8 Theropod teeth from the Judith River Formation of southern Alberta, Canada

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Abstract

Few attempts have been made in the past to identify dinosaur teeth at the species level, and consequently, many have assumed that they cannot be identified. However, a diverse assemblage of theropods from the Judith River Formation of southern Alberta have teeth that are diagnostic at the family, subfamily, generic, and even species levels. Within each taxon, up to four types of teeth can be recognized corresponding to the premaxillary, maxillary, anterior dentary, and posterior dentary regions. Overall tooth shape, cross sections, the position of anterior and posterior carinae, and the morphology of the denticles can be used to identify theropod taxa, regardless of absolute size or maturity. The teeth of *Dromaeosaurus*, *Saurornitholestes*, *Troodon*, tyrannosaurids, and a new genus and species of theropod are described. The identification of theropod teeth has the potential of refining stratigraphic determinations, extending temporal and geographic ranges, indicating relationships, and allowing paleoecological statements to be made on the relative diversity or abundance of certain taxa.

Introduction

Vertebrate paleontologists realized early in the development of the science that certain types of dinosaur teeth were distinctive enough to be diagnosed at the species level (Leidy 1856, 1860, 1868; Cope 1876a,b; Marsh 1892). As better specimens were recovered, many of these tooth genera proved to be nomen dubium. Perhaps the most famous example is that of *Trachodon mirabilis*, a species established on the basis of isolated teeth from the Late Cretaceous of Montana (Leidy 1856). The name was subsequently applied to a flat-headed duckbilled dinosaur, and even became a family (Trachodontidae–Lydekker 1888) and a popular name (trachodonts). With the discovery of better preserved and more diverse specimens from western North America however, it was realized that several species of duckbilled dinosaurs had teeth that were indistinguishable from each other. Furthermore, the type specimens of *Trachodon* turned out to be from crested forms (Lambeosaurinae), whereas the name *Trachodon* had been extended to include skeletons of flat-headed forms (Hadrosaurinae). Lambe (1918) showed the name to be a nomen dubium, and recommended that use of the name be discontinued. Another tooth genus described by Leidy, *Palaeoscincus*, is now known to be an ankylosaurian, but Coombs (this volume) has shown that ankylosaur teeth are only diagnostic at the family level.

Troodon formosus is a name that was established on the basis of a tooth originally thought to have belonged to a lacertilian (Leidy 1856). In 1901, Nopcsa recognized it as a carnivorous dinosaur. However Gilmore (1924) and subsequent workers felt that *Troodon* was a plant-eating pachycephalosaurid. Sternberg (1945, 1951) and Russell (1948) correctly identified it as a small carnivorous dinosaur, and described the first jaws of this animal. Barsbold (1974) was unaware of these references, and put *Troodon* teeth in a different family than the jaws of the same animal. The discovery of a new specimen was necessary before the teeth of *Troodon* were reunited with their jaws and skeletons (Currie 1987a). This checkered history of *Troodon* shows the danger of establishing tooth genera, although in this case the teeth were always distinctive and were always identified as *Troodon*. It is ironic that *Trachodon* and *Troodon* were originally described in the same paper (Leidy 1856) because one shows the futility of using dinosaur teeth to establish new species, while the other shows that tooth genera can be valid.

Theropod teeth are common in the Judith River Formation of southern Alberta, as well as in rocks from many other times and places. This is not surprising because most tooth-bearing theropods had 50 or more functional teeth at any one time during their life. All the

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teeth were replaced several times during the lifetime of the individual. Theropod teeth with roots are recovered in dentigerous bones, but are seldom found in isolation. Worn teeth with resorbed roots are far more common. These shed teeth are often associated with the carcasses of other animals (Buffetaut and Suteethorn 1989), showing that teeth in the process of being replaced tended to be lost while theropods were feeding. In some cases, the evidence suggests that the carnivores were eating carrion (Currie and Dodson 1984), but most of the time it cannot be determined whether or not the prey was killed by an active predator or simply scavenged.

In what is now Dinosaur Provincial Park, there was a strong bias against the preservation of small skeletons (Currie 1987b), and theropods are amongst the rarest of the small species. None of the dromaeosaurids, troodontids, elmisaurids, or other species of small theropods is represented by a complete skeleton. However, many types of small theropod teeth have been found in jaw fragments and in association with partial skeletons. On the other hand, there are numerous complete tyrannosaurid skeletons (Russell 1970) with complete dentitions. Because isolated teeth are much more common than skeletons (even for tyrannosaurids), the following study was undertaken to see if they could be identified.

Usually, the size of theropod denticles are recorded as number of denticles per 5 mm. However, most of the teeth dealt with in this study are too small, and in some cases do not have denticles over a 5 mm length. Those that do usually exhibit strong curvature over a 5 mm length, making it difficult to make an accurate count. Therefore we have opted to measure denticles in this study by either counting the maximum number of denticles per millimeter, or by measuring the proximodistal (in the sense of the tooth rather than the denticle) base length of the largest denticle. Total tooth length often cannot be measured accurately because of wear or breakage at the tip, or because of differences in tooth curvature. The fore-aft basal length (FABL) of the tooth has a relatively constant relationship to the total length (Farlow et al. in preparation), and can be measured easily in most teeth. FABL is therefore the standard against which all other measurements are compared in this paper.

Description

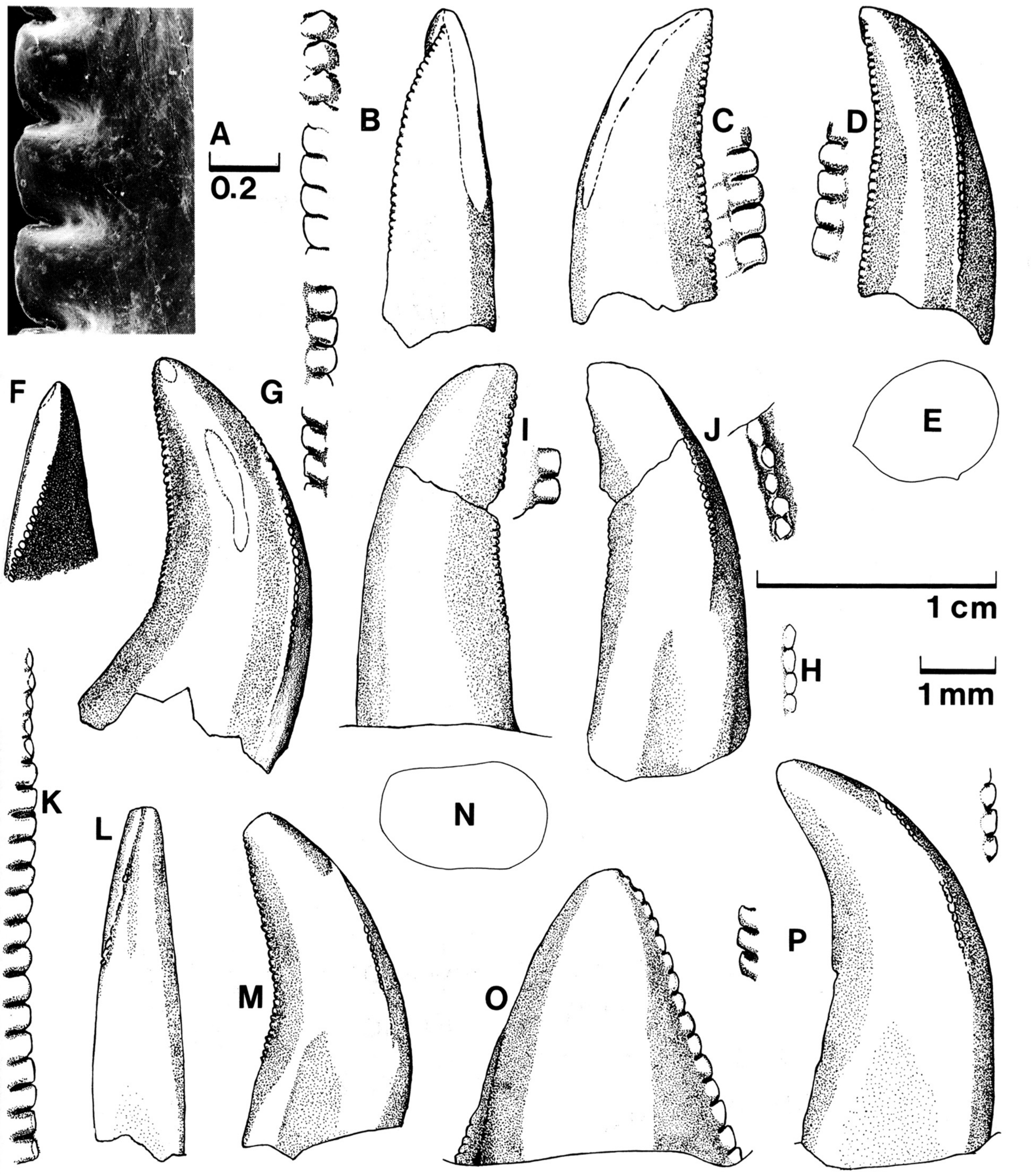
The six families of theropods currently known in the Judith River Formation are the Dromaeosauridae, Troodontidae, Elmisauridae, Caenagnathidae, Ornithomimidae, and Tyrannosauridae. Elmisauridae may be synonymous with Caenagnathidae (Currie and Russell 1988), and therefore may include only toothless species. No North American ornithomimids are known that have teeth, even though teeth are known in the central Asian *Harpimimus* (Barsbold and Perle 1984). Unfortunately, the teeth of *Harpimimus* are only simple pegs that lack serrations (personal observation 1989), and have no significance for determining the relationships of ornithomimids. Of the toothed forms, Dromaeosauridae can be divided into the subfamilies Dromaeosaurinae and Velociraptorinae (Barsbold 1983), and the tyrannosaurids into Aublysodontinae and Tyrannosaurinae (some authors, including Paul 1988b, consider the aublysodonts and tyrannosaurs as distinct families).

