23. Patterns of Distribution of Mammals in the Dinosaur Park Formation and Their Paleobiological Significance

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The organization of Late Cretaceous non-marine vertebrate paleocommunities has been the subject of intensive paleoecological studies. Mammals are an important element of these communities, often showing high levels of diversity and abundance (Russell 1937, 1952; Fox 1979a, 1979b, 1979c, 1980, 1981). In this chapter, changes in the composition of mammalian assemblages through the Dinosaur Park Formation (DPF) of southern Alberta are identified, and differences in the paleoecology of the higher groups of mammals are inferred from these distribution changes.

The DPF contains a rich and diverse vertebrate assemblage, including over 125 taxa of vertebrates (Eberth et al. 2001). An ongoing survey of vertebrate microfossil localities has demonstrated that the diversity and abundance of vertebrates vary through the DPF (Brinkman 1990; Brinkman et al. 1998). On the basis of a comparison of twenty-five localities spanning about 65 m of section, Brinkman (1990) noted that the abundance of remains of some taxa changes stratigraphically. Taphonomic explanations for these patterns were rejected because, with the exception of one locality (Bonebed BB054), the assemblages all show a bias toward preservation of both enamel-covered elements (such as teeth and scales)

and elements that are delicate and/or less physico-chemically resistant. Furthermore, in some cases, elements that are equivalent in size, shape, and density show different distributions. Thus, it was concluded that the distribution patterns have a biological basis. Brinkman (1990) suggested that the changes in abundance are best explained by changes in environment related to the transgression of the Bearpaw Sea, with taxa tracking environmental shifts during the transgression. Because the stratigraphic interval sampled was deposited during the transgression of the Bearpaw Sea, localities that are higher stratigraphically would have been deposited closer to the shoreline. Taxa that are more abundant in localities that are higher stratigraphically than they are at lower stratigraphic intervals would have been more abundant in coastal settings than in more inland settings. For ceratopsians and some other dinosaurs, the hypothesis that these stratigraphic patterns reflect differences in distribution along the coastal plain relative to the shoreline was later tested. This was done by comparing the abundance of dinosaurs and other terrestrial vertebrates in localities along an east–west transect from the relatively more inland area of Dinosaur Provincial Park (the Park) to relatively more coastal localities in the area of the South Saskatchewan River, about 100 km to the east (Brinkman et al. 1998). The general patterns are also supported by a study of the abundance of taxa in the lower half of the Belly River Group (Brinkman et al., in press). Because this interval was deposited during a regression of the inland sea, the pattern of change in abundance of taxa in the lower half of the Belly River Group should mirror the pattern of change in the upper half. This was found to generally be the case.

Not all taxa show significant variation in their abundance through the Belly River Group. For example, hadrosaurs are consistently of high abundance, which suggests that, as a group, they were evenly distributed across the coastal plain. This interpretation is consistent with occurrences of articulated skeletons and isolated elements that show that hadrosaurs were the dominant herbivore in the paleocommunities of the Belly River Group (Dodson 1983). However, in other cases the absence of a trend may be a result of small sample sizes. Subsequent work has suggested that no trends in the abundance of higher groups of mammals were recognized because of the small sample size that was available. Although Brinkman (1990) sees no change in the abundance of mammals through the Belly River Group of the Park, Eberth and Brinkman (1997) note the relatively high frequency of marsupials in the faunal assemblage of a series of estuarine, incised valley fills in the DPF of southern Alberta. On this basis, they suggest that marsupials might be preferentially members of a coastal community. However, because these samples came from a geographically and stratigraphically restricted set of localities, the abundance of marsupials could be a result of specific habitat preference, rather than large-scale environmental differences. To test this hypothesis, we re-examined the pattern of abundance of the major groups of mammals through the DPF.

