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# Vertebrate palaeocommunities of the lower Judith River Group (Campanian) of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages

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## Abstract

A palaeoecological analysis of vertebrate assemblages of the upper Cretaceous Foremost and Oldman Formations based on data from 19 microfossil localities in the Milk River area of southeastern Alberta is presented. R-mode cluster analysis reveals two groups of taxa showing significant difference in their relative abundance. Q-mode cluster analysis, which was used to group sites into clusters containing similar faunal assemblages, resulted in three groups of localities that are highly congruent with their stratigraphic position but not with taphonomic indicators or facies associations. Members of two palaeocommunities are identified based on these distribution patterns. Through comparison with corresponding palaeocommunities previously recognized in Dinosaur Provincial Park, Alberta—about 200 km to the north and largely later in time—the stability of palaeocommunity structure over an approximately 5-million-year time period is evaluated. In general, palaeocommunity structure through the lower beds of the Judith River Group corresponds to the structure of palaeocommunities in the upper beds. Differences can be attributed to extinction events and environmental controls on the north–south distribution of taxa.

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## 1. Introduction

The organization of late Cretaceous dinosaur palaeocommunities has been the subject of inten-

sive palaeoecological studies. Many of these have focused on the Judith River Group (Campanian) of southern Alberta. The diversity of vertebrates and the abundance of palaeontological resources in this unit have allowed statistical approaches to be used to identify palaeocommunities. Generally, palaeocommunities are construed to be groups of taxa that coexisted in a given area or environment and

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were part of a single food (energy) complex. We use the term palaeocommunity rather than palaeofauna because of the explicit assumption that the included taxa were part of a single energy complex. One of the first steps in defining palaeocommunities is to identify groups of geographically restricted, interacting taxa. In one of the first quantitative palaeoecological studies of the Dinosaur Park palaeofauna that attempted to define geographically distinct associations, [Béland and Russell \(1978\)](#) examined the distribution of dinosaur remains across Dinosaur Provincial Park. Differences in the relative abundance of different kinds of dinosaurs in different stratigraphic or geographic regions were interpreted as having a palaeoecological basis. [Dodson \(1983, 1987\)](#) used surface collections from vertebrate microfossil localities as one source of data in a study aimed at establishing the relative abundance of dinosaurs and other vertebrates in exposures of the Judith River Group in Dinosaur Provincial Park. Dodson recognized that vertebrate microfossil localities are significant for studies of the palaeoecology of late Cretaceous non-marine vertebrate palaeocommunities because they are generally taxonomically diverse and include most of the taxa known as macrofossils from the beds in which they occur, as well as the remains of vertebrates known only from the microfossil sites. Also, the large sample sizes obtainable from single localities allows quantitative approaches to be used to develop and test palaeoecological hypotheses. Through comparison of the relative abundance of vertebrates in vertebrate microfossil localities with the relative abundance of vertebrates as documented by articulated specimens, Dodson established the basic structure of the Dinosaur Park palaeofauna.

Palaeoecological complexity within the Dinosaur Park palaeofauna was documented by [Brinkman \(1990\)](#), who used screenwash data from vertebrate microfossil localities preserved in a variety of environmental and stratigraphic settings in the Dinosaur Provincial Park area to identify patterns of distribution of vertebrates throughout this unit. Taxa with a similar stratigraphic distribution were assumed to have coexisted in a given area and have been part of a single food (energy) complex, and thus were members of the same palaeocom-

munity. Since these beds were deposited during the transgressive phase of the Bearpaw Sea, the ecological basis for the distribution patterns was assumed to reflect position on the coastal plain relative to the shoreline. Thus, coastal and inland palaeocommunities were differentiated. The hypothesis that these stratigraphic distribution patterns reflected differences in distribution along the coastal plain relative to the shoreline was later tested by comparing the abundance of taxa in vertebrate microfossil localities along an east–west transect from the relatively more inland Dinosaur Provincial Park area to relatively more coastal localities in the area of the South Saskatchewan River, about 100 km to the east ([Brinkman et al., 1998](#)).

These studies have focused on the upper beds in the group (the Dinosaur Park and the upper Oldman Formations), particularly in the Dinosaur Provincial Park area, and have documented significant palaeoecological complexity within this unit. The lower two thirds of the Judith River Group have remained largely unstudied. One of the goals of palaeoecology is to understand the changes of ecosystems through time, which encompasses evolutionary palaeoecology ([Behrensmeyer and Hook, 1992](#)). Towards this end, a study of the vertebrate assemblages in the lower portion of the Judith River Group was undertaken. The lower beds of the Judith River Group were deposited during the regressive phase of this clastic wedge, so the transition from marine to non-marine environments in this sequence should mirror the transition from non-marine to marine environments that occurred during the transgressive phase of the upper Judith River Group. That this is the case is documented by changes in the sediments. Shoaling upwards parasequences at the base of the Judith River Group are overlain by a paralic succession comprised of complexly interbedded coals, shales and sandstones representing a complex of back-barrier facies, and these are overlain by fluvial sands. At the top of the Judith River Group, fluvial beds are overlain by coals of the Lethbridge Coal Zone and these are overlain by interbedded non-marine sands and marine shales. Because the change in environments through the lower Judith River Group mirrors the change through the upper Judith River Group, the pattern of change of

palaeocommunities preserved in the lower beds should mirror the pattern through the upper beds. Superimposed on this will be differences related to different palaeoenvironmental conditions, so in addition to testing hypotheses of palaeocommunity structure developed previously, the effects of environment and taphonomic processes on palaeocom-

munity structure over the five million year period represented by the Judith River Group in southern Alberta can be evaluated. The objective of this study is to both further our understanding of the structure of the Judith River Group palaeocommunities and examine the stability of this palaeocommunity through this time period.

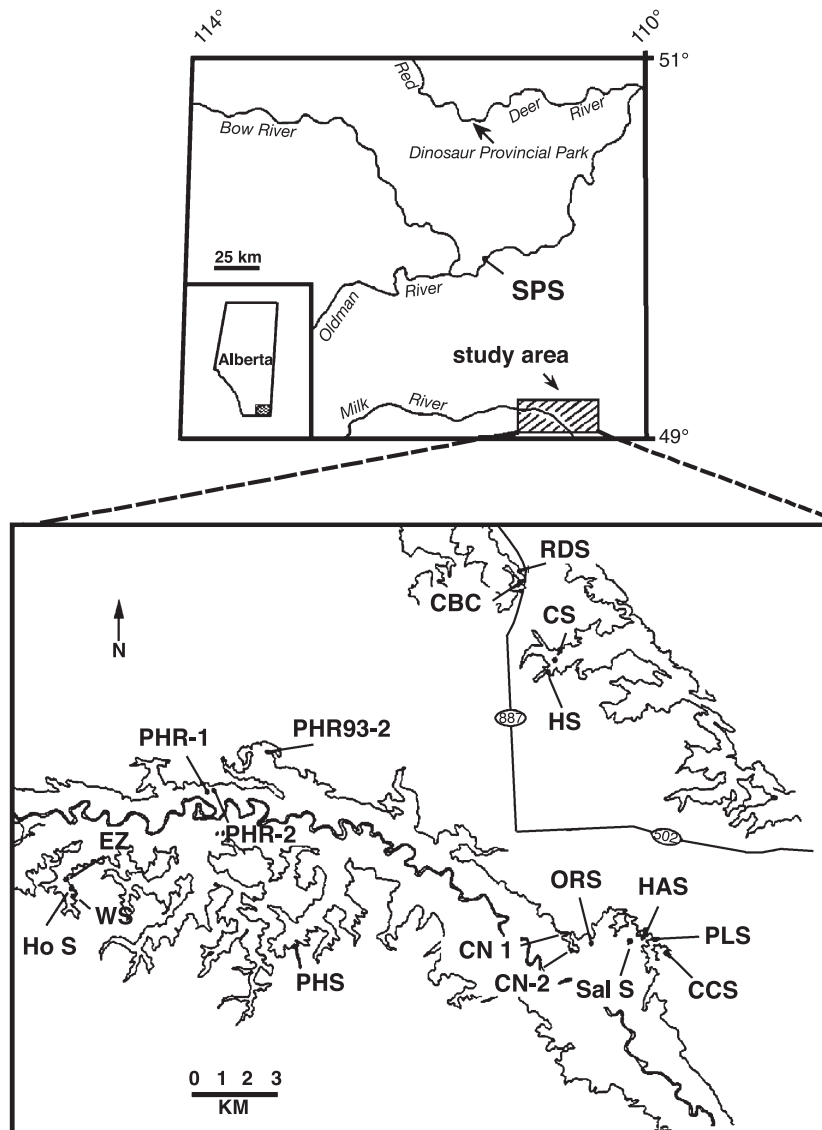


Fig. 1. Locality map showing the geographic distribution of vertebrate microfossil sites from the Judith River Group in southeastern Alberta. The location of the site SPS is shown in the upper map, and the remainder of the 18 sites occur in the Milk River drainage area, as depicted in the lower map.

