J. Paleont., 76(4), 2002, pp. 751–763
0022-3360/02/0076-751$03.00

SMALL THEROPOD AND BIRD TEETH FROM THE LATE CRETACEOUS (LATE CAMPANIAN) JUDITH RIVER GROUP, ALBERTA

JULIA T. SANKEY,[1,2] DONALD B. BRINKMAN,[1] MERRILEE GUENTHER,[2] AND PHILIP J. CURRIE[1]

[1]Royal Tyrrell Museum of Paleontology, P.O. Box 7500, Drumheller, Alberta T0J 0Y0, Canada, and
[2]South Dakota School of Mines and Technology, Museum of Geology and Department of Geology and Geological Engineering, 501 E. Saint Joseph St., Rapid City 57701, <Julia.Sankey@sdsmt.edu>

ABSTRACT—A collection of over 1,700 small theropod teeth from the Judith River Group (Campanian; ~79.5–74 Ma) allows our understanding of the diversity and variation of small theropods in this assemblage to be refined. In addition to the previously recognized taxa, a series of morphologically distinct groups are recognized that may represent distinct taxa in some cases. Teeth with the *Paronychodon*-like features of a flat surface with longitudinal ridges on one side are resolved into a few discrete morphotypes. Two of these are included in *Paronychodon lacustris* and two additional morphotypes are hypothesized to represent distinct taxa, here referred to as *?Dromaeosaurus* morphotype A and Genus and species indet. A. The teeth of *Paronychodon lacustris* and *?Dromaeosaurus* morphotype A share a distinctive wear pattern that suggests tooth functioning involved contact between the flat surfaces of opposing teeth. Two species of *Richardoestesia*, *R. gilmorei* and *R. isosceles*, are present in the assemblage. Additionally, bird teeth are identified in the assemblage and are described in this review.

Bivariate plots were used to document the variation in the theropod teeth, especially in the features that distinguish between *Richardoestesia gilmorei*, *R. isosceles*, *Saurornitholestes*, and *Dromaeosaurus*. Considerable overlap is present in all plots, so although the teeth are morphologically distinct, they are not easily distinguished by quantitative means.

INTRODUCTION

CURRIE ET al. (1990) made the first thorough study of small theropod teeth from the Judith River Group, with detailed descriptions and illustrations of tooth and denticle morphology based on collections in the Royal Tyrrell Museum of Paleontology (RTMP). These features have been used to identify teeth in assemblages ranging from Texas to Alaska (e.g., Rowe et al., 1992; Fiorillo and Currie, 1994; Fiorillo and Gangloff, 2000; Sankey, 2001). Since then, the size of the RTMP's collection of small theropod teeth has greatly increased due to ten additional years of collecting. The development of a screenwashing program (Brinkman, 1990; Baszio, 1997a, 1997b; Peng et al., 2001) has been particularly significant in increasing the sample size of small teeth. Included in this larger sample are additional specimens of some of the rare morphotypes described by Currie et al. (1990). These specimens allow these rare morphotypes to be more precisely defined than previously.

In addition, the larger sample size allows a quantitative approach to be taken to the documentation of the range of variation in the more common morphological groups recognized by Currie et al. (1990). By quantifying the range of variation in features that reflect tooth shape a more rigorous comparison with other assemblages will be possible.

MATERIALS AND METHODS

Fossil sites.—The specimens included in this study are from the Judith River Group (Figs. 1, 2), of southern Alberta. The Judith River Group, comprised of the Foremost, Oldman, and Dinosaur Park Formations, is late Campanian, ~79–74 Ma (Eberth, 1996; Eberth and Hamblin, 1993). Vertebrate microfossil localities have been sampled through this unit (Brinkman, 1990; Peng et al., 2001). Studies of the sedimentology, stratigraphy, palynology, magnetostratigraphy, and radiometric dating (Eberth and Brinkman, 1997; Brinkman et al., 1998) provide a well-constrained stratigraphic framework that allows these sites to be placed in stratigraphic context.

All specimens are in the Royal Tyrrell Museum of Paleontology, and detailed locality information is on file there. In evaluating the taxonomic implications of some of the morphologically distinct but taxonomically problematical teeth, three hypotheses were considered. These are that the morphologically distinct tooth is: 1) a positional variant along the tooth row; 2) a reflection of variation within the population not expressed in each individual; and 3) a distinct taxon. The geographic and stratigraphic distribution of the tooth morphotypes helps select the most parsimonious of these hypotheses since given adequate sample sizes a distinct stratigraphic or geographic distribution supports the hypothesis that a morphologically distinct group of teeth is taxonomically distinct. Although no new taxa are recognized in this study, in some cases a taxonomic hypothesis is most strongly supported by the evidence available. In these cases, the group is described as a distinct morphotype. It is anticipated that with further information on the distribution of these morphotypes, the true nature of their identity will be resolved.

Measurements and photographs.—Tooth measurements are illustrated and described in Figure 3. A Wild M-3 microscope with an ocular micrometer was used by the first author. Measurements are given in millimeters (mm), and are abbreviated: FABL, fore aft basal length; Ht, height; Curv, curvature; CST, cross-sectional thickness; CSS, cross-sectional shape; and Dent/mm, denticles/mm. Photographed specimens were coated with vaporized amonium chloride to highlight surface detail. Measurement resolution is 0.5 mm for denticles/mm and 0.1 mm for denticle width and height.

Statistics and Plots.—The statistical analyses of the Judith River small theropod teeth were done by the third author. Bivariate analyses were accomplished using the statistical analyses program, MINITAB.

The dimensions measured on each tooth and analyzed include: fore aft basal length, curvature, tooth height, cross-sectional thickness, denticles per millimeter, and denticle width and height. Variation resulting from tooth wear and weathering are unavoidably included in these measurements. However, specimens that were obviously worn or weathered were not included in the analyses, so this source of variation did not have a significant effect on the quantitative analysis of the variation.

Basic statistics, including mean and standard deviations, were determined for each taxon in order to quantify the variability within each morphological grouping and to differentiate between morphologically similar teeth, particularly *Dromaeosaurus*, *Saurornitholestes*, *Richardoestesia gilmorei*, and *R. isosceles*. Overall trends in the dimensions with respect to size were also determined, and in some cases, a strong correlation between a variable and size of the tooth was present.

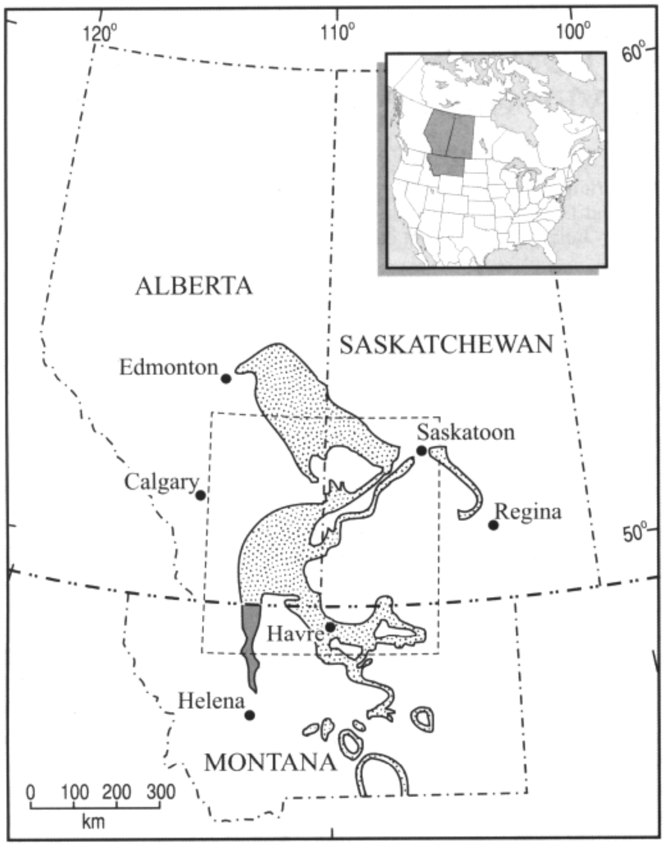

FIGURE 1—Judith River Group outcrop area (hatchured pattern), Alberta and Montana (from Eberth and Hamblin, 1993).

Abbreviations.—The following abbreviations are used: AMNH (American Museum of Natural History, New York); RTMP (Royal Tyrrell Museum of Paleontology, Drumheller, Alberta); and UALVP (University of Alberta, Lab for Vertebrate Paleontology, Edmonton).

SELECTED SYSTEMATIC PALEONTOLOGY

Order SAURISCHIA Seely, 1888
Family DROMAEOSAURIDAE Matthew and Brown, 1922
Genus DROMAEOSAURUS Matthew and Brown, 1922
DROMAEOSAURUS ALBERTENSIS Matthew and Brown, 1922
Figure 4.1–4.8

APPENDIX 1.1

All appendices are available on the *Journal of Paleontology's* supplemental database, ⟨www.journalofpaleontology.org⟩.

Discussion.—The teeth of *Dromaeosaurus albertensis* were distinguished by Currie et al. (1990) primarily by the denticle shape and by the position of the anterior carinae. The denticles were characterized by Currie et al. (1990) as chisel-like in form. Denticle size and shape are similar on both premaxillary and nonpremaxillary teeth. Denticles are almost as wide as high. Denticle tips are slightly rounded to almost flat, and are clearly not pointed. Interdenticle spaces are narrow, so the denticles appear closely spaced. Denticles are larger on the posterior than the anterior carinae. Posterior denticles are usually 0.2 mm wide and 0.3 mm high and usually occur 3 to 3.5/mm (average of 3.4/mm, sample of 42; Fig. 12.2).

