

Theropods from the Cretaceous of Mongolia

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Introduction

Theropods were the most successful lineage of dinosaurs in the sense that they were amongst the first dinosaurs to appear more than 225 million years ago in Late Triassic times, and remained the dominant carnivores until the end of the Cretaceous. Because of their ancestral relationship to birds, it could even be said that they are the most successful group of air-breathing vertebrates today.

Non-avian theropods were never numerically as common as plant-eating dinosaurs, so it is not surprising that they are rare as fossils. Nevertheless, they were diverse and speciose during Mesozoic times. And the peak of their diversity, as presently understood, is represented by fossils from the Upper Cretaceous beds of Mongolia. Numerous sites have produced theropods from Neocomian to Maastrichtian stages, but are particularly strong in the Campanian to Maastrichtian Djadokhta, Baruungoyot and Nemegt 'Mongolian Land Vertebrate Ages' (Jerzykiewicz and Russell, 1991). With the possible exception of equivalent-aged beds in North America, no other region has produced so many fine specimens representing so many species.

Although Mongolia has some of the best Late Cretaceous dinosaur assemblages in the world, earlier intervals are not as well understood. Recent work by a joint Stanford University–Mongolian expedition to the western part of the country has shown the presence of Jurassic sauropods similar to those of north-western China. This strongly suggests that Jurassic carnosaurs similar to *Monolophosaurus jiangi* (Zhao and Currie, 1993) and *Sinraptor dongi* (Currie and Zhao,

1993) from Xinjiang, will eventually be found in Mongolia. Dromaeosaurids, troodontids and ornithomimosaurids have already been found in Early Cretaceous beds of Mongolia, and provide some of the best information available on the ancestry of these groups.

Seven major theropod lineages (dromaeosaurids, oviraptorosaurs, therizinosauroids, troodontids, avimimids, ornithomimosaurids, and tyrannosaurids) lived during Cretaceous Mongolian times (Figure 22.1). All but the therizinosauroids and some families of oviraptorosaurs and ornithomimids were widely distributed in the Northern Hemisphere. The presence in North America of a possible Late Jurassic troodontid and Early Cretaceous dromaeosaurids and oviraptorosaurs suggests that these groups could have originated anywhere in the Northern Hemisphere. North American records of therizinosauroids (Currie, 1992) and avimimids are poor, but suggestive. The assignment to the Ornithomimosauria of the Late Jurassic *Elaphrosaurus* from Africa is completely unfounded (P. Makovicky, pers. comm. 1996). However, a possible ornithomimosaur from the Lower Cretaceous of Spain (Pérez-Moreno *et al.*, 1994) and reports of Lower Cretaceous ornithomimosaurids from Australia (Rich and Vickers-Rich, 1994) indicate that this clade may have originated and diversified somewhere other than Asia. Therizinosauroids and tyrannosaurids are the only two lineages for which a strong case can presently be made for central Asian origins. Even the latter has been questioned following the discovery of *Siamotyrannus* (Buffetaut *et al.*, 1996), although this is at least consistent with an Asian origin for tyrannosaurids.

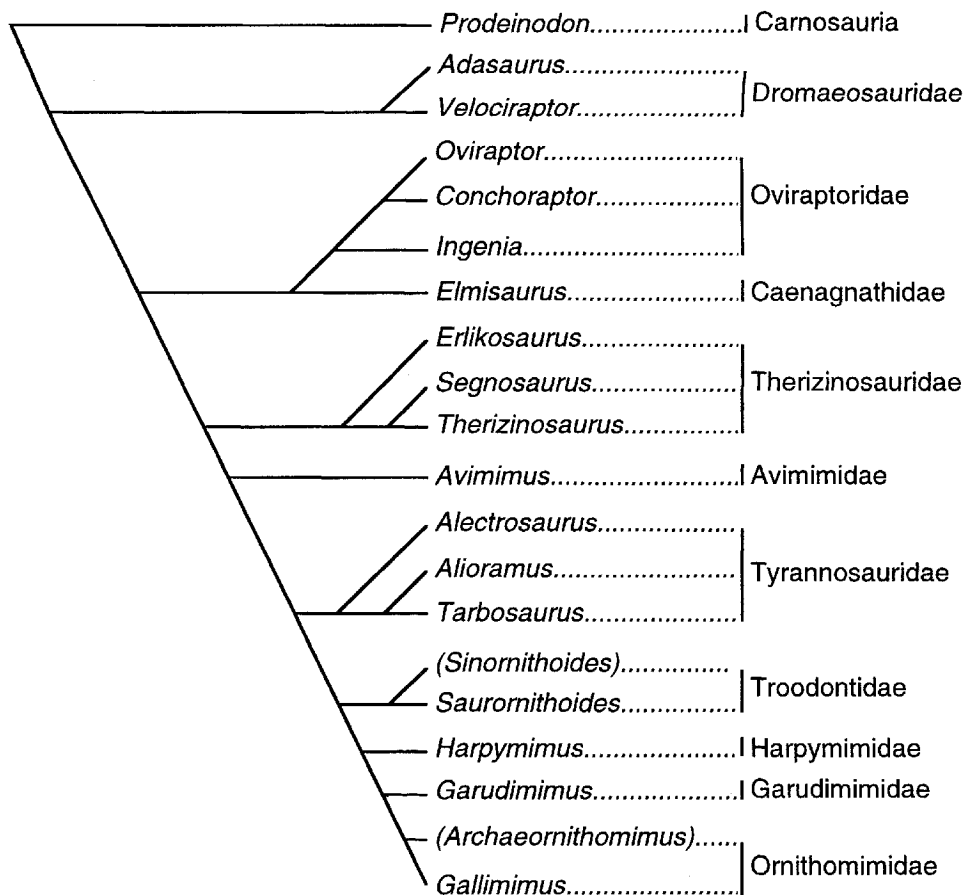


Figure 22.1. Cladogram based on an analysis by Holtz (1994) showing the relationships of the best known Mongolian theropod genera. Genera of unknown affinities (*Bagaraatan*, *Deinocheirus*), and unnamed genera (specimens previously referred to as '*Oviraptor mongoliensis*', 'undescribed giant dromaeosaur' and 'undescribed troodontid') are not included on the cladogram.

Regardless of whether any of the major theropod lineages originated in central Asia, Mongolian discoveries document theropod diversification better than anywhere else. Moreover, the beautiful preservation of so many specimens also permits more precise analysis of their relationships. In this review, each of the seven Mongolian theropod clades is considered, followed by some problematic fossils that represent valid taxa whose relationships are not yet clearly understood.

Systematic survey

Dromaeosauridae

Characteristics. The family Dromaeosauridae is generally subdivided into two subfamilies – Dromaeo-

saurinae and Velociraptorinae. Recent discoveries by the American Museum of Natural History, and restudy of the type specimen of *Dromaeosaurus albertensis* (Currie, 1995) suggests that the two lineages could be separated at a higher taxonomic level (family or higher). Irrespective of the level of distinction, dromaeosaurine and velociraptorine theropods are more closely related to each other than either is to any other known theropod clade.

Dromaeosaurines tend to be more massive animals than velociraptorines of equivalent size. The only animal that can be assigned to this subfamily with certainty is *Dromaeosaurus albertensis* from Upper Cretaceous rocks of North America (Currie, 1995).

What we know about this genus is based almost entirely on the skull, which makes it difficult to compare with specimens that lack skulls. Although some Mongolian taxa have tentatively been referred to this subfamily (Paul, 1988b), this is not meaningful without good cranial material.

In 1989, a giant dromaeosaurid was discovered in Lower Cretaceous rocks of the southeastern Gobi (Perle *et al.*, 1999). *Achillobator* is from approximately the same time period as *Utahraptor* (Kirkland *et al.*, 1993) from the United States, and it is tempting to think that it might be related. Premaxillary tooth size indicates that *Utahraptor* is a velociraptorine, whereas serration size suggests that *Achillobator* might be a dromaeosaurine. Unfortunately, the absence of most of the postcranial skeleton of *Dromaeosaurus* makes these designations tentative.

Dromaeosaurids are easily distinguished from other theropods by many cranial and postcranial autapomorphies (Currie, 1995). These include a slender, T-shaped lacrimal; a T-shaped quadratojugal; a conspicuous lateral extension of the paroccipital process beyond the head of the quadrate; a broad, shallow, shelf-like retroarticular process with a vertical columnar process posteromedially; fusion of the interdental plates to each other and to the margins of the jaws; strongly angled intervertebral articulations in the cervical vertebrae; hyperelongated prezygapophyses in all but the most proximal caudals; hyperelongated anterior projections on all but the most proximal haemal arches; a retroverted pubis; confluence of the greater and lesser trochanters of the femur; and a highly specialized second digit of the foot bearing a sickle-shaped claw.

Record. The best record of dromaeosaurids, which were widespread in the northern hemisphere throughout most of the Cretaceous, comes from Mongolia. A possible dromaeosaurid has been reported from northern Africa (Rauhut and Werner, 1995), but better material is needed to confirm this. Four genera have been described to date, most of which are based on well-preserved material.

Velociraptor mongoliensis is the best known dromaeo-

saurid, having been described originally by Osborn in 1924 on the basis of a skull and partial skeleton from the Djadokhta beds of Bayan Zag (Figures 22.2A and 22.6A). One of the most remarkable dinosaur specimens ever discovered is a complete skeleton of *Velociraptor* from Tögrög preserved in association with a skeleton of *Protoceratops*. Although the association can be interpreted in many ways, the most likely explanation is that the *Velociraptor* had attacked the *Protoceratops* during a sandstorm (Jerzykiewicz *et al.*, 1993; Unwin *et al.*, 1995). Other specimens of *Velociraptor* have been reported from the Baruungoyot beds at Khulsan (Osmólska, 1980, 1982; Norell and Clark, 1992), and the Syuksyuskaya Svita of Kazakhstan (Nesov, 1995), although it has yet to be determined whether or not they represent the same species.