## 2. Geological setting

### 2.1. Localities sampled

Nineteen localities in southeastern Alberta were sampled (Fig. 1). Eighteen of these occur in the Milk River area, about 200 km south of Dinosaur Provincial Park. One site, SPS, is located on the South Saskatchewan River, midway between the Dinosaur Provincial Park and Manyberries areas. These localities have been assigned both a Royal Tyrrell Museum of Palaeontology locality number (indicated with the suffix “L”) and a common name (Table 1). The sites are referred to in this paper by their common name. Land descriptions, UTM coordinates, geological information, and sedimentological and taphonomic details for these sites are provided by Peng et al. (2001, Appendices 1 and 2). The excavated material from the vertebrate microfossil localities was screened using a number 20 American Standard Sieve size screen (mesh size 0.85 mm). Generally, 300 kg were processed from each site. A minimum of 250

identifiable specimens were recovered from each site included in this study. In many sites, this number was greatly exceeded.

### 2.2. Stratigraphic distribution and sedimentological associations of localities

Localities are stratigraphically distributed through the Foremost and Oldman Formations (Fig. 2), which are part of the Campanian Judith River Group (Eberth and Hamblin, 1993). The Foremost Formation includes a sequence of non-marine and brackish-water or marine environments (Ogunyomi and Hills, 1977, Fig. 3). Two localities in the Manyberries area and the single locality from along the South Saskatchewan River are located in the upper part of the Foremost Formation. The Oldman Formation is fully non-marine, and has been divided into three informal units, a lower mud-dominated unit, a middle sand-dominated unit (the Comrey Sandstone zone) and an upper mud-dominated unit (Hamblin, 1997). Vertebrate microfossil localities were sampled from each of these units. Correlations between the Judith River Group in the Dinosaur Provincial Park and Manyberries areas, based on surface and subsurface data, were published by Eberth and Hamblin (1993). The boundary between the Dinosaur Park and Oldman Formations in Dinosaur Provincial Park is approximately equivalent to the boundary between the Comrey Sandstone unit and the upper muddy unit of the Oldman Formation in the Manyberries area. Thus, the Comrey Sandstone zone in the Manyberries area is equivalent to the exposures of the Oldman Formation in Dinosaur Provincial Park and the upper unit of the Oldman Formation in the Manyberries area is temporally equivalent to the lower portion of the Dinosaur Park Formation in the Dinosaur Provincial Park area. The lower muddy unit of the Oldman Formation and the Foremost Formation are below the exposed section in Dinosaur Provincial Park. The base of the Foremost Formation in southern Alberta has been dated radiometrically at 79.14 Ma. The top of the Dinosaur Park Formation has been dated at approximately 74.5 Ma (Eberth and Deino, 1992).

Table 1 summarizes the sedimentary associations of the 19 vertebrate microfossil localities that were sampled. Seventeen are associated with one of two sedimentary facies, in-channel and splay deposits, with identifying characteristics recognized by Eberth

Table 1

Sedimentary facies associations of the 19 vertebrate microfossil localities of the Foremost and Oldman Formations in the Milk River area of southern Alberta

RTMP locality no.	Common name	Sedimentary subenvironments
<i>In-channel deposits</i>		
L1130	PLS	Palaeochannel
L1140	RDS	Palaeochannel
L1133	PHR93-2	Lateral accretion
L1126	Ho S	Lateral accretion
L1123	SPS	Lateral accretion
<i>Splay deposits</i>		
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
<i>Shoreface deposits</i>		
L1124	PHR-1	Regressive lag
L1125	PHR-2	Regressive lag

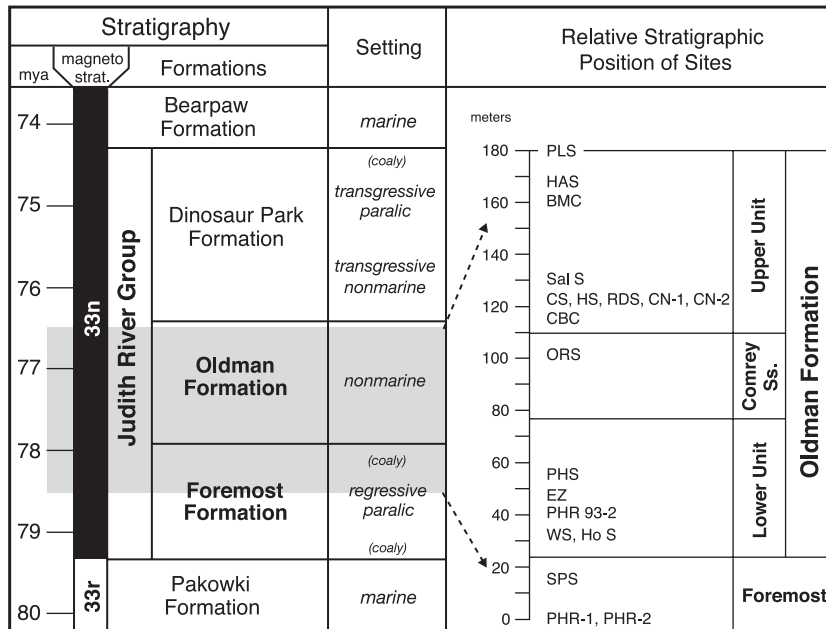


Fig. 2. Stratigraphic positions of the vertebrate microfossil localities sampled from the Judith River Group in the Milk River area of Alberta. Locality coordinates for these sites are on file at the Royal Tyrrell Museum of Palaeontology and are available in Peng et al. (2001, Appendix 1).

(1990). In the in-channel deposits, the vertebrate microfossils were preserved in two settings. In two sites, the fossil material was preserved as a lag at the base of the channel. In the remainder, material was preserved on lateral accretion surfaces. The splay deposits were also of two types, laterally continuous sheets and channel-shaped deposits, termed crevasse splay and crevasse channel in Table 1. The two localities in the Foremost Formation in the Milk River area (PHR-1 and PHR-2) are preserved in shoreface deposits, with vertebrate microfossil remains concentrated along erosional surfaces. This is the first record of vertebrate microfossil localities preserved in this sedimentological setting in the Judith River Group of Alberta.

### 2.3. Taphonomic features

Although these vertebrate microfossil localities are preserved in a variety of sedimentological settings, the specimens show a similar range of preservational features, suggesting that these accumulations are the result of similar taphonomic processes. The following shared preservational features were observed: (1) the assemblages show a similar bias towards enamel-

covered elements, such as teeth and scales; (2) although abraded fragments dominate, elements that are delicate and/or less physico-chemically resistant (e.g., teleost centra and dinosaur eggshell) are also present; (3) samples exhibit similar size-frequency distributions.

