

Saurischian dinosaurs of the Late Cretaceous of Asia and North America

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ABSTRACT

Our understanding of the taxonomic status and distribution (temporal and geographic) of Late Cretaceous theropods and prosauropods from Asia and North America is constantly improving and shows that faunal interchange evidently was underway by the Early Cretaceous. New caenagnathid and segnosaurid specimens recovered from the Judith River Formation of Alberta demonstrate the value of collecting and describing small, isolated specimens. Troodontids, ornithomimids, oviraptorosaurs, elmsaurids, dromaeosaurids, tyrannosaurids and segnosaurids are known now from both central Asia and North America. The absence of five other theropod types from one or the other area is not considered conclusive because of the rarity of the genera involved.

INTRODUCTION

The remains of saurischian dinosaurs are well-known from Upper Cretaceous strata of North America and Asia. Although there are obvious taxonomic and faunal differences between the two continents, recent work suggests that the differences are exaggerated by over-split genera, and collecting and preservational biases.

Tyrannosaurids represent the most derived large theropods, and were the dominant carnivores of Late Cretaceous time. Numerous well-preserved skeletons have been recovered from Canada, China, Mongolia, and the United States, but our understanding of the taxonomic composition of this family is poor. Recent studies by Carpenter (1990) and Bakker and others (1988) suggest that there was a common gene pool in the northern hemisphere.

Other large theropods, including *Deinocheirus* (Osmolska and Roniewicz, 1970), are known only from partial skeletons or isolated bones, and it must be assumed that either these animals were extremely rare or, more likely, that they lived in areas where their skeletons were unlikely to become fossilized.

Small theropods are rare in Upper Cretaceous beds of the northern hemisphere. Their smaller carcasses were more susceptible to destruction by scavengers; ligaments, skin and other connective tissue would deteriorate faster than the thicker, tougher tissues of larger animals; and the light, hollow bones were more likely to be scattered by other animals and the elements. Although the smaller theropods are probably underrepresented in the fossil record, enough material exists to show how diverse these animals had become.

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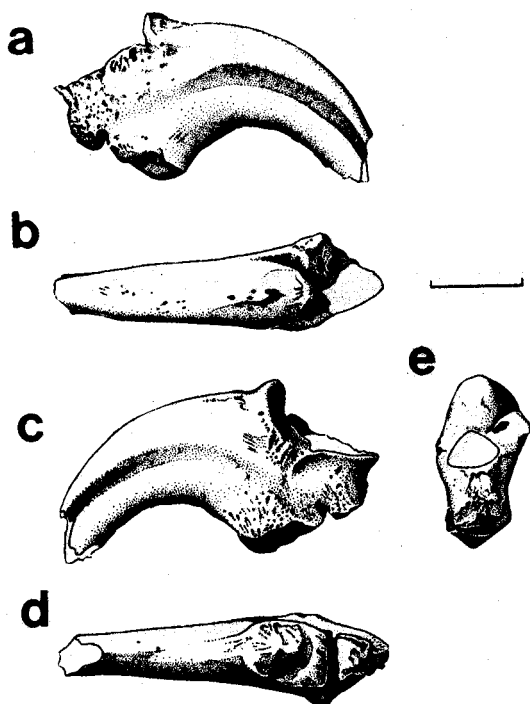


Figure 3. Possible segnosaurid ungual, TMP 79.15.1 in (a, c) lateral/medial, (b) dorsal, (d) ventral, and (e) anterior aspects. Scale-1 cm.

Segnosaurids were originally described as theropods (Perle, 1979) but Paul (1985) convincingly showed that they are best assigned to the Prosauropoda.

Sauropoda

Sauropod dinosaurs are well-known from Upper Cretaceous deposits of central Asia and the United States, but evidently did not inhabit the Cretaceous flood plains of Alberta. Of the Late Cretaceous Asian genera, *Nemegtosaurus* (Nowinski, 1971) and *Quaesitosaurus* (Kurzanov and Bannikov, 1983) have been identified as dicraeosaurine diplodocids, and *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977) as a camarasaurid. North America sauropods such as *Alamosaurus* are titanosaurids, and there is no evidence of sauropod migration between Asia and North America during Late Cretaceous times.