The position of the anterior carina is distinctive in that the anterior carina twists from the anterior edge of the tooth to a more medial position near the tip of the tooth. However, with the larger sample size of theropod teeth available from the Judith River Group, it has become apparent that some tyrannosaurid teeth can also have this feature, especially in the transitional zone between the premaxillary and maxillary teeth, and can be difficult to distinguish from the teeth of *Dromaeosaurus*. In this study, these specimens were distinguished by relying on denticle shape. A thorough review of the isolated tyrannosaurid teeth, which was

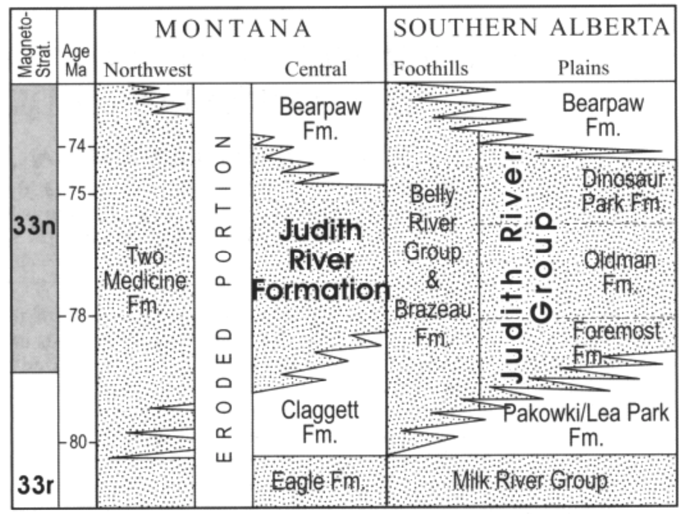

FIGURE 2—Judith River Group (late Campanian) stratigraphy (from Eberth, 1996).

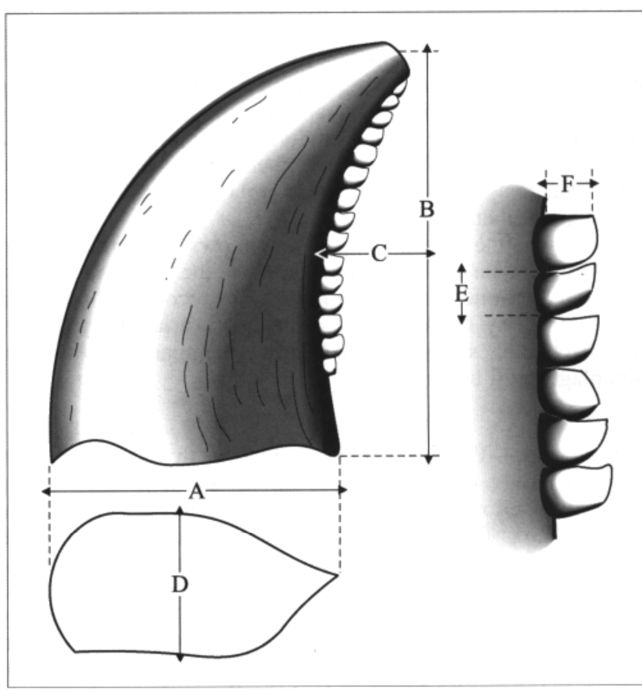

FIGURE 3—Measurements of teeth. A, FABL, fore-aft basal length, not including denticles; B, Greatest height, from crown tip to base (not including root, if unshed tooth) and measured from posterior side; C, Curvature, the greatest distance from posterior carina (not including the denticles) to a perpendicular line from tooth tip to base; D, Cross-sectional thickness, the greatest lateral-lingual cross-sectional tooth thickness; E, Greatest denticle width; F, Greatest denticle height. Denticles/mm, measured midway along the posterior carina.

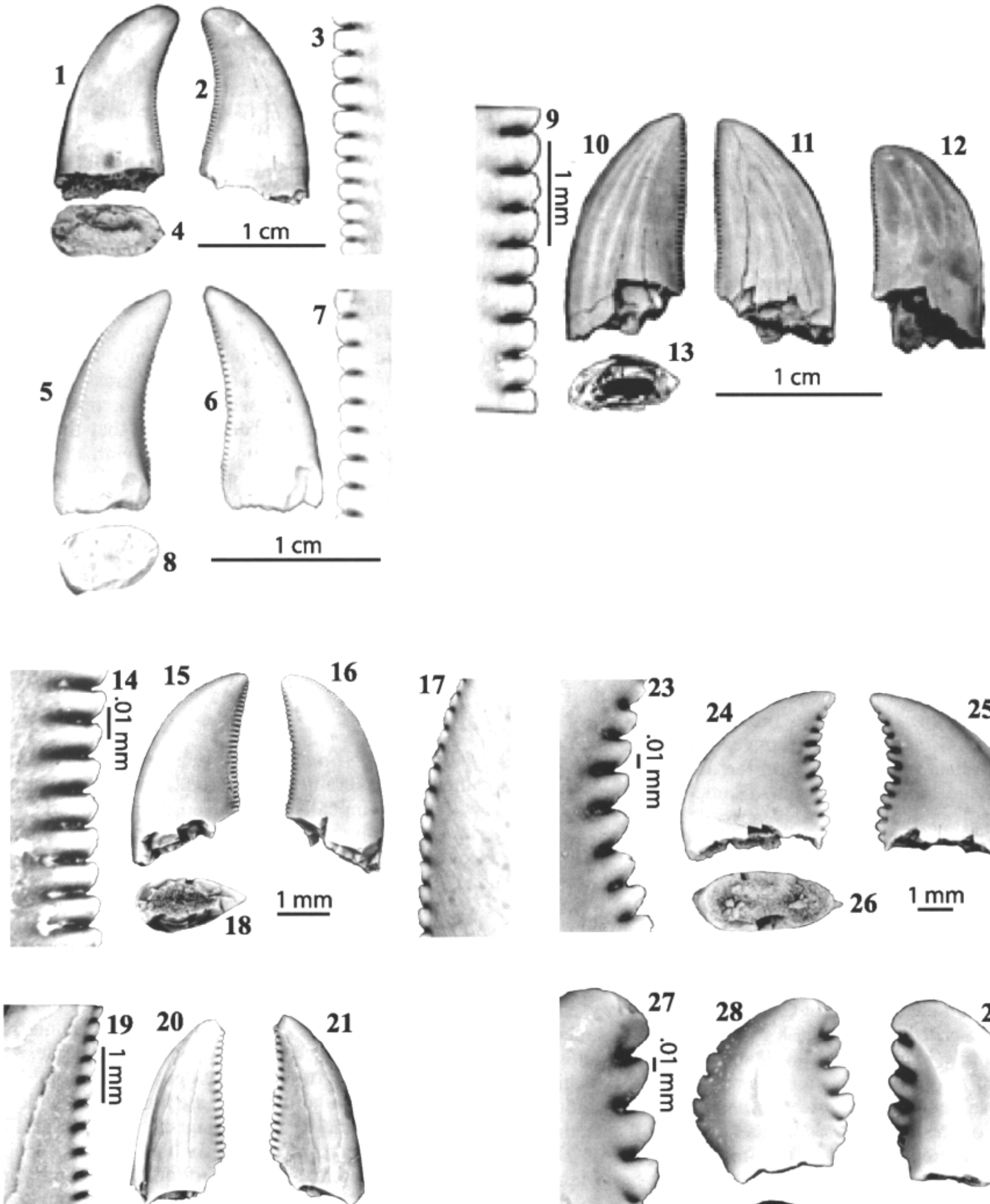

FIGURE 4—Theropod teeth from the Judith River Group, Alberta with views of lingual and labial sides, cross-section through the base of tooth, and close-up of denticles. *1–8, Dromaeosaurus* sp.; *1–4,* RTMP 89.155.2; *5–8,* RTMP 89.36.354, premax. *9–13, Dromaeosaurus* Morphotype A, RTMP 87.50.8. *14–22, Saurornitholestes* sp.; *14–18,* RTMP 95.92.28; *19–22,* RTMP 87.83.1, premax. *23–30, Troodon* sp.; *23–26,* RTMP 86.177.8; *27–30,* RTMP 86.54.66, premax.

not undertaken during this study, is necessary to fully resolve the identification of these teeth of intermediate morphology. A result of the distinctive placement of the carina is that the teeth tend to be sub-rectangular in ventral view (Fig. 4.4, 4.8).

The presence of a series of teeth preserved in jaws in the type specimen allowed Currie et al. (1990) to characterize the variation along the tooth row of *Dromaeosaurus albertensis*. Premaxillary teeth are smaller and less recurved than maxillary teeth. The anterior carinae twists near the tooth tip and extends along the posterior surface of the tooth, so that the carinae are parallel to each other on the same (posterior) surface of the tooth. However, the anterior carina is always more anterior in position. The position of the carina results in a cross section that is round to round-oval, in contrast with those of the non-premaxillary teeth that are more clearly sub-rectangular in basal cross-section. As well, the premaxillary teeth are typically smaller than non-premaxillary teeth (Fig. 6.1). Average dimensions, in a sample of 28 premaxillary teeth are: height, 10 mm; FABL, 5.1 mm; thickness, 3.2 mm; curvature, 0.4 mm. Average dimensions in a sample of sixty-seven non-premaxillary teeth are: height, 12.7 mm; FABL, 6.0 mm; thickness, 3.6 mm; curvature, 0.9 mm. However, there is considerable overlap in the range of variation in shape of the premaxillary and maxillary teeth as illustrated by graphs of the curvature relative to the height and fore-aft basal length (Fig. 6.2, 6.3). Denticle size is consistently 0.2 to 0.3 mm in width (Fig. 12.2).

Wear on *Dromaeosaurus* teeth is typically present on the tips of the teeth. This suggests that the teeth were used for crushing, rather than cutting and slicing. The robustness of the teeth of *Dromaeosaurus albertensis* is consistent with this usage.

?DROMAEOSAURUS Morphotype A
Figure 4.9–4.13

APPENDIX 1.2

Description.—Teeth with *Dromaeosaurus*-like denticles, but with one flat tooth surface and with longitudinal ridges, are grouped together here as *?Dromaeosaurus* morphotype A. The shape of these teeth is distinctive in that the posterior tooth edge is straight, almost perpendicular to the base of the tooth, and the teeth have long fore-aft basal lengths relative to their height. Teeth are large (length average 12.4 mm) and broad (FABL average 6.3 mm). The basal cross-sectional shape is a flattened, stretched out oval. Longitudinal ridges are always present on both sides, but are usually better developed on the convex side. Denticles can occur on both carinae, but are larger on the anterior carinae and are smaller near the base of the tooth. Denticles are large (0.3 mm in width and height) and closely spaced, and consistently occur 3–4/mm. Their tips are rounded, with only a slight point. All the teeth examined have worn surfaces both on the tips and on the base of the flat surface.