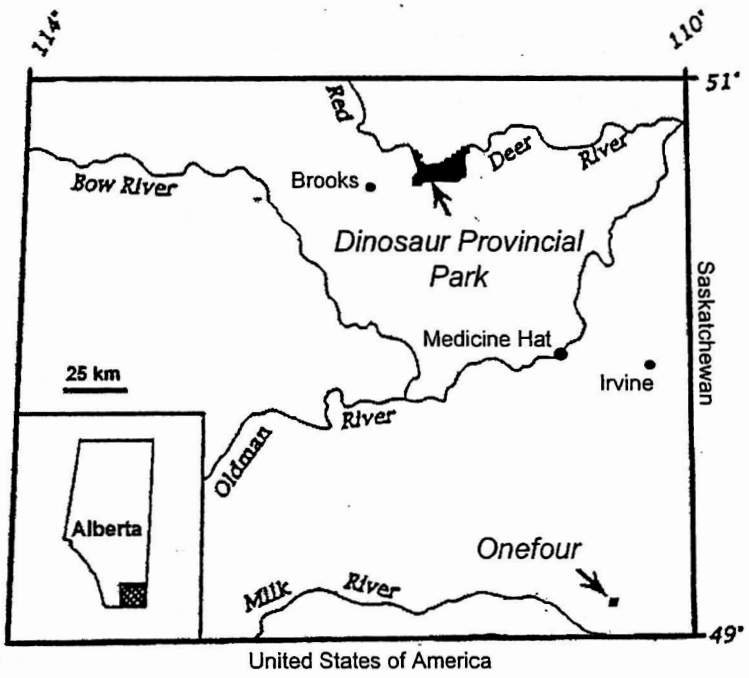

Figure 23.1. Locality map showing the areas from which material used in this study was obtained.

Geology

The DPF is the uppermost formation in the Belly River Group of southern Alberta (Eberth, this volume). It is late Campanian and is dated at 76 to 74.5 mya (Eberth and Deino 1992; Eberth 1997). It was deposited within extensive coastal lowlands adjacent to the Cretaceous Western Interior Seaway during the transgressive phase of the Belly River clastic wedge. Two regions with exposures of this formation are the Park and the Onefour area in southeastern Alberta (Fig. 23.1). In the Park area, the DPF is approximately 70 m thick. The lower 60 m are fluvial beds deposited by a meandering river system. The uppermost 10 m constitute the Lethbridge Coal Zone (Brinkman, Russell et al., this volume), a unit that was deposited in a setting transitional between the fluvial beds below and the fully marine Bearpaw Formation above. Vertebrate microfossil localities are preserved in a variety of facies, including crevasse splay deposits, trough-cross-stratified sandstones, IHS (inclined heterolithic stratified) beds, and mudstones deposited in an oxbow setting (Eberth 1990).

In the Onefour area, the DPF is approximately 30 m thick, with the uppermost 10 m comprising the Lethbridge Coal Zone. In the fluvial beds below the Lethbridge Coal Zone, vertebrate microfossil localities are preserved in trough-cross-stratified sandstones. Localities in the Lethbridge Coal Zone are preserved in a complex of mud-filled channels (Eberth and Brinkman 1997).

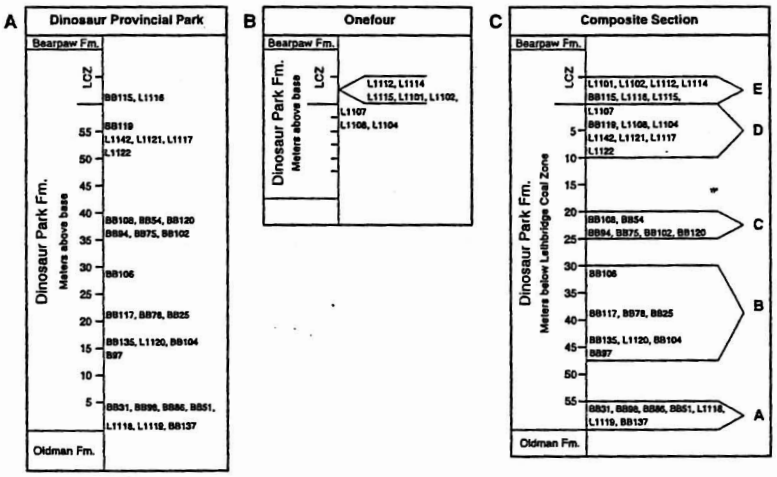

Figure 23.2. Stratigraphic distribution of microvertebrate localities through the Dinosaur Park Formation at (A) Dinosaur Provincial Park and (B) Onefour and (C) a composite section showing the relative position of localities from these two geographic areas. The stratigraphic intervals used in this study are shown in the composite section.