A similar size-frequency distribution has been identified as particularly significant in evaluating taphonomic comparability of vertebrate microfossil sites. 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, and that such variation could result in different taxonomic compositions. The authors suggested that non-diagnostic specimens be used to determine the size-frequency distribution of fossils at different sites, and that if these distributions were sufficiently similar, then taphonomic explanations for faunal differences among the sites could be rejected (Blob and Fiorillo, 1996, p. 431). Thus, in the present study, size profiles of unidentified specimens (Appendix B, Fig. 3) were generated and utilized to quantify differences in size-frequency distributions in each of the vertebrate microfossil localities sampled. These were then compared with one another in order to determine

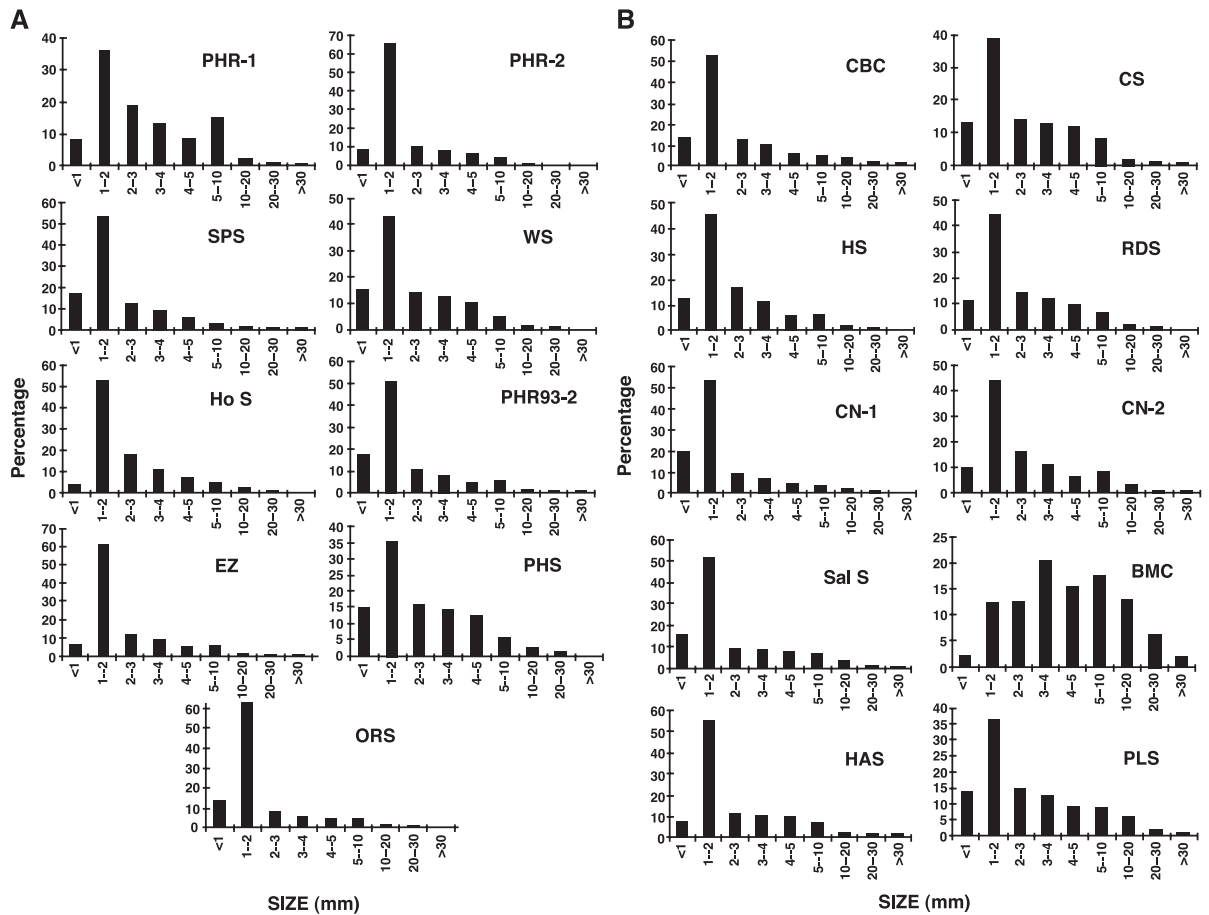


Fig. 3. Size distributions of unidentified vertebrate specimens from vertebrate microfossil localities in the Milk River area. (A) sites in the Foremost and lower and middle units of the Oldman Formation; (B) sites from the upper unit of the Oldman Formation.

whether significant differences are present in the size-frequency distribution of material preserved among the vertebrate microfossil localities.

Specimens less than 10 mm were sorted at increments of 1 mm via the use of American Standard sieves. Those specimens greater than 10 mm were sorted with metal screens at increments of 10 mm. Specimens recovered from the vertebrate microfossil localities examined in this study are predominantly smaller than 10 mm in size (Fig. 3). For all the sites except BMC (the site with the largest size-frequency distribution), the size distributions are skewed toward a range of 1–5 mm, each with a mode of 1–2 mm. In BMC, the mode is 3–4 mm. Non-parametric Kolmogorov–Smirnov tests were applied in the comparison of these size-frequency distributions to test whether or not

this size difference was significant. The null hypothesis that the size-frequency distributions among the sites are not significantly different from each other cannot be rejected at the significance level of 0.05. The similarity in the size-frequency profiles of the vertebrate microfossil localities sampled, together with the similarity in preservational features, suggests a similar degree of transportation and reworking, and reinforces the interpretation that faunal differences have a biological, rather than taphonomic, basis.

The similarity in taphonomic features and size-frequency distribution of material recovered from these sites suggests that processes common to a number of separate environments were involved in the formation of these sites. These could include pre-transport biological processes and cycles of rework-

ing, concentration and deposition in the fluvial and near-shore environments.

### 3. Distribution patterns

#### 3.1. Taxonomic units

The 78 taxonomic groups recognized in the assemblage are reviewed elsewhere (Peng et al., 2001). The number of identifiable elements of each taxon from each vertebrate microfossil locality sampled is listed in Appendix A. Since the number of identifiable elements varies from taxon to taxon, the number of identifiable elements present is not a reflection of the abundance of elements in the original community. However, since the sites being compared are taphonomically similar, differences in the relative abundance of a taxon in the sites being compared should reflect differences in the importance of that taxon in the localities from which the sample was derived. Sample size is significant in estimating whether or not a difference in abundance is significant. Although total sample size per locality is generally high, many of the rare taxa are represented by very few specimens. For example, the xenosaurid lizard is restricted to the lower unit of the Oldman Formation,

but this is based on only two osteoderms collected from two sites. Taxa represented by a small number of specimens were generally lumped together with their close relatives and treated at higher taxonomic levels to give operational taxonomic units with significant sample sizes. However *Rhinobatos*, *Squatirhina* and *Synechodus*, which are each represented by fewer than 10 specimens in total, are treated at the generic level because a study of elasmobranchs from a locality in the same geographic region, but stratigraphically lower in the Foremost Formation, reported abundant specimens of these taxa (Beavan, 1995).

#### 3.2. Stratigraphic distribution of taxa

Range charts showing the distribution of the operational taxonomic units that are not found throughout the sequence (Fig. 4) are based on all available material, and thus include data from surface collected and screenwashed specimens. The pattern of distribution of the two species of *Myledaphus* is most parsimoniously interpreted to be the result of change within a single evolving lineage. If this interpretation is correct, similar transition should be seen at other localities. In the absence of conflicting evidence, these two species are lumped together and treated at the generic level in this study.