Dromaeosaurinae

Dromaeosaurus albertensis is the least specialized of the well-known small theropods of the Judith River Formation. The snout is narrow, and the mandibles are relatively straight bones that meet rostrally in an acute angle. The type specimen (AMNH 5356) includes teeth from all regions of the jaws although most of these are crushed and broken. There are four premaxillary teeth, nine maxillaries, and eleven mandibulars (Colbert and Russell 1969) for a maximum total of 48 tooth positions in the mouth. The third and fifth teeth of the left maxilla, and the third tooth of the right maxilla, are more than 15 mm long when measured in a straight line from the tip to the base of the crown on the back of the tooth, and have a FABL of 7.5 mm. The longest mandibular teeth are 14 mm long, and therefore are not significantly shorter than those of the upper jaw, but the maximum FABL is only 6.7 mm. On the average, the FABL of a dentary tooth is about 9% smaller than one from the upper jaw. As in most theropods, all teeth are set in distinct sockets, and there are interdental plates lingual to the teeth (Currie 1987a). The presence of these interdental plates was not detected for a long time because they co-ossified with adjacent plates and the dentary itself. This condition is comparable with that of *Saurornitholestes* and possibly baryonychids (Charig and Milner this volume), but is distinct from the situation seen in troodontids, tyrannosaurids, a specimen that Gilmore (1924) referred to *Chirostenotes*, and most other theropods.

Dromaeosaurid maxillary and dentary teeth (Fig. 8.1) are laterally compressed so that the FABL of a tooth is as much as double the width. There are denticles on both anterior and posterior carinae, and the denticles are smallest at the proximal and distal ends of the carinae. Most teeth are damaged in the holotype, but the third maxillary tooth of the type specimen has 34 denticles on the anterior carina and 45 on the posterior. The denticles are almost as high as they are long (Fig. 8.1A), and curve only slightly distally towards the tip of the tooth (Figs. 8.1B,D,P). Each denticle is relatively broad (labial-lingual) and chisel-like in form. Blood grooves extend onto the surface of the tooth from between the bases of adjacent denticles on some teeth, but are usually found only near the base of the tooth and tend to be shallow and poorly defined (Figs. 8.1A, 8.7D,G). The blood grooves are oriented perpendicular to the longitudinal axis of the tooth. Abler (in preparation) describes

Figure 8.1. *Dromaeosaurus albertensis*. **A**, SEM photograph of posterior denticles of maxillary tooth (TMP 83.36.8) in labial view. **B–P**, teeth of the holotype (AMNH 5356). **B**, anterior view of 2nd left premaxillary tooth, with mesial (above) and anterior views of enlarged denticles. **C**, labial view of 2nd left premaxillary tooth with enlargement of posterior denticles. **D**, lingual view of 2nd left premaxillary tooth with enlargement of posterior denticles. **E**, cross-section of base of 2nd left premaxillary tooth. **F**, anterodistal view of tip of 4th maxillary tooth showing characteristic twist of anterior carina. **G**, lingual view of 4th right maxillary tooth with labial (above) and lingual (below) enlargements of posterior denticles. **H**, lingual view of anterior denticles of 3rd right maxillary tooth. **I**, labial view of 2nd left dentary tooth with enlargement of posterior denticles. **J**, lingual view of 2nd left dentary tooth with enlargement (in distal aspect) of anterior denticles. **K**, enlargement of denticles along distal region of posterior carina (labial view) of 3rd left dentary tooth. **L**, anterior view of 3rd left dentary tooth. **M**, lingual view of 3rd left dentary tooth. **N**, cross-section of base of 3rd left dentary tooth. **O**, enlargement of lingual view of 3rd right dentary tooth (erupting). **P**, lingual view of 5th dentary tooth with lingual views of posterior (left) and anterior (right) denticles of newly erupted 6th dentary tooth. Centimeter scale bar is for drawings of complete teeth, millimeter scale bar is for "enlargements", and fractional scale bar is for SEM.



an enamel ridge on the midline of each denticle, and finds that the enamel ridges of adjacent denticles meet to form a V-shaped slot. Such ridges and slots are found in the specimen being described, as well as in most other Judithian theropods.

Both the anterior and posterior carinae of any premaxillary tooth of *Dromaeosaurus* are on the lingual side of the tooth. However, because of the narrowness of the snout, the posterior carina is posterolateral to the anterior carina, and the tooth is not D-shaped in section (Figs. 8.1E, 8.6D) as premaxillary teeth are in tyrannosaurids (Figs. 8.6U,X). Denticles on the posterior carinae of the premaxillary teeth tend to be longer than those on the anterior carinae, but their maximum basal length (0.37 mm) is less than that of the anterior carina (0.40 mm).

Maxillary teeth (Fig. 8.1G) of *Dromaeosaurus* tend to be taller and more recurved than the premaxillary teeth. The anterior carina is close to the midline of the tooth near the tip, but not far from the tip twists towards the lingual surface. This characteristic twist (Figs. 8.1F,L) is found on all teeth in the type specimen, and is the easiest way to identify the teeth of *Dromaeosaurus albertensis*.

Dentary teeth of *Dromaeosaurus* (Figs. 8.1I–P) cannot be distinguished from the maxillary teeth in the type specimen. Furthermore, because of the straightness of the jaw and the corresponding similarity of action, anterior dentary teeth cannot be distinguished from more posterior ones. Denticles are found on the anterior carinae at least as far back as the eighth dentary tooth, and are found on the posterior carinae of all teeth.

Velociraptorinae

The most common small theropod is the velociraptorine dromaeosaurid *Saurornitholestes langstoni* (Currie 1987c). Both *Saurornitholestes* and *Deinonychus* were recently synonymized with *Velociraptor* (Paul 1988a), although new material in the collections of the Tyrrell Museum of Palaeontology may show enough differences to support generic distinction. Until the new specimens are described, we have taken the conservative approach of maintaining generic distinction of *Saurornitholestes* and *Velociraptor*.

The snout of a velociraptorine is narrow, as the lower jaws are relatively straight and meet anteriorly in a loose symphysis at an acute angle.

The type specimen of *Saurornitholestes langstoni* (TMP 74.10.5) includes two isolated teeth (Sues 1978). Although it is possible that these associated teeth do not belong to the skeleton, it is more parsimonious to assume association because the skeleton was found by itself (not within a bone-bed), because both the skeleton and teeth can be identified as Velociraptorinae by comparison with other genera, and because one of the teeth includes at least part of a root and therefore could not be the shed tooth of a scavenger. Furthermore, the recent discovery of a partial skeleton (TMP 88.121.39) of this animal confirms the association of teeth and skeleton.

An isolated premaxilla (TMP 86.36.117) has been tentatively identified as *Saurornitholestes*, and includes the bases of four premaxillary teeth as in *Deinonychus* (Ostrom 1969). No maxilla is known for *Saurornitholestes*, but given the number of mandibular teeth and the general similarity of this genus to the other velociraptorines (*Deinonychus* and *Velociraptor*), it is unlikely that there were more than ten maxillary teeth. The identification as *Dromaeosaurus* of two dentaries by Sues (1977a) was incorrect, and UA 12091 and UA 12339 should be assigned to *Saurornitholestes* (Currie 1987a). TMP 88.121.39 includes a complete dentary with 15 teeth. UA 12339 is a slightly larger dentary with 16 alveoli. It seems probable that *Saurornitholestes* had a total of about 60 teeth in the head. The teeth were set in distinct sockets and were bound lingually by interdental plates (Currie 1987a) similar to those of *Dromaeosaurus*.

The teeth of the type specimen (TMP 74.10.5) are 8.9 and 9.2 mm long with FABLs of 3.9 and 4.5 mm respectively. The longest dentary teeth in TMP 88.121.39 are the second, fourth, ninth, and eleventh from the symphysis, all of which are about 9 mm long with a maximum FABL of 5.1 mm. These and all isolated teeth assigned to *Saurornitholestes* are strongly recurved distally, sharply pointed, and laterally compressed (Fig. 8.2). They are easily identified as being velociraptorine because of the great disparity in size of denticles on the anterior and posterior carinae (Fig. 8.3N; Ostrom 1969; Sues 1977b). Anterior denticles are minute, and are usually less than half the length and base width of the posterior denticles. Posterior denticles are smaller than those of *Troodon*, but are more elongate and sharply pointed than those of *Dromaeosaurus*. The denticles are relatively straight and narrow (labial-lingual) for most of their length, but are hooked distally towards the tip of the tooth (Figs. 8.2A,H,L, 8.3N). The interdenticle slits are relatively deep (Figs. 8.7E,H,I). The blood groove is more pronounced than in *Dromaeosaurus*, although it has the same orientation (parallel to the longitudinal axes of the denticles). Amongst the Judithian theropods, the shape of the posterior denticles of velociraptorines is unique (Fig. 8.7).

Two isolated premaxillary teeth (TMP 70.37.1, and NMC 2664, Figs. 8.6E–I) are referred to *Saurornitholestes langstoni* on the basis of similarity of the posterior denticles to those of the type of *Saurornitholestes*. The teeth are flattened lingually, but are not D-shaped in section.

The two teeth found with the type specimen are not associated with either a maxilla or dentary. However, because the denticulate anterior carina extends more than halfway from the tip of the crown in the larger tooth (Figs. 8.2J–L), it may be a maxillary tooth. The smaller tooth (Figs. 8.2C–I) is from the front of the

Figure 8.2. *Saurornitholestes langstoni*. **A**, SEM of posterior denticles in lingual aspect of TMP 80.16.996. **B**, lingual view of TMP 82.24.16. Holotype (TMP 74.10.5) tooth #1 in **C**, anterior; **D**, labial; **E**, posterior; and **F**, lingual views; with **I**, cross-section of base; and enlargements of **G**, anterior and **H**, posterior denticles. Holotype (TMP 74.10.5) tooth #2 in **J**, anterior; and **K**, lingual views; with **L**, enlargement of tip in lingual view. TMP 82.19.366 in **N**, labial; and **O**, lingual views; with **P**, cross-section of base; and **M**, enlargement of labial view of distal denticles. **Q**, enlargement of posterior denticles of TMP 79.8.643 in labial view. **R**, enlargement of posterior denticles of NMC 12410 in labial view. **S**, enlargement of TMP 82.19.180 in lingual view. TMP 82.16.43 in **V**, anterior; and **U**, labial views; with **W**, cross-section of base; and **T**, enlargement of posterior denticles. Scale bars as in Figure 8.1.