Localities Sampled

The areas sampled for vertebrate microfossil localities have a broad stratigraphic distribution (Fig. 23.2A,B). The base of the Lethbridge Coal Zone was used to place localities in the Onefour and Park areas in relative stratigraphic context (Fig. 23.2C). For this sequence, stratigraphic position is expressed in meters below the Lethbridge Coal Zone. Sites within the Lethbridge Coal Zone were not placed in sequence relative to one another.

To obtain statistically significant sample sizes, data from localities within restricted stratigraphic intervals were combined to give a measure of the relative abundance of different groups of mammals in that interval. Five intervals are recognized, labeled A–E in Fig. 23.2C. Three of these are represented by groups of sites that cluster within narrow stratigraphic zones. These are a group of sites located just above the boundary between the Oldman Formation and the DPF (interval A), a group of sites located between 22 and 24 m below the Lethbridge Coal Zone (interval C), and a group of sites within the Lethbridge Coal Zone (interval E). The remaining intervals include the intermediate sites. The sites included in interval B are located between 46 and 31 m below the Lethbridge Coal Zone. The sites included in interval D are located between 2 and 8 m below the Lethbridge Coal Zone.

Methods

Mammals were recovered from twenty-eight sites in the Park area and from eight sites in the Onefour area (Fig. 23.2). Localities were screenwashed using a screen with nine holes per centimeter. With this screen size, incisors and canines of therian mammals were not recovered. To avoid introducing biases, no surface collected material was included in the data used to quantify the abundance of

mammals at a locality. In addition, only dental remains were utilized in this study.

At the generic level, the diversity of therian mammals matches that previously described from the DPF. Relatively few specimens can be identified to species, so at the species level, sample size is small and rare species are not represented in this collection. A comprehensive study of the multituberculates from the DPF has not yet been undertaken. For these reasons, species-level identifications were not attempted. The multituberculate assemblage of the DPF differs from that of the Judith River Formation of Montana in the apparently high diversity of the Cimolomyidae. Three cimolomyid genera can be identified on the basis of isolated teeth. These are *Meniscoessus, Cimolomys,* and an unnamed genus of large body size. A large number of cimolomyid teeth that are generically indeterminate are also present. Morphological diversity indicates that more than one taxon is present in this material. However, in the absence of jaws demonstrating an association between the premolars and molars, the level of diversity remains uncertain.

In general, taphonomic equivalency of the sites sampled is indicated by three criteria: (1) a general similarity in the size-frequency distribution of elements recovered, (2) a similar bias toward enamel-covered elements, such as teeth and scales, and (3) the presence of elements that are delicate and/or less physico-chemically resistant, although abraded fragments dominate. The exceptions are BB054 in the Park and the mud-filled estuarine channel complex in the Onefour area. These sites were deposited under conditions that suggest reduced transport and reworking (Eberth 1990; Eberth and Brinkman 1997). The reduced transportation and reworking are clearly expressed in the relative abundances of terrestrial and aquatic taxa. Because few specimens were recovered from BB054, it does not affect the pattern of abundance of mammals in this interval. However, material from the Onefour channel complex dominates the sample from the Lethbridge Coal Zone. Comparing the Lethbridge Coal Zone assemblage with that from the preceding stratigraphic interval tests the possibility that the apparently high abundance of marsupials in this interval was a result of the differences in taphonomic conditions. In addition, taphonomic effects are minimized because teeth are generally taphonomically similar. Variation is present in size, shape, and density of mammal teeth, but is small compared to the range in shapes and densities of all elements present at a site, which range from light, easily transported teleost centra to compact nodular *Myledaphus* teeth. Mammal teeth form a small subset in this morphological range. Size variation is present but can be excluded as a source of variation in abundance of the major groups of mammals because the taxa represented by larger elements (*Eodelphis* and *Meniscoessus*) show no significant change in abundance through this stratigraphic interval.

