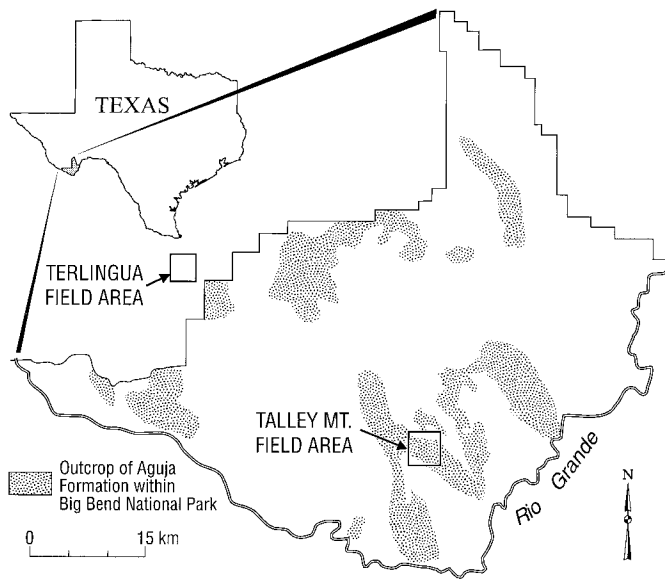


FIGURE 1—Map of Big Bend National Park, west Texas showing area of Aguja Formation outcrops in the Park (stippled). Talley Mountain and Terlingua fossil localities are shown by arrows.

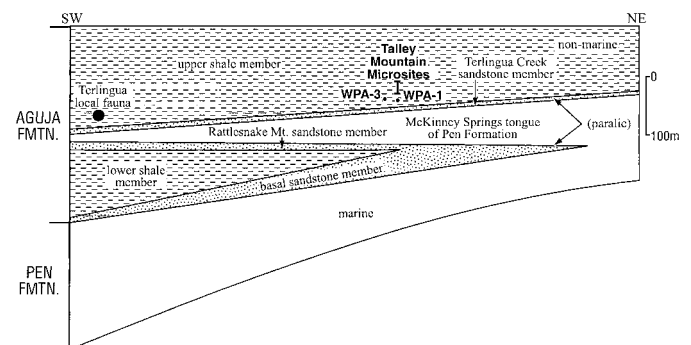


FIGURE 2—Aguja Formation stratigraphy (modified from Rowe et al., 1992) showing positions of the Terlingua (Rowe et al., 1992) and Talley Mt. fossil microsites (Sankey, 1998). The stratigraphic positions of the Talley Mt. microsites above the Terlingua Creek Sandstone are based on Lehman (1985, pl. 3 and written commun., 1998). Formal members of the Aguja Formation are capitalized; informal members are not. WPA-1 and 3 (Work Progress Administration) quarries.

there is a taphonomic bias against recovering large teeth from the conglomerates.

Order SAURISCHIA Seeley, 1888
Family TYRANNOSAURIDAE Osborn, 1905
TYRANNOSAURIDAE indeterminate
Figure 3.3

Description.—V-5580 is a small (2 mm long) carina fragment. Denticles are short (0.5 mm proximally–distally) and wide (0.3 mm at base, anteriorly–posteriorly and 0.5 mm, labially–lingually). Their tops are round in outline; not pointed. There are large spaces (0.1 mm wide) between denticles, and 2.5 denticles/mm.

Material examined.—LSUMG 489:5580.

Discussion.—Tyrannosaurid teeth are more stout and robust than other theropod teeth, and although they are also somewhat laterally compressed, they are more rounded in cross-sectional outline (Abler, 1997). Denticles on both anterior and posterior carinae are approximately equivalent in size. They are large, chisel-shaped, and wider (labially–lingually) than long (proximodistally), and there are about 3/mm (Currie et al., 1990). More details of tyrannosaurid teeth are reported in Abler (1997) and Baszio (1997b).

Even a small tooth fragment such as V-5580 can be identified as tyrannosaurid for the following reasons. Of all the theropods, tyrannosaurids have the largest and widest denticles, especially in the labial–lingual direction. They also have the largest and deepest interdenticle spaces, making the denticles the most widely spaced of any theropod. Also diagnostic is the carina in cross-section: the angle of the tooth below the carina is the widest of any theropod because these teeth are so round and robust. Additionally, denticles are not pointed, but have slightly rounded to flattened tips.