Barsbold (1983) gave a preliminary description of *Adasaurus mongoliensis* from the Nemegt site of Bügiin Tsav. The holotype includes a partial skull and parts of the skeleton. Other specimens include the best preserved dromaeosaurid pelvis (Barsbold, 1983) that clearly shows the retroverted pubis (Figure 22.5A). This animal is distinguished from other dromaeosaurids by the relatively small size of the ungual on the second pedal digit, and by unspecified features of the supporting metatarsal. Barsbold assigned this genus to the subfamily dromaeosaurinae, along with *Dromaeosaurus* and *Deinonycbus*. However, the latter is clearly a velociraptorine (Paul, 1988a), so the criteria used to include *Adasaurus* in the dromaeosaurinae are suspect.

Hulsanpes perlei is based on an incomplete foot from the Baruungoyot Formation of Khulsan (Osmólska, 1982). Most of the similarities to a dromaeosaurid foot are plesiomorphic, and even its identification as a dromaeosaurid is uncertain. Chiappe and Norell believe this to be from another more speciose branch of the Maniraptora (Norell, pers. com.). The small size of the specimen suggests that metatarsal elongation may simply be a juvenile trait, and that negative allometry during ontogeny might have produced a metatarsal with proportions similar to adult *Velociraptor* specimens from the same locality.

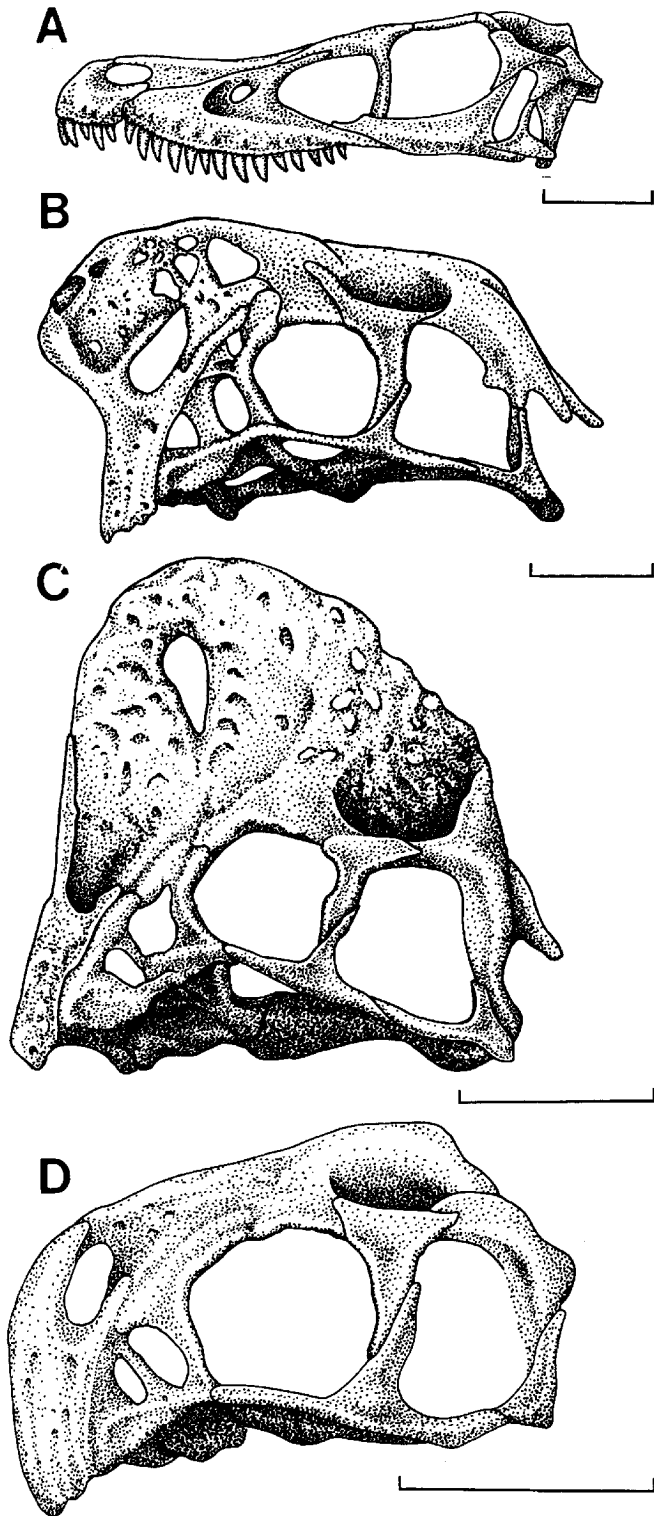


Figure 22.2. Skulls of Mongolian theropods. (A) *Velociraptor*, (B) *Oviraptor*, (C) '*Oviraptor*' *mongoliensis*, and (D) *Conchoraptor*. (A) after Paul (1988a), (B)–(D) after Barsbold *et al.* (1990). Scale bar = 50 mm.

Oviraptorosauria

As presently defined, the Oviraptorosauria includes at least two families – Oviraptoridae and Caenagnathidae. Barsbold (1983) has further subdivided the Oviraptoridae into the subfamilies Oviraptorinae and Ingeniinae. Until recently, caenagnathids were considered to have been restricted to North America. However, Currie *et al.* (1993) reported on the discovery of a caenagnathid, *Caenagnathasia martinsoni*, from the Late Cretaceous of Uzbekistan. Furthermore, it is now apparent that 'Elmisauridae' of Osmólska (1981) is the junior synonym of Caenagnathidae (Currie and Russell, 1988; Sues, 1994). Therefore, the Mongolian species *Elmisaurus rarus* is considered here as a caenagnathid.

Oviraptorosaurs are characterized by many autapomorphies including their toothless, birdlike skulls; loss of the intramandibular joint; fusion of the articular, surangular and coronoid; presence of an unusual jaw articulation with a prominent ridge on the articular; pneumatized vertebral centra, including those of the anterior caudals; and manual unguals with pronounced lips above the interphalangeal articulations.

Oviraptoridae

Characteristics. Mature oviraptorids seem to have ranged in length from one to four meters. Cranially (Figures 22.2B, C), they differ from caenagnathids in having deeper, shorter jaws, a higher, more anteriorly positioned external mandibular fenestra, and a process of the articular-surangular-coronoid ossification that invades the external mandibular fenestra. One of the most interesting differences is that oviraptorids lack the arctometatarsalian condition seen in caenagnathids (Figure 22.6C). The oviraptorid pectoral girdle has a relatively large, well-developed furcula, and the sternum is ossified. It is not known whether caenagnathids also had such a shoulder girdle.

Record. The first oviraptorid skeleton collected at Bayan Zag was associated with a nest of eggs, and was given the name *Oviraptor philoceratops*, which can be translated as 'egg seizer with a fondness for ceratopsian eggs' (Osborn, 1924). However, it has now been

shown (Norell *et al.*, 1995; Dong and Currie, 1996) that this name is inappropriate in the sense that the eggs it was supposed to have been seizing were probably its own. Many oviraptorid skeletons with well-preserved skulls, including embryos (Norell *et al.*, 1994), have been discovered at Djadokhta beds sites in Mongolia and Inner Mongolia. Perhaps the most spectacular locality for oviraptorids is Ukhaa Tolgod, where more than twenty skeletons were discovered in 1993 and 1994 (Dashzeveg *et al.*, 1995). At present, it is not certain whether or not all of these specimens represent *Oviraptor*.

A mature specimen of *Oviraptor philoceratops* has a pneumatized crest over the snout anterior to the orbits (Figure 22.2B). The second and third fingers are subequal in length and each manual ungual has a distinctive dorsoposterior 'lip' that is lacking in the equivalent element in *Conchoraptor*.

A second species of *Oviraptor*, *O. mongoliensis*, was established by Barsbold (1986) on the basis of a well-preserved skull (Figure 22.2C) and partial skeleton from the Nemegt formation at Altan Uul. Subsequent work has suggested to Barsbold (pers. comm., 1996) that this species represents a genus distinct from *Oviraptor*. The crest of this animal is larger than that of *Oviraptor philoceratops*, and the parietal is incorporated into its construction. Although almost the same size as *O. philoceratops*, *O. mongoliensis* apparently has a more lightly built skeleton.

Specimens of *Conchoraptor gracilis* were recovered from Baruungoyot rocks at Hermiin Tsav. They are smaller animals than *Oviraptor philoceratops*, and lack any evidence of a crest (Figure 22.2D). The second and third digits of the hand are subequal in length as in *Oviraptor*, but each ungual lacks the well-developed 'lip' above the interphalangeal articulation.