Discussion.—Currie et al. (1990) recognized that among the teeth that had the features of a flat surface with plications extending along the length of the tooth, the features that had previously been considered diagnostic of *Paronychodon*, were teeth with distinctive denticle morphologies. We follow Currie et al. (1990) in relying on denticle morphology to identify these teeth. The teeth of *Paronychodon*-type with denticles that most closely approach those of *Dromaeosaurus* are here described as a distinct morphotype questionably referred to *Dromaeosaurus*. In addition to the presence of the *Paronychodon*-like features, the teeth of *?Dromaeosaurus* morphotype A differ from the teeth of *Dromaeosaurus albertensis* in having a greater fore-aft basal length relative to their height (Fig. 7.2), being higher relative to their cross sectional thickness (Fig. 7.1), and in having a straighter posterior edge. The teeth of *?Dromaeosaurus* morphotype A do not differ from those of *Dromaeosaurus albertensis* in the height relative to the fore-aft basal length (Fig. 7.3). Denticle size is consistently between 0.2 to 0.3 mm in width (Fig. 12.3).

Because there is no tooth with a *Dromaeosaurus* morphotype A in the type specimen, which has a relatively complete row of teeth preserved, it is unlikely that teeth of this morphology represent variation that is consistently present in an individual. Alternative hypotheses are that such teeth are a result of growth anomalies (a hypothesis suggested by Currie et al., 1990) or that they are taxonomically distinct or that they are part of the normal range of variation present within the population. We consider it likely that these teeth are taxonomically distinct because they have a stratigraphic distribution that differs from that of *Dromaeosaurus albertensis*. Teeth of *Dromaeosaurus albertensis* are restricted to the mid-Campanian Judith River Group and equivalent beds. Late Maastrichtian teeth have been referred to *Dromaeosaurus* (Baszio, 1997b) on the basis of denticle shape, but since they lack the twisted carina that is present in *Dromaeosaurus albertensis*, they can be assumed to be at least specifically distinct. Teeth with the characteristic shape of *?Dromaeosaurus* morphotype A, however, are present in the Latest Maastrichtian (Baszio, 1997b, pl. VI, 88). If the teeth of *?Dromaeosaurus* morphotype A were part of the range of variation present within *Dromaeosaurus albertensis*, then the geographic and stratigraphic distribution of these teeth should be the same as the distribution of the teeth of *Dromaeosaurus albertensis*.

In addition, the pattern of wear on *?Dromaeosaurus* morphotype A teeth is different from that of *Dromaeosaurus albertensis*, suggesting that they functioned differently. In *D. albertensis*, wear is focused on the tips of the teeth, whereas in *?Dromaeosaurus* morphotype A wear is present on both the tips and the bases. The position of these wear facets suggests that the flat sides of the occluding teeth opposed one another, with the tip of one tooth contacting the base of the opposing tooth during the normal functioning of the tooth. The difference in functioning of the teeth implied by these wear patterns is likely to reflect differences in type of food processed and differences in the nature of the jaw movements, which is suggestive of a taxonomic distinction.

Genus SAURORNITHOLESTES Sues, 1978
SAURORNITHOLESTES cf. S. LANGSTONI Sues, 1978
Figure 4.14–4.22

APPENDIX 1.3

Description.—*Saurornitholestes* teeth are recurved, sharply pointed, and laterally compressed. Denticles are straight and narrow (labially-lingually), have deep, narrow interdenticle slits. Posterior carinae have approximately five denticles/mm and the anterior carinae have seven denticles/mm, although many teeth have none. Smaller teeth (probably from immature individuals) have fewer and smaller denticles than larger, more mature ones (Fig. 12.1). Denticle shape varies along the tooth. The denticles towards the apex of the teeth are typically sharply pointed with the point located towards the tip of the tooth, the shape distinctive for the genus (Currie et al., 1990). Near the base of the teeth, the denticles are less strongly pointed, and may become rounded (Fig. 4.14). Denticle size varies along the carina, they tend to be smaller at the base and tip of teeth. The denticles from midway along the carina are rectangular in shape; are higher than wide (height being measured from the tip of the denticle to the base, Fig. 3). In the sample of 99 teeth measured for this study (Appendix 1.3) the height of the denticles varied from 0.1 to 0.3 mm (average, 0.23 mm) and the width varied from 0.1 to 0.2 mm (average, 0.18 mm). Interdenticle spaces vary in size, but are usually small, making denticles tightly packed. Anterior denticles, where present, are distinctly smaller than posterior ones.

Teeth are flattened labio-lingually, and sharply recurved. In basal cross-section, the teeth vary from drop-shaped (Fig. 4.18) to oval or hour-glass shaped. The hour-glass shape, when present is a result of a slight indentation on the lingual surface.

Premaxillary or anterior dentary teeth are medium to large, recurved, narrow, slender teeth with minute or no denticles on the anterior carinae. Anterior and posterior carinae follow the edges of the tooth, although the anterior carinae may twist to be more lingually located near the base of the tooth. The posterior edge forms a fairly straight line. Teeth are oval to flattened oval in cross section. Two premaxillary teeth with the *Paronychodon*-like feature of a flat or concave side and one very convex side are present (Fig. 4.19–4.22). In these teeth, the anterior carina twists and extends along the concave surface and the teeth are round to oval in cross section.

Maxillary or posterior dentary teeth more recurved, denticles present on the anterior carinae. Teeth are oval to flattened oval in cross section. In the sample measured, the teeth of this morphology are typically larger than the anterior teeth. In relationship with the size of the teeth, the denticles are large, for example, 0.3 mm in width and height.

Very small teeth with *Saurornitholestes*-type of denticles (Currie et al., 1990; Fig. 8.2) may be teeth of very young individuals. The teeth are small (about 4.5 mm height; 2 mm FABL), sharply recurved, sharply pointed, labial-lingually flattened, oval/round to oval in cross-section. Posterior denticles are large (example: 0.1 mm width; 0.1 mm height; approximately 5 to 6 denticles/mm; Fig. 12.1) and sharply pointed. Anterior denticles are minute or absent.

Discussion.—*Saurornitholestes langstoni* is the most common small theropod tooth recovered from the Judith River Group in Alberta (Baszio, 1997a). Within the small theropod tooth assemblage of the Judith River Group, the teeth of *Saurornitholestes* are easily recognizable on the basis of denticle morphology and general shape of the teeth. Compared to *Richardoestesia gilmorei*, *Saurornitholestes* teeth are more recurved, and have larger, longer, sharper denticles. Denticles are smaller at the base and tip of teeth, in contrast to *R. isosceles*, which have denticles of more uniform size. *Troodon* teeth are even more recurved, and with larger and more strongly pointed denticles.

Saurornitholestes teeth typically differ from those of *Dromaeosaurus albertensis* in that the teeth are flatter, more gracile, have pointed tips on the denticles, and in that the anterior carina follows the anterior edge of the tooth, rather than twisting lingually as in *Dromaeosaurus*. However, there is gradation between the tooth morphology in these taxa. Figure 8.1–8.4 illustrate this. Figure 8.1 and 8.2 illustrate that both *Dromaeosaurus* and *Saurornitholestes* have large variation in size, reflecting teeth from different tooth positions and ages and of individuals. In Figure 8.3 (CST) *Dromaeosaurus* and *Saurornitholestes* form two distinct groups. Figure 8.4, a histogram of denticles/mm, also shows two distinct groups (*Dromaeosaurus* and *Saurornitholestes*), proving that *Dromaeosaurus* has consistently larger denticles than *Saurornitholestes*. *Saurornitholestes* has a large variability of denticle size, also probably reflecting two or three distinct morphotypes.

The very small teeth with *Saurornitholestes*-like denticles are interpreted as being from young individuals. However, the size of the denticles relative to the size of the tooth is larger than expected given the variation in larger teeth of *Saurornitholestes*. Two premaxillary teeth have a flattened surface like that of teeth of *Paronychodon lacustris* and ?*Dromaeosaurus* morphotype A. These teeth are very rare and cannot be distinguished as a group from the remaining teeth of *Saurornitholestes* on their general shape or wear pattern. Following Currie et al. (1990) we refer these teeth to *Saurornitholestes*.

Wear on *Saurornitholestes* teeth is typically on the side of the teeth near the tip. This, along with the narrow blade-like shape, suggests that the teeth functioned primarily in cutting and slicing.

Family TROODONTIDAE Gilmore, 1924
Genus TROODON Leidy, 1856
TROODON FORMOSUS Leidy, 1856
Figure 4.23–4.30

Description.—(Specimens were not recorded or measured.)

Teeth with large, pointed denticles on the posterior carina, denticles on the anterior carina variably developed or absent. Teeth constricted at the base of the crown. Teeth variable in shape along the tooth row, premaxillary teeth triangular in cross section (Fig. 4.27–4.30), with large carinae. Maxillary teeth (Fig. 4.23–4.26) are laterally compressed, oval in cross section, denticle development of the anterior carina variable, presumably reflecting variation along the jaw. Dentary teeth smaller than maxillary teeth, sharply recurved.

Discussion.—*Troodon* teeth are very distinctive. The variation along the jaw in *Troodon* was described by Currie et al. (1990). Baszio (1997b), Ryan et al. (1998) and Peng et al. (2001) have subsequently illustrated teeth of *Troodon*.

Troodon has a limited geographic and stratigraphic distribution in North America. Baszio (1997b) demonstrated that the reports of *Troodon* teeth in the Milk River Formation are an error resulting from transposing locality and formational information (the Milk River name was used for the locality, and subsequently assumed to be the formation), and subsequently Peng et al. (2001) demonstrated that within a section of the Judith River Group along the Milk River of southern Alberta, *Troodon* teeth are not present in the lower third of the Oldman Formation or below. This first occurrence of *Troodon* was proposed to be a result of the introduction of the genus into the North American dinosaur assemblage from elsewhere. Fiorillo and Gangloff (2000), noting the high abundance of *Troodon* in Campanian localities on the North Slope of Alaska, suggested that *Troodon* is a member of a more northerly community. Teeth from the Late Cretaceous assemblages of Texas that were initially attributed to *Troodon* (Rowe et al., 1992; Sankey, 1998) have been reidentified as pachycephalosaurids (Sankey, 2001). Thus, as suggested by Fiorillo and Gangloff (2000), *Troodon* is likely a member of a northern dinosaur assemblage.

