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Palaeoecology Of Vertebrate Assemblages From The Upper Cretaceous Judith River Group (Campanian) Of Southeastern Alberta, Canada

by

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ABSTRACT

Vertebrate assemblages from the Upper Cretaceous Judith River Group (the Foremost and Oldman formations) in the Milk River area of southeastern Alberta are systematically documented, based on evidence from 19 microfossil localities and 78 identified taxa. These data suggest the presence of at least one previously unidentified taxon, one extinction event, and one immigration event.

Testing for repeatability of sampling is discussed in the context of ensuring representative samples. The maximum likelihood method is introduced for testing the taxonomic representativeness.

Sedimentological examination of the 19 microsites indicates that 17 are associated with one of two sedimentary facies –inchannel and crevasse splay; similar to the situation in Dinosaur Provincial Park (DPP). A third facies association, shoreface, is recognized for two Foremost sites.

The microsites are grouped, using multivariate cluster analysis, on the basis of their taxonomic composition and relative abundance of taxa. Three assemblages are identified. These assemblages are highly congruent with their stratigraphic location, but not with their size profiles or facies associations. Characteristic taxa are summarized for each assemblage, based on the distributional patterns. The upper Foremost assemblage is characterized by 10 taxa restricted to the corresponding unit, with two more occurring in relatively

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high levels of abundance. The upper Oldman assemblage is distinguishable by two taxa restricted to this unit, with three taxa occurring in relatively high levels of abundance. The lower Oldman represents a hybrid assemblage.

Local depositional environmental changes are interpreted as the main contributory factors controlling these distributional patterns of vertebrate assemblages. Based on these distribution patterns, the members of two (inland and coastal) palaeocommunities are identified. The community members generally accord with those previously recognized in DPP, although palaeogeographical differences are evident in patterns of turtle distribution. This dissertation is dedicated to my wife, parents and family for their love and support.

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Chapter 1 Introduction

1.1 General Background

Palaeoecological studies of vertebrate fossil assemblages from the Upper Cretaceous of North America have increasingly focused on two research aspects: the reconstruction of vertebrate palaeocommunities and the investigation of the changes of palaeocommunity structures over periods of time (e.g. Estes, 1964; Estes and Berberian, 1970; Sahni, 1972; Béland and Russell, 1978; Dodson, 1983, 1987; Lehman, 1987; Brinkman, 1987, 1990). One of the fossil-bearing units of the Upper Cretaceous that has been subjected to intensive palaeoecological studies is the Judith River Group (Campanian). The extensive Judith River Group sediments in southern Alberta are renowned worldwide for their remarkably diverse and abundant vertebrate palaeontological resources; in particular, the high quality and quantity of articulated and associated dinosaur materials from Dinosaur Provincial Park (DPP), a UNESCO World Heritage Site. A less spectacular but significant palaeontological resource also exists in the form of vertebrate microfossil localities. These are extremely abundant in the region (e.g. Dodson, 1983, 1987; Brinkman, 1987, 1990; and Eberth, 1990), and provide important palaeoecological information that isolated macrofossils cannot.

Vertebrate microfossil localities (commonly known as microsites) occur in situations where small bones and teeth of vertebrates have become concentrated. Such localities generally yield taxonomically diverse aggregations of remains that include most of the vertebrate taxa known as macrofossils from the beds in which they occur (Dodson, 1983; Brinkman, 1990), as well as the remains of other taxa known only from the microfossil sites. Large sample sizes of vertebrate specimens can be obtained by way of surface collection or through the use of screenwashing techniques. The large samples can then be subjected to quantitative analysis (e.g. Shotwell, 1955, 1958; Estes and Berberian, 1970; Dodson, 1983; Brinkman, 1990). As demonstrated by Brinkman (1990), these features of vertebrate microfossil assemblages, when combined with related sedimentologic and taphonomic information, allow for palaeoecological hypotheses to be erected and tested. Palaeoecological studies of the Judith River Group, which are based on evidence from vertebrate microfossil assemblages, have increased over the past two decades (e.g. Sahni, 1972; Dodson, 1983, 1987; Brinkman, 1987, 1990; Baszio, 1997a).

1.2 Historic Overview of Studies on Vertebrate Microfossil Assemblages

Interest in vertebrate microfossil accumulations has focused essentially upon two aspects: taxonomy and palaeoecology. Taxonomic studies have concentrated on specific vertebrate groups, such as fossil mammals (Fox 1968, 1971), lizards (Gao, 1996) and small theropod dinosaurs (Baszio, 1997b). The description and documentation of vertebrate 'faunas' has been an alternative approach (e.g. Estes, 1964; Sahni, 1972; Brinkman (1990), and such studies provide the basis for further palaeoecological analyses.

Palaeoecological study of the Judith River Group or equivalent strata, based on the information derived from vertebrate microfossil assemblages, was first attempted by Sahni (1972). After having extensively documented vertebrate microfossil assemblages from the Judith River Formation in Montana (broadly equivalent to the Judith River Group of southern Alberta), Sahni reconstructed vertebrate palaeocommunities on the basis of postulated lifestyles of recognized animals and their relative abundance.

Palaeoecological investigation of vertebrate assemblages from the Judith River Group of southern Alberta was first carried out by Béland and Russell (1978). On the basis of a survey of articulated vertebrate remains within the area of Dinosaur Provincial Park, they concluded that the distribution of dinosaurian assemblages exhibited 'important inhomogeneities', both geographically and stratigraphically. The generalized geographical patterns were interpreted as

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being related to variation in habitats. The stratigraphic patterns were suggested to be a reflection of normal environment gradients related to the position relative to the coastline of the Bearpaw sea. Further, Béland and Russell (1978) also noted that palaeoecological interpretations were limited due to data being based only upon the evidence of articulated material, and pointed out that such palaeoecological generalization could be strengthened and modified through examination of other data, such as vertebrate microfossil accumulations.

Dodson (1983) was the first to follow up on this, in a palaeoecological study of dinosaur communities of the Judith River Group of DPP. He incorporated data from vertebrate microfossil assemblages into his study and further suggested that such information is "essential to the understanding of the overall vertebrate community in which the dinosaurs lived" (p. 107). He subsequently (Dodson, 1987) investigated how reliable the data derived from vertebrate microfossil assemblages are for palaeoecological studies, especially those concentrating on dinosaurs. After having surveyed variation in the relative abundance of taxa from vertebrate microfossil localities, Dodson (1987) concluded that: 1) overall, taxonomic composition was stable when various microfossil localities were compared; 2) quantitative assessments were repeatable from site to site, although some variation in the relative abundance of taxa mas present; and 3) the average relative abundance of dinosaurian taxa from the surveyed microsites exhibits a strong correlation with the relative

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abundance of articulated specimens of those dinosaurs. Based upon these findings, Dodson (1987) further suggested that information pertaining to taxonomic composition and relative abundance of taxa derived from vertebrate microfossil assemblages is reflective of the various groups of dinosaurs in the community from which these fossil assemblages originated.

A palaeoecological investigation of aquatic vertebrate communities of the Judith River Group of DPP was carried out by Brinkman (1987) on the basis of a survey of vertebrate microfossil localities. This study demonstrated that stratigraphic patterns in the distribution of taxa are evident among these taxa. Those taxa showing similar stratigraphic patterns were interpreted as being associated with similar ecological factors.

More recently, extensive research on Dinosaur Park Judith River vertebrate microfossil localities has been undertaken. Eberth (1990) dealt with the sedimentology and taphonomy, and Brinkman (1990) documented the palaeoecology. Eberth (1990) suggested that vertebrate microfossil assemblages should be regarded as having originated within the general palaeogeographic area now represented by Dinosaur Provincial Park, and that stratigraphic variation in distribution of vertebrate assemblages throughout the section is reflective of the original variation of these assemblages in the area. Combining the information contained in these analyses of the vertebrate microfossil localities, Brinkman (1990) evaluated the stratigraphic patterns of distribution by applying quantitative analysis to interpret the palaeoecological changes in vertebrate communities associated with a marine transgression. Two palaeoecological assemblages (inland and coastal) were recognized on the basis of the distribution of the taxa through the Judith River Formation. These assemblages are further divided into aquatic and terrestrial palaeocommunities based on the mode of life of included taxa.

The latest palaeoecological work on the Upper Cretaceous of southern Alberta was carried out by Baszio (1997a), who focused on documenting general changes of dinosaur assemblages on the basis of isolated dinosaur teeth from microsites over a rather wide stratigraphical range (over a time span of approximately 20 million years), including the Milk River Formation, the Judith River Group of DPP, Horseshoe Canyon and the Scollard formations in southern Alberta. Baszio (1997a) recognized two distinct dinosaur assemblages: one from the Milk River and Scollard formations, and the other shared by the Judith River Group and Horseshoe Canyon Formation. Within the Judith River Group, apparently, data were only available for the uppermost Oldman and Dinosaur Park formations.

All these palaeoecological studies, however, have been restricted to the upper beds of the Judith River Group (the Dinosaur Park and the upper Oldman formations) and mainly to the area of DPP. The present study expands this by broadening the stratigraphic range and geographic extent of sampling.

1.3 Objectives of This Study

The purpose of this dissertation is to provide a palaeoecological analysis of vertebrate microfossil assemblages from the lower beds of the Judith River Group (including the Foremost and Oldman formations) in the Milk River drainage area of southeastern Alberta and to correlate these with the earlier studies outlined above. Additionally, potential problems that have largely been ignored by previous workers are also addressed, and improvements are suggested to make such studies more comparable in future. This study thus focuses upon three aspects:

1). Documentation of vertebrate fossil assemblages from the lower portion of the Judith River Group from the Milk River area. Due to less abundant articulated material, the vertebrate fossil assemblages from the Judith River Group in the Milk River area are much less well-known than those in DPP. Consequently, these assemblages have heretofore not been systematically documented. This study represents the first extensive collection of vertebrate microfossil remains from the area. A documentation of the systematic palaeontology of the retrieved vertebrate assemblages is provided, which forms the basis for later palaeoecological analysis.

2). Discussion of sampling methods and the representativeness of samples. Surface-collecting and screenwashing, as the two conventional

techniques for sampling vertebrate microfossil accumulations, have been widely used for collecting and compiling data for palaeoecological analysis. In the present study, these two sampling techniques are compared to investigate potential biases inherent in the collecting process. Tests of the repeatability of data gathered from samples are also discussed. The representativeness of samples from vertebrate microfossil localities is tested from two perspectives: the representation of taxonomic diversity and the assessment of minimal quantity of raw sediment for a representative sample. These aspects have not been previously addressed in palaeoecological studies of vertebrate microfossil assemblages. Nevertheless, identification of a sufficient sample from each microsite is a prerequisite for further palaeoecological analysis.

3). Palaeoecological analysis of the vertebrate microfossil assemblages examined. Vertebrate microfossil assemblages are compared on the basis of taxonomic composition and relative abundance of taxa in order to reveal similarities and differences between them. Patterns recognized among these assemblages are then investigated to identify possible palaeoecological correlates; they include the impact of taphonomic biases resulting in sizesorting differences, the role of sedimentary facies associations, the impact of speciation, extinction, or immigration events, and the influence of regional palaeoenvironmental changes. Palaeoecological inferences are then made based upon the stratigraphic distribution of the relative abundance of taxa. Finally, comparisons of palaeoecological interpretations are made between the results of this study and Brinkman's (1990) assessments, to further test and document possible original ecological associations among fossil vertebrates during the period of time when the sediments of the Judith River Group were deposited in southern Alberta.

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The overall objective of this work is to improve and provide a better understanding of the palaeoecology of vertebrate assemblages during the Campanian in southern Alberta, and to further our ability to effectively document and analyze the data gathered.

Chapter 2 Geological Background

In order to investigate and understand the palaeoecological significance of the vertebrate microfossil assemblages retrieved in this study, it is necessary to place them into a geological context. This chapter summarizes the general geological setting of the Upper Cretaceous in southern Alberta, in the context of the following three aspects: palaeogeography, stratigraphy, and the sedimentological and taphonomic framework of vertebrate microfossil localities.

2.1 Palaeogeography Of The Upper Cretaceous Alberta Foreland Basin

During the Late Cretaceous, much of the Western Interior of North America was inundated by the Western Interior Seaway, which extended from what is now the Gulf of Mexico to, at times, the Arctic Ocean (Williams and Stelck, 1975) (Fig. 2.1). Geological study indicates that active tectonics along the western margin of the continent resulted in mountain building, which formed the Canadian Cordillera. As a result of tectonic activity, a broad foreland basin was subsequently produced, in a location congruent with that of the modern southern Alberta Plains. This sedimentary basin is also referred to as the Alberta Foreland Basin. Figure 2.1, shows that the location of the study area in southern Alberta lay in what was, in the Mid-Campanian, a broad, low-lying alluvial plain that extended from the highlands in the west to the Western Interior Seaway in the east. Sediments were transported eastward by alluvial systems and deposited in the Alberta Foreland Basin.

Sea-level fluctuations of the Western Interior Seaway were marked by a series of transgressive/regressive cycles (McGookey, 1972). The western shoreline of the Western Interior Seaway advanced and retreated throughout the Late Cretaceous in response to these cycles (McLean and Jerzykiewicz, 1978; Cant and Stockmal, 1989; Eberth and Hamblin, 1993).



Figure 2.1 Paleogeography of North America during the Mid-Campanian. Alberta is outlined in dashline and the star shows the approximate location of the study area. (Modified from Williams and Stelck, 1975).

2.2 Stratigraphical Setting Of The Upper Cretaceous Alberta Foreland Basin

The regional tectonic activity in the west and the transgression/ regression of the Western Interior Seaway margin in the east of the Alberta Foreland Basin were the major factors in the development of the Late Cretaceous patterns of sedimentation in the region (Cant and Skockmal,1989; Eberth and Hamblin, 1993). Consequently, Upper Cretaceous stratigraphic sections of the Alberta Foreland Basin record a foreland clastic wedge that progressively thins from west to east. This wedge consists of nonmarine deposits in the west of the Alberta sedimentary basin, mostly marine in the east, and in between, an intricate intertonguing of the two (McLean, 1971; Cant, 1989; Cant and Skockmal,1989; Leckie, 1989).

Stratigraphic nomenclature of the Upper Cretaceous strata has been discussed at length (e.g., McLean, 1971; Eberth and Hamblin, 1993; Hamblin, 1997) and will not be addressed here. In this dissertation I essentially follow the nomenclature of Eberth and Hamblin (1993). Figure 2.2 summarizes the stratigraphy of the Upper Cretaceous Alberta Foreland Basin, as interpreted by Eberth and Hamblin (1993).

McLean (1971)	Bearpaw Fm.		Judith River Fm.	Claggett Fm.	Eagle Fm.
Russell & Landes (1940)	Bearpaw Fm.	Oldman Fm.	Foremost Fm.	Pakowki Fm.	Milk River Fm.
Eberth & Hamblin (1993)	Bearpaw Fm.	Dinosaur Park Fm. D Oldman Fm.	ν μ < − × μ κ Foremost	Pakowki Fm.	Milk River Fm.
AGE			U 4 ∑ L 4 Z -	∢z	
MA	;	76	82	88	1 1

FIGURE 2.2 Stratigraphy of the Judith River Group in southern Alberta. Stippled column indicates the stratigraphic range of the exposures in the Milk River area examined in this study. (Modified from Eberth and Hamblin, 1993)

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According to Eberth and Hamblin (1993), the Judith River Group represents an eastward-thinning, non-marine to paralic sedimentary wedge that was deposited along the western margin of the Western Interior Seaway during the middle to late Campanian (80.0-74.5 Ma). In the southern Alberta Plains, the Judith River Group has been further subdivided by Eberth and Hamblin (1993) into three formations, — the Foremost, Oldman, and Dinosaur Park in ascending stratigraphic order. The following is a general geological description of these three formations and their palaeoenvironmental interpretations.

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I. The Foremost Formation This is the lowest formation of the Judith River Group, and is interpreted as a transitional rock unit between the conformably underlying marine Pakowki Formation and the overlying nonmarine Oldman Formation. It comprises both transgressive and regressive sedimentary deposition events (Russell and Landes, 1940; Ogunyomi and Hills 1977; Kwasniowski, 1993). The depositional environments of the formation are considered to be strongly associated with a coastal marine influence, which is comprised of coastal plain, barrier island-shoreface and shoreface, and shallow marginal marine environments (Kwasniowski, 1993; McNeil et al., 1995).

Exposures of the Foremost Formation are mainly distributed along the Milk River Valley in southern Alberta. The sediments of the formation vary greatly at different localities, but are commonly composed of interbedded sandstones, siltstones, mudstones and coals (Russell and Landes, 1940; Ogunyomi and Hills 1977).

Kwasniowski (1993) documented sea-level fluctuations during deposition of the Foremost Formation in southern Alberta, and divided the formation into three informal depositional sequences that are interpreted to have been related to relative sea-level changes. According to Kwasniowski (1993), the lower sequence, characterized by interbedded sandstones, siltstones, claystones and carbonaceous shale with poorly-developed coal seams, represents deposits laid down in an overall regression. The middle sequence is distinctively composed of three mudstone units, which is interpreted as deposits laid down in an overall marine transgression. The upper sequence is characterized by large sandstone bodies, along with clayey siltstones and coal seams, which are considered to represent an overall regression event. In the present study, vertebrate microfossil sites were located in and sampled from only the upper sequence, but vertebrate fossils were also surface-collected from both the lower and middle sequences.

II. The Oldman Formation This formation conformably overlies the top of the Taber Coal Zone of the Foremost Formation and is separated by a regional discontinuity from the overlying Dinosaur Park Formation. The Oldman Formation is characterized by pale, white-to-yellow, fine- to very fine-

grained sandstones (Russell and Landes, 1940). Sedimentological studies by Eberth (1990) and Eberth and Hamblin (1993) suggested that the Oldman Formation represents deposits of shallow, high velocity, lowsinuosity, ephemeral fluvial systems, along with frequent and extensive overbank flooding events. Overall, the Oldman Formation is interpreted to have been deposited in a variety of non-marine fluvial depositional settings on a broad coastal plain along the western margin of the Western Interior Seaway (Eberth, 1990; Eberth and Hamblin, 1993). Depositional environments include freshwater fluvial channels, floodplains and alluvial plains.

According to Eberth (1994), the Oldman Formation in southern Alberta can be further divided informally into three units, which are summarized as follows:

- a lower unit, overlying the Taber Coal Zone, is interpreted to reflect a basin-ward shift of palaeoenvironments from the swampy coastal plain sediments (the Taber Coal Zone) to well drained, alluvial plains sediments. The outcrops of this unit are present and exposed primarily in the Milk River area. Vertebrate microfossil sites are abundant, and are usually associated with sandstones.
- a middle unit, also referred to as the Comrey sandstone [equivalent to the 'Comrey Member' of Hamblin (1997)], represents a regionally consistent sandstone unit that is traceable in the subsurface

throughout southern Alberta (e.g. Hamblin, 1997). The exposures of this unit in the Milk River area are characterized by stacked, multistoried sheet sandstones, often with sharp erosional bases. The sedimentary facies have been interpreted to be the deposits of an extensive, low sinuosity fluvial system with relatively shallow channels (Eberth and Hamblin, 1993; Hamblin, 1997). The outcrops of the middle unit are seen mainly in the Pinhorn Ranch of the Milk River area. Vertebrate microfossil remains are comparatively less abundant in this unit than they are in the other two.

a upper unit, equivalent to the "Upper Siltstone" member of Hamblin (1997), is characterized by isolated palaeochannel sheets, which are generally composed of interbedded siltstone, very fine-to-fine grained sandstone and minor carbonaceous shales. This unit, showing facies somewhat similar to those of the lower unit, is interpreted as representing primarily subaerial floodplain environments, including both overbank and splay deposits (e.g. Hamblin, 1997). The outcrops of this unit are largely exposed along the Milk River drainage. Vertebrate microfossil sites are very abundant and are mainly associated with splay deposits in this unit in the Milk River area.

III. The Dinosaur Park Formation This represents the uppermost unit of the Judith River Group, and consists of alluvial, estuarine and paralic facies (Eberth, 1990; Eberth and Hamblin, 1993). Exposures of this formation are absent or limited in the area of the present study, thus no vertebrate microsites of the Dinosaur Park Formation were found and sampled. However, the sediments of this formation are well preserved and extensively exposed in DPP, where vertebrate microfossil localities are extremely abundant. Extensive studies of these microsites in DPP have been carried out (e.g. Dodson, 1987; Brinkman, 1990; Eberth, 1990).

2.3 Sedimentological and Taphonomic Framework of the Vertebrate Microfossil Localities of the Judith River Group of southern Alberta

The sedimentology and taphonomy of the vertebrate microfossil sites of the Judith River Group in southern Alberta were first discussed by Dodson (1970, 1971), who noted that "concentrated assemblages of small bones (i.e. microsites) characteristically occur in clay pebble sandstones", and that concentrations of such small bones represent hydraulic accumulation which may be associated with "channel backwaters". Further, he also asserted that many vertebrate microfossil remains show no signs of abrasion, and that this may be indicative of the remains having been transported over only small distances. Wood et al.(1988) also documented vertebrate taphonomy in the Judith River Group of DPP, and found that vertebrate microfossil accumulation is associated with channel lag deposits.

A more extensive investigation that specifically focused on the sedimentology and taphonomy of vertebrate microfossil accumulations was carried out by Eberth (1990). He examined 24 microsites that are widely distributed throughout the section of the Judith River Group in DPP, and documented the sedimentology and taphonomy of each site in detail. He concluded that these microsites are associated with two basic sedimentary facies: intraclast deposits (also referred to as in-channel deposits) and contorted siltstone/sandstone deposits (also referred to as splay deposits).

According to Eberth (1990), vertebrate microfossil accumulations associated with the intraclast deposits are considered to represent concentrations of vertebrate microfossils that were locally derived in interchannel areas and subsequently introduced into channels during bank collapse and rip-up events. These vertebrate microfossil concentrations were transported over relatively short distances prior to final burial. The microsites associated with the contorted siltstone/sandstone deposits were interpreted by Eberth (1990) to be concentrations of vertebrate microfossils that were originally distributed on the floodplain and then subsequently accumulated through flooding events (mainly crevasse splays). Such concentrations are often associated with local concentrations of pisidiid clams. Thus, these microsites are considered to be "certainly of local origin on the scale of the splays themselves (100's of m)" (Eberth, 1990: p23).

A complementary palaeoecological study carried out by Brinkman (1990) revealed that vertebrate microfossil remains recovered from both the inchannel and splay deposits are composed of very similar physico-chemically resistant skeletal elements, such as teeth, scales, and centra. Eberth (1990) suggested that the vertebrate microfossil assemblages from both inchannel and splay deposits were concentrated in interchannel environments prior to final transport and burial, and that the differences in relative abundance of taxa associated with their stratigraphic distribution may reflect real differences in local taxonomic abundance through time.

Brinkman (1990) also noted that among the recognized assemblages some taxa, represented by elements that are of similar size, shape and texture, are postulated to have had generally similar life styles, but to exhibit different stratigraphic distribution among microsites. He suggested that such differences are more indicative of biotic causes, than of taphonomic ones. Examples of such taxa listed by Brinkman (1990) are holostean A and holostean B (both represented by small enameled scales), the small theropods <u>Troodon</u> and <u>Saurornitholestes</u> (represented by isolated blade-like teeth), and hadrosaurids and ceratopsians (represented by isolated pebble-like teeth). subjected to "a continuous supply of elements over a long period of time", and were sensitive to local environmental conditions.

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Chapter 3 Material and Methods

In this chapter, I present information pertinent to the study area and the location of the microsites examined, material recovery, methods applied to sorting and curating material, and quantitative methods for estimating abundance of recovered taxa.

3.1 Location Of Vertebrate Microfossil Sites

The field research of the present study focused upon recovering and investigating vertebrate fossils, specifically vertebrate microfossils, from the Judith River Group along the Milk River Valley and in its drainage area near the international border in southeastern Alberta (Fig. 3.1). Exposures of the Judith River Group, mainly composed of the Foremost and Oldman formations in the area, are extensively distributed along the Milk River drainage and adjacent area. FIGURE 3.1 Locality map showing the geographic distribution of vertebrate microfossil sites from the Judith River Group in southeastern Alberta. The location of the site SPS is shown in the upper map, and the remainder of the 18 sites occur in the Milk River drainage area, as depicted in the lower map. Full names and RTMP locality numbers of the sites and a stratigraphic description of each are provided in Appendix I.

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An extensive survey of vertebrate microsites in the study area was carried out mainly during the field seasons from 1993 to 1996, and was organized and led by Dr. D. B. Brinkman of the Royal Tyrrell Museum of Palaeontology (RTMP). Nineteen vertebrate microfossil sites from both the Foremost and Oldman formations were located and subsequently sampled. The geographic distribution of these microsites is presented in Fig. 3.1. Further geographic information on the microsites, including Legal Land Description and Universal Transverse Mercator (UTM) coordinates, is detailed in Appendix I.

Relative stratigraphic relationships of the vertebrate microsites examined in this study are approximated on the basis of the measurement of stratigraphic positions relative to each other and/or to known stratigraphic horizons, such as the Taber Coal Zone. Detailed measurements are presented in Appendix III. Fig. 3.2 summarizes the relative stratigraphic positions of microsites superimposed on the composite section of the Judith River Group in the Milk River area as presented by Eberth and Hamblin (1993, Fig. 22).



Fig. 3.2 Stratigraphic positions of the vertebrate microsites sampled from the Judith River Group in the Milk River area. The composite section in the study area is from Eberth and Hamblim (1993).

3.2 Material Recovery Methods

Two methods are commonly employed for recovering vertebrate microfossils: surface collecting and screenwashing (e.g., Shotwell, 1955, 1958; Estes, 1964; Voorhies, 1969; Brinkman, 1990). Both techniques were applied during the course of the present study. The general procedures for each of these two methods are outlined below, along with a discussion of the potential advantages and disadvantages of each.

I. Surface Collecting

Surface collecting is essentially a method of hand-picking fossils that are exposed and visible on the surface of sediments. It is the most direct and, perhaps, most often applied fossil recovery method used in such field work. It requires no extra tools, and thus is convenient for collecting and preserving specimens that are being weathered and eroded in the field. In this study, surface collecting was conducted at each microsite prior to bulk matrixcollecting, and it was also employed in surveying the associated strata on an extensive basis. Surface collecting allows for a convenient and broad survey of fossil vertebrates within a stratigraphic section and a particular area, and thus can be used as a supplemental method for other methods of collection (see below). However, the surface-collecting method, in general, has the obvious disadvantage of being strongly biased against small specimens and towards large specimens (Wolff, 1975). Other biases of this method include the different interests or experience of collectors, and different total collecting time devoted to different localities. Such biases can be particularly evident for microsites, and they strongly affect abundance data in a manner that makes it much less applicable for some analyses. Further consideration is given to this problem in Chapter 5.

II. Screenwashing

The second method for recovering vertebrate microfossils is the screenwashing technique. It is a well-known collecting method that has been employed by palaeontologists to recover microfossil material of both invertebrates (e.g. Zingula, 1968; Duffield and Warshauer, 1979) and vertebrates (e.g. Hibbard, 1949; McKenna,1962). Such microfossil material might otherwise be overlooked or greatly underestimated if the traditional methods of prospecting are used alone. Thus, screenwashing is considered to be the standard recovery method for vertebrate microfossil material and it has been widely used on Cretaceous sediments since it was first employed in collecting mammal material (McKenna,1962). This technique has proven to be superior to the surface-collecting method for the processing of large samples that yield large numbers of small fossil specimens (Brinkman, 1990). More importantly, screenwashing significantly reduces the biases against small and rare elements encountered in surface-collecting (see Chapter 5), and provides

a way of systematically sampling microsites in a repeatable fashion. This, then, allows for further statistical analyses, such as tests of representativeness of repeated samples and the comparison of taxonomic abundance between and among microsites. Such statistical analyses and a discussion of them are presented in detail in Chapter 5.

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The general process of screenwashing that was applied to the recovery of vertebrate microfossil material in this study is as follows:

- sediment samples were first collected from appropriate microfossil localities and placed into collecting bags. In this study, 20 bags (approximately 20kg per bag) of matrix were collected from each microsite.
- collected matrix was then presoaked under water in buckets for about seven days in order to disaggregate the matrix in preparation for the next step.
- 3) the matrix was finally processed through fine screens using a mechanical shaker, during which a water sprinkler was employed in order to wash away fine-grained sediments. A screen with nine openings per centimeter was used by Brinkman (1990) in his study of vertebrate microfossil localities in DPP. In the present study, a finer screen, with eight openings (less than 1mm diagonally), was employed during matrix washing in order to reveal the possible presence of smaller specimens. The resulting samples indicated that

additional very small specimens, such as <u>Chiloscyllium</u> teeth (<1mm) and <u>Rhinobatos</u> teeth (<1.5mm), were recovered by way of the finer screen. The only exception to this procedure is that the matrix from the PHR-1 site was processed underwater using screenbags in the field.

- 4) the screenwashed concentrate was left to dry on the screens. The weight of washed and dried concentrate samples varied from approximately 2% to 30% of the original matrix weight. Such variance is due to differences in the nature of the sediments, and to the concentration of invertebrate shell material.
- 5) acid preparation was also employed on those samples of screenwashed concentrate that contained a large amount of invertebrate shell fragments. A solution of 10% acetic acid was used to dissolve the shell fragments. Results show that almost all the invertebrate shell fragments were dissolved, while virtually no damage was done to the vertebrate fossils, including small, delicate teleost vertebrae.

3.3 Sorting and Curating Vertebrate Microfossils

After the washed concentrate had been dried, large fragments were picked out. The main task of sorting was carried out using a binocular dissecting microscope to examine concentrate that had been placed on a paper tray marked with 1x1cm grids. All the organic material was picked out and placed in vials, labeled by site, for later taxonomic identification. The residue of the matrix was retained for the assessment of fossil concentration and for possible reexamination.

All of the sorted specimens were then closely examined and identified to the lowest possible taxonomic level (for details see Chapter 4). Each major group of vertebrates recovered was allotted an accession number that was designated by the Royal Tyrrell Museum of Palaeontology. Within a major group, a catalogue number corresponding to the accession number was given to a specimen or set of specimens of each element of an identified taxon. All the identified specimens were then placed in vials labeled with information including a catalogue number, skeletal element identification, taxonomic name, name of microsite, and source of stratigraphic formation. Recovered specimens that were not able to be identified in this study were also kept in separate vials or containers, and labeled with microsite name and stratigraphic formation. These unidentified specimens were also separated into different size groups for the examination of the size frequency distribution at each site

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(for details see Chapter 7). Both the identified and unidentified specimens were counted for the compilation of data matrices and for later numerical analyses.

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3.4 Quantitative Methods For Estimating Abundance Of Fossil Vertebrates

Quantification of Specimens Using the screenwashing technique, vertebrate microsites yield a large number of specimens of fossil vertebrates. These specimens are represented by teeth and disarticulated, small skeletal elements. In order to estimate the relative abundance of taxa (the number of individuals per taxon) present in fossil assemblages, based upon the recovered specimens, it is very important to choose appropriate methods. A variety of quantitative methods for estimating the number of individuals per taxon in fossil vertebrate assemblages have been developed and are discussed extensively in palaeoecological studies (e.g., Shotwell 1955, 1958; Grayson, 1978, 1984 and Badgley, 1986).

Badgley(1986) reviewed these approaches and concluded that different quantitative methods are suited to different agencies of natural sampling that have been responsible for the formation of particular assemblages, in the context of their taphonomy. She found that the minimum number of elements (MNE) of a taxon is the best method for estimating the abundance of individuals preserved at localities in which specimens are widely dispersed and accumulated as isolated specimens, such as that typically found at vertebrate microsites. The MNE is a modification of the minimum number of identified specimens (NISP), which counts only disassociated elements. This measure attempts to eliminate the effects of fragmentation that occurs during preservation, exposure, and collection. Brinkman (1990) adopted this approach in his vertebrate microfossil study [but warned that each end of a salamander centrum may be counted as a separate element because the hourglass-shaped vertebrae tend to break in the middle and the resulting fragments appear identical]. Blob and Fiorillo (1996), in an effort to reduce the false representation of one element as several, due to breakage during screenwashing, were more restrictive in that they only counted elements that were more than half complete. Such adjustment, however, is not universally applicable to vertebrate specimens, as it cannot adequately deal with the aforementioned hourglass-shaped salamander vertebrae, or with turtle shell elements which are particularly prone to fragmentation. Few examples of turtle shell elements that are more than half complete have been recovered from any microsite in the present study, even though turtle shell fragments may be abundant.

The breakage of specimens due to screenwashing can generally be recognized during the process of sorting, and thus this problem has been alleviated in the present study by way of specimen repair. Moreover, such a problem can be minimized if the comparison of relative abundance is

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conducted for the same taxon between different microsites. The reasons are as follows: first, all the specimens are counted in the same way; second, it is safe to assume that the probability of fragmentation among the same elements of a taxon should be the same when the samples are subjected to the same sampling (screenwashing) process.

The disadvantage of the MNE quantitative method is that it cannot account for associations among elements, and it will distort the estimated abundance of taxa when associated and unassociated specimens are counted in the same manner. Evidently, the associated specimens tend to be overestimated. Therefore, modifications of the method proposed by Brinkman (1990) were adopted in the present study in order to ensure consistency and appropriate comparison. The modifications of MNE include counting specimens that are prone to fragmentation as separate elements (such as salamander vertebrae and turtle shells) and reducing the number of associated specimens through specimen repair. In order to further alleviate the disadvantage of overestimating elements that are associated due to breakage, other measures were also taken in later numerical analyses, such as excluding those elements from data.

Relative Abundance Of Taxa The number of elements of an individual taxon, as discussed above, in a standard sample may not be directly used as a measure of abundance to compare different microsites because the concentration of vertebrate fossils varies among microsites. Approximately the

different numbers of specimens (for instance, the identified specimens vary from 7375 from PHR-1 to 233 from BMC; for details see Appendix II). Thus, relative abundance of taxa can be introduced to moderate this problem.