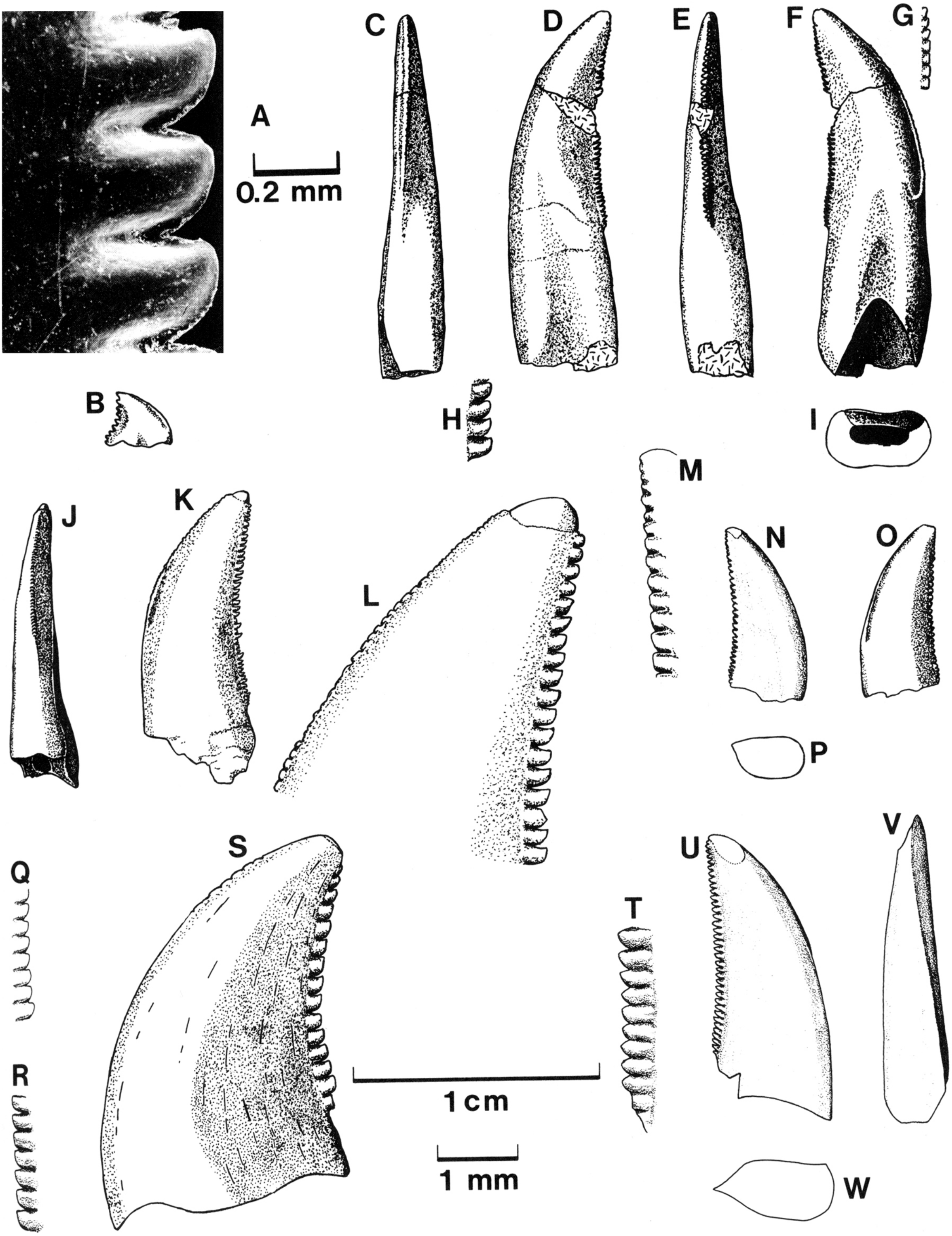
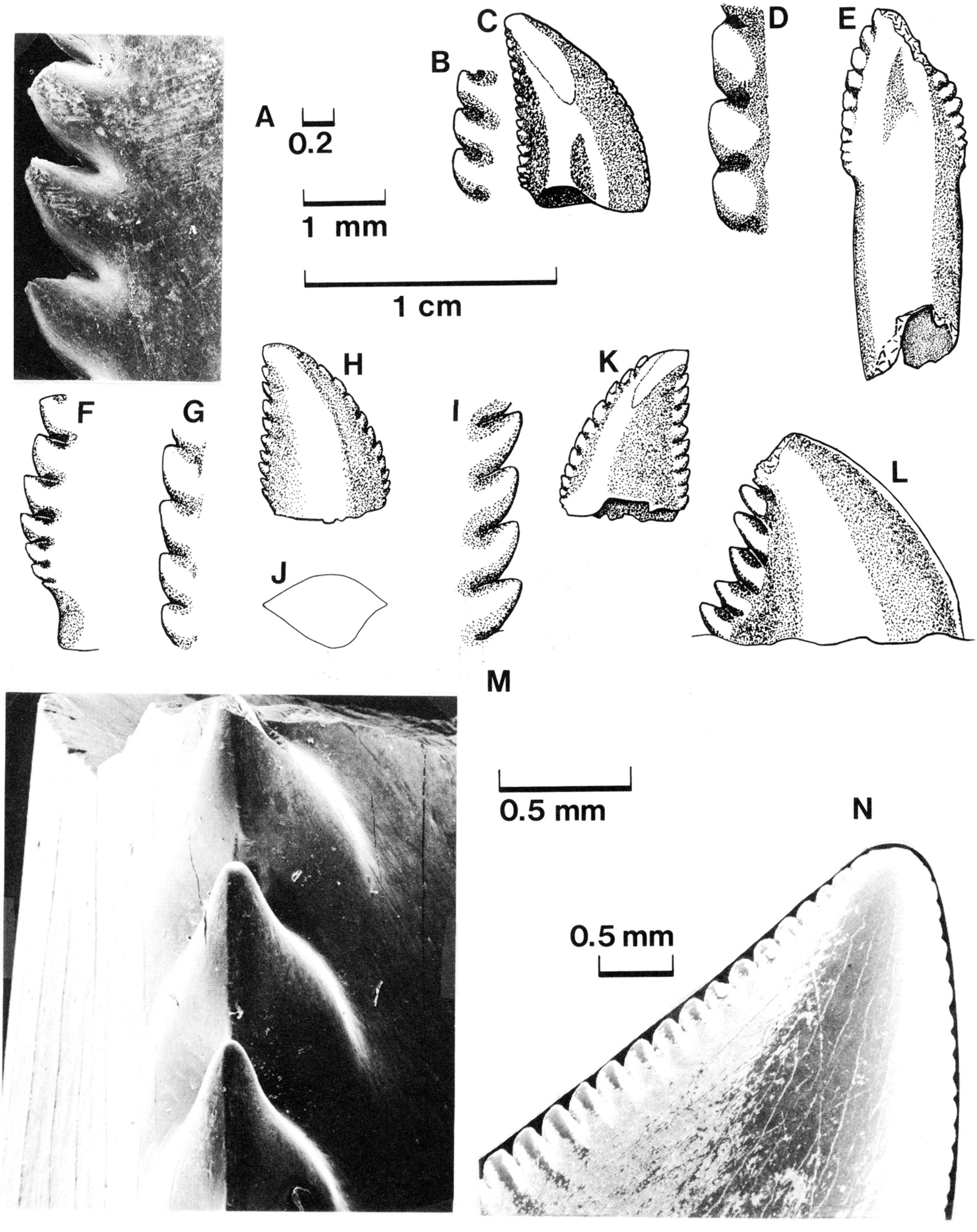


Figure 8.3. *Troodon formosus*. **A**, SEM of posterior denticles in labial view of maxillary tooth (TMP 83.45.7). TMP 85.6.186 (maxillary tooth) in **C**, lingual view; with **B**, an enlargement of posterior denticles. TMP 85.6.3 (premaxillary tooth) in **E**, lingual view; with **D**, enlargement of anteromedial denticles showing worn tips. **F,** enlargement of proximal denticles on posterior carina of TMP 83.36.215. TMP 83.36.214 (maxillary tooth) in **H**, labial; and **K**, lingual views; with **J**, cross-section of the base; and enlargements of **G**, anterior, and **I**, posterior denticles in lingual view. **L**, enlargement of distal end of mandibular tooth of TMP 83.12.11 in lingual view. **M**, SEM of posterior denticles of *Troodon formosus* (TMP 83.45.8) in posterior view. **N**, SEM of labial view of tip of tooth of *Saurornitholestes langstoni* (TMP 78.9.96). Scale bars as in Figure 8.1.



left dentary. As pointed out by Sues (1978), there are about five denticles per millimeter on the posterior carina, and seven on the anterior. Individual denticles on the posterior carina are not only broader at the base than the anterior ones, but are considerably longer and sharper as well.

Teeth in the third and fifth alveoli of the dentary of TMP 88.121.39 lack denticles on the anterior carina. However, the distal ends of the anterior carinae probably did have denticles (as in more posterior teeth of the same dentary, which have six denticles per millimeter) that have simply been worn off. Nevertheless, there are many isolated teeth of *Saurornitholestes* from Dinosaur Provincial Park that do lack anterior denticles (Figs. 8.2N,O,U,V), indicating that the presence or absence of denticles on the anterior carinae of dentary teeth is variable. There are four denticles per millimeter on the posterior carinae of TMP 88.121.39.

There are many small isolated teeth identified as *Saurornitholestes* (Fig. 8.2B), in which the posterior denticles are relatively large compared to the FABLs of the teeth, but are somewhat smaller than the denticles of larger teeth. In TMP 81.20.259, the FABL is 2.6 mm and there are seven denticles per millimeter on the posterior carina. This trend is consistent with other theropods (Farlow et al., in preparation) where young individuals tend to have fewer, smaller denticles on their teeth than more mature animals.

Troodontidae

Troodon formosus is currently the only species of troodontid recognized in the Judith River Formation (Currie 1987a), and includes specimens previously referred to *Stenonychosaurus inequalis*, *Polyodontosaurus grandis*, and *Pectinodon bakkeri*. There are three teeth preserved in the premaxilla of MOR 430, but this bone is incomplete and a fourth tooth may have been present as in *Saurornithoides* (Barsbold 1974). A maxillary fragment of *Troodon formosus*, NMC 12392, has parts of nine alveoli preserved. However, comparison with troodontid material from Asia suggests that there would have been a total of 15–20 maxillary teeth. The dentary teeth of *Troodon* are smaller and more numerous (35) than those in the upper jaw. *Troodon*, therefore, had more than 100 functional tooth positions, which is a higher tooth count than any other theropod from the Judith River Formation. Premaxillary teeth are set in sockets, whereas most of the dentary teeth are arranged in a dental groove, and are held in position by interdental bone around the roots. There are no interdental plates lingual to the teeth. Instead, the teeth are constricted between crown and root, and held in place by a partial ring of interdental bone around the constriction (Currie 1987a). The constriction would have been below the gum line on the crown of the tooth, and the enameled surface of the crown extends to the level of the constriction labially, anteriorly and posteriorly, but on some teeth, it ends at the gum line on the lingual surface.

