

## THEROPOD TEETH FROM THE JUDITH RIVER FORMATION (UPPER CRETACEOUS) OF SOUTH-CENTRAL MONTANA

ANTHONY R. FIORILLO<sup>1</sup> and PHILIP J. CURRIE<sup>2</sup>

<sup>1</sup>Museum of Paleontology, University of California,  
Berkeley, California 94720;

<sup>2</sup>Royal Tyrrell Museum of Palaeontology, P.O. Box 7500,  
Drumheller, Alberta, Canada T0J 0Y0

**ABSTRACT**—Theropod teeth are some of the most diagnostic fossils from dinosaur assemblages, with taxonomic utility to the genus or even species level. One hundred and twenty-nine teeth, representing five theropod taxa, have been recovered from eight localities along a 75 km east-west transect in the Judith River Formation of south-central Montana. Unlike the pattern of distribution observed for the Judith River Formation in Alberta, no geographic or temporal differentiation of the theropod faunas seems to have occurred in this formation in south-central Montana.

### INTRODUCTION

Since the first discoveries of isolated dinosaur teeth (e.g., Leidy, 1856), it has been recognized that teeth have some degree of taxonomic utility. With the discovery of more complete specimens through time, some taxa based on teeth have later been recognized as *nomen dubium* (e.g., *Trachodon mirabilis*). However, rather than dispute all dinosaur taxa based on isolated teeth, it has been shown that isolated dinosaur teeth have differing degrees of taxonomic utility. For example, Horner (1990) showed that the teeth of hadrosaurs are diagnostic at the subfamily level. In contrast, Coombs (1990) showed that isolated teeth of ankylosaurs and pachycephalosaurs provide very little taxonomic utility at the subordinal level. Of these dinosaurian groups, only the teeth of small theropods provide reliable criteria for generic and specific identification (Currie et al., 1990).

Isolated theropod teeth are fairly common in dinosaur-bearing deposits. This abundance is not surprising considering that most tooth-bearing theropods had 50 or more teeth in their jaws (Currie et al., 1990) and that these teeth, as with those of most other dinosaurs, were continually replaced during the life time of these animals. The vast majority of these isolated teeth lack roots and represent shed teeth. Although some may have fallen out as their replacement teeth erupted, the majority were probably shed when theropods bit prey animals. Theropods apparently did not routinely chew the bones of their prey (Fiorillo, 1991a), but the bite forces generated by these animals would have been more than sufficient to remove any loose teeth. The common association of shed theropod teeth with the carcasses of herbivorous dinosaurs (Buffetaut and Suteetham, 1989; Gallup, 1989; Horner, 1987; Ostrom, 1970) provides direct evidence of this scenario. Indirect evidence is provided by the frequency

of recovery of teeth that have passed through the digestive system. These teeth are easily identified because their surfaces have been etched by digestive acids which often remove the enamel entirely. One suspects that if the teeth fell out at any time other than prey utilization, they would have been swallowed. Of course, some of the teeth lost during feeding would also have been ingested, but overall the recovery of swallowed, shed teeth is less than 5 percent.

The purpose of this paper is three-fold. First, this report, utilizing characters provided by Currie et al. (1990), will document both the geographic and stratigraphic distribution of various theropod teeth found in the Judith River Formation of south-central Montana. In fulfilling this objective, this paper will then update the theropod data presented for the respective distributions in an earlier paper (Fiorillo, 1989a). The second point of this paper will be to describe an unusual series of theropod teeth recovered from several sites in southern Montana, while the third aspect of this paper is to document the relative abundances of each taxon present and to discuss the paleoecological significance of the entire sample.

In the early 1980s, an amateur fossil collector uncovered the first bones from a major dinosaur bone bed in the Judith River Formation of south-central Montana. Subsequent investigation of this formation by joint University of Pennsylvania/Academy of Natural Sciences of Philadelphia field-crews have discovered numerous other fossil sites (Fig. 1) ranging from bone beds to microvertebrate localities (Dodson, 1986; Fiorillo, 1987a, b, 1989a, b, 1991b).