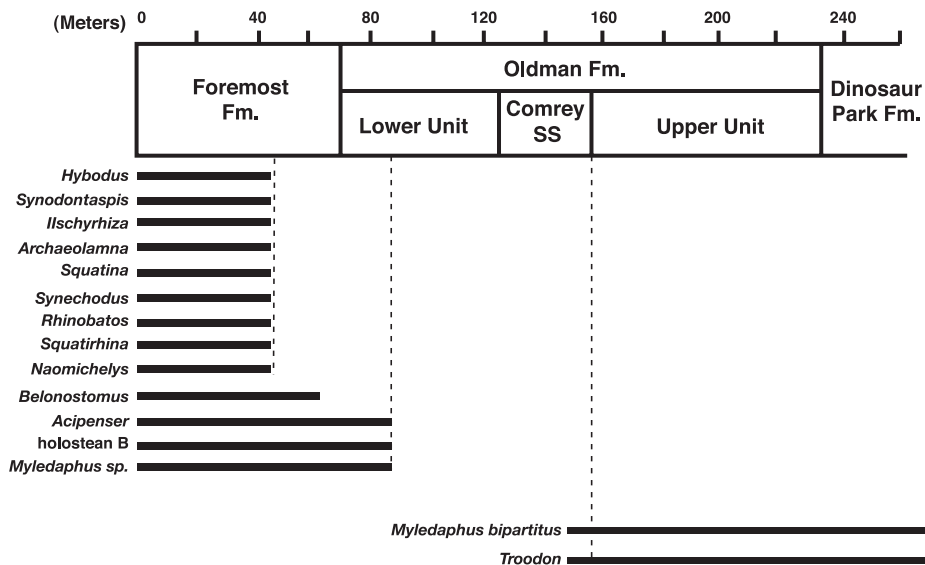


Fig. 4. The stratigraphic distributions of taxa from vertebrate microfossil localities in the Judith River Group in the Milk River area that are of limited stratigraphic distribution within the section sampled.

### 3.3. Cluster analysis

To identify groups of co-occurring taxa, cluster analysis was employed. Kovach (1989) demonstrated that the average linkage clustering method, when used with the Spearman rank order correlation coefficient, is the most suitable for palaeoecological data, which are typically non-normally distributed and have the potential for noisiness (i.e., possible randomness of occurrence of rare taxa). This approach is used here. Both R-mode and Q-mode cluster analyses were undertaken. The R-mode and the Q-mode are two basic approaches that have been widely applied in community studies (e.g., Dodd and Stanton, 1990). The R-mode analysis groups taxa into clusters with a similar pattern of distribution. The Q-mode analysis groups sites into clusters that share a similar fossil assemblage. The results of the R- and Q-mode cluster

analyses are shown in Figs. 7 and 8. The R-mode analysis results in the recognition of three major groups (Fig. 5, groups 1, 2 and 3). The Q-mode cluster analysis of the sites (Fig. 6) also reveals three major groups (groups I, II and III). A chart superimposing the R- and Q-mode cluster analyses and including data on the relative abundance of each taxon (Fig. 7) provides an overview of the range of variation in abundances of each taxon within each of these groups.

### 4. Palaeoecological interpretations

Three possible explanations for the groups of sites identified by the Q-mode cluster analysis can be considered. These are that the groups are the result of: (1) taphonomic processes, (2) palaeoecological

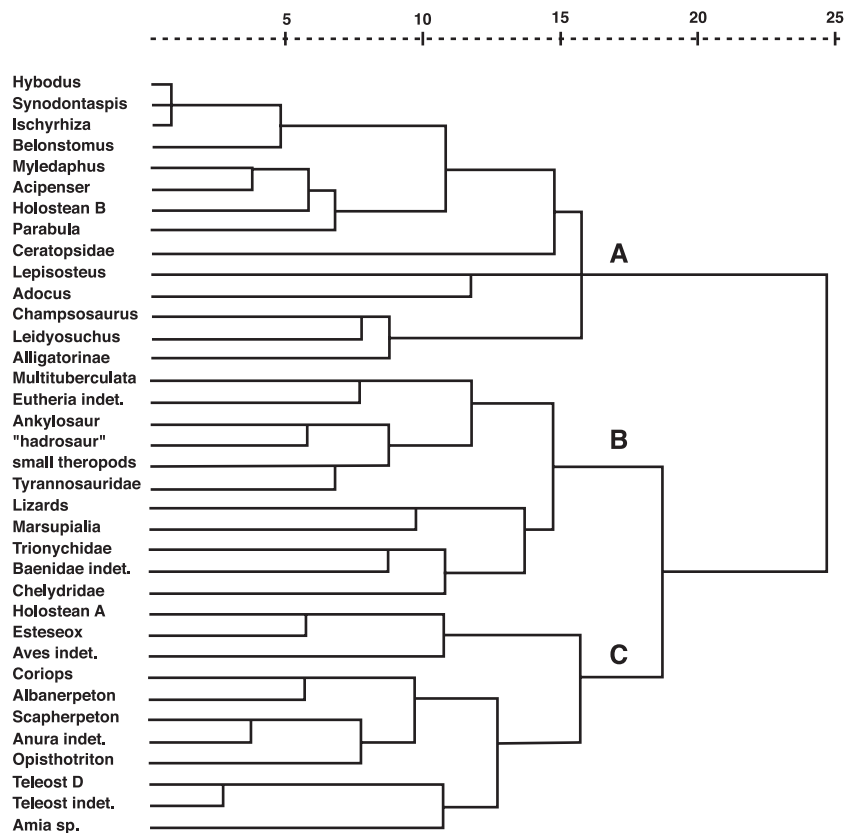


Fig. 5. Dendrogram from R-mode cluster analysis (using average linkage) of the vertebrate assemblages from the 19 microsites from the Judith River Group in the Milk River area. Shading indicates the three different groupings. The horizontal scale represents the rescaled distance cluster measure.



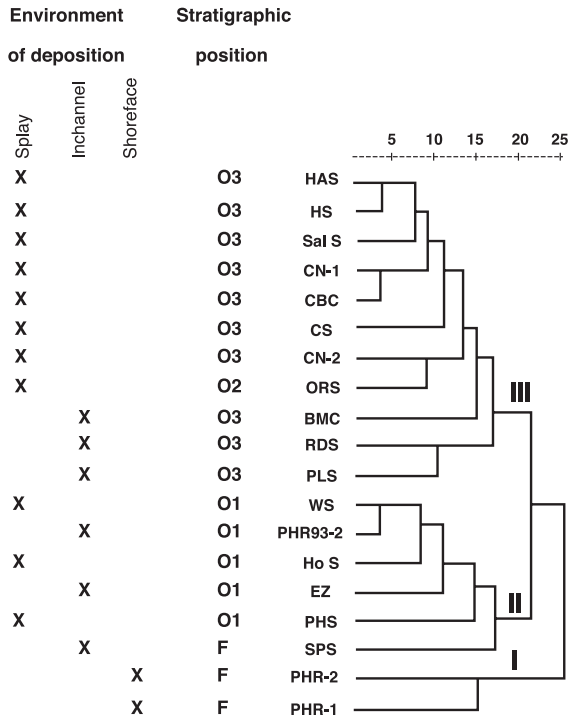


Fig. 6. Dendrogram from Q-mode cluster analysis (using average linkage) of the 19 microsites from the Judith River Group in the Milk River area, with the 3 associated sedimentary facies and the stratigraphic position of the localities superimposed. The horizontal scale represents the rescaled distance cluster measure. Abbreviations: F, Foremost; O1, lower unit of Oldman Formation; O2, middle unit of the Oldman Formation; O3, upper unit of the Oldman Formation.

differences in the local environment of deposition or (3) regionally significant differences in palaeocommunity composition. To resolve between these alternatives, the clusters can be compared with a series of criteria reflecting taphonomic processes, local environment of deposition and stratigraphic patterns of distribution, to identify the factors most strongly associated with them.

To test the hypothesis that the sites group for taphonomic reasons, the groups were examined for a correlation with size-frequency distributions. This was done by undertaking a cluster analysis of sites based on the size-frequency distribution of contained material and comparing the groupings resulting from these two cluster analyses. No correlation is present (Fig. 8).

To test for the presence of a correlation between local environment of deposition and groupings of the sites resulting from the cluster analysis, the types of sedimentary facies associated with each locality were

superimposed upon the dendrogram produced by the cluster analysis (Fig. 6). The two major types of sedimentary facies—in-channel and crevasse splay—are not closely related to the groupings in the dendrogram. However, the two microsites deposited in the shoreface facies (PHR-1 and PHR-2) do group together.