CONCLUSIONS

There are unquestionable similarities between the theropod faunas of the Late Cretaceous of Asia and North America. In both areas, there is a diverse array of

The Judith River (Oldman) Formation of Dinosaur Provincial Park (Alberta, Canada) and the Nemegt Formation of the Mongolian People's Republic are two of the richest dinosaur faunas known, and include a variety of theropod species. Both are Campanian (Karczewska and Ziembinska-Tworzydło, 1983), although the Nemegt is considered by some (Fox, 1978) to be younger in age.

The similarities between the Asian and North American theropod faunas from the Late Cretaceous are very striking and show that there must have been faunal interchange throughout the Campanian, and possibly earlier. New specimens from Alberta, documented here, show that more of the Asian forms were present in North America than had been previously thought.

DISCUSSION

Troodontids are well-known but rather enigmatic theropods (Russell, 1969; Barsbold, 1974; Russell and Sequin, 1982; Currie, 1985, 1987a; Wilson and Currie, 1985). They were large-brained animals that possessed more birdlike characteristics than other theropods. The second pedal digit bore a raptorial claw that was probably carried off the ground, and was reserved for use as an offensive weapon. This characteristic also developed in the dromaeosaurids, and has been used to unite these families into the Deinonychosauria (Gauthier, 1986). However, troodontids and dromaeosaurids are fundamentally different in other significant features, and it seems more likely that the specialized second pedal digit evolved independently in the two lineages. Dromaeosaurids are in fact very primitive theropods, whereas troodontids share a suite of derived characters with ornithomimids, elmsaurids and tyrannosaurids (Currie, in prep.).

Currie (1987a) has recently demonstrated that only one species of troodontid, *Troodon formosus* (= *Stenonychosaurus inequalis*), can at present be identified in North America. There are some slight differences in tooth structure that suggest Maastrichtian troodontids from North America, originally described as *Saurornithoides* sp. (Estes, 1964) and redescribed as *Pectinodon bakkeri* (Carpenter, 1982), may eventually turn out to be a valid second species of *Troodon* (*T. bakkeri*).

Two species of troodontid are presently known from Asia; *Saurornithoides mongoliensis* and *Saurornithoides junior* (Barsbold, 1974). If both species are valid, there are enough cranial differences from the North American form to support generic distinction. However, differences between *S. mongoliensis* and *S. junior* could also be interpreted as sexual or individual variation. If these species were synonymized, then the classification could be further simplified by recognizing the Asian form as *Troodon mongoliensis* (Paul, 1988).

A new species of troodontid from the Nemegt Formation will be described in the near future (Barsbold and Osmolska, written commun., 1987) on the basis of a specimen with the distinctive foot structure of a troodontid. Another specimen from the Lower Cretaceous Dzunbainskaya Svita (Albian) at the Khamareen Us locality of Mongolia (Osmolska, written communication, 1987) is a more primitive troodontid than either *Troodon* or *Saurornithoides*. As troodontid teeth are also known from the Milk River Formation (lower Campanian) of Alberta (uncatalogued specimens in Royal Ontario Museum 1967 field expedition collections), it still cannot be

determined whether this family originated in Asia, North America, or somewhere else. Teeth from the Lower Cretaceous Cedar Mountain Formation (Nelson and Crooks, 1987) that were identified as troodontid are more likely velociraptorine. The absence of troodontid teeth from the Lower Cretaceous of North America would support a hypothesis of Asian origin.

Ornithomimidae

The bulbous parasphenoid of ornithomimids is an unusual, derived character that suggests these animals may be more closely related to troodontids than to any other theropods (Osmolska, Roniewicz and Barsbold, 1972; Currie 1985). The most primitive ornithomimids, *Harpimimus* (Barsbold and Perle, 1984) and *Garudimimus* (Barsbold, 1981) are both from Mongolia.

Deinocheiridae

Deinocheirus mirificus is poorly known, only one partial skeleton having been described to date (Osmolska and Roniewicz, 1970). The arms of this animal are so enormous for a theropod that there is little doubt that it can be assigned to its own family, although some have suggested affinities with the ornithomimids. No specimens found in North America can be assigned to this family.