Juvenile tyrannosaurid teeth (including fragments) are often found with small theropod teeth in Late Cretaceous microvertebrate sites (Currie et al., 1990). V-5580 fits the above descriptions for tyrannosaurid teeth and compares well with illustrations in Currie et al. (1990) and Abler (1997). There are many small carina fragments in the collection, but all have considerably smaller denticles and are probably from small theropods. Based on this collection from the conglomerates, tyrannosaurids were rare in the fauna.

Fewer tyrannosaurids than small theropods have been found in the Aguja; most are isolated teeth from channel lags (Lehman, 1985). Although theropod teeth were recovered from the WPA quarries, they were not identified (Lehman, 1982; Davies and Lehman, 1989). Rowe et al. (1992) reported that there was at least one large tyrannosaurid in the Terlingua local fauna and Standhardt (1986) reported three tyrannosaur morphotypes from the uppermost Aguja. This scarcity in the Talley Mt. and other microsites from the Aguja suggests that tyrannosaurids were uncommon in this area. This scarcity makes further investigation of dinosaur teeth from microsites in the Aguja especially important.

Genus SAURORNITHOLESTES Sues, 1978
SAURORNITHOLESTES cf. LANGSTONI Sues, 1978
Figure 3.8–3.10

Description.—All specimens are teeth or fragments of teeth. V-5659 is an unshed tooth. Specimens are small (less than 7 mm long), flattened labio-lingually, and sharply recurved. FABLs vary from 2.6 to 9 mm. Denticles on the posterior carinae are considerably larger than those on the anterior carinae; although not all anterior carinae have denticles. Denticles are longer than wide: 0.1 to 0.2 mm antero-posteriorly in width and 0.1 to 0.3 mm high. Denticle tips are rounded to sharply pointed (pointing toward the tip of the tooth), depending partly on the condition of

the tooth. Unshed, less worn teeth, such as V-5659 (Fig. 3.10), have sharper denticle tips. Interdenticle spaces vary in size, but are usually small, and the denticles closely spaced. Posterior denticle counts vary from 4–7/mm. In basal cross-section, the teeth are flattened ovals; some even have a slight indentations on the lingual surfaces.

Material examined.—LSUMG 140:6139, 6140, 6183, 6185; 489:5659; 491:5950; 492:5158.

Discussion.—(Modified from Currie et al., 1990 and Baszio, 1997b). *Saurornitholestes* teeth are recurved, sharply pointed, and laterally compressed. Denticles are straight and narrow (labially–lingually), hook distally near the tooth tip, and have deep interdenticle slits. Posterior carinae have approximately five denticles/mm and the anterior carinae have seven denticles/mm, although many teeth have none. Immature individuals have fewer and smaller denticles than more mature ones (Farlow et al., 1991). Unworn denticle shape varies, and is not always sharply pointed as stated in Currie et al. (1990), but is always chisel-shaped and not rounded as in *Troodon* (Baszio, 1997b). Compared to *Richardoestesia gilmorei*, *Saurornitholestes* teeth are more recurved, flattened, and have larger, longer, sharper denticles. *Troodon* teeth are even more recurved, and have the largest, sharpest denticles of any theropod. *Dromaesaurus* teeth are rounder, more robust, have more flattened denticle tips, and have distinctive anterior carinae that twist lingually.

The specimens are all small, flattened, recurved teeth that compare well to *Saurornitholestes langstoni* in the RTMP collections and literature (Currie et al., 1990; Rowe et al., 1992; Fiorillo and Currie, 1994; Baszio, 1997b). Small carinae fragments with denticles that closely resemble *Saurornitholestes langstoni* are present in the collection, but are too fragmentary for definite referral.