All three groups correlate strongly with stratigraphic distribution. Group I includes the sites in the middle portion of the Foremost Formation. Group II includes all the sites from the uppermost Foremost Formation and the lower unit of the Oldman Formation. Group III includes all of the sites from the middle and the upper unit of the Oldman Formation (Fig. 6). This pattern is consistent with the hypothesis that the groupings of taxa with similar stratigraphic distributions are ecologically based assemblages reflecting regionally significant differences in palaeocommunity composition with respect to distance from the shoreline.

The R-mode analysis of individual taxa (Fig. 5) identifies groups of taxa that tend to share a similar distributional pattern. To identify the relationship between abundance and stratigraphic position, taxa that occur throughout the sequence were examined for changes in relative abundance through the section. For this, the section was subdivided into the three stratigraphic intervals identified by the Q-mode cluster analysis. These are: (1) the lower Foremost Formation, (2) the upper Foremost Formation and the lower muddy unit of the Oldman Formation and (3) the Comrey Sandstone interval plus the upper muddy unit of the Oldman Formation. In order to test whether or not significant changes in abundance of taxa with respect to stratigraphic position are present, the Kruskal–Wallis test, a non-parametric ANOVA (Hollander and Wolfe, 1973; Zar, 1996), was employed. This test compares the relative abundance of each taxon among the three stratigraphic intervals, with each site being treated as one sample in its stratigraphic interval. Rank-order was used as a measure of the relative abundance of each taxon in a locality, with the most abundant taxon receiving the rank of one. The rank mean was assigned to ties. As is apparent in Fig. 9, some taxa show a successive change in abundance through the section, while for others the change is concentrated between two stratigraphic units. Pairwise Mann–Whitney tests were performed to determine whether the difference in abundance of a taxon between

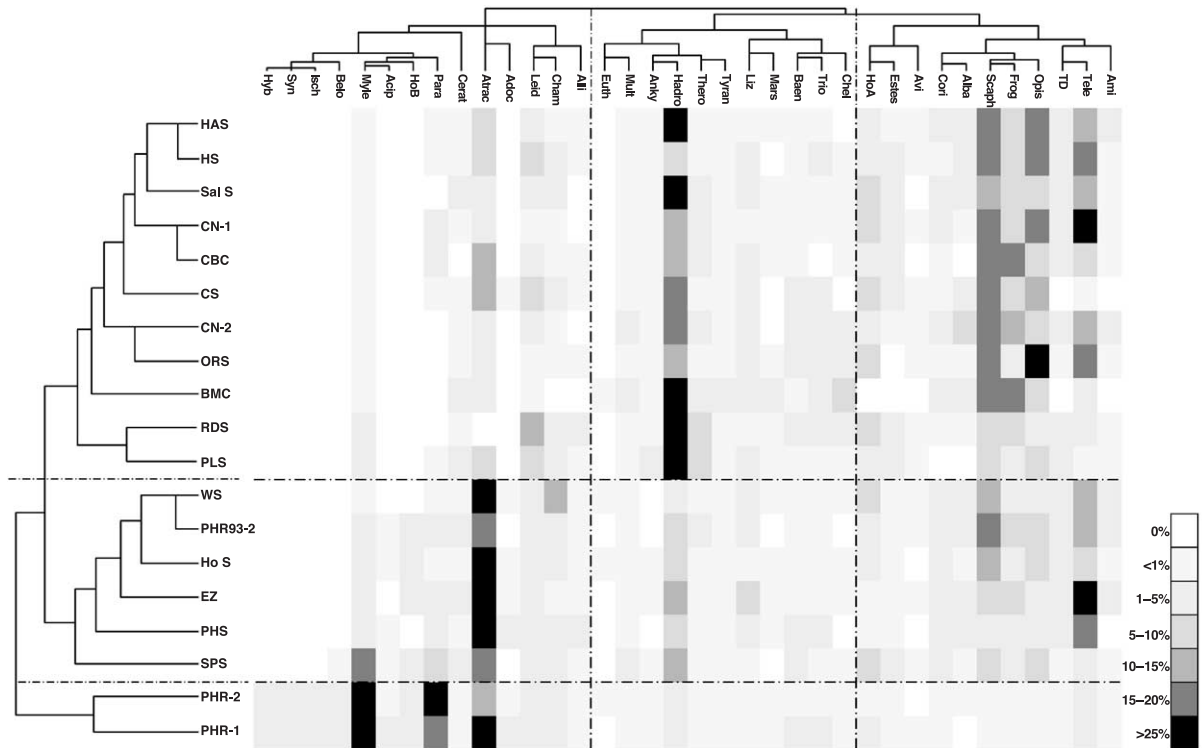


Fig. 7. Dendrograms of Q- (left) and R-mode (top) cluster analysis of the vertebrate assemblages of the Judith River Group in the Milk River area. The data matrix is displayed between the dendrograms. The legend on the right shows the relative abundance of taxa (in percentage). Dashed lines indicate the different clusters. Acronyms for the microsites are explained in Fig. 2 and Table 1. Taxon abbreviations are as follows: Acip., Acipenserids; Adoc, *Adocus*; Alba, *Albanerpeton*; Alli, Alligatorines; Ami, *Amia*; Anky, Ankylosaurids; Atrac, *Atractosteus*; Avi, Avians; Baen, Baenidae; Belo, *Belonostomus*; Cerat, Ceratopsids; Cham, *Champsosaurus*; Chel, Chelydrids; Cori, *Coriops*; Estes, *Estesesox*; Euth, Eutheria; Frog, Anurans; Hadro, Hadrosaurids; HoA, Holostean A; HoB, Holostean B; Hyb, *Hybodus*; Isch, *Ischyrhiza*; Leid, *Leidyosuchus*; Myle, *Myledaphus*; Opis, *Opisthotriton*; Para, *Paralbula*; Scaph, *Scapheperon*; Syn, *Synechodus*; TD, Teleost D; Tele, Teleosts; Thero, Theropods; Trio, Trionychids; Tyran, Tyrannosaurids.

two stratigraphic intervals is significant. The results of Kruskal–Wallis and Pairwise Mann–Whitney tests are presented in Table 2.

Cluster 1 of the R-mode cluster analysis includes all the taxa that show a significant decrease in abundance (Fig. 9), plus the taxa included in the cluster analysis that had a restricted stratigraphic distribution. These are *Hybodus*, *Synechodus*, *Ischyrhiza* and *Belonostomus*. Of the 10 taxa in cluster 1 that are present in each of the 3 stratigraphic intervals, 4 (*Myledaphus*, *Paralbula*, holostean B and *Adocus*) show a successive decrease in abundance through each of the 3 units sampled. The remaining 6 have a pattern in which the change in abundance is concentrated between two units. In the case of phyllodontids, *Leidyosuchus*, alligatorines, *Champsosaurus* and ceratopsids, the change in abun-

dance is concentrated between the lower two stratigraphic intervals (the Foremost and lower Oldman Formations). For *Atractosteus*, the change in abundance is concentrated between the lower and upper Oldman units.

Cluster 2 includes only taxa that do not show significant changes in their relative abundance. Thus, this cluster includes taxa that are equally abundant in the Foremost and Oldman Formations.

Cluster 3 includes all the taxa that show a significant increase in abundance (Fig. 10), and three taxa included in cluster 3 that show no significant stratigraphic change when their distribution is tested with the Kruskal–Wallis test. For all the taxa that increase in abundance, the increase occurs between the lower and middle stratigraphic intervals.