In 1981, Barsbold set up the oviraptorid subfamily Ingeniinae. He subsequently (1986) elevated this to family level. At present, there is only one species, *Ingenia yanshini*, within this clade, represented by more than half a dozen skeletons from the Baruungoyot of Hermiin (Figures 22.5B and 22.6B). This a small, but relatively robust oviraptorosaur characterized by a

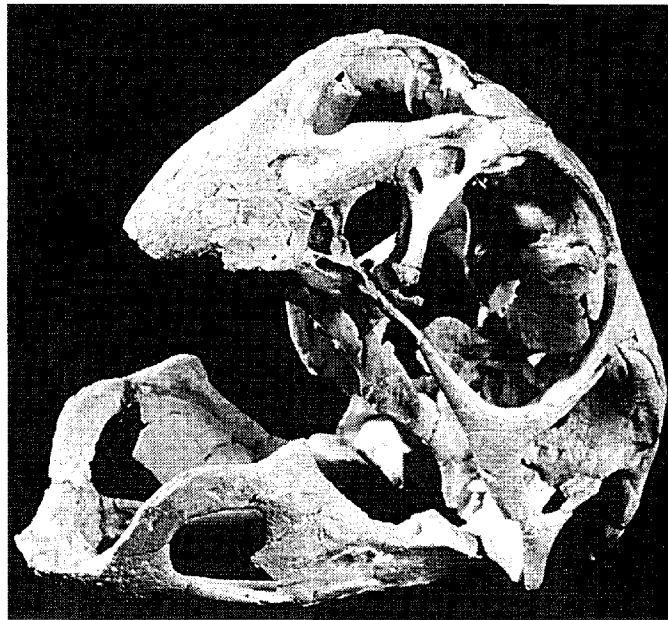


Figure 22.3. Anterolateral view of a beautiful oviraptorid skull in the collections of the Palaeontological Institute in Moscow (courtesy of P. Rich).

skull that apparently lacks a crest, and by a hand in which the first finger is longer and more powerful than the second and third fingers. The manual unguals are significantly longer than the corresponding penultimate phalanges, and lack posterodorsal lips above the articulations.

Caenagnathidae

Characteristics. Caenagnathids are more poorly understood than oviraptorids at present because of the incomplete nature of all skeletons. There appear to be two distinct lineages (which will be referred to here as caenagnathines and elmisaurines), one characterized by *Chirostenotes* from North America, and the other by *Elmisaurus* from both Mongolia and North America (Osmólska, 1981; Currie, 1989). Until recently, caenagnathines were known primarily from their lower jaws, which tend to be longer and lower than those of oviraptorids. Like oviraptorids, the braincase is highly pneumatized, although the basal tubera and basiptyergoid processes are aligned vertically (Sues, 1994).

Most were 2–3 m in length at maturity, and had unfused, arctometatarsalian tarsometatarsi (Currie and Russell, 1988). No cranial material can be assigned with confidence to the Elmsaurinae, although the small size of *Caenagnathasia martinsoni* (Currie *et al.*, 1993) suggests that it may belong to this lineage. Elmsaurines were much smaller animals than caenagnathines, perhaps 1 m in length, but, nevertheless, had fused arctometatarsalian tarsometatarsi.

Record. Two caenagnathids are currently recognized from central Asia. *Caenagnathasia martinsoni* is from the Upper Turonian Bissekty Svita of Uzbekistan and possibly from the Bostobe Svita (probably Santonian) of Kazakhstan (Currie *et al.*, 1993). It is not unreasonable to think that its remains may also be found in Mongolia. Only dentaries have been identified to date, and these suggest that *Caenagnathasia* was a small animal that weighed less than 5 kg at maturity.

Elmsaurus rarus is based on partial skeletons from the Nemegt Formation at the Nemegt locality (Osmólska, 1981). These include hands, feet, and fragments of limb bones (Figure 22.6D). The hand looks remarkably similar to that of *Chirostenotes* from North America (Currie, 1990), but the more slender tarso-metatarsus differs in being fused.

Therizinosauroidea (Alxosauridae, Therizinosauridae)

Although the first therizinosauroid specimens were found in the Irendbasu Formation of Inner Mongolia in 1923, there has been a lot of confusion about their relationships. The Irendbasu specimens were erroneously considered to belong to the tyrannosaurid *Alectrosaurus* (Mader and Bradley, 1989), *Therizinosaurus cheloniformis* from Mongolia was originally identified as a turtle (Maleev, 1954), and *Nanshiungosaurus brevispinus* from China was referred to the Sauropoda (Dong, 1979). In fact, they were not recognized as a distinct theropod taxon for 57 years (Perle, 1979), and their true nature remained obscure until much later (Russell and Dong, 1993a, b).

Many characters separate therizinosauroids from other theropods. These include small bulbous teeth

with denticles aligned parallel to the longitudinal axis of each tooth; widely spaced cervical zygapophyses; elongate, highly pneumatic cervical vertebrae; tall neural arches in the anterior dorsal vertebrae; very broad hips; opisthopubic pelvis; deep preacetabular process of the ilium, which is strongly deflected outwards in *Segnosaurus* and *Nanshiungosaurus*; short postacetabular region of the ilium; relatively short metatarsus, less than a third the length of the tibia; and a functionally quadridactylous foot in which the proximal end of the first metatarsal reaches the tarsus.

Two families of therizinosauroids are recognized by Russell and Dong (1993a, b). Alxosauridae encompasses the more primitive, generally smaller therizinosauroids of the Lower Cretaceous, whereas therizinosaurids are more derived, Upper Cretaceous forms.

Alxosauridae

Characteristics. Alxosaurids are considered to be less derived than therizinosaurids in having teeth that extend to the front of the jaw, unfused cervical ribs, only five sacral vertebrae, a relatively small deltopectoral crest on the humerus, well developed ligament pits in the manual phalanges, and an elongate ilium with only moderate preacetabular expansion.

Record. At present, only one genus is included in the Alxosauridae. *Alxosaurus elesitaiensis* is known from several partial skeletons collected from Lower Cretaceous (Albian?) strata in the Alxa (Alashan) Desert of Inner Mongolia. These remains suggest that it was a medium-sized dinosaur about four meters in length and 400 kg in weight. There are more teeth (40) in the dentary than there are in known therizinosaurids. Although its remains are unreported from Mongolia, its association with Early Cretaceous dinosaurs that are known from Mongolia suggests that it will be found north of the border.

Therizinosauridae

Characteristics. The generally larger therizinosaurids are distinguishable from alxosaurids in lacking teeth at the front of the mouth (Figure 22.4A), and in having

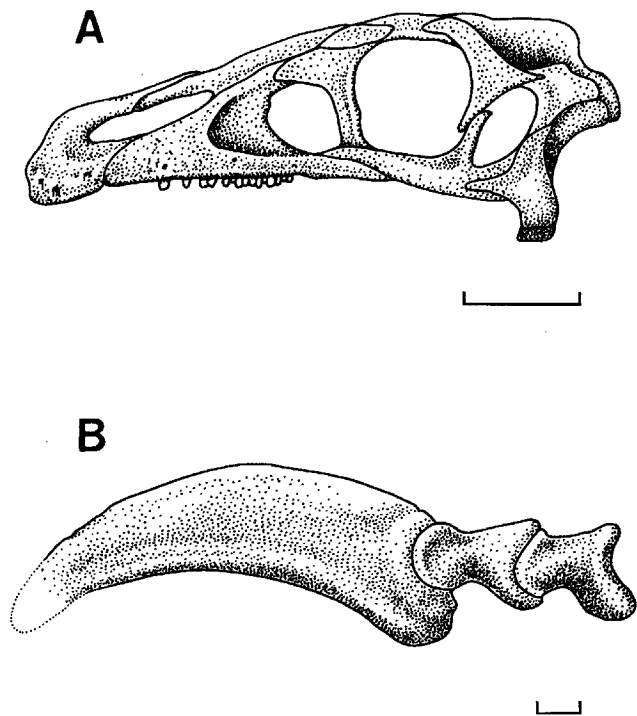


Figure 22.4. Fossil remains of Mongolian therizinosaurids. (A) Skull of *Erlikosaurus*, (B) phalanges of manual digit II of *Therizinosaurus*. (A) after Clark *et al.* (1994), (B) after Barsbold (1976). Scale bar = 50 mm for (A) and 10 mm for (B).

cervical ribs that are fused to the vertebrae, six sacral vertebrae, a large deltopectoral crest, shallow ligament pits in the manual phalanges (Figure 22.4B), and a shorter ilium with significant preacetabular expansion.

Therizinosaurids were a diverse assemblage of theropods that are relatively common at sites that seem to represent lake and river deposits. There are fewer teeth in therizinosaurids than there are in *Alxasaurus*, the anterior teeth having been lost and presumably replaced by a horny bill. This suggested to Barsbold and Perle (1980) that they may have been piscivorous, although Paul (1984) presented a strong case for herbivorous therizinosaurids.

Record. The holotype of *Erlikosaurus andrewsi* was recovered from Bayanshiree strata (Upper Cretaceous) of Baishin Tsav (Perle, 1981). Remains attributed to this animal have also been recovered from the Irendabasu beds of Inner Mongolia (Currie

and Eberth, 1993). (Note that the name has been spelled both as *Erlikosaurus* and '*Erlicosaurus*' by the original author and subsequent workers. The former spelling should be considered correct in that it was used first, and in that the animal is named after 'Erlik', a lamaist deity.) *Erlikosaurus* is smaller than most therizinosaurids, but the unguals are more trenchant (Figure 22.4B). It is the only therizinosaurid known from well preserved, well described cranial material (Clark *et al.*, 1994; Figure 22.4A). Notably, the premaxilla is edentulous, the maxillary teeth are inset from the side of the face, there are 31 dentary teeth, the external naris is relatively larger than those of other theropods, the parasphenoid-basisphenoid complex is highly pneumatic, there is a distinct depression around the otic region in the side of the braincase, and the coronoid bone has been lost from the lower jaw. Although some of these characters are similar in oviraptorosaurs, troodontids, ornithomimids, and other theropods, details allow one to distinguish *Erlikosaurus* easily from other taxa (Clark *et al.*, 1994). It is not yet known how widespread most of these characters are in other therizinosaurids.

The type specimen of *Enigmosaurus mongoliensis* consists of a relatively large pelvis from the Bayanshiree strata of Khar Hötöl. It is possible that this specimen might belong to *Erlikosaurus* (Barsbold, 1983), for which the pelvis is unknown.