The Judith River Formation in the area of south-central Montana (Golden Valley and Wheatland counties) varies in thickness from 70 m to more than 120 m. Contact with the underlying Claggett Formation and the overlying Bearpaw Formation can usually be readily located lithologically and paleontologically

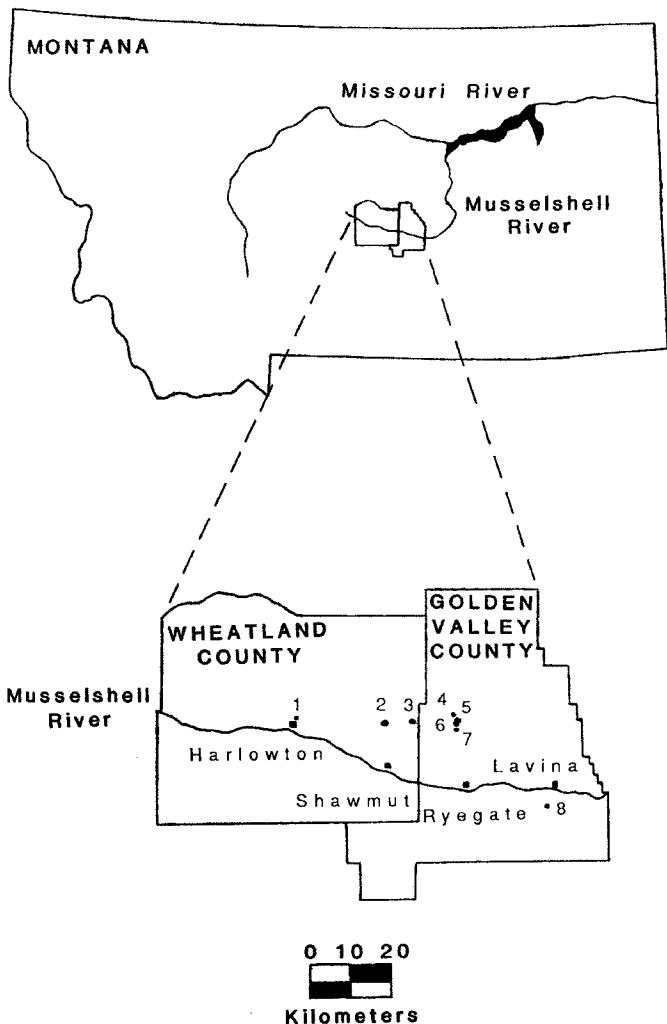


FIGURE 1. Locations of the eight sites that yielded the theropod teeth discussed in this report. The numbers 1-8 correspond to the following localities; (1) Ox Hill Quarry, (2) Antelope Head Quarry, (3) Careless Creek Quarry, (4) Emily's Ankle Quarry, (5) Top Cat Quarry, (6) Hidden Valley Quarry, (7) Blackbird Ridge Quarry, and (8) Jensen Ranch Mini-site.

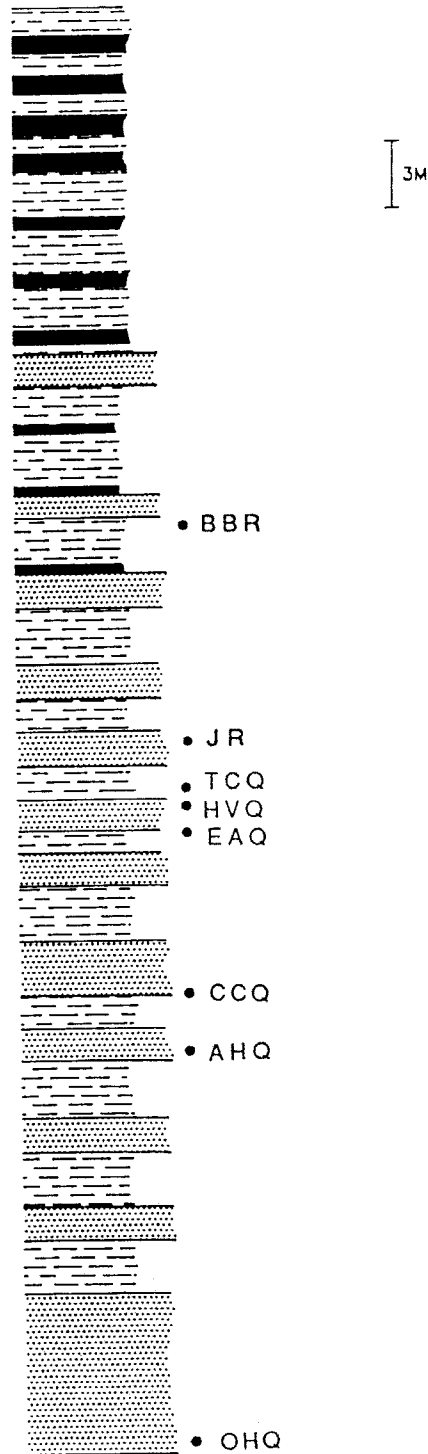


FIGURE 2. Generalized stratigraphic section for the Judith River Formation in the Musselshell Valley with the relative stratigraphic position of each of the quarries mentioned in this paper. The dotted pattern corresponds to sandstone bodies, the hyphenated pattern refers to siltstones, and the black pattern corresponds to coal (both lignitic and bituminous).