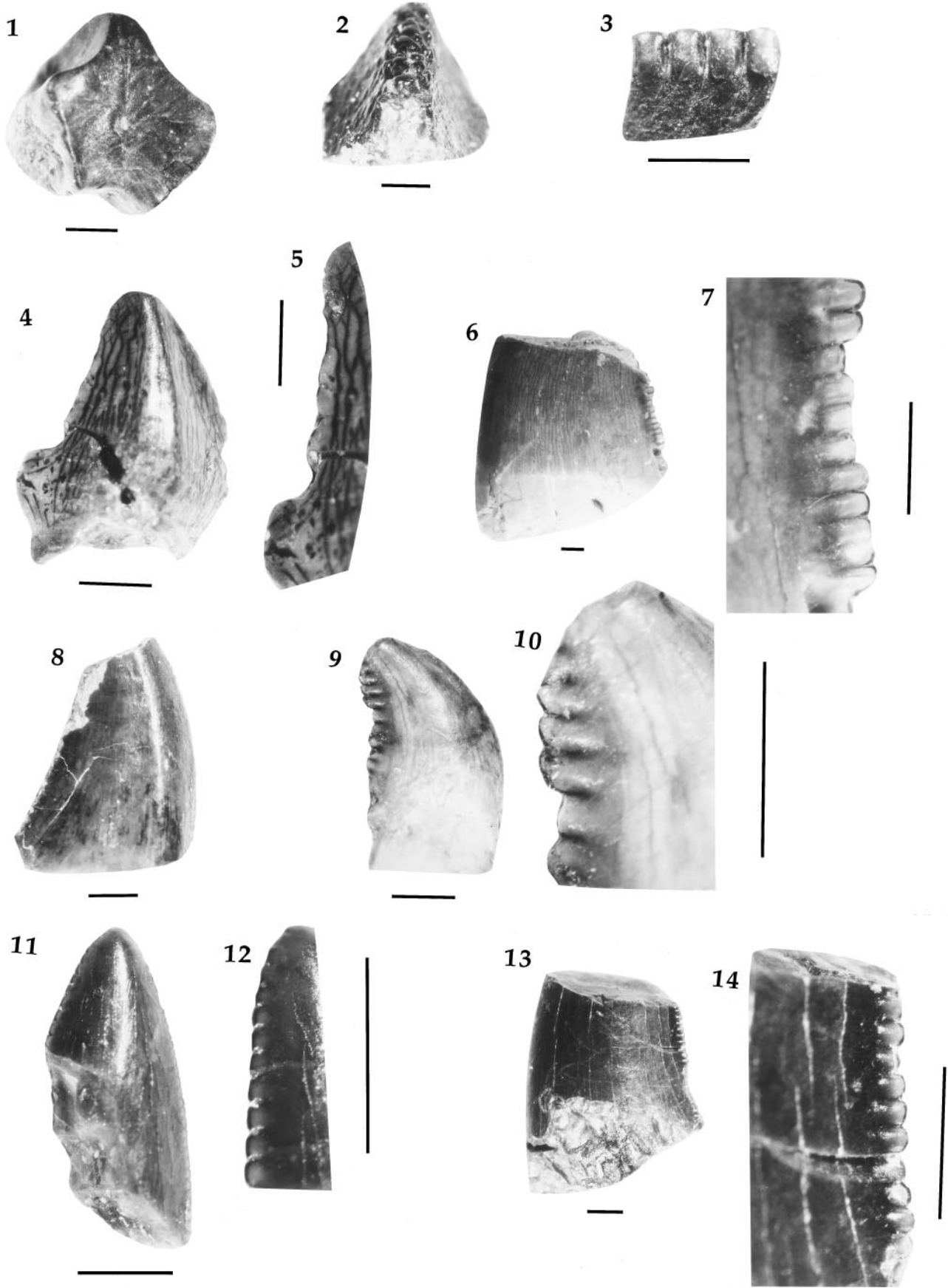
Saurornitholestes langstoni teeth are the most common small theropod teeth recovered from the Campanian through Maastrichtian deposits in Alberta (Baszio, 1997a). Each individual had approximately 60 small, socketed teeth. Teeth from the type *S. langstoni* (TMP 74.10.5) are 8.9 and 9.2 mm long and have FABLs of 3.9 and 4.5 mm respectively (Currie et al., 1990).

Saurornitholestes cf. *langstoni* has been identified in the Milk River, Oldman, Dinosaur Park, Horseshoe Canyon, and Scollard formations of Alberta; the Frenchman Formation of Saskatchewan; and the Lance Formation of Wyoming. It is the most abundant theropod in the Milk River and Horseshoe Canyon formations, but is slightly less abundant in the Dinosaur Park and Scollard formations (Baszio, 1997a). This pattern suggests that *Saurornitholestes langstoni* may have preferred wetter, more closed habitats. This is supported by the fact that many *Saurornitholestes* specimens were recovered from the Terlingua microsite, an estuarine deposit within the Aguja (Rowe et al., 1990), but few from the Talley Mt. microsites. Several *Saurornitholestes* sp. teeth were recovered from the uppermost Aguja Formation (LSUMG VL-113; Standhardt, 1986).