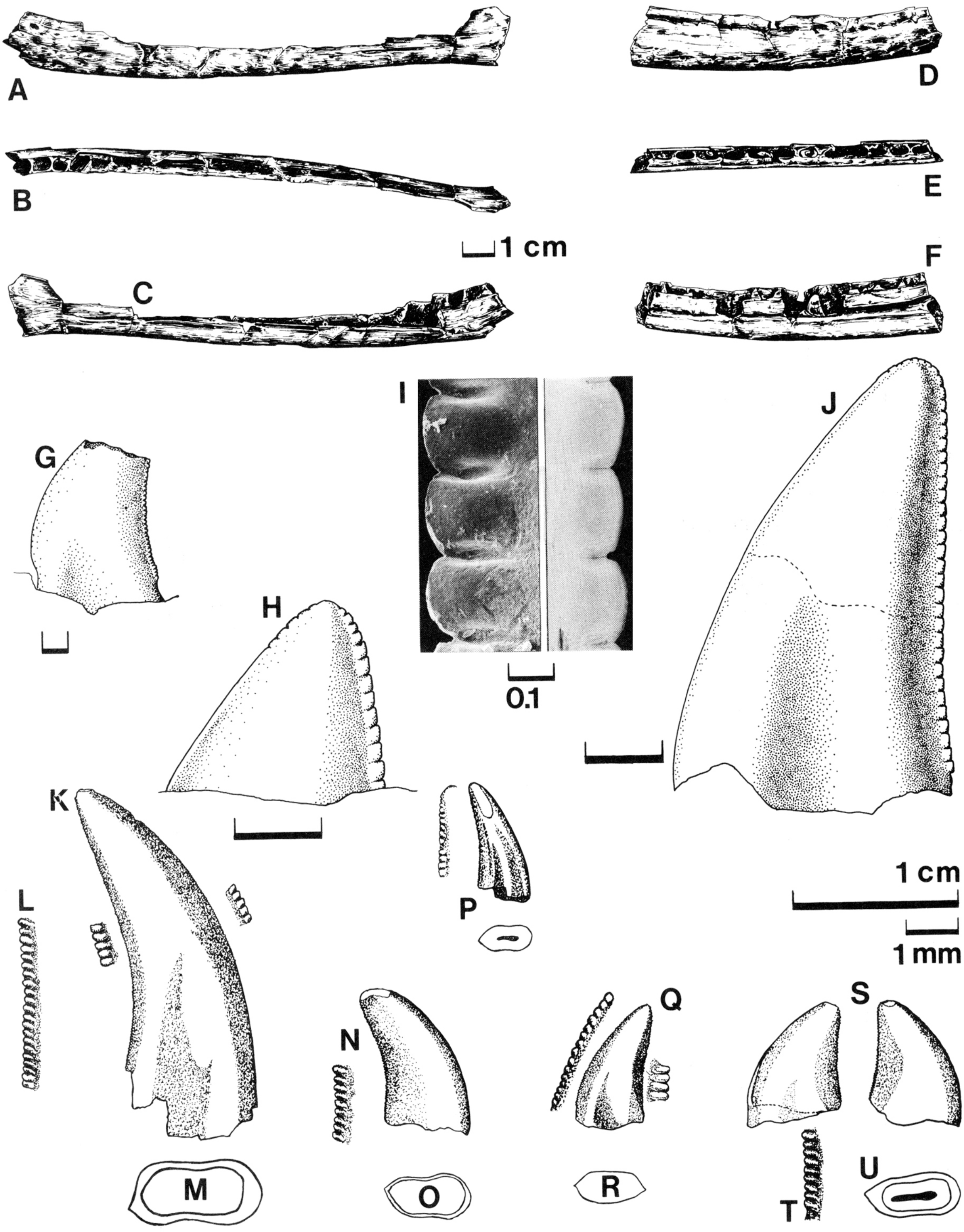
The front of the troodontid snout is relatively wide, and the distal ends of the lower jaws curve towards the midline as in toothless caenagnathids and ornithomimids, but in contrast with the jaws of dromaeosaurids and tyrannosaurids. The snout of a tyrannosaurid is fairly broad however, and in this sense is more similar to the snout of a troodontid than to that of a dromaeosaurid. The development of "incisiform" (in this sense, with both carina on the posterior surface) teeth is clearly related to the orientations of the jaws anteriorly, and it is not surprising that troodontids and tyrannosaurids have incisiform teeth in the premaxilla, and that troodontids have incisiform teeth at the front of the dentary.

The carinae of a premaxillary tooth (Figs. 8.3, 8.6) are both on the posterior side of the tooth, as in tyrannosaurids. In contrast with the latter family however, the premaxillary tooth of a troodontid is triangular in section rather than D-shaped (Currie 1987a). There are large denticles on both carinae of a troodontid premaxillary tooth (Figs 8.3D, E). In the type specimen (ANSP 9259), there are seven "posterior" denticles and ten "anterior" denticles (Currie 1987a). All denticles are strongly hooked with the pointed tips (Fig. 8.3M) turned toward the distal end of the tooth. The denticles are larger than those found in any other Judithian theropod, with a basal diameter measuring up to 0.7 mm in TMP 82.20.259, less than 1.5 denticles per millimeter (compare this with BHI 1281, a 9 cm long tooth of *Tyrannosaurus* that has denticles with the same basal diameter). As reported previously (Currie 1987a), the denticles on the posterior carina of premaxillary teeth tend to be longer than those of the anterior carina, but have a smaller basal diameter. The grooves between successive denticles form distinct, rounded pits, at the centres of which are found the interdenticle slits (Figs. 8.7B,F).

Maxillary teeth of *Troodon* (Figs. 8.3G–K) have long, recurved crowns, are laterally compressed, and have carinae on the rostral and posterior surfaces. TMP 65.23.32 is a centimeter long with a FABL of 5.7 mm, and TMP 88.96.2 has a FABL of 6.7 mm. In general shape, the denticles and their associated blood grooves and pits (Figs. 8.3A, 8.7B,F) are the same as the denticles of premaxillary teeth. However, maxillary denticles are smaller than premaxillary ones, and the posterior ones reach a maximum length of 0.5 mm with basal diameter of 0.5 mm (TMP 65.23.32). There can be more than thirty anterior denticles, which are smaller than the 20 or so on the posterior carina. In TMP 65.23.32, the basal diameter of the largest anterior denticle is 0.35 mm, but its height is only 0.1 mm. The "serrated" carina follow the midline of the tooth, and extend from the gum line to the tip of the tooth.

The dentary teeth of *Troodon* are considerably smaller than the maxillary ones (Currie 1987a). The

Figure 8.4. *Richardoestesia gilmorei*. Holotype (NMC 343): **A**,**B**,**C**, left; and **D**,**E**,**F**, right dentary fragments in **A**,**D**, lateral; **B**,**E**, dorsal; and **C**,**F**, lingual views; with lingual views of **G**, 13th right; **H**, 17th right; and **J**, sixth right dentary teeth. **I,** SEMs of labial view of denticles at mid-length of the tooth and lingual view of distal denticles. **J**, lingual view of sixth right dentary tooth. TMP 83.45.2 in **K**, labial view with enlargements of anterior and posterior denticles; **L**, enlargement of proximal denticles of posterior carina; and **M**, cross-section of the base of the tooth. TMP 80.8.298 in **N**, labial view; with **O**, enlargement of posterior denticles and cross-section of the base. TMP 84.89.274 in **P**, labial view with enlargement of posterior denticles and cross-section of the base. TMP 83.129.11 in **Q**, lingual view with enlargements of anterior and posterior denticles; and **R**, cross-section of the base of the tooth. TMP 80.16.1230 in **S**, lingual and labial views; with **T**, enlargement of proximal posterior denticles in labial view; and **U**, cross-section of base. **G**, **H**, **J**, scale bars represent 1 mm. **L**–**U**, scale bars as in Figure 8.1.



maximum length of any mandibular tooth is 6 mm with a FABL of less than 5 mm. The anterior dentary teeth, because of the curvature of the jaw, are similar to the premaxillary teeth in that both carinae are clearly on the lingual side of the tooth. At least the first half dozen or so dentary teeth have denticles on both anterior and posterior carinae, although the posterior denticles are larger than the anterior ones. The posterior denticles are larger and less numerous on these anterior teeth than they are on more posterior dentary teeth. In contrast with the premaxillary teeth, the "anterior" denticles are not wider at the base than the posterior denticles, the former having a maximum diameter of 0.5 mm compared with 0.6 mm for posterior denticles. Posterior mandibular teeth lack denticles on the anterior carina.

The teeth of juvenile troodontids have been described (Currie 1987a). The basal widths of the denticles are only slightly smaller on average than those of mature teeth, so it is not surprising that there are fewer denticles on the smaller teeth. For example, TMP 79.8.635 is a posterior dentary tooth with a length of 4 mm, and bears only eight denticles on the posterior carina, the largest of which has a basal diameter of 0.5 mm. In contrast, the 20th mandibular tooth of TMP 83.12.11 is 5 mm long, and has at least 11 posterior denticles, the largest of which has a basal diameter of 0.45 mm.

Troodontid teeth found in the Milk River Formation (ROM collections) and the Horseshoe Canyon Formation (TMP, NMC collections) are essentially identical to those of the Judith River Formation. The troodontid *Saurornithoides* teeth from Mongolia are similar in size and shape (Barsbold 1974), but the posterior maxillary teeth lack anterior denticles, making them difficult to distinguish from posterior dentary teeth except by relative size. The distinctive shape of the troodontid denticle is found in *Saurornithoides* (teeth found with IVPP 2206883, Djadokhta Formation of Bayan Manduhu, Inner Mongolia). Teeth from the Lower Cretaceous Cedar Mountain Formation identified as troodontid (Nelson and Crooks 1987) are more likely from a velociraptorine because the denticles are too small (there are 12 posterior denticles per millimeter in their figures) and elongate. Troodontid teeth from the Maastrichtian Frenchman, Hell Creek, Lance, and Scollard Formations, as well as from the Prince Creek Formation of Alaska, are somewhat different from the Judithian teeth of southern Alberta (personal observations) and may eventually prove to represent a distinct species.

Theropoda *incertae sedis*

In 1924, Gilmore named *Chirostenotes pergracilis*, based on a pair of articulated mani. In the same paper, he described a pair of jaws found several miles away, and arbitrarily referred them to *Chirostenotes* because of their long, slender nature. The left dentary of NMC 343 is almost complete, lacking only small parts of the rostral and caudal ends (Figs. 8.4A–C), and is 193 mm long. Gilmore's suggestion that each jaw would have had at least 18 teeth is correct, and the number would not have exceeded 20. NMC 343 represents a theropod that had more teeth in its jaws than any other known Judithian carnivore except *Troodon*. Given that there were 18–20 dentary teeth, a conservative estimate based on relative tooth counts in other theropods suggests there would have been at least 3 premaxillary and 11 maxillary teeth on each side of the skull for a total minimum of 66 teeth in the head. The maximum number would have been less than 90.