The minimum number of identifiable specimens—which is the best indicator of abundance of individuals at sites with widely dispersed, isolated specimens (Badgley 1986)—was used as a basis for

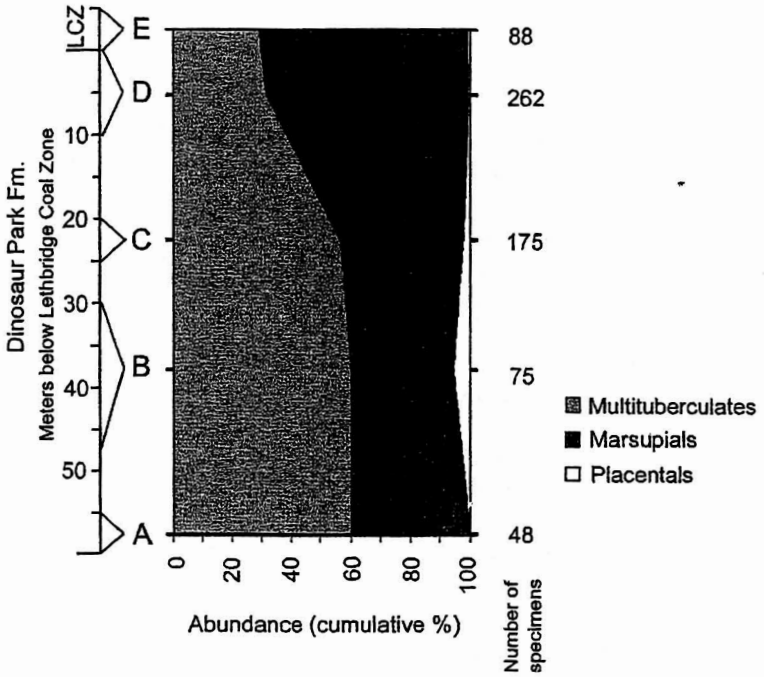

Figure 23.3. Changes in the relative abundance of the three major groups of mammals through the Dinosaur Park Formation, Alberta. The number of specimens from each interval is shown on the right of the chart.

estimating relative abundance. Because the tooth counts differ in therians and multituberculates, the relative abundance of teeth identified at a locality is not a direct measure of their taxonomic abundance in the original community. However, because the elements being considered are taphonomically similar and the localities sampled were subject to similar taphonomic processes, differences in the composition of mammalian assemblages should reflect differences in the original source communities.

All material is catalogued in the collections of the Royal Tyrrell Museum of Palaeontology.

Results

Variation in the composition of the mammalian assemblage through the DPF was first evaluated by considering differences in the relative abundances of the three major groups of mammals (multituberculates, marsupials, and placentals) as a percentage of the entire assemblage of mammals through this formation. A plot of the abundances of these taxa against stratigraphic position (Fig. 23.3) indicates a decrease in multituberculates and an increase in marsupials through the sequence. Placentals have their greatest abundance in the second stratigraphic interval, where they constitute approximately 5 percent of the mammals present. Above and below this interval, they constitute about 1 percent of the mammals present.

The statistical significance of the greater abundance of marsupials in the upper stratigraphic intervals was tested by using a bino-

mial test for differences in the proportion of marsupials relative to other mammals in successive stratigraphic intervals. The abundances of marsupials (Pmarsup) in the successive units are as follows: A, Pmarsup = 0.41; B, Pmarsup = 0.35; C, Pmarsup = 0.41; D, Pmarsup = 0.68; and E, Pmarsup = 0.70. The differences in the proportions of marsupials in the lower three intervals are not significantly different from zero, and the differences in proportions of marsupials in the upper two intervals are not significantly different from zero. However, proportions of marsupials in the lower three intervals are significantly less than in the upper two intervals at a 95% confidence interval. The number of placentals recovered is not sufficiently large to show that their higher abundance in lower stratigraphic intervals is significant.