5. Discussion

5.1. Palaeocommunity organization within the lower Judith River Group

Brinkman (1990) argued that, given taphonomically equivalent samples, taxa sharing a similar distribution can be interpreted as members of a similar palaeocommunity. The taphonomic equivalency of the sites included in this study is indicated by the similarity in the bias towards enamel-covered elements, the presence of both abraded fragments and elements that are delicate and/or less physico-chemically resistant (e.g., teleost centra and dinosaur eggshell), and the size-frequency distribution of non-diagnostic material present. Thus, ecological factors can be regarded as the primary controlling factor for these distribution patterns. Since the groups of sites recognized in the Q-mode cluster analysis correlate most strongly with stratigraphic position, ecological factors related to stratigraphic position are identified as the most likely factors determining the palaeocommunity composition. The sites that cluster in group I (the lower two sites in the Foremost Fm.) would have been deposited in coastal settings, sites in group III

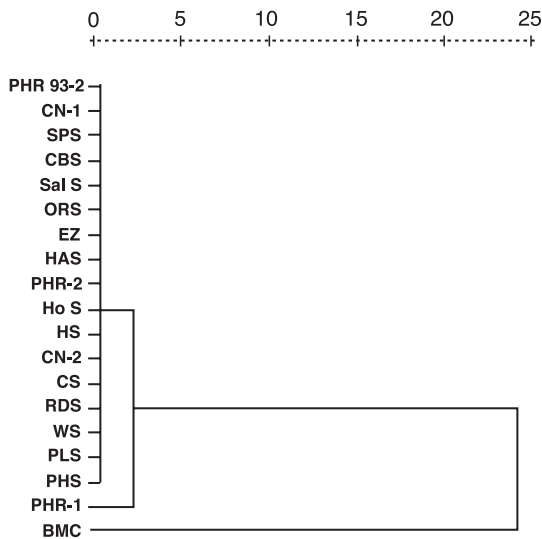


Fig. 8. Dendrogram from cluster analysis (using average linkage) on the size profiles of unidentified specimens among the 19 microsites from the Judith River Group in the Milk River area. Acronyms for the microsites are explained in Fig. 2 and Table 1. The horizontal scale represents the rescaled distance cluster measure.

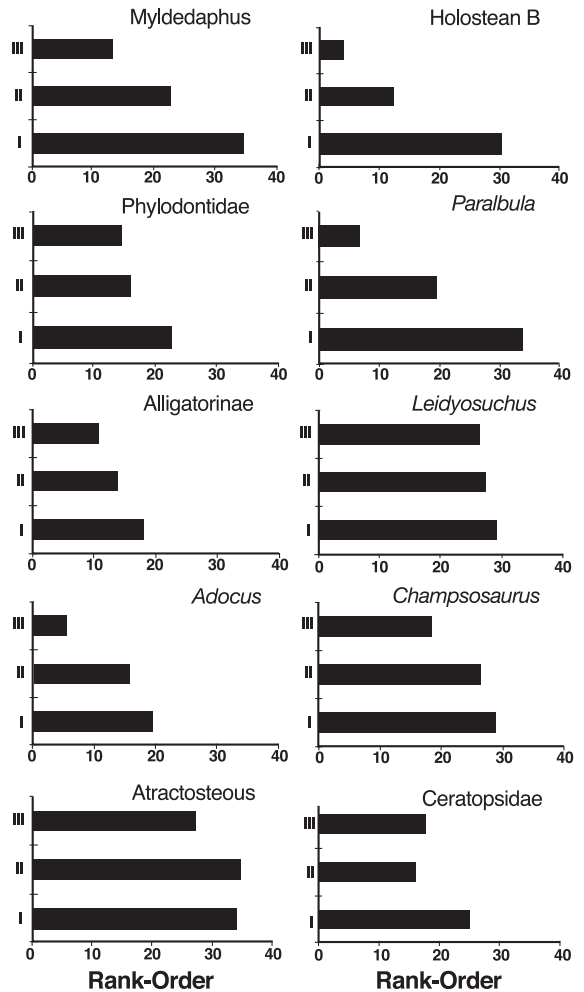


Fig. 9. Graphs showing taxa with a significant decrease in abundance through the Judith River Group in the Milk River area. The abundance is the average of the Rank order abundance for that taxon in all the vertebrate microfossil localities from that unit. The results of Kruskal–Wallis and Mann–Whitney tests for these taxa are listed in Table 2. I=upper Foremost, II=lower Oldman, III=upper Oldman.

would have been deposited farthest from the coastline in the most inland setting of the sites sampled, and sites in group II (the sites in the uppermost Foremost Fm. and the lower Oldman Fm.) would have been deposited in an area between the coastal and inland settings. Thus, taxa in cluster 1, which are all more abundant in the lower stratigraphic intervals than they are in the higher stratigraphic intervals, can be interpreted as preferentially members of a coastal palaeocommunity. Most of the taxa in cluster 3 also

Table 2

Results of the Kruskal–Wallis 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

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

For the Mann–Whitney test at a 95% level of confidence, *p*-values of 0.05 or less indicate that the difference in abundance of the two units being compared is significant. Abbreviations: F2=the upper Foremost, 01=the lower Oldman, 02=the upper Oldman unit.

show a stratigraphic pattern of distribution, in that they are more abundant in the higher stratigraphic intervals than they are in the lower stratigraphic intervals. Thus, this cluster can be interpreted as being preferentially members of an inland palaeocommunity. To these can be added the taxa not included in the analysis that show a restricted taxonomic distribution. Thus, *Nao-michelys*, *Archaeolamna*, *Squatina*, *Rhinobatos*, *Squatirhina* and *Synechodus*, which are restricted to the base of the sequence, are included in the group of taxa that are preferentially members of the coastal palaeocommunity, and *Troodon* is included in the inland palaeocommunity (Table 3).

Community membership, the aspect of palaeocommunity organization that is the focus of this study, is one of the first steps in palaeocommunity reconstruction. A further step is the estimate of relative abundance of a taxon within a palaeocommunity, and the degree to which a taxon is restricted to a palaeocommunity. The

variation in the degree to which a taxon is restricted to a palaeocommunity is illustrated by combining the results from both Q-mode and R-mode analyses (Fig. 7). Group I is distinguished by the high abundance of taxa that are identified as members of the coastal palaeocommunity. Within this assemblage, *Myledaphus*, *Belonostomus*, *Paralbula* and *Atractosteus* are of particularly high abundance. Group III, which includes all the sites from the upper Oldman and the uppermost site from the middle Oldman unit (ORS), is distinguished by the high abundance of taxa that are here identified as members of an inland assemblage. Within this assemblage, *Scapherpeton*, *Opisthotriton*, teleost indet. and anurans are of particularly high

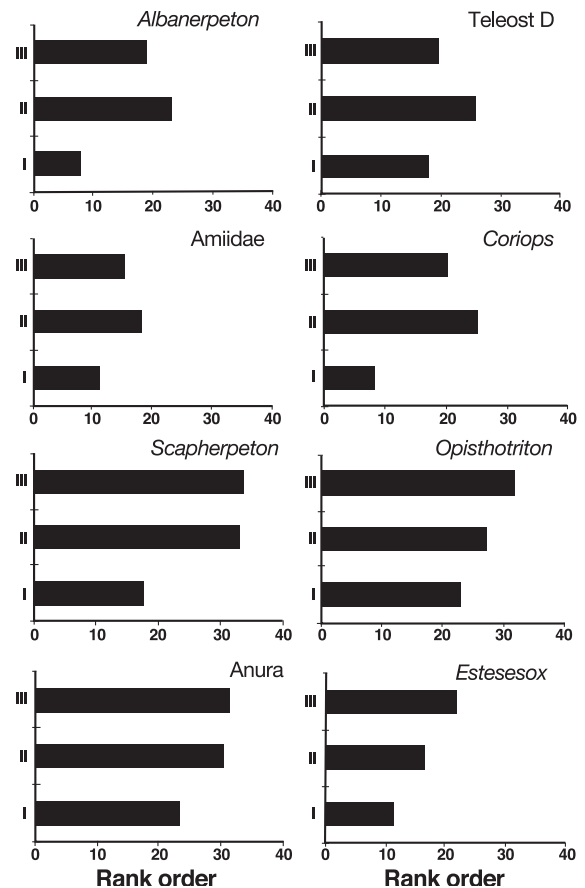


Fig. 10. Graphs showing taxa with a significant increase in abundance through the Judith River Group in the Milk River area. Abundance is the average of the rank order abundance for that taxon in all the vertebrate microfossil localities from that unit. The results of Kruskal–Wallis and Mann–Whitney tests for these taxa are listed in Table 2.

