

Theropoda

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Theropoda (which means "beast foot") is a name proposed by O. C. Marsh in 1881 for all the meat-eating dinosaurs known at that time, including *Allosaurus*, *Compsognathus*, *MEGALOSAURUS*, and other fossils that are now recognized as TYRANNOSAURIDAE. This lineage, which includes all of the known meat-eating dinosaurs, first appeared in the Triassic and survived more than 160 million years. In fact, because birds are the direct descendants of theropods, the theropod lineage is still very successful today and has a history of 230 million years.

Theropods tend to be rare but diverse at most localities. Two exceptions are the GHOST RANCH *Coelophys* bone bed and the CLEVELAND-LLOYD QUARRY (which is dominated by *Allosaurus*). Theropods usually make up less than 20% of the fossils recovered at any site. Although rare in numbers, theropods are very diverse. About 40% of approximately 300 genera of dinosaurs currently recognized as valid are theropods, which also comprise approximately 50% of the recognized families of dinosaurs. This compares well with mammals, in which approximately half of the recognized families are carnivores, insectivores, piscivores, and/or omnivores. Because of their relative rarity but high diversity, theropod interrelationships are not as well understood as those of most taxa of herbivorous dinosaurs, and theropod taxonomy is more volatile and susceptible to change.

The clades Theropoda and Sauropodomorpha form two stem-based sister taxa that make up the Saurischia. Theropoda can be defined in a stem-based sense to include birds and all other theropods more closely related to birds than to Sauropodomorpha, such as *Plateosaurus* and *Diplodocus*.

Usually theropods were slender, long-legged, bipedal animals that were capable of moving faster than contemporary herbivorous dinosaurs (Fig. 1). Most have blade-like teeth with serrated ridges (see TOOTH SERRATIONS). The claws, especially on the hand, are usually recurved and end in sharp points. Unlike most ornithischian dinosaurs, theropods always have

hollow limb bones. They also show a tendency toward having pneumatic bones (cranial and axial) in the front part of the body (see CRANIOFACIAL AIR SINUS SYSTEMS; POSTCRANIAL PNEUMATICITY). In some theropods (OVIRAPTOROSAURIA), pneumatic bones are found as far back as the middle of the tail, and in birds most of the bones of the limbs and limb girdles can also be air-filled. None of these characters are unique to theropods, even though they are significant aspects of theropod appearance. Even the elaborate pneumatic systems shared by nonavian theropods and birds are similar to those of pterosaurs and sauropods, suggesting pneumaticity might be a primitive character that was secondarily lost in ornithischians and prosauropods. The absence of such pneumatism in *Lagosuchus* and other dinosaurian out-groups suggests that it developed convergently, however.

Unique characters that define Theropoda are found in the skull and postcranial skeleton. The lacrimal extends onto the top of the skull, there is a well-developed intramandibular joint, prominent processes (epiphyses) are found above the postzygophyses of cervical vertebrae, the prezygapophyses of caudal vertebrae are elongate, there are at least five sacral vertebrae and a transition point in the tail, the scapular blade is strap-like, the humerus is less than half the length of the femur, the manus is elongate although the outer two fingers are reduced or lost, there are distinctive ligament attachment pits on the distal extensor surfaces of the metacarpals, the penultimate phalanges of the manus are elongate, the ilium has an enlarged preacetabular region, the distal end of the pubis is expanded, there is a shelf-like ridge of bone near the head of the femur for the attachment of muscles, and the fibula is strap-like and attached to a crest on the side of the tibia.

Specimens discovered in Upper Triassic (Carnian) rocks of Argentina include some of the oldest and most primitive dinosaurs that are currently known. One of these animals, *Herrerasaurus*, was for a long time considered too primitive to be classified as either