Oviraptorosauria

Two, or possibly three, families can be assigned to the Oviraptorosauria: Caenagnathidae, Oviraptoridae and possibly the Elmsauridae. The oviraptorids of Mongolia are the best known oviraptorosaurs (Osborn, 1924; Osmolska, 1976; Barsbold, 1977, 1981), and the partial skeletons of as many as three genera have been collected (Barsbold, 1986). This family is not represented in North America, although there is no doubt about their relationship to the Caenagnathidae from Alberta. *Caenagnathus* is well-established on the basis of the lower jaws of two individuals (Sternberg, 1940; Cracraft, 1971). The toothless jaws of *Caenagnathus collinsi* are long and shallow, in contrast with the short, deep jaws of *Oviraptor*, but share a suite of derived characters not seen in any other theropods. Although the earliest known occurrence of oviraptorosaurs is from Asia, the fact that caenagnathid jaws are less derived suggests that these animals may have evolved first in North America.

Currie and Russell (1988) have presented evidence to suggest that the elmsaurid genus *Chirostenotes* may be the senior synonym of *Caenagnathus*. The known specimens of elmsaurids from Asia and North America are not complete enough to resolve this identification, but do strongly suggest that they are oviraptorosaurs. *Elmsaurus* has similar hands and feet to *Chirostenotes*, but is a smaller animal with a fused tarsometatarsus (Currie, 1988). Several specimens have been collected from the Nemegt Formation of Mongolia (Osmolska, 1981), and there are

two fused tarsometatarsals from Alberta (Currie, 1990).

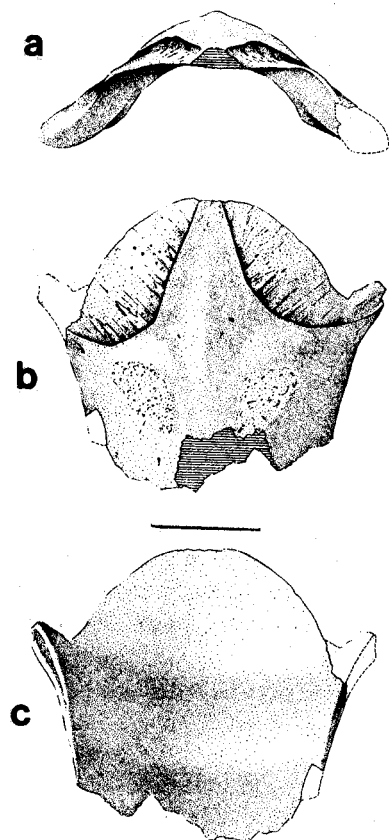


Figure 1. cf. *Caenagnathus*, TMP 81.19.252, parietal in (a) anterior, (b) dorsal and (c) ventral views. Scale-1 cm.

An isolated parietal (Fig. 1) from Dinosaur Provincial Park, may be that of a caenagnathid. Like the parietal of *Oviraptor*, it is more expanded than the parietals of other theropods, and it lacks a sagittal crest. The bone is incomplete caudally, so the shape and size of the nuchal crest is unknown. As in most other theropods (Currie, 1987b), the fused parietals have a median process that projects rostrally between the caudal ends of the paired frontals. Although this process was broken off in TMP 81.19.252, it is highly probable that it overlapped the frontals near its tip. Lateral to this process, the frontal broadly overlaps a shelf on the parietal (Fig. 1b), and fits snugly into a slot posteriorly where it is overlapped slightly by the parietal (Fig. 1a). The surface of the synarthrose is covered by low ridges that are oriented rostrolaterally. There is a rostrolateral process preserved on the right side that shows the parietal helped form the base of the dorsal portion of the postorbital bar as in other theropods. It cannot be determined whether the parietal extended far enough to actually contact the postorbital bone. The ventrolateral margins of the bone (Fig. 1c) are slotted longitudinally for strong contact with the laterosphenoid. Two regions on the dorsal surface of the bone are pitted in an unusual manner. Because of the positions of these areas, it seems likely that these represent points of attachment for

temporal muscles. The cancellous bone inside the parietal is not unusual for a theropod, whereas that of *Oviraptor* is highly pneumatic. Although assignment of TMP 81. 19. 252 to the Oviraptorosauria is reasonable, it is not possible to identify it as a species of *Caenagnathus*, *Chirostenotes* or *Elmisaurus* without the discovery of better specimens.