(Fiorillo, 1989a, b, 1991b). Although bone-producing levels are scattered throughout the lower three-quarters of the Judith River Formation, the majority of the quarries are concentrated within the middle third of the formation (Fig. 2).

The fauna from this area includes fish, salamanders, crocodiles, turtles, lizards, champsosaurs, pterosaurs, dinosaurs and mammals. Of the dinosaur remains, the majority are isolated elements. Careless Creek Quarry is noteworthy for its yield of associated dinosaur material (Dodson, 1986; Fiorillo, 1987b, 1989a, 1991b).

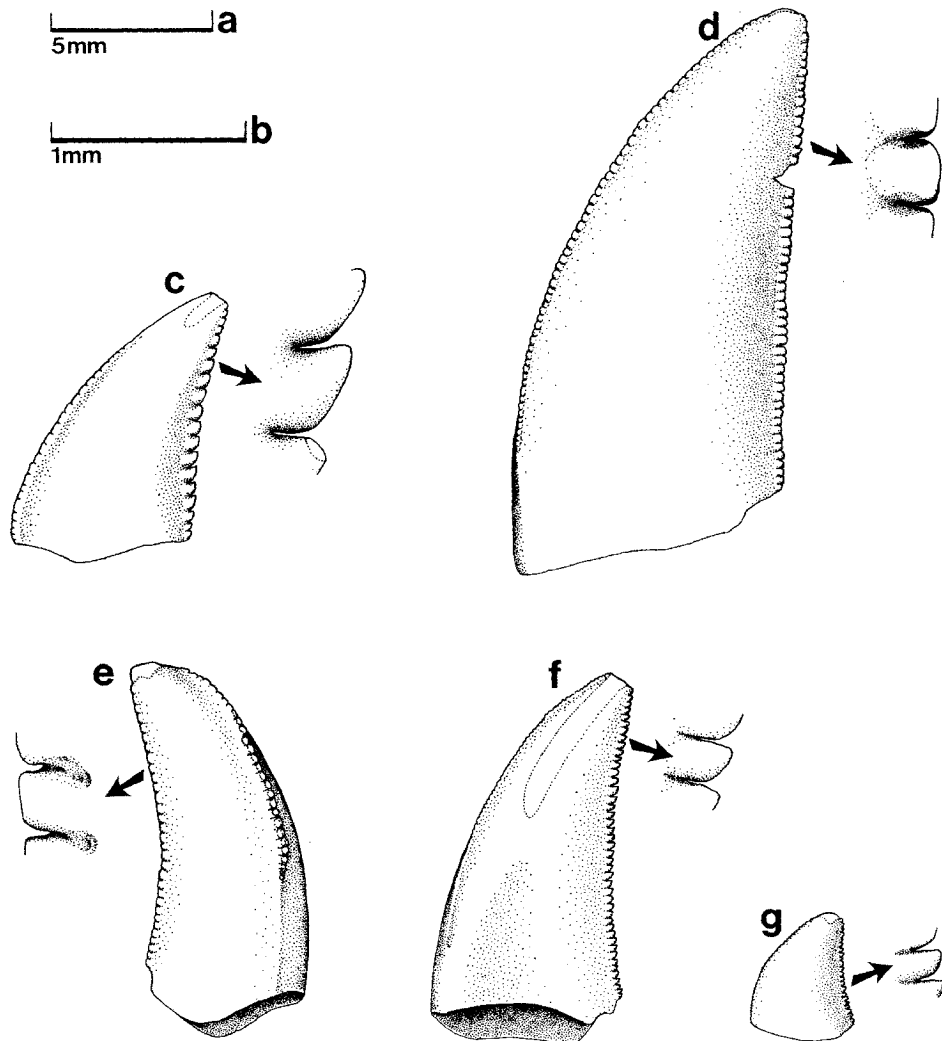


FIGURE 3. Comparison of the denticles and teeth of the theropods from the Judith River Formation of south-central Montana. The scale shown in a corresponds to the illustrations of the teeth, and the scale shown in b corresponds to the illustrations of the denticles. c, a maxillary tooth of *Troodon* (ANSP 15950). d, unknown large theropod (ANSP 15962). e, anterior maxillary tooth of *Dromaeosaurus* (ANSP 15963). f, tooth of *Saurornitholestes* (ANSP 15957). g, tooth of *Saurornitholestes* (ANSP 15824).