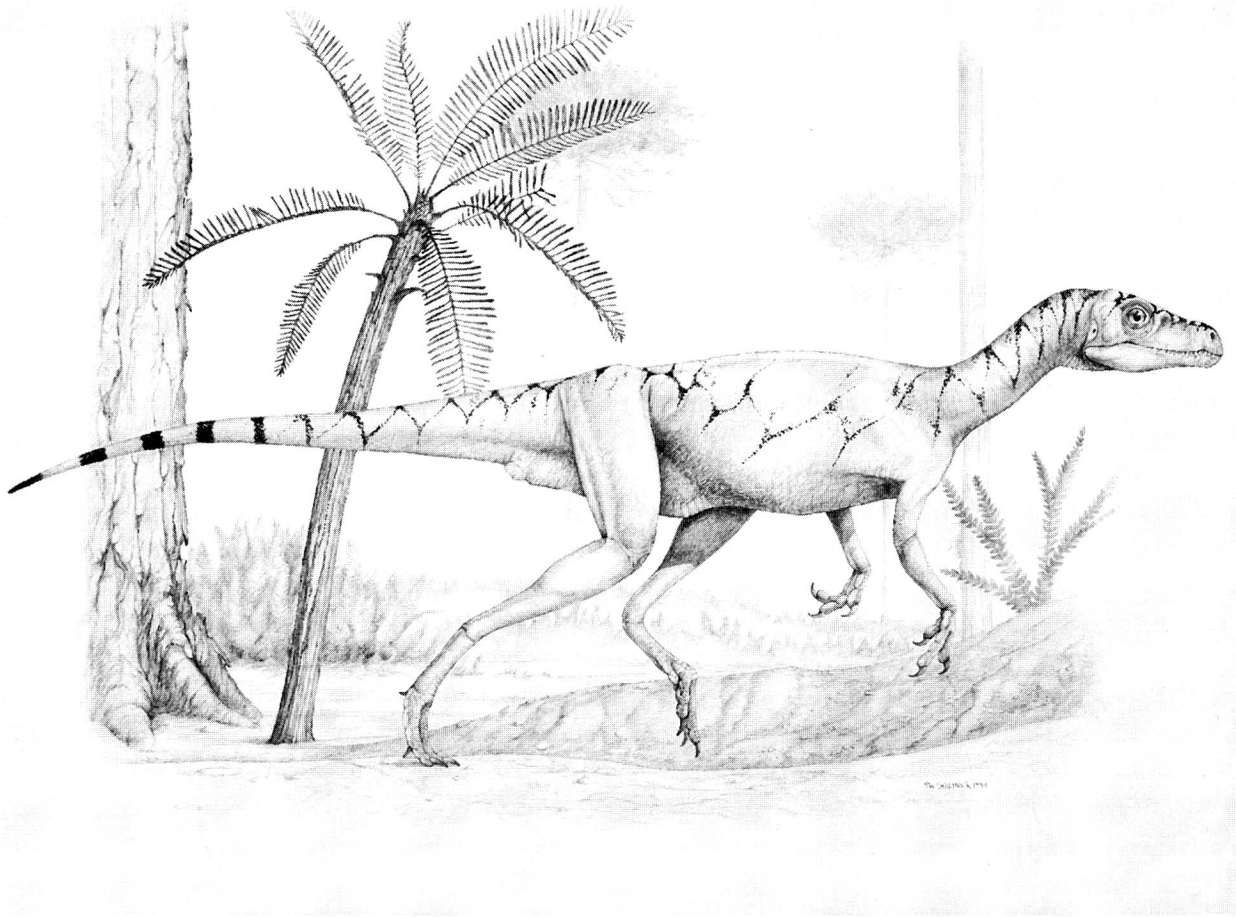


FIGURE 1 In some phylogenetic hypotheses, *Eoraptor* is thought to be near the root of the theropod clade (illustration by M. Skrepnick). See the endpapers of this book for a hypothesis of dinosaur phylogeny.

saurischian or ornithischian. However, the recovery of better specimens in recent years suggests that this animal has a moveable joint in the middle of the lower jaw (Sereno and Novas, 1993) like all but a few theropods that have secondarily fused this articulation.

Members of the HERRERASAURIDAE are also considered as basal theropods by some authors because of the elongate prezygapophyses in the distal part of the tail. However, because herrerasaurids have only two sacral vertebrae, short necks, a manus in which the third finger is longest, and a well-developed metatarsal V, some researchers consider them either as outside DINOSAURIA or as basal saurischians (Gauthier, 1986; Holtz and Padian, 1995).

Another 1-m-long animal found in the same rocks as *Herrerasaurus* is anatomically closer to what would be considered the ancestral morphotype of both sau-

rischian and ornithischian dinosaurs. *Eoraptor* lacks the intramandibular joint and probably is not a theropod.