Dromaeosauridae

Dromaeosaurids are the most diverse group of small theropods known from the Upper Cretaceous strata of the northern hemisphere. Two lineages can be distinguished, mostly on the basis of cranial features. *Velociraptor*, *Deinonychus*, and *Saurornitholestes* form a single clade, the Velociraptorinae, characterized by low, narrow snouts and a highly developed raptorial pedal claw (phalanx II—3). Denticles on the anterior carina of the teeth are significantly smaller than those on the posterior carina, whereas in most other theropods they are subequal in size. Some authors (e. g., Paul, 1984, 1988) believe that these three genera should be synonymized, although the three species would remain distinct. Velociraptorine teeth are found in most North American terrestrial microvertebrate sites from the Cloverly Formation (Aptian-Albian) to the Maastrichtian formations (Currie, Rigby and Sloan, 1990). Those teeth recovered from the Maastrichtian beds differ slightly from those of earlier forms in being generally shorter, more recurved and sharper, which suggests that a new species will probably be diagnosed upon the discovery of adequate skeletal material.

The dromaeosaurines (*Dromaeosaurus*, *Adasaurus* and possibly *Hulsanpes*) are much rarer animals on both continents. There is not enough material available to determine whether or not any of these animals are congeneric. Currie (1987b) has suggested that there may be a second dromaeosaurine in the Judith River Formation. Dromaeosaurines seem to have been stockier, more powerful animals than the velociraptorines. The teeth are closer to those of tyrannosaurids in possessing short, chisel-shaped denticles that are subequal on rostral and caudal carina.

Gilmore (1924) briefly described a pair of theropod jaws that he tentatively assigned to *Chirostenotes*. At present, it appears more likely that *Chirostenotes* was a toothless caenagnathid, and therefore these jaws must belong to another undescribed theropod from the Judith River Formation. The teeth of this animal are very distinctive in shape and denticulation (Currie, Rigby and Sloan, 1990) and can be traced from lower Campanian strata (Russell, 1935) upwards into basal Paleocene beds in North America. No teeth of this kind have been described from central Asia.

Tyrannosauridae

Tyrannosaurids are the distinctive, large carnivores that formed the top of the food chain during the Late Cretaceous. They are not closely related to the large Jurassic theropods, but may have come from smaller forms like *Marshosaurus* (Madsen, 1976). *Alioramus* (Kurzban, 1976) appears to be a relatively primitive, long-snouted tyrannosaurid from the Upper Cretaceous of Mongolia. *Aublysodon mi-*

randus, a poorly known, small theropod from Campanian and Maastrichtian beds of North America (Molnar, 1978; Molnar and Carpenter, 1989), has D-shaped premaxillary teeth and the derived skull roof of the tyrannosauridae, and appears to be the least specialized tyrannosaurid known.

The large tyrannosaurids (*Tyrannosaurus*, *Albertosaurus*, *Daspletosaurus*, *Nannotyrannus*, *Gorgosaurus*, and *Tarbosaurus*) are well represented by good skeletal material, but are in need of further description and revision (Bakker, Williams and Currie, 1988). Although taxonomic resolution remains unresolved, (Carpenter, 1990; Bakker, Currie and Williams, 1988), there is no doubt about the close relationship of North American and Asian forms. Where faunas are well-known, there appear to invariably be two or three species of tyrannosaurid present at any single locality in Campanian or Maastrichtian beds. Study of microvertebrate sites in Alberta shows that juvenile tyrannosaurid teeth are more common than the teeth of any single species of small theropod. This suggests that juvenile tyrannosaurids were competing successfully with small theropods.

Shanshanosauridae

Shanshanosaurus huoyanshanensis is known from a single crushed skull and partial skeleton from the Campanian-Maastrichtian Subashi Formation of China (Dong, 1977). It is currently placed in its own family, and nothing is known of its distribution or relationships.

