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Theropod Dinosaurs of the Cretaceous

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INTRODUCTION

Tyrannosaurus rex is unquestionably the most famous dinosaur, probably because of its awesome size and appearance, and its apparent strength, agility and prowess. In spite of its fame, the anatomy and relationships of *Tyrannosaurus* and its kin remain poorly understood. By Late Cretaceous times (about 65 to 100 million years ago), carnivorous dinosaurs (theropods) had reached their peak of diversity in the Northern Hemisphere, and there were many specialized species of all sizes.

The Upper Cretaceous beds of central Asia (Mongolian People's Republic and the People's Republic of China) and western North America (especially Alberta and Montana) have produced the greatest diversity of theropod remains. At least thirteen species of carnivorous dinosaurs are known from the Judith River Formation of Dinosaur Provincial Park (Alberta), and from the Nemegt Formation of Mongolia. Although the species have been called different names on each continent, they nevertheless represent closely related forms, indicating the presence of connections between the continental masses. Members of the Canada-China Dinosaur Project are making direct comparisons between Asian and North American taxa, and comparing the depositional environments that they are associated with. This will help us to understand the relationships, evolution, and dispersal of Cretaceous dinosaurs. Because the intercontinental connections lay within the arctic circle, recent discoveries in Alaska (by the University of California at Berkeley and the University of Alaska) and Canada's arctic islands (by the National Museum of Canada and Memorial University) of dromaeosaurid, troodontid and tyrannosaurid theropods also have a direct bearing on these studies.

Theropods are not as common as ornithischian dinosaurs, and specimens of some of the smaller species are extremely rare. Some carnivorous dinosaurs, such as *Caenagnathus* (described in 1940 by R.M. Sternberg, the grandson of C.H. Sternberg), are only known from distinctive but isolated bones. In recent years, a greater emphasis has been put on the recovery and identification of small specimens, including isolated bones and teeth. In Asia, this led to the discovery of forms such as *Elmisaurus* and *Hulsanpes*, which have been described on the basis of distinctive hand and foot elements. In North America, *Elmisaurus* has been identified from similar material. The recovery of thousands of theropod teeth from microvertebrate screen-washing sites has made possible the identification of theropod taxa by their teeth. This has greatly increased our understanding of faunal associations, as well as the geographic and temporal range of at least some of the theropods.

Because so few theropods are known from complete skeletons, problems certainly exist with names being given to different parts of skeletons. For example, a tooth from the front of a skull collected in Montana was given the name *Troodon*, while other teeth found in Wyoming were called both *Saurornithoides* and *Pectinodon*; a jaw from Alberta was called *Polyodontosaurus* and several partial skeletons from Alberta were named *Stenonychosaurus*. All of these turned out to be from the same species, *Troodon formosus*, once they were analyzed critically and compared with more recently discovered specimens (Currie, 1987). Nevertheless, in spite of some taxonomic uncertainties, the high diversity of Late Cretaceous theropods seems to be real.

Recent studies suggest that some fundamental reevaluation of theropod classification is necessary. Some species that were once thought to have been related are in fact only distant cousins, whereas others that appear very different physically are much more closely related.

CRETACEOUS THEROPODS OF THE NORTHERN HEMISPHERE

Coelurosaurs. -- Some six families of small to medium-sized coelurosaurs were common in the Cretaceous of the Northern Hemisphere. Dromaeosaurid theropods became well known to the public with the discovery and description of *Deinonychus* (Ostrom 1969), a small form with an enlarged claw on its foot adapted for disembowelling or skewering prey. Although *Deinonychus* is from the Lower Cretaceous of Montana, closely related forms (*Velociraptor* from Asia, *Saurornitholestes* from North America) are common in the Upper Cretaceous. All workers have recognized the similarities of these three genera and have included them in their own subfamily, the Velociraptorinae. Some workers, including Paul (1988), have taken it a step further and recognize them as three distinct species of the same genus, *Velociraptor*. Isolated teeth are easy to identify because the serrations on the back are much larger than those on the front.