The most readily identifiable isolated dinosaur fossils are the commonly encountered teeth of theropods. Most of these teeth belonged to small theropods, although approximately one-quarter of the teeth can be attributed to a large theropod.

#### SYSTEMATIC PALEONTOLOGY

Descriptions for *Dromaeosaurus albertensis*, *Saurornitholestes langstoni*, *Troodon formosus*, and *Richardoestesia gilmorei* are brief because the teeth of these taxa have been described and illustrated in detail elsewhere (Currie, 1987; Currie et al., 1990). A summary of the occurrence of each of these taxa with respect to locality is provided in Table 1. Numbers refer to specimens in the Academy of Natural Sciences of Philadelphia (ANSP).

Order SAURISCHIA  
Suborder THEROPODA  
Family DROMAEOSAURIDAE  
Subfamily DROMAEOSAURINAE

*DROMAEOSAURUS ALBERTENSIS*  
Matthew and Brown, 1922

**Referred Specimens**—15827, 15959, 15963 (Fig. 3e), 17639, 17805, 17960, 17798, 18108, 18110.

**Discussion**—Nine teeth can be attributed to *Dromaeosaurus* cf. *albertensis* based on the size and shape of the denticles, and the characteristic twist of the anterior carina (Currie et al., 1990). One (ANSP 15959) is clearly a premaxillary tooth. Currie et al. (1990) reported that they could not distinguish between maxillary and dentary teeth. However, the anterior den-

ticles on maxillary teeth tend to start closer to the base of the tooth than those of the dentary, and it is evident that ANSP 15950 (Fig. 3c) is an anterior maxillary tooth.

#### Subfamily VELOCIRAPTORINAE

##### *SAURORNITHOLESTES LANGSTONI* Sues, 1978

**Referred Specimens**—ANSP 15808, 15810, 15811, 15814, 15815, 15817, 15818, 15819, 15823, 15824 (Fig. 3g), 15825, 15826, 15828, 15829, 15831, 15833, 15838, 15939, 15943, 15945, 19546, 15948, 15949, 15951, 15953, 15954, 15955, 15956, 15957 (Fig. 3f), 15958, 15960, 15975, 16195, 16197, 16198, 16199, 16225, 16226, 16227, 16228, 16229, 17646, 17648, 17649, 17773, 17774, 17775, 17776, 17777, 17778, 17781, 17783, 17785, 17786, 17787, 17788, 17789, 17801, 17802, 17803, 17962, 17963, 18002, 18006, 18100, 18103, 18105, 18109, 18112, 18118, 18122.

**Discussion**—The most commonly recovered theropod teeth are easily recognized as *Saurornitholestes langstoni* (Fig. 3f, g) by their strong lateral compression, by the shape of their denticles, and by the disparity in size of the anterior and posterior denticles (Currie et al., 1990). The premaxillary teeth are not as flat in section, and both carina are positioned on the lingual side of the tooth. Approximately 15 percent of this tooth sample represent premaxillary teeth. The dental formula (premaxillary : maxillary : dentary) was estimated (Currie et al., 1990) as 4:10:16, which, if correct, predicts that 15 percent of the teeth recovered should be premaxillary.

Two isolated teeth associated with the type specimen of *Saurornitholestes langstoni* have denticles on both the anterior and posterior carinae, although the anterior denticles are much smaller than the posterior denticles (Sues, 1978). Currie et al. (1990) point out that the presence or absence of denticles on the anterior carina is variable, even within the same jaw. With respect to this tooth sample of *S. langstoni*, approximately half of the teeth have denticles on both carinae.