Infraorder MANIRAPTORA Gauthier, 1986
Family unknown
Genus RICHARDOESTESIA Currie, Rigby, and Sloan, 1990

RICHARDOESTESIA cf. *GILMOREI* CURRIE, RIGBY, AND SLOAN, 1990 *Description.*—V-6237 is a fragment of a small tooth (~2 mm long). It is oval in basal cross-section (1.1 mm, labial–lingual; 2.2 mm, antero–posterior), slightly flattened (labial–lingual), and slightly recurved. Denticles are minute (8–9/mm), uniform in size along the carinae, closely packed (with minute interdenticle spaces), and are not present on the anterior carinae of this specimen. Denticles have flattened to slightly rounded tips. The tooth is indented at the base as in bird teeth (Currie, personal commun., 1999).

Material examined.—LSUMG 489:6237.



Discussion.—(Modified from Currie et al., 1990 and Baszio, 1997b) *Richardoestesia gilmorei* was a small theropod that had long jaws with little lateromedial curvature. Dentaries have 18–19 teeth. Teeth are small, flattened labiolingually, recurved, and pointed. Anterior mandibular teeth are relatively straight and slightly convex; posterior mandibular teeth are shorter and more recurved. Most characteristic are the minute denticles (0.15 mm long), the smallest of any Cretaceous theropod. Although denticles are variable in shape, their tips are straight. Denticles are usually only present on the posterior carinae, and there are up to 9 denticles/mm.

Richardoestesia gilmorei (Currie et al., 1990) was described from the Judith River Formation of Alberta. Although isolated teeth are variable, they can be distinguished from *Richardoestesia* n. sp. (straight form) by the curvature in the proximal part of the tooth. Teeth are typically smaller than those of *Saurornitholestes*, but are also oval to slightly labial-lingually flattened in cross section. Denticles in *Richardoestesia* are unique: they are minute, the smallest of any theropod. Denticles are usually not present on the anterior carinae, but if they are present, are minute.

V-6237 matches the descriptions and illustrations of *R. gilmorei* (Currie et al., 1990). Because *R. gilmorei* is such a common taxon in the Judith River Group of Alberta, it is interesting that only one specimen was recovered from the Talley Mt. microsites, and only seven specimens were referred to *Richardoestesia* from the Terlingua local fauna (personal observation, 1998). More specimens of *Richardoestesia* n. sp. than *R. gilmorei* were recovered from the Talley Mt. microsites.

Genus RICHARDOESTESIA Currie, Rigby, and Sloan, 1990
RICHARDOESTESIA ISOSCELES new species
Figure 3.11, 3.12

Diagnosis.—(Modified from *Richardoestesia* sp. in Currie et al., 1990 and Baszio, 1997b). Teeth straight; narrow; shaped like an isosceles triangle in lateral view (as mentioned for *Richardoestesia* sp. in Currie et al., 1990 and in Baszio, 1997b). Shape of tooth in basal cross-section is labio-lingually flattened oval. Denticles minute (0.1 mm in height and in antero-posterior width); square; uniformly-sized from base to tip of tooth; extend length of carinae. Anterior denticles, if present, often considerably smaller than posterior denticles. Interdenticle spaces usually minute and barely visible; denticles closely spaced. Denticle tips straight or faintly rounded, but not pointed. 7–11 denticles/mm.

Etymology.—In reference to the shape of the tooth in lateral view: an isosceles triangle.

Type.—Holotype, LSUMGS 489:6238.

Referred specimens.—LSUMG 489:6233, 6234, 6235; 492:6264; A.M. 8113 (fig. 69b in Estes, 1964); RTMP 91.170.9.

Occurrence.—Aguja Formation, Big Bend National Park, Texas; Milk River, Oldman, Dinosaur Park, Horseshoe Canyon, and Scollard formations, Alberta; Frenchman Formation, Saskatchewan; and Lance Formation, Wyoming (Currie et al., 1990; Baszio, 1997a); Hell Creek Formation, North and South Dakota (personal observation).

Discussion.—Currie et al. (1990) first recognized that straight teeth of *Richardoestesia*, referred to as *Richardoestesia* sp., probably represent a taxon distinct from *R. gilmorei*. Baszio (1997b)

and Peng (1997), both working on dinosaur teeth from Late Cretaceous deposits in Alberta, recognized additional specimens of the straight *Richardoestesia* form, also referring them to *Richardoestesia* sp.