The teeth of NMC 343 are set in distinct sockets (Figs. 8.4B,E) as in all Judithian theropods except *Troodon*. The jaws are straight, and it is evident that they met in an acute angle rostrally, rather than curving to meet each other as in *Troodon*. The shallow Meckelian groove is similar to that of *Saurornitholestes*. There are interdental plates (Fig. 8.4F), in contrast with *Troodon*, but, unlike *Dromaeosaurus* and *Saurornitholestes*, the adjacent centers of interdental bone do not cover the entire base of the tooth lingually. In fact, adjacent interdental plates do not seem to touch each other, with the possible exception of the third and fourth plates on the left dentary. Amongst Judithian theropods, the interdental plates of NMC 343 are closest in appearance and morphology to those of tyrannosaurids. This is clearly a primitive characteristic however, and cannot be used by itself to indicate relationship. Nevertheless, the primitive nature of the interdental plates do show that this animal is neither a dromaeosaurid nor a troodontid.

Most of the teeth of NMC 343 fell out of the jaws before burial and fossilization. The roots of four teeth were found in the sockets, however. Three of these four broken teeth were in the process of being replaced, and developing teeth are preserved within the shells of the older teeth. At least an additional seven unerupted teeth were found within sockets where the functional teeth had either fallen out or been broken off. As pointed out by Gilmore (1924), as many as three teeth in different stages of development were found in each alveolus. The germ teeth develop lingual to the older teeth in the anterior half of the tooth socket. Each developing tooth is twisted somewhat so that the anterior carina is more medial in position than the posterior carina. As a tooth became larger, it would migrate laterally and posteriorly, and would rotate until the anterior and posterior carina were aligned. Tooth development was confined to the tooth sockets and there appears to have been little reworking of the interdental bone, in contrast with *Troodon* where there appears to have been more reworking of the interdental bone.

Two types of laterally compressed teeth were found in NMC 343. The anterior dentary teeth are elongate, relatively straight teeth (Fig. 8.4I). They are distinctive because the posterior margin of the tooth, when viewed from the side, is convex at the distal end rather than concave as it is in all other Judithian theropods. At least the first eight dentary teeth seem to fit this pattern. The average antero-posterior length – which approximates the FABL – of five anterior alveoli is 4.6 mm. The crown appears to have been at least 50% longer (proximodistally) than the FABL. The sixth right dentary germ tooth has a complete crown, although the enamel appears to have been incompletely formed on the proximal half of the tooth.

More posterior teeth of NMC 343 are distinctive in that they are more recurved (Fig. 8.4G). The average lateromedial width of a dentary alveolus is not significantly variable along the jaw. However, the base of a mid to posterior tooth is longer, with an average alveolar length (roughly equivalent to the FABL) of 5.5 mm.

There are a few denticles at the distal end of the anterior carina (Fig. 8.4I) of the sixth, eighth, and seventeenth dentary teeth, and the denticles wrap around the tip of the tooth onto the posterior carina. Each denticle is small and relatively simple in form (Figs. 8.4J, 8.7C), and hooks slightly toward the distal end of the tooth. There are interdenticle slits as in other theropods. The posterior denticles of NMC 343 are easily distinguished from those of *Dromaeosaurus*, *Saurornitholestes*, *Troodon*, and the tyrannosaurids because of their small size. There are six denticles per millimeter on the sixth dentary tooth, and five denticles per millimeter on the thirteenth. However, these denticles are short and measure less than 0.15 mm from base to tip. The denticles taper slightly, but are not hooked distally as much as they are in *Saurornitholestes* and *Troodon*. Because these teeth had not erupted by the time of death, the lack of pronounced distal hooking cannot be attributed to tooth wear.

No postcranial skeletal remains were found with NMC 343, but the same or similar teeth (Figs. 8.4N,Q,S) as those of this specimen are relatively common in the Judith River Formation. Other teeth can be referred to the same genus because of similarity of denticular size and shape, although the teeth do not necessarily have the same shape (Figs. 8.4K,P). Nevertheless, it is assumed that these teeth do represent the same species of theropod, but that they may represent teeth from the upper jaws. The labial view of the teeth in NMC 343 cannot be seen because they are covered by bone. In some isolated teeth attributed to this animal, the denticles look like "stacked bananas" in labial aspect (Figs. 8.4L,N,T) because of the blood grooves between the denticles. This unusual feature can be used to identify isolated teeth with small denticles that are different in overall tooth shape and anterior denticulation from the known mandibular teeth.

Some of the isolated teeth that can now be attributed to the same animal as NMC 343 have previously been identified as possible sebecosuchian teeth (Sahni 1972). Langston (1956) gives a list of characteristics that can be used to distinguish sebecosuchians from "carnosaurs." However, most small theropods can be distinguished from carnosaurs using some of the same characters (lateral compression, "lenticular" cross sections). Other characters cited by Langston (relative length of the root, fluting, length of denticulate portion of carina) either have not been seen in the Judithian teeth identified as sebecosuchians, or are not present. NMC 343 is unquestionably a theropod, rather than a sebecosuchian crocodile, and it is highly probable that so are all teeth from the Judith River Formation previously identified as sebecosuchian.

There is a considerable variety of teeth from Dinosaur Provincial Park that have the same small denticles seen in NMC 343. By comparison with this specimen, many of these can be identified as anterior or posterior dentary teeth. But others do not seem to be mandibular teeth. TMP 83.45.2 (Fig. 8.4K) is an elongate, fang-like tooth with denticles on both anterior and posterior carinae. We have no hesitation in referring this specimen to the same species as NMC 343 because of the minute size and shape of the denticles. The posterior denticles are hooked slightly distally, and, as in *Saurornitholestes*, are markedly larger than the anterior denticles.

When Gilmore (1924) referred NMC 343 tentatively to *Chirostenotes pergracilis*, it was hoped that additional skeletal material would be recovered to confirm or refute this referral. Although additional specimens of *Chirostenotes* have been found (Currie and Russell 1988), small theropods remain some of the rarest animals recovered and there is still no way of confirming Gilmore's identification after more than six decades. Currie and Russell (1988) presented evidence to suggest that *Chirostenotes* (exclusive of the referred dentaries) may even be synonymous with the toothless *Caenagnathus*. Russell (1984) suggested that the teeth are similar to isolated *Paronychodon* teeth, but the presence of small denticles on the posterior carinae and the absence of longitudinal ridges makes this association unlikely. However, there are many isolated teeth recovered from Dinosaur Provincial Park that are the same as those of NMC 343. Because NMC 343 is so distinctive, because teeth referrable to the same species of animal are so common, and because continued referral of NMC 343 to *Chirostenotes* is both confusing and probably misleading, we hereby propose to name a new genus and species of small theropod. It is conceivable that more complete specimens may eventually show that this animal is in fact synonymous with either *Chirostenotes pergracilis* or *Elmisaurus elegans* (Currie 1989).

Dinosauria Owen 1842
Theropoda Marsh 1881
Maniraptora Gauthier 1986
Family unknown
Richardoestesia n. gen.

Etymology. In honour of Richard Estes, whose

1964 paper on Lance Formation microvertebrate fossils demonstrated the use of theropod teeth in faunal studies.

Diagnosis. Small carnivorous dinosaur. Elongate jaw with little lateromedial curvature. 18–19 teeth per dentary. Anterior mandibular teeth relatively straight with convex posterior outline in lateral view for at least the distal half of tooth. More posterior teeth are relatively short and recurved. Denticles shorter than in other known Judithian theropods with a length of 0.15 mm. There are up to five denticles per millimeter on the posterior carina of mandibular teeth.

Genoholotype. NMC 343.

Richardoestesia gilmorei n. sp.

Etymology. In honour of G. W. Gilmore who first described this specimen in 1924.

Holotype. NMC 343, the remains of a pair of dentaries with unerupted and germ teeth.

Horizon and locality. Judith River (Oldman) Formation, Dinosaur Provincial Park, Alberta (Section 30, Twp. 20, Rge. 11, W4M).

Diagnosis. In contrast with Maastrictian teeth of *Richardoestesia*, some curvature is always present in the proximal portion of tooth.

Isolated teeth of *Richardoestesia gilmorei* are quite varied in shape and size. Although teeth of this species are common, no premaxillary teeth have been identified with certainty. TMP 81.16.194 (Figs. 8.6J–M) may be a premaxillary tooth of this species because its denticles are minute in comparison with those of premaxillary teeth in other theropods.

Teeth of *Richardoestesia* have also been identified in the Lower Campanian Milk River Formation (Russell 1935), the Scollard Formation of Alberta, the Frenchman Formation of Saskatchewan, the Hell Creek Formation of Montana, and the Lance Formation of Wyoming (Estes 1964; Carpenter 1982). Both longer straight teeth and recurved shorter teeth are known. As in *Richardoestesia gilmorei*, the serrations are often limited to the posterior carina, and individual denticles are minute. Many teeth from these formations are different, however, in that there is virtually no curvature evident in lateral view, and the teeth resemble an elongate, isosceles triangles. We suspect that the Maastrichtian teeth represent a difference species of *Richardoestesia*, which will be described later. However, the presence of identical teeth in the Lower Campanian Milk River Formation is perplexing in light of the virtual absence of this form in the Late Campanian Judith River and Horseshoe Canyon Formations.