#### Family TROODONTIDAE

##### *TROODON FORMOSUS* Leidy, 1856

**Referred Specimens**—ANSP 15937, 15947, 15950 (Fig. 3c), 15964, 17642, 17780, 17795, 18005.

**Discussion**—A total of eight teeth can be reasonably attributed to *Troodon formosus*. In a recent study of *T. formosus*, Currie (1987) distinguished between premaxillary, maxillary, and anterior structure and posterior dentary teeth, based on various aspects of tooth structure. In this sample of theropod teeth, specimens ANSP 17642, ANSP 17780, and ANSP 17795 are identified as premaxillary teeth, specimens ANSP 15947, ANSP 15950 (Fig. 3c) and ANSP 18005 are attributed to the maxilla, while specimens ANSP 15937 and ANSP 15964 are from the dentary.

#### Family incertae sedis

##### *RICHARDOESTESIA GILMOREI* Currie et al., 1990

**Referred Specimens**—15824, 15942, 15952, 17647, 17782, 17784, 17983, 18101, 18104, 18114, 18115, 18119.

**Discussion**—Currie et al. (1990) described, based on jaws and isolated teeth, a new genus of theropod, *Richardoestesia gilmorei*, from the Upper Cretaceous of western North America. All teeth described by Currie et al. were dentary or maxillary teeth. The most readily identifiable characteristic of these teeth are the very small height and length of the denticles. In their description of the teeth of *R. gilmorei*, Currie et al. (1990) differentiated between anterior and posterior teeth based on general tooth height and curvature.

A total of 12 teeth from the Judith River Formation of south-central Montana can be referred to *Richardoestesia gilmorei*. Of these teeth, 10 are considered to be posterior teeth based on the well-developed curvature of the tooth.

#### Theropod "A"

**Referred Specimens**—ANSP 15807, 15832, 15834, 15961, 15962 (Fig. 3d), 15965, 15966, 15968, 15970, 15971, 15972, 15973, 15974, 17186, 17333, 17470, 17471, 17472, 17521, 17574, 17791, 17792, 17793, 17794, 17800, 17804, 18102, 18116.

**Discussion**—Twenty-eight teeth of a large theropod were recovered. Virtually all of these specimens have broken bases so actual tooth height is unknown. However, the largest reasonably complete tooth (ANSP 17333) has a height of 69 mm. These teeth have a few unusual characters that distinguish them from the teeth of the typical Upper Cretaceous theropods, the Tyrannosauridae.

In other theropods, identification of premaxillary teeth is based on the lingual positions of both the anterior and posterior carinae (Currie et al., 1990). With this as the criterion, approximately 20 percent of the large theropod teeth assigned to theropod "A" are identified as premaxillary.

Aspects of the structure of the denticles on these teeth show significant differences from tyrannosaurid teeth. The denticles of tyrannosaurid teeth grade into the body of the tooth, forming a smooth transition from denticle to the tooth body, whereas the denticles of theropod "A" teeth clearly end rather than grade into the tooth body. The denticles of the Montana teeth are similar to those of tyrannosaurids in having a longer labiolingual axis than proximodistal axis (Currie et al., 1990), although this is true for the teeth of most large theropods. Functionally, this was necessary because the disproportionately small denticles of large theropods were processing much greater volumes of animal tissue, and were more likely to encounter bone. Wider denticles were thereby able to resist breakage and protect the sharp edges between the denticles that cut the muscle fibers. The wide, chisel-like denticles

TABLE 1. Distribution of theropod taxa. The abbreviations, from left to right, refer to Ox Hill Quarry, Antelope Head Quarry, Careless Creek Quarry, Emily's Ankle Quarry, Top Cat Quarry, Hidden Valley Quarry, Blackbird Ridge Quarry, and Jensen Ranch Mini-Site. The order of the listing of the various localities reflects the relative position of each site along an approximate 75 km east-west transect.

Taxon	Locality							JR
	OHQ	AHQ	CCQ	EAQ	TCQ	HVQ	BBR	
<i>D. albertensis</i>	X		X			X	X	
<i>S. langstoni</i>			X	X	X	X	X	
<i>T. formosus</i>		X	X	X	X	X		
<i>R. gilmorei</i>			X	X		X	X	
Theropod "A"	X	X	X	X	X	X	X	X

of large theropods were not as efficient as separating muscle fibers as the narrow, hooked, and sharply pointed denticles of small theropods, but this was compensated for by the greater strength of the jaws.

The ratio of denticle length to height for these teeth varies only slightly from 1:1 to 1:1.5. The denticles appear on both the anterior and posterior carinae and are of approximately equal size on either carina. On some teeth the denticles gradually increase in size distally, while on other teeth no clear reduction in size is observable.