Based on large collections of dinosaur teeth in the RTMP, teeth from *R. isosceles* and *R. gilmorei* have been identified from the Milk River, Oldman, Dinosaur Park, Horseshoe Canyon, and Scollard formations of Alberta; the Frenchman Formation of Saskatchewan; the Lance Formation of Wyoming (Baszio, 1997a); and the Hell Creek Formation of North and South Dakota (personal observation). However, the two taxa have different relative abundances at different sites, reflecting their different paleoecologies: *R. isosceles* is abundant in the Milk River, Scollard, Lance, and Hell Creek formations and is rare in the Oldman, Dinosaur Park, and Horseshoe Canyon formations; the latter units representing wetter, more closed habitats (Baszio, 1997a). The presence of *R. isosceles* in the Talley Mt. area supports the interpretation that the Aguja had dry, open habitats. Baszio (1997b) suggested that *R. isosceles*, with its small, straight, and pointed teeth, may have been specialized as a fish-eater. Alternatively, it may have been specialized for insect-eating.

This is the first record of *R. isosceles* in the Aguja Formation. Rowe et al. (1990) mentioned that small, bird-like theropod teeth occur in the Terlingua fauna; perhaps *R. isosceles* is also present. The presence of *R. isosceles* in the Aguja Formation demonstrates for the first time that this was widely occurring taxon within the Western Interior.

Family and genus undetermined
Figure 3.6, 3.7, 3.13, 3.14

Description.—Both specimens are large fragments of large, robust, and recurved teeth. FABLs of V-5483 and V-6239 are 9.0 and 5.5 mm, respectively. In basal cross-section, V-6239 is round to oval, but V-5483 is slightly more flattened labio-lingually. Denticles are small (0.2 mm high and 0.1 mm wide) and there are 3.5 to 5.5/mm. Denticle tips are only slightly rounded, and are clearly not pointed. Interdenticle spaces are narrow, making the denticles closely spaced.

Material examined.—LSUMG 488:5483; 489:6239.

Discussion.—The teeth are most similar to *Dromaeosaurus* in the RTMP collections and in Currie et al. (1990) and Baszio (1997b). They are large, stout (round to oval in cross section), and recurved, and have denticles with flat (not pointed) tips. However, in Talley Mt. teeth, the anterior carinae do not twist lingually as they do in *Dromaeosaurus* (Currie et al., 1990). The teeth are different from *Saurornitholestes*, which are smaller, more sharply recurved, more flattened labial-lingually, and have more sharply pointed denticles. Based on tooth size, the teeth could also be from young tyrannosaurids, but the denticle shape and size is not tyrannosaurid-like. Because the teeth do not fit any previous descriptions, they may be from a new taxon.

DISCUSSION

Prior to this work, the Terlingua local fauna was the only late Campanian microvertebrate fauna known for the Aguja. The Talley Mt. microsites provide important additional information on

←

FIGURE 3—Dinosaur teeth from the Talley Mt. microsites. 1, Hadrosaurid; hatchling or juvenile (LSUMG 489:5538, occlusal view); 2, Ceratopsian tooth fragment (LSUMG 488:6230, occlusal view); 3, Tyrannosaurid tooth fragment, close-up of denticles (LSUMG 489:5580); 4, 5, Pachycephalosauridae, lateral view and close-up (LSUMG 140:6117); 6, 7, Undetermined family and genus, lateral view and close-up of denticles; (LSUMG 488:5483); 8, *Saurornitholestes* cf. *langstoni*, lateral view (LSUMG 140:6139); 9, 10, *Saurornitholestes* cf. *langstoni* unshed tooth, lateral view and close-up of denticles; (LSUMG 489:5659); 11, 12, *Richardoestesia isosceles* n. sp., lateral view and close-up of denticles; (LSUMG 489:6238); 13, 14, Undetermined family and genus, lateral view and close-up of denticles; (LSUMG 489:6239). All scale bars are 1 mm.

the dinosaurs that were present in the area. Late Campanian microsites in such southern areas are important because we know less about the composition and diversity of dinosaurs from these areas. Although Lehman (1997) considers the late Campanian northern and southern vertebrate assemblages distinct ("Corythosaurus" and "Kritosaurus" provinces), before this study a direct comparison between the southern- and northernmost contemporaneous microsites had not been made.