Theropoda can be divided into two basal stem groups. CERATOSAURIA are known from Upper Triassic to Upper Jurassic rocks and may include the Cretaceous ABELISAURIDAE of South America and Africa. Characteristic forms are *Coelophysus* and *Syntarsus*. *Dilophosaurus* was a related genus that had attained a relatively large size by Early Jurassic times. These three animals have been united with *Ceratosaurus* of the Late Jurassic into the Ceratosauria, although the union is based on relatively few derived features. The second stem taxon, TETANURAE, includes two major branches known as the CARNOSAURIA and COELUROSAURIA. Distinctive tetanuran characters include the presence of a large opening (maxillary fenestra) in front of the antorbital fenestra, the presence of a fur-



FIGURE 2 *Ornithomimus* have been excavated from Maastrichtian and Campanian age sediments of the Denver, Kaiparowits, Judith River, and Horseshoe Canyon Formations of Alberta, Colorado, and Utah (illustration by D. Braginetz).

cula, and extensive contact between the first and second metacarpals. Other characters that were used to set up the Tetanurae, such as the loss of the fourth finger and the presence of an obturator process on the ischium, are not as universal as they were once thought to have been (Currie and Zhao, 1993).

The carnosaurs were once united primarily by large size, but recently it has become widely accepted that some of the largest theropods (tyrannosaurids) are in fact overgrown coelurosaurs as proposed more than 70 years ago (von Huene, 1926), whereas large Abelisaurids and *Ceratosaurus* seem to represent more primitive taxa. Even though many genera have been removed from the Carnosauria, the clade still includes well-preserved Jurassic forms such as *Allosaurus* and the Sinraptoridae (Currie and Zhao, 1993). Currently, it is not clear whether the Late Cretaceous Carcharodontosaurids are late-surviving carnosaurs (Sereno *et al.*, 1996) or abelisaurids.

Coelurosauria is made up of all taxa closer to birds than to *Allosaurus* and includes a wide diversity of mostly Cretaceous forms, including DROMAEOSAURI-

DAE, ELMISAURIDAE, ORNITHOMIMOSAURIA, OVIRAPTOROSAURIA, THERIZINOSAURIA, TROODONTIDAE, TYRANNOSAURIDAE, and AVES. Elmisauridae may be a junior synonym of Caenagnathidae, and segnosaurs are included in the Therizinosauria. Gauthier (1986) redefined the Coelurosauria to include ornithomimids and a clade he referred to as the MANIRAPTORA. The latter has been redefined by Holtz (1996) to include only all theropods closer to birds than to ornithomimids. He went on to establish the taxon Maniraptoriformes, defined as the most recent common ancestor of *Ornithomimus* and birds and all descendants of that common ancestor (Fig. 2). Maniraptoriformes are characterized by a pulley-like wrist joint that allowed the hand to be folded back against the body. This characteristic was secondarily reduced or lost in ornithomimids and tyrannosaurids. Recently discovered compsognathids (see FEATHERED DINOSAURS) have well-preserved hands that suggest that this character was more widespread among coelurosaurs. Although they dominated northern continents, new evidence suggests that nonavian coelurosaurs had spread to

the southern continents by the end of the era (Novas, 1996). Birds, the most successful theropod taxon, first appeared in the Late Jurassic and had attained a worldwide distribution before the nonavian theropods disappeared at the end of the Cretaceous.

There has been considerable speculation about which families of theropods are most closely related to birds (see BIRD ORIGINS). The most bird-like theropods are mostly Late Cretaceous forms, although this probably reflects preservational biases because small theropods are very poorly known in Jurassic rocks. Most Cretaceous theropod families clearly had long independent histories before they appear in the fossil record. Avimimids, oviraptorids, and ornithomimids were the most bird-like in appearance because of the convergent evolution of toothless, beaked skulls. Dromaeosaurids are currently considered to be the most likely avian ancestral stock, but troodontids show many bird-like characters as well. Both families are represented by well-preserved skeletons from Lower Cretaceous rocks, and Late Jurassic dromaeosaurid and troodontid teeth have also been reported.