One of the most universal characteristics of tyrannosaurids (including *Alectrosaurus* and *Aublysodon*) is the presence of well-developed "blood grooves" emerging from between the denticles and extending obliquely towards the base of the tooth (Currie et al., 1990; Abler, 1992). These are particularly well developed on the lingual side of the posterior carina, and are present in virtually every clearly identified tyrannosaurid tooth. Similar grooves can occasionally be found on the teeth of more primitive large theropods, but they are never as well developed or as consistent. The absence of these grooves from the theropod "A" teeth from the Judith River Formation of south-central Montana suggests that the teeth were not derived from a tyrannosaurid.

These characteristics of the teeth are consistent throughout the sample, regardless of overall size of the tooth. In this sense, these teeth are similar to tyrannosaurid teeth, which show little change in tooth structure from juveniles to adults (Currie et al., 1990; Farlow et al., 1991).

Comparison with the teeth of other large non-tyrannosaurid theropods indicates a strong similarity between the teeth of this sample and those of *Allosaurus* and other more primitive theropods. The structure of the denticle region on the teeth of *Dryptosaurus aguilunguis*, the problematic theropod from the eastern United States (Molnar, 1990), suggests the presence of a slightly developed "blood groove," a feature not present on the teeth of theropod "A." The preservation of the teeth of *D. aguilunguis* is poor, however, and a more thorough comparison is not available. This comparison reveals that the characters found on the teeth

of the large Judith River theropod from south-central Montana can be considered to be primitive. Because these teeth are isolated, with unclear affinities, it is the opinion of the authors that naming a new genus and species would be premature.

Although most of the non-premaxillary teeth are laterally compressed, approximately one-third of the teeth that show good definition of the form of the body of the tooth are inflated. In contrast, maxillary and all but the first few dentary teeth of tyrannosaurids are all laterally compressed (Currie et al., 1990).

## PALEOECOLOGICAL INFERENCES

Several workers have discussed the utility of disarticulated and unassociated vertebrate remains for making paleoecological interpretations (e.g., Badgley, 1986; Dodson, 1987). Using patterns of frequency and occurrence of microvertebrate remains compared to similar patterns of articulated remains, Dodson (1987) argued that microvertebrate faunal assemblages provide reasonable information, at least at the familial level, of relative abundances of taxa from a given site. Badgley (1986) suggested that given assemblages of disarticulated vertebrates with low probabilities of association, then individual specimen counts provide a reasonable estimate of relative abundances of taxa within an ancient ecosystem. The relative abundance of teeth can, at present, only give a rough idea of the relative abundance of the animals from which they are derived. These estimates will be refined as sample size increases, and by taking into account the number of teeth in the jaws of specific theropods (*D. albertensis*, for example, had 48 functional tooth positions, compared with more than 100 in *T. formosus*) and their replacement rates (Erickson, 1991). The specimens used in this study are assumed to have a low probability of association due to the taphonomic setting of each of the localities. Therefore, individual specimen counts are used here as an estimate of ecological relative abundance at each site.

Tables 2 and 3 provide specimen counts and relative percentages, respectively, of each taxon per site, while Table 4 provides a summary total of specimen counts and relative percentages of each of the theropod taxa discussed above. The most common theropod tooth

TABLE 2. Specimen totals per site. Abbreviations as in Table 1.

Taxon	Locality							
	OHQ	AHQ	CCQ	EAQ	TCQ	HVQ	BBR	JR
	N = 1	N = 11	N = 52	N = 23	N = 14	N = 9	N = 16	N = 1
<i>D. albertensis</i>	1	0	3	0	0	2	3	0
<i>S. langstoni</i>	0	0	37	12	10	4	9	0
<i>T. formosus</i>	0	1	4	1	1	1	0	0
<i>R. gilmorei</i>	0	0	3	4	0	1	4	0
Theropod "A"	0	10	5	6	3	1	2	1

TABLE 3. Percent representation per site. Abbreviations as in Table 1.