The Aguja faunas are late Campanian and are some of the southern-most of this age. Albertan faunas of this age are some of the northern-most known and are from the uppermost Dinosaur Park (~75 Ma) and lowermost Horseshoe Canyon (~72 Ma) formations (Eberth and Ryan, 1992). Numerous Campanian through Maastrichtian microvertebrate sites, yielding hundreds of isolated dinosaur teeth, have been collected by the RTMP and UALVP in Alberta. These collections, from the Milk River (84–82.5 Ma), Oldman and Dinosaur Park (79.5–74 Ma), Horseshoe Canyon (72–67 Ma), and Scollard (65–60 Ma) formations span 20 mys (Eberth and Ryan, 1992). The taxonomy and relative abundances of the dinosaur teeth from these deposits were studied by Baszio (1997a, 1997b) and the general paleoecological trends by Brinkman (1990). I compared the dinosaur teeth from the Aguja fauna (Talley Mt. and Terlingua microsites only) to those from Alberta (Tables 1 and 2).

Based on dinosaur teeth from microvertebrate sites only, more dinosaur taxa occur in the individual Albertan formations than in the Aguja. Although compared to contemporaneous formations from Alberta and Montana, the Aguja has a smaller outcrop area and has had fewer paleontologists working on it (Lehman, 1997), its lower dinosaur diversity is probably real. Of the theropods, *Saurornitholestes* cf. *langstoni* (Sues, 1978), *Richardoestesia isosceles*, and *R. gilmorei* (Currie et al., 1990) occur in both areas. However, *Troodon*, *Paronychodon*, and *Dromaeosaurus*, present in all but the Milk River Formation in Alberta, are absent from the Aguja. Further work in progress on the Aguja will clarify this pattern.

In Alberta, *R. isosceles* is more abundant in the geologic units that represent open, drier habitats (Baszio, 1997a), and its presence in the Talley Mt. microsites probably reflects similar conditions. Paleoecologically, the late Campanian Talley Mt. microsites are more similar to the lower Scollard Formation (~66 Ma) than to more contemporaneous units like the upper Dinosaur Park and lower Horseshoe Canyon formations, which represent wetter conditions with more closed vegetation. The dinosaur assemblages from the Aguja and Scollard formations have the following similarities: 1) *R. isosceles* is more abundant than *R. gilmorei*; 2) *Troodon* and *Dromaeosaurus* are absent or rare; and 3) pachycephalosaurids are present to common.

Many of the teeth from the Talley Mt. microsites are small and probably represent hatchlings or young individuals. This is the first evidence that many of these dinosaur taxa nested in the area. Although pieces of eggshells were collected by Standhardt from the Late Cretaceous deposits in Big Bend (personal observation, 1998), no complete eggs or nests have been found in the area. Geologic evidence in the Talley Mt. area, such as the *Chasmosaurus* bonebeds (Davies and Lehman, 1989) and the sedimentology of the carbonate cemented sandstone conglomerates (Sankey, 1998), suggest that the area was not only well drained, but was arid.

CONCLUSIONS

The Talley Mt. microsites and associated magnetostratigraphy support Lehman's (1997) biogeographic division of southern and northern late Campanian vertebrate faunas. Southern faunas were paleoecologically distinct from contemporaneous northern faunas. Animals were probably more arid-adapted and less diverse. In

fact, the dinosaur faunas of the Talley Mt. and Terlingua microsites, both from the lower part of the upper shale member of the Aguja, are more similar, paleoecologically, to the Latest Cretaceous (~66 Ma) Scollard (Alberta) and Hell Creek formations (South and North Dakota) in the following: 1) *Richardoestesia isosceles* is more abundant than *R. gilmorei* (Currie et al., 1990); 2) *Troodon* and *Dromaeosaurus* is absent to rare; and 3) pachycephalosaurids are present to common.

The connection between drier climate and lower dinosaur diversity in the late Campanian of west Texas predicts that lower diversity in the latest Cretaceous northern assemblages was also due to climatic differences. This conclusion has implications for the causes of the Late Cretaceous extinctions; a progressive decrease in dinosaur diversity throughout Maastrichtian times may reflect local environmental changes and gradual extinction.