Within the Theropoda, certain evolutionary trends can be observed over the course of their Mesozoic history. In the skull, pneumatization of the snout becomes more pronounced in advanced theropods, and accessory antorbital openings appear in front of the antorbital fenestra. By the Cretaceous, most theropods seem to have had a degree of stereoscopic vision with the eyes facing more forward than they had been in earlier forms. The brains had become relatively larger (see INTELLIGENCE; PALEONEUROLOGY), especially in the smaller theropods. The epiphyses in cervical vertebrae tended to be lost in more advanced theropod lineages as the neck took on a stronger curvature and the vertebrae became regionally more distinct from each other. The fingers tended to become more elongate in coelurosaurs, and there is a strong tendency for further reduction of the number of fingers. Many of the Jurassic theropods had three functional fingers (Fig. 3) with only a vestige of the fourth, and the fourth is completely lost in allosaurids. Tyrannosaurids independently reduced the number of fingers to two, and *Mononykus* retained only the first finger. In the hips, the distal expansion of the pubis became an enlarged boot in many of the theropod families, and the obturator foramen of the ischium opens up into a notch proximal to the obturator process. The limbs of theropods became progressively

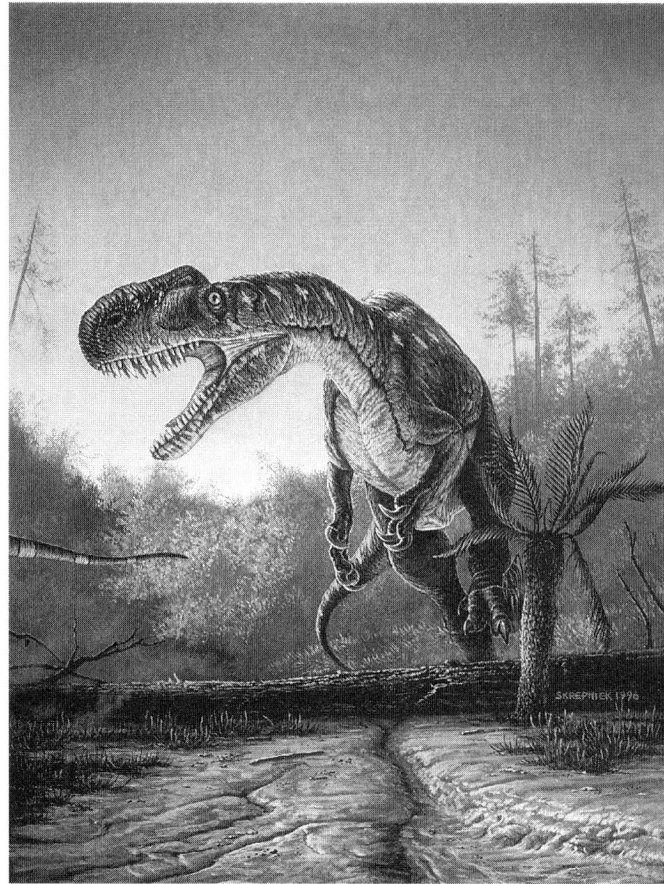


FIGURE 3 Carnosaurs like *Monolophosaurus* may have been agile predators or lumbering scavengers (illustration by M. Skrepnick).

longer over time, especially the tibia, fibula, and the metatarsals. The lengthening of leg elements and changes in proportions reflect faster running abilities. As theropods became faster, they needed more control and better shock absorption in their feet. The ascending process of the astragalus became much higher, extending as much as 25% of the length of the tibia. The lower end of the fibula and the calcaneum had a tendency to become smaller, and the latter element was lost as a distinct element in some families. Theropods had three toes (second to fourth) that functioned in support, although therizinosaurids had secondarily enlarged the first metatarsal to support an enlarged first digit, whereas dromaeosaurids and troodontids became functionally didactylous. The upper part of the third metatarsal became narrow and splint-like in most of the Late Cretaceous theropods, and metatarsals II and IV contacted each other at the top (Holtz, 1994). The lower end of the third metatarsal would have contacted the ground first when a theropod was running. Through a system

of bony contacts and elastic ligaments, the shock of impact was transferred to, and dissipated through, the adjacent metatarsals, thereby reducing the chance of foot injuries (Wilson and Currie, 1985). In elmsaurids, avimimids, and birds, the heads of the three main metatarsals fused with the distal tarsals to form a unified tarsometatarsal bone.