To determine whether or not the changes in relative abundance of the three major groups of mammals was a result of an increase or a decrease in the abundance of particular lower-level taxa, the stratigraphic distribution of mammals that could be identified to lower taxonomic levels was considered. Therians and multituberculates were considered separately. Within the therians, four taxa were considered: placentals, the marsupial family Peradectidae (including the genera *Turgidodon* and *Alphadon*), and the nonparadectid genera *Eodelphis* and *Pediomys* (Table 23.1). Among the multituberculates, five genera were considered (Table 23.2). Because few of the mammals from the lowest stratigraphic interval (interval A) could be referred to these taxonomic categories, the mammals of this interval were lumped with those from interval B. The grouping of the mammals from these two stratigraphic intervals is unlikely to obscure distributional patterns because the two intervals have only small differences in proportions of the major groups of mammals.

Changes in abundance of the lower-level taxa of mammals can be shown graphically (Fig. 23.4). Among the therians, the tendency for placentals to be more abundant in the lower stratigraphic intervals than they are in the higher intervals is apparent (Fig. 23.4). Placentals are also more diverse in the lower stratigraphic intervals (Table 23.1). However, because they are never abundant compared to other mammalian taxa and because sample sizes are small, this difference in diversity could be a reflection of the sample sizes. No trends are obvious in the abundance of marsupials, although *Pediomys* is unusually abundant in the Lethbridge Coal Zone (stratigraphic unit E, Fig. 23.4). Among the multituberculates, *Cimexomys* and *Mesodma* consistently decrease in abundance through the four stratigraphic intervals, although the changes are minor and not statistically significant (Fig. 23.5). Thus the change in abundance of placentals, marsupials, and multituberculates through the DPF is not accompanied by a significant change in relative abundance of lower-level taxa.

TABLE 23.1.
Counts of teeth of therian mammals from vertebrate microfossil localities in the Dinosaur Park Formation, Alberta, sampled for this study. The range of stratigraphic intervals A to E is shown in Figure 23.1.

Locality	Stratigraphic position	Placentalia indet.	*Gypsonictops*	*Deltatheroides*	*Paranyctoides*	Marsupialia indet.	*Turgidodon*	*Turgidodon/Alphadon*	*Pediomys*	*Eodelphis*
Strat interval E										
L1116	LCZ					5	3	1	1	1
L1115	LCZ	1				16	2	2	5	1
L1101	LCZ					15	1	1	2	
L1102	LCZ					1	2			1
L1112	LCZ								1	
L1114	LCZ					1				
Total interval E		1	0	0	0	38	8	4	9	3
Strat interval D										
L1117	54					1				
L1143	53						1			
L1142	53					1	1		0	1
L1122	52									1
L1107	58					2		0	0	3
L1108	56	2				105	15	11	19	6
L1104	56					5	1	2		
Total interval D		2	0	0	0	114	18	13	19	11
Strat interval C										
BB054	38	1				18	3	3	3	4
BB120	37	1				8	1		9	2
BB108	38									
BB102	37					9	2		1	4
BB075	36			1		1			1	
BB094	36				1	1		1		
Total interval C		2	0	1	1	37	6	4	14	10
Strat interval B										
BB025	23					1				
BB078	21					2				
BB117	22	1	1			5		1	1	1
BB104	17		1		1	9		1	2	
L1120	15									
BB135	15					4				
BB097	14					1				
Total interval B		1	2	0	1	22	0	2	3	1

TABLE 23.1. (*continued*)

Locality	Stratigraphic	Placentalia	*Gypsonictops*	*Deltatheroides*	*Paranyctoides*	Marsupialia	*Turgidodon*	*Turgidodon/Alphadon*	*Pediomys*	*Eodelphis*
Strat interval A										
BB031	1								1	
BB098	1								1	
BB086	1					4	2		2	
BB051	1					3	2	2		
L1118	0					2				
L1119	0									
BB137	0					1				
Total interval A		0	0	0	0	10	4	2	4	

Discussion

Changes are present in the relative abundances of the major groups of mammals through the DPF. Assemblages that are higher stratigraphically have, on average, relatively more marsupials and relatively fewer placentals than do sites that are lower stratigraphically. Because the sites are taphonomically similar, taphonomically based explanations for these distribution patterns are unlikely. A number of biologically based explanations for changes in abundance can be considered. These include evolutionary changes in the taxa present, climate change, and general changes in environment. There is no evidence from morphological studies of mammals in this interval for evolutionary change during deposition of the DPF. Indeed, the Judithian mammal assemblage is notable for its stability over a long period of time. Changes in climate during this time have not been documented. However, there were environmental changes related to the transgression of the Bearpaw Sea. Therefore, the general pattern of variation in the abundance of placentals, marsupials, and multituberculates in vertebrate microfossil localities is attributed to variation in their abundance in the communities from which the fossil assemblages were derived. This variation is in turn related to shifts in the geographical distribution of the communities as they tracked the environmental changes accompanying this transgression. This relationship implies that marsupials, which are relatively more abundant in higher stratigraphic intervals, were probably relatively more abundant closer to the coast, whereas

TABLE 23.2.