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Relative abundance of taxa is an important parameter in ecological studies that attempt to express the proportion of a particular taxon in an entire assemblage. Percentage and rank-order are the two measures most commonly applied in palaeoecological studies. However, it has been argued that percentage is an unsatisfactory measure because an increase in the abundance of one taxon will result in an apparent decrease in the abundance of all others (Grayson, 1984; Briks and Gordon, 1985; and Brinkman, 1990). Brinkman (1990) pointed out that unimportant variation in the abundance of the most common taxa may obscure patterns in the occurrence of rare taxa within assemblages where a few taxa are dominant. In order to ameliorate this problem, he suggested that rank-order is a better measure of relative abundance of taxa for the analysis of vertebrate microfossil assemblages. Such ordinal level data, however, may result in the loss of certain details of information, and are also not suitable for some statistical analyses.

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Chapter 4 Systematic Palaeontology

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Vertebrate fossil assemblages from the Judith River Group in the Milk River area are much less well-known than those in DPP, due to much less abundant articulated material. Thus, abundant vertebrate microfossil assemblages have become a very significant source for documenting the diversity of vertebrate fossils from the Judith River Group in the Milk River area. Due to the incomplete nature of vertebrate microfossil material and scarce references, taxonomic identification in microsite studies is often a difficult, tedious task. In an attempt to alleviate the situation, a detailed description of all identified vertebrate microfossils, along with accompanying photographic plates, is provided in this chapter, with emphasis being placed upon identifying and distinguishing known vertebrate microfossils.

The fossil vertebrate material described below includes the identified specimens from the microsites examined in the present study through both screenwashed and surface-collected samples. The following classificatory schemes are essentially followed: Chondrichthyes (Cappetta, 1987), Osteichthyes (Lauder and Liem, 1982; Nelson, 1984), Amphibia (Estes, 1964; Duellman and Trueb, 1994), Squamata (Estes, 1983; Estes et al., 1988; Gao and Fox, 1996), Testudines (Gaffney and Meylan, 1988), Crocodylia (Wu et al., 1996), Ornithischia (Horner, 1990; Weishampel and Horner, 1992), Saurischia (Currie et al., 1990), and Mammalia (Fox, 1996, pers comm.). The specimens are assigned to the lowest possible taxonomic level, but between taxa this lowermost designation varies due to differences in the quality of preservation. The following descriptions and documentation provide a complete taxonomic list of fossil vertebrate material recovered from the microsites examined in this study, with an emphasis on distinguishing and identifying disarticulated microvertebrate material.

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Class Chondrichthyes Huxley 1880 Subclass Elasmobranchii Bonaparte 1838

Elasmobranch fossils, represented mainly by tooth material, have been predominantly recovered from PHR-1 and PHR-2, and sporadically from other sites. Eight genera have been identified in this combined collection, consisting of 4754 specimens. Having highly distinctive morphologies, they are readily separable from other microvertebrate fossils.

Order Euselachii Hay 1902 Family Hybodontidae Owen 1846 <u>HYBODUS</u> Agassiz 1837

Plate 1, a-c.

Material: <u>Hybodus</u> teeth (RTMP96.71.1 and -2) have been retrieved from only the PHR-1 and PHR-2 sites. They are represented mostly by a main (central) cusp, lacking a tooth root. Only one tooth (RTMP96.71.1) exhibits partial preservation of a root.

Description and Discussion: <u>Hybodus</u> teeth are readily identifiable by the presence of a low, rather mesio-distally expanded crown, with a distinctively robust, tall principal cusp (Case 1978; Cappetta, 1987).

In addition to the aforementioned features, the teeth recovered in this study bear prominent mesial and lateral carinae on the principal cusp and distinct plications extending up to half of the principal cusp height. The lateral cusplets are poorly-developed or absent. These teeth are evidently referable to the genus, <u>Hybodus</u>.

<u>Hybodus</u> teeth have also been described by Case (1978, 1987) from the Judith River Formation of Montana and the Mesaverde Formation of Wyoming, and by Beavan (1996) from the Foremost Formation of southern Alberta. Case (1978, 1987) erected two species of the genus, <u>H</u>. <u>montanensis</u> and <u>H</u>. wyomingensis, essentially on the basis of size differences. One of the features

listed for <u>H</u>. <u>montanensis</u> by Case (1987, p.6), the absence of plications, contradicts with his description and illustration (Case, 1978, p.180, text-fig. 2). Thus, this feature is here considered to be questionable for distinguishing the two species. More complete material is needed to clarify this. Until then, the teeth retrieved from this study are assigned to the genus <u>Hybodus</u>. These teeth are, in general, very similar to those recovered from the upper Judith River Group of DPP (Brinkman, 1990).

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Order Lamniformes Berg 1958

Family Odontaspididae Müller & Henle 1839

SYNODONTASPIS White 1931

Synodontaspis hardingi (Cappetta & Case 1975)

Plate 1, d-g.

<u>Odontaspis hardingi</u> Cappetta & Case 1975: p. 20, Pl. 7, figs. 1-16. <u>Odontaspis sanguinei</u> Case 1978: p. 190, Pl. 4, figs. 12. <u>Carcharias hardingi</u> Beavan 1995: p. 68, Pl. II, figs. c-g.

Material: <u>Synodontaspis</u> teeth (RTMP96.71.3 and .4) have been recovered from the PHR-1 and PHR-2 sites of the Foremost Formation.

Description: The teeth are referable to <u>Synodontaspis</u> on the basis of the following features: they possess a tall, slender central cusp and single pair of lateral cusplets; the central cusp is sigmoidal in profile view of each edge;

the lingual face is smooth, and some bear week, irregular longitudinal ridges; the labial face is flat, with some short longitudinal ridges at the foot of the crown; the cutting edges of the central cusp are prominent and thinly enameled; the roots are bi-lobed, with a deep nutritive groove on the lingual protuberance.

Discussion: This genus is one of the most common fossil sharks found in the Upper Cretaceous deposits of marine and estuarine facies in North America (Cappetta, 1987). Such teeth have been identified under two generic names--<u>Carcharias</u> and <u>Synodontaspis</u> (e.g. Case, 1978; Siverson, 1992, 1995; Welton and Farish, 1993; Beavan, 1995), resulting in some confusion. Cappetta (1987) suggested that <u>Carcharias</u> is a *nomen oblitum* [because <u>Carcharias</u> has been placed on the Official Index of Rejected Generic Names in Zoology (Name no 1747, Opinion 723.5b, 1963)]. I have here applied the generic name <u>Synodontaspis</u>. The teeth recovered in this study are referable to <u>Synodontaspis</u> hardingi.

Family Cretoxyrhinidae Glückman 1958

ARCHAEOLAMNA Siverson 1992

Archaeolamna kopingensis Siverson 1992

Plate 1, h-m.

<u>Plicatolamna arcuata</u> Herman 1973: p. 311, Pl. 8, fig. 4; Case 1978: p. 191, Pl. 4, figs. 5-6; Case 1987: p. 10, Pl. 3, figs. 6-13. <u>Archaeolamna kopingensis</u> Siverson 1992: p. 534, Pl. 2, figs. 16-20.

Material: Teeth of <u>Archaeolamna</u> have been recovered from only the PHR-2 site. This sample includes both lateral and posterior teeth (RTMP96.71.5).

Description: These teeth display a triangular, broadly-based central cusp that is labio-lingually strongly compressed and distally curved; a single pair of lateral cusplets is present, having a similar triangular form to that of the main cusp, and are somewhat divergent from it. A lingual protuberance with nutritive pits is prominently developed.

Discussion: <u>Archaeolamna</u> teeth can be readily distinguished from those of <u>Synodontaspis</u> by the presence of a triangular and broadly-based central cusp.

Order Orectolobiformes Applegate 1972 Family Orectolobidae Jordan & Fowler 1903 <u>SQUATIRHINA</u> Casier 1947 <u>Squatirhina roessingi</u> Case 1987

Plate 2, a-d

Squatirhina roessingi Case 1987: p. 20, Pl. 6, figs. 1a-6e.

Material: Specimens referred to <u>Squatirhina</u> <u>roessingi</u> are oral teeth. They are catalogued as RTMP96.71.6 and RTMP96.71.9.

Description: These oral teeth are minute; with the largest dimension less than 3mm. The central cusp is slender and sharply-pointed. The welldeveloped labial flange extends ventrally and close to the root area. The shoulders on either side of the central cusp are narrow, with a shallow notch between cusp and shoulder. The cutting ridges on the shoulders often rough and discontinuous, indicative of being vestigial cusplets. The root is dorsoventrally thin, with a prominent groove on the ventral surface, which divides the root base lingo-labially into two.

Discussion: The teeth recovered in this study are similar in features described above to those of <u>S</u>. <u>roessingi</u> recovered from the Mesaverde Formation of Wyoming (Case, 1987), and are thus assigned to that species. The teeth of <u>S</u>. <u>roessingi</u> resemble, in general appearance, those of <u>Squatina</u>,

but are readily distinguishable by the presence of a prominent nutrient groove on the basal attachment surface. These teeth of <u>S</u>. <u>roessingi</u> represent the first record of this taxon reported from the Upper Cretaceous of Alberta.

Family Hemiscylliidae Gill 1862

CHILOSCYLLIUM Müller & Henle 1837

Chiloscyllium missouriense Case 1979

Plate 2, e-g

<u>Chiloscyllium missouriense</u> Case 1979: p. 224, Pl. 1, fig. 2; Case 1987: p. 19, fig. 7.

Material: <u>Chiloscyllium</u> is represented by minute teeth (<1mm). It is one of the most widely (second to <u>Myledaphus</u>) distributed elasmobranch taxa in this collection. Specimens have been recovered from the following sites: PHR-2 (RTMP96.71.14), SPS (RTMP96.71.15), WS (RTMP96.71.16), PHR93-2 (RTMP96.71.17), CS (RTMP96.71.18) and CN-1 (RTMP96.71.19). Unlike <u>Myledaphus</u>, however, specimens are not common and only one tooth has been recovered from the sites, except for PHR-2 and SPS.

Description: The crown is generally smooth (some have minor folds), with a long, broadly-based cusp. A pair of accessory cusplets is either poorlydeveloped or absent. The labial flange is prominent and round, and the root is low and cordiform in ventral view. The basal attachment surface is concave, with a large central nutrient foramen. The lingual root protuberance is penetrated by a foramen.

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Discussion: Case (1979) described a species, <u>C</u>. <u>missouriense</u>, based on teeth, from the Judith River Formation of Montana. He later assigned more material from the Mesaverde Formation of Wyoming to the same species (Case, 1987). The <u>Chiloscyllium</u> teeth identified in the present study are also referable to this species, although they differ in the variable presence of a pair of cusplets which are absent from the teeth from Wyoming and Montana. The current findings represent the first occurrence of this genus in the Upper Cretaceous of Alberta.

Herman (1977) noted that the specimens examined by Estes (1964, fig. 2, a, b: U. C. no. 56272 and 53901) were mistakenly identified as symphyseal teeth of 'Lonchidion selachos', and that they belong to the Orectolobiformes. These specimens appear to closely resemble the teeth of <u>C</u>. <u>missouriense</u> recovered in this study. Thus, they are here suggested to be referable to this taxon.

Order Rajiformes Berg 1940

Family Rhinobatidae Müller & Henle 1838

RHINOBATOS Linck 1790

Rhinobatos casieri Herman 1977

Plate 2, h-i

<u>Rhinobatos casieri</u> Herman 1977: p. 126, figs.5-9; Case 1987: p. 22, Pl. 5, figs.3a-5c; Welton & Farish 1993: p. 131, figs. 1-4. <u>Rhinobatos</u> sp. Case et al. 1990: p. 1092, figs.12, 13.

Material: <u>Rhinobatos</u> (RTMP96.71.13) teeth have been recovered from only the PHR-2 site. They are minute, with a maximum dimension less than1.5mm.

Description: The crown is smooth and is mesio-distally longer than it is labio-lingually. On the lingual side, the crown sends a long median lingual uvula towards the base of root, and this is flanked by similarly-sized (in width), but shorter mesial and distal lingual marginal uvulae. The lateral protuberances are distinctly separated from the median protuberance by grooves, except for the region close to the dorsal crown. The root is massive and is separated by a deep groove into two lobes, each of which bears a lateral triangular process. A pair of nutrient foramina is present at the base of each triangular process. **Discussion**: The <u>Rhinobatos</u> teeth reported here represent the first occurrence of this taxon from the Judith River Group of southern Alberta. They have, however, been described from the Upper Cretaceous of Montana (Cappetta, 1987). Although it has not been confirmed in extant species of the genus, tooth sexual dimorphism was proposed by Cappetta (1987) and Case et al. (1990) for fossil forms. Only one type of tooth (the 'female' morph) has been recovered from site PHR-2. Whether this represents a preservational bias or whether it is due to other causes remains to be clarified by further study.

Family Sclerorhynchidae Cappetta 1974

ISCHYRHIZA Leidy 1856

Ischyrhiza mira Leidy 1856

Plate 2, j-m

<u>Ischyrhiza mira</u> Leidy 1856: p. 221; Storer & Johnson 1974: p. 712, fig.1; Case 1978: p. 196, Pl. 3, figs. 4, 5; Case 1987: p. 24, Pl. 13, figs. 1a-e; Beavan 1995: p. 75, Pl. 5 & 6, figs. h-i.

Material: The retrieved specimens of <u>Ischyrhiza</u> include oral teeth (RTMP96.71.10), and one rostral tooth (RTMP96.71.11) from PHR-2.

Description: The oral teeth are referred to the genus on the basis of the following features: crown smooth, mesio-distally expanded with a single, short cusp and low, but rather broadly expanded shoulders; cusplets absent; labial

flange well-developed; cutting ridges prominent on cusp and the labial margin of shoulders (some teeth also have a cutting edge on the labial flange); root relatively high, with a flat basal attachment surface; a deep nutrient groove subdividing the root into two triangular lobes, a condition typical of the holaulacorhizous form (Cappetta, 1987). The rostral tooth is typical of the genus in its form: the crown laterally is compressed, with sharp cutting edges both anteriorly and posteriorly; and it is also covered with smooth enameloid, and slightly sinuous anteroposteriorly.

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Discussion: Both the oral teeth and the rostral tooth described above exhibit the typical morphology associated with <u>Ischyrhiza mira</u> (Case, 1978, 1987; Cappetta, 1987), and can be referred to this species with certainty. The oral teeth are often more common and are readily identifiable by the presence of broad and low shoulders and the holaulacorhizous type of root (Cappetta, 1987).

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Rhinobatoidei incertae sedis

MYLEDAPHUS Cope 1876

Specimens referred to <u>Myledaphus</u> are represented mainly by isolated teeth, and they were retrieved from 18 of the 19 microsites examined in this study.

Myledaphus bipartitus Cope 1876

Plate 3, a-c

Myledaphus bipartitus Cope 1876: p. 260; Lambe 1902: p. 28, Pl. 19, figs. 1-2;
Sternberg 1909: p. 78, fig.13; Estes 1964: p. 15, Pl. 1, figs. 7-8; Sahni
1972: p.344; Johnson & Storer 1974: p. 15, fig.7; Case 1978: p. 198, Pl.
5, figs. 6-8; Carpenter 1979: p. 41, fig.7a-b; Breithaupt, 1982: p. 131.

Material: The specimens referable to the species include isolated teeth (RTMP96.71.29-37), and centra (RTMP96.71.38-39) and dermal denticles (RTMP96.71.40-42).

Description: Tooth size ranges from 1.3 mm high by 2.1 mm wide, to 3.7 mm high by 5.7 mm wide. The teeth are of the typical configuration for the genus, having a hexagonal crown and a bifid root that is invariably smaller in all dimensions than the crown. They are also distinctive in the following features: the flat occlusal surface is divided into two by a transverse ridge that

is slightly arched labially, and bears numerous parallel enameloid folds that extend labio-lingually; and the flattened sides of crown are prominently marked with a series of vertical striations (wrinkles) that are often continuous with the enameloid folds on the occlusal surface.

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Discussion: The teeth of <u>M</u>. <u>bipartitus</u> are readily identifiable by their distinctive form and by the presence of the prominent wrinkles on the lateral surface of the crown and the enameloid folds on the occlusal surface. This type of tooth is among the most widespread of elasmobranch fossils in the Upper Cretaceous deposits of North America (e.g. Lambe, 1902; Sternberg 1926; Sahni, 1972; Estes, 1964). <u>Myledaphus</u> teeth recovered from the Upper Judith River Group of DPP were also referable to this species (Brinkman, 1990).

<u>Myledaphus</u> sp.

Plate 3, d-f

<u>Myledaphus bipartitus</u> Russell 1935: p. 120, Pl. 2, fig. 1; Case 1987: p. 28, fig.11; Beavan 1995: p. 74, Pl. 5, figs. e-g.

Material: The specimens referred consist of isolated teeth, and they are catalogued as RTMP96.71.20—28.

Description: The teeth included are very similar in overall configuration to those of \underline{M} . <u>bipartitus</u>, but they are also distinctly different in that: i) they lack

a series of perpendicular wrinkles on the flattened lateral surfaces of the crown; and ii) the occlusal surface of the teeth is generally smooth and plain, with a poorly-developed transverse ridge (sometimes absent), and is devoid of parallel enameloid folds.

Discussion: Teeth referable to this taxon were found to be very abundant in the microsites of the Foremost Formation. They have also been reported and described in the Milk River Formation (Russell 1935). It is suggested that these <u>Myledaphus</u> teeth may represent different species for the following reasons:

- They show distinct and consistent morphological differences from those of <u>M</u>. <u>bipartitus</u>, as described above;
- A great number of <u>Myledaphus</u> teeth covering a wide size range recovered from many different microsites suggests it is highly unlikely that the morphological differences represent simply individual variation;
- Stratigraphically, these distinctive teeth have so far been consistently retrieved only from the Milk River and the Foremost formations in Alberta. Conversely, those of <u>M</u>. <u>bipartitus</u> are known from comparatively higher stratigraphic deposits.

More detailed examination is needed to formally describe these teeth as representing a new species. For now, they are referred to <u>Myledaphus</u> sp.

Order Squatiniformes Buen 1926 Family Squatinidae Bonaparte 1838 <u>SQUATINA</u> Dumeril 1906 <u>Squatina hassei</u> Leriche 1929

Plate 3, g-i

Squatina hassei Leriche 1929: p. 68; Welton & Farish 1993: p. 77, figs. 1-2.

Material: <u>Squatina</u> teeth (RTMP96.71.7 and .8) have been recovered from sites PHR-1and PHR-2. Surface collecting has indicated that they are also present in the Lower Foremost Formation.

Description: The tooth crown is smooth, mesio-distally elongate, and bears a short, triangular cusp. The tooth shoulders are low, with sharp cutting ridges extending continuously across the shoulders and cusp. A labial flange is well-developed and forms a distinct, rounded apron. The root is low and triangular in ventral view. The basal attachment surface varies from flat to slightly concave, and is perpendicular to the crown. The lingual root protuberance is prominent and covered with enameloid on its upper part. Multiple nutrient foramina are evident on the lingual root protuberance. A comparatively large central nutrient foramen is present at the center of the ventral surface of the root. This foramen is connected to a smaller foramen at the tip of the lingual root protuberance through a canal, a condition representative of hemiaulacorhize root morph. According to Cappetta, (1987), the hemiaulacorhize refers to an elasmobranch root that has a central hollow basal face with an open central foramen that communicates by a medio-internal foramen canal with the foramen on the lingual root protuberance.

Discussion: <u>Squatina</u> teeth are very close in their general appearance to those of <u>Squatirhina</u> and <u>Cretorectolobus</u>, an orectolobid shark known from the Judith River Formation of Montana (Case, 1978). As noted by Welton and Farish (1993), <u>Squatina</u> teeth are, however, readily distinguishable from those of <u>Squatirhina</u> and <u>Cretorectolobus</u> by the absence of the nutrient groove on the ventral surface of the root. Galeomorphii incertae ordinis Cappetta 1987

Family Palaeospinacidae Regan 1906

SYNECHODUS Woodward 1888

Synechodus turneri Case 1987

Plate 3, j-l

<u>Synechodus turneri</u> Case 1987: p. 8, Pl. 2, figs. 1-5. <u>Paraorthacodus turneri</u> Beavan 1995: p. 73, Pl. IV, figs. e-f. <u>Synechodus</u> sp. Case 1973: p. 129, fig. 109; Beavan 1995: p. 73, Pl. IV, figs. g-i.

Material: This genus is represented by only a single complete tooth (RTMP96.71.12), recovered from the PHR-2 site.

Description: This specimen is a very small anterior tooth (6mm wide and 4mm high). Its principal cusp is straight, and is flanked by five pairs of lateral cusplets. Enamel folds are prominent on both the labial and lingual faces, which cover mainly the lower half of the crown. The base of the crown on the labial face overhangs the root by a way of slight bulge. The lateral cusplets are short, and are not distinctly separate from one another or from the cusp. The cutting ridges on the cusplets are united and join those of the central cusp to form a continuous, sigmoidal sharp edge in occlusal view. The lingual root protuberance is well-developed and exhibits many nutrient foramina. The root is thick, and its baseline is arched in labial view while straight in lingual view. Some deep grooves are prominent on the labial side of the root, each displaying a single foramen at its base.

A. 1997 - 4

Discussion: This genus is relatively rare, and has not yet been discovered in the Upper Judith River Group of DPP. Synechodus teeth can be readily confused with those of Paraorthacodus, another genus of the same family, due to their similar dental morphology. According to Cappetta (1987). Synechodus is distinguishable mainly by the presence of its short, blunt lateral cusplets that are not distinctly separated from each other, in contrast to the teeth of Paraorthacodus that bear high, sharp lateral cusplets that are well separated from each other, and from the main cusp, by notches reaching the level of the root. In addition, Synechodus teeth are generally much smaller in size (<10mm high) than those of Paraorthacodus (up to 20mm high). Among the species of the genus, the tooth (RTMP96.71.12) is closely similar to those of S. turneri in general size, in the lateral cusplets that are not independent of the central cusp and of each other, and in the enamel folds that cover mainly the lower half of the crown (Case, 1987). Thus, it is referred to this species: S. <u>turneri</u>.

Class Osteichthyes Order Acipenseriformes Family Acipenseridae Genus indet.

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Plate 4, a-b

Material: Sturgeon specimens recovered in this study are predominantly represented by fragments of dermal skull elements, and are catalogued as RTMP96.77.20-25.

Description: These specimens are referable to the family Acipenseridae on the basis of the distinctive sculpture patterns on the surface, which are typical of those of extant species of sturgeons. The distinctive sculpturings are the numerous flattened or crested ridges on the dorsal surface of the dermal cranial elements, which commonly radiate from the center of an element. The identification of these elements is often difficult due to their fragmentary nature.

Discussion: Two genera of acipenserids, Acipenser and

Protoscaphirhynchus, have been described from the Upper Cretaceous of North America (Estes, 1964; Wilimovsky, 1956). Differences in sculpture patterns of cranial elements are unknown between the two genera. The specimens retrieved in this study are here referable only to the family Acipenseridae due to their fragmentary nature, although most specimens of sturgeons recovered from the Upper Cretaceous of North America have been referred to <u>Acipenser</u> (e.g. Estes 1964; Estes et al.1969; Brinkman, 1990). A skeleton of a sturgeon has recently been discovered in DPP (Brinkman, 1996 pers. comm.). Study of this specimen may provide more information about its morphology.

Order indet.

Holostean A

Plate 4, g-j

Material: Holostean A, described by Brinkman (1990, p.43, figs.3A-C), is represented predominantly by bony scales. The scales retrieved in this study are referable to holostean A, and catalogued as RTMP96.77.45-62.

Description: Scales representing holostean A are small, ganoid, and greatly reduced in thickness when compared to those of <u>Atractosteus</u>. The peg-and-socket structures for articulation with anterior and posterior scales are well-developed, with a ridge extending between the peg-and-socket on internal surface. The lateral surface of each scale is covered with shiny ganoine, but lacks ornamentation. Holostean A scales retrieved in this study are very similar in morphology to those from the Dinosaur Park Formation of DPP (Brinkman, 1990).

Holostean B

Plate 4, c-f

Material: Holostean B was named by Brinkman (1990, p.43, fig.3D) for the second type of holostean scale recovered from the Dinosaur Park Formation of DPP. Such scales have also been retrieved from the microsites examined in this study. Specimens are catalogued as RTMP96.77.63-67.

Description and Discussion: Holostean B scales are similar to those of holostean A in overall shape and in the reduction of scale thickness, as well as in the presence of a well-developed peg-and-socket articulation. They differ, however, in that holostean B scales are generally larger and more elongate than holostean A scales, although a few holostean B scales are shorter (see Plate 4c,d), probably reflecting variation over the body surface. They are also different in that the lateral surface in a holostean B scale is ornamented with a series of continuous or broken shiny ganoine ridges extending laterally to the free edge of the scale. The stratigraphic distribution of holostean A and B scales is significantly different in that either both co-occur in microsites but have very different abundances between microsites, or only one type occurs independently at different microsites (see discussion below). Similar patterns of stratigraphic occurrence were also found by Brinkman (1990). Thus, it is highly unlikely that they simply represent sexual dimorphism or positional differences within the body of a fish.
Order Aspidorhynchiformes Family Aspidorhynchidae <u>BELONOSTOMUS</u> Agassiz 1834 <u>Belonostomus longirostris</u> (Lambe 1902) Plate 4, k, l, q

<u>Diphyodus</u> <u>longirostris</u> Lambe 1902: p. 30. <u>Belonostomus longirostris</u> Estes 1964: p. 22, figs. 12-14.

Material: <u>Belonostomus</u> material recovered in this study is represented by scales and jaw fragments, and consists of specimens RTMP 96.77.68-71.

Description: The jaw fragments mostly represent the predentary portion of the lower jaw. They are laterally compressed and ventrally rather rounded. On the lateral surface they bear many longitudinal, rounded ridges, which are coated with ganoine. Dorsally, the predentary has a concave surface, on which a single row of large teeth is carried in the middle and two rows of small, closely-spaced teeth are present along the lateral edges.

Scales of <u>Belonostomus</u> are elongate, rectangular, and covered with a layer of smooth, shiny ganoine on the exposed outer surface. This surface is divided longitudinally into two facets, one lateral and one medial, the former being lower and narrower than the latter. The interior face of the scale shows a corresponding subdivision of its surface, with the lateral surface being lower

and narrower than the medial. As a result, in cross-section the lateral portion of the scale is thinner than the medial. The ganoine coating is absent from the inner surface. The peg-and-socket articulation with anterior and posterior scales is generally poorly-developed.

Discussion: Jaw fragments of <u>Belonostomus</u> are readily identified by the characteristic arrangement of three rows of teeth and by the ornamentation on the outer surface. Scales of this taxon are easily separable from those of <u>Atractosteus</u> by their general shape and the subdivided external surface; and differ from those of holostean A and B in that the peg-and-socket articulation is poorly-developed and that they lack ornamentation on the surface.

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Order Lepisosteiformes Hay 1929

Family Lepisosteidae Cuvier 1825

ATRACTOSTEUS Rafinesque 1820

Atractosteus occidentalis (Leidy 1856)

Plate 4, m-p

Lepisosteus occidentalis Leidy 1856: p.73; Estes 1964: p.43, fig.21; Estes et al. 1969: p.11; Sahni 1972: p.345; Breithaupt 1982: p.132.
<u>Clastes occidentalis</u> Cope 1884: p.73.
<u>Atractosteus occidentalis</u> Wiley 1976: p. 66.

Material: <u>Atractosteus</u> specimens recovered from the microsites examined in this study are represented predominantly by scales, although a few isolated teeth and centra of <u>Atractosteus</u> were also retrieved. Referred specimens include the following: RTMP96.77.1-19.

Description: The scales of <u>Atractosteus</u> are rectangular, thick, and heavy, with well-developed peg-and-socket articulations, and are typical of the ganoid type of scale as represented in modern garfishes. They represent the thickest scales of all osteichthyan fishes recovered from the microsites examined in this study. The thickness of the scales, however, varies among specimens retrieved, which may be indicative of a regional difference within the body of fish. The teeth of <u>Atractosteus</u> are elongate and sharply-pointed. They are capped by bulbous, translucent tips. As a result, a constricted neck is prominent between the tip and crown. The tooth crown is ornamented on the surface with rather dense, longitudinal striations. The centra of <u>Atractosteus</u> are rather heavily built and opisthocoelous, a condition readily distinguishable from that of other osteichthyan fishes. Wiley (1976) suggested the opisthocoelous vertebrae are apomorphic for the family Lepisosteidae.

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Discussion: Wiley (1976) discussed the phylogeny of the family Lepisosteidae and assigned the material that was often referred to <u>Lepisosteus</u> <u>occidentals</u> from the Upper Cretaceous in North America to <u>Atractosteus</u> <u>occidentals</u>. This taxonomic arrangement is followed here. The scales of <u>Atractosteus occidentals</u> are abundant in the Upper Cretaceous of North America (e.g. Estes, 1964;Brinkman, 1990). They represent one of the most abundant specimens retrieved from most of the microsites examined in this study. Isolated teeth of <u>Atractosteus</u> are relatively rare. They are easily confused with those of <u>Champsosaurus</u> due to their similar size and general form. They can be distinguished, however, on the basis of the presence of the bulbous, translucent tip and the constricted neck between the tip and crown (see Plate 40) in <u>Atractosteus</u>, a feature that is absent in <u>Champsosaurus</u>.

Order Amiiformes

Family Amiidae Bonaparte 1837

Genus indet.

Plate 5, a-f

Material: The specimens of amiids recovered from the microsites examined in this study are represented by jaws, toothplates (RTMP96.77.143 to RTMP96.77.159) and centra (RTMP96.77.160 to RTMP96.77.174).

Description: Lower jaws of amiids are relatively abundant and are represented by dentaries. They are rather robust and bear only a single row of teeth. The tooth-bearing coronoid bones located on the medial face of the dentary are often not preserved. The premaxilla is a relatively short, plate-like element, with one row of large teeth along the edge. It has a flat, broad dorsal articulatory surface for the receipt of the nasals. The maxilla is a comparatively slender element, with a characteristic long, rod-like process projecting anteriorly for articulation with the premaxilla. Only a single row of small teeth is present on the maxilla. The toothplates are mostly represented by pterygoids, which are characterized by bearing a single row of large teeth on the edge and multiple rows of small teeth medially. Parasphenoid toothplates are rare, but are distinctive in that they bear numerous tiny teeth. All the toothplates are constructed from condensed bony plates, contrasting with the highly cancellous toothplates of Coriops. Amiid vertebrae are distinctive in that the centra are

greatly shortened antero-posteriorly, the dorsal portion of each centrum is antero-posteriorly thicker than the ventral, and the centra have oval, rather than concave, ends with shallow pits on the surface.

Discussion: Amiid fossil material has been found to be abundant in the Late Cretaceous of North America (Estes, 1964; Estes and Berberian, 1969; Estes et al., 1969; and Brinkman, 1990). The specimens described above can be referred to the family Amiidae with certainty based on the features described above. The identification at a lower level, however, is uncertain due to the incomplete, isolated nature of the material.

Subdivision Teleostei Müller 1846 Order Elopiformes Sauvage 1875 Family Phyllodontidae Sauvage 1875 Subfamily Paralbulinae Estes 1969a <u>PARALBULA</u> Blake 1940 <u>Paralbula casei Estes 1969a</u>

Plate 5, j-l

<u>Paralbula casei</u> Estes 1969a: p.323, figs. 3a-f, 6c-e; Estes 1969b: p.11; Case & Schwimmer 1988: p.299, figs. 6.21-22. ?<u>Paralbula</u> sp. Sahni 1972: p.345, figs. 7**R-S**.

Material: <u>Paralbula</u> specimens retrieved in this study are predominantly represented by isolated teeth, along with a few fragmentary basibranchial and parasphenoid tooth plates. The referred specimens are RTMP96.77.72 -87.

Description: Unworn <u>Paralbula</u> teeth are hemispherical and, on the dorsal surface, bear coarse, rugose structures radiating from the centre. A basal rim with striated edges is present at the base of the crown. On the ventral surface a basilar foramen is evident in the centre. It appears that the foramina of unworn, replacement teeth are large, and that those of functional (usually worn) teeth have a comparatively smaller basilar foramen. It is thus postulated that the basilar foramen of the replacement tooth shrinks to a small opening, as it begins to move up and become a functional tooth. This is

accomplished by the development of a thin layer of dentine that surrounds the foramen. As a result of this, the pulp cavity is almost closed. Such a morphological transition may be directly related to the strengthening of functional teeth, with more dentine being built up.

The partial basibranchial toothplate (RTMP96.77.72, plate 4j) reveals that the occlusal surface is convex, with the larger teeth being aggregated towards the centre of the toothplate and the smaller ones towards the edges. This arrangement of teeth is not, however, seen in the parasphenoid toothplate (RTMP96.77.83), on which teeth of various sizes are randomly distributed on its surface. The parasphenoid toothplate displays a slightly concave occlusal surface. Both surfaces of the toothplate are curved to some degree. A very thin bony layer is present on the attachment surface of the tooth plate. Both the basibranchial and parasphenoid tooth plates reveal that replacement teeth are irregularly stacked, as was described by Estes (1969), and that about four generations of teeth are present on the toothplates.

Discussion: The majority of the isolated teeth and toothplates retrieved can be definitely assigned to <u>Paralbula casei</u>. The recovery of relatively complete parasphenoid tooth plates indicates that these may have been curved, which contrasts with the interpretation of Estes (1969) who stated that the toothplates of <u>P</u>. casei lack a sigmoid curvature.

Subfamily Phyllodontinae Dartevelle & Casier 1949

gen. indet.

Plate 5, m-o

Material: Isolated teeth and tooth stacks, catalogued as RTMP96.77.175-193.