Table 3

Summary of composition two different vertebrate palaeocommunities hypothesized on the basis of stratigraphic distributions in the Judith River Group in the Milk River area

Coastal	Inland
<i>Hybodus</i>	Coriops
<i>Synodontaspis</i>	Esocoids
<i>Ischyrhiza</i>	Amiids
<i>Archaeolamna</i>	Teleost D
<i>Squatina</i>	Scapherpeton
<i>Rhinobatos</i>	Opisthotriton
<i>Squatirhina</i>	Albanerpeton
<i>Synechodus</i>	Anurans
<i>Myledaphus</i>	Troodon
<i>Belonostomus</i>	
Acipenserids	
<i>Atractosteus</i>	
<i>Parabula</i>	
Holostean B	
Phyllodontids	
<i>Leidyosuchus</i>	
Alligatorines	
<i>Champsosaurus</i>	
<i>Adocus</i>	
Ceratopsids	

abundance. Group II, which includes all the sites in the lower Oldman unit and SPS, is an intermediate assemblage. *Scapherpeton* and teleost indet., two of the members of the inland assemblage, and *Atractosteus*, one of the members of the coastal assemblage, are also of high abundance in these sites. Among the taxa that show no significant change in abundance through the stratigraphic interval measured, hadrosaurs are of highest abundance.

### 5.2. Palaeocommunity stability through the Judith River Group

Through a comparison of the results of this study with the results of a study of palaeocommunity membership in the upper portion of the Judith River Group (Brinkman, 1990), the composition of palaeocommunities across southern Alberta during the 5 million years represented by this interval can be evaluated. Table 4 provides a comparison of the taxa identified as preferentially members of inland and coastal palaeocommunities of the Manyberries area with their counterparts in the upper Judith River Group in the Dinosaur Provincial Park area. The coastal assemblages of these two areas show the greatest

number of differences, with over half of the taxa included in the coastal assemblage in the Manyberries area not identified as members of the coastal assemblage in the Dinosaur Provincial Park area. These contrasts are diminished, however, if differences resulting from dissimilar taxonomic treatments are taken into account. Two of the taxa identified as members of the coastal assemblage in the Manyberries area were not recognized in Dinosaur Provincial Park assemblages by Brinkman (1990), although they were subsequently shown to be present in his samples. These are the alligatorines, which Brinkman lumped with

Table 4

Comparison of members of vertebrate palaeocommunities recognized in this study and by Brinkman (1990)

	Milk River region (this study)	DPP (Brinkman, 1990)
Coastal	<i>Hybodus</i>	<i>Hybodus</i>
	<i>Myledaphus</i>	<i>Myledaphus</i>
	<i>Belonostomus</i>	<i>Belonostomus</i>
	<i>Atractosteus</i>	<i>Atractosteus</i>
	<i>Parabula</i>	<i>Parabula</i>
	holostean B	holostean B
	<i>Leidyosuchus</i>	<i>Leidyosuchus</i>
	<i>Champsosaurus</i>	<i>Champsosaurus</i>
	ceratopsids	ceratopsids
	<b><i>Synodontaspis</i></b>	<b><i>Paratarpon</i></b>
	<b><i>Ischyrhiza</i></b>	<b><i>Basilemys</i></b>
	<b><i>Archaeolamna</i></b>	<b><i>Aspideretoides</i></b>
	<i>Squatina</i>	
	<i>Rhinobatos</i>	
	<i>Squatirhina</i>	
	<i>Synechodus</i>	
	<i>Naomichelys</i>	
	<b>acipenserids</b>	
	<b>phyllodontids</b>	
	<b>alligatorines</b>	
<i>Adocus</i>		
Inland	<i>Coriops</i>	<i>Coriops</i>
	amiids	amiids
	teleost D	teleost D
	teleost indet.	teleost indet.
	holostean A	<i>holostean A</i>
	<i>Scapherpeton</i>	<i>Scapherpeton</i>
	<i>Opisthotriton</i>	<i>Opisthotriton</i>
	anurans	anurans
	Troodon	Troodon
	<b>esocoids</b>	<b>pachycephalosaurids</b>
	<i>Albanerpeton</i>	
	<b>bird</b>	

Taxa listed in boldface are those showing differences between the two studies.

*Leidyosuchus*, and phyllodontids, which Brinkman lumped with *Paralbula*. The two assemblages are also different in the presence of a series of marine sharks in the Milk River area coastal palaeocommunity that were not recovered in vertebrate microfossil localities in the Dinosaur Provincial Park area sampled by Brinkman (1990). However, a shark-dominated assemblage from the uppermost Lethbridge Coal Zone in the Dinosaur Provincial Park area described by Beavan and Russell (1999) and interpreted by them as a marine assemblage, includes many of the same shark taxa. Thus, their absence in the coastal assemblages of the non-marine beds of the Dinosaur Park Formation cannot be attributed to biogeographic patterns or extinction events. However, facies-related controls on their occurrence may be functioning in this case. These sharks are present in the Manyberries area only in vertebrate microfossil localities preserved in shoreline facies, a facies that has not been sampled in the Dinosaur Provincial Park area (Fig. 6).

The remaining contrasts represent potentially significant differences in the palaeocommunity composition of these two areas. In some cases, hypotheses concerning the palaeoecological significance of the differences can be developed from the patterns of distribution of the taxa.

The inclusion of the turtle *Naomichelys* in the Milk River area coastal palaeocommunity, but not in the Dinosaur Provincial Park coastal assemblage can be attributed to an extinction event. This taxon first occurs in the lower Cretaceous (Hay, 1908) and is abundant in the early Campanian Milk River Formation of southern Alberta, but is not known in the interior of North America above its occurrence in the Foremost Formation. Thus, the absence of this taxon from the coastal palaeocommunity of the Dinosaur Park area can be hypothesized to be a result of its extinction in the Western Interior.

The differences in the palaeocommunity membership of the turtle *Adocus* and the large elopomorph fish *Paratarpon* may reflect north–south biogeographic differences between these two areas. *Adocus* is present in the Dinosaur Provincial Park area, but is very rare and has not been recovered from any of the vertebrate microfossil assemblages that have been screened for the Dinosaur Park area. It is present in most screen-washed samples from the Manyberries area and is frequently encountered in surface collections in this

area. *Paratarpon* is present in the Dinosaur Park Formation in the Manyberries area (Bardack, 1970), but has not been recovered below the Dinosaur Park Formation and has not been reported from the Judith River Group of Montana or from Campanian beds further south. There is no evidence for a physical barrier between these two geographic areas, but climatic differences can be hypothesized on the basis of the more northerly position of Dinosaur Provincial Park. However, the difference between these areas is only 2° latitude, so the climatic differences are likely to be minor. Alternatively, these distribution patterns may reflect differences in the fluvial systems, such as the presence of larger meandering rivers in the Dinosaur Park Formation.

The remaining differences between the coastal assemblages of the two areas include the presence of *Basilemys* and *Aspiteroides* in the coastal assemblage of the Dinosaur Provincial Park area, but not the Manyberries area, and the inclusion of acipenserids in the coastal palaeocommunity in the Manyberries area, but not in Dinosaur Provincial Park. At present, there is no palaeoecological explanation for these differences.

The inland assemblages of the 2 areas are very similar, with 9 of the 10 taxa included in the inland assemblage in Dinosaur Provincial Park also being included in the inland assemblage in the Manyberries area. The differences that are present are reduced if different taxonomic treatments are accounted for. Esocoids were included in teleost indet. by Brinkman (1990), so these two categories can be considered to be equivalent, at least in part. As well, *Albanerpeton* material was not identified by Brinkman (1990), although it was subsequently shown to be present in his material (Gardner, 2000). Thus, it is presently of unknown distribution in Dinosaur Provincial Park.