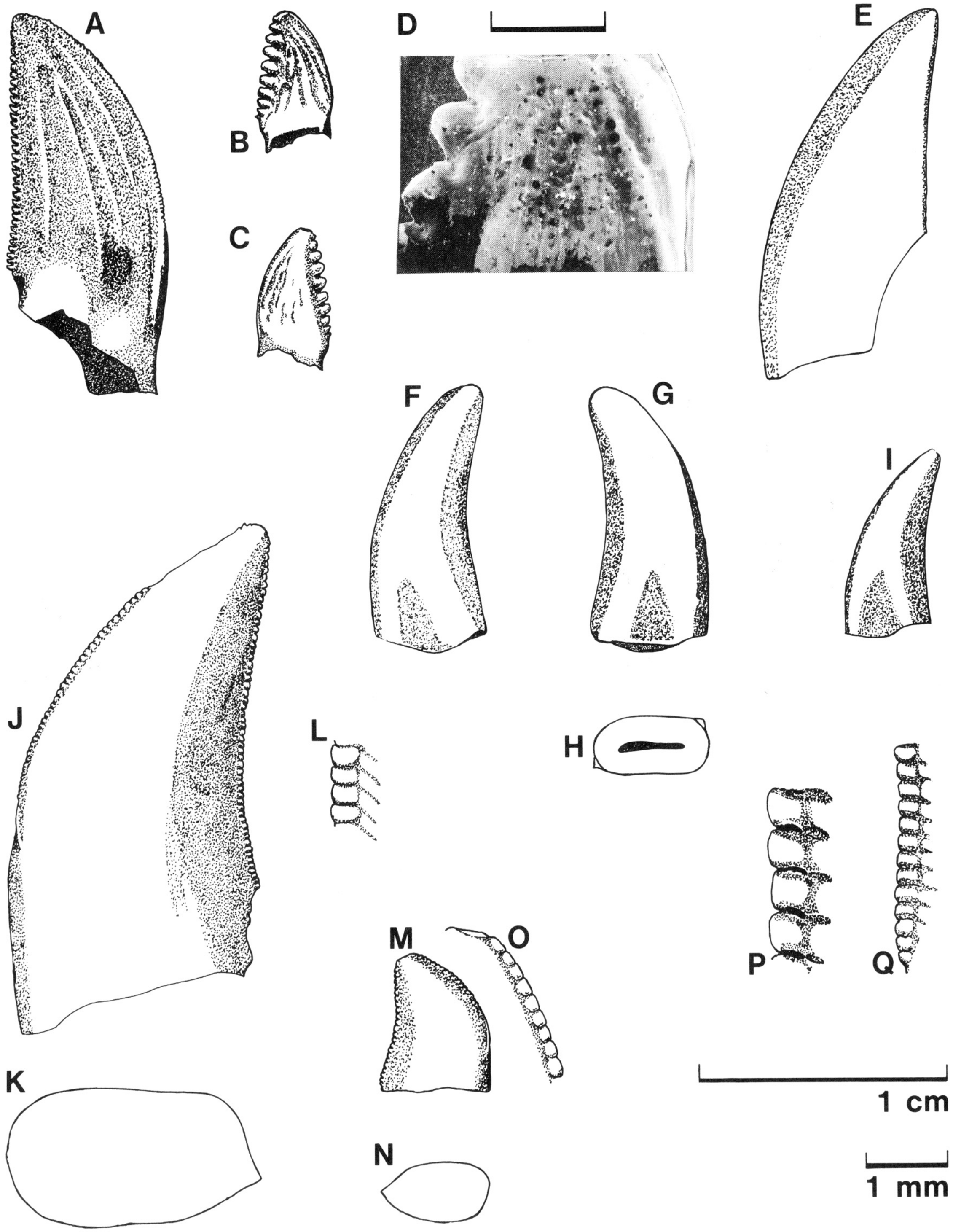
Indeterminate small theropod teeth

Teeth of *Paronychodon lacustris* (Cope 1876a) are found throughout Upper Cretaceous beds (Russell 1935; Sahni 1972; Armstrong-Ziegler 1980; Lehman 1981; Carpenter 1982; Breithaupt 1985; Standhardt 1986) but remain enigmatic because of lack of association with skeletal remains. Junior synonyms include *Zapsalis abradens* (Cope 1876b) and *Dipriodon caperatus* (Marsh 1892). *Paronychodon* teeth are flat on one side and usually bear three or more longitudinal ridges. The other side of the tooth is convex, and can either be smooth or have longitudinal ridges as well. *Paronychodon* teeth are highly variable in shape and size. Most lack serrations but others can have denticles on either the posterior carina, or on both anterior and posterior carinae. The denticles provide the clue to identifying the true nature of these teeth. "*Paronychodon*" teeth (that is, flattened and ridged on one side and convex on the other) from Dinosaur Provincial Park usually bear serrations that identify them as *Troodon* (Figs. 8.5B,C,D; Currie 1987a, Fig. 5S), *Saurornitholestes* (Fig. 8.5A), and possibly *Dromaeosaurus* (TMP 82.19.7). One might suspect that this type of tooth is from the symphysis of the mandibles as proposed by Marsh (1892), who thought the flat surfaces of the teeth on the symphysis appressed against each other. However, many of these teeth can be identified as maxillaries or from the posterior region of the dentary. It appears more likely that these teeth represent growth abnormalities. Theropod teeth develop along the medial wall of the tooth socket and remain flattened against this wall until the root of the older and more lateral functional tooth is resorbed and the new tooth is ready to erupt. By this time, a new germ tooth has often started to develop medial to the erupting tooth. The flattened, ridged lingual surface of a "*Paronychodon*" tooth was possibly caused by prolonged contact with the medial wall of the socket. The pitted surface (Fig. 8.5D) of many of these teeth supports the notion of abnormal growth. Because most "*Paronychodon*" teeth can be referred to known genera, the name *Paronychodon lacustris* should be restricted to non-serrate forms. These tend to be more common in Maastrichtian beds, and conceivably may represent a distinct taxon of theropod.

A number of teeth in the Judith River Formation can be identified as theropods on the basis of size and shape, but lack serrations entirely (Figs. 8.5E–L). In almost all cases, the tooth surface has a chalky grey appearance, and the surface is sometimes pitted. These may be shed teeth, swallowed during feeding (Argast et al. 1987). The enamel surface of the teeth, including denticles, would have been removed by digestive acids before the teeth were expelled from the body. In some of these teeth, the bases of the denticles can still be seen as a line of circles along the anterior and posterior margins of the laterally compressed teeth.

Some small theropod teeth cannot be identified with certainty. Many of these have denticles that are morphologically similar to those of *Dromaeosaurus*. However, the anterior carina does not twist from the lingual surface to the midline of the tooth as it approaches the tip. It is possible that this type of tooth may represent a distinct species of dromaeosaurid, or a gracile, small form of tyrannosaurid.

Figure 8.5. Miscellaneous theropod teeth from the Judith River of southern Alberta. **A**, "*Paronychodon*" (*Saurornitholestes*) tooth (TMP 79.15.3) in lingual view. **B**, **C**, "*Paronychodon*" (*Troodon*) tooth (TMP 85.30.1) in lingual and labial views. **D**, SEM of lingual surface of TMP 79.8.635, "*Paronychodon*" (*Troodon*), scale = 0.5 mm. **E**, **F**, **G**, **H**, **I**: "digested" teeth. **E**, TMP 82.19.180. TMP 80.13.34 in **F**, labial; and **G**, lingual views; with **H**, cross-section of the base. **I**, TMP 82.20.255. **J–Q**: tyrannosaurid teeth. TMP 81.19.263 in **J**, lingual view; with **L**, enlargement of posterior proximal denticles in labial view; and **K**, cross-section of the base. TMP 82.20.47 in **M**, lingual view; with **Q**, enlargements of posterior proximal denticles, and **O**, anterior distal denticles; and **N**, cross-section of base. **P**, enlargement in lingual aspect of posterior denticles of a 6 cm long tooth (NMC 1592). Scale bars as in Figure 8.1.



Tyrannosauridae

In going through collections of small theropod teeth, it is not surprising that a large number of juvenile tyrannosaurid teeth are found. These teeth tend to be stouter than those of dromaeosaurids or troodontids, but are still laterally compressed (Fig. 8.5N). They are simply scaled down versions of large tyrannosaurid teeth. At present, no juvenile tyrannosaurid skulls have been collected from the Judith River Formation. The smallest one known, TMP 86.144.1, is a half-grown individual with dentary teeth up to 36 mm long. In this specimen, serrations are relatively large on both anterior and posterior carinae, with three denticles per millimeter. A small tyrannosaurid maxilla (TMP 85.11.3, 25 cm long) has teeth with 2.5 denticles per millimeter. There are numerous isolated maxillary and dentary teeth that were obviously shed from much younger individuals. TMP 81.19.263 (Fig. 8.5M) is only 15.5 mm long, and bears three denticles per millimeter on the anterior carina and 3.5 denticles per millimeter on the posterior. TMP 79.10.59 is smaller (9.8 mm long with a FABL of 7.2 mm), and has 3.5 denticles per millimeter. In larger individuals, the denticles are smaller relative to tooth length, but are absolutely larger in basal diameter and denticle height (TMP 80.16.864 is a typical tyrannosaur tooth with a length of 80 mm and up to 2 denticles per millimeter along the anterior and posterior carina). As in more mature Judithian tyrannosaurid teeth, the denticles of juvenile tyrannosaurs are relatively stout and chisel shaped. The denticles of tyrannosaurids are wider labially-lingually than they are long proximodistally. This represents a compromise between the strength needed by the denticles of teeth that were biting into bone, and the need for serrations for cutting meat (Abler in prep.). Tyrannosaurid denticles (Fig. 8.7A) do not curve distally towards the tip of the tooth, but do possess sharp ridges of enamel along the midline. Long, distinctive blood grooves are found between the bases of the denticles, oriented towards the base of the tooth (Figs. 8.5L,P,Q, 8.7A). These grooves are especially evident on the lingual surface of the tooth between denticles on the posterior carina in the proximal half of the tooth. Other aspects of tyrannosaurid tooth form and function are being studied by Farlow et al. (in prep.), and by Abler (in prep.).

Aublysodon mirandus (Figs. 8.6V–X) is a peculiar type of small premaxillary tooth originally described by Leidy (1868) from the Judith River Formation of Montana. In his original description, both serrated and nonserrated teeth were identified as *Aublysodon*, although Marsh (1892) restricted the name to the non-serrated form, and described two more species. The same teeth have been found in virtually every Upper Cretaceous Formation in North America.

Considering that all *Aublysodon* teeth are less than 20 mm long, one might suspect that *Aublysodon* represents an early ontogenetic stage of known tyrannosaurids, two of which have been described from the Judith River Formation (Russell 1970). However, there are serrated premaxillary teeth of tyrannosaurids (Figs. 8.6R–U) that are almost the same size as those of *Aublysodon*. Furthermore, the median ridge between the carina on the posterior surface of the premaxillary tooth of *Aublysodon* is more strongly developed distally than it is in either the juvenile or mature serrated tyrannosaurid teeth. This still leaves the possibility that *Aublysodon* could represent a juvenile morph of one of the large tyrannosaurid species, with juveniles of the other species having serrated premaxillary teeth. The remote possibility also exists that serrated and unserrated premaxillary teeth represent different sexes.

It is, however, more likely that *Aublysodon* represents a distinct taxa in the Judith River Formation. Identical teeth recently were recovered from the Iren Dabasu Formation at Erenhot, People's Republic of China (IVPP 170788104). The Asian "*Aublysodon*" teeth belong to *Alectrosaurus* (Perle pers. comm. 1989), a theropod related to tyrannosaurids. The Jordan theropod (Molnar 1978) was recently referred to as *Aublysodon molnaris* (Paul 1988b), and has been redescribed formally by Molnar and Carpenter (1990) as *Aublysodon*, because of its non-serrate premaxillary teeth that are D-shaped in cross-section. The maxillary teeth are serrated, laterally-compressed, blade-like structures (Molnar and Carpenter 1990), and may well turn out to be the same as the unidentified Judithian teeth referred to above as a possible dromaeosaurid or gracile tyrannosaurid.