Segnosaurus galbinensis is from Bayanshiree strata of Amtgai, Baishin Tsav, Khar Hötöl and Uirilge Khudag in southeastern Mongolia (Barsbold and Perle, 1980), and from the Irendabasu formation of Inner Mongolia (Currie and Eberth, 1993). Specimens include the lower jaw (with 25 teeth) and much of the skeleton (Figure 22.5C, 22.6E). The front of the jaw is toothless and the anterior teeth are somewhat curved, whereas the posterior ones are smaller and straight.

Although Maleev (1954) originally thought the unguals of *Therizinosaurus cheloniformis* were from a sea turtle, Rozhdestvenskii (1970) and Osmólska and Roniewicz (1970) recognized that it was a theropod. A complete front limb and shoulder girdle was described by Barsbold (1976), and the hind limb was described

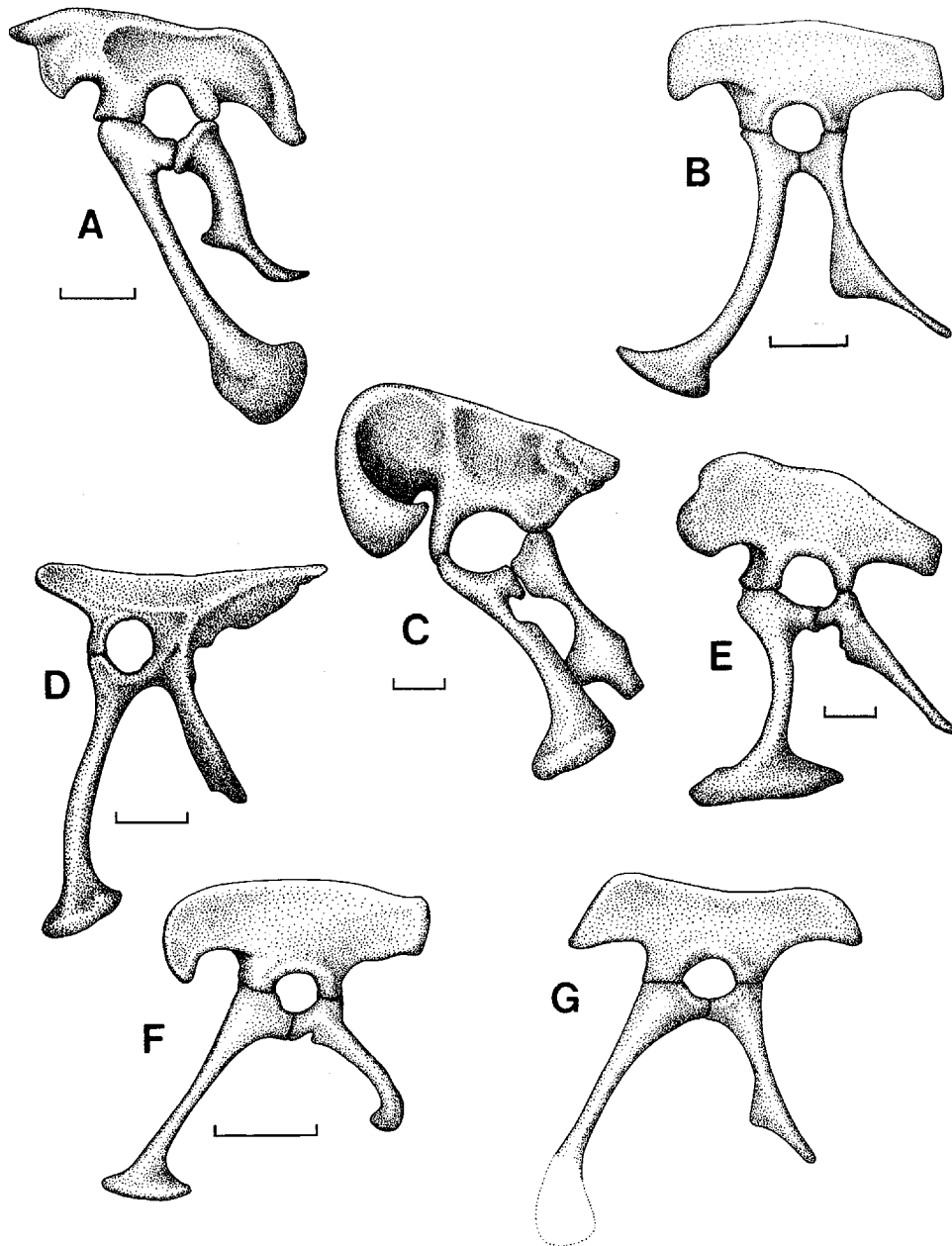


Figure 22.5. Pelvic girdles of Mongolian theropods. (A) *Adasaurus*, (B) *Ingenia*, (C) *Segnosaurus*, (D) *Avimimus*, (E) *Tarbosaurus*, (F) *Gallimimus*, (G) *Saurornithoides*. (A), (C) and (G) after Barsbold (1983), (B) after Barsbold *et al.* (1990), (D) after Kurzanov (1987), (E) after Maleev (1974), and (F) after Barsbold and Osmólska (1990). Scale bar = 50 mm for (A), (B), (D) and (F) and 20 mm for (C) and (E).

and figured by Perle (1982), but neither seemed to resolve the systematic position of this species. The discovery of *Alxasaurus* allowed Russell and Dong (1993a, b) to demonstrate an association between *Therizinosaurus* and ‘segnosaurs’. *Therizinosaurus che-*

loniformis remains, which consist mostly of parts of the front and hind limbs, have also been recovered from Nemegt beds near the Nemegt locality.

Therizinosaur remains are also found in Kazakhstan and Uzbekistan (Nesov, 1995), but are too incomplete

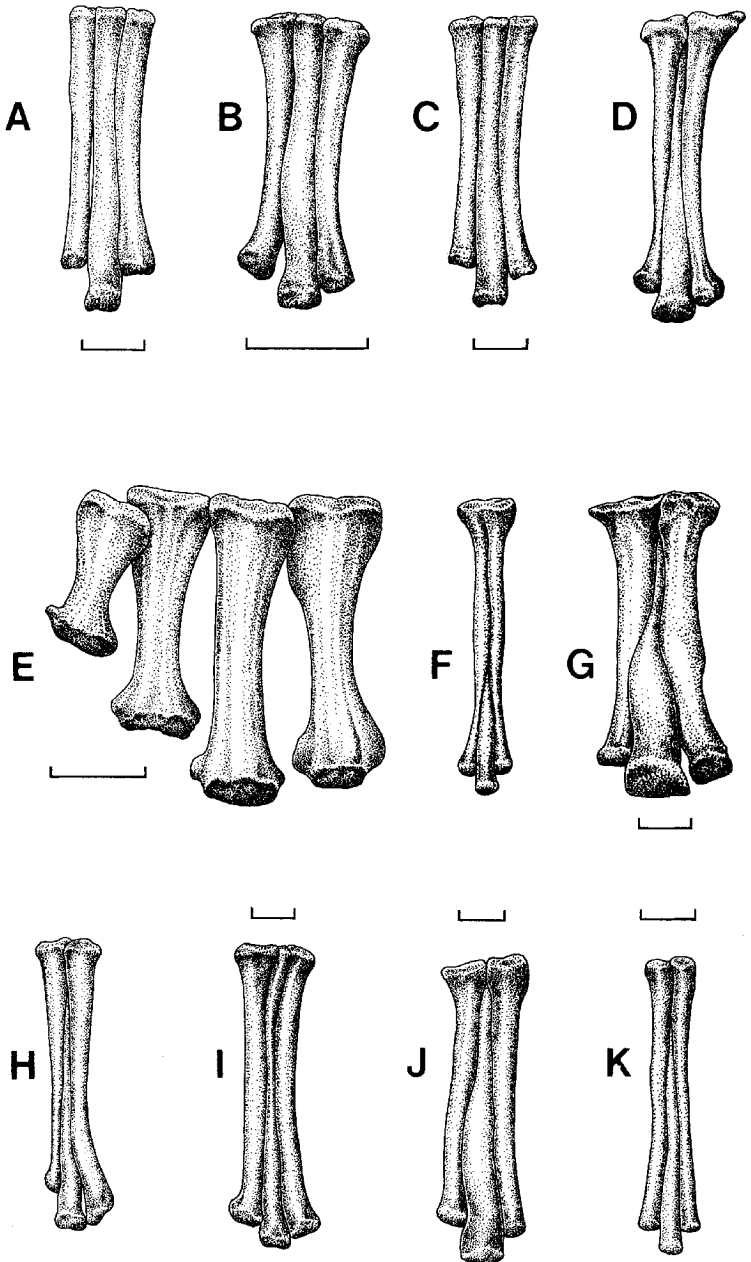


Figure 22.6. Metatarsi of Mongolian theropods. (A) *Velociraptor*, (B) *Ingenia*, (C) *Oviraptor*, (D) *Elmisaurus*, (E) *Segnosaurus*, (F) *Avimimus*, (G) *Tarbosaurus*, (H) *Tochisaurus*, (I) *Harpymimus*, (J) *Garudimimus*, and (K) *Gallimimus*. (A), (C) after Barsbold (1983), (B) after Barsbold *et al.* (1990), (D) after Osmólska (1981), (E) after Perle (1979), (F) after Kurzanov (1987), (G) after Maleev (1974), (H) after Kurzanov and Osmólska (1991), and (I), (J), and (K) after Barsbold and Osmólska (1990). Scale bar = 50 mm except for (E) and (G) = 100 mm.

for more specific identification at present. Recently, eggs with embryos from central China (Henan and Hubei provinces) have been referred to as therizinosauroids (Currie, 1996).