Dromaeosaurus is an extremely rare dromaeosaurid, but a well preserved skull and partial skeleton was collected in Alberta in 1916. Although it shares a number of derived characters in the skull and foot with *Velociraptor*, it is a more massive animal that has a more primitive type of tooth. Therefore, it has been referred to a distinct subfamily, the Dromaeosaurinae. Several of the central Asian forms, including *Adasaurus*, are provisionally referred to the same subfamily.

A number of Asian and North American species with unusual, toothless skulls have been assigned to the Caenagnathidae. Three genera (*Conchoraptor*, *Ingenia*, *Oviraptor*) are represented in central Asia by relatively good specimens. The North American *Caenagnathus* is only known from two specimens that show the distinctive toothlessness of the jaws. The lower jaws are more primitive than those of the Asian genera in that they are relatively longer and lower, suggesting that caenagnathids may have evolved in North America. In fact, *Microvenator*, a poorly known form from the Lower Cretaceous Cloverly Formation, has some characteristics that suggest that it may be a caenagnathid.

The elmisaurids *Elmisaurus* and *Chirostenotes* have a peculiar type of hand with a long, slender outer finger, and also share many similarities in the foot. *Chirostenotes* is a man-sized theropod known from several partial skeletons from North America. *Elmisaurus* is more progressive in the fusion of foot elements, even though it is a smaller animal. *Elmisaurus rarus* was described from Asia, and *Elmisaurus elegans* from Alberta.

Avimimus is a bird-like animal from China and Mongolia that is referred to as a bird by some workers, and as a dinosaur by others. The skull is very birdlike with its inflated braincase and toothless mouth; but it lacks diagnostic characters of birds, such as feathers or quill nodes on the forearm. Individuals of this turkey-sized genus are smaller than *Elmisaurus*, but show a higher degree of fusion of hand and foot bones.

Troodon and *Saurornithoides* are North American and Asian representatives of a highly derived family of theropods known as the Troodontidae. *Troodon formosus* was first described in 1856 on the basis of a distinct type of small tooth with large serrations. Although many such teeth were recovered in subsequent years, more than 130 years passed before a skeleton was identified for *Troodon*. "*Stenonychosaurus*" (a peculiar, man-sized theropod with a relatively large brain) had been described in 1932, but none of the skeletons included teeth, so its true identity was not realized until a "*Stenonychosaurus*" jaw was discovered with *Troodon* teeth in it (Currie, 1987). "*Stenonychosaurus*" gained a certain amount of notoriety when one paleontologist made a projection of what this dinosaur might have looked like (extrapolating from evolutionary trends) if it had continued to evolve. The resultant "dinosauroid" (Russell and Seguin, 1982) is hypothetical and not a real animal, but it does make the point that theropods were becoming larger brained, with more efficient locomotion.

Troodontid teeth are distinct from those of other theropods because of their relatively large serrations, and there is no problem recognizing them throughout Upper Cretaceous beds of the Northern Hemisphere. Based on tooth morphology, it appears likely that there are two distinct species in North America. Two species of *Saurornithoides* have been described from Asia, but these may ultimately turn out to be indistinguishable. Another Late Cretaceous form, *Borogovia*, is known only from Asia. Troodontid teeth from the Lower Cretaceous Cedar Mountain Formation of North America were referred incorrectly to the Troodontidae (Nelson and Crooks, 1987) and the only Lower Cretaceous troodontids known are unnamed specimens from Mongolia and China. This suggests that Asia may have been the birthplace of the family.

Ornithomimids are similar to ostriches in body form and size. These long-legged runners have toothless jaws, large eyes, and relatively large brains. The most primitive ostrich-mimic dinosaurs were found in Asia. *Harpimimus* has some teeth at the front of the jaws, but all later forms had toothless beaks. *Garudimimus* is more primitive than other Late Cretaceous forms, and is usually put in its own subfamily. Numerous specimens of *Archaeornithomimus* have been collected near Erenhot in China. Similar specimens from New Jersey have been referred to the same genus, although this is mostly on the basis of primitive characters, which generally have no taxonomic significance. *Dromiceiomimus*, *Ornithomimus*, and *Struthiomimus* are the Late Cretaceous forms from North America, and *Gallimimus* and *Anserimimus* are their Mongolian relatives.