ACKNOWLEDGMENTS

This work was part of my Ph.D. dissertation (1998) at Louisiana State University in Baton Rouge, and I thank J. Schiebout (major advisor), A. Bouma, J. Hazel, J. Lorenzo, J. Wrenn, and G. Wise (committee members) for advice, and the LSU Museum of Natural Science and the Department of Geology and Geophysics for financial and technical support. The Dinosaur Society and the U.S.–Canada Fulbright Program supported the Albertan side of this research and I greatly appreciate the support and advice from my Albertan advisors, R. Fox, P. Currie, D. Eberth, and especially to D. Brinkman for many hours of discussion about Albertan theropods. Fossils were collected in Big Bend National Park (BBNP) under permit #BIBE-N-50.001. Assistance is appreciated from BBNP personnel P. Koepf, V. Davilla, and M. Fleming. S. Ting and R. Hubert did the initial lab work for this research, and museum volunteers (T. Aherns, C. Moore, J. Ramcharan, M. Schneider, and S. Wachter) helped with the remainder. J. Sankey assisted with the field work. M. Eggart (LSU) drew Figures 1 and 2. B. Creisler gave advice on the correct nomenclature for *Richardoestesia isosceles*. I also appreciate discussions with T. Lehman, T. Rowe, W. Langston, and A. Weil and comments from two reviewers. Access to the fossil collections of the Royal Tyrrell Museum of Paleontology (Drumheller, Alberta) and the Vertebrate Paleontology Laboratory, Texas Memorial Museum, University of Texas at Austin is appreciated.

REFERENCES

- ABLER, W. L. 1997. Tooth serrations in carnivorous dinosaurs, p. 740–741. In K. Padian, and P. J. Currie (eds.), *Encyclopedia of Dinosaurs*. Academic Press, San Diego.
- BASZIO, S. 1997a. Investigations on Canadian dinosaurs: palaeoecology of dinosaur assemblages throughout the Late Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg*, 196:1–31.
- BASZIO, S. 1997b. Investigations on Canadian dinosaurs: systematic palaeontology of isolated dinosaur teeth from the Latest Cretaceous of south Alberta, Canada. *Courier Forschungsinstitut Senckenberg*, 196:33–77.
- BRINKMAN, D. B. 1990. Paleoeology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 78:37–54.
- CIFELLI, R. L. 1995. Therian mammals of the Terlingua Local Fauna (Judithian), Aguja Formation, Big Bend of the Rio Grande, Texas. *Contributions to Geology, University of Wyoming*, 30:117–136.
- COLBERT, E. H., AND R. T. BIRD. 1954. A gigantic crocodile from the Upper Cretaceous beds of Texas. *American Museum Novitates*, 1688:1–22.
- COPE, E. D. 1869. Synopsis of the extinct Batrachia, Reptilia, and Aves of North America. *Transactions American Philosophical Society*, 14:1–252.
- CURRIE, P. J., J. K. RIGBY, JR., AND R. E. SLOAN. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada, p. 107–