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Description and Discussion: These teeth resemble typical Paralbula teeth in their general 'button' shape, but differ in their large size (usually about 2-3 times larger). These large teeth are also different in that the replacement teeth are tightly stacked immediately below the functional teeth, and each tooth is very thin and has a sculptured occlusal surface. The pulp cavity is absent. Most specimens recovered represent isolated tooth stacks. They are similar to those of Phyllodus (Estes, 1969, Fig.1 G-I), which are also found as isolated. stacked teeth. Estes (1969) interpreted them as the enlarged central teeth of the tooth plate of the basibranchial. However, the earliest teeth of Phyllodus that have so far been found are from the Early Paleocene. Due to the incompleteness of all known basibranchial toothplates of P. casei, it remains unclear as to whether the enlarged central teeth are present or not. This tooth type could represent the earliest record of the subfamily Phyllodontinae, or may simply represent the enlarged central teeth of <u>P</u>. <u>casei</u>. Additional material and study are needed to solve this. Until such time, they are referred to as Phyolldontinae gen. indet..

Family Elopidae Romer 1966

PARATARPON Bardack 1970

Paratarpon apogerontus Bardack 1970

Plate 6, a-b

Paratarpon apogerontus Bardack 1970: p. 3, Pl. 1, fig.1; Brinkman 1990: p. 42.

Material: A nearly complete centrum obtained from a surface-collecting sample.

Description and Discussion: This specimen is the largest fish centrum recovered in the present study. It possesses prominent edges on both anterior and posterior ends. Numerous fine lamellae running parallel to one another are located between the anterior and posterior faces.

Bardack (1970) first described <u>Paratarpon</u> on the basis of and articulated postcranial skeleton from the Oldman Formation (equivalent to the Judith River Group here) of Alberta. More material of <u>Paratarpon</u>, including isolated centra and partial skeletons, was subsequently recovered from the Judith River Group of DPP, and was assigned to the same species (Brinkman, 1990). The centrum recovered in the present study is clearly referable to this taxon on the basis of its morphology. It is readily distinguished from any other teleosts by its size.

Family Abulidae

CORIOPS Estes 1969b

Coriops amnicolus Estes 1969b

Plate 5, g-i

Coriops amnicolus Estes et al. 1969: p. 12.

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Material: Specimens referable to <u>Coriops</u> are represented by only fragmentary basibranchial and parasphenoid tooth plates, and comprise specimens RTMP96.77.88-105.

Description and Discussion: The teeth on the toothplate are generally short and blunt, and are fused to it. The toothplate proper is constructed of cancellous bone, with the attachment surface being highly perforated. Teeth with broken crowns indicate that the pulp cavities were open, by a way of a few small foramina, to the cavities within the toothplates. The toothplates of <u>Coriops</u> are distinguishable from those of amiids because of their cancellous bony plates. Amiid toothplates are highly compact bony plates. Similar toothplates of both <u>Coriops</u> and amiids have been reported from the Judith River Group of DPP (Brinkman, 1990).

Order Salmoniformes Bleeker 1859 Suborder Esocoidea Bleeker 1859 Family Esococidae Cuvier 1817 <u>ESTESESOX</u> Wilson et al. 1992 <u>Estesesox foxi</u> Wilson et al. 1992

Plate 6, c-f

Material: Specimens of esocoids recovered from the microsites in this study are represented by palatines, premaxillae, and jaw fragments (RTMP96.77.26-44).

Description: Esocoid fishes are distinctive in having hinged, depressible teeth (Wilson et al., 1992). Tooth crowns on the esocoid toothbearing elements retrieved in this study were mostly lost during preservation. As a result, only "C"-shaped tooth bases remain. The esocoid palatine, similar to those described by Wilson et al (1992, p. 843, fig. 5), is generally straight, and bears multiple rows of hinged, depressible teeth, with a prominent longitudinal ridge on the dorsal side (Plate 6d). The premaxillae are very thin elements, with only a single row of depressible teeth. The lower jaws are comparatively robust and bear several rows of depressible teeth anteriorly, and fewer rows posteriorly.

Discussion Two esocoid genera--<u>Estesox</u> and <u>Oldmanesox</u>, have been described by Wilson et al (1992) on the basis of lower jaws from the Upper Cretaceous of southern Alberta. Nevertheless, most of the lower jaws

recovered in this study are referable with certainty to <u>Estesox</u> on the basis of the feature that all dentary teeth are depressible with multiple rows anteriorly and fewer posteriorly. The lower jaws of <u>Oldmanesox</u>, according to Wilson et al (1992), differ in the presence of a single row of large, fixed (rather than depressible) teeth posteriorly. Due to the fragmentary nature of specimens recovered, none of the lower jaw fragments can be surely referred to this genus. In addition, although Wilson et al.(1992) did not include premaxillary specimens, these can be identified by the presence of a single row of depressible teeth, similar to those of Esox (Plate 6e).

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Order indet.

Teleost D

Plate 6, g-i

Material: Teleost D, described by Brinkman (1990, p44, figs. E, F), is represented by a group of centra found in the Dinosaur Park Formation of DPP. This type of centrum has also been recovered from microsites examined in this study. They comprise specimens RTMP96.77.106 to RTMP96.77.123.

Description: These centra are distinctive in having two large, circular pits for the attachment of the neural arch, with a small pit between these, and the presence of a long transverse processes and a mid-ventral pit.

Teleost D specimens retrieved in this study are abundant and can be readily distinguished from other teleost centra. They differ very little morphologically from those from the Dinosaur Park Formation of DPP.

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Teleost indet.

Plate 6, j-m

In addition to teleost D, further abundant teleost centra were also recovered from microsites examined in this study. They include specimens RTMP96.77.124 to RTMP96.77.142. Apparently, these represent teleost centra of many different types. A study of these teleost centra is ongoing (Brinkman, 1997 pers. comm.). For the present, therefore, they are simply referred to as teleost indet.. Class Amphibia

Family Scapherpetonidae

SCAPHERPETON Cope 1876

Scapherpeton tectum Cope 1876

Plate 7, a-e, j

Scapherpeton tectum Cope 1876: p. 355; Estes 1964: p. 62, fig. 33.;

Sahni 1972: p. 348; Carpenter 1979: p. 41, figs. 9a, b; Breithaupt 1982: p. 134.

Hemitrypus jordanianus Cope 1876: p. 358.

Hedronchus sternbergi Cope 1876: p. 359.

Material: Abundant specimens referable to <u>Scapherpeton</u> have been recovered from the microsites examined in this study. They consist of isolated vertebrae and dentaries, and are catalogued as RTMP96.78.62-80.

Description: The majority of the specimens of <u>Scapherpeton</u> are trunk vertebrae. They are diagnostic in being amphicoelous and having teardropshaped cotyles, and in lacking basapophyses and having a variably developed subcentral keel. According to Estes (1964), some isolated atlantes have been referred to this taxon. They are mostly represented by robustly built centra from which the neural arches have been detached. The atlas has a characteristically-shaped anterior end that bears an intercotylar process (odontoid) and two lateral cotyles for articulation with the condyles of the skull. The intercotylar process is massive and has a prominent, ball-like condyle at its end and a constricted (neck-like) base that connects with the centrum proper. The dorsal surface of the process is grooved and continuous with the neural canal. The lateral cotyles flanking the intercotylar process are dorso-ventrally depressed and oval in shape, a characteristic of this taxon. The ventral side of centrum is flat, with a variable number of foramina.

Some isolated lower jaw elements can be assigned to this taxon. Most of these specimens are dentaries, which are slender, elongate, and prominently curved medially. This contrasts with the condition in <u>Opisthotriton</u>, in which the dentaries are straight. The symphysis is extended posteriorly, forming an ovoid vertical plate. The subdental shelf is low and somewhat parallel with the ventral edge of the dentary. As a result, the tooth roots tend to be relatively long, extending over half the height of the dentary. A similar isolated dentary has been referred to the same taxon (Estes, 1964). The crowns of the teeth are mostly broken off. The preserved roots are anteroposteriorly compressed and closely spaced.

Discussion: Several species of <u>Scapherpeton</u> were described by Cope (1876), based upon disarticulated material from the Judith River Formation of Montana. Only one species, <u>S</u>. <u>tectum</u>, was considered to be valid by Auffenberg and Goin (1959), based upon a review of the genus. Isolated specimens of this taxon have been discovered in a wide range of the Upper Cretaceous deposits, including the Milk River Formation of southern Alberta (Fox, 1972, Table1), the Judith River Group of DPP (Brinkman, 1990, Faunal

list), the Judith River Formation of Montana (Cope, 1876; Fiorillo, 1989), the Hell Creek and Lance formations of Wyoming (Estes, 1964), the Laramie Formation of Colorado, and the Foremost and Oldman formations of southeastern Alberta (this study).

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Family Batrachosauroidae

OPISTHOTRITON Auffenburg 1961

Opisthotriton kayi Auffenburg 1961

Plate 7, f-i, m

<u>Opisthotriton kayi</u> Auffenburg 1961: p. 456, figs. 1-5; Estes 1964: p. 81, figs. 38-41; Estes et al. 1969: p. 13; Sahni 1972: p. 350; Carpenter 1979: p. 43, figs. 13, 14a, b; Breithaupt 1982: p. 134.

Material: Specimens herein referred to this genus consist of dentaries and vertebrae, and are catalogued as RTMP96.78.81-99.

Description: The typical trunk vertebrae are identifiable by a combination of features as follows: the centrum is opisthocoelous, but the anterior condyle is somewhat rudimentary and is pitted in the center; a pair of basapophyses are prominent on the ventro-posterior region of the centrum; and a subcentral keel is well-developed. Atlantes referred to <u>Opisthotriton</u> by Estes (1964) have also been recovered in this study. This identification was confirmed by the discovery of an articulated specimen from the Paleocene of

Wyoming (Estes, 1975). The atlantes resemble those of <u>Scapherpeton</u> in general form, but differ in that the intercotylar process is poorly-developed, being expressed as a thin, shelf-like structure without a constricted base. The lateral cotyles of the atlas are generally round, in contrast to those of <u>Scapherpeton</u>, in which they are oval.

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Isolated dentaries of <u>Opisthotriton</u> are distinguishable in that each is narrow anteriorly and widens greatly posteriorly, both dorsally and ventrally. The subdental shelf is high in the dorsal half of the dentary. As a result, the marginal tooth roots tend to be very low, in contrast with those of the dentaries referred to <u>Scapherpeton</u>. The subdental shelf, along with the baseline of the tooth row, rises toward the posterior end. A nearly complete left lower jaw (RTMP96.78.78) from BCC site reveals that the tooth number appears to be lower than that of <u>Scapherpeton</u>, despite the fact that most tooth crowns are missing. It greatly resembles the lower jaws of <u>Opisthotriton</u> from the Lance Formation of Wyoming (see Estes, 1964, Fig.39).

Discussion: <u>Opisthotriton</u> was described, based upon isolated vertebrae, from the Lance Formation of Wyoming (Auffenberg, 1961). More material was subsequently recovered from the same deposits, and was described in detail by Estes (1964). Since then, <u>Opisthotriton</u> material has been reported from other Cretaceous deposits, such as the Milk River Formation of southern Alberta (Fox, 1972, Table1), the Judith River Group of DPP (Brinkman, 1990, Faunal list), the Judith River Formation of Montana (Fiorillo, 1989), the Hell Creek and Lance formations of Wyoming (Estes, 1964), the Laramie Formation of Colorado, and the Foremost and Oldman formations of southeastern Alberta (this study). The <u>Opisthotriton</u> vertebrae recovered here show a strong resemblance to those from the Judith River Group of DPP and those from other deposits. They are referable to <u>O</u>. <u>kavi</u>, since the genus is monospecific. Estes (1964) also described isolated elements other than vertebrae and dentaries, such as vomers, premaxillae and maxillae, and referred them to the same taxon. Such isolated elements were also recovered from the microsites examined in this study. However, the association of these elements with the isolated vertebrae of <u>O</u>. <u>kavi</u> can not be established here due to the fragmentary nature of these specimens. They are described as Caudata indet. (see description below).

It is interesting and noteworthy that <u>Opisthotriton</u> material tends to cooccur with that of <u>Scapherpeton</u>, at least throughout the microsites examined in this study. The proportion of <u>Scapherpeton</u> versus <u>Opisthotriton</u> specimens is quite consistent at about 2:1 among these microsites. Similar patterns have also been noted among the microsites of the Judith River Group of DPP (Brinkman, pers. comm.), and may also be evident among the localities in the Lance Formation of Wyoming (Estes, 1964).

Order Caudata Oppel 1811

gen. indet.

Plate 7, k, l, n-q

Material: Additional specimens identified as Caudata indet. consist of isolated vomers, fused opisthotics-exoccipitals, quadrates, premaxillae, maxillae and postdentary bones. They are catalogued as RTMP96.78.100-175.

Description and Discussion: Vomers are represented by their anterior portions. They are somewhat similar in general form to those of <u>Habrosaurus</u> (Estes, 1964: figure 36a). Each consists of a vertical lateral edge and a flat medial plate. The process for articulation with the premaxilla is present at the anterolateral corner of the lateral edge. A row of teeth is closely attached to the medial side of the lateral edge. Tooth number ranges from five to eight, in contrast with that of <u>Habrosaurus</u>, in which nine are present. The medial plate varies in its width among the specimens retrieved: some are relatively narrow strips and some are rather wide and short. These elements are noticeably different from those of <u>Opisthotriton</u> in that they are elongate and triangular in shape (Estes, 1964: figs.40a-c; 1965: fig 3A). Estes (1964) referred a single vomer to <u>Scapherpeton</u>, but it was not illustrated, and features diagnostic to the genus were not identified.

Among the tooth-bearing caudate elements recovered in the present study, isolated premaxillae and maxillae are identifiable. The premaxillae are recognizable on the basis of their shortness, lingual-curvature and their dorsoposteriorly projecting nasal process. The premaxillary teeth are often missing. In many instances, only the wide nasal process is preserved. The posterior edge for articulation with the maxilla varies from short and oblique to high, with vertical surfaces. Isolated maxillae are recognizable by their straight, slender morphology and the presence of a dorsal process. The position of the dorsal process varies among specimens – arising from the anterior to the middle portion of the maxilla proper. Most of the maxillae are rather fragmentary, missing their teeth and the dorsal portion of the dorsal process. None of the maxillae can be certainly referred to either <u>Scapherpeton</u> (Estes, 1964: Fig.33a) or <u>Opisthotriton</u> (Estes, 1964: Figs.41d,e). Additional material and further study are needed to clarify their taxonomic assignment.

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Abundant caudate fused opisthotic-exoccipital complexes were identified. These are readily recognizable based on the presence of a small ovoid and small medial articulatory facet. Each complex is robustly built and the opisthotic is fused laterally to the exoccipital. Some specimens display a large jugular foramen between the opisthotic and exoccipital. The exoccipital bears the prominent, posteriorly-oriented condyle and the medial facet. This facet is smaller than the condyle and forms an articulation with the intercotylar process of the atlas. The condyle is generally ovoid, with a rough, flat surface for articulation with the cotyle of the atlas. The ovoid condyle matches well with the oval-shaped cotyle of the atlas of <u>Scapherpeton</u> (see description above) and thus these isolated elements may be assignable to <u>Scapherpeton</u>. No examples of such opisthotic-exoccipital complexes bearing condyles with round articulatory surfaces, which match the round cotyles of the atlas of <u>Opisthotriton</u>, have been certainly identified here. This may be due to the incompleteness of the material.

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Isolated quadrates of caudates are all represented by their articular portions. Each quadrate is a pillar-like element, with a concave articulatory surface at its distal end. Two different types of quadrate, described here as Type A and B, are recognizable. Type A is distinctive in that the articulatory surface is large and deeply concave, and in that the shaft is elongate and is evidently smaller in cross-section than is the articulatory end. The lateral surface bears a large, shallow depression as the articulatory facet for the ventral process of the squamosal. The anterior surface is expanded medially and bears numerous, small nutrient foramina. Type B differs in that the articulatory surface is saddle-like and expanded laterally, and in its stout and short shaft. The articulatory facet for the squamosal is present on the anterolateral edge of the shaft, far above the articulatory end, which contrasts with Type A, in which the articulatory surface closely approaches the articulatory end of the quadrate. Type A is much more abundant than Type B. Although Type A is somewhat similar to that of <u>Opisthotriton</u>, as described by Estes

(1965), its referral to that genus cannot be confirmed until additional associated material is retrieved.

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Isolated caudate postdentary complexes, typically consisting of the articular, prearticular and angular, were recovered. These specimens are identifiable on the basis of the presence of a large, semicircular, and convex articulatory condyle at the posterior end. A foramen is present on the outer surface, below the condyle. The articular, prearticular and angular are so highly fused that sutures are not evident. The anterior portion of the postdentary is slender and elongate, and dorsally forms a vertical, thin plate. Such isolated postdentaries have not yet been reported or described from other Cretaceous deposits of North America, although similar elements have been found in the Judith River Group of DPP (Brinkman, 1996 pers. comm.).

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Order Allocaudata Fox & Naylor 1982 Family Albanerpetontidae Fox & Naylor 1982 <u>ALBANERPETON</u> Estes & Hoffstetter 1976 <u>Albanerpeton</u> sp

Plate 8, a-e

Material: Specimens referable to <u>Albanerpeton</u> are represented by isolated premaxillae, maxillae, frontals, dentaries and trunk vertebrae. They are catalogued as RTMP96.78.100-145.

Description: The premaxillae, maxillae and dentaries are very similar to those of <u>Albanerpeton</u> that have been recovered from the Milk River Formation and described in detail by Fox and Naylor(1982). The dentary is distinctive in the presence of a lobate, interdigitating symphysis, which is one of the diagnostic features of <u>Albanerpeton</u>. All these jaw elements bear nonpedicellate, pleurodont teeth. Isolated frontals have also been identified. Each is generally triangular and plate-like, with the anterior end narrowing almost to a point and the posterior end widening. A pair of small articulatory facets for articulation with the nasals is present. These extend antero-laterally close to the anterior end of the frontal. The dorsal surface of the frontal is sculpted, the patterns of which are similar to those described for anurans in which pitted circles are encompassed by continuous ridges. The sculpting on <u>Albanerpeton</u> frontals is, however, comparatively finer and the ridges are lower. A few trunk vertebrae can be tentatively assigned to <u>Albanerpeton</u> (Plate 8a, b). They are small and elongate, with low neural arches and poorly-developed neural spines. Their centra are smooth ventrally and lack the subcentral keels and basapophyses that are typical of <u>Opisthotriton</u>. Both ends of the centra are deeply concave and round in shape, in contrast to those of <u>Scapherpeton</u> vertebrae that have teardrop-shaped cotyles.

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Discussion: Material of <u>Albanerpeton</u> is readily distinguishable from that of other caudates recovered from these deposits by the features described above. This taxon has been found widely in the Cretaceous deposits of North America (e.g. Fox & Naylor 1982). Its recovery from the microsites examined in this study represents the first record of this taxon from the Foremost and Oldman formations of southern Alberta. A review of albanerpetonid material at lower taxonomic level is ongoing (Gardner, 1996 pers. comm.). For now, the material recovered in this study is temporally referred to the genus.

83

Order Anura Giebel 1845

Family indet.

Plate 8, f-n, p-r

Material: Specimens referable to anurans are represented by cranial elements, presacral and sacral vertebrae, humeri, and ilia. They are catalogued as RTMP96.78.1-61.

Description: Cranial fragments are the most abundant specimens. They are distinguishable in that their outer surfaces bear distinctive sculpturing formed by dense and continuous ridges bounding numerous subequally sized circles. A few cranial fragments, nevertheless, display different and irregular sculpturing patterns. Among these cranial specimens, complete and partial jaws (including maxillae and dentaries), squamosals, and frontoparietals are identifiable. The tooth-bearing elements reveal very small, pointed teeth with evident cement deposited at their bases. As a result, the roots of such teeth are affixed together and are hard to separate. This condition can be readily distinguished from that of caudates, in which the roots are clearly separate.

The vertebrae are, in general morphology, typical of those of extant frogs. Most of them, lacking neural arches, are represented by centra. Among the presacrals, four types of centra are evident: procoelous, amphicoelous, opisthocoelous, and biconvex. The procoelous centra are most abundant, followed by the amphicoelous and opisthocoelous types. Only one centrum (RTMP96.78.46) was found to be biconvex; a very unusual condition among anurans. Until more specimens are recovered, it is here interpreted as an individual variation. Sacral vertebrae are distinctive, as they are for extant frogs, in that they bear posterior bicondylar articulatory facets. A relatively complete sacrum (RTMP96.78.60) indicates that the transverse processes (diapophyses) are rather wide antero-posteriorly, a feature considered to be primitive (Trueb, 1973).

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The ilium of anurans is identifiable in that its elongate shaft curves anteriorly and is essentially rod-like, with a compressed oval cross-section, and in that the acetabular fossa is large and occupies over a half of the ventral portion of the ilium proper. A large depressed area is prominent on the medial surface, opposite the lateral acetabular fossa. Such specimens can be confused with the ilia of salamanders retrieved from the same microsites examined in this study, due to their similar appearance. They are distinguishable, however, in that salamander ilia are relatively slender, with a sigmoidal shaft and a rather round cross-section, and a small acetabular fossa that is about one-third the length of the ilium proper (Plate 80).

Humeri of anurans are represented only by their distal ends. Each is distinctive in the presence of a large, ball-like articulatory condyle, which is typical of those of extant anurans.

Discussion: The anuran specimens described above are readily distinguishable from other microvertebrate specimens on the basis of their

characteristic form, such as the sculptured cranial elements, and the peculiar form of the vertebrae and ilia. All anuran material recovered to date from the Cretaceous deposits of North America is represented by disarticulated skeletal elements (Estes, 1964, 1969; Brinkman, 1990). The taxonomic assignment of these Cretaceous specimens is tentative (e.g. Estes. 1964), due to the lack of articulated specimens and poor documentation. Additional specimens and further study are required to determine the identity of these Cretaceous anurans. Currently, they are only identifiable as Anura, family indet.. Class Reptilia Linnaeus 1758 Subclass Diapsida Osborn 1903 Infraclass Lepidosauromorpha Benton 1983 Superorder Lepidosauria Haeckel 1866 Order Squamata Oppel 1811 Suborder Lacertilia Owen 1842

Fossil lacertilian material is well-known from the Upper Cretaceous of North America (for example, Gilmore, 1928; Estes, 1964, 1983; Gao and Fox, 1991). Recently Gao and Fox (1996) extensively documented the lacertilians of the Late Cretaceous, especially those from the Judith River Group of southern Alberta. Abundant lacertilian material was recovered from the microsites examined in the present study. In the following descriptions of these specimens, the taxonomic and morphological terms applied by Gao and Fox (1996) have been adopted except where noted.

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Infraorder Scincomorpha Camp 1923

Family Teiidae Gray 1827

SOCOGNATHUS Gao & Fox 1991

Socognathus unicuspis Gao & Fox 1991

Plate 9, a-c

<u>Socognathus unicuspis</u> Gao & Fox 1991: p. 146, Pl. 3, figs. 1-8, text-fig. 7; Gao & Fox 1996: p. 25, figs. 8-9.

Material: Specimens referable to this taxon are: RTMP96.74.1, an incomplete dentary (Ho S); RTMP96.74.2, a fragmentary dentary (PHS); RTMP96.74.3a-c, one nearly complete right maxilla, a partial left maxilla and a dentary (CS); RTMP96.74.4, jaw fragments (PLS).

Description: <u>Socognathus</u> dentaries are identifiable on the basis of their strong mandibular symphysis that bears a well-developed ventral buttress, and their teeth that are subpleurodont and unicuspid, with the cusp being pointed and posterolingually-inclined. This cusp is always flanked by a strong anterior ridge and a weak posterior one, with faint striations present on the lingual face of the cusp between the anterior and posterior ridges. A nearly complete right maxilla (RTMP96.74.3a, Plate 9a) shows overall similarity to those (UALVP 29910-11) described by Gao and Fox (1996, Figs.9D, E). This specimen (RTMP96.74.3a) bears somewhat antero-posteriorly compressed anterior teeth. The completely preserved 12th tooth, however, lacks this morphology and is short. The premaxillary process of the maxilla is short, and dorsally bears a medially-extended and concave surface that floors the external naris. The nasal process of the maxilla is partially preserved, and its interior surface differs from that of <u>Chamops</u>, a teiid described from the Lance Formation of Wyoming (e.g., Estes, 1964), in that the two depressions described by Gao and Fox (1996) are less distinctively separated from one another. A partial left maxilla (RTMP96.74.3b) was also recovered from the same microsite (CS) as RTMP96.74.3a. The two are almost mirror images of each other in morphology and also are very similar in size, and thus may be from the same individual.

Discussion: <u>Socognathus unicuspis</u> was described by Gao and Fox (1991) on the basis of incomplete dentaries and maxillae from the Upper Judith River Group of southern Alberta. Such material has not been positively identified from any other deposits so far. The specimens recovered in the present study represent the earliest stratigraphic occurrence of this taxon.

LEPTOCHAMOPS Estes 1964

Leptochamops sp.

Plate 9, d, f-h

Material: Specimens referred to <u>Leptochamops</u> are: RTMP96.74.5, a partial dentary (PHR-1); RTMP96.74.6, a right partial dentary (PHR-2); RTMP96.74.7, three dentary fragments (WS); RTMP96.74.8, four dentary

fragments (EZ); RTMP96.74.9, three dentary fragments (PHR93-2); RTMP96.74.10, a dentary fragment (Sal S); RTMP96.74.11, four jaw fragments (HS); RTMP96.74.12, three jaw fragments (HAS); RTMP96.74.13, two jaw fragments (CN-1); RTMP96.74.14, two jaw fragments (CN-2); RTMP96.74.15, four partial dentary (ORS); RTMP96.74.16, seven fragmentary jaw elements (BCC); RTMP96.74.17, a partial left dentary (RDS); and RTMP96.74.18, four jaw fragments (BMC).

Description: The tooth-bearing specimens of this taxon can be identified on the basis of their characteristic tooth morphology--high-crowned, slender, cylindrical and tricuspid. Among the specimens referred, RTMP96.74.18 (a right dentary from BMC) is the best-preserved, despite the absence of a small segment from its middle, and a broken posterior end. It bears 10 complete teeth, which are incipiently tricuspid anteriorly and typically tricuspid posteriorly. All the teeth are closely spaced. The subdental shelf is robust anteriorly and gradually thins dorso-ventrally posterior to the 7th tooth, and it exhibits a slight upward curvature at each end. The anterior end reveals that the mandibular symphysis was weak, lacking the well-developed ventral buttress that is evident in the dentary of Socognathus.

Discussion: Two nominal species of <u>Leptochamops</u> have been described: <u>L</u>. <u>denticulatus</u> and <u>L</u>. <u>thrinax</u>. <u>L</u>. <u>denticulatus</u> was initially described from the Lance Formation of Wyoming (Gilmore, 1928; Estes, 1964), and subsequently specimens from the Hell Creek Formation of Montana (Estes, et al., 1969), and the Frenchman Formation and the Upper Judith River Group of southern Alberta (Gao and Fox, 1996) were referred to this species. L. thrinax was described by Gao and Fox (1991) on the basis of dentaries from the Upper Judith River Group of southern Alberta. It is considered to be separable from L. denticulatus on the basis of dentary teeth that are more robust, more widelyspaced and fewer in number, and a straighter subdentary shelf. RTMP96.74.18, as described above, resembles UALAP29772 (Gao and Fox, 1996, Fig. 16E) in tooth morphology, and both of these specimens differ from L. thrinax in that the subdental shelf curves upwards on both anterior and posterior ends, and that the teeth are closely-spaced. Interestingly, RTMP96.74.18 reveals the presence of striations on the lingual side of the crown apices, a condition unknown for either of the nominal species so far described. Comparable lingual striations were noted by Denton and O'Neill (1995) to be present on a teild described from the Upper Cretaceous Marshall Formation of New Jersey (Denton and O'Neill, 1995, see Fig.3). The presence of lingual striations was interpreted by Denton and O'Neill (1995) to be a derived character shared by Chamops and Prototeius, but the striations on Chamops were later argued, by Gao and Fox (1996), to be due to individual variation. The presence of lingual striations on the specimens described here suggests that this feature is widely shared by Upper Cretaceous teilds and that the absence of such striations on some specimens may be due to tooth wear. Additional study is needed to further clarify this. The specimens of dentaries

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referable to <u>Leptochamops</u> are, however, too fragmentary to enable more precise identification, and they are thus referred to <u>Leptochamops</u> sp.

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GERONTOSEPS Gao and Fox 1991

Gerontoseps irvinensis Gao and Fox 1991

Plate 9, e

<u>Gerontoseps</u> <u>irvinensis</u> Gao and Fox 1991: p. 149, Pl. 5, figs. 1-4, text-fig. 10; Gao and Fox 1996: p. 34, figs. 13, 14A-D.

Material: RTMP96.74.19, a nearly complete left dentary from the PLS site.

Description: This dentary is referable to <u>Gerontoseps irvinensis</u> on the basis of the following features: a shallow element with a narrow but deep *sulcus dentalis*; subpleurodont, unicuspid teeth, with symmetrical anterior and posterior crests. This dentary (RTMP96.74.19) is similar to UALVP29760-61 (Gao and Fox, 1996, Fig.14C, D) in that the splenial is not fused to it, although an articulatory facet is evident along the posterior and postero-ventral side of the subdental shelf. RTMP96.74.19 still carries the 15 anteriormost teeth, of which four are complete.

Discussion: <u>G. irvinensis</u> has only been reported from the Upper Judith River Group of Alberta (Gao and Fox, 1991,1996). Although RTMP96.74.19 is the only specimen of this taxon recovered in this study, it represents the first record of this taxon discovered outside the type locality and from a relatively lower stratigraphic section. This specimen also supports the interpretation of Gao and Fox (1996) that the fusion of the splenial with the dentary along their dorsal contact represents ontogenetic variation, rather than being a diagnostic feature of the taxon, as previously stated (Gao and Fox, 1991).

Infraorder Anguimorpha Fürbringer 1900 Family Anguidae Gray 1825 <u>ODAXOSAURUS</u> Gilmore 1928 <u>Odaxosaurus</u> cf. <u>priscus</u> Gao and Fox 1996 Plate 9, i-j

Odaxosaurus priscus Gao and Fox 1996: p. 70, figs. 29, 30A-F.

Material: RTMP96.74.25, incomplete right dentaries (RDS); RTMP96.74.26, a left partial dentary (CS).

Description: All three dentaries are referable to <u>Odaxosaurus</u> on the basis of their tooth morphology. The dentary teeth are characteristic in being strongly compressed antero-posteriorly and transversely elongate and rectangular in cross section, and in possessing a truncate crown with a horizontal cutting edge. A right dentary (RTMP96.74.25a) bears three teeth that are closely spaced, the middle one complete and the other two missing the

crown tips. The teeth are pleurodont, and each has a basal foramen on the lingual side. The complete tooth reveals that the crown is similar to that of <u>O</u>. <u>priscus</u> (Gao and Fox, 1996), and is less truncated than that of <u>O</u>. <u>piger</u>. No striations are evident on the medial face of the crown. According to Gao and Fox (1996), the teeth of <u>O</u>. <u>priscus</u> bear week striations. A second dentary (RTMP96.74.25b), bearing nine consecutive teeth with broken crowns, reveals that the teeth are closely spaced, and that the *sulcus dentalis* is absent. The third dentary (RTMP96.74.26) is smaller and bears four teeth that are also closely spaced, one being complete. The cutting edge of the complete crown is absent, apparently the result of wear.

Discussion: <u>O</u>. <u>piger</u> was initially described from material from the Lance Formation of Wyoming (Gilmore, 1928). Material referred to the taxon has also been reported from the Hell Creek Formation of Montana, the Laramie Formation of Colorado (Carpenter, 1979), and the Scollard and the Frenchman formations of Alberta (Gao and Fox, 1996). The second species of the genus, <u>O</u>. <u>priscus</u>, was erected by Gao and Fox (1996) on the basis of material from the Upper Judith River Group of Alberta. <u>O</u>. <u>priscus</u> is, according to Gao and Fox (1996), different from <u>O</u>. <u>piger</u> in the dentary tooth count being lower due to wider spacing of the teeth, and the crown being less strongly truncated and less heavily striated medially. The three dentaries recovered in this study resemble those of <u>O</u>. <u>priscus</u> in the presence of a less strongly truncated crown, but they also reveal that the teeth are closely spaced, which is different
from the condition found in <u>O</u>. <u>priscus</u>, but similar to that of <u>O</u>. <u>piger</u>. Moreover, it is evident that the maxillae referred to <u>O</u>. <u>priscus</u> by Gao and Fox (1996) have closely-spaced teeth. Therefore, it is likely that the closely-spaced dentary teeth exhibited by UALVP29896 and 29897 (Gao and Fox, 1996, Figs.30A,B) could be the result of individual variation. Such a feature is not a good diagnostic character for the species on the basis of what is currently known. Nevertheless, the dentaries recovered in this study are tentatively referable to <u>O</u>. <u>priscus</u> on the basis of their similarity of tooth crown structure. They apparently represent, to date, the earliest stratigraphic occurrence of <u>Odaxosaurus</u>.

cf. Odaxosaurus piger (Gilmore 1928)

Plate 10, a-d

<u>Peltosaurus piger</u> Gilmore 1928: p.136, PI.26, figs. 4, 6; Sahni 1972: p.354, figs. 8G, H; Estes 1964: p.121, fig. 57b.
 <u>Odaxosaurus obliquus</u> Gilmore 1928: p.158, PI.28, figs. 3, 5.
 <u>Pancelosaurus piger</u> Meszoely 1970: p.105.
 <u>Odaxosaurus piger</u> Breithaupt 1982: p.136; Gao & Fox 1996: p.68, fig. 28.