Deinocheirus mirificus is poorly known, only one partial skeleton having been found. The arms of this animal are extremely long (2.4 m), and the size was used to establish a new family of theropods known as the Deinocheiridae, although it may simply be a highly derived ornithomimid. There is no evidence of *Deinocheirus* in North America.

Carnosaurs. -- Theropods of the carnosaur family Tyrannosauridae are among the best known dinosaurs, especially *Tyrannosaurus rex*. In recent years, numerous new skeletons have been recovered, especially in Alberta (Currie and Britt, 1989), Montana, South Dakota, and Mongolia. In addition, museum specimens are being restudied, resulting in the recognition of previously unidentified taxa, such as *Nanotyrannus* (Bakker et al., 1988). The tyrannosaurids are anatomically distinct from all other theropods, and as a family are easily defined. However, the recognition of individual species is difficult because ontogenetic, sexual, and individual variation is not well understood for any member of this family. This is compounded by the individual biases of workers in establishing the generic level. Some recognize *Albertosaurus*, *Alectrosaurus*, *Aublysodon*, *Daspletosaurus*, *Gorgosaurus*, *Nanotyrannus*, *Tarbosaurus* and *Tyrannosaurus* as valid tyrannosaurids, whereas others (Paul, 1988) recognize no more than three of these genera. Two other Asian forms, *Indosuchus* and *Alioramus*, may be tyrannosaurids, but more information is needed on existing specimens.

Aublysodon is a type of tooth described more than a century ago. Like the premaxillary teeth of *Albertosaurus*, *Tyrannosaurus*, and their kin, *Aublysodon* teeth are D-shaped in cross-section. What is different is that they lack serrations. All *Aublysodon* teeth are small, and it is possible that these are tyrannosaurid baby teeth that were replaced by more normal, serrated teeth as individuals grew up. Although *Aublysodon* could still be shown to be a juvenile of one of the other tyrannosaur species, the discovery and identification of baby tyrannosaurid teeth with serrations suggest that this is unlikely. A partial skull found in Montana, often referred to as the "Jordan theropod," is being redescribed as *Aublysodon*.

There were other theropods during the Late Cretaceous in Asia and North America, but specimens are not complete enough to do more than hint at their relationships. *Chilantaisaurus* from China, *Labocania* from Mexico, and isolated teeth from the United States suggest that tyrannosaurids were not the only large predators in the Northern Hemisphere. Small teeth shaped like isosceles triangles are common in the Upper Cretaceous beds of North America, and have also been recovered from Paleocene channels in Montana. At one time these were identified as sebecosuchian crocodile teeth on the basis of tooth shape and the small size of the serrations. Even though these teeth are relatively common, only a single pair of jaws can be associated with them. The jaws are unquestionably from a theropod. Specimens like these and others from Asia do not give us a clear understanding of the animals they represent, but do indicate that theropods were as diverse as modern carnivores.

THEROPOD RELATIONSHIPS

If we ignore poorly understood taxa, most theropods found in the Northern Hemisphere's Upper Cretaceous beds can be assigned to six families -- Dromaeosauridae, Caenagnathidae, Elmisauridae, Troodontidae, Ornithomimidae, and Tyrannosauridae. The history of our understanding of the interrelationships of these families has been chaotic, but as our knowledge of theropod anatomy improves, the "family tree" should become more stable.

The long-standing view was that theropods could be assigned to two groups, the Coelurosauria and the Carnosauria. Gauthier (1986) and others have shown that all large theropods cannot be assigned to the Carnosauria, nor are all small theropods coelurosaurs.