Counts of teeth of multituberculate mammals from vertebrate microfossil localities in the Dinosaur Park Formation, Alberta, sampled for this study. Stratigraphic position is within the Lethbridge Coal Zone (LCZ) or meters below the Lethbridge Coal Zone. The range of stratigraphic intervals A to E is shown in Figure 23.1.

Locality	Stratigraphic position	Multituberculate indet	*Meniscoessus*	*Cimolomys*	*Cimolodon*	*Mesodma*	Cimolomyidae	*Cimexomys*
Strat interval E								
L1116	LCZ	2	1	2				
L1115	LCZ	5		2		3	3	
L1101	LCZ	5	1	1				
L1102	LCZ							
L1112	LCZ							
L1114	LCZ							
Total interval E		12	2	5	0	3	3	0
Strat interval D								
L1117	54	1	1	1				
L1143	53							
L1142	53	1				2		
L1122	52		1	1				
L1107	58	2	1	2		1		
L1108	56	47				6	2	3
L1104	56	2	2	3	1		1	
Total interval D		53	5	7	1	9	3	3
Strat interval C								
BB054	38	15	5	3	1	6	2	6
BB120	37	10	7	11		3	3	
BB108	38	1				1		
BB102	37	3	2			3	3	
BB075	36	1		2	1	3	1	
BB094	36	2	1	3		1		
Total interval C		32	15	19	2	17	9	6
Strat interval B								
BB025	23	1						1
BB078	21	3						
BB117	22	9	1	2		1		2
BB104	17	4	1	1		7		3
L1120	15	2						1
BB135	15	3	1	1			1	
BB097	14	1		1				1
Total interval B		23	3	5	0	8	1	8


D

TABLE 23.2. (*continued*)

Locality	Stratigraphic position	Multituberculate indet	*Meniscoessus*	*Cimolomys*	*Cimolodon*	*Mesodma*	Cimolomyidae	*Cimexomys*
Strat interval A								
BB031	1	1				1		
BB098	1					2		
BB086	1	6				2		1
BB051	1	4	1	3		3		2
L1118	0	1						
L1119	0	1				1		
BB137	0							
Total interval A		13	1	3	0	9	0	3

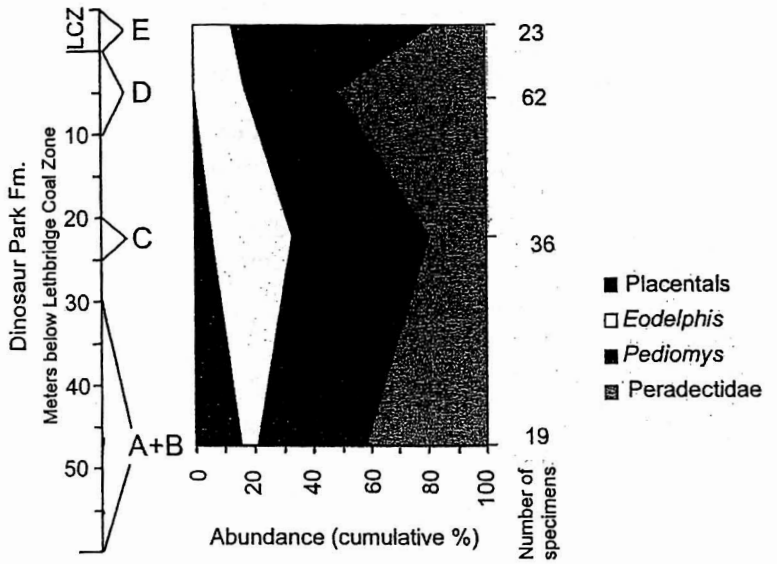

Figure 23.4. Stratigraphic distribution of lower-level taxa of therians through the Dinosaur Park Formation, Alberta. The number of specimens from each interval is shown on the right of the chart.

multituberculates were probably relatively more abundant in inland settings. The higher abundance of placentals in the lower stratigraphic intervals suggests that they also probably preferred a more inland setting.