Segnosauridae

An unusual frontal (Fig. 2) described by Sues (1978) as a theropod may represent the segnosaurid *Erlicosaurus*. A second specimen (TMP 81.16.231, Figs. 2e-g) was recently recovered from the Judith River Formation of Dinosaur Provincial Park. The frontal is roughly triangular, and compares most closely to ornithomimid frontals (Currie, 1987b). The interfrontal suture is at an acute angle to the dorsal surface, showing that the frontal sloped lateroventrally from the midline (Fig. 2b). The dorsal surface is slightly depressed between the orbital rim and the midline, and there is a well-defined, relatively straight ridge that marks the rostral extent of the temporal musculature (Fig. 2a). The nasals appear to have been separated caudally by the frontals, which they overlapped. The prefrontal also overlapped the frontal (Figs. 2a,e), and probably reached the orbital rim. The lacrimal suture is well defined on the ventral surface of the frontal (Figs. 2b,f), and in contrast with ornithomimids (Currie, 1987b) does not extend posteriorly beyond the limit of the prefrontal. The orbital rim is pitted and rough in NMC 12355, and smooth in TMP 81.16.231. The orbital ridge (Figs. 2b,f) on the ventral surface of the frontal is very deep (Fig. 2g), and formed an appreciable part of the rostro-lateral wall of the braincase.

An isolated ungual (Fig. 3) from the Judith River Formation of Alberta is unusual in that the flexor tubercle is well developed and extends posteriorly below the articulation with the penultimate phalanx. The only Cretaceous animal that I am

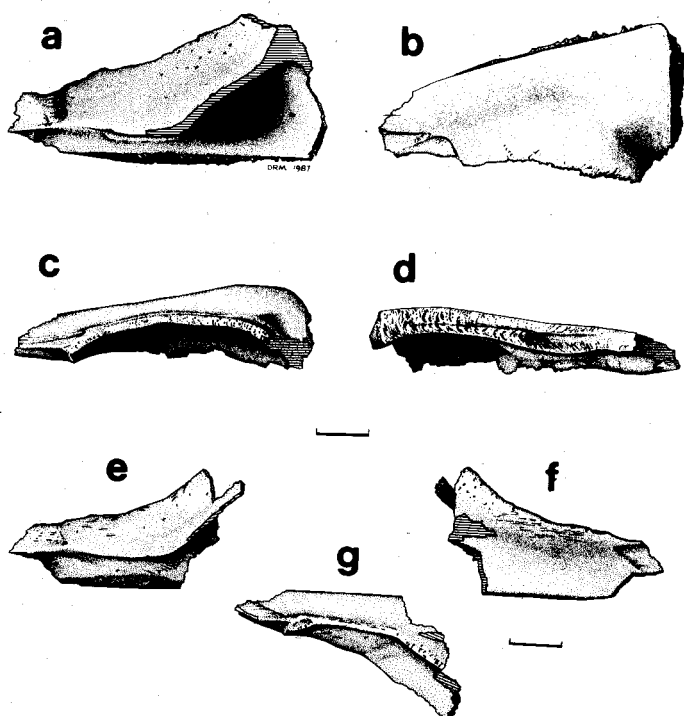


Figure 2. Segnosaurid frontals from the Late Cretaceous of Alberta, Canada. NMC 12349 in (a) ventral, (b) dorsal, (c) lateral, and (d) medial views. TMP 81.16.231 in (e) ventral, (f) dorsal, and (g) lateral views. Scale bars -1 cm.

aware of with this unusual articulation is *Segnosaurus* (Perle, 1981). It should be pointed out however that the ungual resembles the manual ungual of *Chirostenotes* if the articulation is ignored, and it is possible that the distinctive nature of the articulation may have been produced by disease or injury.

Russell (1984) briefly reported on an unusual astragalus from the Hell Creek Formation that he identified as being from a segnosaurid.

Therizinosaurus was originally thought to have been an enormous turtle (Maleev, 1954) with claws exceeding a metre in length. Although little skeletal material has been discovered since the original description, this gigantic animal is generally considered to be a theropod (Barsbold, 1981). Similarities in the humerus suggest it may turn out to be a segnosaurid (Osmolska, oral commun. 1987). There is no evidence to suggest that this animal ever inhabited North America.

Enigmosaurus mongoliensis (Barsbold, 1983) is appropriately named and little can be said about its anatomy or distribution at this time. Better material may show it to be a segnosaurid (Osmolska, oral commun. 1987).