Avimimidae

Characteristics. Avimimids are small, turkey-sized theropods with unknown affinities. When discovered, *Avimimus portentosus* was identified as a bird (Kurzanov, 1981, 1987), though subsequent workers have tended to treat *Avimimus* as a small theropod. A short, deep premaxilla and the front of a lower jaw suggest that this animal was toothless. The braincase is inflated and rather birdlike, there is a reduced postorbital bar, and much of the skull roof is fused. The humerus is relatively long and slender, like that of a bird, but retains a theropod-like deltopectoral crest. The ulna supposedly has papillae for attachment of feathers, but these features are not distinct enough to be sure of their presence. There is a fused carpometacarpus. The hips are very broad, the ilium has a large intertrochanteric shelf (Figure 22.5D), the pubic canal is very broad, and the sacrum includes seven coossified vertebrae. The tarsometatarsus is coossified, but the distal ends of the metatarsals are separate (Figure 22.6F). The third metatarsal is constricted between the second and fourth metatarsals as in arctometatarsalian theropods including ornithomimosauroids, troodontids and caenagnathids. Other than the fact that the fifth metatarsal is included in the fused tarsometatarsus, this structure most closely resembles that of *Elmsaurus*. The vertebrae exhibit some similarities, such as the presence of hypapophyses on the anterior dorsals, to those of troodontids and ornithomimosauroids. Although reconstructed with a short tail by Kurzanov (1987), caudal vertebrae found in China, and the structure of the hips and femur suggest that *Avimimus* may have had a long, tapering tail. A number of isolated vertebrae, tarsometatarsi and unguals have been found in Upper Cretaceous strata of North America that closely resemble those of Mongolian avimimids (collections of Royal Tyrrell Museum of Palaeontology).

Record. *Avimimus portentosus* was recovered from several Djadokhta beds sites in southeastern and

southwestern Mongolia. In addition to that, many isolated avimimid bones have been collected for more than 70 years from the Irendbasu Formation exposed near Erenhot in Inner Mongolia (Currie and Eberth, 1993), and in 1975 at Baishin Tsav (Kurzanov, pers. comm., 1991). Whether these two earlier occurrences represent the same species or not cannot be determined at this time.

Troodontidae

Characteristics. The Troodontidae is one of the most birdlike families of non-avian theropods. They were relatively gracile animals that were less than 3 m in length at maturity. The eyes are large, and because of the narrow snout and broad postorbital region, they face forward and have overlapping fields of view. Relative brain size is large, with that of the North American species *Troodon formosus* being the largest of any dinosaur presently known. Many of the skull bones are pneumatized, with air invading facial and palatal bones from the nasal region, and pneumatopores entering the braincase from the throat via the eustachian tube and the middle ear. The pneumatic parasphenoid has expanded into a bulbous, balloon-like structure. The teeth are relatively small, but are numerous and easily identified because of their relatively large, hook-like denticles. The premaxillary teeth are almost triangular in cross-section, whereas the teeth in the lower jaw are smaller than those in the upper jaw. Unlike other theropods, there are no interdental plates in the lower jaws, and the teeth are held in place by a ring of dental bone that wraps around a constriction between the root and crown of each tooth.

Postcranially, troodontids were highly adapted for a cursorial existence. In fact, limb proportions suggest that in terms of running speed they were probably second only to ornithomimids. Like dromaeosaurids, the second toe of the foot bore an enlarged raptorial claw that was kept off the ground to maintain its sharpness. Because only digits three and four contacted the ground, there are some unusual adaptations in the metatarsus. The second metatarsal, which supports the raised, raptorial claw, is reduced to a relatively thin bone. Like caenagnathids, ornithomimids, tyran-

nosaurids and several other types of Cretaceous theropods, the proximal part of the third metatarsal has been reduced to a small splint. Most of the weight of the animal therefore had to be borne by the fourth metatarsal, which is relatively larger in troodontids than in any other theropods.

Troodontids have many characteristics that make them one of the most easily defined clades in the Theropoda. However, defining their position amongst the theropods has not been as simple. Great importance was placed in the past on the presence in both dromaeosaurids and troodontids of the highly modified second digit of the foot with its enlarged claw. Because of this, the two families are usually included in a clade known as the Deinonychosauria (Colbert and Russell, 1969). However, fundamental differences in anatomical details suggest that this adaptation was attained independently (Currie and Peng, 1993). Similar changes in the second pedal digit seem to have also occurred in the Argentinian theropod *Noasaurus* (Bonaparte and Powell, 1980), and in at least one modern bird known as the seriema. A higher number of derived characters are shared by troodontids and ornithomimosaurids, which led Holtz (1994) to establish a clade that he called the Bullatosauria.

Record. The Troodontidae is best known from the Upper Cretaceous strata of Asia and North America, although it was clearly a well established family in Asia during Early Cretaceous times. The identification of teeth (*Koparion*) as those of troodontids from the Upper Jurassic Morrison Formation of the United States (Chure, 1994) would be more convincing if diagnostic postcranial elements are recovered. This is compounded by the fact that basal ornithomimosaurids and other theropods can have troodont-like teeth. However, given the highly derived nature of Early Cretaceous troodontids, it is not unlikely that the family traces its origins back into the Jurassic.

Numerous species of troodontids have been described from Mongolia and adjacent parts of China and Uzbekistan. The earliest, and incidentally the most complete, troodontid is *Sinornithoides youngi* (Russell and Dong, 1993a, b) from the Lower Cretaceous rocks of the Ordos Basin in Inner

Mongolia. This was a small animal weighing only about 2.5 kg. Although it was a young animal, the degree of ossification and the relative proportions of the body suggest it was almost fully grown. A partial troodontid skeleton from the Lower Cretaceous Khamaryn Us locality of Mongolia (Barsbold *et al.*, 1987) is from a larger animal that may represent a distinct, unnamed species.

Saurornithoides mongoliensis was the first troodontid described from Asia (Osborn, 1924). The holotype was recovered from the Djadokhta beds at Bayan Zag, and specimens from equivalent aged beds are generally referred to this species. These include a small specimen from Bayan Mandahu in Inner Mongolia (Currie and Peng, 1993) that suggests that troodontid juveniles had disproportionately long, but slender metatarsals.

A second, somewhat larger species, *Saurornithoides junior*, was established on the basis of a lovely skull and partial skeleton from the Nemegt beds of Bügiin Tsav. In addition to size, this species has more teeth than *S. mongoliensis* (Barsbold 1974). *Borogovia gracilicrus* (Osmólska, 1987) is another troodontid collected from the Nemegt beds of Mongolia, but has only been reported so far from the Altan Uul IV locality. It is based on partial hind limbs, which include a distinctive second toe with a straight ungual. A third Nemegt genus and species of troodontid, *Tochisaurus nemegtensis*, was established on the basis of a metatarsus (Kurzanov and Osmólska, 1991; Figure 22.6H). Unfortunately, there is no significant overlap in the known specimens of these three Nemegt genera, which were recovered from the same geographic area, and it is conceivable that they all represent the same species.

Troodontid teeth and isolated cranial and postcranial bones from Iren Dabasu (Currie and Eberth, 1993) in Inner Mongolia and Jiayin in Heilongjiang, China, cannot be distinguished from *Saurornithoides* on the basis of size or morphology. A joint Mongolian–American expedition has recently recovered the skull of a new, as yet undescribed genus of troodontid (Novacek *et al.*, 1994) and troodontid teeth attributed to *Troodon asiamericanus* and *Pectinodon* have

been described from the Khodzhakul Formation (Cenomanian) of Uzbekistan (Nesov, 1995).

Although *Archaeornithoides deinosauriscus* was described as a small, birdlike theropod, Elzanowski and Wellnhofer (1993) also speculated on the possibility that this animal, from the Djadokhta Formation of Bayan Zag, was a juvenile troodontid. The characters suggesting that it is not a troodontid include the presence of a wide palatal shelf and the absence of denticles on the teeth. However, new troodontid specimens from Montana show that these animals do have broad palatal shelves. Furthermore, the lack of denticles on the carina of the teeth of such a small animal is not surprising considering the fact that the teeth are less than half the size of the smallest known troodontid teeth. It is therefore quite possible that *Archaeornithoides deinosauriscus* might eventually be shown to be a very young specimen of *Saurornithoides mongoliensis*.

Although troodontid fossils clearly represent a diverse clade within the Cretaceous of Mongolia and neighbouring parts of China, the incompleteness of most specimens makes it difficult to determine evolutionary trends within the family. There is a tendency for the troodontid species to increase in size over time, and for them to increase the number of teeth. *Sinornithoides* and *Saurornithoides mongoliensis* have 18 maxillary teeth, *Saurornithoides junior* has 19–20, and the new, undescribed specimen evidently had at least 30.

Ornithomimosauria

The best fossils documenting the evolution and diversification of 'bird mimics' come from Mongolia. Three ornithomimosaur families are presently recognized – Harpymimidae, Garudimimidae and Ornithomimidae – and all of them are represented in Mongolia (Barsbold and Osmólska, 1990). *Pelecanimimus polyodon*, from the Lower Cretaceous of Spain, has also been identified as an ornithomimosaur (Pérez-Moreno *et al.*, 1994), but cannot be assigned to any of these three families.