There are differences in the teeth and denticles amongst tyrannosaurid species (Farlow pers. comm.). However, tyrannosaurid taxonomy is currently under review by a number of authors, and it would be pointless to attempt to key out these differences until the teeth can be associated with valid taxa.

Discussion

Theropod teeth from the Judith River Formation are diagnostic, and can usually be identified by size, shape, and pattern of denticulation. The denticles are diagnostic enough (Fig. 8.7) that only a portion of a tooth is usually necessary for identification. Most of the problems encountered with identification of theropod teeth relate to the absence of sufficient associated skeletal material.

Theropod teeth show little ontogenetic variation. Juvenile teeth are simply scaled down versions of teeth of more mature individuals, although juvenile teeth have fewer (but relatively larger) denticles. There does not appear to have been any significant increase in the number of teeth (Madsen 1976; Colbert 1989) as theropods matured, whereas increase in tooth rows is a common phenomena amongst ornithischians (Chapter 15).

In the Judith River Formation, a large proportion of the theropod teeth less than 2 cm long are from juvenile tyrannosaurids and *Aublysodon*. Of the remaining

Figure 8.6. Comparison of premaxillary teeth from the Judith River Formation of Dinosaur Provincial Park. First left premaxillary tooth of *Dromaeosaurus* (TMP 81.16.461) in **A**, lingual; and **B**, posterior views; with **C**, enlargement of anterior and posterior denticles in lingual view; and **D**, cross-section of base of tooth. Left premaxillary tooth (cf. *Saurornitholestes*, TMP 70.37.1) in **E**, lingual; and **F**, posterior views; with **G**, enlargement of anterior and posterior denticles in lingual view; and **I**, cross-section of base of tooth. **H**, enlargements of anterior and posterior denticles of NMC 2664 (cf. *Saurornitholestes*), a 2nd or 3rd premaxillary tooth. TMP 81.16.194 (cf. *Richardoestesia*) in **J**, lingual; and **K**, posterior views; with **L**, enlargement of posterior denticles; and **M**, cross-section of the base. NMC 1267 (*Troodon*) in **N**, lingual; and **O**, posterior views; with **P**, enlargements of denticles in lingual view; and **Q**, cross-section of base of tooth. NMC 41104 (juvenile tyrannosaurid) in **R**, lateral; and **S**, posterolingual views; with **T**, enlargement of denticles; and **U**, cross-section of base. TMP 82.19.367 (*Aublysodon*) in **V**, ?lateral; and **W**, posterolingual views; with **X**, cross-section of the base.

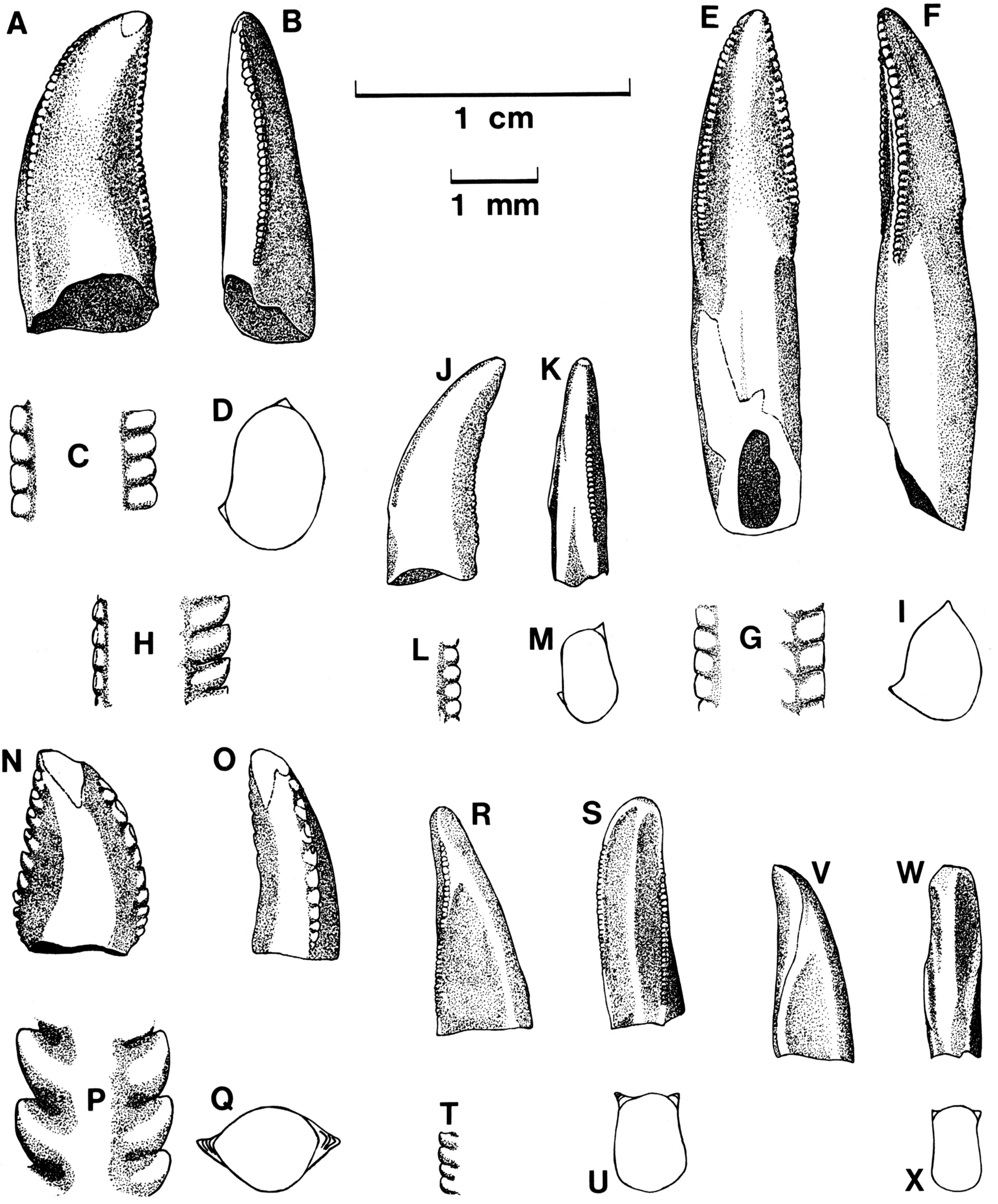
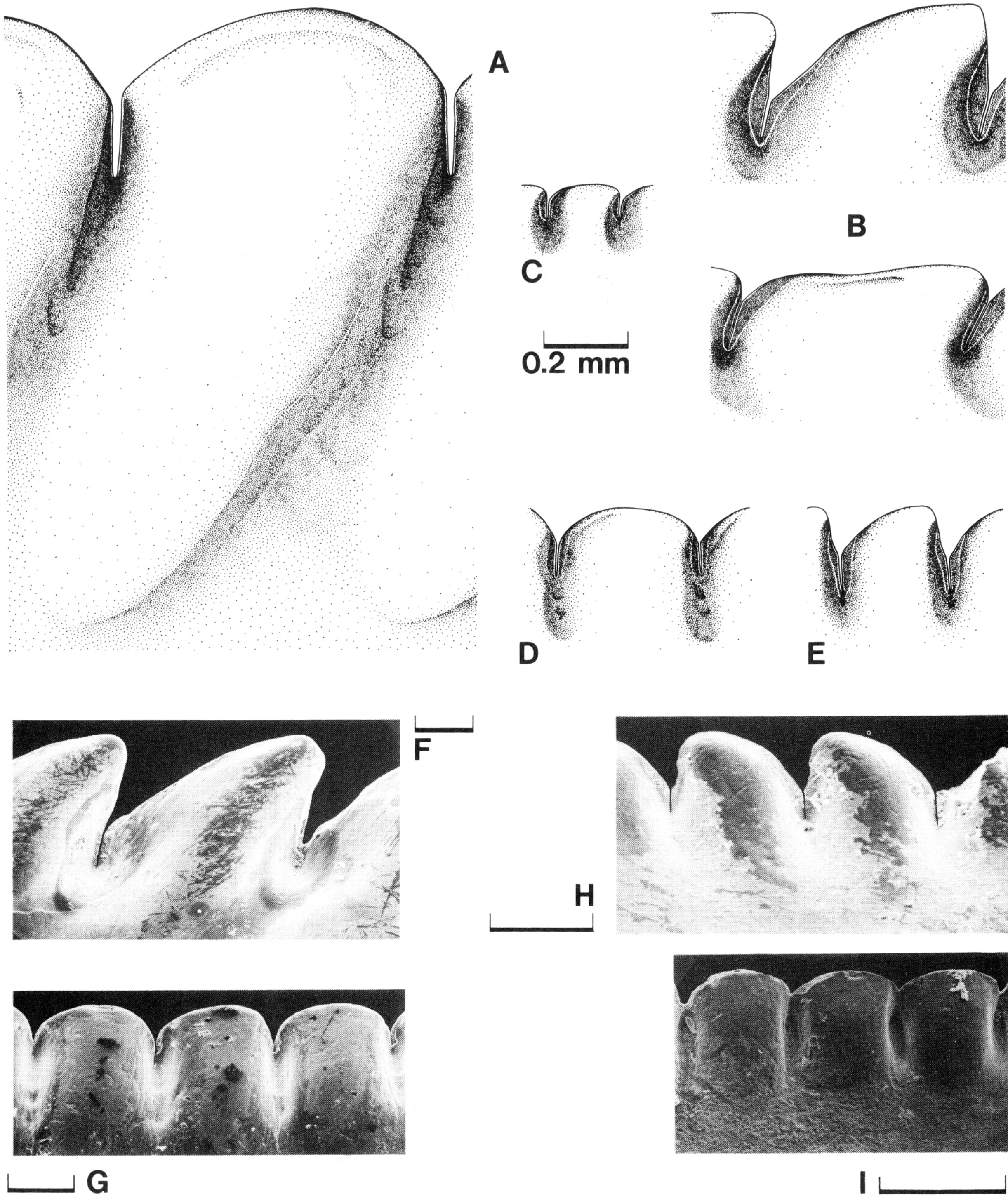