Infraorder MANIRAPTORA Gauthier, 1986
Family unknown
Genus RICHARDOESTESIA Currie, Rigby, and Sloan, 1990
RICHARDOESTESIA cf. R. GILMOREI Currie, Rigby, and Sloan, 1990
Figure 5.1–5.8

APPENDIX 1.4

Description.—Teeth small (3 to 12 mm in height), recurved, oval in basal cross-section, and slightly flattened (labial-lingually). Isolated teeth vary in curvature from almost completely straight (0.1 mm curvature) to strongly recurved (0.7 mm curvature). Teeth are indented at the base, a feature also seen in bird teeth and the teeth of *Troodon*. Cross sectional shape varies from oval to a flattened oval. Denticles are small to minute. Posterior denticle widths and heights are 0.1 mm or less, and occur 5 to 11/mm, depending on tooth size (Fig. 12.4). Denticle size varies slightly along the carinae, with smaller ones at the base and tip. Anterior denticles, where present, are usually minute and considerably smaller than posterior ones. Interdenticle spaces are small. Denticle tips can be slightly pointed, rounded, or flattened.

Discussion.—*Richardoestesia gilmorei* was erected by Currie et al. (1990) on the basis of a lower jaw containing a single replacement tooth and a series of isolated teeth. The isolated teeth were referred to the genus on the basis of features of the denticles, particularly their small size. Denticles in *Richardoestesia* are the smallest of any Late Cretaceous theropod. Denticles are usually not present on the anterior carinae, and minute where they are present.

Two general morphologies were present in the *Richardoestesia* material available to Currie et al. (1990), teeth that were tall and straight, and teeth that were shorter and more recurved. Currie et al. (1990) considered the possibility that these two morphologies represented variation along the tooth row, with the straight teeth

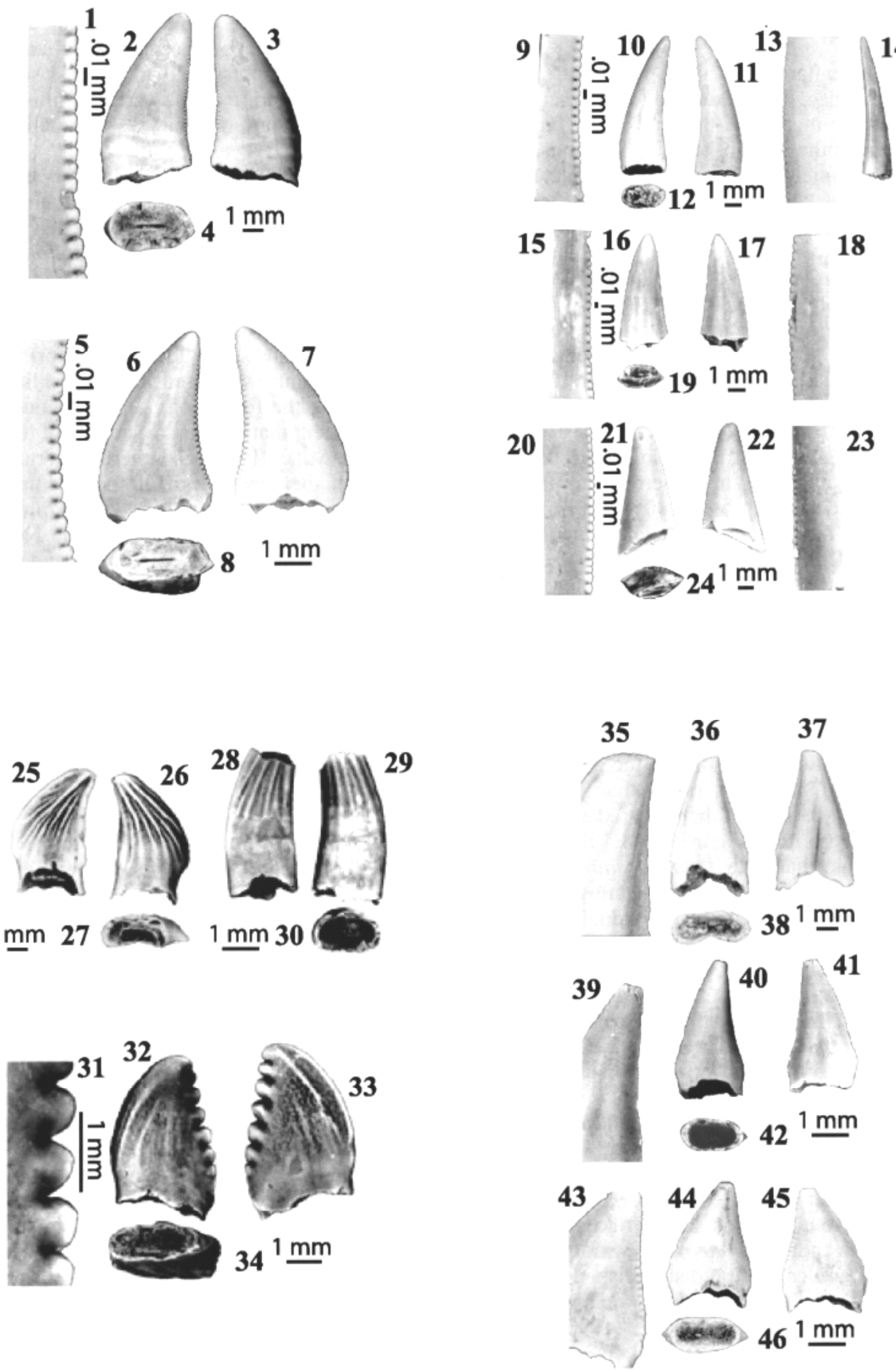

FIGURE 5—Theropod teeth from the Judith River Group, Alberta with views of lingual and labial sides, cross-section through base of tooth, and close-up of denticles. *1–8, Richardoestesia gilmorei*; *1–4,* RTMP 87.80.35; *5–8,* RTMP 88.91.28. *9–24, Richardoestesia isosceles*; *9–14,* RTMP 96.142.19; *15–19,* RTMP 89.136.56; *20–24,* RTMP 84.36.97. *25–27, Paronychodon lacustris* Morphotype B, RTMP 2000.19.2. *28–30, P. lacustris* Morphotype A, RTMP 88.211.66. *31–34,* cf. Troodontidae indet., RTMP 2000.21.11. *35–46,* Bird teeth; *35–38,* RTMP 87.4.19; *39–42,* RTMP 96.62.51; *43–46,* RTMP 86.172.53.

being more anterior in position, but concluded that they were most likely representatives of two distinct taxa. This was followed by Baszio (1997b), who referred to the straight *Richardoestesia* teeth as *Richardoestesia* sp. Sankey (2001) subsequently named these teeth *R. isosceles*. *Richardoestesia gilmorei* (Currie et al., 1990) can be distinguished from *Richardoestesia isosceles* by the curvature in the proximal part of the tooth. Tooth shape in *R. gilmorei* is similar to that *Saurornitholestes*, but the maximum tooth size of *Richardoestesia gilmorei* is less than that of *Saurornitholestes*.

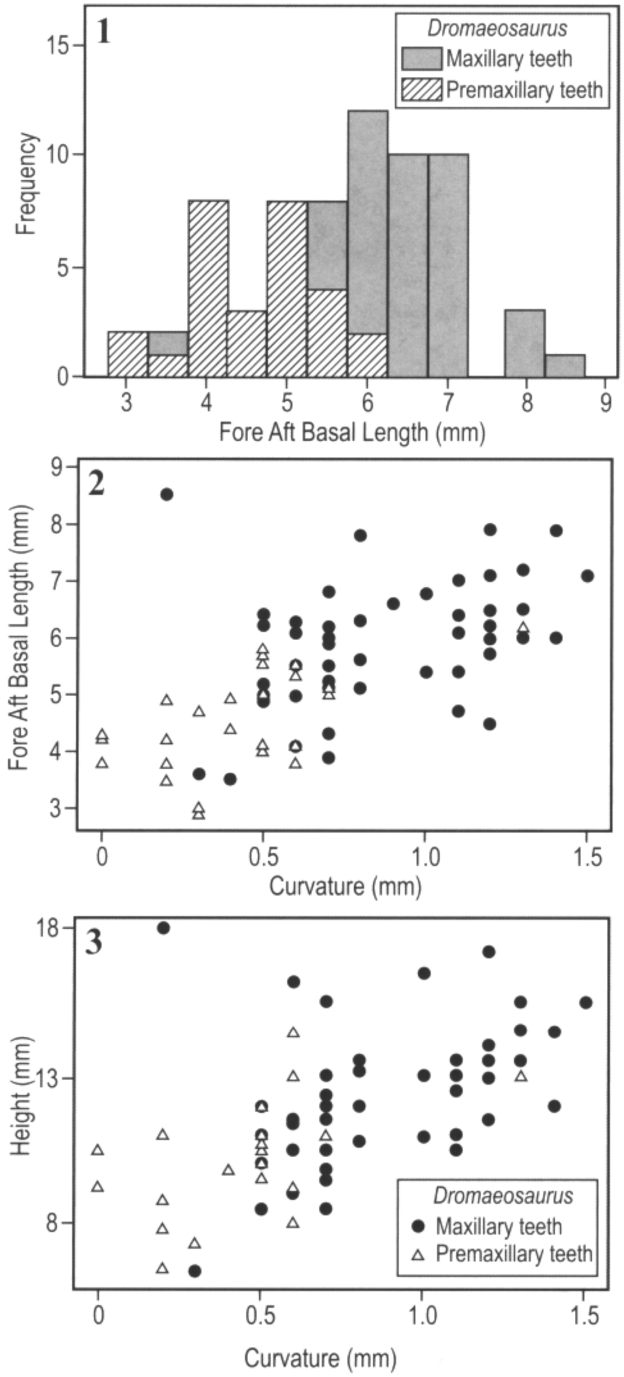

FIGURE 6—*Dromaeosaurus* premaxillary and maxillary teeth. *1*, Histogram of FABL (Fore-aft basal length); *2*, FABL and curvature; *3*, curvature and height.