Ornithomimosaurians are generally man-sized animals, although they have lightly built, birdlike

heads and bodies. As in troodontids, the eyes are huge, and there is a bulbous parasphenoid. Most are toothless, a convergence with oviraptorids, and the jaws would have been encased by keratinous rhamphothecae. Toothed forms have either numerous, very small teeth (*Pelecanimimus*) or relatively few, poorly developed, peglike teeth (*Harpymimus*). As in dromaeosaurids, the premaxilla has a dorsoposterior process that excludes the maxilla from the nasal opening. In ornithomimosaurians, however, this process is relatively longer, and separates the maxilla and the nasal to the level of the antorbital fossa. The lower jaws are slender and elongate, and the jaw articulation is in an anterior position ventral to the postorbital bar. The cervical vertebrae constitute about 40% of the length of the presacral vertebral column. Metacarpals II and III are almost the same length, and the first metacarpal is more than half of that length. In fact, with the exception of *Harpymimus*, the first metacarpal is usually only slightly shorter than either of the other two. The manual unguals are either weakly curved or straight, and have flexor tubercles that are more distally positioned than they are in other theropods. An ornithomimosaur ilium has an anteroventrally hooked process, the ischium is shorter than the pubis, and there is a wide pubic canal. The metatarsus/tibia ratio is higher than those of other theropods. The first toe is lost in all ornithomimosaurians except *Garudimimus*.

Ornithomimosaur remains are widely distributed in other parts of Asia, including China (Dong, 1992), Kazakhstan, Tadjikistan, and Uzbekistan (Nesov, 1995).

Harpymimidae

Characteristics. Only one harpymimid has been found to date. There are teeth in the jaws of these animals, although they are not well-formed, appear to lack enamel, and may even have been covered over by a keratinous bill (Barsbold and Osmólska, 1990). The humerus is not twisted as it is in more advanced ornithomimosaurians, and the first metacarpal is not as elongate. The metatarsus (Figure 22.6I) seems to have been relatively shorter in that the length is only five times the width of the unit, compared with 7.5 to 9

times the length in ornithomimids. Perhaps more significant is the fact that the third metatarsal is not as constricted as it is in ornithomimids, and that it still separated the second and fourth metatarsals. However, there is some damage to the specimen (Osmólska, pers. com.) in this region, and this feature is uncertain. *Record.* The only specimen of *Harpymimus okladnikovii* was recovered from the Aptian–Albian Shinekhudag beds of Dundgov'. It includes a skull and part of a skeleton, both of which need to be properly described before the systematic position of this species can be understood.

Garudimimidae

Characteristics. A single, well-preserved skull and its incomplete postcranial skeleton are all that are known of the Garudimimidae. Like more advanced ornithomimosaurids, there is a bulbous parasphenoid, and the jaws are edentulous. However, the postorbital region of the skull is relatively longer, and the jaw articulation is positioned posterior to the postorbital bar. The degree of constriction of the proximal end of the third metatarsal is intermediate between that of harpymimids and ornithomimids (Figure 22.6J). The first pedal digit has been retained, in contrast to ornithomimids where it is absent.

Record. The type specimen of *Garudimimus brevipes* was collected from the Cenomanian–Turonian Bayanshiree beds of Baishin Tsav. *Garudimimus* may actually be found in the same rocks that produce specimens of *Archaeornithomimus* (Currie and Eberth, 1993), a fact that could potentially lead to much confusion.

Ornithomimidae

Characteristics. Most ornithomimid genera from Mongolia are well represented by multiple skulls and skeletons. Each animal has metacarpals and fingers that are almost equal in length, a metatarsus that is more than two thirds the length of the tibiotarsus, a proximally pinched third metatarsal that permits proximal contact between metatarsals II and IV (Figure 22.6K), and loss of the first digit of the foot.

Record. The first ornithomimid described from central Asia was named *Ornithomimus asiaticus* by Gilmore

(1933), but was subsequently renamed *Archaeornithomimus asiaticus* by Russell (1972). This ornithomimid is poorly known, even though its remains occur in bonebeds in the Irendabasu Formation of Inner Mongolia, and thousands of partial skeletons and isolated bones have been collected (Currie and Eberth, 1993). The Irendabasu Formation is generally considered to be Cenomanian in age, but is best considered Early Senonian, and may ultimately prove to be as young as Campanian (Currie and Eberth, 1993).

Gallimimus bullatus is the best known ornithomimid, thanks to the recovery of several nearly complete skeletons with skulls from the Nemegt formation at Altan Uul, Bügiin Tsav, Nemegt, and Tsagaan Khushuu (Osmólska *et al.*, 1972). The youngest of these was only about 0.5 m high at the hips, while the largest was close to 2 m in the same dimension.

The Nemegt beds at Bügiin Tsav also produced the type and only specimen of *Anserimimus planinychus* (Barsbold, 1988). This partial skeleton is different from other Mongolian ornithomimids because of the powerful development of the deltoid crest of the humerus (which has never been illustrated), and because of peculiar, flattened unguals on the manus.

Tyrannosauridae

Tyrannosaurids are normally divided into two subfamilies – the Tyrannosaurinae, and the poorly understood Aublysodontinae. These large theropods are most readily characterized by their premaxillary teeth, which are D-shaped in cross-section, incisiform, and are smaller than most of the maxillary and dentary teeth. The cheek teeth are mediolaterally inflated, and can be subcircular in cross-section. This is correlated with increased tooth strength that reduced the chances of damage when bone was encountered during feeding. The nasals coossify in mature individuals, and their dorsal surfaces are rugose. In all species, the prominent nuchal crest extends double the height of the supraoccipital above the foramen magnum. Presacral vertebral centra are relatively shorter anteroposteriorly than those of other theropods. This, the reduction of the forelimbs,

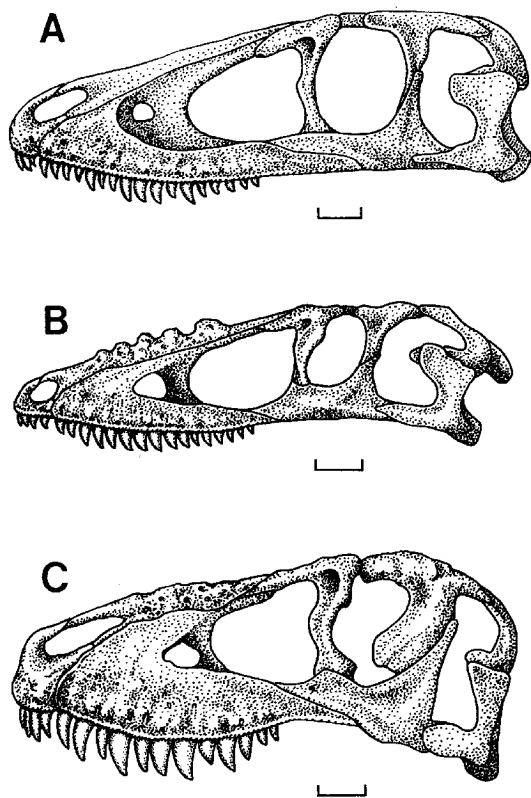


Figure 22.7. Skulls of Mongolian tyrannosaurids. (A) *Alectrosaurus*, (B) *Alioramus*, (C) *Tarbosaurus*. (A) after Perle (1977), (B) after Kurzanov (1976), and (C) after Maleev (1974). Scale bar = 50 mm for (A) and (B) and 100 mm for (C).

and the loss of all but manual digits I and II may be correlated with lightening of the front end of the skeleton. The legs are relatively long for such large animals, suggesting that they were fast movers. The feet are arctometatarsalian, with elongate metatarsals, the third one of which is proximally constricted.

Aublysodontinae

Characteristics. Aublysodontine tyrannosaurs seem to have all been medium sized theropods that grew to less than 5 m in length. Both *Aublysodon*, from North America, and *Alectrosaurus* (Figure 22.7A), from Central Asia, lack denticles (serrations) on their premaxillary teeth. In the latter, there are 17 maxillary, and 19 dentary teeth, which are higher numbers than counts for tyrannosaurine genera. The first two or three maxillary teeth are incisiform (Perle, 1977). The

teeth are narrower and more bladelike than those of their later, more specialized cousins. The skulls of these animals are relatively low and long, although this is, in part, a function of small size in that juvenile tyrannosaurines have similar cranial proportions. The dorsal surface of the fused nasal unit is smooth. The front limbs of *Alectrosaurus* are relatively large compared with advanced tyrannosaurids like *Tarbosaurus* (Perle, 1977), but the few measurements published resemble those of similar-sized individuals of *Gorgosaurus libratus*. Newly recovered specimens from Mongolia and Inner Mongolia suggest that there are many other postcranial characters, especially in the front limbs and hips, that distinguish *Alectrosaurus* from other tyrannosaurids.

Record. *Alectrosaurus olseni* was described by Gilmore (1933) on the basis of parts of two different skeletons from the Iren Dabasu site near the modern city of Erenhot, Inner Mongolia. Perle (1977) and Mader and Bradley (1989) recognized that the robust arms that were supposed to belong to *Alectrosaurus* were in fact from a segnosaur, but that the hind limbs were unquestionably tyrannosaurid. The first specimens of this animal from Mongolia were described by Perle (1977) on the basis of cranial and postcranial material recovered from Baishin Tsav. Several partial, undescribed skeletons of *Alectrosaurus* collected from southeastern Mongolia are in the collections of the museum in Ulaanbaatar, and another new specimen was recently collected from Erenhot in China. *Aublysodon* and *Alectrosaurus* remains have been reported from Kazakhstan, Tadjikistan and Uzbekistan (Nesov, 1995), although none of the specimens are complete enough for proper identification.

Tyrannosaurinae

Characteristics. Tyrannosaurines include some of the largest and most derived predators amongst the theropods, and large specimens of *Tarbosaurus* from Mongolia reached lengths of more than 12 m. Tyrannosaurines can be distinguished from aublysodontines in that they have serrated premaxillary teeth, have fewer than 17 maxillary teeth that are absolutely and relatively taller, have maxillary and dentary teeth

that are labiolingually thicker, and have fused nasals with rugose dorsal surfaces.