125. In K. Carpenter and P. J. Currie (eds.), *Dinosaur Systematics: Perspectives and Approaches*. Cambridge University Press, Cambridge.
- DAVIES, K. 1983. Hadrosaurian dinosaurs of Big Bend National Park, Brewster County, Texas. Unpublished M.A. thesis, University of Texas at Austin, Austin, 236 p.
- DAVIES, K., AND T. M. LEHMAN. 1989. The WPA Quarries, p. 32–42. In A. B. Busbey, III and T. M. Lehman (eds.), *Vertebrate Paleontology, Biostratigraphy, and Depositional Environments, Latest Cretaceous and Tertiary, Big Bend Area, Texas*. Guidebook, Field Trip Nos. 1a, b, c, Society of Vertebrate Paleontology 49th Annual Meeting, Austin, Texas.
- EBERTH, D. A., AND M. RYAN. 1992. Stratigraphy, depositional environments and palaeontology of the Judith River and Horseshoe Canyon formations (Upper Cretaceous) South Alberta, Canada. Abstracts AAPG/SEPM Annual Meeting, Calgary, 1–107.
- ESTES, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. University of California Publications in Geological Sciences, 49:1–187.
- FARLOW, J. O., D. L. BRINKMAN, W. L. ABLER, AND P. J. CURRIE. 1991. Size, shape, and serration density of theropod lateral teeth. *Modern Geology* 16:161–198.
- FIORILLO, A. R., AND P. J. CURRIE. 1994. Theropod teeth from the Judith River Formation (Upper Cretaceous) of southcentral Montana. *Journal of Vertebrate Paleontology*, 14:74–80.
- FORSTER, C. A., P. C. SERENO, T. W. EVANS, AND T. ROWE. 1993. A complete skull of *Chasmosaurus mariscalensis* (Dinosauria: Ceratopsidae) from the Aguja Formation (late Campanian) of west Texas. *Journal of Vertebrate Paleontology*, 13:161–170.
- GAUTHIER, P. 1986. Saurischian monophyly and the origin of birds, p. 1–55. In K. Padian (ed.), *The Origin of Birds and the Evolution of Flight*. Memoirs of California Academy of Science, 8.
- HORNER, J. R. 1990. Evidence of diphyletic origination of the hadrosaurian (Reptilia: Ornithischia) dinosaurs, p. 179–187. In K. Carpenter and P. J. Currie (eds.), *Dinosaur Systematics: Perspectives and Approaches*. Cambridge University Press, Cambridge.
- LEHMAN, T. M. 1982. A ceratopsian bone bed from the Aguja Formation (Upper Cretaceous), Big Bend National Park, Texas. Unpublished M.A. thesis, University of Texas at Austin, Austin, 209 p.
- LEHMAN, T. M. 1985. Stratigraphy, sedimentology, and paleontology of Upper Cretaceous (Campanian-Maastrichtian) sedimentary rocks in Trans-Pecos, Texas. Unpublished Ph.D. dissertation, University of Texas at Austin, Austin, 299 p.
- LEHMAN, T. M. 1989. *Chasmosaurus mariscalensis*, sp. nov., a new ceratopsian dinosaur from Texas. *Journal of Vertebrate Paleontology*, 9: 137–162.
- LEHMAN, T. M. 1991. Sedimentation and tectonism in the Laramide Tornillo Basin of west Texas. *Sedimentary Geology*, 75:9–28.
- LEHMAN, T. M. 1997. Late Campanian dinosaur biogeography in the Western Interior of North America, p. 223–240. In D. A. Wolberg and E. Stump (eds.), *Dinofest International, Proceedings of a Symposium Sponsored by Arizona State University*. Special Publication, Academy of Natural Sciences, Philadelphia.
- MARSH, O. C. 1881. Principal characters of American Jurassic dinosaurs, Pt. V. *American Journal of Science* (ser. 3), 21:417–423.
- MARSH, O. C. 1888. A new family of horned Dinosauria from the Cretaceous. *American Journal of Science*, 36:477–478.
- MARSH, O. C. 1890. Additional characters of the Ceratopsidae with notice of new Cretaceous dinosaurs. *American Journal of Science* (ser. 3), 39: 418–426.
- MATTHEW, W. D., AND B. BROWN. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. *Bulletin of the American Museum of Natural History*, 46:367–385.
- OSBORN, H. F. 1905. *Tyrannosaurus* and other Cretaceous carnivorous dinosaurs. *Bulletin of the American Museum of Natural History*, 21: 259–265.
- PENG, J. 1997. Palaeoecology of vertebrate assemblages from the upper Cretaceous Judith River Group (Campanian) of southeastern Alberta, Canada. Unpublished Ph.D. dissertation, University of Calgary, Calgary, 312 p.
- ROWE, T., R. L. CIFFELLI, T. M. LEHMAN, AND A. WEIL. 1992. The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos, Texas. *Journal of Vertebrate Paleontology*, 12:472–493.
- SANKEY, J. T. 1998. Vertebrate paleontology and magnetostratigraphy of the upper Aguja Formation (late Campanian), Talley Mountain area, Big Bend National Park, Texas. Unpublished Ph.D. dissertation, Louisiana State University, Baton Rouge, 263 p.
- SEELEY, H. G. 1888. The classification of the Dinosauria. *Report British Association for the Advancement of Science*, 1887:698–699.
- STANDHARDT, B. R. 1986. Vertebrate paleontology of the Cretaceous/Tertiary transition of Big Bend National Park, Texas. Unpublished Ph.D. dissertation, Louisiana State University, Baton Rouge, 298 p.
- STERNBERG, C. M. 1945. Pachycephalosauridae proposed for dome-headed dinosaurs, *Stegoceras lambei* n. sp., described. *Journal of Paleontology*, 19:534–538.
- SUES, H.-D. 1978. A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta Canada. *Zoological Journal of the Linnean Society*, 62:381–400.
- SUES, H.-D., AND P. M. GALTON. 1987. Anatomy and classification of the North American Pachycephalosauria (Dinosauria: Ornithischia). *Palaeontographica Abt. A*, 198:1–40.
- WEIL, A. 1992. The Terlingua local fauna: stratigraphy, paleontology, and multituberculate systematics. Unpublished M.A. thesis, University of Texas at Austin, Austin, 120 p.
- WEISHAMPEL, D. B., AND J. R. HORNER. 1990. Hadrosauridae, p. 534–561. In D. B. Weishampel, P. Dodson, and H. Osmolska (eds.), *The Dinosauria*. University of California Press, Los Angeles.