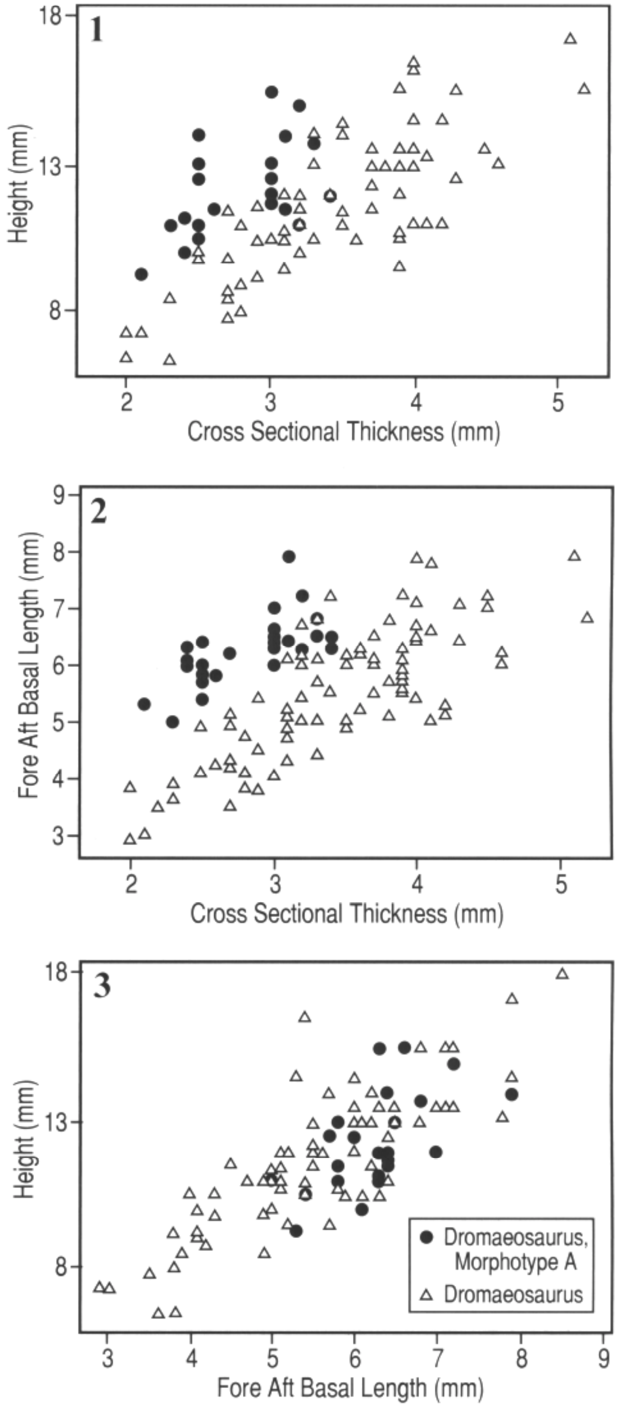

FIGURE 7—*Dromaeosaurus* and *Dromaeosaurus* Morphotype A teeth. *1*, *2*, Plots of cross-sectional thickness (cst) with height and FABL; *3*, plot of height and FABL.

RICHARDOESTESIA ISOSCELES Sankey, 2001
Figure 5.9–5.24

APPENDIX 1.5

Description.—Teeth tall and narrow, straight or slightly recurved, when straight, shaped like an isosceles triangle in lateral view. Teeth not constricted at the base of the crown as in bird or *R. gilmorei* teeth. Some teeth are slightly recurved lingually when seen in anterior view, with the labial surface of the tooth slightly convex and the lingual surface slightly concave (Fig. 5.14). Curvature, where present, is less than 0.3 mm (Fig. 5.10, 5.11). Flat surfaces on the labial and lingual sides of recurved teeth, yield cross-sectional shape more trapezoidal than oval (Fig. 5.12). Straight teeth without flat surface at base have oval basal cross section (Fig. 5.24). Posterior denticles (Fig. 5.9, 5.15, 5.20) are consistently minute (Fig. 12.5), square-shaped, uniformly-sized along tooth, and extend the length of the carinae. Denticle bases

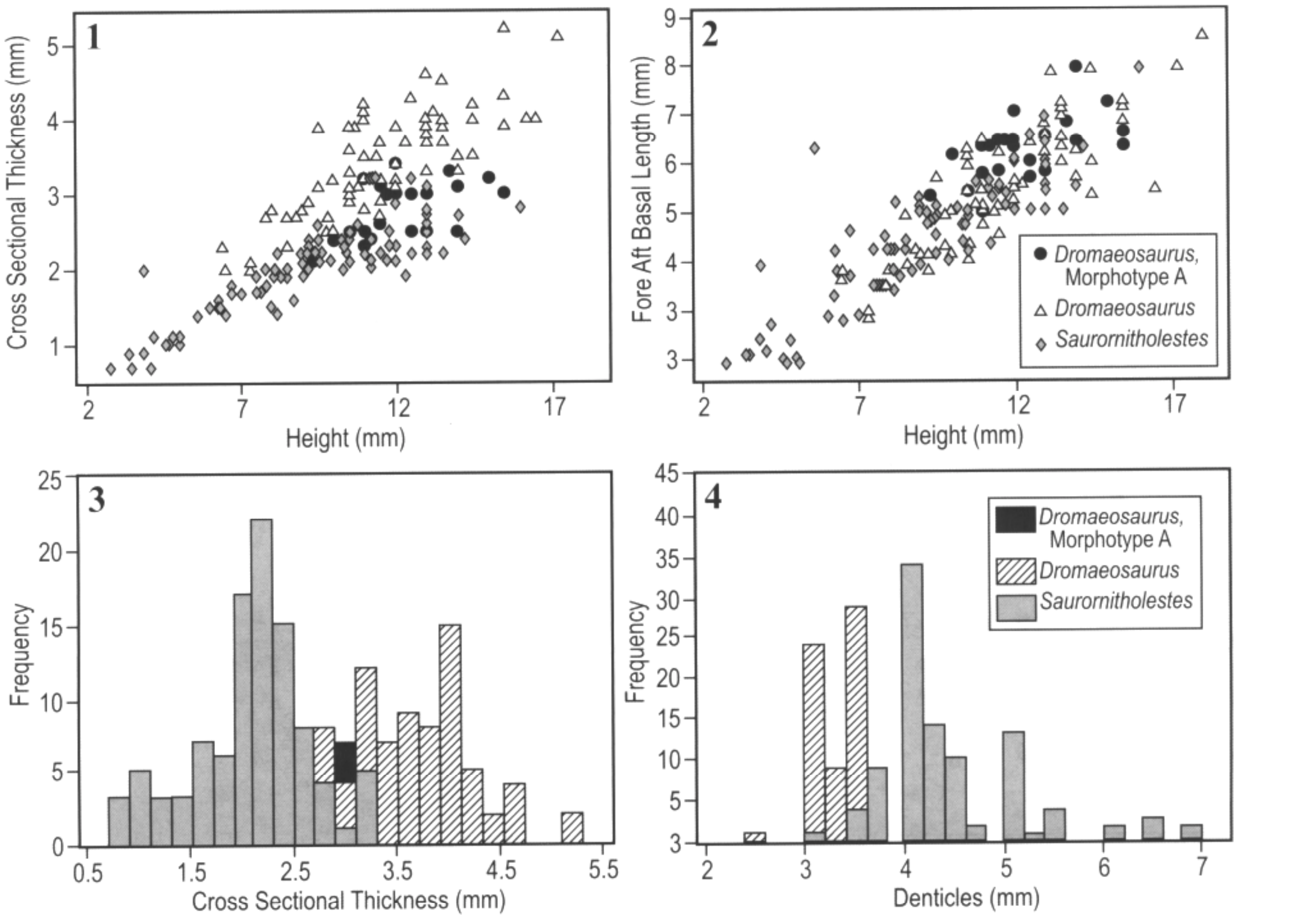

FIGURE 8—*Dromaeosaurus*, *Dromaeosaurus* Morphotype A, and *Saurornitholestes*. *1*, Plot of height with cross-sectional thickness (CST); *2*, plot of height and FABL; *3*, histogram of CST; *4*, histogram of denticles/mm.

are not inflated as in small tyrannosaurid and *Dromaeosaurus* teeth. In larger teeth, denticles have large interdenticle spaces. Denticles on the anterior carinae are either slightly to considerably smaller than posterior denticles. Denticle widths and heights are usually 0.1 mm or less, and occur from 5 to 12/mm, depending on tooth size. Denticle tips are straight or slightly rounded, but not pointed.

Discussion.—The teeth of *Richardoestesia isosceles* have long been recognized as morphologically distinct but have only been recently recognized as taxonomically distinct. Estes (1964; Fig. 69b) illustrated a tooth that is referable to *R. isosceles*, and suggested that it might be a juvenile theropod tooth. Currie et al. (1990) suspected that the Maastrichtian specimens might be a distinct taxon, but considered the material from the

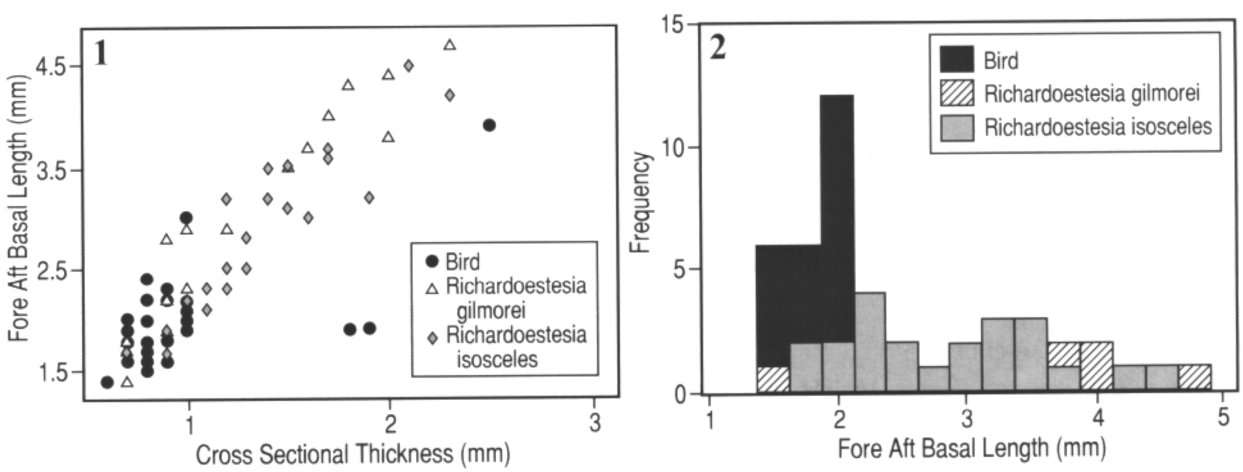

FIGURE 9—*Richardoestesia gilmorei*, *R. isosceles*, and Bird. *1*, Plot of FABL and CST; *2*, histogram of FABL.