Theropods had a universal distribution, and specimens have been found from the North Slope of Alaska to Antarctica. Nevertheless, the ecological preferences of theropods are poorly understood, mostly because of the rarity of specimens in the vast majority of the species.

Wherever herbivorous dinosaurs are found, theropods are also recovered. The environmental extremes were the coastal lowlands of Late Cretaceous western North America (see JUDITH RIVER WEDGE) and the deserts of central Asia. The DJADOKHTA FORMATION (Upper Cretaceous) of Mongolia and equivalent beds in China represent dry, stressful environments that were suitable for only a few species of dinosaurs. Although hundreds of skeletons have been collected at these sites, the dinosaurian diversity is low, and none of the animals was more than 4 m long. Other

than a few isolated teeth and bones that appear to have been washed in from other environments or reworked from older sediments, tyrannosaurids are not found in the Djadokhta. However, small theropods, including dromaeosaurids (Fig. 4), oviraptorids, and troodontids, seem to have been relatively common in these stressed environments (Dashzeveg *et al.*, 1995).

Theropod genera were less restrained than ornithischian genera by climate and vegetation and seem to have had wider geographic ranges, as in modern Carnivora (Farlow, 1993). DINOSAUR PROVINCIAL PARK and DEVIL'S COULEE represent two synchronous but distinct habitats separated by approximately 300 km. There was a more consistent source of water at Dinosaur Park 75 million years ago that produced a well-watered, well-vegetated ecosystem. Devil's Coulee was farther from the coastline and was undoubtedly drier on at least a seasonal basis. Reflecting differences in the food resources, the composition of herbivores was different, with the hadrosaurs *Corythosaurus* and *Lambeosaurus* dominating in Dinosaur Provincial Park and *Hypacrosaurus* in Devil's Coulee. Ankylosaurs also seem to have been rarer in Dinosaur