Record. Numerous tyrannosaurines have been described from Mongolia since their discovery by the first Russian expedition to the Nemegt Valley in 1946. Tyrannosaurids are relatively common in this region. The Russians collected seven more or less complete skeletons in the 1940s, the Polish–Mongolian expeditions excavated at least three more, and at least six more skeletons are housed in Ulaanbaatar. Even today, there are reports of *Tarbosaurus* specimens being found and left in the field. Why there are so many of these large carnivores found in the Nemegt Formation is a matter for considerable speculation (Osmólska, 1980). Tyrannosaurid fossils recovered from Kazakhstan are sometimes referred to *Tarbosaurus* (Nesov, 1995), whereas teeth and poorly preserved remains of large tyrannosaurids from the Upper Cretaceous of the Heilongjiang (Amur) River of Russia and China, and other parts of China (Dong, 1992) are almost certainly attributable to *Tarbosaurus*.

Tyrannosaurs from Mongolia were originally described by Maleev (1955a, b, 1974) as *Tyrannosaurus bataar*, *Tarbosaurus efremovi*, *Gorgosaurus lancinator* and *Gorgosaurus novojilovi*. Rozhdestvenskii (1965) considered all Nemegt tyrannosaurs to be different growth stages of a single species, *Tarbosaurus bataar*. This has been generally accepted, although Carpenter (1992) used the type specimen of '*Gorgosaurus*' *novojilovi* to establish *Maleevosaurus novojilovi*. Most of the characters used to separate '*Maleevosaurus*' from specimens generally referred to as *Tarbosaurus* are differences in proportions that are ontogenetically controlled. Juvenile tyrannosaurs have lower, more elongate skulls than the adults, which means that the relative proportions of the fenestrae and individual bones (including the maxilla and dentary) go through some extreme changes. The moderate size of the lacrimal horn is not unexpected considering the well rounded, low nature of the dorsal surface of the lacrimal in *Tarbosaurus* (Figure 22.7C, 22.8). The jugal of '*Maleevosaurus*' appears to be very slender (Maleev, 1974), but it has also been damaged and is not complete. Although apparent fusion of the neural arch to

the centrum and the calcaneum to the astragalus (Maleev, 1974) might indicate that the only specimen of '*Maleevosaurus*' represents a mature individual, the scapula is not fused to the coracoid, suggesting that it is immature.

Olshevsky (1995a, b) has gone one step further in recognizing three tyrannosaurids from the Nemegt Basin. He resurrected *Tarbosaurus efremovi* for the 12 m long tyrannosaur, accepted Carpenter's *Maleevosaurus novojilovi*, and set up a third genus, *Jengbizkhan*, for the large (15 m) individual that Maleev called '*Tyrannosaurus*' *bataar*. Olshevsky followed many of Maleev's original ideas in characterizing *Jengbizkhan*, thereby accepting as diagnostic many of the features that other workers felt were ontogenetically controlled.

In my own research on ontogenetic series of specimens of *Gorgosaurus libratus* and *Daspletosaurus torosus* from Alberta, Canada, I can see trends that suggest *Maleevosaurus* and *Jengbizkhan* are junior synonyms of *Tarbosaurus*, as was proposed by Rozhdestvenskii (1965). In examining the many fine tyrannosaurid specimens in Moscow, Warsaw and Ulaanbaatar, I have never found differences significant enough to convince me that *Tarbosaurus bataar* should be subdivided. That does not mean that further research will not reveal convincing differences, but at the present time the most conservative approach is to accept only *Tarbosaurus bataar*.

There is one other tyrannosaurid from the Nemegt Formation. *Alioramus remotus* is from the Nogoön Tsav beds of the Ingenii Höövör valley (Kurzanov, 1976; Figure 22.7B). Based on a single specimen, this medium-sized tyrannosaurid is easily distinguished from *Tarbosaurus* by its higher tooth count and by a series of bumps on the nasals. The maxilla has 16, possibly 17 teeth, and the dentary has 18 teeth, compared with a maximum of 13 maxillary and 15 dentary teeth in *Tarbosaurus*. The bumps on the nasals are rather irregular, so it is possible that the number (five) will prove to be variable in other specimens of *Alioramus*. As pointed out by Kurzanov (1976), the skull is longer and lower than those of *Tarbosaurus*, *Albertosaurus*, *Daspletosaurus* and *Tyrannosaurus*. However, skull pro-

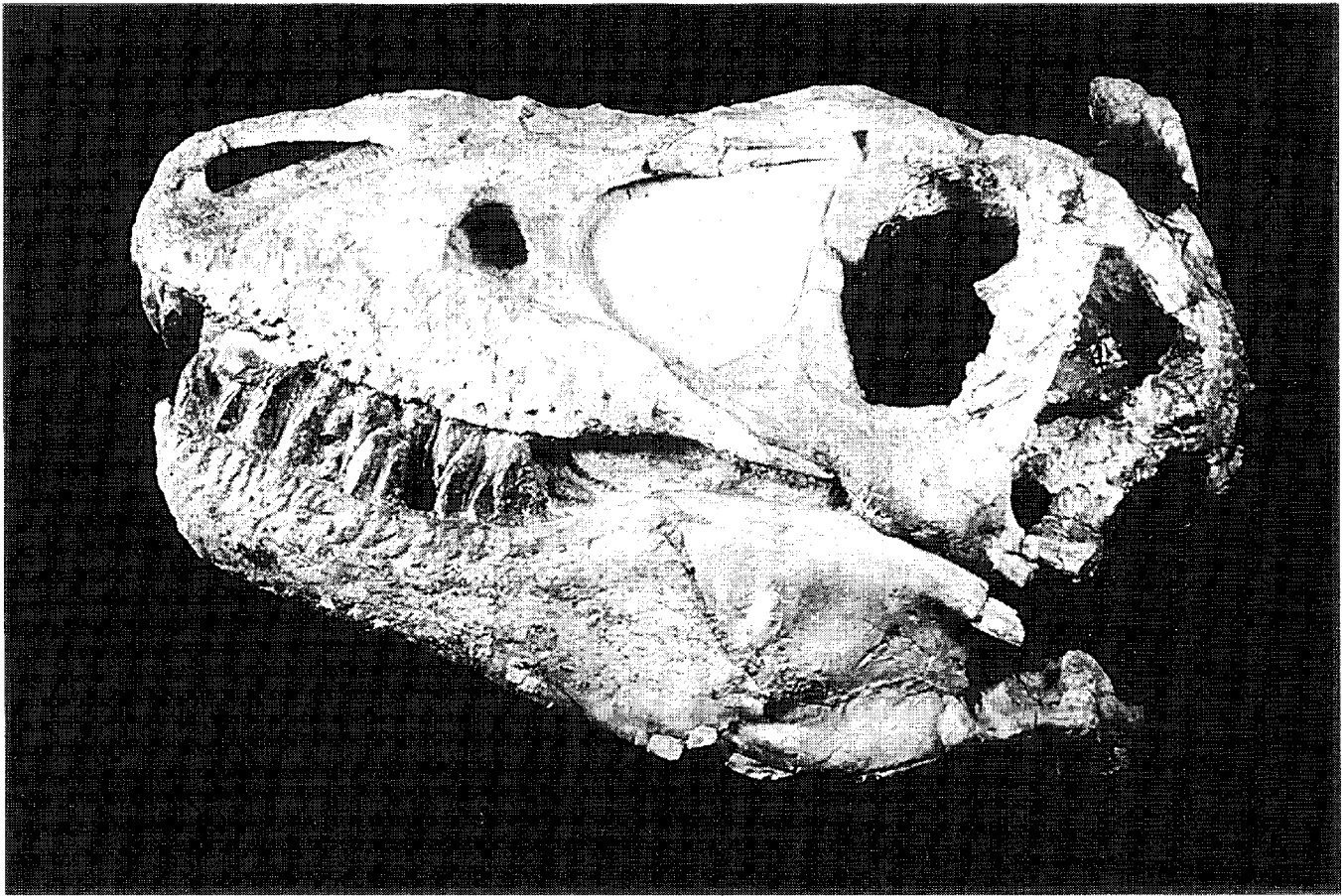


Figure 22.8. Skull of *Tarbosaurus* in left lateral view. (Courtesy of P. Rich.)

portions in tyrannosaurids are dependant on size and age, and juveniles of the other genera have skull proportions that are the same as those of *Alioramus*. The type specimen has a beautifully preserved braincase with a broad nuchal crest and a downturned occiput. These and other characters suggest that *Alioramus* is most closely related to *Tarbosaurus* in Asia, and to *Daspletosaurus* and *Tyrannosaurus* in North America.

Theropods of uncertain systematic position

Asiamericana asiatica

Nesov (1995) described small theropod teeth and jaws from the Bissekty Svita (Upper Turonian) of Uzbekistan and the Dabrazinskaya Formation (Santonian) of Kazakhstan as *Asiamericana*. Although these almost fish-like theropod teeth are distinctive, the systematic position of this theropod cannot be determined at this time.

Bagaraatan ostromi

An unusual medium-sized theropod described by Osmólska in 1996 is based on an incomplete skeleton from the Nemegt formation at the Nemegt locality. The type specimen of *Bagaraatan ostromi* includes a mandible with a shallow but massive dentary, and a fibula that is fused distally to both the tibia and the coossified astragalus and calcaneum. A more complete specimen is needed to determine the systematic position of this animal within the Theropoda.

Deinocheirus mirificus

The Deinocheiridae was erected to include only a single specimen of *Deinocheirus mirificus*, consisting of a remarkably large pair of front limbs, the shoulder girdle and assorted fragments (Osmólska and Roniewicz, 1970). The scapula is long and slender, the forelimbs are elongate, and the three fingers end in

long, strong unguals. The relative proportions of the front limb elements are suggestive of ornithomimids (Osmólska and Roniewicz, 1970), with the manus being only slightly longer than the radius, and the first metacarpal being only 5% shorter than the second. The great length of the arms (close to 2.5 m) is more suggestive of therizinosaurids, however, which is one reason Barsbold (1976) included both types of animals in a new suborder that he called the Deinoceriosauria. This has not received widespread acceptance, and it is clear that the taxonomic position of *Deinocheirus* will not be resolved without more complete specimens. The single specimen of *Deinocheirus mirificus* was collected from Nemegt strata at Altan Uul III.