Material: Isolated osteoscutes (RTMP96.74.27-36)

Description: All of these osteoscutes are basically rectangular, with the length exceeding the width. Each possesses an anterior gliding surface which,

in life, was overlapped by another osteoscute lying anterior to it; and an exposed, posterior surface that is sculptured with irregular pits and ridges. The two extremities are separated by a groove. The smooth gliding surface varies from about one third to one half of the length of the osteoscute. There is no evidence of suturing along the lateral edges. Two different types of osteoscute are recognizable among the material recovered. The first has lateral edges that bear smooth, oblique surfaces, one facing dorsally and the other ventrally. This suggests that they provide for lateral overlapping of adjacent osteoscutes. Such osteoscutes evidently represent those of the flanks (Meszoely, 1970, 1973). The second is larger and thicker, and bears a prominent median keel on the exposed surface. The smooth lateral surfaces both face either lateroventrally or laterally, indicating that this type of osteoscute overlapped adjacent ones. They are evidently representative of mid-dorsal osteoscutes (Meszoely, 1970).

Discussion: These osteoscutes show a great resemblance to those of <u>Odaxosaurus</u> (Estes, 1964; Meszoely, 1970) in their general constitution and in the sculpturing of the exposed surfaces. The mid-dorsal osteoscutes recovered in this study, however, differ in that a median ridge is prominent and that both smooth lateral surfaces face latero-ventrally, contrasting with those of <u>Odaxosaurus piger</u> in which no median keel is present and the lateral surfaces face latero-dorsally, indicating overlap by adjacent osteoscutes (Meszoely, 1970). Gao and Fox (1996) described a second species of <u>Odaxosaurus – O</u>. <u>priscus</u>, on the basis of dentaries from the Upper Judith River Group of Alberta (see above). Similar specimens were recovered from the microsites examined in this study, from which these osteoscutes were also retrieved. The similar lateral body osteoscutes, but somewhat different mid-dorsal ones, when compared to O. <u>piger</u>, is further suggestive of the presence of a second species of <u>Odaxosaurus</u>.

Family Necrosauridae Hoffstetter 1943

COLPODONTOSAURUS Estes 1964

Colpodontosaurus cf. cracens Estes 1964

Plate 9, o-p

<u>Colpodontosaurus cracens</u> Estes 1964: p. 128, fig. 60; Estes et al.1969: p. 20; Gao & Fox 1996: p. 74, figs. 31A-C.

Material: RTMP96.74.20, three partial dentaries from site SPS; RTMP96.74.21, a right partial dentary from site Ho S; RTMP96.74.22, a left dentary and two partial maxillae from site WS; RTMP96.74.23, a dentary fragment and a partial maxilla from site CN-1; and RTMP96.74.24, a right and a left dentary from site ORS.

Description: RTMP96.74.24a is the most complete dentary, missing only small portions of the anterior and posterior ends. It is slender, and similar in general form to those typical of <u>Colpodontosaurus</u> (see Estes, 1964, Fig.60; Gao and Fox, 1996, Fig. 31B). It differs, however, in that the tooth row curves strongly upward at both ends. The subdental shelf is relatively well-developed. thicker anteriorly and gradually thins toward the posterior end. The sulcus dentalis is very shallow anteriorly and is absent in the posterior half of the dentary. The intramandibular septum is poorly developed. This dentary bears 10 complete or nearly complete teeth, and four tooth bases. These teeth are low-crowned and constricted at their tip, with expanded bases and a thin tooth wall, which are all typical of <u>Colpodontosaurus</u> teeth. The complete teeth all exhibit essentially straight shafts without recurved tips, in contrast to those of the holotype of the type species of the genus (see Estes, 1964, Fig.60), which has strongly recurved crown tips. Another specimen (RTMP96.74.24b) from the same site (ORS) (the posterior portion of a left dentary) carries three complete teeth and two tooth bases, all of which have straight shafts, without recurved tips. Four large, round basal foramina are present on the lingual side. The teeth with broken crowns reveal that they are hollow and that the tooth wall is thinner labially than lingually. Such a thin tooth wall is also found in RTMP96.74.21, RTMP96.74.23a,b and RTMP96.74.24a. Two partial dentaries (RTMP96.74.20a,b) bear three and two complete teeth, respectively. These teeth are generally similar to those of the specimens described above, but differ in that the crown is taller and is comparatively less strongly constricted. They are similar to the teeth of Litakis gilmorei (Estes, 1964) in having relatively high crowns. According to Estes (1964), the teeth of L. gilmorei are,

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however, different in having anterior and posterior ridges, resulting in an incipiently tricuspid appearance. Thus, these dentaries (RTMP96.74.20a, b) are still referred to <u>Colpodontosaurus</u> on the basis of their expanded tooth bases and the presence of a poorly-developed intramandibular septum.

Three incomplete maxillae (RTMP96.74.22b,c; and RTMP96.74.23b) are assigned to this taxon on the basis their tooth morphology, which is very similar to that of the dentary teeth described above.

Discussion: Colpodontosaurus cracens was previously known only from Maastrichtian deposits, including those of the Lance Formation of Wyoming. the Hell Creek Formation of Montana, and the Scollard Formation of Alberta (Estes, 1964, 1983; Estes et al., 1969; Gao and Fox, 1996). The specimens recovered in this study are referable to Colpodontosaurus on the basis of the following features: dentary slender, with a poorly-developed intramandibular septum; teeth low-crowned and thinly walled, with the base expanded and lacking striations. They also represent, for the first time, specimens with complete and numerous teeth. The recurved crown tips of the holotype were reconstructed by Estes (1964). Gao and Fox (1996) noted that the teeth of UALVP29782 have a relatively straight shaft and that a slightly recurved tip is present on the single nearly complete tooth. All the specimens recovered in this study clearly show that the teeth have a straight shaft and lack recurved crown tips. They also represent the first record of Colpodontosaurus from the Judith River Group of Alberta.

Family Helodermatidae Gray 1837

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PARADERMA Estes 1964

cf. Paraderma bogerti Estes 1964

Plate 9, I

<u>Paraderma bogerti</u> Estes 1964: p. 132, figs. 64, 65; Gao & Fox 1996: p. 82, figs. 34, 35.

Material: RTMP96.74.37, a complete marginal tooth (PHS), RTMP96.74.38, a nearly complete tooth (BMC). and RTMP96.74.39, a marginal tooth (CS).

Description: RTMP96.74.37 is laterally compressed but rather robust. The crown is straight and strongly trenchant, with a slightly recurved tip. Both the anterior and posterior cutting edges are sharp, but lack serration. A shallow venom groove is evident extending from the base along the anterior cutting edge to close to the tip. Such a groove is not present along the posterior edge. The tooth base is moderately expanded lingually, and bears infoldings on its surface. A basal foramen is evident at the bottom of the base on the lingual side. It is not clear whether RTMP96.74.37 is a dentary or maxillary tooth.

Discussion: All the three teeth (RTMP96.74.37-39) are comparable to those of <u>Paraderma bogerti</u> (Estes, 1964; and Gao and Fox, 1996) in their

general shape, and especially in the presence of a shallow venom groove along the anterior edge. In <u>Labrodioctes</u>, another helodermatid from the Judith River Group described by Gao and Fox (1996), the venom groove is absent on the anterior edge but present on the posterior edge. Although Gao and Fox (1996) questioned the reported occurrence (Sahni, 1972) of this taxon in the Judith River Group and considered it to be restricted to the deposits of the Lance Formation, the specimens recovered in this study confirm its occurrence in the Judith River Group of southern Alberta.

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Family Helodermatidae Gray 1837

genus indet.

Plate 10, e-h

Material: Isolated osteoderms (RTMP96.74.52-65).

Description: These osteoderms range in maximal length from 1.5mm to 6mm. They are readily distinguishable from other lizard osteoderms in being thick and heavily-constructed. They possess an outer surface that is slightly concave and highly tuberculate, and an interior surface that is convex, smooth and endowed with markings that probably represent growth rings. Two distinctive types of osteoderms are present: one is generally oval-shaped and small; the other is rectangular or subrectangular, and larger. They are interpreted as regional variants within individuals. **Discussion**: These isolated osteoderms are comparable to those of helodermatids (e.g. <u>Heloderma texana</u>, Stevens, 1977), in being thick and robust, and in bearing a tuberculate outer surface. They cannot be referred to either of the two known helodermatids from the Judith River Group. Thus, they are here referred to as Helodermatidae genus and species indet.. Such helodermatid osteoderms represent the first report of this taxon from the Upper Cretaceous of North America, although similar material has also been recovered from the Judith River Group of DPP (Brinkman, 1997 pers. comm.).

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Family Xenosauridae Cope 1886

Genus indet.

Plate 10, i

Material: Isolated osteoderms (RTMP96.74.66-67).

Description and Discussion: These osteoderms are transversely elongate, wedge-shaped, slenderly-built elements. A prominent ridge is present on the external surface, extending between the two pointed ends and dividing the surface into an anterior and a posterior one. Both anterior and posterior surfaces incline toward the ridge. The external surface is sculptured with small pits, while the interior surface lacks sculpture and is flat. They are readily distinguishable from the osteoderms of helodermatids in their different shape, in lacking tuberculate ornamentation, and in their slender construction. An isolated xenosaurid frontal with fused osteoderms was described by Gao and Fox (1996) from the Judith River Group in DPP but was only referred to the family.

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Family Varanidae Gray 1827

PALAEOSANIWA Gilmore 1928

cf Palaeosaniwa canadensis Gilmore 1928

Plate 9, k

<u>Palaeosaniwa canadensis</u> Gilmore 1928: p. 83; Estes 1964: p. 135, fig. 66; Gao & Fox 1996: p. 90, figs. 37, 38. <u>Megasaurus robustus Gilmore 1928: p. 157, Pl. 27, figs. 1, 1a.</u>

Material: All referable specimens are isolated marginal teeth, and are catalogued as RTMP96.74.40-51.

Description: These isolated marginal teeth are evidently shed ones, as indicated by the presence of a large pit at the attachment end, resulting from resorption in the process of replacement, and the missing crown base. The crown length of these teeth ranges from about 2 mm to 4 mm. They are laterally compressed and trenchant, with sharply-pointed tips. Both the anterior and posterior edges bear micro-serration. The whole tooth surface is coated with a layer of shiny enamel. No venom grooves are evident on any teeth. **Discussion**: These marginal teeth resemble the isolated teeth of <u>Palaeosaniwa canadensis</u>, described by Estes (1964), in general shape, and in the presence of micro-serration on the anterior and posterior cutting edges. Gao and Fox (1996) described some jaw fragments from the Judith River Group of southern Alberta, and referred them to <u>P. canadensis</u>. They suggested that the micro-serration on the teeth that they described are slightly different from those illustrated by Estes (1964, Fig. 66) from the Lance Formation of Wyoming. Such a difference is not evident on the isolated teeth recovered in the present study.

Superfamily Varanoidea Camp 1923

Family indet.

Plate 9, m-n

Material: Fragments of jaw elements (RTMP96.74.68-75).

Description and Discussion: These specimens are mostly partial dentaries with broken tooth crowns. They are referred to the Varanoidea primarily on the basis of the presence of the infolded crown bases that are evident, as well as the absence of a subdental shelf. Nevertheless, they are too incomplete to allow further taxonomic assignment.

Order Cryptodira Cope 1868

Suborder Eucryptodira Gaffney 1975

The turtle specimens recovered are all carapace and plastron fragments. They are catalogued as RTMP96.79.1-63.

Family Baenidae Cope 1882

gen. indet.

Plate 10, j

Material: Shell fragments (RTMP96.79.45-63).

Description and Discussion: These shell fragments are diagnostic in being heavily built, smooth and devoid of shell sculpture, and in the presence of shallow sulci. Three genera of baenids, <u>Plesiobaena</u>, <u>Boremys</u>, and <u>Neuranchyles</u>, have been reported from the Upper Cretaceous deposits of southern Alberta (e.g. Gaffney, 1972), but the material recovered in the present study is too fragmentary to be identified at the generic level.

Family Chelydridae Agassiz 1857

gen. indet.

Plate 10, k

Material: Shell fragments (RTMP96.79.28-43)

Description and Discussion: Chelydrid shell fragments are identifiable on the basis of a thin shell and the presence of deep sulci, prominent ridges and corrugations on the carapace. Isolated peripheral bones (RTMP96.79) are distinctive in bearing deep sulci and deep pits for articulation with the ribs. These chelydrid specimens are noticeably smaller than most of the other turtle specimens from the same microsites.

Chelydrid specimens have been reported from the Lance Formation of Wyoming and referred to 'Chelydridae gen. indet.' (Estes, 1964; Hutchison & Archibald, 1986). According to Hutchison and Archibald (1986), these specimens, represented by disarticulated shell fragments, were mistakenly referred by Estes (1964) to "the Emydidae near <u>Pseudemys</u>". Evidently, the chelydrid material recovered in the present study exhibits resemblance to that from the Lance Formation and is thus referred to that taxon. Similar material of chelydrids has also been reported from the Judith River Group of DPP (Brinkman, 1990).

<u>Emarginochelys</u> <u>cretacea</u>, an articulated skeleton from the Hell Creek Formation of Montana, was originally described by Whetstone (1978) as a chelydrid but is now recognized to be a kinosternoid turtle (Meylan and Gaffney, 1989).

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Family Adocidae Cope 1870 ADOCUS Cope 1868 Adocus sp. Plate 10, I

Material: Shell fragments, catalogued as RTMP96.79.20-27.

Description: These specimens are characteristic in bearing very fine ornamentation on the shell fragments. Such ornamentation is comprised of numerous shallow pits bounded by low ridges in a regularly-arranged series of lines, also referred to as punctate sculpturing (Meylan and Gaffney, 1989). This contrasts with the shell ornament of trionychids which consists of deep pits and high, wavy ridges.

Discussion: The osteology of <u>Adocus</u> was well documented by Meylan and Gaffney (1989) on the basis of a nearly complete skeleton from the Hell Creek Formation of Montana. Shell fragments of <u>Adocus</u>, readily identifiable based upon their distinct punctate sculpturing, have been recovered abundantly from Upper Cretaceous deposits of North America. Further specific identification based upon shell sculpture pattern within this genus, however, has been the subject of debate (Brown, 1907; Gilmore, 1919, White, 1972). Estes et al. (1969) noted that two types of <u>Adocus</u> shell sculpture are typical of the Late Cretaceous specimens: a very fine type with eight to ten pits per centimeter, and a more well-defined type with six to seven pits per centimeter. They found that all the Hell Creek specimens exhibited the former type, and thus suggested that the two sculpture patterns are not simply variants indicative of different shell areas. However, the specimens recovered from the microsites examined in this study reveal that the number of pits varies from five to ten per centimeter. Some fragments of peripheral bones also reveal that the pits of the sculpture on the ventral side are relatively larger and more laterally elongate than those on the dorsal side. Thus, the variation that Estes et al. (1969) noted is likely a result of variation on the shell of a single species.

<u>Adocus</u> was considered by Estes and Berberian (1970) to be restricted to Maastrichtian strata. Recent work has indicated that it has a wider temporal and stratigraphic range of distribution in southern Alberta, including the Upper Milk River Formation (personal observation), the Foremost and Oldman formations (this study), and the Dinosaur Park Formation (Brinkman, 1990).

Family Nanhsiungchelyidae Yeh 1966

BASILEMYS Hay 1902

Basilemys sp.

Plate 10, m

Basilemys sp Russell, 1935, 1964; Sahni, 1972; Brinkman, 1990.

Material: Shell fragments, only known from surface-collected samples from WS.

Description and Discussion: Shell fragments of <u>Basilemys</u> can be readily identified by their rough, coarse sculpture with only three to four pits per cm, in contrast to that of <u>Adocus</u> which is relatively fine, smooth, and with more than five pits per cm (e.g. Estes et al., 1969). <u>Basilemys</u> shell fragments are also distinguishable from other turtles known from the Upper Cretaceous in their considerable thickness (e.g. Sahni, 1972). <u>Basilemys</u> material recovered in this study is very similar to that from DPP (Brinkman, 1990).

Family Trionychidae Gray 1870

gen. indet.

Plate 10, n

Material: shell fragments (RTMP96.79.1-19).

Description and Discussion: Trionychid specimens can be readily recognized on the basis of their distinctive shell sculpture patterns. These patterns vary from numerous pits of various shapes encompassed by irregular and rounded ridges, to arrays of many grooves segregated by wavy ridges. Such ornament has been widely considered to be characteristic of the family Trionychidae, but it has been considered to be of dubious taxonomic significance at lower taxonomic levels (Estes 1964, Nicholls 1972, Gaffney 1979, Gardner and Russell 1994). Gardner and Russell (1994) noted that the sculpture patterns of trionychids are irregular and that they may vary within an individual shell and also probably during ontogeny. Recently, Gardner et al. (1995) documented trionychid fossils from the Judith River Group of North America, and concluded that only two genera (Aspideretoides and Apalone) and four species are valid after reviewing three genera and 15 nominal species of trionychids that had been previously described. Sculpture pattern on dorsomedian carapace is listed by Gardner et al. (1995) as one of diagnostic features for the three species of Aspideretoides. Nevertheless, the shell

material recovered in the present study is too fragmentary to be identified with certainty to the generic level.

Family *incertae sedis* <u>NAOMICHELYS</u> Hay 1908

Plate 10, o

Naomichelys sp.

Material: A single shell fragment (RTMP96.79.44) of this taxon was retrieved, from PHR-1, through screenwashing.

Description and Discussion: <u>Naomichelys</u> shell material is very distinctive in bearing numerous, pillar-like tubercles on the dorsal surface, which makes it easily segregable from other turtles. This genus first occurs in the Lower Cretaceous (Hay, 1908). The recovery of this genus from site PHR-1 (the Upper Foremost Formation) represents, to date, its most recent stratigraphic occurrence. Surface collecting in the present study has indicated that <u>Naomichelys</u> material is found in the lower portion of the Foremost Formation.

Order Crocodylia Gmelin 1788 Family Crocodylidae Cuvier 1808 <u>LEIDYOSUCHUS</u> Lambe 1907 <u>Leidyosuchus</u> sp.

Plate 11, a-b, f

Material: Specimens of <u>Leidyosuchus</u> recovered are represented by isolated teeth and scutes. They are catalogued as RTMP96.73.1-38.

Description: The isolated teeth are typical of those of the genus, with two different forms being evident: cone-shaped teeth with smooth or faint striations (the smaller ones tending to be more strongly striated); and bulbous, low-crowned teeth that are finely striated and oval in cross-section, with an evident neck at the base of the crown. The former are more abundant than the latter within the microsites examined in the present study.

Two types of scutes are also present: one has deeply pitted sculpture and is relatively thick; the other has smaller and shallower pits and a relatively thin body.

Discussion: <u>Leidyosuchus</u> is, according to Wu et al.(1996), the most primitive member of the Eusuchia, and material has been frequently retrieved from the Upper Cretaceous of North America. The stratigraphic record of the genus includes the Judith River Group and the Edmonton Group of southern Alberta, the Judith River, the Two Medicine and the Hell Creek formations of Montana and the Lance Formation of Wyoming. Another less common nonalligatorine eusuchian, <u>Prodiplocynodon</u>, was described by Mook (1941) based on material from the Lance Formation of Wyoming. So far, no example of this taxon has been reported from the Judith River Group of Alberta or elsewhere. Thus, the material recovered in the present study is assigned to <u>Leidyosuchus</u> sp..

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Subfamily Alligatorinae Kälin 1955

gen. indet.

Plate 11, c-e

Material: Specimens referable to alligatorines consist only of isolated teeth (RTMP96.73.39-.53).

Description and Discussion: Associated material of alligatorines recovered from the Upper Cretaceous of North America reveal that they possessed several distinctive crushing teeth in the posterior region of the jaws (Wu et al., 1996). Such teeth are generally bulbous, low-crowned and laterallycompressed, and are diagnostic in having wide, horizontally-worn crown tips. The worn crowns indicate that the teeth were functional in the crushing actions performed by the jaws. Carpenter and Lindsey (1980) suggested that these Cretaceous alligators fed on shelled animals, such as clams and turtles. Three genera of the Alligatorinae have so far been discovered in the Upper Cretaceous of North America: <u>Albertochampsa</u> from the Judith River Group of southern Alberta (Erickson, 1972); <u>Brachychampsa</u> from the Hell Creek Formation of Montana (Gilmore, 1911; Norell et al., 1994); and <u>Stangerochampsa</u> from the Horseshoe Canyon Formation of southern Alberta (Wu et al., 1996). The isolated alligatorine crushing teeth retrieved in this study, with their horizontally-worn crowns, can be readily segregated from those of <u>Leidyosuchus</u>, which bear different, laterally worn (often to a much smaller degree) crowns associated with different feeding habits. The crushing teeth of Cretaceous alligatorines, with their horizontally-worn crowns, are all similar in general form among the three known genera (Wu, 1997 pers. comm.), and the isolated crushing teeth recovered in this study can only be identified as Alligatorinae gen. indet.. The non-crushing teeth of alligatorines are presumably included with Leidyosuchus teeth.

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Suborder Choristodera Cope, 1877 Family Champsosauridae Cope 1877 <u>CHAMPSOSAURUS</u> Cope 1877 <u>Champsosaurus</u> sp.

Plate 10, g-j

Material: Specimens referred to this taxon include fragments of jaws, isolated teeth and centra, catalogued as RTMP96.73.54-93.

Description and Discussion: Jaw fragments (RTMP96.73. 73-82) are represented mainly by dentaries. They are robustly built and are often preserved with their teeth attached. The crowns of most of these teeth are broken, leaving only the bases. As result, the acrodont mode of tooth attachment is evident, and the large pulp cavity is revealed in the base of each tooth. Isolated teeth (RTMP96.73.54-72) are slender, cone-shaped, and bear faint striations. Some carry antero-posterior keels on the crowns. They can be confused with those of isolated <u>Atractosteus</u> teeth, which are similar in both form and size. <u>Atractosteus</u> teeth are, however, different in that they have a translucent tip and a prominent neck between the tip and the crown.

Isolated champsosaur centra (RTMP96.73.83-.93) are predominately representative of the presacral region, but a few caudals have also been retrieved. The largest measures 20 mm in length and the smallest 4 mm. They are amphiplatyan and cylindrical, as is typical of champsosaurids.

Order Ornithischia Seeley 1888 Suborder Ornithopoda Marsh 1881 Family Hadrosauridae Cope 1869

The Hadrosauridae as a monophyletic group has been widely accepted, but Horner (1990) challenged the idea and suggested that the family is of diphyletic origin. In the cladogram he presented, the Hadrosaurinae was considered to be the sister group of <u>Iguanodon</u>, while the Lambeosaurinae is considered to be the sister group of <u>Ouranosaurus</u>. Horner (1990) further argued that both subfamilies were postulated to have arisen from separate stem species and to represent two families. However, more recent phylogenetic work by Weishampel et al. (1993) advocates the monophyly of the family. Further, Fastovsky and Weishampel (1996) also suggested that the latter hypothesis (hadrosaurids as a monophyletic group) is more parsimonious than Horner's (1990) (hadrosaurids with separate origins). Thus, the traditional taxonomic arrangement is accepted here.

Hadrosauridae gen. indet.

Plate 12, a-d

Material: Specimens referable to hadrosaurids are represented by isolated teeth, most of which are functional teeth with worn crowns. They are catalogued as RTMP96. 83.1-19.

Description and Discussion: The Hadrosaurinae and Lambeosaurinae share similar forms of dentition, which are distinctive in consisting of multiple tooth families, with three to five successional teeth present at each tooth location (see Weishampel and Horner, 1992: Fig.26.8). Each tooth is composed mainly of dentine, with an enamel layer present only on one side of the crown (the labial side of the maxillary teeth and lingual side of the dentary teeth--Horner, 1990; Weishampel and Horner, 1992). The crown of an unworn hadrosaurid tooth (RTMP96.83.16) is, on the enameled side, diamond-shaped. with its dorso-ventral height being much greater than its antero-posterior width. A prominent median ridge spans the dorso-ventral height of the crown face and divides it into two symmetrical halves. Most isolated teeth are represented by the majority of the crown, with a worn crown apex and broken root. These fragmentary teeth are identifiable on the basis of the presence of the median ridge and the radiating dentine deposits evident on the worn surface of the crown.

Taxonomic utility of hadrosaurid teeth has not been considered in great detail, but has been thought to be limited (Lull and Wright, 1942; Gilmore, 1953; Coombs, 1988). Coombs (1988) stated that tooth morphology shows considerable variability within a single individual and that their morphology shows "substantial overlap among different species, genera and even subfamilies of Hadrosauridae". Nevertheless, it has also been noted that the crown morphology of the two subfamilies (Hadrosaurinae and Lambeosaurinae) is not identical. In the hadrosaurids there is a straight, median ridge, and the crown-root angle is greater than 145°, while in the lambeosaurids there is sinuous, median ridge, and the crown-root angle ranges between 120-140° (Sternberg, 1935; Langston, 1960; Weishampel and Horner, 1990, 1992). Due to the lack of roots on most of the isolated teeth recovered in the present study, it is not possible to assign them to either Hadrosaurinae or Lambeosaurinae. Thus, they are identified as Hadrosauridae gen. indet., on the basis of the morphology of the median ridge.

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Suborder Ceratopsia Marsh 1890 Infraorder Neoceratopsia Sereno 1986 Family Ceratopsidae Marsh 1890

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gen. indet.

Plate 12, e-f

Material: Specimens recovered here are represented by isolated tooth fragments, catalogued as RTMP96.83.20-38.

Description and Discussion: The isolated ceratopsian teeth recovered in this study are mostly functional ones, as is indicated by their greatly-worn crowns. Among vertebrate microfossils recovered in the present study, they may be potentially confused with isolated hadrosaurid teeth. Ceratopsian teeth are recognizable, however, in that the dorso-ventral ridge of the crown is located in the anterior half of the occlusal surface, and secondary ridges are often present. This contrasts with the condition in hadrosaurid teeth, in which a single, median ridge is present. The worn surface of ceratopsian teeth reveals that the dentine was deposited parallel to the crown surface, not in a radiating pattern as is evident in hadrosaurid teeth. Isolated ceratopsian teeth also differ in that they bear a prominent cingulum at the base of the enameled occlusal surface. Such isolated ceratopsian teeth have been found in abundance in vertebrate microfossil assemblages of the Upper Cretaceous of North America (e.g. Estes, 1964; Sahni, 1972; Brinkman, 1990; Baszio, 1997).

Suborder Ankylosauria Osborn 1923

Family Nodosauridae Marsh 1890

gen. indet.

Plate 12, g

Material: Specimens referable to nodosaurids are represented only by isolated teeth (RTMP96.70.12-22)

Description and Discussion: Ankylosaurian teeth, in general, have leaf-shaped and generally labio-lingually compressed crowns, with an apical cusp and secondary cusps along the crown edge. The two ankylosaurian families – the Nodosauridae and Ankylosauridae (Coombs, 1990; Weishampel and Horner, 1992) – display significantly different tooth morphologies. Nodosaurid teeth are distinctive in being highly labio-lingually compressed, in having vertical grooves that are coincident with the notches between adjacent marginal cusps on the crown flanks, and in the presence of a conspicuous basal cingulum.

Family Ankylosauridae Brown 1908

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gen. indet.

Plate 12, h-j

Material: Isolated teeth referable to ankylosaurids include specimens catalogued as RTMP96.70.1-11.

Description and Discussion: The teeth of the family Ankylosauridae are generally smaller than those of nodosaurids, and differ from them in the absence of a distinct basal cingulum and in the presence of less welldeveloped vertical grooves on the crown flanks. Ankylosaurid teeth have a swollen base instead of a basal cingulum, and the vertical grooves are not in alignment with the notches between adjacent marginal cusps.

Ankylosauria fam. indet.

Plate 12, k-l

Material: Specimens referable to ankylosaurians are represented by disarticulated osteoderms of the dermal armor (RTMP96.70.32-33).

Description and Discussion: The armor osteoderms recovered in this study are small (the greatest dimension less than 2cm) and thus most likely represent the smaller ossification that fill the spaces between transversely arranged rows of large armor plates (see Weishampel and Horner, 1992: fig.22.13). These small osteoderms, a variety of shapes, can be identified on the basis of the density of the bone that constitutes them. No further information can be gleaned from them that is pertinent to a more precise taxonomic assignment. Among the microsites sampled in the present study, sites CS and HAS have yielded unusually abundant isolated small osteoderms. Similar variation in abundance patterns was also noted by Brinkman (1990) among the microsites of DPP.

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Suborder Pachycephalosauria Maryanska & Osmolska 1974 Family Pachycephalosauridae Sternberg 1902

gen. indet.

Plate 12, m-n

Material: Specimens referred to pachcephalosaurids are represented only by isolated teeth (RTMP96.70.23-31).

Description and Discussion: These isolated teeth are relatively small and have crowns that are triangular and labio-lingually-compressed, and crown edges that bear evident denticles, with the apical denticle prominently stronger than the marginals. A small, complete tooth (RTMP96.70.29) reveals that only three to four marginal denticles are present. A cingulum is well-developed on the anterior and posterior portion of the teeth. A vertical ridge extends from the tip of the crown to the base and vertically divides the crown flank into two symmetrical halves. The tooth root, as shown in RTMP96.70.29 (plate 12m), is long (about twice the crown height), but is noticeably narrower than its crown. The fully-developed root and a strong wear on the crown indicate that RTMP96.70.29 is a functional rather than replacement tooth, despite its rather small size (4mm high and 1.5mm wide).

Order Saurischia Seeley 1888

Suborder Theropoda Marsh 1881

Much of our current understanding of theropod dinosaur biology and diversity, particularly that of small theropods, is based upon the form and interpretation of dental material from the Upper Cretaceous of North America. Currie et al (1990) demonstrated that theropod teeth display diagnostic features that are distinctive at the family, generic and even specific levels. Identification of theropod teeth in the present study is essentially based upon the descriptions provided by Currie et al (1990).

Abundant theropod material has been collected from the Upper Judith River Group of DPP and has been documented by Brinkman (1990) and Currie et al. (1990). Recently, tooth material from small theropods has been described from the Milk River Formation and the Horseshoe Canyon Formation in southern Alberta (Baszio,1997). Although theropod teeth have occasionally been surface-collected from the Lower Judith River Group (including the Foremost and Oldman formations), the theropod tooth specimens recovered from the microsites examined in this study represent the first systematic collection in this stratigraphic section of southern Alberta. This new material allows a more complete documentation of theropod teeth, including variation of their morphology and patterns of their stratigraphic distribution, in the Upper Cretaceous of southern Alberta.

A total of 384 small theropod and bird teeth have been recovered from the microsites examined in this study, consisting of 327 retrieved from screenwashing and 57 from surface collecting. This material is described below.

Family Dromaeosauridae Matthew and Brown 1922

DROMAEOSAURUS Matthew and Brown 1922

Dromaeosaurus albertensis Matthew and Brown 1922

Plate 13, a, b, d

Dromaeosaurus albertensis Matthew and Brown 1922; Colbert and Russell 1969: p.66; Currie et al. 1990: p.109, fig. 8.1; Fiorillo & Currie .1994: p. 77, fig. 3e; Rowe et al., 1992: p. 482, fig. 5 G-I.

Material: Isolated teeth (catalogued as RTMP96.62.1-3, and 69, 70). The teeth of this genus were relatively rarely encountered (only seven) in the microsites examined. **Description and Discussion**: The most diagnostic feature is that the anterior serration curves off from its anterior edge near the tip of tooth (see Plate 12b). Such teeth are often strongly compressed, resulting in the cross-section being different from that of tyrannosaurid premaxillary teeth (Currie et al, 1990), which is typically "D"-shaped. Other diagnostic features, as summarized by Currie et al.(1990), are that the denticles are as long as they are wide and are less sharply-pointed than those of <u>Saurornitholestes</u> teeth, and that the size difference between anterior and posterior denticles is smaller than it is for the teeth of <u>Saurornitholestes</u>.

In general, the teeth of <u>Dromaeosaurus</u> can be identified by the characteristic anterior serrated ridge that deviates from the anterior edge near the tooth tip. This diagnostic feature of some <u>Dromaeosaurus</u> teeth (e.g. RTMP96.62.70), as represented in this collection, appears to be less distinctive than that seen in previously described and more typical <u>Dromaeosaurus</u> teeth, and instead appears to be more similar to that of some <u>Saurornitholestes</u> teeth (e.g. RTMP96.62.6). This type of <u>Dromaeosaurus</u> tooth can, however, still be identified as such on the basis of the presence of a less pointed and relatively straight and less recurved tip, and on the presence of labio-lingually broad denticles and similarly sized anterior and posterior denticles. It is difficult to distinguish the <u>Dromaeosaurus</u> teeth in this collection from those recovered from the Milk River, or DPP formations, although size variation may be present among them. Throughout the Upper Cretaceous strata of southern Alberta,

<u>Dromaeosaurus</u> is always a relatively rare theropod (4.32-9.47% of the total theropod contingent) (Currie et al, 1990 and Baszio, 1997).

SAURORNITHOLESTES Sues 1978

Saurornitholestes langstoni Sues 1978

Plate 13, c, e-f

<u>Saurornitholestes</u> <u>langstoni</u> Sues 1978; Currie 1987:p.78; Currie et al.1990: p. 110, fig. 8.2; Fiorillo & Currie .1994: p. 77, fig. 3f, g; Rowe et al., 1992: p. 482, fig. 5 A-C.

Material: Isolated teeth (RTMP96.62.4-22). The teeth of

<u>Saurornitholestes</u> recovered from the microsites studied here represent some of the most abundant small theropod material in this collection.

Description: The teeth of <u>Saurornitholestes</u> are most readily distinguished by the following diagnostic features: strong compression labiolingually; strongly recurved, sharply pointed tips; denticles that are chisel-like, labio-lingually compressed at the base, and distinctly different in denticle size between the anterior and posterior denticles. Those recovered from the microsites examined in this study have anterior denticles that are either smaller than the posterior denticles or they are absent. Currie et al (1990) suggested that the teeth without anterior denticles may be present within the jaw, along with those with anterior denticles. The <u>Saurornitholestes</u> teeth in this collection that lack anterior denticles are interpreted as worn, replacement teeth.