Dromaeosaurids have generally been included with troodontids (=saurornithoidids) in a taxon known as the Deinonychosauria. This association is based on the presence in both families of the specialized claw on the inner toe, leaving only two toes in contact with the ground. However, representatives of these two families are very different from each other in all other specialized characteristics. The braincase of *Dromaeosaurus* is no more progressive than those of Late Triassic theropods, and most of the foot is unusually primitive for a Late Cretaceous form. Furthermore, the raptorial digit is structurally different in the two families, suggesting that it developed independently. Dromaeosaurids are different from troodontids in that the first joint of the second toe is not significantly longer than the second joint.

Dromaeosaurids are clearly the most primitive group of Late Cretaceous theropods. The braincase, limb proportions and most characteristics are not significantly different from those of *Coelophysis* and other early theropods. Nevertheless, they do have a number of derived characters not found in other theropod genera, including the enlarged, sharply recurved claw on the elevated second toe of the foot and long, bony processes of the vertebrae that stiffen the tail.

Caenagnathids have highly derived, birdlike skulls that lack teeth, probably bore a horny bill, have many pneumatic openings, and often have an inflated crest over the nasal region. The postcranial skeleton is more primitive, however, and looks like a typical theropod. Some features of the hand are similar to those of elmisaurids, but other characteristics are more primitive. Caenagnathids were the first dinosaurs discovered with clavicles (the collar bone or "wishbone" of birds), the absence of which had previously been used to show that dinosaurs could not have been ancestral to birds. Bony sternals ("breastbones") have also been found in Asian caenagnathids.

Currie and Russell (1988) presented evidence to suggest that the elmisaurid genus *Chirostenotes* may be the senior synonym of *Caenagnathus*. Unfortunately, there is no anatomical overlap between the specimens, and the least ambiguous approach is to assume that they are different until better specimens are described. Specimens of *Oviraptor* discovered recently in China and Mongolia show that caenagnathids and elmisaurids have differences in the foot that would support separation at the family level.

The remaining families of Cretaceous theropods share a number of derived characters that suggest a closer relationship than has been suspected until now. The third metatarsal (the bones in the sole of your foot are metatarsals) is pinched at the top between the second and fourth metatarsals in elmisaurids, avimimids, troodontids, ornithomimids, and tyrannosaurids. By itself, this characteristic is not significant. However, papers in progress by Bakker, Currie and Lietch, and Currie and Zhao will show that troodontids, ornithomimids, and tyrannosaurids have many derived characters in the braincase that are not found in other theropods. The most prevalent of these is a series of pneumatic sinuses in the skull bones that connect directly to the middle ear, and from there via the eustachian tube to the throat.

Elmisaurids, as previously noted, do show some similarities with caenagnathids. But if fusion of foot elements is a progressive characteristic, then elmisaurids are more advanced theropods. The skull is normally the best part of the skeleton for determining relationships, and unfortunately no elmisaurid skulls have been identified.

Whereas five bones of the foot are fused into a bird-like tarsometatarsus in *Elmisaurus*, a sixth bone (the fifth metatarsal) is also included in *Avimimus*. The similarities in the foot suggest that *Avimimus* may have been derived from elmisaurid dinosaurs. The skull is enigmatic, however, showing similarities in its toothlessness with caenagnathids, ornithomimids, and birds.

Troodontids and ornithomimids have both extended the air ducts from the middle ear into a balloon-like structure (the bulbous parasphenoid) at the front of the braincase. This is such a specialized feature that it suggests close relationship between these families. This suspicion finds support in the highly pneumatic skull bones, enlarged brain, and specializations of the foot.

Troodontids have many characteristics that distinguish them from other theropods. As previously mentioned, the claw of the second toe has become a specialized weapon as in dromaeosaurids, although this has been accomplished in a different manner. Because this specialized toe was held off the ground, the other two toes became more powerful in order to carry the animal's weight. The eyes face forward, the brain is large, the teeth are small and numerous but bear coarse serrations, interdental plates (bone that covers the inside bases of the teeth) have been lost, and the crown and root of each tooth are separated by a constriction.

Troodontids have many birdlike characteristics that indicate at the very least that birds are as closely related to dinosaurs as they are to any other group of vertebrates. These characteristics include a relatively large, bird-like brain, an elaborate system of air ducts that pass from the middle ear into many of the skull bones, and the presence of a constriction between the crown and root of any tooth (although we do not normally think of birds having teeth, they are present in some Mesozoic forms).