The stratigraphic control of patterns documented here seems to reflect variation in the relative abundances of the major groups of mammals across the coastal plain during deposition of the Belly

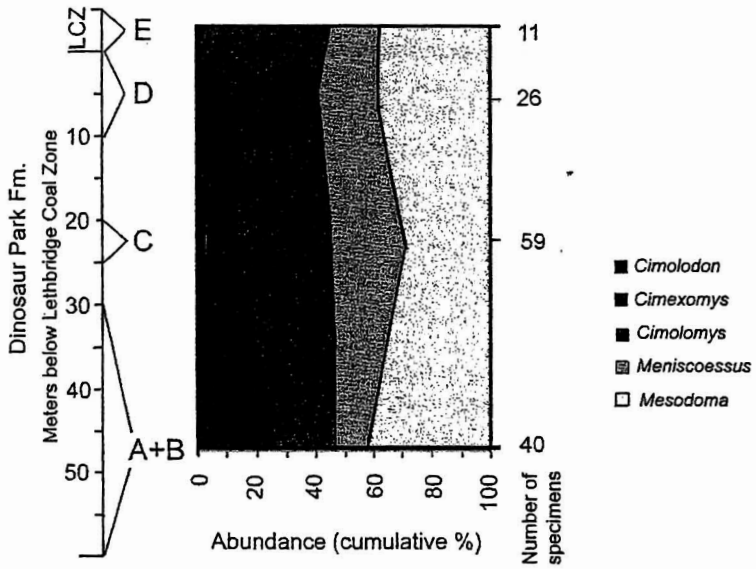

Figure 23.5. Stratigraphic distribution of lower-level taxa of multituberculates through the Dinosaur Park Formation, Alberta. The number of specimens from each interval is shown on the right of the chart.

River Group. The hypothesis makes several predictions about the distribution of mammals in time and space and can be tested by further collection and study of specimens. For example, the hypothesis predicts that at any single time, marsupials will be more abundant in eastern localities than they are in contemporaneous localities in the west. The hypothesis also predicts that changes in the abundance of mammals through the lower half of the Belly River Group will mirror the changes in the DPF.

Mammal distributions in the DPF provide additional evidence regarding the complexity of the Park paleocommunities. At present, there is no way of knowing the specific paleoecological interactions with the environment or associated taxa that led to these distribution patterns. Locomotor adaptations of Cretaceous mammals, plant distributions, variation in substrate consistency, and the amount of open water are just a few of the factors that could have influenced the patterns. Whatever the influences were, they were stable through to the end of the Cretaceous because continental-scale distribution patterns of higher groups of mammals parallel their distribution patterns in the DPF. For example, in the late Maastrichtian of North America, placentals are relatively more abundant in the more inland Scollard Formation than they are in the more coastal Lance Formation (Lillegraven 1969). This pattern has been confirmed by subsequent descriptions of late Maastrichtian mammalian assemblages (Hunter and Pearson 1996). Furthermore, the hypothesis that marsupials preferred wet, coastal areas is consistent with the difference in abundances of marsupials in Asia and North America (Cifelli 2000), because these coastal environments and marsupials are poorly represented in the Late Cretaceous of Asia. The discovery of assemblages from wet coastal environments in the Campanian of Asia will test this hypothesis.

Acknowledgments. Julia Sankey was able to work with her coauthors on the Cretaceous mammals of the Park thanks to a Fulbright Postdoctoral Research Fellowship in 1999. We thank the many participants in the Field Experience Program of the Royal Tyrrell Museum of Palaeontology for their efforts in locating microvertebrate localities and collecting specimens for this paper. Mary Lee Eggart and Lisa Pond (Louisiana State University) drafted Figure 23.1. The paper benefited from the comments of two anonymous reviewers.

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