Discussion: One hundred and sixty-nine teeth of <u>Saurornitholestes</u> have been recovered through screenwashing and 41 from surface-collecting. They exhibit similar morphological variation to that of typical of specimens recovered from other Upper Cretaceous strata in the area (Brinkman, 1990 and Currie et al., 1990). <u>Saurornitholestes</u> teeth have been found to be the most abundant (47.63-64.81%) of theropod teeth retrieved from the Upper Cretaceous deposits of southern Alberta (Currie et al,1990), and represent 64.81% of all the small theropods in this collection, versus 45% from the Milk River Formation (Baszio, 1997) and 47.63% from the Dinosaur Park Formation of DPP (Currie et al, 1990).

Family Troodontidae Gilmore 1924

TROODON Leidy 1856

Troodon formosus Leidy 1856

Plate 13, g-l

<u>Troodon formosus</u> Leidy 1856: p. 72; Russell 1948: p. 629; Sahni 1972: p. 359, fig. 9L-M; Currie et al. 1990: p. 113, figs. 8.3A-M; Fiorillo & Currie 1994: p. 77, fig. 3c; Rowe et al., 1992: p. 482, fig. 5 J-M.
<u>Stenonychosaurus inequalis</u> Sternberg 1932:
<u>Polyodontosaurus grandis</u> Gilmore 1932: p. 117.

Cf. <u>Saurornithoides</u> sp. Estes 1964: p.142, fig. 69a. <u>Pectindon bakeri</u> Carpenter 1982: p. 129, fig. 3a-c.

Material: Isolated teeth (RTMP96.62.33-36, and -59, -60). The <u>Troodon</u> specimens recovered in this study include 23 complete and partial teeth from screenwashed samples and two from surface-collected samples.

Description: <u>Troodon</u> teeth are distinctive in the presence of large, sharply-pointed denticles, with a count of only two denticles per mm (Currie et al, 1990). Such a count is lower than that of any other known small theropod. Other diagnostic features include the robust, recurved and biconvex crowns, and the weak constriction between the crown and root. <u>Troodon</u> teeth can be easily distinguished from those of all other theropods by their characteristic denticles: the largest denticles of any known small theropod. The teeth of <u>Troodon</u> recovered in this study show little variation in their morphology and are not distinguishable from those recovered from other Upper Cretaceous strata in the region.

Discussion: <u>Troodon</u> teeth are readily distinguishable from other small theropod teeth by the characteristic form of their denticles. Baszio (1997) clarified that <u>Troodon</u> tooth specimens previously claimed to be from the Milk River Formation by Currie et al (1990) were actually collected from the Judith River Group. Thus, it is suggested that the <u>Troodon</u> teeth recovered from the Oldman Formation in the course of this study, perhaps represent the earliest occurrence of this animal in North America (for further discussion see Chapter 7).

Family incertae sedis.

<u>RICHARDOESTESIA</u> Currie et al. 1990

Thirty examples of the teeth of <u>Richardoestesia</u> were recovered in this collection, including 26 from screenwashing and 4 from surface-collecting samples.

Description and Discussion: <u>Richardoestesia</u> teeth have the following diagnostic features [modified from Currie et al (1990)]: they are slender and labio-lingually compressed; their denticles are minute and are smaller than those of any other known theropod; and the denticle count is as high as eight per mm. Many of the <u>Richardoestesia</u> teeth recovered in this study exhibit weak longitudinal striations at the base of the crown.

Two types of <u>Richardoestesia</u> tooth crowns are evident: one has a recurved tip (typical of theropod crowns); the other has a straight crown with a non-recurved tip, with the crown being triangular in lateral view. The latter are often longer than the former. Baszio (1997) identified them as representing two different species. This assignment is adopted here. Thus, the <u>Richardoestesia</u> teeth recovered in this study can be referred to two species as follows:

Richardoestesia gilmorei Currie et al. 1990

Plate 14, a-e

Theropoda incertae sedis Carpenter 1982: p.130, fig.6.

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<u>Richardoestesia gilmorei</u> Currie et al. 1990: p. 117, figs. 8.6J-M; Baszio,

1997b: p. 38, pl. IV, fig. 49; Rowe et al., 1992: p. 482, fig. 5 D-F.

Material: Isolated teeth (RTMP96.62.23-32, and -66).

Discussion: This species has been relatively commonly found in Upper

Cretaceous strata, and is represented by those of <u>Richardoestesia</u> teeth that are diagnostic in having typical recurved crowns.

Richardoestesia sp. Baszio 1997

Plate 14. f-g

Theropoda ? *incertae sedis* Russell 1935: p.123, fig.9; Estes 1964:
p. 143, fig. 69b.
?Sebecosuchia Sahni 1972: p. 351, figs. 8Y, Z
<u>Richardoestesia</u> sp. Baszio 1997: p. 40, Pl. V, figs. 61-68.

Material: Isolated teeth referable to this species are catalogued as RTMP96.62.26 and .31.

Discussion: The teeth of <u>Richardoestesia</u> sp. are readily

distinguishable from those of the other species in having straight crowns. This type of tooth has been reported from the Milk River Formation (Russell, 1935),
the Judith River Formation of Montana (Sahni, 1972), and the Lance Formation of Wyoming (Estes, 1964), but they were not named. Currie et al. (1990) referred these teeth to <u>Richardoestesia</u> and suspected that they represent a different species of the genus due to their distinctve morph. More specimens retrieved by Baszio (1997) confirm Currie et al.'s (1990) observation. This is also reinforced by the specimens recovered in this study.

Family incertae sedis

PARANYCHODON Cope 1876

Paranychodon lacustris Cope 1876

Plate 14, h-k

<u>Paranychodon lacustris</u> Cope 1876: p. 256; Russell 1935: p. 26, PI.2, fig. 8; Estes 1964: p.143; Estes et al. 1969: p.25, Pl. 1d, e; Sahni 1972: p. 360, figs. 8S, T, 9J, K; Carpenter 1982: p.130, fig.4; . <u>Tripriodon caperatus</u> Marsh 1889: PI.3 figs. 18-22.

Material: Isolated teeth (RTMP96.62.37-47, and -67, -68). Eighteen

<u>Paranychodon</u> teeth were recovered from screenwashed samples obtained during the course of this study.

Description and Discussion: The teeth of this taxa are recognized by having distinct longitudinal ridges on one or both sides of the tooth crown and in lacking denticles. All such teeth recovered in this study are of small size.

Currie et al. (1990) showed that <u>Paranychodon</u> teeth are highly variable in shape, and suggested that the name <u>Paranychodon lacustris</u> be restricted to the non-serrate teeth with distinct longitudinal ridges. They referred those teeth with similar forms but bearing serrations to different small theropods (see Currie et al., 1990: p. 118, fig.8.5 A-C).

The teeth of <u>Paranychodon</u> are widespread in the Upper Cretaceous deposits of North America, but current understanding of the genus is poor as there is nothing known of associated material. They are, however, distinctive in terms of the diagnostic features described above. Although the <u>Paranychodon</u> teeth recovered in this study are relatively rare in absolute number, they are nonetheless distributed widely among the studied microsites.

Family Tyrannosauridae Osborn 1905

genus. indet.

Plate 14, I

Material: Isolated teeth (RTMP96.62. 71-90).

Description and Discussion: Tyrannosaurid teeth can often be identified by their very large size, and their elongate and recurved crown bearing stout and chisel-like denticles. Juvenile or small teeth of tyrannosaurids are basically scaled-down versions of large ones, and, as such, are clearly stouter than those of other small theropods that possess teeth of equivalent length. Both large and juvenile tyrannosaurid teeth were retrieved in this study, and they are very similar in morphology to those from other Upper Cretaceous strata. The incompleteness of the material makes it difficult for precise assignment at lower taxonomic level.

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AUBLYSODON Leidy 1868

Aublysodon sp.

Plate 14, m-n

Material: Isolated premaxillary teeth (RTMP96.62.48-49). Only five Aublysodon teeth were recovered from the microsites examined in this study.

Description and Discussion: According to Molnar and Carpenter (1990), <u>Aublysodon</u> teeth are restricted to the small non-serrated premaxillary teeth with a D-shaped cross-section, in contrast with those of other tyannosaurids that bear distinct serration. The five premaxillary teeth recovered in the present study are assignable to this genus. However, Currie et al (1990) questioned the valid status of this genus because it was described only from tooth material. Until further study of the genus is conducted, this type of premaxillary tooth is temporaily referred to <u>Aublysodon</u> sp..

Class Aves

gen. indet. Plate 14. o-p

Material: Isolated teeth (RTMP96.62.50-65). Twenty seven teeth recovered in this study have been referred to Aves, genus indet..

Description and Discussion: The teeth of Aves genus indet. differ from other known theropod teeth in the following features: they are small, stout but strongly laterally-compressed; the crown is slightly recurved; enamel carinae are present on both anterior and posterior edges, but they lack definitive denticles; and they are prominently constricted at the base of the crown. Such teeth can be easily distinguished from the non-serrated teeth of <u>Paranychodon</u> as they lack striations on the tooth surface. Confusion of such teeth with those of specimens of small <u>Leidyosuchus</u> is possible, but they are segregable on the basis of the greater degree of lateral compression and their more pronounced recurved profile. They also differ from the teeth of known Cretaceous toothed birds (e.g. <u>Hesperornis</u> and <u>Ichthyornis</u>) in general form, suggesting that they represent one or more as yet described avian taxa of the Late Cretaceous.

Class Mammalia

Plate 15, a-t

Plentiful mammalian material was recovered from the microsites examined in this study. There are 188 identified specimens retrieved from the microsites from screenwashed samples. They are predominantly represented by isolated teeth and fragments of jaws, and are catalogued as RTMP96.82.1-188.

Fossil mammals from the Upper Cretaceous of southern Alberta, particularly the Milk River and the Dinosaur Provincial Park formations, have been extensively collected and documented by Fox (e.g. Fox, 1968a, 1971, 1976, 1979a, and 1984). Mammalian material from the Oldman and the Foremost formations in the Milk River region, however, have been comparatively poorly-collected and are thus not well documented. The mammalian specimens retrieved in the present study represent the first extensive collection from the region. Table 4.1 is a taxonomic listing of mammals from the microsites examined in the present study, as determined by Dr. Richard Fox of the University of Alberta. Detailed description and documentation of these taxa can be found in the following publications by Fox (1968a, 1968b, 1970, 1971a, 1971b, 1977, 1979a, 1979b, 1979c, 1980 and 1984). **TABLE 4.1** Classificatory summary of mammals from the microsites sampled from the Judith River Group of Milk River area. Numbers indicate the number of identifiable elements for generic and lower level of taxa.

Class Mammalia Subclass Allotheria
Order Multituberculata
Suborder Taeniolabidoidea
Family Cimolomvidae
Meniscoessus maior7
Cimolomvs clarki1
?Cimolodon sp
Suborder Ptilodontoidea
Family Ectypodontidae
Mesodma cf primaeva4
Mesodma cf antiqua6
Cimexomys sp
Subclass Theria
Infraclass Metatheria
Order Marsupialia
Family Pediomyidae
Pediomys prokrejcii1
Pediomys sp
Family Stagodontidae
Eodelphis sp2
Family Peradectidae
Turgidodon russelli10
Turgidodon praesagus4
Infraclass Eutheria
Order Deltatheridia
Family Paleoryctidae
Cimolestes sp1
Order Insectivora
Family Leptictidae
Gypsonictops cf lewisi1
Paranyctoides sternbergi1

Teeth of Chondrichthyes

- a-c, <u>Hybodus</u>. a, (RTMP96.71.1) lingual view of lateral tooth
 with partial root; b, (RTMP96.71.2) labial view; c, (RTMP96.71.1)
 labial view.
- d-g, <u>Synodontaspis</u> <u>hardingi</u>. (RTMP96.71.4): d, anterior tooth in labial view; e, lingual view; f, lateral tooth in lingual view; g, labial view.

h-m, <u>Archaeolamna kopingensis</u>. (RTMP96.71.5): h and i,
lateral tooth in labial view; j and m, anterior tooth in labial and
lingual view; k and l, lateral tooth in labial view.



Teeth of Chondrichthyes

a-d, Squatirhina roessingi. (RTMP96.71.9): a, lingual;

b, labial; c, lingual; d, labial view.

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- e-g, <u>Chiloscyllium missouriense</u>. e, (RTMP96.71.14) ventral view of root; f, (RTMP96.71.19) lingual view; g, (RTMP96.71.19) labial view.
- h-i, <u>Rhinobatos casieri</u>. (RTMP96.71.13): h, lingual; i, labial view.
- j-m, <u>Ischyrhiza mira</u>. (RTMP96.71.10): j and k, labial view; I and m, lingual view.



Teeth of Chondrichthyes

- a-c, <u>Myledaphus bipartitus</u>. (RTMP96.71.35): a, lingual; b, occlusal;
 c, basal view.
- d-f, <u>Myledaphus</u> sp.. (RTMP96.71.20): d, lingual; e, occlusal;

f, basal view.

g-i, <u>Squatina hassei</u>. (RTMP96.71.8): g, basal; h, lingual;

i, labial view.

j-l, <u>Synechodus turneri</u>. (RTMP96.71.12): j, labial; k, lingual;

I, occlusal view.



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Specimens of Osteichthyes

a-b, Acipenseridae gen. indet.. Cranial elements in external view:a, (RTMP96.77.21); b, (RTMP96.77.20).

c-f, Holostean B. Bony scales: c, (RTMP96.77.64) external;

d, (RTMP96.77.64) internal; **e**, (RTMP96.77.63) external; **f**, (RTMP96.77.63) internal view.

g-j, Holostean A. Bony scales: g, (RTMP96.77.60) external;
 h, (RTMP96.77.60) internal; i, (RTMP96.77.49) internal; j, (RTMP96.77.49) external view.

k,I,q, <u>Belonostomus longirostris</u>. Bony scales: k, (RTMP96.77.68) internal; I, (RTMP96.77.70) external view. Jaw element: q, (RTMP96.77.71) occlusal view.

m-p, <u>Atractosteus occidentalis</u>. Bony scale(RTMP96.77.1):
m, external; n, internal view. Tooth (RTMP96.77.194): o, lateral view. Vertebra (RTMP96.77.195): p, ventral view.



Specimens of Osteichthyes

a-f, Amiidae gen. indet.. Vertebra (RTMP96.77.169): a, anterior;

b, dorsal view. Lower jaw (RTMP96.77.153): c, lateral; d, medial view. Toothplate (RTMP96.77.147): e, ventral;

f, dorsal view.

g-i, <u>Coriops amnicolus</u>. Toothplate (RTMP96.77.95): g, ventral;h, dorsal; i, lateral view.

j-l, <u>Paralbula casei</u>. Toothplate (RTMP96.77.72): j, occlusal view. Tooth (RTMP96.77.73): k, basal; l, occlusal view.

m-o, Phyllodontinae gen. indet. Tooth stacks: m, lateral (RTMP96.77.175); n, basal (RTMP96.77.176); o, occlusal view (RTMP96.77.176).



Specimens of Osteichthyes

a-b, Paratarpon apogerontus. Vertebra (unaccessioned specimen):

a, ventral; **b**, anterior view.

c-f, Estesesox foxi. Palatines: c, occlusal view (RTMP96.77.38);

d, dorsal view (RTMP96.77.35). Right premaxilla

(RTMP96.77.38): e, medial view. Left dentary (RTMP96.77.36): f, medial view.

g-i, Teleost D. Vertebra (RTMP96.77.119): g, dorsal;

h, anterior; i, ventral view.

j-m, Teleost indet. Vertebrae: j, dorsal (RTMP96.77.135);

k, ventral (RTMP96.77.135); **I**, ventral (RTMP96.77.138); **m**, dorsal view (RTMP96.77.138).



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Specimens of Amphibia

- a-e,j, <u>Scapherpeton tectum</u>. Trunk vertebra (RTMP96.78.71):
 a, lateral; b, ventral; c, anterior view. Atlas (RTMP96.78.148): d, ventral; e, anterior view. Left lower jaw (RTMP96.78.2146): j, medial view.
- f-i, m, Opisthotriton kayi. Trunk vertebra (RTMP96.78.95):

f, ventral; **i**, lateral view. Atlas (RTMP96.78.149): **g**, ventral; **h**, anterior view. Right lower jaw (RTMP96.78.147): **m**, medial view.

k, I, n-q, Caudata gen. indet. Right vomer (RTMP96.78.150):

k, ventral view. Opisthotic-exoccipital (RTMP96.78.169): I, posterior view. Right maxilla (RTMP96.78.168): n, lateral view.
Left quadrate (RTMP96.78.188): o, anterior view. Left quadrate (RTMP96.78.206): p, posterior view. Postdentary bone (RTMP96.78.207): q, lateral view.



Specimens of Amphibia

a-e, Albanerpeton sp.. Trunk vertebra (RTMP96.78.144):

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a, ventral; b, lateral view. Frontal (RTMP96.78. 136): c, dorsal view. Left lower jaw (RTMP96.78.107): d, medial view. Right premaxilla (RTMP96.78.121): e, medial view.

f-n, p-r, Anura gen. indet. Cranial element (RTMP96.78.17):

f, external view. Right squamosal (RTMP96.78.11): g, external view. Right maxilla (RTMP96.78.34): h, lateral view. Maxillae in medial view: i, (RTMP96.78.36); I,(RTMP96.78.31). Trunk vertebrae in ventral view: j, (RTMP96.78.45); k, (RTMP96.78.46); m, (RTMP96.78.50). Left ilia in lateral view: n, (RTMP96.78.226); p, (RTMP96.78.227). Humeri: q, (RTMP96.78.56); r, (RTMP96.78.59).

o, Caudata gen. indet. Left ilium (RTMP96.78. 228): o, lateral view.



Specimens of Lacertilia

a-c, Socognathus unicuspis. Right maxilla (RTMP96.74.3a):

a, medial view. Right dentaries in medial view: b,

(RTMP96.74.3c); c, (RTMP96.74.4).

- d, f-h, Leptochamops sp. Right maxilla (RTMP96.74.16):
 - d, medial view. Jaw elements: f, lateral view (RTMP96.74.16);h, (RTMP96.74.16). Right dentary (RTMP96.74.15): g, medial

view.

- e, <u>Gerontoseps</u> <u>irvinensis</u>. Left dentary (RTMP96.74.19) in medial view.
- i-j, Odaxosaurus cf priscus. Left dentary (RTMP96.74.26):

i, medial view. Jaw element (RTMP96.74.25): j, partial.

- k, cf <u>Palaeosaniwa</u> <u>canadensis</u>. Marginal tooth (RTMP96.74.42) in lateral view.
- I, cf <u>Paraderma bogerti</u>. Marginal tooth (RTMP96.74.37) in medial view.
- m-n, Varanoidea fam. indet. Jaw elements in medial view:m, (RTMP96.74.71); n, (RTMP96.74.72).
- o-p, <u>Colpodontosaurus</u> cf <u>cracens</u>. Left dentary (RTMP96.74.24b):
 o, lateral view. Right dentary (RTMP96.74.24a): p, medial view.



Specimens of Lacertila and Cryptodira

- a-d, cf Odaxosaurus piger Osteoscutes in external view:
 - **a**, (RTMP96.74.30); **b**, (RTMP96.74.31); **c**, (RTMP96.74.33);
 - d, (RTMP96.74.36).

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e-h, Helodermatidae gen. indet. Elongate osteoderms

(RTMP96.74.60): e, external; f, internal view. Round osteoderm (RTMP96.74.62): g, internal; h, external view.

- i, Xenosauridae gen. indet. Half complete osteoderm (RTMP96.74.67) in external view
- j, Baenidae gen. indet. Shell fragment (RTMP96.79.45) in external view.
- k, Chelydridae gen. indet.. Costal fragment (RTMP96.79.41) in external view.
- I, <u>Adocus</u> sp. Carapace fragment (RTMP96.79.20) in external view.
- m, <u>Basilemys</u> sp.. Peripheral fragment (unaccesioned specimen) in external view.
- n, Trionychidae gen. indet. Carapace fragment (RTMP96.79.1) in external view.
- o, <u>Naomichelys</u> sp. Carapace fragment (RTMP96.79.44) in external view.















Specimens of Crocodylia and Choristodera

a-b, <u>Leidyosuchus</u> sp.. Teeth in lateral view: **a**, (RTMP96.73.5); **b**, tooth with partial root (RTMP96.73.19).

c-e, Alligatorinae gen. indet. Posterior teeth in lateral view:

c, (RTMP96.73.47); d, (RTMP96.73.43); e, (RTMP96.73.53).

f, cf. Leidyosuchus sp. Scute (RTMP96.74.25) in external view.

g-j, <u>Champsosaurus</u> sp.. Tooth (RTMP96.73.62): g, lateral view.
Jaw element (RTMP96.73.77): h, occlusal view. Trunk vertebra (RTMP96.73.83): i, dorsal; j, lateral view.



Specimens of Ornithischia

a-d, Hadrosauridae gen. indet. Isolated teeth: a, lateral

(RTMP96.83.12); b, occlusal (RTMP96.83.12); c, lateral

(RTMP96.83.14); d, lateral view (RTMP96.83.16) (unworn tooth).

e-f, Ceratopsidae gen. indet. Teeth in lateral view: e,

(RTMP96.83.20); f, (RTMP96.83.21).

g, Nodosauridae gen. indet. Isolated tooth (RTMP96.70.17) in labial view

h-j, Ankylosauridae gen. indet. Isolated teeth: h, labial (RTMP96.70.11); i, labial (RTMP96.70.10); j, lingual view (RTMP96.70.10).

- k-I, Ankylosauria fam. indet. Isolated osteoderm (RTMP96.70.32): k, internal; I, external view.
- m-n, Pachycephalosauridae gen. indet.. Teeth: m, lingual view (RTMP96.70.25) (with root); n, lingual view (RTMP96.70.28).

C b a d 1 e













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Teeth of Theropoda

- a-b, d, <u>Dromaeosaurus</u> <u>albertensis</u>. Premaxillary teeth in lingual view: a,(RTMP96.62.1); b, (RTMP96.62.2). d, marginal (RTMP96.62.3) in lingual view.
- c, e-f, <u>Saurornitholestes langstoni</u>. Lateral view: c, (RTMP96.62.13);
 e, (RTMP96.62.9); f, (RTMP96.62.6).

g-I, Troodon formosus. Lingual view: g, (RTMP96.62.34);

h, (RTMP96.62.60) (premaxillary). i, labial view (RTMP96.62.60).
Lateral view: j, (RTMP96.62.36); k, (RTMP96.62.35);
I, (RTMP96.62.60).



Teeth of Theropoda and Aves

a-g, Richardoestesia. R. gilmorei: Lateral view: a, (RTMP96.62.25);

b, (RTMP96.62.23); **c**, (RTMP96.62.30); **d**, (RTMP96.62.32);

e, (RTMP96.62.64). <u>R</u>. sp.: f, (RTMP96.62.26); g, (RTMP96.62.31).

h-k, <u>Paranychodon lacustris</u>. Lateral view: h, (RTMP96.62.40);
i, (RTMP96.62.42); j, (RTMP96.62.44); k, (RTMP96.62.43).

I, Tyrannosauridae gen. indet. (RTMP96.62.71) in lateral view.

m-n, <u>Aublysodon</u> sp. Isolated premaxillary teeth: m, lingual

(RTMP96.62.48); n, lateral view (RTMP96.62.49).

o-p, Aves gen. indet.. Lateral view: o, (RTMP96.62.55);

p, (RTMP96.62.50).

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Teeth and Jaws of Mammalia

a, e-f, <u>Mesodma antiqua</u>. a, left maxillary fragment with P^1 and P^2 (RTMP96.89.28) in ventral view. Left M₁ in occlusal view:

e, (RTMP96.89.29)); f, (RTMP96.89.26).

b-c, <u>**Cimolomys**</u>. <u>**C**</u>. <u>**clarki**</u> (RTMP96.89.8): **b**, left M¹ in occlusal view.

<u>C</u>. sp. (RTMP96.89.14): **c**, left M² in occlusal view.

d, Cimolomyidae gen. indet. Left M² (RTMP96.89.19) in occlusal view.

h-i, n-p, r, <u>Turgidodon</u>. <u>T. russelli</u>: h, right dentary with P₃ and M₂ (RTMP96.89.41) in lateral view; i right dentary with M₄ (RTMP96.89.42) in lateral view; n, right M³ (RTMP96.89.43); r, left M³ (RTMP96.89.44) in occlusal view. <u>T. praesagus</u>: o, right M² (RTMP96.89.45), p, right M³ (RTMP96.89.46) in occlusal view.

j-m,q, Pediomys. P. clemensi: Left dentaries with M3:

- j, lateral (RTMP96.89.47); k, lateral (RTMP96.89.48); l, occlusal view (RTMP96.89.48). <u>P</u>. sp.: m, of left dentary with M_3 (RTMP96.89.49) in lateral view; q, left M_4 (RTMP96.89.50) in occlusal view.
- s, <u>Paranyctoides</u> <u>sternbergi</u>. Right M² (RTMP96.89.51) in occlusal view.
- t, Eutheria gen. indet.. Left M³ (RTMP96.89.52) in occlusal view.


Chapter 5 Sampling and the Representativeness of Samples

Because of the scant attention that has been given to the problem of sampling and the representativeness of samples in the study of vertebrate microsites, a more detailed evaluation of these matters was undertaken as a part of the current study. "Large" or "sufficient" samples are commonly assumed and emphasized in practice, while those that intuitively appear to be "too small" are rejected for consideration in statistical analysis.

The way in which a "large" sample size can be demonstrated to be sufficiently representative of a microfossil site requires investigation as it has important implications for the appropriate quantitative comparison of samples taken from different localities.

Consideration of sampling and its representativeness of taxonomic diversity and abundance in vertebrate microsites, is undertaken in a three-fold manner in this chapter. First, a test of repeatability of samples in the process of sampling is performed and discussed. Second, representation of taxonomic diversity of samples is tested. Finally, consideration is given to how a minimal quantity of raw sediment is assessed to ensure that a representative sample results.

5.1 Sampling: Test of Repeatability

Repeatability of sampling from a microsite is essential to ensure that samples are representative of that site. Furthermore, it is imperative that the comparisons of abundance of taxa between different microsites do not reflect sampling artifacts due to insufficiently large samples having been examined, rather than real differences or similarities of abundance of taxa. That samples from vertebrate microfossil sites are highly repeatable has heretofore been assumed, but tests of such an assumption have not been attempted to date on such material. Such tests necessitate laborious sampling procedures. To test for the representativeness of samples in this study, three independent samples from microsite WS (from the lower unit of the Oldman Formation) were examined.

The first sample was taken during the 1994 field season, with 20 bags of matrix (20 kg per bag) collected. This sample was screenwashed and sorted by the author.

The second sample, which consisted of 10 bags of matrix (20 kg per bag), was taken by D. Brinkman of the Royal Tyrrell Museum of Palaeontology in the 1990 field season. The sample was subsequently screenwashed and sorted before the current research project started.

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The third sample was assessed based upon surface-collecting of the same microsite during the 1993 field season. During surface-collecting, only specimens which were exposed and visible on the surface of the microsite were collected. Thus, no sediment matrix was collected.

The first and second samples were both screenwashed, but they were collected and processed by different researchers and at different times. Thus, they can be treated as independent samples, as can the surface-collecting sample which was subjected to a totally different sampling procedure. The abundance data retrieved from these three samples are presented in Table 5.1a.

In order to examine the potential of the three samples to reveal both the distribution and abundance of taxa, taxon-abundance histograms were first constructed for each (Fig. 5.1). The first sample was used as a reference because it contained the largest number of specimens.

A non-parametric test, known as the Kolmogorov-Smirnov (K-S) test, was employed to determine the probability that the three samples were drawn from the same population (i.e. to test if the three samples reflect the same distribution of taxonomic abundance within the same microsite). Due to the difference in the number of specimens retrieved in the three samples, the K-S test was applied to data transformed to relative abundance of taxa (Table 5.1b).

Таха	Surface-collected Sample	Screenwashed (this study)	Screenwashed [Brinkman(1990)]
Myledaphus	0	9	4
Hybodus	0	0	0
Acipenser	0	0	0
Belonostomus	0	11	1
Atractosteus	114	404	172
Amia	4	11	14
holostean A	0	138	28
holostean b	0	25	2
Paralbula	0	16	3
escoids	0	15	1
Coriop	0	35	1
teleost D	1	28	17
teleost indet.	1	225	10
Opistotriton	0	38	2
Scapherpeton	0	216	50
frogs	0	75	4
Leidyosuchus	9	82	33
Champsosaurus	6	214	11
trionychids	13	14	6
baenids	1	0	0
chelydrids	4	5	21
Adocus	2	8	2
Basilemys	11	1	7
hadrosaur	9	61	28
ankylosaur	1	0	1
small theropods	4	9	2
tyrannosaurids	0	3	4
ceratopsians	1	8	5
lizards	0	49	16
mam mais	0	6	4
Total	181	1706	449

TABLE 5.1a Data on the vertebrate microfossil assemblage of the WS site as compiled from three different samples. Counts indicate the numbers of identifiable elements.

TABLE 5.1b Data on the vertebrate microfossil assemblage of the WS site as compiled from three different samples. Numbers indicate the relative abundance of taxa in precentage.

Taxa	Surface-collected Sample	Screenwashed (this study)	Screenwashed [Brinkman(1990)]
Myledaphus	0.00	0.53	0.89
Hybodus	0.00	0.00	0.00
Acipenser	0.00	0.00	0.00
Belonostomus	0.00	0.64	0.22
Atractosteus	62.98	23.68	38.31
Amia	2.21	0.64	3.12
holostean A	0.00	8.0 9	6.24
holostean b	0.00	1.47	0.45
Paralbula	0.00	0.94	0.67
escoids	0.00	0.88	0.22
Coriop	0.00	2.05	0.22
teleost D	0.55	1.64	3.79
teleost indet.	0.55	13.1 9	2.23
Opistotriton	0.00	2.23	0.45
Scapherpeton	0.00	12.66	11.14
frogs	0.00	4.40	0.89
Leidyosuchus	4.97	4.81	7.35
Champsosaurus	3.31	12.54	2.45
trionychids	7.18	0.82	1.34
baenids	0.55	0.00	0.00
chelydrids	2.21	0.2 9	4.68
Adocus	1.10	0.47	0.45
Basilemys	6.08	0.06	1.56
hadrosaur	4.97	3.58	6.24
ankylosaur	0.55	0.00	0.22
small theropods	2.21	0.53	0.45
tyrannosaurids	0.00	0.18	0.89
ceratopsians	0.55	0.47	1.11
lizards	0.00	2.87	3.56
mammals	0.00	0.35	0.89
Total	100%	100%	100%



Fig. 5.1. Bar charts showing distribution of taxa within and among three different samples of the vertebrate assemblage from the WS site. Sample 1 (the largest) was used as a reference sample and all other samples are plotted against its axes.

The results (Table 5.2) indicate that the two screenwashed samples are not significantly different from each other in their distributions of the relative abundance of taxa. In contrast, the surface-collected sample is significantly different in distribution of relative abundance of taxa from the two screenwashed samples.

TABLE 5.2. Results of Kolmogorov-Smirnov tests for similarity among the three independent samples from the WS site. Top number represents maximum difference for pairs of samples; bottom number represents two-sided probability that samples came from the same distribution.

	Sample 1	Sample 2	Sample 3
Sample 1	<u>0.000</u> 1.000		
Sample 2	<u>0.143</u> 0.899	<u>0.000</u> 1.000	
Sample 3	<u>0.429</u> 0.008	<u>0.357</u> 0.042	<u>0.000</u> 1.000

This result reinforces the assumption that both screenwashed samples are representative of the real relative abundance of taxa. The difference in the number of specimens retrieved from these two samples seems to have resulted from the different amounts (200 kg vs 400 kg) of matrix that were collected and processed, as well as because a finer screen was used during the screenwashing of the first sample, permitting retention of very small specimens. Both samples, however, were adequate enough to represent the taxonomic diversity and relative abundance of taxa in the vertebrate microfossil assemblage.

The significantly different sample that was accumulated as a result of surface-collecting evidently reflects the strong biases that are inherent in this sampling procedure, as discussed in Chapter 3. Examination of this sample clearly reveals that the collection was strongly biased toward large specimens, such as turtle shell fragments and champsosaur vertebrae, and toward specimens that have distinctive forms and are easily spotted, such as theropod teeth and crocodile teeth and scutes. In contrast, the collection was biased against small specimens, such as small champsosaur teeth, fish vertebrae, and salamander and frog fragments. This further supports the suggestion in Chapter 3 that surface-collected samples of microsites are evidently inappropriate for the compilation of abundance data and that they should not be subjected to the same statistical analysis, due to the aforementioned sampling biases.

Given the results outlined above, it is concluded that the method of sampling employed in this study is adequate to reveal appropriate relative abundance data, which allows for the effective comparison of samples taken from different microsites. 5.2 Testing of Taxonomic Completeness Of Samples

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A sufficient sample from a microsite should contain specimens that reflect the taxonomic complement of that microsite. In other words, a question that should be addressed is: how well or to what extent do the taxa recovered from a sample represent the original proportion of taxa in a microsite?

An approach to community analysis that is applied to modern ecological studies, the maximum likelihood method, developed by Cohen (1959, 1961), was employed here to evaluate whether or not a sample is taxonomically representative of a source assemblage. This statistical approach was essentially devised to estimate the total number of taxa in a community, including rare taxa not yet collected, when the taxonomic abundance distribution is lognormal (Krebs, 1989).

If the distribution of taxon abundance of a microsite is lognormal, then the microfossil assemblage in the locality can be assumed to have a structure similar to a lognormally-distributed community. Thus, this approach can be useful in assessing the representativeness of taxa for a sample from a microsite.