Although *Troodon* is identified as a member of the inland assemblage in both areas, its distribution suggests that its stratigraphic distribution may be a reflection of its introduction into the assemblage as an immigrant from the north. *Troodon* is present in localities in the upper unit of the Oldman Formation but absent from the lower unit and from the Foremost Formation. It is also absent from the underlying Milk River Formation (Baszio, 1997a). Thus, the *Troodon* teeth recovered from the Oldman Formation in the course of this study represent the earliest occurrence

of this taxon in North America. Since troodontids are present in the Early Cretaceous of Central Asia (Barsbold et al., 1987; Russell and Dong, 1993; Currie and Peng, 1993), the group may have been introduced into North America from central Asia during the time of deposition of the Judith River Group. Alternatively, its first appearance in the Judith River Group may represent a range extension of a taxon that is more typically northern in its distribution. The second of these explanations is consistent with the observation that a high abundance of *Troodon* in early Maastrichtian localities in the north slope of Alaska suggests that it may have been a member of a northern vertebrate assemblage (Fiorillo and Gangloff, 2000).

The two remaining differences are the inclusion of pachycephalosaurids in the inland assemblage of Dinosaur Provincial Park but not the Manyberries area, and the inclusion of birds as members of the inland assemblage in the Manyberries area but not Dinosaur Park. These differences may be a reflection of biologically significant differences in palaeocommunity composition in these two areas, although sample sizes are small and further data are necessary to confirm this.

## 6. Conclusions

Palaeocommunity reconstruction is a complex, multistep process, with levels of interpretation ranging from considerations of palaeocommunity membership to relative abundance and interactions between palaeocommunity members. The goal of this study was to identify the distinctive members of palaeocommunities in the lower beds of the Judith River Group of southern Alberta. Data from vertebrate microfossil localities revealed two general associations of vertebrates in the lower Judith River Group. These are hypothesized as representing palaeocommunities that occupied distinct areas on the coastal plain with respect to the coastline. The results of this comparison demonstrate that, although palaeocommunity associations were generally stable through the time period documented by the Judith River Group, some palaeoecologically significant differences are present. One extinction event and a possible immigration event are identified. As well, the presence of a northern biogeographic zone including

the Dinosaur Provincial Park area and a southern biogeographic zone including the Manyberries area is indicated by differences in comparable palaeocommunities in these two areas. A northern and southern vertebrate assemblage has been hypothesized on the basis of the distribution of vertebrates during the mid-Campanian across western North America (Lehman, 1997). A northern and southern assemblage of small theropods was hypothesized by Baszio (1997b), and differences in the turtles of the Campanian of Mexico and Alberta were noted by Rodriguez de la Rosa and Cevallos-Ferria (1998). The greater abundance of *Adocus* in the southern localities in Alberta, and of *Paratarpon* in the more northern localities in Alberta suggests that biogeographic trends are also present within the much more limited geographical area of southern Alberta.

Although we attribute some compositional differences in these palaeocommunities to latitude, immigration and extinction, the overall compositions of inland and coastal palaeocommunities were stable through the five million years during which the Judith River Group was deposited. In this context, our palaeocommunities resemble chronofaunas (Olson, 1952), which have been interpreted as developing in response to ecological and environmental stability. Thus, the presence of multiple palaeocommunities that are compositionally stable during the mid-Campanian suggests that this was a time of environmental and climatic stasis in southern Alberta.

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Chelydridae indet.	21	1	4	14	5	2	0	15	0	3	0	1	9	15	23	6	10	12	2
<i>Naomichelys</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Baenidae indet.	93	2	18	2	11	1	4	16	13	4	5	6	5	8	10	6	14	2	2
<i>Champsosaurus</i> sp.	97	213	50	17	214	6	18	37	27	7	6	14	1	2	4	2	9	0	10
Alligatorinae indet.	10	15	5	3	9	2	1	3	11	1	1	0	0	0	1	2	18	0	3
<i>Leidyosuchus</i> sp.	112	190	33	28	73	11	19	90	40	19	20	82	11	5	3	19	100	1	27
Ceratopsidae indet.	52	12	2	3	8	11	10	10	2	15	10	12	18	2	5	17	19	5	6
Nodosauridae indet.	4	2	2	0	0	1	0	3	0	1	2	1	0	0	2	0	1	1	8
Ankylosauridae indet.	4	6	0	2	0	0	0	2	2	0	3	1	0	1	3	1	5	0	2
Pachycephalosauridae indet.	2	0	2	0	1	1	0	2	0	0	0	1	0	0	0	0	2	3	1
"Hadrosaur" indet.	178	263	162	83	61	101	65	219	93	132	268	108	136	50	99	87	295	54	128
<i>Dromaeosaurus</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0	0
<i>Saurornitholestes</i>	7	18	2	6	7	1	11	6	7	5	8	4	10	1		7	41	4	25
<i>Richardoestesia</i>	3	3	0	2	0	0	0	2	0	0	2	2	0	2	2	3	7	0	1
<i>Troodon</i>	0	0	0	0	0	0	0	1	0	0	0	0	2	1	0	4	12	0	2
<i>Paranychodon</i>	0	1	2	0	2	0	1	1	1	1	2	3	0	1	1	0	0	1	2
<i>Aublysodon</i>	2	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0	1	0	0
Tyrannosauridae indet.	5	9	1	2	3	1	0	4	2	2	1	1	3	0	1	3	3	4	3
Aves indet.	3	0	3	0	3	1	1	2	0	0	2	4	2	1	3	0	2	0	1
<i>Meniscoessus major</i>	1	3	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
? <i>Cimolodon</i> sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Cimolomys clarki</i>	0	1	0	1	0	0	0	0	0	0	0	2	0	0	0	1	0	1	0
<i>Mesodma</i> cf. <i>primaeva</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	0
<i>Mesodma</i> cf. <i>antiqua</i>	0	0	0	0	0	1	0	0	0	0	1	1	0	0	0	2	0	2	0
<i>Cimexomys</i> sp.	0	0	0	1	0	0	0	0	1	0	0	3	0	0	0	2	0	0	0
Cimolomyidae indet.	3	0	0	1	0	0	0	0	0	0	3	0	0	0	0	1	0	1	1
Multituberculata indet.	2	2	29	3	2	1	1	3	4	4	6	1	2	4	2	2	3	5	2
<i>Pediomys prokrajci</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
<i>Pediomys</i> sp.	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Eodelphis</i> sp.	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Turgidodon russelli</i>	0	2	0	0	2	0	0	0	1	1	0	0	0	0	0	0	0	4	1
<i>Turgidodon praesagus</i>	1	0	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0
Peradectidae indet.	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Marsupialia indet.	0	0	0	0	0	0	0	2	2	0	1	0	3	0	4	2	2	2	0
<i>Cimolestes</i> sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gypsonictops</i> cf. <i>lewisii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Paranyctoides sternbergi</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Eutheria indet.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Theria indet.	0	0	9	0	0	0	0	4	0	0	0	0	0	1	2	0	1	0	0

## Appendix B

Size profiles (counts) of unidentified specimens from 19 vertebrate microsites from the Judith River Group in the Milk River area. Acronyms for the sites are explained in Fig. 2.

Sieve (mm)	PHR-1	PHR-2	SPS	Ho S	WS	EZ	PHR93-2	CS	PHS	Sal S	HAS	HS	CNI	CN2	ORS	CBC	RDS	BMC	PLS
>30	16	3	4	2	2	2	3	2	0	4	5	2	2	3	1	5	0	17	6
20–30	39	6	5	13	14	5	19	6	7	5	5	15	24	6	11	15	6	51	15
10–20	125	47	27	40	38	16	30	23	16	38	26	33	49	24	41	66	21	105	86
5–10	1333	282	85	131	148	104	165	82	43	95	164	183	100	87	155	181	98	144	140
4–5	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
2–3	1682	921	462	506	462	242	322	139	124	148	299	549	301	171	278	461	218	104	247
1–2	3248	6304	1966	1669	1412	1206	1693	392	284	826	1531	1487	1645	518	2406	1862	689	102	612
0–1	736	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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