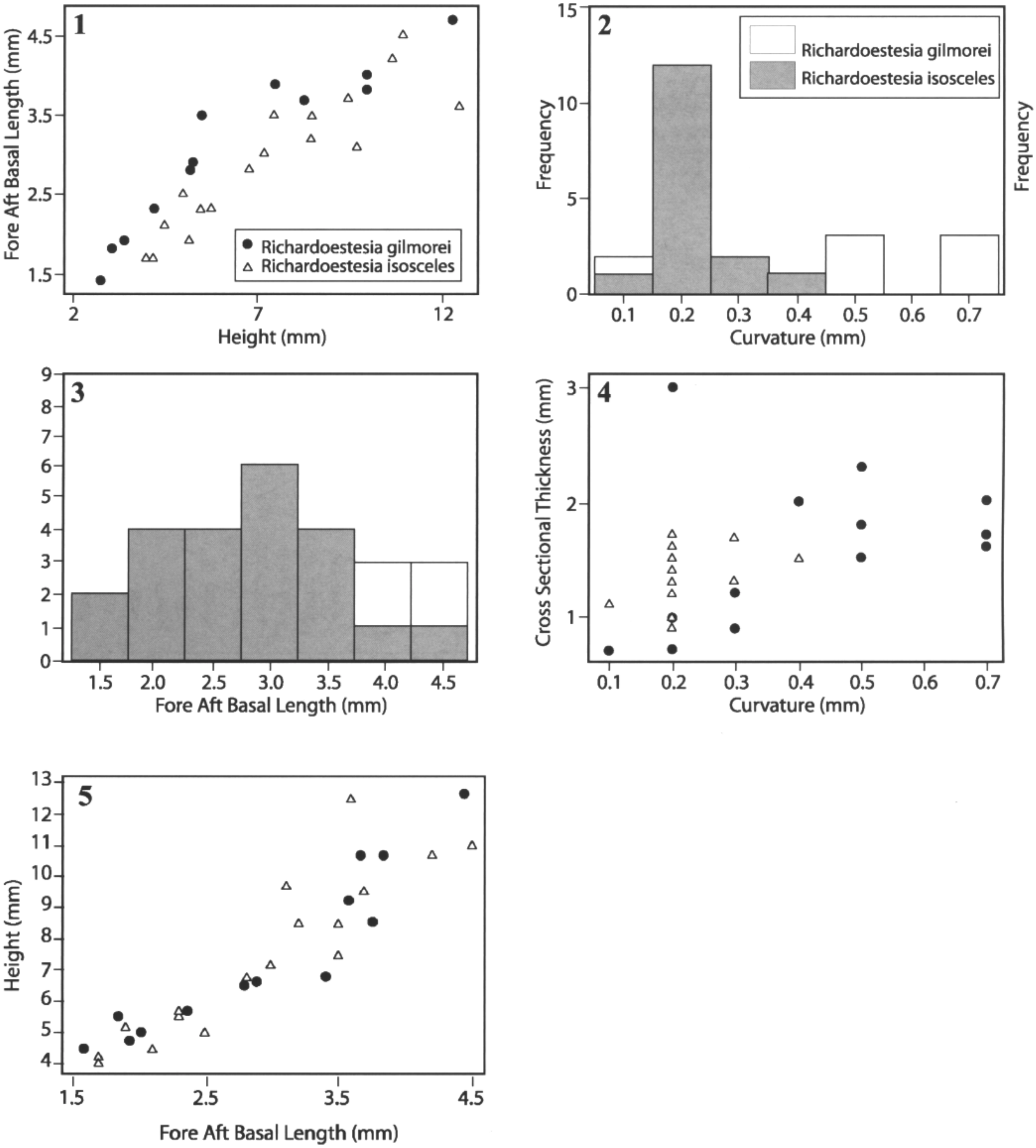

FIGURE *10*—*Richardoestesia gilmorei* and *R. isosceles*. *1*, Plot of height and FABL; *2, 3,* histograms of curvature and FABL; *4,* plot of curvature and CST; *5,* plot of FABL and CST.

Campanian localities to be referable to *R. gilmorei*. Baszio (1997b) and Peng et al. (2001) both considered the teeth of *R. isosceles* to be taxonomically distinct, and referred to them as *Richardoestesia* sp. Baszio (1997a) recognized that the abundance of *R. isosceles* changes through the Late Cretaceous sequence. In Alberta, *R. isosceles* is more abundant in the Milk River and Scollard Formations, geologic units that represent, drier habitats (Baszio, 1997a). Sankey (2001) reported on material from the Aguja Formation in Texas and formally named the taxon.

Richardoestesia isosceles is included in the genus *Richardoestesia* because of the presence of small denticles. However, the

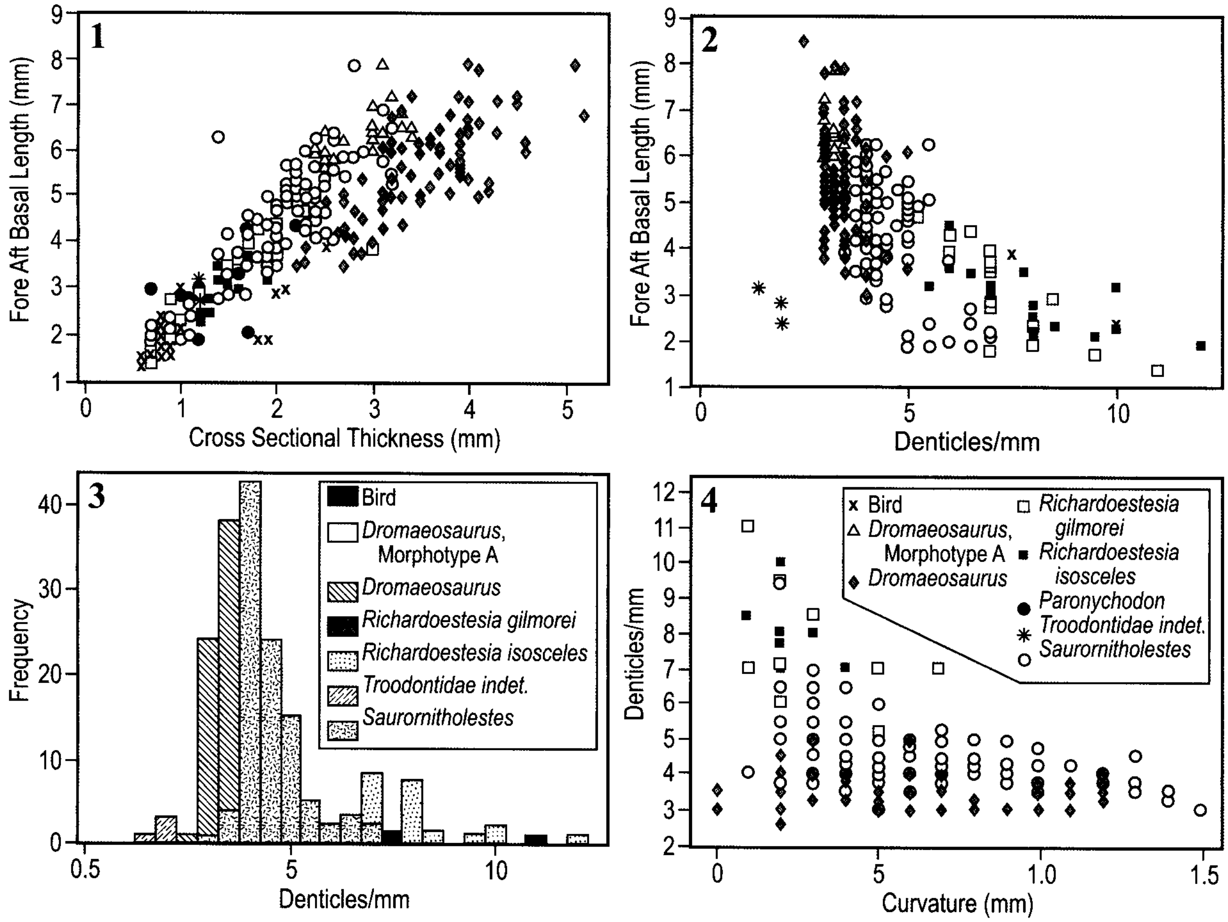

FIGURE *11*—Bird, *Dromaeosaurus* Morphotype A; *Dromaeosaurus*; *Richardoestesia gilmorei*, *R. isosceles*; *Paronychodon*, *Saurornitholestes*, and cf. Troodontidae. *1*, Plot of FABL and CST; *2*, plot of FABL and denticles/mm; *3*, histogram of denticles/mm; *4*, plot of curvature and denticles/mm.

shape of the denticles in *Richardoestesia gilmorei* and *isosceles* is different. In *R. gilmorei* they are not square-shaped and they have small interdenticle spaces. *Richardoestesia isosceles* typically has serrations on both anterior and posterior edges.

Although *Richardoestesia gilmorei* and *R. isosceles* form two morphologically distinct groups, some overlap is present in proportions (Fig. 10.1, 10.4, 10.5). *R. gilmorei* is generally shorter than *R. isosceles* (Fig. 10.1), more recurved (Fig. 10.2, 10.4), and larger (Fig. 10.3). Although the teeth of R. *isosceles* appear generally thicker than those of *R. gilmorei*, the two taxa are not distinguished by a plot of FABL and height (Fig. 10.5). Rather, this graph shows that the teeth vary, reflecting different tooth positions and ages in the sample. Distinct wear facets were not observed on teeth of *Richardoestesia isosceles*. Based on the straight, narrow, pointed teeth, Baszio (1997b) considered *Richardoestesia isosceles* a fish-eater.

Family Unknown
Genus PARONYCHODON Cope, 1876
PARONYCHODON LACUSTRIS Cope, 1876
Figure 5.23–5.30

APPENDIX 1.6

Description.—We follow Currie et al. (1990), who restricted *Paronychodon lacustris* to those teeth with the features of a flattened surface, numerous and well developed longitudinal ridges, and no denticles. We refer the more bilaterally symmetrical teeth with minute denticles to *Richardoestesia gilmorei*, *R. isosceles*, or bird.

Within this restricted definition of *P. lacustris*, we recognize two morphotypes:

Morphotype A: teeth are larger (usually approximately 8 mm high and 4.2 mm CST), straighter (only slightly recurved), and are not constricted at the crown base. Numerous well developed longitudinal ridges occur on both surfaces of the teeth, usually approximately 10 on convex surface and 4 to 6 on flat surface. Some of the ridges do not extend the length of the tooth, but are restricted to the wider, bottom half of the tooth. Ridges on the convex surface are not as well developed as those on the flat surface.