Ornithomimids, with the exception of *Harpimimus*, have all lost their teeth, and replaced them with a horny bill. The primitive *Garudimimus* from Mongolia has retained a vestigial inner (first) toe as most theropods have, but other ornithomimids have lost it. The limbs of ornithomimids are well adapted for running, and the claws are almost hoof-like in progressive forms.

Deinocheirus is larger than known members of the Ornithomimidae, but has specializations in its hands (e.g., nearly equal metacarpal lengths) that suggest close relationship. Some assign it to its own family (the Deinocheiridae), but others conclude that is simply a gigantic ornithomimid with no unique features.

Tyrannosaurids are a tightly knit family of theropods with incisors that are D-shaped in section, reduced forelimbs with only two functional fingers, and a suite of less significant but derived characters that are not found in other theropods.

Birds are closely related to theropods (see Gauthier and Padian, this volume), but it is worth noting that many of the specialized characters shared by these animals are so far known only in Cretaceous (not Triassic or Jurassic) theropods. The absence of more progressive forms in the earlier beds when birds first appear is a problem, but may simply reflect the inadequacies of the fossil record. Bird fossils are rare in Upper Cretaceous beds, but do indicate that a variety of diverse forms was already present.

THEROPOD BIOLOGY

There are problems in comparing theropods from different localities because of distance between geographic areas, and differences in time and/or ecosystems. Differences between North American and Asian theropods are normally attributed to geographic separation. Nevertheless, it is highly probable that at least some carnivorous dinosaur species had intercontinental distributions. Some authors already regard *Saurornitholestes* as a junior synonym of *Velociraptor*, *Saurornithoides* as the same as *Troodon*, and *Tarbosaurus* as either *Tyrannosaurus* or *Albertosaurus*. Distinct but closely related species of *Elmisaurus* have been described for both Alberta and Mongolia.

There are also problems in determining how closely related species on the same continent are. For example, two species of *Saurornithoides* have been described from successive formations in Mongolia. Aside from the fact that the Nemegt Formation is younger than the Djadokhta Formation, the depositional environments and their associated faunas are quite different, so it is reasonable to suspect that they may be different species. However, the characteristics that have been used to diagnose the two species are unlikely to hold up when more material is found. A juvenile specimen of *Saurornithoides mongoliensis* from the Djadokhta of China is more different from the type specimen of this species than the type is from *Saurornithoides junior*.

This example shows some of the most fundamental problems that we have in theropod studies. The specimens are usually not well enough preserved to give us a complete understanding of the anatomy of carnivorous species. Even if specimens are reasonably complete, English, Chinese, Russian and even Mongolian language publications usually do not adequately describe or illustrate the material. Specimens are given names, often without considering the variability that any species can have (individuals of a single species can look quite different from each other, especially if there are differences in sex or age). Species are also established by perceived differences in geographic location or differences in time. But theropods were mobile animals that probably had wide geographic ranges that encompassed numerous ecosystems, and therefore one would expect to find a species in more than one formation.

Given our poor understanding of theropod anatomy and the confusion caused by naming species on inadequate material or faulty assumptions, it is not surprising that theropod relationships are also poorly understood. The long-standing practice of assigning small species to the "Coelurosauria" and big individuals to the "Carnosauria" was both simplistic and wrong (Gauthier, 1984, 1986).

International travel is easier today than it has been, and this has given workers increased opportunities to study the specimens themselves and to make direct comparisons. Such work has also been facilitated by the wider availability of casts. There are probably more people collecting dinosaurs today than there ever has been, so new, often better specimens are available. Collecting techniques are more sophisticated, yielding better information on the paleoenvironments and paleoecosystems. Dating techniques are improving, and this is giving researchers another framework within which to evaluate theropod speciation. Although theropod classification has become quite volatile in recent years, the interrelationships of these animals are much better understood.