According to Krebs (1989), the lognormal distribution of a data set can be generally recognized by the use of a Whittaker plot (Fig. 5.2). The Whittaker plot is a taxon-abundance curve, in which the x axis represents the

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FIGURE 5.2 Theoretical Whittaker plot of taxa abundance data showing two different distributions: logarithmic series (producing a nearly straight line), and lognormal (predicting a reverse S-shaped curve). (from Krebs, 1989).

ranks of n taxa from 1 (the most abundant taxon) to n (the least abundant taxon). This is plotted against the y axis, which reflects the relative abundance of taxa on a log scale. In a Whittaker plot, a lognormal distribution produces a reverse S-shaped curve, which is different from the logarithmic series which is graphed as a straight line.

A lognormal distribution of a variable is defined as that distribution in which the logarithm of the variable is normally distributed (Parkin and Robinson, 1992). The goodness-of-fit of the lognormal distribution to the data of relative abundance of taxa from a microsite can be tested by performing the Lilliefors test (Wilkinson, 1990), after the data are log transformed.

Data for each microsite were recompiled first by excluding taxa that are absent from that site, and the remaining taxa were subsequently rank-ordered on the basis of their relative abundance. A plot of the data for each microsite was then generated, using SYSTAT 5.05 for Windows. The resulting plots appear to conform, in general, to what would be expected for lognormal curves for all of the data (Figs. 5.3a-e).

Lilliefors goodness-of-fit tests were performed on the log-transformed data to detect departures from normality. These tests can be used as tests of lognormality for original data (Parkin and Robinson, 1992). The test results, presented in Table 5.3, reveal that no distribution is significantly different from the lognormal distribution.



including PHR-1, PHR-2, SPS and WS. The curves exhibit lognormal series (see discussion in text).



including Ho S, EZ, PHR93-2 and Sal S. The curves exhibit lognormal series (see discussion in text). FIGURE 5.3b Whittaker plots of abundance data from vertebrate microsites in the Milk River area,





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including CN-1, CN-2, CBC and RDS. The curves exhibit lognormal series (see discussion in text). FIGURE 5.3d Whittaker plots of abundance data from vertebrate microsites in the Milk River area,



FIGURE 5.3e Whittaker plots of abundance data from vertebrate microsites in the Milk River area, including ORS, CCS and PLS. The curves exhibit lognormal series (see discussion in text). 182

TABLE 5.3. Result of Lilliefors goodness-of-fit test on the log-transformed data, showing difference from normal distribution. Maxdif,maximum difference between a observed distribution and a normal distribution;Lilliefors probability (2-tail), two-tailed probability that an observed distributionis insignificantly different from a normal distribution.

Variable	N-Of-Cases	Maxdif	Lilliefors Probability (2-Tail)
PHR1	39.000	0.143	0.142
PHR2	44.000	0.144	0.123
SPS	33.000	0.104	0.466
HOS	31.000	0.121	0.282
WS	35.000	0.124	0.187
ΕZ	32.000	0.131	0.168
PHR93-2	29.000	0.088	0.886
CS	33.000	0.119	0.265
PHS	29.000	0.119	0.363
SAL S	27.000	0.100	0.715
HAS	32.000	0.151	0.062
HS	30.000	0.135	0.172
CN1	29.000	0.114	0.426
CN2	27.000	0.164	0.062
ORS	32.000	0.148	0.074
CBC	28.000	0.098	0.716
RDS	31.000	0.116	0.341
BMC	22.000	0.104	0.855
PLS	29.000	0.115	0.422

Following the confirmation of the lognormal distribution of the data, Cohen's maximum likelihood methods were applied to the relative abundance data in order to estimate the representation of the number of taxa recovered from each microsite. The general calculating procedure of Cohen's methods, as provided by Krebs (1989), is outlined briefly as follows:

1). Calculate the mean (X) and variance (S^2) of the log-transformed abundance of taxon *i* (x_i). The observed (recovered) number of taxa (S_r) is treated as the sample size.

2). Calculate parameter y:

$$y = S^2 / (X - X_0)^2$$

where y= the parameter of lognormal distribution

 $X_0 = \log(0.5) = -0.30103$ (log10 is used)

3). Correction factor \emptyset corresponding to the parameter of lognormal distribution (y) can be obtained (Krebs, 1989, p. 354, Table 10.5).

4). Calculate corrected estimates of the mean and variance of the lognormal distribution from the equations

$$\hat{u} = X - \mathcal{O}(X - X_0)$$
$$\hat{o}^2 = S^2 + \mathcal{O}(X - X_0)^2$$

where \hat{u} = estimate of the true mean of the lognormal

distribution;

 \hat{o}^2 =estimate of the true variance of the lognormal

distribution

5). Calculate the standardized normal deviate Z from the following equation:

$$Z = (X_0 - \hat{u}) / \hat{o};$$

and then get the corresponding probability (p) of the Z from the standard normal distribution. Finally, the estimated number of taxa (S_e) in a microsite can be calculated using the following formula:

$$S_r = S_e * (1-p)$$

where S_e = estimate of the number of taxa in a microsite

assemblage;

S_r= recovered (observed) number of taxa in a

sample

The results of the above analyses for all the microsites examined in this study are presented in Table 5.4, which demonstrates that the taxa recovered from all the samples taken represent a significant proportion of the original vertebrate assemblages of the microsites examined in this study.

TABLE 5.4. Proportions (in percentage) of recovered taxa relative to the estimated taxa from microsites of the Judith River Group in Milk River area.

PHR-1	PHR-2	SPS	Ho S	ws	ĒZ	PHR93-2
0.956	0.980	0.957	0.960	0.967	0.965	0.973
CS	PHS	Sal S	HAS	HS	CN-1	
0.964	0.971	0.957	0.977	0.969	0.960	
CN-2	ORS	СВС	RDS	BMC	PLS	
0.965	0.967	0.972	0.974	0.978	0.970	

5.3 Estimating the Minimal Volume of Sediment for a Representative Sample

Subsequent to the demonstration that a sample from a microsite is representative and that the specimens of fossil vertebrates recovered are taxonomically representative of that microsite, it is necessary to determine the minimal volume of sediment needed to obtain a representative sample. This can be estimated by the use of a multiple subsampling procedure. An extensively collected microsite, Michael's site, from the Milk River Formation of southern Alberta, was used as an example by subjecting it to the following analysis.

About 454 kg of sediment was collected from this microsite. This sample was screenwashed, yielding approximately 7.6 kg of concentrate. Prior to specimen sorting, the extracted concentrate was subdivided into nine equal subsamples (0.83 kg each). The subsamples were then arranged in random order, and labeled accordingly. These subsamples were then each sorted sequentially. Identified vertebrate elements were stored separately from those of other subsamples. Numbers of new taxa recovered from each subsample were recorded cumulatively during the course of sorting and identification.

The cumulative count of taxa from each subsample was then plotted against the cumulative mass of the nine subsamples. The resultant curve is similar to a rarefaction curve (Fig. 5.4). The total number of taxa recovered from the microsite is 22, based on the known extensive collections. This number of taxa was reached during the sorting of the seventh subsample. Further sorting of subsequent subsamples resulted in no additional new taxa being recovered.

Thus, it can be stated that the last subsample (the seventh) yielding a new taxon represents the minimal cumulative sample that is required to be representative of the site. As portrayed by the curve (Fig.5.4), the total number of taxa (22) corresponds with the point for the seventh subsample, at which point the cumulative mass of concentrate was 5.81 kg. Thus, the minimum amount of sediments excavated from the microsite required to reveal 22 taxa can be estimated as follows:

(5.81 / 7.6) x 454 = 351.25 kg

This result confirms that the 454 kg of sediment collected from Michael's site was adequate enough to be representative of the taxonomic diversity and abundance at the site. Nevertheless, the intention of this analysis was to present one way that could lead to the assessment of minimal volume of sediment for a representative sample from a microsite. The estimated minimal volume of sediment (351.25 kg) is, under no circumstance, widely applicable to other microsites, but it could serve as a reference volume when other microsites are sampled.



FIGURE 5.4 A plot showing the cumulative number of taxa recovered with cumulative mass of subsamples for Michael's site. The dashed line indicates the point of cumulative subsamples where all the 22 taxa are included.

In summary, it is of fundamental importance to test the representative nature of samples collected from vertebrate microsites before further comparisons with other microfossil assemblages are performed. The maximum likelihood method may provide a useful tool for the analysis of vertebrate microfossil assemblages, although the lognormal distribution of the taxa within a microfossil assemblage has still to be demonstrated. Equally, repeated sampling may provide an important means of estimating the minimal volume of sediment that provides exhaustive coverage of fossil taxa from a given microfossil locality.

Chapter 6 Sedimentological and Taphonomic Examination of the Vertebrate Microfossil Localities Sampled in This Study

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Sedimentological and taphonomic information has been considered crucial for palaeoecological analysis (e.g. Behrensmeyer, 1990; Brinkman, 1990; Blob and Fiorillo, 1996). The sedimentological investigation provides essential information for understanding the palaeoenvironments in which animals lived, died, and were buried. This information is also crucial for understanding how biotic and abiotic components of the original ecosystems interacted with one another (e.g. Eberth, 1990; Behrensmeyer and Hook, 1992). The taphonomic information provides the means to document potential biases that may have occurred during the process of preservation of a fossil assemblage. Such taphonomic biases can strongly affect palaeoecological data and the reconstruction of the original ecological associations. For instance, Badgley (1986) suggested that different counting methods should be applied for estimating taxonomic abundance of fossil assemblages in accordance with different taphonomic biases (details see Chapter 3); Blob and Fiorillo (1996) demonstrated that different size-sorting due to taphonomic biases can result in biased representation of vertebrate fossil assemblages (for further discussion see Chapter 7).

Sedimentological and taphonomic studies of vertebrate microfossil localities in DPP by Eberth (1990) (see review in Chapter 2) have provided a framework for the investigation of the vertebrate microfossil localities sampled in this study. The host sediments of the 19 microsites examined in this study were examined in the field by Drs. D. A. Eberth and D. B. Brinkman of the Royal Tyrrell Museum of Palaeontology, upon which the following sedimentological interpretations of the microsites are based. The sedimentological and taphonomic descriptions of the microsites as they appear in the unpublished field notes of D. A. Eberth (1997) are reproduced in Appendix III.

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In this chapter, sedimentological and taphonomic interpretations of these sites are provided, along with comparisons among the sites themselves, and also with those from DPP.

6.1 Sedimentological and Taphonomic Interpretations of the Vertebrate Microfossil localities in the Milk River Area

Eberth (1997 pers. comm.) concluded that 17 of the 19 microsites examined in this study are associated with one of two sedimentary facies, inchannel and splay deposits, similar to those recognized by Eberth (1990) in DPP. Two microsites (PHR-1 and PHR-2) are interpreted as being associated with shoreface deposits, which are different from those of the other microsites. Table 6.1 summaries the sedimentary facies associations of these 19 microsites.

	RTMP locality no.	Common name	Sedimentary facies association
/	n-channel deposits		
	L1130	PLS	Palaeochannel lag
	L1140	RDS	Palaeochannel lag
	L1133	PHR93-2	Lateral accretion
	L1126	Ho S	Lateral accretion
	L1123	SPS	Lateral accretion
	Splays deposits		
	L1131	HAS	Crevasse splay
	L1141	BMC	Crevasse channel
	L1135	Sal S	Crevasse splay
	L1137	CN-1	Crevasse splay
	L1136	CN- 2	Crevasse splay
	L1132	HS	Crevasse splay
	L1134	CS	Crevasse splay
	L1139	CBC	Crevasse splay
	L1138	ORS	Crevasse splay
	L1129	PHS	Crevasse splay
	L1128	EZ	Crevasse splay
	L1127	WS	Crevasse splay
ing ang a sa tao tao tao tao tao tao tao tao tao ta	Shoreface deposits		
	L1124	PHR-1	Regressive lag
	L1125	PHR-2	Regressive lag

TABLE 6.1 Sedimentary facies associations of the nineteen vertebrate microfossil localities of the Foremost and Oldman formations in the Milk River area of southern Alberta.

Among the sites that are associated with in-channel deposits, RDS, PLS and PHR93-2 are associated with palaeochannel lags. RDS and PLS show similar sedimentary and taphonomic features in that both host lithosomes comprise medium to large scale trough cross-stratified sandstones, and both exhibit the presence of abundant, fragmentary-to-complete valves of unionids. The presence of articulated unionid valves in both sites suggests that the unionid material experienced relatively short distance transportation. Ho S and SPS are similar to one another in regard to their association, with lateral accretion and in the presence of small shell fragments of gastropods and pisidiids. Vertebrate microfossils in PHR93-2 were produced from a transition from trough cross-stratified sandstone to inclined heterolithic stratification, suggesting that they were deposited on lateral accretion surfaces. PHR93-2 is, however, different from the others in the conspicuous absence of invertebrate shell material.

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The microsites that are associated with crevasse splay deposits (Table 6.1, Appendix III) are similar in their general sedimentological and taphonomic features to those of DPP that were documented by Eberth (1990). For instance, the sedimentary structures of the host lithosome are only locally developed, and are often dominated by graded, horizontally-laminated sediments. All these sites, except for BMC, exhibit sharp, flat bases, a non-channelized geometry, and are commonly associated with aquatic invertebrate assemblages, including shell fragments of unionids, pisidiids and gastropods.

As pointed out by Eberth (1990), unionids are generally regarded as having been inhabitants of well-oxygenated, slow-to-fast-moving aquatic environments such as rivers, while pisidiids are quiet water forms inhabiting ephemeral to perennial standing water environments, such as floodplain ponds.

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Differences in invertebrate assemblages preserved with the vertebrate microfossils are noticeable among these microsites. For example, PHS, EZ, CN-2, CBC, SAS, HS and CS are similar to one another in the presence of both unionid and pisidiid shell fragments, while HAS, ORS, WS and CN-1 exhibit a conspicuous absence of unionid material, with their invertebrate assemblages being dominated by pisidiids. BMC is distinctively different from the others in the absence of invertebrate shell material and in that its host lithosome exhibits a lenticular geometry (Appendix III). Because of this, it is suggested that BMC formed in a levee area as a crevasse channel deposit (Eberth, 1997, pers comm.).

PHR-1 and PHR-2 are interpreted as being associated with shoreface deposits, in which vertebrate microfossil remains are concentrated at a regressive erosional surface (Appendix III). Both sites occur at the base of a massive sandstone, which sits sharply on the fourth parasequence of the middle (mudstone) succession (Kwasniowski, 1993). Vertebrate fossils from PHR-1 and PHR-2 comprise remains of both marine (such as sharks) and nonmarine (such as amphibians and lizards) environments (see Chapter 4). Nevertheless, PHR-2 differs from PHR-1 in that the former site has abundant invertebrate shell fragments, while in the latter site such elements are very rare. Although these two sites show a distinctly different facies association from those of the other microsites examined in this study, the teeth and skeletal remains of vertebrates yielded from PHR-1 and PHR-2 exhibit taphonomic features that are generally similar to those from others. For instance, the size frequency distribution of vertebrate microfossils is not different from those of other sites (see discussion in Chapter 7). The vertebrate microfossil elements, in general, exhibit a degree of abrasion similar to those of other microsites. The presence of delicate fish centra and jaw elements, and small mammal jaw elements in PHR-1 and PHR-2 suggests that the vertebrate concentrations experienced transportation over only short distances.

Thus, it is suggested, based upon the aforementioned observations, that the sedimentological and taphonomic framework of the vertebrate microsites in DPP is essentially similar to the vertebrate microsites examined in this study (Eberth, 1997, pers comm.). Furthermore, it is assumed that these vertebrate microfossil assemblages contain taxa that were of generally local origin, and that stratigraphic variation in relative abundance of the taxa reflects real differences in relative abundance of the taxa in the area over the depositional time period.

The assumptions that the microsites, although preserved in different sedimentary facies, were subjected to similar taphonomic processes are

supported by examination of the following taphonomic characteristics of the vertebrate microfossil remains from the sites in this study:

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- the compositions of teeth and skeletal elements recovered from the microsites are very similar to those of the microsites in DPP, typically comprising small teeth, scales, and centra;
- the co-occurrence of elements that are delicate and less physicochemically resistant, such as fragile teleost centra and dinosaur eggshell;
- 3) in some cases taxa that had generally similar life styles and that are represented by elements that are similar in size, shape and texture, exhibit different stratigraphic distribution among microsites. They include holostean A and holostean B, <u>Troodon</u> and other small theropods, hadrosaurid and ceratopsian remains, different types of teleosts, and the two different types of <u>Myledaphus</u> teeth. In these cases, the differences in distribution cannot be attributed to taphonomic processes but are better attributable to differences in the biology of the animals. Such similar taphonomic features are also indicated by Brinkman (1990) in the microsites of DPP.
- vertebrate microfossil assemblages from splay deposits are often associated with invertebrate remains, such as pisidiid clams, which were not transported over great distances. This is very similar to assemblages found in DPP (see discussion above);

The sedimentology of the vertebrate microfossil sites examined in this study shows great similarities to that of the microsites in DPP, in their strong association with two basic sedimentary facies. The vertebrate microfossils from the microsites in this study and those of DPP are demonstrated above to share taphonomic characteristics. Such sedimentological and taphonomic patterns of vertebrate microsites recur through the Judith River Group in southern Alberta. This forms the basis for a later discussion of the palaeoecology of the vertebrate microfossil assemblages examined in this study in terms of comparisons with those of DPP. Behrensmeyer (1991: p.327) pointed out that "recurring patterns of preservation indicate that the vertebrate record is more structured than random in its sampling of faunas through time", and that this provides "a more reliable basis for assessing the effects of taphonomic processes on the palaeocommunity strucures".

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Chapter 7 Possible Palaeoecological Interpretations Of The Vertebrate Microfossil Assemblages

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Two basic and important sets of information about each vertebrate microfossil assemblage—its taxonomic composition and the relative abundance of the included taxa—have been documented respectively in Chapters 4 (taxonomic identification) and in 3 (quantification of specimens). These parameters allow for the analysis of the vertebrate microfossil assemblages and comparisons among them, in order to further test palaeoecologic inferences. In this chapter, the vertebrate microfossil assemblages recovered from nineteen microsites are first compared on the basis of their taxonomic composition and the relative abundance of taxa, in order to identify similarities and differences and to reveal potential patterns. Possible palaeoecologic correlates that may be responsible for the recognized patterns among the assemblages are then explored.

7.1 Comparison Of Vertebrate Microfossil Assemblages

The taxonomic composition and relative abundance of taxa for the vertebrate microfossil assemblages are summarized in Appendix II. While all the assemblages display high taxonomic diversity, different degrees of diversity are evident. For instance, the assemblage with the highest diversity (PHR-2)

yielded 48 taxa, whereas that with the lowest diversity (BMC) yielded only 32. Each assemblage is also characterized by its dominant taxa (those that are most abundant). For example, <u>Myledaphus</u>, <u>Paralbula</u> and <u>Atractosteus</u> are the most abundant taxa retrieved from PHR-2, whereas the BMC site has as its most abundant taxa in <u>Scapherpeton</u> and Anura indet.. To examine overall differences and similarities among all of the included assemblages, a multivariate statistical approach, cluster analysis, was employed.

Cluster analysis has been widely applied in palaeoecological studies, particularly in the context of community analysis (e.g. Mello and Buzas, 1968; Orloci, 1978; McKinney and Zachas, 1986; Kovach, 1989; Oboh, 1992). This statistical method is essentially a classificatory technique, the main purpose of which is to divide the variables of the study into discrete groups based upon their similarity or dissimilarity (Pielou, 1984; Davis, 1986; Romesburg, 1990). Here, vertebrate assemblages are compared on the basis of their taxonomic composition and their relative abundance of taxa. As a result, those assemblages that are relatively similar are clustered together, and this allows for patterns to be summarized. Such analysis is often known as Q-mode analysis in ecological studies (Jones, 1988; Dodd and Stanton, 1990).

A variety of different clustering methods and similarity or distance measures are available for use on such data (e.g. Wishart, 1978; Pielou, 1984; Jones, 1988). After careful examination of the commonly-used combinations of clustering methods and similarity measures on a set of fossil plant data, Kovach (1989) demonstrated that the average linkage clustering method, when used with the Spearman Rank Order Correlation Coefficient, is the most suitable for palaeoecologic data, which are typically non-normally distributed and have the potential for "noisiness" (i.e. possible randomness of occurrence of rare taxa). He suggested that the choice of similarity measure for palaeoecologic data must allow for the noise which taphonomic processes, such as differences in size sorting and transportation, impose on the data. The data set from the vertebrate microfossil assemblages in the present study, as discussed in Chapter 3, exhibits similar properties to those described by Kovach (1989).

Furthermore, Brinkman (1990), in a palaeoecologic study of vertebrate microfossil assemblages from DPP, suggested that the rank-order serves as a better relative abundance measure than percentage representation for such data. He employed the Spearman Rank Order Correlation Coefficient as a measure in order to determine the significant changes in relative abundance of taxa in their stratigraphic distributions throughout the section in DPP.

Cluster analysis is herein applied to the vertebrate microfossil assemblages recovered from 19 microsites in the Milk River region, using the Spearman Rank Order Correlation Coefficient as a distance measure, and the Average Linkage clustering method. The microsites were compared and clustered on the basis of taxonomic composition and relative abundance of

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taxa. The statistical analysis was performed using the computer software SPSS for Windows (Release 6.0).

Cluster analysis resulted in a dendrogram (Fig. 7.1). Three major groupings are distinguishable among the nineteen sites: Group I (PHR1, PHR2), Group II (PHS, EZ, HOS, PHR93.2, and WS), and Group III (PLS, RDS, BMC, ORS, CN2, CS, CBC, CN1, Sal S, HS, and HAS). Dodd and Stanton (1990) suggested that each of the resultant groupings from a Q-mode analysis represent a homogeneous group, because the average similarity value for sites within a group is greater than the average similarity value between sites in different groups.

The homogeneity of the groupings of sites is further reinforced by the fact that they are, in general, reflective of their location in the stratigraphic section. Group I comprises the sites from the base of the upper unit of the Foremost Formation; Group II includes all the sites from the uppermost Foremost Formation and the lower unit of the Oldman Formation; and Group III consists of all sites from the upper portion of the Comrey and the upper unit of the Oldman Formation.

What are the major factors that contribute to the similarities and differences of these vertebrate microfossil assemblages, and that result in the distinctive grouping of sites? The major possibilities that have been commonly raised and discussed in palaeoecologic studies are addressed below.






- The groupings among the microsites are primarily related to different taphonomic processes. Blob and Fiorillo (1996) suggested that even vertebrate microsites that are associated with the same sedimentary processes may be subjected to different degrees of size-sorting. As a result of such taphonomic processes, vertebrate assemblages could be biased differently in their taxonomic composition and relative abundance of taxa.
- 2) The groupings of microsites essentially reflect the similarities or differences between vertebrate assemblages produced by similar or different small, local-scale habitats in the Milk River region during the Campanian. To illustrate, microsites clustered in the same group may represent those that are strongly associated with similar or the same sedimentary facies, while those in a different group may be the resultant products of different sedimentary facies. Certain sedimentary facies are usually correlated with certain local habitats, such as river-associated channel sediments and floodplainassociated crevasse splays.
- 3) Modifications of taxonomic compositions through speciation, extinction and immigration events, may be contributory factors that result in the differences of vertebrate assemblages and consequently affect the groupings of the microsites. According to Eberth and

Hamblin (1993), the Judith River Group in the study area is of middle to late Campanian age and the deposition of the section (about 230 m thick) spanned approximately 5 Million years (75-80 Ma).

4) The groupings of the microsites may represent local environmental shifts in the region during the Campanian. As reviewed in Chapter 2, geological evidence indicates that marine transpression and regression strongly affected depositional environments during the Late Cretaceous in southern Alberta. By way of illustration, the depositional environment of the Foremost Formation has been considered to be strongly associated with marine coastal areas (Ogunyomi and Hills 1977; Kwasniowski, 1993). The coastal environment then shifted to a primarily freshwater fluvial inland environment in the overlying Oldman Formation. Such regional palaeoenvironmental fluctuations through time would likely affect the vertebrate assemblages in terms of both taxonomic composition and the relative abundance of taxa. Brinkman (1990) showed that the patterns of vertebrate microfossils as related to their stratigraphic distribution in DPP are reflective of depositional environmental changes through time in the region, and the regional ecological zonation of vertebrate communities.

These factors can independently or jointly contribute to the formation of a vertebrate microfossil assemblage. Thus, it is essential to carefully examine

these factors if further palaeoecologic extrapolations are to be made. Each of the factors will be investigated in the following sections to determine which role, and to what extent, each played in affecting the aforementioned distinctive patterns among the vertebrate microfossil assemblages retrieved from the microsites examined in this study.

7.2 Potential Taphonomic Biases: Size-Sorting Of Vertebrate Microfossils

Blob and Fiorillo (1996) demonstrated that the size frequency distribution of vertebrate microfossil concentrates may vary among sites, even those occurring in the same sedimentary facies. This variability was interpreted as being due to quantitative differences in sedimentary processes, such as different degrees of size-sorting. The authors indicated that such variations in size frequency distributions of specimens could result in biases in the relative abundance of taxa and taxonomic compositions recovered from microsites and that taphonomic, rather than biotic, agencies may be primarily responsible. Two localities yielding vertebrate microfossils from the Upper Cretaceous Judith River Formation of south-central Montana were used as examples to illustrate this. One locality was shown to yield vertebrate remains strongly biased towards small specimens, resulting in an underestimation of taxa that are often represented by large sized specimens, such as turtles; conversely, the other was biased towards large specimens and will thus underrepresent taxa normally represented by small specimens.

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During their analysis, Blob and Fiorillo (1996) examined only the diagnostic (i.e. identified) specimens in revealing the differences in the size frequency distribution of specimens. Nevertheless, they admitted that using the identified specimens caused a 'complication' in their analysis, because certain vertebrate fossils are often represented only by remains of characteristic sizes and shapes. For instance, Myledaphus is predominantly represented by small teeth, and turtles are mainly represented by comparatively large shell fragments. If turtles were more abundant in the original assemblage, the fossil assemblage would have more large elements. To mitigate such problems, the authors suggested that non-diagnostic (unidentified) specimens be used to "determine the fossil size and shape profiles of sites instead of diagnostic specimens"; and that "if profiles based on the non-diagnostic specimens were sufficiently similar, then taphonomic explanations for faunal differences among the sites could be rejected" (Blob and Fiorillo, 1996; p. 431).

In the present study, vertebrate fossils, including both identified and unidentified, were sorted and retained during sampling. Unidentified specimens were utilized to examine and test the possible differences in size frequency distributions among the aforementioned 19 microsites, in order to determine whether or not different taphonomic processes could produce significantly different degrees of size sorting.

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The size profiles of unidentified specimens are presented in Table 7.1a. Specimens less than 10 mm were sorted at increments of 1 mm via the use of American Standard sieves. For instance, specimens screened through a 1 mm sieve size were considered to be in the range of 0—1 mm, and those trapped between 1 mm and 2 mm sieves were within the range of 1—2 mm. Those specimens greater than 10 mm were sorted with metal screens at increments of 10 mm. It was noted that specimens greater than 10 mm comprise a small proportion of the samples, with the exception of the BMC site (Table 7.1b).

Specimens recovered from the microsites examined in this study are predominantly smaller than 10 mm in size (see Table 7.1b). The size profiles of samples of unidentified specimens are further demonstrated by the plots of size frequency distributions for each microsite (Figs. 7.2a-d). For all the sites, except BMC, the size distributions are evidently skewed toward the size range of 1—5 mm, each with a mode of 1—2 mm (BMC: mode 3—4 mm). Non-parametric Kolmogorov-Smirnov tests were applied in the comparison of these size frequency distributions. The results are summarized in Table 7.3. The null hypothesis that the size frequency distributions among the sites are not significantly different from each other can not be rejected at the significance level of 0.05.

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Sieve(mm)	PHR-1	PHR-2	SPS	Ho S	MS	EZ	PHR93-2	cs	SHd	Sal S	HAS	HS	CN1	CN2	ORS	СВС	RDS	ccs	PLS
>30	16	ю	4	5	7	5	ю	7	0	4	с У	2	Ν	ю	.	5	0	17	9
2030	36	9	5	13	14	Ω	19	9	7	5	S	15	24	9	11	15	9	51	15
1020	125	47	27	40	38	16	30	23	16	38	26	33	49	24	41	66	21	105	86
510	1333	282	85	131	148	104	165	82	43	96	164	183	100	87	155	181	98	144	140
45	736	511	201	203	328	110	134	113	98	121	245	185	143	65	156	199	144	126	151
3-4	1215	705	332	312	392	173	241	126	112	136	272	366	221	118	216	334	181	168	210
23	1682	921	462	506	462	242	322	139	124	148	299	549	301	171	278	461	218	104	247
12	3248	6304	1966	1669	1412	1206	1693	392	284	826	1531	1487	1645	518	2406	1862	689	102	612
01	136	829	645	102	495	128	556	131	119	248	198	401	621	106	511	533	176	16	232
Total	9130	9608	3727	2978	3291	1986	3163	1014	803	1621	2745	3221	3106	1098	3775	3656	1533	833	1699

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Sieve (mm)	PHR-1	PHR-2	SPS	Но S	MS	EZ PH	IR93-2	CS	SHG	Sal S	HAS	H	CN1 (CN2	ORS	CBC	RDS	BMC	PLS
>30	0.18	0.03	0.11	0.07	0.06	0.10	0.09	0.20	0.00	0.25	0.18	0.06	0.06 (0.27	0.03	0.14	0.00	2.04	0.35
2030	0.43	0.06	0.13	0.44	0.43	0.25	0.60	0.59	0.87	0.31	0.18	0.47	0.77 (J.55	0.29	0.41	0.39	6.12	0.88
1020	1.37	0.49	0.72	1.34	1.15	0.81	0.95	2.27	1.99	2.34	0.95	1.02	1.58	2.19	1.09	1.81	1.37	12.61	5.06
510	14.60	2.94	2.28	4.40	4.50	5.24	5.22	8,09	5.35	5.86	5.97	5.68	3.22	7.92	4.11	4.95	6.39	17.29	8.24
45	8.06	5.32	5.39	6.82	9.97	5.54	4.24	11.14	12.20	7.46	8.93	5.74	4.60 5	5.92	4.13	5.44	9.39	15.13	8.89
34	13.31	7.34	8.91	10.48	11.91	8.71	7.62	12.43	13.95	8.39	9.91 1	1.37	7.12 1(0.75	5.72	9.14	11.81	20.17	12.36
23	18.42	9.59	12.40	16.99	14.04	12.19	10.18	13.71	15.44	9.13 1	10.89 1	7.04	9.69 15	5.57	7.36	12.61	14.22	12.48	14.54
12	35.58	65.61	52.75	56.04	42.90	60.73	53.53	38.66	35.37	50.96 5	55.77 4	6.17 5.	2.96 47	7.18 6	3.74	50.93	44.94	12.24	36.02
01	8.06	8.63	17.31	3.43	15.04	6,45	17.58	12.92	14.82	15.30	7.21 1	2.45 1:	9.99	9.65 1	3.54	14.58	11.48	1.92	13.66
<10	98.03	99.42	99.03	98.15	98.36	98.84	98.36	96.94	97.14	97.10 9	9.69.9	8.46 9	7.59 96	. <u>99</u> 9	8.60	97.65	98.24	79.23	93.70

TABLE 7.1b Size profiles (percentage) of unidentified specimens from nineteen vertebrate microsites from the Judith River Group in the Milk River area.

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Figure. 7.2a Size distributions of unidentified specimens from microsites in the Milk River area.



Figure. 7.2b Size distributions of unidentified specimens from microsites in the Milk River area.



Figure. 7.2c Size distributions of unidentified specimens from microsites in the Milk River area.



Figure. 7.2d Size distribution of unidentified specimens from the BMC site in the Milk River area

TABLE 7.3 Results of Nonparametric Kolmogorov-Smirnov two sample tests for similarity in the size distributions of unidentified specimens from nin eteen microsites from the Judith River Group in the Milk River area. Numbers represent probability that samples came from the same dis

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	PHR1	PHR2	SPS	NOS	ws	EZ	PHR932	cs	PHS	SALS	HAS	HS	CN1	CN2	ORS	CBC	RDS	BMC	PLS
PHR1	1.000																		
PHR2	0.662	1.000																	
SPS	996.0	0.966	1.000																
HoS	0.662	0.966	1.000	1.000															
ws	1 000	0.307	0.966	0.966	1.000														
EZ	0.662	0.966	0.966	0.966	0.662	1.000													
PHR932	0.662	0.966	1.000	1.000	0.966	0.966	1.000												
cs	996 0	0.307	0.966	0.662	0.966	0.662	0.662	1.000											
SHd	1.000	0.307	0.966	0.662	0.966	0.307	0.662	0.662	1.000										
SALS	0.966	0 966	0.966	0.966	0.662	0.966	0.966	0.662	0 662	1.000									
HAS	0.662	0.966	0.966	0.966	0.662	0.966	0 966	0.307	0.307	0.966	1.000								
HS	0 966	0.662	0.966	0.966	1.000	0.966	0.966	0.966	0.966	0.966	0.662	1.000							
CN1	0.662	0.966	0.966	1.000	0 662	0.966	1.000	0.662	0.662	0.966	0.966	996.0	1.000						
CN2	996.0	0.662	0.966	0.966	0.966	0.966	0.966	0.662	0.662	0.966	0.966	996:0	0.966	1.000					
ORS	0.307	1.000	0.966	1.000	0.662	0.966	0.966	0.307	0.662	0.662	0.662	0.966	1.000	0.662	1.000				
CBC	0 966	0.966	0.966	0.966	0.966	996 0	1.000	0.966	0.966	0.966	0.966	996 0	0.966	0.966	0.966	1.00			
RDS	996 0	0.662	0.966	0 966	0.966	0 662	996 0	0.966	0.662	0.662	0.662	0.966	996.0	0.966	0.662	0.966	1 000		
BMC	0.662	0.111	0.662	0.307	0.662	0 111	0.307	0 966	0.966	0.307	0.111	0.662	0.307	0.307	0.307	0.662	0.307	1.000	
PLS	0.966	0.662	0.966	0.662	0.966	0.662	0.662	1.000	0.966	0.966	0.662	0.966	0.662	0.966	0.307	0.966	0.966	0.966	1.000

A cluster analysis, using the aforementioned clustering method and similarity measure, was also employed to examine how the microsites are grouped on the basis of the size profiles of these specimens. The result (Fig. 7.3) shows that most sites are clustered together with high coefficients, with the BMC sites being distinctly separate from the rest. In the dendrogram, PHR-1 also exhibits certain differences from the main group. Such differences may be attributed to the reason that screenbags with slightly coarser screen size were used during screenwashing of the site, which resulted in fewer small specimens being retrieved (for details see Chapter 3).