Morphotype B: teeth are smaller (usually approximately 4.5 mm long and 2 mm wide), more recurved, with a distinct constriction below the crown, and with a 'heel' or cingulum on the posterior side of the base of the crown.

In both morphotypes A and B, the shape of the teeth in basal cross section are narrow ovals, with an indentation on the concave surface. Well-developed longitudinal ridges are consistently present and prominent on both surfaces of the tooth. Compared to Morphotype A, the ridges radiate out from tip of tooth instead of being oriented in parallel lines.

Discussion.—*Paronychodon lacustris* was described by Cope (1876). Although the type specimen was never illustrated, Estes (1964) examined it and stated that it was the same as those illustrated in Marsh (1881) and Russell (1935).

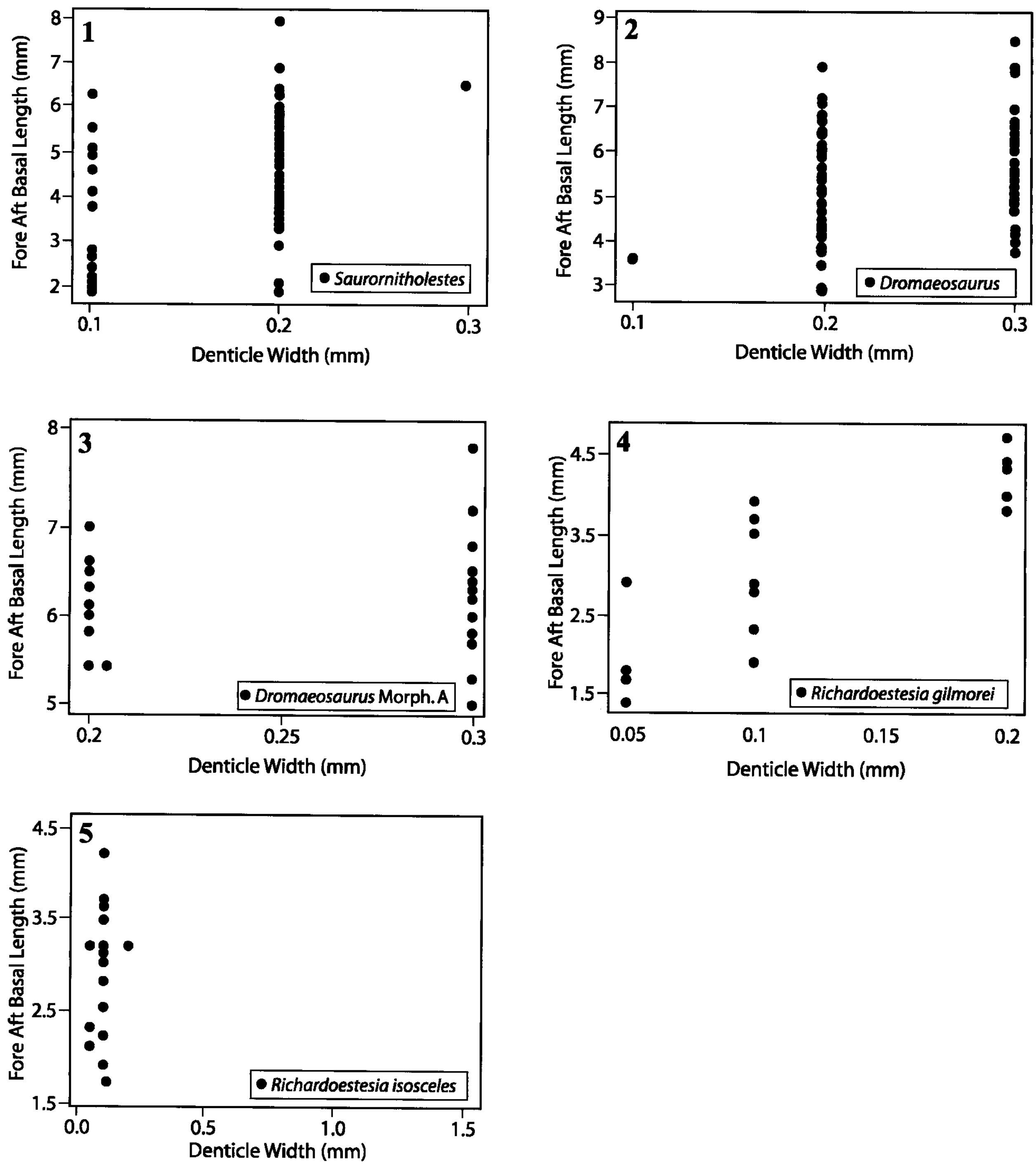

FIGURE 12—Plots of denticle width and FABL. *1*, *Saurornitholestes*; *2*, *Dromaeosaurus*; *3*, *Dromaeosaurus* Morphotype A; *4*, *Richardoestesia gilmorei*; *5*, *Richardoestesia isosceles*. Resolution of denticle measurement is 0.1 mm.

Estes (1964) considered the presence of a flattened surface with longitudinal wrinkles as diagnostic features of *P. lacustris*. Thus he included in this taxon teeth that are here described as ?*Dromaeosaurus* morphotype A. Carpenter (1982) followed Estes in the definition of *Paronychodon*, and referred teeth from the Lance and Hell Creek Formations in Wyoming and Montana to *P. lacustris*. Currie et al. (1990) considered the features of a flat surface on one side of the tooth with longitudinal ridges on that surface to be the defining feature of *Paronychodon*, but suggested that the taxon *Paronychodon lacustris* should be restricted to the teeth without serrations. They identified teeth having one flat side with longitudinal ridges; one convex side; and denticles as "*Paronychodon*"-like teeth of *Troodon*, *Saurornitholestes*, or *Dromaeosaurus*, depending on their denticle morphology. They interpreted these "*Paronychodon*"-like teeth as growth abnormalities. Baszio (1997b) followed Currie et al. (1990) in the restricted definition of *Paronychodon lacustris* but showed that in the Milk River Formation, teeth of *Paronychodon lacustris* vary in their cross sectional shape from teeth that are flat on one surface to teeth that are convex on both surfaces. He suggested that this variation reflected variation along the tooth row.

Among the teeth of *Paronychodon lacustris* from the Judith River Group of Alberta, two distinct morphologies are present, recognized here as morphotype A and morphotype B. Both morphotypes conform to the definition of Currie et al. (1990) in that the teeth are flat on one side, have longitudinal ridges on the flat side, and are without serrations. As well as being different in size and degree of curvature, they differ in the presence of a constriction at the base of the crown of the tooth in morphotype B but not A. The difference in the development of constriction between the crown and the root is surprising since this has been interpreted as a significant feature reflecting patterns of development and implantation (Currie et al., 1990). At present we treat the two morphotypes as variation within an individual, presumably reflecting variation along the jaw. This can be tested by the stratigraphic and geographic distribution of teeth of these two morphologies. If correctly interpreted as variation within a single individual, the stratigraphic and geographic distribution of these teeth should be identical.

Wear on the teeth of *Paronychodon lacustris*, like that of ?*Dromaeosaurus* morphotype A, is present on the tip and the base of the flat surface. At the first stages of wear, the surfaces of the ridges are worn, in extreme cases the entire flat surface of the tooth is worn. This suggests that tooth function involved grinding between opposing flat surfaces.

cf. TROODONTIDAE indeterminate
Genus and species indeterminate A
Figure 5.31–5.34

APPENDIX 1.7

Description.—Teeth convex on one side and flattened or concave on the other; enamel pitted on the flat to concave surface; two well-developed longitudinal ridges present on flat surface, one ridge extending from the apex denticle to near the base of the enamel and the second extending along the anterior carinae; ridges variably developed on the convex surface; anterior carina smooth and unserrated; posterior carina deeply serrated, apical denticle incorporated into the tip of the tooth; denticles rounded in outline, without pointed tips, larger than in any other theropod tooth, sizes ranging from 0.4 to 0.6 mm in anterior-posterior width, and usually occur 2/mm; denticles are also wider labial-lingually than any other theropod; basal constriction present below the crown and above the root; root round in cross-section.

Discussion.—The teeth here described as genus and species indeterminate. They match those that Estes (1964) referred to *Saurornithoides*. Carpenter (1982) included Estes' *Saurornithoides* in "*Pectinodon bakkeri*" (now *Troodon*) and mentioned that Estes no longer considered referral to *Saurornithoides* correct. Currie et al. (1990) suggested that the single specimen of a tooth of this type that he had available was actually an abnormally developed tooth of *Troodon*. This identification was based primarily on the presence of large denticles and a constriction of the tooth at the base of the crown, both features also present in *Troodon*. While the denticles of gen. and sp. indet. A are similar to those of *Troodon* in being of large size, they differ considerably in shape. The denticles are rounded, rather than pointed, and the apical denticle is formed by the tip of the tooth. Thus morphologically, the teeth of gen. and sp. indet. A are distinct from those of *Troodon*.

In addition, the teeth have a distinct distribution pattern compared to the teeth of *Troodon* in the Judith River Group. *Troodon* is found throughout the Dinosaur Park Formation and the middle and upper Oldman Formation (Peng et al., 2001), while the specimens of gen. and sp. indet. A have only been recovered from localities at the uppermost Dinosaur Park Formation. As well, the teeth of gen. and sp. indet. A were not reported in assemblages in Alaska, where *Troodon* teeth are abundant (Fiorillo and Gangloff, 2000). This distinct distribution pattern, together with the distinct morphology, suggests that these teeth are from a taxon distinct from *Troodon*. However, additional data are necessary to confirm this.

One feature of note is the consistent pitting on the flat surface of the teeth. The pitted surface of the teeth of gen. and sp. indet. A has been interpreted as a pathological feature. However, since it is present in all the teeth of this group, including specimens from the Late Maastrichtian, and was not seen in other kinds of teeth, it can be interpreted as a normal feature of these teeth. None of the available teeth show distinct wear facets.

Class AVES Linnaeus, 1758
Order indeterminate
Figure 5.35–5.46

APPENDIX 1.8

Description.—Teeth are small (1.6 to 3 mm in height), laterally compressed, straight, indented at their base, with no or minute denticles, and some with a thin carina on both the anterior and posterior edges. Most teeth are short and squat, with a round base and a triangular crown. Some are narrower, but still conical in shape. Teeth are oval to oval-flattened in cross section.

Discussion.—The teeth described are identified as pertaining to birds because of their similarity with those of *Hesperornis*. The toothed bird *Baptornis* is known in the assemblage on the basis of postcranial elements (Tokaryk and Harington, 1992). However, this identification is tentative because small non-avian dinosaurs with similar teeth have recently been described (Xu et al., 2000).