Nanshiungosaurus brevispinus (Dong, 1979) is based on a partial skeleton from the Upper Cretaceous from southeastern China that appears to have been from a segnosaurid based on similarities in pelvic structure. The vertebrae are highly pneumatic, showing that the animal was much lighter than its bulky appearance would sug-

theropods in any single formation, reaching a peak in the two best known faunas (Judith River Formation of Alberta, Nemegt of Mongolia) which each have at least 13 species (Table 1).

The degree of similarity between Asian and North American theropods is unclear because of taxonomic confusion and the palaeoecological differences between the regions. Taxonomic confusion comes from the rarity of well-preserved theropod skeletons, preservational differences and inadequate comparative work on specimens. Genera previously known only from Mongolia have been discovered in Alberta recently because of improved collecting techniques (Currie, 1987c) that sample drier, 'more upland' palaeoecosystems that more closely resemble those of Asia.

The North American Upper Cretaceous terrestrial formations are well-dated by interspersed marine beds and radiometric dating of volcanic ashes (Eberth, 1990). The Asian formations are not well-dated, as workers have had to rely on terrestrial faunal and floral comparisons with North America. Consequently, any discussion of earliest known occurrences of theropod lineages (to determine where they originated) would employ circular reasoning based solely on the relative 'primitiveness' of the animals. Freshwater invertebrates, charophytes, and ostracods, for example, can be used to correlate with regions where dating is better defined. Such an extensive analysis still needs to be done, but the data are available.

Troodontids, ornithomimids, caenagnathids/oviraptorids, elmsaurids, dromaeosaurids (Dromaeosaurinae, Velociraptorinae), tyrannosaurids, and segnosaurids are known from both central Asia and North America. Unfortunately the jaw described by Gilmore (1924) as '*Chirostenotes*' was found in isolation, so it is not surprising that this fragmentary form has not turned up in Asia. Similarly, the lack of deinocheirids, therizinosaurids, enigmosaurids and shanshanosaurids from North America may simply reflect the rarity of specimens, and our poor understanding of their taxonomic positions.

It is certain that faunal interchange was underway between the regions during Early Cretaceous time, and that it continued throughout the Late Cretaceous. Amongst the theropods, velociraptorines are known from Lower Cretaceous strata of North America, and troodontids and ornithomimids from the Lower Cretaceous of Asia. Dromaeosaurines, elmsaurids and tyrannosaurids, as presently understood, are restricted to the Late Cretaceous of the northern hemisphere and the origins of these families are obscure. Oviraptorids are known only from Asia and caenagnathids only from Alberta, but these families are unquestionably a taxonomic unit easily distinguished from other theropod families. Segnosaurids are more diverse in Asia, but their fossil record is too poor to say anything about intercontinental connections. No single sauropod family is found in Upper Cretaceous strata of both North America and Asia.

Solving some of the problems associated with Cretaceous faunal interchange is a major objective of the Canada-China Dinosaur Project, initiated in 1986 by the Institute of Vertebrate Palaeontology (Beijing), the National Museum of Canada (Ottawa), the Tyrrell Museum of Palaeontology, and the Ex Terra Foundation (Edmonton). Over the course of the project, researchers from the two countries will have an opportunity to study each others specimens and data, to compare the techniques used in collection, preparation and analysis, and to study the occurrence of fossils in their sedimentological context in the field.

Table 1. Distribution of Late Cretaceous saurischians (excluding sauropods in central Asia and North America)