Embosaurius minax

Two vertebrae from the Lower Cretaceous of Kazakhstan were originally described as *Embosaurius* by Ryabinin (1931). They may be megalosaurid (Nesov, 1995).

Euronychodon asiaticus

The tooth genus *Euronychodon* was established on the basis of teeth from southern Europe, but Nesov (1995) proposed the species *E. asiaticus* for teeth he recovered from the Bissekty Svita (Upper Turonian) of Uzbekistan. The affinities of this small theropod are unknown.

Itemirus medullaris

A well-preserved braincase from the Turonian beds of the Kyzylkum Desert of Uzbekistan was described by Kurzanov (1976) as *Itemirus medullaris*. Although he originally referred to it as a carnosaur, it is much closer in all but one respect (the laterally excavated basiptyergoid process) to a dromaeosaurid braincase (Currie, 1995). The Dzharakhuduk locality has produced many isolated theropod specimens, including dromaeosaurid teeth and bones, but without a more complete skeleton, *Itemirus* should not be assigned to the Dromaeosauridae.

Prodeinodon mongoliensis

Teeth from the Ondaisair and Öösh Formations (Early Cretaceous) of Mongolia have been referred to as *Prodeinodon mongoliensis* (Osborn, 1924). The teeth demonstrate that there was at least one species of large theropod in Mongolia at that time, but give no information on the type of theropod to which they might belong.

Shanshanosaurus buoyanshanensis

Olshevsky (1995b) has allied *Shanshanosaurus buoyanshanensis* from the Maastrichtian Subashi Formation of Xinjiang, China, with the aublysodontine tyrannosaurs because of its unserrated, incisiform, premaxillary teeth (Dong, 1977) and booted pubis. The reported presence of procoelic cervical vertebrae is incorrect, and re-examination of the type specimen (Currie and Dong, in prep.) suggests that it may be a juvenile *Tarbosaurus*.

Conclusions

To date, 33 theropod species representing at least eleven families have been described from Mongolia. It is doubtful whether all of these species are valid, but it is almost certain that at least 25 of them are (Table 22.1). An additional five theropods from neighbouring regions in China, Kazakhstan and Uzbekistan can be expected to be found eventually in Mongolia, and other species described from these regions, such as *Chilantaisaurus* and *Phaedrolosaurus* from China, may well turn out to be valid, and may also turn up in Mongolia. Furthermore, additional theropods will no doubt be discovered in Mongolia as the result of intensive collecting activity at established and newly discovered localities.

The diversity of Mongolian theropods gives us one of the best windows available on theropod evolution, including the origin of birds. Even though all of the small theropods discovered in Mongolia so far lived too late in time to have been bird ancestors, their superb preservation allows us to make detailed anatomical comparisons with birds. Furthermore, many of the Mongolian lineages seem to have originated

Table 22.1. *Theropods from Mongolia and adjacent regions. The first column lists the maximum number of species that have been proposed for central Asia, the second column is the most conservative interpretation of the first column, and the third gives the 'age' of the species according to Jerzykiewicz and Russell (1991)*

<i>Achillobator giganticus</i>	<i>Achillobator giganticus</i>	Lower Cret.
<i>Adasaurus mongoliensis</i>	<i>Adasaurus mongoliensis</i>	Nemegt
<i>Alectrosaurus olseni</i>	<i>Alectrosaurus olseni</i>	Bayanshiree
<i>Alioramus remotus</i>	<i>Alioramus remotus</i>	Nemegt
<i>Alxasaurus elesitaiensis</i>	*	**China
<i>Anserimimus planinychus</i>	<i>Gallimimus bullatus</i>	Nemegt
<i>Archaeornithomimus asiaticus</i>	? <i>Archaeornithomimus</i>	**China
<i>Archaeornithomimus bissektensis</i>	<i>Archaeornithomimus bissektensis</i>	**Uzbekistan
<i>Archaeornithoides deinosauroiscus</i>	<i>Saurornithoides mongoliensis</i>	Djadokhta
<i>Asiamericana asiatica</i>	<i>Asiamericana asiatica</i>	**Uzbekistan
<i>Avimimus portentosus</i>	<i>Avimimus portentosus</i>	Djadokhta
<i>Bagaraatan ostromi</i>	<i>Bagaraatan ostromi</i>	Nemegt
<i>Borogovia gracilicrus</i>	<i>Saurornithoides mongoliensis</i>	Nemegt
<i>Caenagnathasia martinsoni</i>	? <i>Elmisaurus</i>	**Uzbekistan
<i>Conchoraptor gracilis</i>	<i>Conchoraptor gracilis</i>	Baruungoyot
<i>Deinocoelurus mirificus</i>	<i>Deinocoelurus mirificus</i>	Nemegt
<i>Elmisaurus rarus</i>	<i>Elmisaurus rarus</i>	Nemegt
<i>Enigmosaurus mongoliensis</i>	<i>Erlikosaurus andrewsi</i>	Bayanshiree
<i>Erlikosaurus andrewsi</i>	<i>Erlikosaurus andrewsi</i>	Bayanshiree
<i>Euronychodon asiaticus</i>	<i>Euronychodon asiaticus</i>	**Uzbekistan
<i>Gallimimus bullatus</i>	<i>Gallimimus bullatus</i>	Nemegt
<i>Garudimimus brevipes</i>	<i>Garudimimus brevipes</i>	Bayanshiree
<i>Harpymimus okladnikovii</i>	<i>Harpymimus okladnikovii</i>	Shinekhudag
<i>Hulsanpes perlei</i>	<i>Velociraptor mongoliensis</i>	Baruungoyot
<i>Ingenia yanshini</i>	<i>Ingenia yanshini</i>	Baruungoyot
<i>Itemirus medullaris</i>	<i>Itemirus medullaris</i>	**Uzbekistan
<i>Jenghizkhan bataar</i>	<i>Tarbosaurus bataar</i>	Nemegt
<i>Maleevosaurus novofilovi</i>	<i>Tarbosaurus bataar</i>	Nemegt
<i>Monolophosaurus jiangi</i>	*	**China
<i>'Oviraptor' mongoliensis</i>	<i>Oviraptor mongoliensis</i>	Nemegt
<i>Oviraptor philoceratops</i>	<i>Oviraptor philoceratops</i>	Djadokhta
<i>Prodeinodon mongoliensis</i>	<i>Prodeinodon mongoliensis</i>	Öösh
<i>Saurornithoides junior</i>	<i>Saurornithoides mongoliensis</i>	Nemegt
<i>Saurornithoides mongoliensis</i>	<i>Saurornithoides mongoliensis</i>	Djadokhta
<i>Shanshanosaurus buoyanshanensis</i>	*	**China
<i>Segnosaurus galbinensis</i>	<i>Segnosaurus galbinensis</i>	Bayanshiree
<i>Sinraptor dongi</i>	*	**China
<i>Sinornithoides youngi</i>	? <i>Sinornithoides</i>	**China
<i>Tarbosaurus efremovi</i>	<i>Tarbosaurus bataar</i>	Nemegt
<i>Therizinosaurus cheloniformis</i>	<i>Therizinosaurus cheloniformis</i>	Nemegt
<i>Tochisaurus nemegtensis</i>	<i>Saurornithoides mongoliensis</i>	Nemegt
<i>Troodon asiamericanus</i>	<i>Saurornithoides mongoliensis</i>	**Uzbekistan
Undescribed troodontid	Undescribed troodontid	Djadokhta
<i>Velociraptor mongoliensis</i>	<i>Velociraptor mongoliensis</i>	Djadokhta

Notes:

A single asterix (*) means nothing has been found in Mongolia to indicate the presence of this species, although the probability of its discovery there is high. Double asterices (**) indicate the country of origin for species not presently known in Mongolia. A question mark refers to specimens already found in Mongolia that may eventually be identified as non-Mongolian genera.

during Jurassic times, and share with birds derived characters that would have been present in the ancestors of both these theropods and birds. Dromaeosaurids are considered by many experts to be the sister group of birds, but other authors have also made a case for a closer relationship between troodontids and birds. Several of the theropod families represented in Mongolia, including avimimids and caenagnathids, are so birdlike that they were originally identified as birds.

The large number of well preserved specimens from Mongolia also presents palaeontologists with opportunities to assess the morphological variation (individual, sexual and ontogenetic) of theropod species. Although such studies will inevitably lead to a reduction in the apparent diversity of Mongolian theropods, they will provide a much firmer foundation for understanding other aspects of dinosaurian biology, such as palaeoecology. Tyrannosaurids are one of the best examples from Mongolia of animals that can be used to assess variation because: (1) there are many well-preserved skulls and skeletons; (2) half-grown to adult individuals are known; and (3) their North American cousins have been used to demonstrate both ontogenetic and sexual variation. The large number of specimens and elaborate display crests on the skulls of some oviraptorids also make them prime candidates for such studies.

The fine preservation of Mongolian theropods has given science some of the best information on theropod behaviour through taphonomic studies. Examples include the predatory behaviour of *Velociraptor*, and the egg-laying and brooding behaviour of *Oviraptor* (Norell *et al.*, 1995). But there is still much to be learned. Why, for instance, are so many crested oviraptorids found at Ukhaa Tolgod?

Mongolia has clearly established itself as the 'Mecca' for specialists on theropod dinosaurs and an ever-increasing flow of exciting new discoveries is likely to insure this eminent position long into the future.

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