Small teeth of *Richardoestesia gilmorei*, *R. isosceles*, and bird can be especially difficult to distinguish. In Figure 9.1 (FABL vs. CST), bird teeth, which are usually the smallest teeth in the sample, fall along a regression line that includes *R. gilmorei* and *R. isosceles*. Figure 9.2 (histogram of FABLs of all three taxa), also shows a large amount of overlap between these taxa. However, they can be distinguished on morphological features since *R. isosceles* teeth are not indented at their base and *R. gilmorei* are more recurved, have larger denticles, and lack the distinctive hour-glass shape of the base of the bird teeth.

DISCUSSION

The goal of this project was to document variation in theropod teeth present in the Judith River Group of Alberta. This was accomplished by first describing the taxa present and then quantifying the range of variation in linear measurements in a series of bivariate plots. In particular, our goals were to: 1) distinguish between *Richardoestesia gilmorei* and *R. isosceles*; 2) quantify the variation in morphological features that distinguish *R. gilmorei*, *Saurornitholestes*, and *Dromaeosaurus*; 3) describe the variation in the teeth of *Paronychodon*. *Troodon*, which is morphologically very distinct, was not studied in detail.

All the theropod taxa plotted together (Fig. 11) show that the taxa occupy distinct areas on the plots, but that considerable overlap is present. In the plot of cross sectional thickness relative to fore-aft basal length, bird and ?*Dromaeosaurus* morphotype A show the least amount of variation (Fig. 11.1). Denticles/mm varies little in ?*Dromaeosaurus* morphotype A, *Dromaeosaurus albertensis*, and gen. and sp. indet. A, but is more variable for *Saurornitholestes*, *Richardoestesia gilmorei*, *R. isosceles*, and bird (Fig. 11.2, 11.3).

With the large sample size, a series of morphologically distinct groups are recognized that, in some cases, may represent distinct taxa. Teeth with the *Paronychodon*-like features of a flat surface with longitudinal ridges on one side can be resolved into a few discrete morphotypes. Two distinct morphotypes are included in *Paronychodon lacustris*, and two additional morphotypes, ?*Dromaeosaurus* morphotype A and gen. and sp. indet A, are hypothesized to represent distinct taxa. The teeth of *Paronychodon lacustris* and ?*Dromaeosaurus* morphotype A share a distinctive wear pattern that suggests tooth functioning involved contact between the flat surfaces of opposing teeth. The stratigraphic and geographic distribution of these taxa through the Late Cretaceous of North America will test this taxonomic hypothesis. Two species of *Richardoestesia*, *R. gilmorei* and *R. isosceles* Sankey (2001), are present in the assemblage. Additionally, bird teeth are identified in the assemblage and are included in this review.

The greater diversity of theropods indicated by these taxonomic conclusions will require a revision of patterns of change in diversity of dinosaurs through the Late Cretaceous. Theropod diversity from the Judith River Group is often used as a standard for the Late Campanian. Based on this study, theropod diversity appears to have been lower in the late Maastrichtian than it was in the late Campanian. However, the taxonomic hypotheses presented here need to be supported by additional data, and samples from younger time periods need to be studied in order to understand theropod diversity trends during the final ten million years of the Cretaceous. In particular, taxonomic studies should be made on Maastrichtian theropod teeth and standardized collections of microvertebrate sites from late Maastrichtian deposits should be made.

ACKNOWLEDGMENTS

This work was part of Sankey's Fulbright postdoctoral research fellowship in Alberta (1999) and the Haslem position (1999 to present), Museum of Geology and Department of Geology and Geological Engineering, South Dakota School of Mines and Technology (SDSM&T), Rapid City. Guenther's research was supported by a graduate research fellowship from the SDSM&T. Many of the fossils from the One Four and South Saskatchewan River sites were collected by J. Peng. We thank the many volunteers who have helped collect the fossils used in this study, and the RTMP which has supported this research. We are grateful to M. L. Eggart and L. Pond (Louisiana State University), who drafted all of the figures and to S. Baszio and T. Fiorillo who reviewed an earlier version of this paper.

REFERENCES

BASZIO, S. 1997a. Investigations on Canadian dinosaurs: palaeoecolo, v of dinosaur assemblages throughout the Late Cretaceous of south A.-berta, Canada. Courier Forschungsinstitut Senckenberg, 196:1–31.

BASZIO, S. 1997b. Investigations on Canadian dinosaurs: systematic palaeontology of isolated dinosaur teeth from the Latest Cretaceous of south Alberta, Canada. Courier Forschungsinstitut Senckenberg, 196: 33–77.

BRINKMAN, D. B. 1990. Paleoecology of the Judith River Formation (Campanian) of Dinosaur Provincial Park, Alberta, Canada: evidence from vertebrate microfossil localities. Palaeogeography, Palaeoclimatology, Palaeoecology, 78:37–54.

BRINKMAN, D. B., M. J. RYAN, AND D. A. EBERTH. 1998. The paleogeographic and stratigraphic distribution of ceratopsids (Ornithischia) in the upper Judith River Group of Western Canada. Palaios, 13:160–169.

CARPENTER, K. 1982. Baby dinosaurs from the Late Cretaceous Lance and Hell Creek formations and a description of a new species of theropod. Contributions to Geology, University of Wyoming, 20(2):123–134.

COPE, E. D. 1876. Descriptions of some vertebrate remains from the Fort Union beds of Montana. Proceedings of the Academy of Natural Sciences of Philadelphia, 248–261.

CURRIE, P. J., J. K. RIGBY, JR., AND R. E. SLOAN. 1990. Theropod teeth from the Judith River Formation of southern Alberta, Canada, p. 107–125. *In* K. Carpenter and P. J. Currie (eds.), Dinosaur Systematics: Perspectives and Approaches. Cambridge University Press, Cambridge.

EBERTH, D. A. 1996. Judith River Wedge, p. 379–385. *In* P. J. Currie and K. Padian (eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego.

EBERTH, D. A., AND D. B. BRINKMAN. 1997. Paleoecology of an estuarine, incised valley fill in the Dinosaur Park Formation (Judith River Group, Upper Cretaceous) of Southern Alberta, Canada. Palaios, 12: 43–58.

EBERTH, D. A., AND A. P. HAMBLIN. 1993. Tectonic, stratigraphic, and sedimentologic significance of a regional discontinuity in the upper Judith River Group (Belly River wedge) of southern Alberta, Saskatchewan, and northern Montana. Canadian Journal of Earth Science, 30: 174–200.

ESTES, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. University of California Publications in Geological Sciences, 49:1–187.

FIORILLO, A. R., AND P. J. CURRIE. 1994. Theropod teeth from the Judith River Formation (Upper Cretaceous) of south-central Montana. Journal of Vertebrate Paleontology, 14:74–80.

FIORILLO, A. R., AND R. A. GANGLOFF. 2000. Theropod teeth from the Prince Creek Formation (Cretaceous) of Northern Alaska, with speculations on Arctic dinosaur paleoecology. Journal of Vertebrate Paleontology, 20(4):675–682.

GAUTHIER, P. 1986. Saurischian monophyly and the origin of birds, p. 1–55. *In* K. Padian (ed.), The Origin of Birds and the Evolution of Flight. Memoirs of California Academy of Science, 8.

GILMORE, G. W. 1924. A new coelurosaurid dinosaur from the Belly River Cretaceous of Alberta. Geological Survey of Canada Bulletin, 38:1–12.

LEIDY, J. 1856. Notice of remains of extinct reptiles and fishes, discovered by Dr. F. V. Hayden in the Bad Lands of the Judith River, Nebraska Territory. Academy of Natural Sciences Philadelphia Proceedings, 8: 72–73.

LINNAEUS, C. 1758. Systema naturae per regna tria naturae, 10th edition, revised, 2 volumes. Holmiae, L. Salmii.

MARSH, O. C. 1881. Principal characters of American Jurassic dinosaurs. Pt. V. American Journal of Science (ser. 3), 21:417–423.

MATTHEW, W. D., AND B. BROWN. 1922. The family Deinodontidae, with notice of a new genus from the Cretaceous of Alberta. Bulletin of the American Museum of Natural History, 46:367–385.

PENG, J.-H., A. P. RUSSELL, AND D. B. BRINKMAN. 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman Formations of the Judith River Group (Campanian) of Southeastern Alberta: an illustrated guide. The Provincial Museum of Alberta, Natural History Occasional Paper No. 25, 54 p.

ROWE, T., R. L. CIFFELLI, T. M. LEHMAN, AND A. WEIL. 1992. The Campanian Terlingua local fauna, with a summary of other vertebrates from the Aguja Formation, Trans-Pecos, Texas. Journal of Vertebrate Paleontology, 12:472–493.

RUSSELL, L. S. 1935. Fauna of the Upper Milk River beds, Southern Alberta. Transactions, Royal Society of Canada, 3(29):115–127.

RYAN, M. J., P. J. CURRIE, J. D. GARDNER, M. K. VICKARYOUS, AND J. M. LAVIGNE. 1998. Baby hadrosaurid material associated with an unusually high abundance of *Troodon* teeth from the Horseshoe Canyon Formation, Upper Cretaceous, Alberta, Canada. Gaia 15:123–133.

SANKEY, J. T. 1998. Vertebrate paleontology and magnetostratigraphy of the upper Aguja Formation (late Campanian), Talley Mountain area, Big Bend National Park, Texas. Ph.D. dissertation, Louisiana State University, Baton Rouge, 263 p.

SANKEY, J. T. 2001. Late Campanian southern dinosaurs, Aguja Formation, Big Bend, Texas. Journal of Paleontology, 75(1):208–215.

SEELEY, H. G. 1888. The classification of the Dinosauria. Report British Association for the Advancement of Science, 1887:698–699.

SUES, H.-D. 1978. A new small theropod dinosaur from the Judith River Formation (Campanian) of Alberta Canada. Zoological Journal of the Linnean Society, 62:381–400.

TOKARYK, T. T., AND D. R. HARINGTON. 1992. *Baptornis* sp. (Aves: Hespernithiformes) from the Judith River Formation (Campanian) of Saskatchewan, Canada. Journal of Paleontology, 66:1010–1012.

XU, X., Z. ZHONGHE, AND W. XIAOLIN. 2000. The smallest known non-avian theropod dinosaur. Nature, 408:705–708.

ACCEPTED 27 AUGUST 2001