This dendrogram (Fig. 7.3) is very different from the one generated on the basis of the data on relative abundance of taxa, with the same clustering method (average linkage) being used. If the taphonomic bias of size sorting played a major role in the preservation of the vertebrate concentrates among the sites, the dendrogram generated on the basis of size profile data would be expected to be similar to, if not the same as, the dendrogram on the basis of taxonomic data. Thus, it is suggested that the taphonomic bias of size sorting among these sites is not significantly different, and that size sorting did not affect the formation of taxonomic assemblages in a significant way.



profiles of unidentified specimens among the 19 vertebrate microsites from the Judith River Group in the Milk River area FIGURE 7.3 Dendrogram from cluster analysis (using Average Linkage) on size

7.3 Potential Sedimentary Facies Associations

As discussed in Chapter 6, the microsites investigated in this study are associated with three different sedimentary facies, each representing a different sedimentary process that was involved in the formation of a microfossil assemblage. Different sedimentary processes may dictate different taphonomic histories of microsites, which consequently affect the contents of vertebrate microfossil assemblages. Thus, it must be investigated to what extent the different sedimentary processes involved in the preservation of vertebrate microfossils contributed to the similarities and differences of the vertebrate assemblages revealed through cluster analysis.

If such differences in sedimentary facies played a major role in the selection of vertebrate microfossil assemblages that result in the groupings characteristic of the microsites, then the prediction would be that microsites that group together should be associated with similar, if not the same, sedimentary facies, and that different groupings should represent different sedimentary facies.

To test this prediction, the types of sedimentary facies associated with each microsite (see Chapter 6, Table. 6.1) were superimposed upon the dendrogram of the microsites (Fig. 7.4). Two different types of correlation are evident between the sedimentary facies and the groupings of microsites: INCHANNEL



FIGURE 7.4 Dendrogram of the vertebrate microsites from the Judith River Group in the Milk River area, with the three associated sedimentary facies superimposed.

- the two major types of sedimentary facies in-channel and crevasse splay – are not all clustered together, and they appear not to be closely related to the groupings in the dendrogram.
- the third type of sedimentary facies shoreface, known only from the Foremost Formation, is separated from the others and correlated with microsite group I (including PHR-1 and PHR-2).

That the two major sedimentary facies (inchannel and splay) do not exhibit strong correlation with the grouping patterns of microsites is interpreted as evidence that these two different sedimentary facies did not play a major role in the grouping of vertebrate microfossil localities resulting from the cluster analysis. To illustrate, these vertebrate microfossil assemblages were preserved through two different sedimentary processes, but they are not affected by such differences. A similar observation was also made by Brinkman (1990) for the microsites that are associated with the same two sedimentary facies in DPP. A simple and obvious explanation for this is that the source of skeletal material making up the vertebrate concentrates were similar or the same. This is consistent with the suggestion of Eberth (1990) that vertebrate microfossils were concentrated in the interchannel area and were subsequently preserved through sedimentary events (mainly crevasse splay and channel). Eberth (1990) also suggested that microfossils in such microsites experienced a short distance of transportation. Further, the

taphonomic biases in size sorting, as demonstrated above, are not significantly different among the microsites that have experienced different sedimentary processes.

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All these reinforce the interpretation that the groupings among these microsites revealed through cluster analysis represent homogeneous groups. Behrensmeyer (1991) also pointed out that if similar taxonomic compositions and abundance of taxa are indicated from assemblages with different taphonomic histories, then it provides a strong basis for the argument that these assemblages are persistent, spatially homogeneous groups.

The third sedimentary facies (shoreface), associated with two microsites (PHR-1 and PHR-2), are clustered together and segregated from the others. Such a correlation is interpreted as evidence that the Group I microsites in the dendrogram are clustered together because of their different facies association. These two microsites yielded vertebrate microfossils that include taxa from both marginal marine and nearshore non-marine environments where the microsites were preserved. The marginal marine environments are distinctively characterized by the presence of marine taxa, such as sharks, which are absent from the other assemblages (for details see discussion in Chapter 8).

Thus, Group I (consisting of PHR-1 and PHR-2) in Fig. 7.1 is interpreted to be a homogeneous group, in the sense that this group records the vertebrate assemblages of marginal marine and adjacent shoreline environments in the area during the period in which they were preserved. This interpretation is additionally supported by the fact that these two microsites, as described in Chapter 6, are located at the same stratigraphic horizon and share similar taphonomic characteristics.

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7.4 Influences of Speciation, Extinction and Immigration Events

Speciation, extinction and immigration events could affect the taxonomic composition of vertebrate assemblages. In general, taxa whose occurrences are restricted to a certain level of strata but are absent in any higher strata are considered to be extinct. However, caution must be exercised here because of the existence of Lazarus-taxa (Jablonski, 1986; Evans and Hecht, 1993). The earliest occurrence of a taxon in all known strata is correspondingly interpreted to coincide with a speciation event.

Among the vertebrate microfossil assemblages recovered in this study, the aforementioned events are apparently infrequent, and only occur among rare taxa. The only case of an extinction event is the turtle <u>Naomichelys</u>, which first occurred in the Lower Cretaceous but is only found as high in the section as the upper unit of the Foremost Formation (Hay, 1908, and see discussion in Chapter 4). Since this is the last known occurrence of this turtle, its absence in higher strata can be assumed to be because of its extinction. Two species of <u>Myledaphus, M</u>. sp. and <u>M</u>. <u>bipartitus</u>, show distinctively different but restricted distributions: the former occurs in strata lower than the middle unit of the Oldman Formation, while the latter occurs in the upper unit of the Oldman and above (for details see discussion in Chapter 8). This probably represents a case of a speciation event.

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Immigration events may also affect the taxonomic composition of vertebrate assemblages. One example identified is the small theropod Troodon. This taxon, represented by isolated teeth recovered from the microsites sampled in this study, has a distinct pattern of stratigraphic distribution, being common in the upper unit of the Oldman Formation but absent from the lower unit. A similar pattern of stratigraphic distribution has also been found in the Upper Judith River Group of DPP, with abundant Troodon teeth occurring relatively more frequently in the Oldman Formation than those in microsites in the higher Dinosaur Park Formation (Brinkman, 1990). The Troodon tooth specimens reported from the Milk River Formation by Currie et al. (1990) have now been clarified to be from the Judith River Group (Baszio, 1997). This suggests that the <u>Troodon</u> teeth recovered from the Oldman Formation in the course of this study perhaps represent the earliest occurrence of this animal in North America. Since troodontids have been recovered from the Early Cretaceous and Late Cretaceous of Central Asia (Barsbold et al., 1987; Russell and Dong, 1993; Currie and Peng, 1993), it is postulated that North American troodontids arrived by a way of immigration from central Asia during the Late Cretaceous (Campanian). Since this is the

only case found among the vertebrate assemblages examined in the present study, it should not strongly affect the general patterns of microsite groupings. Other possible examples are two lacertilian genera, <u>Socognathus</u> and <u>Odaxosaurus</u>. Their occurrences in the Oldman Formation recognized in this study, represent, to date, their earliest stratigraphic records (see discussion in Chapter 4). However, the lacertilian fauna has been less extensively collected and studied in the Foremost Formation, so the significance of such occurrences is uncertain.

These aforementioned taxa, with the exception of <u>Myledaphus</u> sp., are comparatively rare in all of the vertebrate microfossil assemblages included in this study. For instance, <u>Naomichelys</u> is represented by only one specimen, and <u>Odaxosaurus</u> by four specimens. It is postulated that "noise" would be introduced into the data by these rare taxa through possible random processes. In order to reduce such "noise", cluster analyses were performed on two types of data; one involved the exclusion of rare taxa, and the other the incorporation of these taxa at a higher taxonomic level. No change is evident between the results of the two cluster analyses. Thus, the aforementioned minor evolutionary modifications should not have affected the patterns of groupings of the vertebrate microfossil assemblages.

7.5 Possible Influence Of Regional Depositional Environmental Changes On The Vertebrate Assemblages

With the above factors being rejected as determinants of the differences and similarities among the vertebrate microfossil assemblages, the observed variations point to the explanation that regional depositional environmental change was the main cause. As summarized in Chapter 2, sedimentologic evidence indicates that the strata in which the studied microsites are located document an overall depositional environment change from more coastal to more inland. As a result, the vertebrates that lived in the area may have been forced to respond to the environmental shift, which is reflected in the differences of the vertebrate microfossil assemblages from different sites. These changes in the vertebrate microfossil assemblages are postulated to have been primarily ecologically driven.

A palaeoecologic study of the vertebrate microfossil assemblages in DPP by Brinkman (1990) and a sedimentological study by Eberth (1990) provide compelling evidence that regional depositional environmental changes were the major factors that determined the differences in the local vertebrate assemblages. Brinkman (1990) concluded that the patterns of stratigraphic distribution of taxa reflect the ecological zonation of the Upper Cretaceous Alberta foreland plain in which the beds were deposited. The vertebrates that were more abundant in the beds associated with coastal environments were considered to be members of a community that lived in a zone close to the shoreline, while those that were more abundant in the beds associated with inland environments were considered to be members of a community that lived in a zone with a more inland environment. Brinkman (1990) noted that similar palaeoecological interpretations have been postulated in studies of other assemblages of taxa, such as marine invertebrates (e.g. Bailey and Tedesco, 1986) and non-marine vertebrates (Wilson, 1988).

Thus, the patterns in the groupings of the microsites, revealed through cluster analysis on the basis of taxonomic composition and relative abundance of taxa, are interpreted as being reflective of changes of vertebrate assemblages in response to the regional environmental transitions from coastal to inland. The microsites grouped together are more similar to one another in their vertebrate assemblages, due to generally similar depositional environments, than they are to those in different groupings, as a result of different environments. As demonstrated in the dendrogram, the microsites sampled from the same stratigraphic units are clustered together, and the groupings from the Oldman Formation are more similar to one another than they are to the group from the Foremost Formation, with the exception of the SPS site. As discussed in Chapter 6, SPS, occurring in the upper portion of the third unit of the Foremost Formation, is associated with inchannel deposits-lateral accretion, which is evidently different from the shoreface deposits associated with the other two Foremost sites (PHR-1 and PHR-2).

Sedimentological study by Kwasniowski (1993) suggested that the upper portion of the third unit represents deposits of a coastal plain with fluvial channels, floodplain swamps and bogs, whereas the lower portion of the same unit (where PHR-1 and PHR-2 occur) represents the remains of a foreshore environment. Therefore, the environmental shift from a marginal marine to a coastal plain environment (with floodplain swamps and fluvial channels) within the third unit is apparently the determinant that resulted in the differences between the assemblage retrieved from SPS and those from PHR-1 and PHR-2. The grouping of SPS with those microsites from the lower unit of the Oldman Formation (Group II) is probably a result of the similar environment they shared.

Among Group III, ORS is the only site from the middle unit of the Oldman Formation, while the rest are from the upper unit. That ORS is clustered with those from the upper unit is suggestive of their similar vertebrate assemblages, which probably resulted from similar environments. ORS is also close stratigraphically to those of the upper units (Fig. 7.1).

To summarize, the three recognized groups of vertebrate assemblages are considered to be reflective of the response of vertebrate assemblages to regional environment changes in the area. These groupings are also, in general, reflective of their stratigraphic location in congruence with the three stratigraphic units (the upper unit of the Foremost Formation, the lower unit of the Oldman Formation, and the upper unit of the Oldman Formation). Therefore, it is concluded that each of the recognized groups of microsites represents a homogeneous group which recorded a vertebrate assemblage in an associated environment over a period of time in the area.

Chapter 8 Stratigraphic Patterns In Abundance Of Taxa And Their Palaeoecological Interpretations

Palaeoecological studies have demonstrated that stratigraphic changes in abundance of taxa provide important information for the analysis of palaeocommunities (e.g. Wilson, 1988; Brinkman, 1990). For instance, Brinkman (1990) reconstructed vertebrate palaeocommunities on the basis of stratigraphic patterns of relative abundance of taxa through the section in DPP, and associated palaeoenvironmental interpretations derived from geological evidence.

As discussed in Chapter 7, it is suggested: i) that the three groups of microsites identified in this study reflect the results of the responses of the vertebrate assemblages retrieved from those sites to regional environment changes during the Campanian; ii) that these groupings are also, in general, reflective of their stratigraphic location congruent with the three stratigraphic units (the upper unit of the Foremost Formation, the lower unit of the Oldman Formation, and the upper unit of the Oldman Formation); and iii) that each of the recognized groups of microsites represents a homogeneous group that recorded a vertebrate aggregation in a certain associated environment over a period of time in the area.

This allows for further investigation of how a specific taxon or group of taxa in the vertebrate assemblages reacted to the regional environmental

changes, as indicated by geological evidence. To facilitate the investigation, the aforementioned three stratigraphic units that coincide with the three groupings of microsites were treated as successive stratigraphic horizons, and each microsite in its grouping as one sample from the associated unit. The only site (ORS) from the middle unit of the Oldman Formation is included with those of the upper unit, which comprise Group III. Thus, the stratigraphic distribution of taxa can be examined on the basis of the grouped microsites through the three sequential stratigraphic horizons.

Behrensmeyer (1991) pointed out that utilizing multiple fossil samples that experienced varying taphonomic histories within a given stratigraphic unit greatly reduces the overall impact of taphonomic bias on fossil assemblages. The present groupings of microsites are consistent with this assumption. To illustrate, each site in a group of microsites is treated as one sample; hence such a group of microsites can be considered as multiple samples from their associated stratigraphic unit. Such treatment can also reduce variance due to the relative abundance of taxa, especially those rare taxa, between microsites within the same group. Differences in relative abundance of taxa observed through the stratigraphic horizons thus are more likely to represent real changes, as opposed to being the result of sampling variations within the same group.

The vertebrate microfossil assemblages from the three units evidently exhibit differences in taxonomic composition and abundance of shared taxa (Appendix II). Through the stratigraphic section, three general distributional patterns in the change of relative abundance of taxa are recognized:

- a) taxa showing restricted stratigraphic distribution, i.e. a taxon occurs in only a part of the section studied. This results in differences in taxonomic composition among the assemblages of the three units;
- b) taxa shared among the assemblages throughout the stratigraphic section that demonstrate changes in the relative abundance of those taxa among them. Such changes include overall increase or decrease through the three units.
- c) taxa showing no apparent changes in their abundance through the stratigraphic section.

These patterns are first documented, and then are subjected to palaeoecological interpretations.

8.1 Restricted Stratigraphic Distributions of Taxa: Differences in Taxonomic Composition

The most notable difference in taxonomic composition among the assemblages is that some taxa show different and restricted ranges of distribution among the three stratigraphic units. For example, a taxon can be found in only one of the three stratigraphic, or, conversely, it may be present in two units but absent in the third. This restricted range in the occurrence of a taxon was recognized on the basis of not only the screenwashed samples but also the surface-collected samples and other known collections.

The patterns of restricted stratigraphic distribution are depicted in graphical form (Fig. 8.1). The restricted stratigraphic distribution of taxa results in differences of taxonomic composition among the vertebrate microfossil assemblages recovered from the three stratigraphic units. Since these taxa occur at earlier and later times in other localities, their patterns of distribution in this study section cannot be attributed to extinction, speciation, or immigration events. Thus, the most likely factor accounting for these distributions is local ecological control.

Taxa showing restricted stratigraphic range of distributions among the three units are summarized as follows:

1) Taxa found to be restricted to the upper unit of the Foremost Formation: <u>Hybodus</u>, <u>Synodontaspis</u>, <u>Ischyhiza</u>, <u>Belonostomous</u>,



FIGURE 8.1 Graph showing restricted stratigraphic distributions of taxa from microsites in the Judith River Group of the Milk River area.

- Archaeolamna, Squatina, Rhinobatos, Squatirhina, and Synechodus. Among these taxa, the last three are each represented by fewer than 10 specimens, but another collection by Beavan (1996), focusing on fossil elasmobranch fishes in the same region of the Foremost Formation, recovered more abundant specimens of <u>Rhinobatos</u>, <u>Squatirhina</u> and <u>Synechodus</u>.
- Taxa, such as <u>Acipenser</u> and holostean B, found in both the upper unit of the Foremost Formation and the lower unit of the Oldman Formation, but absent from the upper unit of the Oldman Formation.
- 4) Taxa found in both the lower and the upper units of the Oldman Formation, consisting of the lizard, <u>Socognathus</u>, and the mammal, <u>Mesodma</u>, but their sample sizes are small. Another lizard, <u>Paraderma</u>, also shows a similar distribution, but is represented only by three specimens from three different sites. Therefore, it is not included until more sampling has been conducted.

One other possible restricted stratigraphic range is that of xenosaurid material, which was found only in the lower unit of the Oldman Formation. However, it is represented by only two osteoderms, one per site. As this distributional range may be subject to stochastic occurrence, the material was rejected from further consideration pending further sampling.

8.2 Changes In Relative Abundance Of Shared Taxa

In addition to those that show restricted stratigraphic distribution, taxa shared by the assemblages exhibit changes in their relative abundance through the section. These changes in abundance were examined among the three stratigraphic horizons that are represented by the three units. To document the patterns of change, the average value of the relative abundance of a taxon from all of the grouped microsites within the same unit was plotted against the stratigraphic position of that unit. The rank-order was used as measure of the relative abundance of a taxon. Such a measure was generated, using Microsoft Excel for Windows (Version 7.0), on the basis of the abundance of each taxon within an assemblage in ascending order. In this approach, the most abundant taxon receives the highest rank and the least abundant is ranked the lowest among all the taxa in an assemblage from a microsite. The rank mean was assigned to ties.

Two general patterns of change in abundance of taxa were observed through the three stratigraphic horizons. They are: a) overall decrease in relative abundance of taxa through the stratigraphic section (Fig. 8.2); and b) overall increase in relative abundance of taxa through the stratigraphic section (Fig. 8.3). Even so, each pattern, a decrease or increase, also exhibits variation in its changes. For instance, the decrease in abundance of a taxon









can be directional (i.e. a consistent decrease through the horizons, see Fig. 8.2) or non-directional (i.e. a decrease at the mid-point of the horizon, followed by a slight increase at the top, although the abundance overall decreases through the section, see Fig.8.4a, b). The magnitudes of the changes in the abundance of taxa also vary among the three stratigraphic horizons.

In order to quantify and test whether or not these stratigraphic patterns of relative abundance of taxa are significant, a non-parametric statistical method, the Kruskal-Wallis test, was employed. The Kruskal-Wallis test, a non-parametric ANOVA (Hollander and Wolfe, 1973; Zar, 1996), compares the relative abundance of each taxon among the three stratigraphic units, during which each site is treated as one sample in its unit. The results are presented in Table 8.1, and indicate that there are two groups of taxa showing significant changes in their relative abundance among the stratigraphic units. Group A includes taxa that exhibit significant decrease; group B contains those that show significant increase. Taxa that do not show significant changes as a result of the test are not listed in Table 8.1.

Pairwise Mann-Whitney tests were subsequently performed on the individual taxa comprising these two groups to further determine the direction of changes. The Mann-Whitney test was used to detect at which point such differences occur, that is, whether the significant changes in the relative abundance of a taxon occurred between the upper Foremost and the lower Oldman unit, or between the upper Foremost and the upper Oldman unit, or








TABLE 8.1 Results of the Kruskal-Wallis tests and Pairwise Mann-Whitney tests for changes in relative abundance of vertebrates in the upper Foremost, the lower Oldman and upper Oldman formations in the Milk River area.

ТАХА	Kruskal-Wallis test		Mann-Whitney test p value		
	test statistic	p value	F2/O1	F2/O2	01/02*
A. Taxa decreasing in abundance in the section					
<u>Atractosteus</u> <u>Myledaphus</u> <u>Paralbula</u> holostean B phyllodontids <u>Leidyosuchus</u> alligatorids <u>Champsosaurus</u> <u>Adocus</u> ceratopsids	11.21 10.82 13.39 12.54 6.29 5.93 5.94 8.12 10.04 5.96	0.004 0.005 0.001 0.002 0.041 0.050 0.048 0.017 0.007 0.046	0.746 0.013 0.012 0.009 0.042 0.048 0.041 0.043 0.015 0.033	0.041 0.001 0.002 0.040 0.046 0.038 0.033 0.038 0.038 0.046	0.039 0.034 0.023 0.012 0.864 0.915 0.107 0.099 0.048 0.619
B. Taxa increasing in abundance in the section <u>Coriops</u> esocoids amiids teleost D <u>Scapherpeton</u> <u>Opisthotriton</u> <u>Albanerpeton</u> anurans	7.78 6.90 6.28 6.26 6.12 6.55 6.27 7.43	0.020 0.033 0.041 0.042 0.045 0.038 0.041 0.024	0.011 0.032 0.033 0.043 0.029 0.039 0.008 0.008 0.040	0.033 0.011 0.044 0.756 0.027 0.031 0.022 0.038	0.686 0.113 0.107 0.061 0.864 0.128 0.653 0.788

* F2=the upper Foremost, O1=the lower Oldman, O2=the upper Oldman unit

between the lower Oldman upper and the upper Oldman unit. The results are summarized in Table 8.1. Taxa in both group A (except <u>Atractosteus</u>) and B show significant changes in their relative abundance between the upper Foremost and the lower Oldman unit. Such changes are also indicated between the upper Foremost and the upper Oldman unit, except for teleost D. Interestingly, the changes between the lower Oldman and the upper Oldman unit, are shown to be insignificant among all the taxa in group B. In contrast, taxa in group A, including <u>Myledaphus</u>, <u>Paralbula</u>, holostean B, and <u>Adocus</u>, exhibit a significant decrease, while the rest in the group do not. The significant changes in the relative abundance of <u>Myledaphus</u>, <u>Paralbula</u>, holostean B, and <u>Adocus</u> between the two Oldman units are indicative of the differences between the two vertebrate assemblages.

A cluster analysis, in which taxa are grouped on the basis of their similarities in distribution among the microsites, was also performed to further document the patterns of stratigraphic distribution in the abundance of taxa. This method is often referred to as R-mode cluster analysis, in contrast with the Q-mode discussed above. The R-mode and the Q-mode are two basic approaches that have been widely applied in community studies (e.g. Jones, 1988; Dodd and Stanton, 1990). In R-mode analysis, taxa that share patterns of change or co-occurrence are grouped together, whereas those with distributions that are not strongly correlated or mutually exclusive are placed in different clusters. The Spearman Rank Order Correlation Coefficient as a distance measure, and the Average Linkage as a clustering method were also applied in the R-mode analysis, in order to maintain consistency with the Q-mode analysis. The R-mode analysis results in three major groups (Fig. 8.5: clusters A, B, and C). Within each cluster, taxa are more similar to one another, in their stratigraphic changes of abundance, than they are to those taxa in other groups. These three groups of taxa are generally congruent with the groups of taxa showing different stratigraphic patterns recognized through the Kruskal-Wallis and Mann-Whitney tests. For example, cluster A includes taxa that decrease in abundance through the stratigraphic section (plus those showing restricted distribution to lower Foremost unit), cluster C consists of taxa that show increase in their relative abundance (except for holostean A, birds and teleost indet.), and cluster B consists of those taxa that do not show significant changes in their relative abundance.

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A diagram, combining the results from both Q-mode and R-mode analyses, was constructed (Fig. 8.6). In this figure, the data matrix is displayed in graphic form between the dendrograms for both the cluster analyses of microsites and taxa. Thus, the structure in the original data can be seen along with the results of the cluster analyses.

On the basis of the above recognized patterns, it becomes evident that each of the three groups of microsites is distinguishable by its characteristic taxa. For instance, Group I (PHR-1 and PHR-1) differs from other two in the



assemblages from the 19 microsites from th Judith River Group in the Milk River area. Shadings indicate FIGURE 8.5 Dendrogram from R-mode cluster analysis (using Average Linkage) on the vertebrate three different groupings. **FIGURE 8.6** Dendrograms of Q- (left) and R-mode (top) cluster analysis of the vertebrate assemblages of the Judith River Group in the Milk River area. The data matrix is displayed between the dendrograms. Legend on the right shows relative abundance of taxa (in percentage). Dashed lines indicate the different clusters.



presence of taxa that show restricted distribution to the Foremost Formation. including Hybodus, Synodontaspis, Ischyhiza, Archaeolamna, Squatina, Rhinobatos, Squatirhina, Synechodus, Myledaphus sp., Belonostomous, acipenserids and Naomichelys, plus those that show significant decrease in abundance towards the Oldman Formation, such as Paralbula and Atractoteus, which are common taxa in the assemblage. Group III, including all sites from the upper Oldman and ORS from the middle Oldman unit, is characterized by dominant taxa such as Scapherpeton, Opisthotriton, anurans and also by the absence or rarity of taxa, such as acipenserids, holostean B, Paralbula and Adocus, which are abundant in the other two groups. Myledaphus bipartitus and Troodon, which are restricted to the upper stratigraphic unit, are also considered to be characteristic taxa of Group III. Group II (including all the sites in the lower Oldman unit and SPS) appears to be a hybrid assemblage characterized by sharing taxa from both Group I and Group III, such as Atractosteus, Paralbula, Champsosaurus, Adocus, and holostean B (shared with Group II), and Scapherpeton, Opisthotriton, anurans, teleosts and hadrosaurids (shared with Group III) which represent the common taxa in this assemblage. This group is readily distinguishable from Group I by the absence of chondrichthyan teeth (including Hybodus, Synodontaspis, Ischyhiza, Archaeolamna, Squatina, Rhinobatos, Squatirhina, Synechodus), and differs from Group III in the absence of Myledaphus bipartitus and Troodon, and in the presence of acipenserids and Myledaphus sp. that are absent from Group III.

8.3 Palaeoecological Interpretations of the Patterns of Stratigraphic Distribution in Abundance of Taxa

The recognized stratigraphic patterns of the abundance of taxa discussed above, along with palaeoenvironmental information derived from geological evidence, provide a basis for palaeoecological interpretations.

Interpretation of the Restricted Stratigraphic Distributions of Taxa

Taxa showing restricted stratigraphic distributions are interpreted as representing those characteristics of the assemblage (or assemblages) preserved in that stratigraphic unit (or units). The reasoning behind this assertion is as follows:

- Sedimentologic evidence has indicated that the three stratigraphic units investigated document an overall depositional environmental shift from a marine-influenced coastal to a more freshwater inland environment;
- 2) The taxonomic composition and abundance of the vertebrate microfossil assemblages have been demonstrated above to be primarily influenced and determined by changes of source communities in response to the environmental changes.

For example, taxa that are restricted to the lower Foremost Formation, such as Hybodus, Synodontaspis, Ischyhiza, Belonostomous, Archaeolamna, <u>Squatina</u>, <u>Rhinobatos</u>, <u>Squatirhina</u>, and <u>Synechodus</u>, are interpreted to have been adapted to live in marine-influenced coastal areas in which they were preserved. With the situation having shifted to a freshwater inland environment in the same area, the ranges of these animals were affected and their absence reflects a retreat of coastal areas as a result of the regression of the Western Interior Sea.

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In a study on elasmobranch fossils, Beavan and Russell (submitted) indicated that some of the taxa recovered from the Foremost Formation, such as, <u>Hybodus</u>, <u>Synodontaspis</u>, <u>Ischyhiza</u>, and <u>Archaeolamna</u>, were also present in the terrestrial-marine transitional Lethbridge Coal Zone of the Dinosaur Park Formation in DPP. Later reappearance of these elasmobranch taxa in the strata associated with the transgression of the Bearpaw Sea in DPP, reinforces the interpretation given here. Therefore, these taxa are considered to be members of a coastal vertebrate community.

The teeth of <u>Myledaphus bipartitus</u> also appear to be restricted to the upper Oldman in the studied section, but this taxon is not interpreted as being a member of an inland community for the following reasons: 1) <u>M. bipartitus</u> is a rare taxon in the upper Oldman assemblage (represented by comparatively few specimens), 2) the occurrence of <u>M. bipartitus</u> teeth in the upper Oldman is recorded as the earliest appearance of this taxon (suggestive of a speciation event), 3) <u>M. bipartitus</u> in the higher strata of DPP was interpreted as a member of coastal community (due to the significant increase of its abundance along

with an environmental shift from inland to coastal – Brinkman, 1990), and 4) the teeth of <u>Myledaphus</u> (combining both species), as revealed above (Table 8.1), show a significant decrease toward the upper Oldman through the section. Therefore, <u>Myledaphus</u>, including both <u>M. bipartitus</u> and <u>M. sp.</u>, are interpreted as members of the coastal community.

Interpretation of Significant Changes in Abundance of Taxa

It was suggested above that differences among vertebrate microfossil assemblages are due to the responses of the taxa to palaeoenvironmental shifts during the period of time when the beds were being laid down. Geological and sedimentologic evidence indicates that the stratigraphic section where the microsites are found documents a trend in the palaeoenvironment from coastal to inland (i.e. the shoreline of the Western Interior Seaway moved away from the region toward the east). Therefore, the observation that taxa show significant changes in their abundance through the three stratigraphic horizons is interpreted as reflecting differentiation of habitats due to palaeoecological zonation across the foreland plain during the period of time of deposition.

Taxa showing a significant decrease in abundance are most common in the upper unit of the Foremost Formation, and are interpreted as being members of vertebrate communities that were associated with coastal environments or lived in coastal areas. Those showing significant increase in their abundance are most common in the upper unit of the Oldman Formation, and are consequently interpreted as members of vertebrate communities that were associated with freshwater environments or that lived in inland areas. On the basis of these criteria and the interpretation of taxa showing restricted distribution, members of two different communities (coastal and inland) are thus recognized and are summarized in Table 8.2.

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Those taxa that do not show significant changes in their relative abundance through the stratigraphic section are, according to the same criteria, indeterminate pertaining to their community memberships. Nevertheless, in a reconstruction of palaeocommunities of vertebrates in DPP, Brinkman (1990) interpreted these taxa with similar stratigraphic distribution as members of both inland and coastal communities. **TABLE 8.2** Summary of taxa hypothesized to be indicative of two differentvertebrate palaeocommunities, based upon their stratigraphic distributions inthe Judith River Group in the Milk River area.

Coastal	Inland
<u>Hybodus</u>	Coriops
<u>Synodontaspis</u>	esocoids
Ischyhiza	amiids
Archaeolamna	teleost D
<u>Squatina</u>	Scapherpeton
<u>Rhinobatos</u>	Opisthotriton
<u>Squatirhina</u>	Albanerpeton
Synechodus	anurans
Myledaphus	
<u>Belonostomous</u>	
acipenserids	
<u>Atractosteus</u>	
Paralbula	
holostean B	
phyllodontids	
<u>Leidyosuchus</u>	
alligatorids	
Champsosaurus	
Adocus	
ceratopsids	

8.4 Comparison with the Vertebrate Microfossil Assemblage of DPP

Brinkman (1990) documented vertebrate assemblages and their stratigraphic patterns on the basis of numerous microsites from the Judith River Group in DPP. He also provided palaeoecological interpretations of the stratigraphic patterns recognized among the assemblages. The present study focuses upon the same Judith River Group, but the beds are stratigraphically lower in section (including the upper Foremost Formation and the Oldman Formation) and are more southerly in their distribution. This allows for these palaeoecological interpretations to be compared and tested. Furthermore, this allows for the understanding of ecologically driven changes of vertebrate assemblages through the Late Cretaceous in southern Alberta.

8.4.1 Comparison of Taxonomic Compositions

The vertebrate microfossil assemblages from the Foremost and the Oldman formations in the Milk River region are generally very comparable in taxonomic composition to those from the upper Oldman and the Dinosaur Park formations in DPP (see faunal list in Brinkman, 1990). Table 8.3 summarizes the differences between the two assemblages.

The absence of small elasmobranch taxa in DPP, as listed in Table 8.3, was possibly due to minor differences in the application of retrieval techniques **TABLE 8.3** Comparison of vertebrate microfossil assemblages of the Judith River Group between Milk River area and DPP in southern Alberta, showing the list of taxa that are different between the two.

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	Milk River Region	DPP Assemblage
Таха	Assemblage	(Brinkman, 1990)
Elasmobranch: Squatirhina Synechodus Rhinobatos Chiloscyllium Squatina	Present	Absent*
Albanerpeton	present	absent*
Naomichelys	present	absent
Adocus	common	extremely rare
Basilemys	rare	common

*some taxa may not have been retrieved due to differences in screen size applied during screenwashing in DPP (for further discussion see the text).

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(i.e. a finer screen was used in the present study during the screenwashing process). Because the specimens of the aforementioned taxa are generally small in size (for details see Chapter 4), they will have not been recovered with the coarser screens applied by Brinkman (1990). Likewise, these taxa were not recovered by Beavan and Russell (submitted) presumingly because the same coarse screen was also utilized in retrieving fossil remains from a site in the uppermost Dinosaur Park Formation of DPP. However, the possibility cannot be eliminated that the difference reflects a faunal difference in the two regions. Considering that: 1) the Milk River assemblage is more southerly in its location; and 2) that most of these elasmobranch taxa have been recovered from the Upper Cretaceous of more southerly regions, such as Montana (Case, 1978, 1987), and Texas (Welton & Farish, 1993), a possible explanation for such a taxonomic difference is the result of a difference in geographic distribution (i.e. they occurred most commonly in an area south of DPP).

Phyllodontids and <u>Albanerpeton</u> were not previously recognized in the upper Judith River Group of DPP (Brinkman 1997, pers. comm.), although these taxa are present.