The increased capability of identifying theropods by only parts of their skeletons is now giving us a better handle on their distribution and ecology. The ability to identify teeth is especially promising because thousands of teeth are recovered from screen-washing microvertebrate sites. We now know that during Late Cretaceous times, dromaeosaurids, caenagnathids, elmisaurids, troodontids, ornithomimids, and tyrannosaurids were distributed across the Northern Hemisphere. At least three of these families lived within the Arctic Circle. Dromaeosaurids, caenagnathids, and troodontids lived both in the forested coastal lowlands of Asia and North America, and in the semi-arid deserts of central Asia. Ornithomimids and tyrannosaurids seemed to avoid the latter environments, although at least one specimen of *Tyrannosaurus rex* is from a drier paleoenvironment in North America.

We have a few clues to theropod behavior. The analysis of anatomical characteristics remains the best source of information on lifestyles. It is easy to imagine dromaeosaurids and tyrannosaurids eating flesh because of their teeth and claws. The dietary preferences of these animals are confirmed by the presence of shed teeth (these are not broken teeth, but loose teeth that were being replaced by new ones) mixed in with the skeletons of herbivores, and by the marks that the serrated teeth left on the bones of their prey. Although some have postulated that tyrannosaurids were scavengers rather than hunters, anatomical clues such as limb proportions suggest that they were efficient hunters and killers. This is also true of dromaeosaurids, which had developed the inner claw of the foot into an effective weapon for killing. Both tyrannosaurids and dromaeosaurids were opportunists, however, and would not have turned away from the carcasses of animals that died by other means. In Dinosaur Provincial Park, several hundred bodies from a herd of *Centrosaurus* show extensive evidence of having been eaten, although the probable cause of death was drowning or disease. A tooth-marked velociraptorine skeleton from Alberta shows that dromaeosaurids would even eat their own dead.

It is not as easy to interpret the dietary preferences of other theropods. Troodontids have many sharply pointed teeth with large serrations, but the teeth are relatively small. Binocular vision, a large brain, and specializations in the hands and feet suggest that they may have been eating smaller prey like lizards and mammals. *Oviraptor* means "egg stealer," a name earned when the first specimen was found next to a nest of herbivorous dinosaur eggs. With its toothless mouth and highly movable skull, eggs may well have formed part of its diet. But the jaws are very deep and powerful, and it may also have used them for crushing molluscs. Ornithomimids have long, slender, toothless jaws that seem poorly adapted for killing and eating other animals. Nevertheless, each jaw would have been sheathed in a horny bill, just as those of birds are today, and meat still could have formed part of its diet.

Late Cretaceous theropods are generally not found in bonebeds (in contrast with *Coelophysis* at Ghost Ranch, or the predator trap represented by the Cleveland-Lloyd Quarry in Utah). Several skeletons of *Deinonychus* were recovered from a single site in Montana, suggesting that dromaeosaurids may have hunted in packs. A very rich bed of *Archaeornithomimus* skeletons in China indicates that some ornithomimids were gregarious. Footprint sites in western Canada show that medium-sized theropods may have moved in groups of up to half a dozen animals, whereas large theropods hunted singly, in pairs, or triplets.

Nests of theropod eggs have not been identified with certainty. Eggs with embryos from Montana may be from *Troodon*, but unfortunately the embryos are too immature to confirm the identification. Nests of small (up to 7 cm), almost round eggs from China and Mongolia were probably laid by dromaeosaurids, caenagnathids, elmisaurids, and troodontids, but lack any associated skeletal material for positive identification. Nests of slightly larger but similar eggs are found in China in beds where *Archaeornithomimus* is common, so we may have ornithomimid eggs. Finally, large round eggs from central Asia are generally attributed to sauropods, but alternatively some may have been laid by tyrannosaurids.

Theropod studies have come a long way in the past decade, and we have a much better understanding of theropod anatomy, taxonomy, evolution, growth, physiology, behavior and ecology. The relationship between theropods and birds is better understood now. Nevertheless, most of our information is still based on relatively few specimens, most of which are incomplete, and most of which come from only two regions. Clearly, we still have much to learn about the carnivorous dinosaurs of the Late Cretaceous.