Figure 8.7. Comparison of denticles of Late Cretaceous theropods from southern Alberta. Drawings (**A–E**) done to same scale to show relative sizes of denticles, and all oriented so that tip of tooth is to the right. **A**, *Tyrannosaurus rex*, TMP 81.6.1 (Willow Creek Formation, Maastrichtian), lingual view of denticle mid-length along the posterior carina of a functional dentary tooth (FABL = 28.5 mm). **B**, *Troodon formosus*, TMP 82.20.320, reversed image of lingual view of eighth denticle from the distal end of the posterior carina, and (below) lingual view of eleventh denticle from proximal end of the anterior carina of an anterior maxillary tooth (FABL = 5.5 mm). **C**, *Ricardoestesia gilmorei*, NMC 343, reversed image of ninth denticle from distal end of posterior carina of germ tooth in 17th tooth position of dentary (FABL is between 5 and 5.5 mm). **D**, *Dromaeosaurus albertensis*, TMP 81.26.48, labial view of denticle from middle of posterior carina of an anterior dentary tooth (FABL = 7.0 mm). **E**, *Saurornitholestes langstoni*, TMP 78.9.96, lingual view of eighteen denticle from distal end of posterior carina of an isolated, shed tooth. **F**, *Troodon formosus*, TMP 83.45.8, lingual view of fourth denticle from the proximal end of the posterior carina of a premaxillary tooth (FABL = 6.5 mm). **G**, *Dromaeosaurus albertensis*, TMP 81.26.48, same as **D**. **H**, *Saurornitholestes langstoni*, TMP 74.10.5 (holotype), labial view of tenth and eleventh denticles from distal end of posterior carina (FABL = 4.5 mm). **I**, *Richardoestesia gilmorei*, NMC 343, labial view of denticles on posterior carina of sixth dentary tooth (FABL = 3.7 mm). All scales = 0.2 mm. FABL = fore-aft basal length.



teeth studied (sample size = 424), *Saurornitholestes* teeth are the most common (47.63%), followed by *Troodon* (19.53%), *Richardoestesia* (18.05%), *Dromaeosaurus* (9.47%), "*Paronychodon*" (3.25%), and unknown/unidentified forms (2.07%).

We do not know if troodontid and dromaeosaurid species replaced their teeth at the same rate. However, if we assume they did, then the number of teeth for each species can be divided by the approximate number of teeth in the head to give an idea of how common the small theropods were in relation to each other. Because *Troodon* had nearly twice the number of teeth in the mouth as *Saurornitholestes*, one can assume that the smaller number of *Troodon* teeth recovered is a firm indication that this animal was less common than the velociraptorine. However, Currie (1987c) reported that *Troodon* and *Saurornitholestes* frontals are found in equal numbers in Dinosaur Provincial Park, which suggests that they were equally common. This may indicate that velociraptorines had much higher tooth replacement rates than troodontids, and clearly indicates that estimating the abundance of theropod species on the basis of their shed teeth cannot be done with confidence. Based on the recovery of both teeth and skeletal parts, *Dromaeosaurus* was a rare form. *Richardoestesia* is also well represented by isolated, shed teeth. However, this animal is known from only jaws and teeth, and no other skeletal parts have ever been identified. Interestingly, the number of teeth found corresponds closely to the recovery of identifiable *Chirostenotes* remains.

While we are ignorant of replacement rates of theropod teeth, they must be conspicuously faster than predicted by Johnston (1979), who interpreted the growth lines of tyrannosaurid teeth as annual. Although theropod skeletons are rare, shed theropod teeth are common as isolated elements, and are usually found mixed with herbivore skeletons. For example, Ostrom (1969) noted that *Deinonychus* teeth (and no others) were found associated with *Tenontosaurus* remains at fourteen sites in the Cloverly Formation. This suggests that theropods lost one or more teeth with each meal. Yet known theropod skulls and jaws invariably have most tooth positions occupied. Taken together, these two facts suggest that tooth replacement was rapid and constant. Tooth life may have been of the same order of magnitude as that in extant crocodiles, which Edmund (1962) measured as nine to sixteen months.

Tooth morphology varies within the jaws of single individuals, depending on tooth position. In tyrannosaurids and *Dromaeosaurus*, premaxillary teeth are distinguishable from maxillary/dentary teeth. In *Saurornitholestes*, premaxillary, maxillary, and dentary teeth differ enough from each other to permit identification into these groupings. Anterior dentary teeth are distinct from posterior dentary teeth in *Richardoestesia*, but the situation in the upper jaw bones is unknown. *Troodon* demonstrates the greatest degree of heterodonty amongst the Judithian theropods, with four distinct tooth morphs within a single individual.

All of the tooth types characteristic for *Saurornitholestes, Dromaeosaurus, Troodon, Richardoestesia*, and the Tyrannosauridae are found in the Lower Campanian Milk River Formation of southern Alberta, and up into the Upper Campanian beds of the Horseshoe Canyon Formation near Drumheller. *Richardoestia* teeth found in the Milk River Formation include some that are perfectly straight, in contrast with those from the Judith River Formation of Alberta and Montana, which are always slightly curved at the base. The Milk River Formation *Richardoestesia* teeth are identical to those of the Maastrichtian Scollard, Frenchman, Hell Creek, and Lance Formations. This suggests either a similarity of environments between the Milk River and Maastrichtian formations, or that the straight *Richardoestesia* teeth just have not been found to date in the Judith River Formation. Neither explanation is very satisfying when balanced with other lines of evidence. Amongst other theropod teeth recovered, "*Paronychodon*" teeth (in the collections of the Royal Ontario Museum and the University of Alberta) recovered from the Milk River Formation are also closer in appearance to Lancian, rather than Judithian, teeth of this type.

A variety of small theropod teeth have been identified in Paleocene deposits in Montana (Sloan et al. 1986), thereby opening up the possibility that dinosaurs did survive beyond the Cretaceous–Tertiary boundary. The problem of whether or not these teeth have been reworked from older sediments cannot be solved unequivocally at this time (Bryant et al. 1986; Argast et al. 1987), and stronger evidence will be required to convince most workers that some dinosaurs may have survived into the Paleocene.

The possibility that fossil materials may have been reworked emphasizes the potential problem of assigning too much importance on isolated teeth in paleoecological studies. Teeth can be reworked several times from older sediments, or they can be brought in by flowing water from upstream ecosystems. The latter situation also applies to both isolated bones and articulated skeletons (a floating or rolling carcass can be carried great distances downstream before decomposition of the soft tissue is complete), whereas isolated bones can also be reworked from older sediments. Reworking and transport can be discounted in many cases, however, by taking into account relative abundance, degree of postmortem wear, and knowledge of rates of accumulation in the depositional environments.

Tooth and jaw morphology in Judithian theropods provides little insight into their relationships. The fused interdental plates of *Saurornitholestes* and *Dromaeosaurus* represent a derived condition from that seen in most thecodonts (Ewer 1965) and primitive theropods (Welles 1984; Raath this volume). However, the teeth of *Dromaeosaurus* differ from those of *Saurornitholestes*, *Velociraptor*, and *Deinonychus* in carina position and denticulation. These facts support inclusion of *Dromaeosaurus* and *Saurornitholestes* in separate subfamilies of the Dromaeosauridae. Troodontids are characterized by the increased disparity in size between teeth of the upper and lower jaws (this character is more extreme in *Baryonyx*, Charig and Milner this volume), by increased differentiation of teeth, by loss of the interdental plates, and by the enlarged size of the denticles. Because the front of the snout is wider than it is in most theropods, the carinae of anterior teeth have shifted to the posterior surfaces as they have in the premaxillae of tyrannosaurids. This is clearly parallel evolution related to the width of the front of the jaws, and has been accomplished in two different ways. Troodontid anterior teeth are triangular in section, whereas the premaxillary teeth of *Aublysodon* and other tyrannosaurids are D-shaped.

There are few clues as to the relationships of *Richardoestesia*. The fine denticulation and high number of teeth are reminiscent of more primitive theropods like *Coelophysis* (TMP 84.63). The form of the interdental plates is the same as in tyrannosaurids, but this is a primitive character.

In assessing relationships based on denticulation patterns, it should be remembered that the denticles perform a function related to the killing and eating of prey. It is not surprising then that denticle morphology falling within the range of variation expressed in Theropoda can also be found in such diverse forms as sharks (Frazetta 1988), lizards, thecodonts, and saber-tooth tigers (Martin 1980). The denticles in *Richardoestesia* are generalized and tell us little about diet preference. Tyrannosaurid denticles are broad and strong and are a compromise between the requirements of cutting through flesh and bone. The long, slender hooked posterior denticles of *Saurornitholestes* were well adapted to slicing flesh off of bones. Grazing tooth marks on TMP 88.121.39 show how *Saurornitholestes* teeth were used parallel to the surface of the bone rather than perpendicular to it. The shorter, broader denticles of *Dromaeosaurus*, in conjunction with the more massive skull, suggests that this animal probably was biting through the smaller bones of its prey. The enlarged, sharply pointed but broad-based denticles of troodontids probably gave the animals the option of slicing efficiently through soft material or into bone. The denticles are as large as those of tyrannosaurids, but are more sharply pointed and are hooked distally. This suggests that they were capable of cutting meat more efficiently than the large carnivores.

Tooth shape and wear facets merit more detailed study in theropods because they also provide dietary clues. The anterior dentary teeth of *Richardoestesia* are straight, whereas the more posterior ones curve back towards the throat. It is easy to imagine that these teeth would have been useful for piercing and holding insects and other soft-bodied prey. The cheek teeth of dromaeosaurids and troodontids tend to show their greatest wear at the distal end of the anterior carina, whereas premaxillary teeth show more wear on the lingual surface. In spite of their relatively small size, the premaxillary teeth of tyrannosaurids are almost invariably worn on the lingual surface. The carinae are frequently worn completely away on these teeth, making it difficult in some cases to determine whether or not there were denticles. "Wear" facets on tyrannosaurid cheek teeth are more difficult to interpret because there is little consistency in position. It appears more likely that flakes of enamel were spalling off as the animal bit into bone, and that the edges of these damaged surfaces would subsequently wear smooth. Some tyrannosaurid teeth were reduced to nubbins by breakage and wear before being shed and replaced (Carpenter 1979; Farlow and Brinkman 1987).

In conclusion, the ability to identify theropod teeth is another tool that can be used to determine the relative age of Mesozoic beds, and/or to provide information on paleoenvironments. Both temporal and geographic ranges of some theropods can be extended by recognition of their teeth. Relative abundance of theropod taxa is indicated by the numbers of teeth recovered, but this cannot be a precise indication because of our ignorance on replacement rates and, in some cases, the numbers of teeth in the skull. Some taxa are still known only by their teeth. Morphology of teeth and jaws can indicate relationships of certain taxa.

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