Taxon	Locality							JR
	OHQ	AHQ	CCQ	EAQ	TCQ	HVQ	BBR	
<i>D. albertensis</i>	100	0	6	0	0	25	19	0
<i>S. langstoni</i>	0	0	70	50	71	39	50	0
<i>T. formosus</i>	0	9	8	5	7	12	0	0
<i>R. gilmorei</i>	0	0	6	18	0	12	25	0
Theropod "A"	0	91	10	27	22	12	12	100

type, either large or small, is *Saurornitholestes langstoni*. The next most abundant theropod teeth are those assigned to the large theropod. The remaining three taxa, *Dromaeosaurus albertensis*, *Troodon formosus*, and *Richardoestesia gilmorei*, are present in nearly equal numbers. Although the actual percentages vary somewhat from site to site this pattern remains consistent regardless of which site is considered. Based on this consistency, certain paleoecological inferences can be made.

The Ox Hill Quarry site has only produced one theropod tooth, thus far, and therefore does not provide reasonable faunal data other than the presence of *D. albertensis* very low in the section. Similarly the Jensen Minisite produced only one specimen. Any further discussion of the stratigraphic distribution of theropods will concern the remaining, more productive, localities. Based on the stratigraphic distribution of these faunas (Fig. 2), it is clear that there is little variation in the composition of these theropod faunas throughout the middle third of the Judith River Formation. This middle third represents approximately 40 m of section. The consistency of the theropod faunas through this section contrasts with the pattern of theropod distributions identified for the 90 m of section for the Judith River Formation of southern Alberta (Béland and Russell, 1978). In their review of the distribution of dinosaurs throughout Dinosaur Provincial Park, they noted a slight reduction in the abundance of theropods towards the top of the section.

Similar to the vertical distribution of theropod teeth from south-central Montana, the horizontal distribution also shows no strongly preferred pattern of theropod occurrence or frequency (Table 5). There is only a slight suggestion that the large theropod declines in

TABLE 4. Summary of occurrence of taxa for all sites. (Total sample: 129 teeth.)

Taxon	Specimen totals	Percent of sample
<i>D. albertensis</i>	9	7
<i>S. langstoni</i>	72	56
<i>T. formosus</i>	8	6
<i>R. gilmorei</i>	12	9
Theropod "A"	28	22

TABLE 5. Simple Matching coefficient (Sneath and Sokal, 1973) table for AHQ, CCQ, EAQ, TCQ, HVQ, and BBR faunas. Because of their small sample sizes OHQ and JR were omitted from this comparison. Notice that there is no preferred pattern of faunal change along the east-west transect.

	AHQ	CCQ	EAQ	TCQ	HVQ	BBR
AHQ	1.0					
CCQ	0.4	1.0				
EAQ	0.6	0.8	1.0			
TCQ	0.8	0.6	0.8	1.0		
HVQ	0.4	1.0	0.8	0.6	1.0	
BBR	0.2	0.8	0.6	0.4	0.8	1.0

abundance from west to east and *R. gilmorei* increases in abundance from west to east (Tables 1–3). This contrasts with the distribution of fish remains throughout this approximately 75 km transect (Fig. 1). The distribution of fishes indicates a change from a more marine- or brackish-water influenced setting in the east to a more fresh-water setting in the west (Fiorillo, 1989a). The pattern of consistency with respect to the theropod remains here again contrasts with the study of Béland and Russell (1978), where they point out changes in the horizontal distribution of dinosaurs through a 34 km transect in the Dinosaur Provincial Park region.

Although patterns of differentiation may have been present in the ecosystem of the Judith River Formation of southern Alberta, these patterns are not evident in south-central Montana. This may have been due to a more homogeneous terrestrial environment existing in south-central Montana versus that of southern Alberta. Certainly the dinosaur fauna of southern Alberta is much more extensive than that of south-central Montana (Béland and Russell, 1978; Currie, 1987; Fiorillo, 1989a, b). This suggests that the Judithian dinosaur fauna of southern Montana constituted a separate biogeographic region (Fiorillo, 1988), based on the primitive nature of some of the taxa such as *Avaceratops lammersi* (Dodson and Currie, 1990) and the large theropod discussed above. A basic environmental difference between these regions, such as homogeneity of the environment in southern Montana compared to the region farther north, may have been a contributing factor to this biogeographic differentiation.

#### ACKNOWLEDGMENTS

Field work for this project was funded largely by National Science Foundation grants EAR 84-08446 and EAR 87-21432. The authors thank Drs. Hans-Dieter Sues, James Farlow, and Dale Russell for reviewing this manuscript. The authors also thank Ted Daeschler, collection manager at the Academy of Natural Sciences of Philadelphia, for providing access to the materials used in this paper. This manuscript is University of California Museum of Paleontology contribution number 1594.

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