	1	2	3	4	5	6	7	8
Troodontidae								
<i>Troodon</i> sp.	—	—	—	—	—	—	—	8
<i>Troodon formosus</i>	—	—	3	—	5	—	7	—
<i>Saurornithoides</i> sp.	—	2	—	4	—	6	—	—
<i>Saurornithoides mongoliensis</i>	—	2	—	—	—	—	—	—
<i>Saurornithoides junior</i>	—	—	—	—	—	6	—	—
<i>New species</i> (Osmolska, written comm., 1987)	—	—	—	—	—	6	—	—
Ornithomimidae	1	—	3	—	5	6	7	8
<i>Archaeornithomimus asiaticus</i>	1	—	—	—	—	—	—	—
<i>Ornithomimus edmontonicus</i>	—	—	—	—	5	—	—	—
<i>Struthiomimus altus</i>	—	—	—	—	5	—	7	—
<i>Dromiceiomimus samueli</i>	—	—	—	—	5	—	—	—
<i>Dromiceiomimus brevitertius</i>	—	—	—	—	—	—	7	—
<i>Garudimimus breviceps</i>	1	—	—	—	—	—	—	—
<i>Gallimimus bullatus</i>	—	—	—	—	—	6	—	—
Deinocheiridae	—	—	—	—	—	6	—	—
<i>Deinocheirus mirificus</i>	—	—	—	—	—	6	—	—
Caenagnathidae	—	—	—	—	5	6	7	—
<i>Caenagnathus collinsi</i>	—	—	—	—	5	—	—	—
<i>Caenagnathus sternbergi</i>	—	—	—	—	5	—	—	—
Elmisauridae	—	—	—	—	5	6	7	—
<i>Chirostenotes pergracilis</i>	—	—	—	—	5	—	7	—
<i>Elmisaurus elegans</i>	—	—	—	—	5	—	—	—
<i>Elmisaurus rarus</i>	—	—	—	—	—	—	6	—
Oviraptoridae	—	—	—	—	—	—	—	—
<i>Oviraptor philoceratops</i>	—	2	—	—	—	—	—	—
<i>Oviraptor mongoliensis</i>	—	—	—	—	—	6	—	—
<i>Ingenia yanshini</i>	—	—	—	4	—	—	—	—
<i>Conchoraptor gracilis</i>	—	—	—	4	—	—	—	—
Shanshanosauridae	—	—	—	—	—	—	—	—
<i>Shanshanosaurus huoyanshanensis</i>	1	—	—	—	—	—	—	—
Dromaeosauridae	1	2	3	4	5	6	7	8
<i>Dromaeosaurus</i> sp.	—	—	—	—	5	—	7	—
<i>Dromaeosaurus albertensis</i>	—	—	—	—	5	—	—	—
<i>Saurornitholestes</i> sp.	—	—	3	—	—	—	7	8
<i>Saurornitholestes langstoni</i>	—	—	—	—	5	—	—	—
<i>Velociraptor</i> sp.	—	2	—	4	—	6	—	—
<i>Velociraptor mongoliensis</i>	—	2	—	—	—	—	—	—
<i>Hulsanpes perlei</i>	—	—	—	4	—	—	—	—
<i>Adasaurus mongoliensis</i>	—	—	—	—	—	6	—	—
" <i>Chirostenotes</i> " jaws	1	—	3	—	5	—	7	8
Tyrannosauridae	1	2	3	4	5	6	7	8
<i>Alectrosaurus olseni</i>	1	—	—	—	—	6	—	—
<i>Alioramus remotus</i>	1	—	—	—	—	—	—	—
<i>Aublysodon mirandus</i>	—	—	—	—	5	—	7	8
<i>Gorgosaurus libratus</i>	—	—	—	—	5	—	—	—
<i>Daspletosaurus torosus</i>	—	—	—	—	5	—	—	—
<i>Daspletosaurus</i> n. sp.	—	—	—	—	—	—	7	—
<i>Albertosaurus sarcophagus</i>	—	—	—	—	—	—	7	—
<i>Tarbosaurus bataar</i>	—	—	—	—	—	6	—	—
<i>Tarbosaurus novo-jilovi</i>	—	—	—	—	—	6	—	—
<i>Nanotyrannus lancensis</i>	—	—	—	—	—	—	—	8

<i>Tyrannosaurus rex</i>	-----8
<i>Tyrannosaurus luanchuanensis</i>	1-----
Saurischia Inc. Sed., Segnosauria	1-----56--
Segnosauridae	1-----56--
" <i>Erlcosaurus</i> " sp.	-----5---
<i>Erlcosaurus andrewsi</i>	-----6---
<i>Nanschiungosaurus brevispinus</i>	1-----
<i>Segnosaurus ghalbiensis</i>	1-----
Therizinosauridae	-----6---
<i>Therizinosaurus cheloniformis</i>	-----6---
Enigmatosauridae	1-----
<i>Enigmatosaurus mongoliensis</i>	1-----

1, other; 2, Djadokta/Bayn Dzak; 3, Milk River; 4, Barun Goyot; 5, Judith River; 6, Nemegt; 7, Horseshoe Canyon; 8, Hell Creek/Lance Creek/Scollard.

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