The absence of <u>Naomichelys</u> from DPP is probably due to its extinction, as discussed before. That <u>Adocus</u> was found to be extremely rare throughout the DPP beds (Brinkman, 1990), but common particularly in the Foremost Formation in the Milk River area, was suggested by Peng et al. (1995) to be due to a difference in geographical range (with the animal being more abundant in the south of its distribution). Conversely, another turtle, <u>Basilemys</u>, was found to have an opposite pattern of occurrence, i.e. it is relatively more common in the DPP deposits but rare in the present study beds. Thus, it may be that <u>Basilemys</u> had a more northerly distribution during the time of deposition in southern Alberta.

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Although additional work is needed to sort out the taxonomic details of lizards and mammals from DPP, preliminary observations indicate that they are generally similar to those from the Milk River region (Brinkman 1997, pers. comm.).

Thus, the two assemblages from the Judith River Group in the Milk River region, and in DPP, are generally comparable in taxonomic compositions of non-dinosaurian vertebrates, although palaeogeographical and evolutionary influences are also evident.

8.4.2 Comparison of the Recognized Community Members

Brinkman (1990) documented the vertebrate palaeoecology of the upper section of the Judith River Group in DPP and recognized members of two different vertebrate palaeocommunities (see Brinkman, 1990: p.51, Table 4). The present study has focused upon the vertebrate palaeoecology of the lower section of the Judith River Group in the Milk River region. However, both studies have led to a similar identification of members of vertebrate palaeocommunities (Table 8.2). As mentioned above, the stratigraphic section of the Judith River Group in the study area documents a general environmental shift from coastal to inland, which is the reverse of that seen in DPP (a general change from inland to coastal environment) (e.g. Eberth, 1990; Brinkman, 1990). Although similar criteria were applied in both studies, the spatial and temporal differences of the vertebrate assemblages, along with the reverse environmental shifts, established by the two studies, provide a rather robust test of the palaeoecological inferences made for the Late Cretaceous vertebrate assemblages of southern Alberta.

Table 8.4 summarizes the recognized members of two different communities in the two studies. The results of these studies are generally congruent with one another, although differences are also evident. Such differences may be attributed to evolutionary influences, such as the extinction of <u>Naomichelys</u>, possibly a speciation event of <u>Myledaphus</u>, and differences in palaeogeographical distribution, such as <u>Adocus</u> (southerly distributed) versus <u>Basilemys</u> (more northerly distributed) and possibly most of the chondrichthyans listed (see discussion above). The differences are also the result of taxa not being recognized in DPP, such as <u>Albanerpeton</u>, or possibly not retrieved as a result of different screen sizes applied, such as small shark teeth.

Therefore, the members of the vertebrate communities previously recognized in DPP (Brinkman, 1990) are generally duplicated in the Judith

TABLE 8.4 Comparison of members of vertebrate palaeocommunities recognized in this study and by Brinkman (1990). Taxa listed in bold face represent those that are different between the two studies.

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	Milk River Region	DPP
	(This study)	(Brinkman, 1990)
Coastal	Hybodus Myledaphus Belonostomous Atractosteus Paralbula holostean B Leidyosuchus Champsosaurus ceratopsids Synodontaspis Ischyhiza Archaeolamna Squatina Rhinobatos Squatirhina Synechodus acipenserids phyllodontids alligatorids Adocus	Hybodus Myledaphus Belonostomous Atractosteus Paralbula holostean B Leidyosuchus Champsosaurus ceratopsids Paratarpon Basilemys Aspideretes
Inland	<u>Coriops</u> amiids teleost D <u>Scapherpeton</u> <u>Opisthotriton</u> anurans <u>esocoids</u> <u>Albanerpeton</u>	<u>Coriops</u> amiids teleost D <u>Scapherpeton</u> <u>Opisthotriton</u> anurans holostean A teleost indet.

River Group of the Milk River area. This finding reinforces the palaeoecological inferences of Brinkman (1990). It also provides evidence for monitoring the ecologically driven changes of vertebrate communities during the Late Cretaceous southern Alberta.

8.5 Discussion of the Dinosaur Assemblages from the Judith River Group

After surveying dinosaur assemblages, defined on the basis of isolated teeth, from vertebrate microfossil localities in the Upper Cretaceous strata of southern Alberta, Baszio (1997a) recognized two distinct dinosaur assemblages — the Judith River / Horseshoe Canyon; and the Milk River / Scollard. He noted that the two dinosaur assemblages are different from each other in the following aspects:

- <u>Richardoestesia</u> sp. is less abundant in the Judith River / Horseshoe Canyon assemblage;
- <u>Paranychodon</u> is relatively rare in the Judith River / Horseshoe Canyon assemblage;
- <u>Troodon</u> exhibits a relatively high occurrence in the Judith River / Horseshoe Canyon assemblage;
- 4) Protoceratopsid dinosaurs are relatively more abundant in the Milk River/ Scollard assemblage.

However, the data utilized by Baszio (1997a) in his analyses for the Judith River Group were restricted only to the Dinosaur Park Formation and the uppermost Oldman Formation in DPP, because samples from earlier beds (the lower portion of the Oldman and the Foremost formations) were not available. Samples taken in the present study allow for further documentation of the dinosaur assemblage from a more complete stratigraphic range of the Judith River Group in southern Alberta.

<u>Theropod Dinosaurs</u> As described in Chapter 4, seven theropod dinosaurs have been identified, based on isolated teeth from the microsites examined in this study: <u>Dromaeosaurus</u>, <u>Saurornitholestes</u>, <u>Troodon</u>, <u>Richardoestesia</u>, <u>Paranychodon</u>, <u>Aublysodon</u> and Tyrannosauridae gen. indet..

Table 8.5 summarizes the relative abundance of these taxa. In compiling the data of relative abundance of taxa (in percentage) among theropod dinosaurs, Baszio (1997a) included Aublysodon teeth with those of Tyrannosauridae gen. indet. as Tyrannosauridae. A similar procedure has been adopted here to facilitate comparison. Based on data from the present study, it is evident that the overall relative abundance of these theropods from the lower Judith River Group exhibits great similarity to that of this group in DPP, and apparent difference from the abundance data for theropods of the Milk River Formation. For instance, <u>Richardoestesia</u> sp. is comparatively rare, representing 1.37% of the theropod teeth recovered from the lower Judith River Group (2% in DPP), in contrast to 16% of the Milk River assemblage; Troodon makes up 7.51% (8% in DPP), while it is absent in the Milk River Formation. Statistical comparison of the proportions of Richardoestesia sp. between the Judith River and the Milk River were made using two-tailed z-tests (Zar, 1996; p.553). Results indicate that the proportions of Richardoestesia sp. in the Judith River assemblage from both the DPP and this study area are

TABLE 8.5 Comparisons of relative abundance of theropod dinosaurs among the lower JRG (Foremost and Oldman formations) in this study, the Upper JRG in DPP, and the Milk River Formation in southern Alberta. JRG = Judith River Group.

	Lower JRG (This study)	Upper JRG (Baszio, 1997)	Milk River Fm. (Baszio, 1997)
Dromaeosaurus	1%	3%	0%
Saurornitholestes	58%	56%	45%
<u>Richardoestesia</u> sp.	1%	2%	16%
<u>R</u> . <u>gilmorei</u>	9%	11%	19%
Troodon	8%	8%	0%
<u>Paranychodon</u>	7%	4%	10%
Tyrannosauridae	16%	15%	10%
Total number of specimens	293	296	830

significantly different from its representation of the Milk River assemblage (with p<0.0001). Similar tests indicate that <u>Paranychodon</u> in DPP is significantly different in its proportional representation when compared to the Milk River assemblage (p=0.002), whereas its proportion in the present study area shows insignificant difference from that in the Milk River assemblage (p=0.093) (Tables 8.6, 8.7).

Thus, the interpretation by Baszio (1997a) that the Judith River theropod dinosaur assemblage is different from that of the Milk River Formation is reinforced, based on the data from the lower Judith River Group generated in the present study. The addition of the data from this study also suggests that:

- the significantly lower occurrence of <u>Richardoestesia</u> sp., noted by Baszio (1997), in DPP is consistent with the pattern in the lower Judith River Group;
- 2) <u>Paranychodon</u> from the uppermost Judith River Group in DPP exhibits a significantly lower occurrence than it does in the Milk River Formation, but this taxon from the lower Judith River Group does not differ significantly in its relative abundance when compared to the Milk River assemblage. This may suggest that the relative abundance of <u>Paranychodon</u> exhibits variation within the Judith River Group.

The occurrence of <u>Troodon</u> in the Oldman Formation, as discussed in Chapter 7, has been suggested to represent an immigration event. This taxon **TABLE 8.6** Results of two-tailed z-tests comparing proportions of<u>Richardoestesia</u> sp. and <u>Paranychodon</u> between the assemblages of the lowerJRG and the Milk River Formation of southern Alberta.

Таха	Lower JRG (This study)	Milk River Fm. (Baszio, 1997)	Z	Significance level
<u>Richardoestesia</u> sp.	1%	16%	6.479	p<0.0001
Paranychodon	7%	10%	1.679	p=0.093

TABLE 8.7 Results of two-tailed z-tests comparing proportions of<u>Richardoestesia</u> sp. and <u>Paranychodon</u> between the assemblages of the upperJRG and the Milk River Formation of southern Alberta.

Таха	Upper JRG (Baszio, 1997)	Milk River Fm. (Baszio, 1997)	Z	Significance level
<u>Richardoestesia</u> sp.	2%	16%	6.189	p<0.0001
Paranychodon	4%	10%	3.069	p=0.002

occurs in only the upper Oldman and the Dinosaur Park formations and higher strata. This also results in the absence of <u>Troodon</u> from the Foremost Formation and the lower and middle units of the Oldman Formation, as well as from the Milk River Formation.

Ornithischian Dinosaurs Four main groups of ornithischian dinosaurs, Ankylosauria, Ceratopsia, Pachycephalosauria and Hadrosauridae, have been identified from the microsites sampled from the Foremost and Oldman formations in this study (see Chapter 4). A total of 2871 isolated teeth of these taxa were recovered. However, no protoceratopsid teeth have been identified. This is a strong indication that protoceratopsid dinosaurs did not occur or were extremely rare in the area at the time that the Foremost and Oldman formations were deposited. Thus, the absence or rare occurrence of protoceratopsid dinosaurs is consistent throughout the Judith River Group.

In conclusion, the samples from the lower Judith River Group (including the Foremost and the Oldman formations) in this study generally support Baszio's (1997) observation that the dinosaur assemblage of the Judith River Group is different from that from the Milk River Formation in southern Alberta. The main differences between the two dinosaur assemblages are the significantly lower occurrence of <u>Richardoestesia</u> sp. and the absence or rare occurrence of protoceratopsids throughout the Judith River Group. Nevertheless, the data from this study also indicate that <u>Paranychodon</u> varies in its relative abundance within the Judith River Group, and that the appearance of <u>Troodon</u> in the upper Oldman Formation represents an immigration event, it being absent from the Foremost and the lower and middle Oldman formations.

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Chapter 9 SUMMARY AND CONCLUSIONS

In this final chapter, I first present a summary of my conclusions concerning the palaeoecology of the Foremost and Oldman formations of southeastern Alberta, on the basis of evidence from vertebrate microfossil localities. Secondly, I consider, in the context of the results of this and previous studies, the importance and significance of microsites in palaeoecologic studies, their applications, potential problems and implications.

9.1 Summary of Results

The results of this study are summarized below, with the order of presentation following the sequential chapters laid out in the dissertation.

- Extensive field work focused on the Judith River Group in the Milk River area of southeastern Alberta resulted in the discovery of nineteen vertebrate microfossil localities (stratigraphically distributed in the section of the Foremost and Oldman formations), and yielded over 30,000 identified vertebrate specimens.
- Vertebrate assemblages from the Upper Cretaceous Judith River Group (including the Oldman and Foremost formations) of southeastern Alberta are systematically examined and documented for the first time, on the basis

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of the evidence from the vertebrate microfossil localities. 78 taxa are identified, including six different major groups: Chondrichthyes; Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia. Taxonomic description for recognized taxa is provided, with emphasis on criteria for identification.

3) Investigation of the methods employed in collecting and sampling fossil vertebrates from microsites suggests that a) the surface-collecting method is biased against small specimens, although such collection can be used for documenting palaeoecological data pertaining to the presence and absence of taxa; b) test of repeatability of sampling by screenwashing (a commonly applied and less biased technique for systematic sampling of microsites) is needed to ensure that representative samples are employed in further analysis; c) Cohen's (1961) maximum likelihood method can be used to test whether or not a sample is taxonomically representative of a source assemblage (microsite); and d) the minimal volume of sediment for a representative sample from a microsite is assessed, using Michael's Site (an extensively collected microsite in the Milk River Formation) as an example, which suggests that 351.25 kg of sediment is adequate for this site.

- 4) Sedimentological and taphonomic examination of the microsites in the Milk River area indicates that 17 of 19 microsites exhibit two recurrent sedimentary facies associations (inchannel and crevasse splay) similar to those in DPP. A third facies association (shoreface) is also recognized for the two microsites from the Foremost Formation.
- 5) The sampled microsites are compared, using multivariate cluster analysis (Q-mode), with respect to their taxonomic composition and relative abundance. The resultant groupings of microsites, generally congruent with their stratigraphic location, are suggested to represent homogenous groups. Taphonomic biases of size-sorting, suggested by Blob and Fiorillo (1996), are not indicated among these microsites. Analysis of facies association among the microsites suggests that the two most common sedimentary facies are not correlated with the recognized groupings of microsites and thus are interpreted as not being contributory factors. Two types of Myledaphus teeth with distinctively different stratigraphic distributions are suggested to be associated with a possible speciation event giving rise to M. bipartitus. The disappearance of Naomichelys above the Foremost Formation is interpreted as an extinction event. The first occurrence of Troodon in the upper Oldman Formation is suggested to be the result of an immigration event. Modifications of the taxonomic composition of the vertebrate assemblages studied here through such events are considered

to be very limited, since the only one example was identified for each. Regional depositional environmental change, from coastal to inland, as suggested by geological evidence, is interpreted as the main contributory factor that determines the patterns of microsite groupings.

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6) Stratigraphic distributions of taxa are examined and documented through the section, using grouped microsites as multiple samples for each unit. Three general patterns of stratigraphic distribution of taxa are recognized: a) taxa showing restricted stratigraphic distribution, i.e. the occurrence of a taxon in only a part of the section studied; b) taxa shared among the assemblages throughout the stratigraphic section that demonstrate changes (including overall increase or decrease) in the relative abundance of that taxon; c) taxa showing no apparent or directional changes in their abundance through the stratigraphic section. Non-parametric statistical approaches (the Kruskal-Wallis and Mann-Whitney tests) are employed in determining the significance of such changes. Such patterns, along with the results from further R-mode multivariate cluster analysis, allow for comparison and documentation of the characteristic taxa of each of the three recognized assemblages (the upper Foremost, lower Oldman and upper Oldman). The upper Foremost assemblage differs from other two in the presence of taxa that show restricted distribution to the Foremost Formation (Hybodus, Synodontaspis, Ischyhiza, Archaeolamna, Squatina,

<u>Rhinobatos</u>, <u>Squatirhina</u>, <u>Synechodus</u>,., <u>Belonostomous</u>, acipenserids and <u>Naomichelys</u>), plus those that show significant decrease in abundance towards the Oldman Formation, such as <u>Myledaphus</u> sp., <u>Paralbula</u> and <u>Atractosteus</u>, which are common taxa in the Foremost assemblage. The lower Oldman represents a hybrid assemblage characterized by a sharing of common taxa with both the upper Foremost and the upper Oldman, such as <u>Atractosteus</u>, <u>Paralbula</u>, <u>Champsosaurus</u>, <u>Adocus</u>, and holostean B (shared with the upper Foremost), and <u>Scapherpeton</u>, <u>Opisthotriton</u>, anurans, teleosts and hadrosaurids (shared with the upper Oldman. The upper Oldman assemblage is characterized by dominant taxa, including <u>Scapherpeton</u>, <u>Opisthotriton</u>, anurans, and also by the first appearance of <u>Myledaphus bipartitus</u> and <u>Troodon</u>, and the absence or rarity of taxa such as acipenserids, holostean B, <u>Paralbula</u> and <u>Adocus</u>, which are abundant in the other two groups.

7) Palaeoecological interpretation of the recognized patterns of stratigraphic distribution of taxa resulted in the recognition of two vertebrate (inland and coastal) palaeocommunities. Comparisons of these results with those in DPP suggest that taxonomic composition of vertebrate assemblages is quite comparable in both study areas of southern Alberta for the period of time when the Judith River Group beds were deposited. The identified members of two vertebrate communities in the Milk River area generally duplicate those previously recognized in DPP, although evolutionary and palaeogeographical influences were also evident between them.

8) Data from the Foremost and Oldman microsites indicate the dinosaur assemblage from the lower beds in the present study area is generally consistent in its structure with that of the uppermost Judith River Group in DPP, although variation is also evident, such as the absence of <u>Troodon</u> and the relatively high occurrence of <u>Paranychodon</u> in the lower Judith River Group. This also supports Baszio's (1997) assertion that the dinosaur assemblage from the Judith River Group is different from that from the Milk River Formation.

9.2 General Conclusions

Undoubtedly, vertebrate microfossil accumulations have not only provided significant information for documenting and understanding fossil vertebrate assemblages of the Upper Cretaceous southern Alberta, but also have become a very important source of information in the study of palaeoecology of vertebrate assemblages and their interactions with associated palaeoenvironments. This study demonstrates that taxonomically diverse vertebrate assemblages can be retrieved and documented from vertebrate microfossil localities. Such assemblages include not only most of the vertebrate taxa known from articulated remains in the beds in which they occur, but also those taxa known only from the vertebrate microsites. Large sample sizes of vertebrate specimens can be obtained through the use of screenwashing or surface collecting techniques. The large samples can then be subjected to quantitative analysis, which allows for further palaeoecologic inferences to be made and tested.

Before palaeoecologic interpretations can be made based upon differences or similarities among a group of assemblages, it must first be established that such differences or similarities are not sampling artifacts. This study demonstrates that careful evaluation of samples from microsites is necessary to ensure the representativeness of the samples. Such representative samples allow for appropriate abundance data to be complied and further used for the effective and valid comparison of samples taken from different microsites.

Sedimentological and taphonomic examination is an essential part in the palaeoecologic study of microsites. These sources provide important contextual information for understanding the interpretation of palaeoenvironments in which animals lived, died, and were preserved, and how biotic and abiotic components of the original ecosystems interacted with one another. Such information also provides the means to document potential biases that may have occurred during the process of preservation of a fossil assemblage. Before it is concluded that palaeoenvironmental (ecological)

changes were the chief determinants that result in differences between assemblages, the potential roles of taphonomic processes and sedimentary facies associations must be evaluated. Such factors may themselves produce outcomes that could result in differential interpretation of vertebrate assemblages from different microsites. Other possible factors that could affect differences in the structures of vertebrate assemblages, such as evolutionary changes, extinction and immigration events, should also be assessed. Combined with sedimentological interpretation of palaeoenvironments, the stratigraphic differences in relative abundance of taxa can be used to reconstruct vertebrate palaeocommunities.

The results of this study suggest that the vertebrate assemblages known from microsites of the Judith River Group in the Milk River area and DPP of southern Alberta exhibit generally similar modifications in response to palaeoenvironmental changes as a result of sea-level oscillations. Such ecological changes over a long period of time are reflected in the modifications of vertebrate assemblages as a result of long-term environmental changes, and provide an example for understanding of changes of ecosystems through time, a theme recently advocated for evolutionary palaeoecology (Behrensmeyer and Hook., 1992).
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APPENDIX I Names, catalogue numbers, Legal Land Description Universal Transverse Mercator (UTM) coordinates and geological information of vertebrate microfossil localities from the Judith River Group in the Milk River area of southeastern Alberta

SPS (Suffield Pumping Station Site)

RTMP no. **L1123**

 Legal Land Description:
 LSD 13, Sec 11, Tp.13, Rg 9, W4.

 UTM:
 5546650 m N, 490100 m E
 Zone 12

Map name: Suffield Map number: 72E/14

Formation: Foremost Horizon: Upper unit Environment of deposition: lateral accretion

<u>PHR-2</u> (Pinhorn Range #2)

RTMP no. L1124

Legal Land Description: LSD 4, Sec 22, Tp. 2, Rg 7, W4. UTM: 5442025 m N, 509350 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Foremost Horizon: Upper unit Environment of deposition: shoreface

PHR-1 (Pinhorn Range #2)

RTMP no. <u>L1125</u>

Legal Land Description: LSD 1, Sec 21, Tp. 2, Rg 7, W4. UTM: 5442050 m N, 509200 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Foremost Horizon: Upper unit Environment of deposition: Shoreface

Ho S (Hoodoo site)

RTMP no. <u>L1126</u>

Legal Land Description: LSD 4, Sec 7, Tp. 2, Rg 7, W4. UTM: 5438725 m N, 504500 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Lower unit Environment of deposition: inchannel ÷. .

RTMP no. <u>L1127</u>

Legal Land Description: LSD 5, Sec 7, Tp. 2, Rg 7, W4. UTM: 5438950 m N, 504450 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Lower unit Environment of deposition: splay

EZ (EZ site)

RTMP no. L1128

Legal Land Description: LSD 5, Sec 7, Tp. 2, Rg 7, W4. UTM: 5439150 m N, 504350 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Lower unit Environment of deposition: splay

PHS (Pinhorn South Site)

RTMP no. <u>L1129</u>

Legal Land Description: LSD 2, Sec 2, Tp. 2, Rg 7, W4. UTM: 5436950 m N, 511725 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Lower unit Environment of deposition: splay

PLS (Prairie Level Site)

RTMP no. **L1130**

Legal Land Description: LSD 6, Sec 36, Tp. 1, Rg 6, W4. UTM: 5436000 m N, 523050 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: inchannel

HAS (Hanna's Ankylosaur Site)

RTMP no. L1131

Legal Land Description: LSD 10, Sec 36, Tp. 1, Rg 6, W4. UTM: 5436500 m N, 523150 m E Zone 12 Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: splay

HS (Hanna's Site)

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RTMP no. <u>L1132</u>

Legal Land Description: LSD 8, Sec 34, Tp. 2, Rg 6, W4. UTM: 5445550 m N, 520300 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit

PHR 93-2 (Pinhorn Ranch #93-2)

RTMP no. L1133

Legal Land Description: LSD 13, Sec 23, Tp. 2, Rg 7, W4. UTM: 5443175 m N, 511100 m E Zone 12

Map name: Calib Coulee

Map number: 72E/2

Formation: Oldman Horizon: Lower unit Environment of deposition: inchannel

<u>CS</u> (Confluence Site)

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RTMP no. L1134

Legal Land Description: LSD 9, Sec 34, Tp. 2, Rg 6, W4. UTM: 5445850 m N, 520500 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: splay

<u>Sal S</u>. (Salamander Site)

RTMP no. <u>L1135</u>

Legal Land Description: LSD 9, Sec 35, Tp. 1, Rg 6, W4. UTM: 5436350 m N, 521900 m E Zone 12

Map name: Calib Coulee Map number: 72E/2 Formation: Oldman Horizon: Nesmos unit Environment of deposition: spaly

<u>CN-2</u> (Cecil Nesmos #2)

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RTMP no. <u>L1136</u>

Legal Land Description: LSD 12, Sec 35, Tp. 1, Rg 6, W4. UTM: 5436100 m N, 520800 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: spaly

<u>CN-1</u>(Cecil Nesmos #1)

RTMP no. <u>L1137</u>

Legal Land Description: LSD 16, Sec 34, Tp. 1, Rg 6, W4. UTM: 5436600 m N, 520575 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: splay

ORS (Old Road Site)

RTMP no. L1138

Legal Land Description: LSD 10, Sec 35, Tp. 1, Rg 6, W4. UTM: 5436300 m N, 521750 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Middle unit Environment of deposition: splay

<u>CBC</u> (Come-By-Chance)

RTMP no. **L1139**

Legal Land Description: LSD 2, Sec 10, Tp. 3, Rg 6, W4. UTM: 5448650 m N, 519550 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: channel

RTMP no. L1140

Legal Land Description: LSD 6, Sec 10, Tp. 3, Rg 6, W4. UTM: 5449025 m N, 519400 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: inchannel

<u>BMC</u> (Big Muddy-Channel Site)

RTMP no. L1136

Legal Land Description: LSD 5, Sec 31, Tp. 1, Rg 5, W4. UTM: 5435950 m N, 524950 m E Zone 12

Map name: Calib Coulee Map number: 72E/2

Formation: Oldman Horizon: Nesmos unit Environment of deposition: crevasse channel

Taxa	PHR-1	PHR-2	SPS	Ho S	WS	EZ	PHR93-2	CS	PHS	Sal S	HAS	HS	CN-1	CN-2	ORS	CBC	RDS	BMC	PLS
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Total	7375	6750	1738	1761	1782	720	813	1176	967	469	1301	1163	1150	289	747	779	942	233	358

Appendix II. Data matrix of vertebrate assemblages from microsites of the Foremost and Oldman formations in the Milk River area in southeastern Alberta. The numbers indicate the number of identifiable elements.

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Appendix III Sedimentological and Taphonomic Description of Vertebrate Microfossil Localities

The sedimentological and taphonomic description of the microsites herein was reproduced based upon unpublished field notes by D. A. Eberth (1997).

On the basis of sedimentology, these microsites are interpreted as being subdivisible into three sedimentary facies: in-channel deposits; crevasse splays deposits; and shallow marine deposits.

Key: O_1 =The lower unit of the Oldman Formation; O_2 =The middle unit of the Oldman Formation; O_3 =The upper unit of the Oldman Formation; F_2 =The upper unit of the Foremost Formation.

INCHANNEL DEPOSITS

PLS (O_3) : 4.5m below the double bentonite at the top of the section.

Vertebrate microfossil elements are concentrated in the basal 20 cm of a 1.9 m thick, fine-grained sandstone body. The host lithosome is composed of thinning-upward sets of medium- to large-scale trough cross-beds. The fossil-bearing bed represents an intraformational lag, which has a sharp contact on a rooted siltstone, with locally-cemented ironstone. Vertebrate microfossils are associated with incomplete and complete unionid valves, coaly debris, coalified wood and uncemented mudstone pebbles.

RDS— (O_3) : in the same area as the CBC site, but 5.5m higher in the section.

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The RDS fossil concentrate crops out within the lower 1.5m of a 4.5m thick multistorey, lenticular sandstone body (representing a palaeochannel deposit). Vertebrate fossils in RDS are associated with fragmentary to complete unionid valves, contorted mudstone, fine-grained sandstone, caliche clasts, and shale rip-ups, along with large unidentified dinosaurian skeletal fragments. The RDS lithosome represents a stacked succession of lags, and passes up into medium- to large-scale cross-beds.

PHR 93-2-(O1): 24.5m above the top of the Taber Coal Zone.

PHR93-2 occurs at the base of a palaeochannel deposit. The host lithosome is a 1.25m thick, fining-upward sandstone body, composed of 75 cm, large-scale trough cross-beds which then pass into heterolithic inclined beds. The heterolithic beds comprise fine-grained sandstone with abundant plant debris. Vertebrate microfossil remains occur in the transition from the crossbedding to the heterolithic inclined beds. Invertebrate shell material is conspicuously absent.

Ho S— (O_1) : just adjacent to the coulee housing Wendy's site, and 8.5m above the top of the Taber Coal Zone.

Ho S occurs in a 50 to 75 cm thick, silty sandstone body, which displays a complexly stratified, ripple laminated, and heterolithic succession. Above the host lithosome are abundant contorted heterolithic beds which contain organic
and coaly debris. It probably represents a complexly interbedded lateral accretion in a palaeochannel succession. Vertebrate microfossil remains are associated with abundant, small fragments of mainly gastropod and pisidiid shells and plant debris.

SPS—(F₂): located at Suffield Pumping Station in the South Saskatchewan River area, the only one that is not from the Milk River area. This site is immediately below the Taber Coal Zone.

The vertebrate microfossil concentrates occur at the base of fine grained, silty sandstone, associated with abundant shell fragments of gastropods and some pisidiids and small carbonaceous plant debris.

CREVASSE SPLAYS DEPOSITS

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BMC— (O_3) : 17m below the double bentonite at the top of the section.

BMC occurs at the base of a muddy, sandy, clayey, siltstone/ sandstone. The brownish lower portion of the host lithosome indicates the presence of rich plant fragments. The lithosome fines and lightens upward into muddy, grey-togreen siltstone, which contains coalified roots. The entire host lithosome is a lens-shaped deposit that is 25 m wide and 75cm thick at its deepest. Vertebrate microfossils are associated with abundant tree branches and gymnosperm leaves. A large, complete theropod phalanx was also found very close to the microsite. Invertebrate shell material is strikingly absent in this site. **CBC**— (O_3) : located in the same area as RDS, but is 5.5m stratigraphically lower. It is suggested that CBC is at the base of the upper unit of the Oldman Formation

CBC occurs in a 60cm thick, sandy, clayey siltstone. The host lithosome shows very poor internal organization and becomes coarser upward, which may suggest multiple flood events. Vertebrate microfossils, concentrated at the flat base of the lithosome, are associated with shell fragments, mainly unionids with some gastropods and pisidiids and poorly-sorted caliche clasts.

EZ—(O₁): 27.5m above the top of the Taber Coal Zone.

EZ occurs at the base of a 1.5m thick carbonaceous, clayey, silty sandstone and mudstone. The host lithosome is evidently contorted, indicative of multiple lags. Vertebrate microfossils are associated with abundant shell fragments of pisidiids, unionids and gastropods.

HS and CS—(O₂)

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The two sites are associated with muddy sandstones. And their vertebrate microfossil remains are mixed with small invertebrate shell fragments, most of which are pisidiid shells, with some unionid shell fragments.

These two sites were not revisited for sedimentological and taphonomic examination after being sampled due to their location in privately-owned land. Because they are located in the adjacent coulees and close to RDS, it is estimated that their stratigraphical horizon is about the same as that of RDS in the section. **PHS**— (O₁): 35m above the top of the Taber Coal Zone.

PHS occurs in a tabular, flat-bedded, carbonaceous, clayey, silty sandstone. The host lithosome is about 75cm thick, and fines upward into siltstone, with the presence of contorted structure and local iron staining. Vertebrate microfossils are associated with coaly fragments, plant debris, and shell fragments of unionids, gastropods and pisidiids.

ORS— (O_2) : 7m below the base of the upper unit.

ORS occurs in a muddy, carbonaceous, clayey, silty sandstone body. The host lithosome is 1.5m thick, and fines upward into a muddy, sandy, carbonaceous siltstone. Vertebrate microfossils are associated with predominantly pisidiid shell fragments that are very well sorted. No obvious shell fragments of unionids are present.

CN-1— (O_3) : 6m above the top of the middle unit.

Vertebrate microfossils in CN-1occur in a 1.5m thick, massive siltstone. The host lithosome is tabular, flat-bedded, and fines upward. Abundant shell fragments of unionids and gastropods are associated with the vertebrate microfossil remains.

CN-2— (O_3) : 4.5m above the uppermost sandstone sheet of the middle unit.

CN-2 occurs in a 1.1m thick, muddy, clayey, silty sandstone. The host lithosome contains rich organic material, which is indicated by its evident brown

color. Vertebrate microfossil remains are associated with abundant predominantly pisidiid shell fragments.

HAS—(O₃): 14.5m below the double bentonite layers of the section.

HAS occurs in a 1.0m thick, brown, organic-rich, clayey, silty sandstone. The host lithosome is a vaguely to poorly developed planar stratified type, with the upper half being contorted and without obvious sedimentary structures. Vertebrate microfossil remains are associated with abundant shell fragments of pisidiids and very few unionids, and with coalified plant debris.

Sal S—(O₃): about 20 to 30m above the middle unit.

The vertebrate fossil concentrate in SAS occurs in a 0.75 to 1.0m thick, tabular, carbonaceous, silty sandstone. The host lithosome pinches out 30m to the north, and passes into stacked ripple laminations with local ironstone 20m to the south. Vertebrate microfossils are associated with abundant shell fragments of gastropods and unionids, and poorly-sorted plant debris.

WS-(O1): about 10m above the Taber Coal Zone.

WS occurs in a 30 to 50cm thick, clayey, silty sandstone. The host lithosome is somewhat contorted, with interbeds of clean and carbonaceous sandstone, and represents a part of a stacked splay succession. Vertebrate microfossil remains are associated with abundant shell fragments of mainly unionids and some small, disarticulated gastropods, along with abundant carbonaceous to coaly plant debris.

SHOREFACE DEPOSITS

PHR-1—(F₂): at the base of the third unit of the Foremost Formation, 25m below the Oldman Formation.

Vertebrate microfossils in PHR-1 occur at the base of a massive (about 3.5m thick), fine-grained sandstone body, which rests sharply on the underlying dark marine shales of the fourth parasequence of the middle (mudstone) succession. The overlying sandstone body comprises low angle to planar sets of ripple-laminated sandstone, with a massive and pebbly base that is traceable about 10m laterally. It is interpreted as a regressive surface of erosion that is related to a drop in relative sea-level. Vertebrate microfossil remains, including both marine and non-marine, are associated with carbonaceous plant debris, with conspicuously rare invertebrate shell fragments.

PHR-2—(F_2): sits in the stratigraphic horizon equivalent to PHR-1, but is about 400m east of the PHR-1 site.

Vertebrate microfossil remains at the PHR-2 site are concentrated at the base of a 3.5m thick sandstone, which comprises alleviating silty sand and finely laminated shales. The host lithosome sits with sharp contact on the fourth parasequence of the middle (mudstone) succession. The lateral extent of the site is traceable for a few meters. Abundant invertebrate shell fragments

of <u>Corbula</u>, <u>Ostrea</u> and other unidentified marine clams are associated with the vertebrate microfossils.