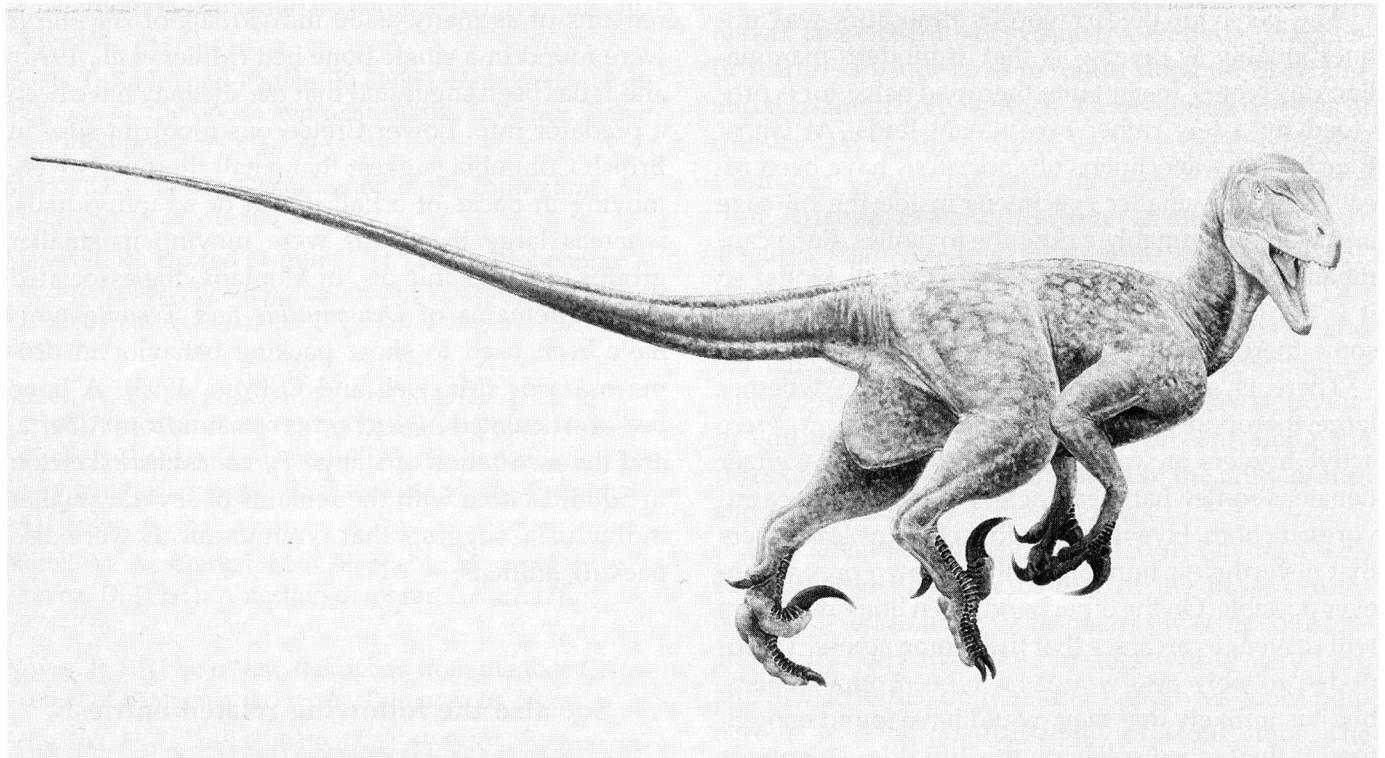


FIGURE 4 *Utahraptor* possessed, like all dromaeosaurs, a large hyperextended trenchant unguis. Such a structure must have rendered dromaeosaurs especially threatening to prey (illustration by D. Braginetz).

Provincial Park. However, evidence suggests that the carnivores of the two sites are the same taxa—*Gorgosaurus libratus*, *Saurornitholestes langstoni*, and *Troodon formosus* being the most common ones.

Isolated small theropod bones and teeth are more common than those of large theropods in most Cretaceous localities, but smaller species tend to be rarer as articulated skeletons. It is difficult to determine how large the populations of small theropods might have been in relation to prey species because nondinosaurian animals would have comprised a large part of their diets. Ornithomimids may also have been omnivorous and are indeed very common at some sites. Immature large theropods probably competed with small species of theropods, which could explain the virtual absence of small theropods at most known dinosaur localities of the Jurassic. However, it is also possible that in some large theropod species, the juveniles associated with mature animals in packs or family groups, and therefore would not have been competing directly with the small species of theropods. There is some evidence to suggest that tyrannosaurids maintained family groups, so it is not surprising that the greatest diversity of small theropods is found in paleoenvironments where tyrannosaurids were the large predators.

The behavior of carnivorous dinosaurs was unquestionably as diverse as that of modern mammalian carnivores. Insight into theropod behavior is provided by a few rather exceptional finds. At Ghost Ranch, larger specimens of *Coelophysis* have been recovered with smaller specimens inside the rib cage and were presumably eating the juveniles. Such cannibalism is widespread in animals of all kinds, so it is not surprising that it was practiced by at least some theropods.

There is some controversy concerning whether large theropods, especially *Tyrannosaurus rex*, were active hunters or scavengers. The hunter/scavenger debate is somewhat meaningless because most carnivores are both. Hyenas are highly efficient scavengers that nevertheless hunt and kill their own prey whenever possible. On the other hand, even lions and tigers will scavenge carcasses that they come across. Theropods probably also would have been opportunists, but it is unlikely that they would have found enough food if they relied solely on this lifestyle. Theropods almost universally have limb proportions that exceed

those of the assumed prey animals and were presumably faster animals. This relationship would not have been maintained if the big theropods were all scavengers. There is at least one example of a theropod (*Velociraptor*) that attacked a living herbivore (*Protoceratops*) in Cretaceous Mongolia (see DROMAEOSAURIDAE).

Evidence of nesting behavior is known for *Oviraptor* (Norell *et al.*, 1995; Dong and Currie, 1996) and *Troodon* (Varricchio *et al.*, 1996), thanks to the fortuitous recovery of adult skeletons associated with nests of eggs.

Full and partial skeletons of at least 1000 individuals of *Coelophysis* at Ghost Ranch in New Mexico (Schwartz and Gillette, 1994) strongly suggest that this dinosaur was gregarious. Such large accumulations of theropods do not appear to have been uncommon during Late Triassic and Early Jurassic times. There is a similar accumulation of skeletons in Zimbabwe of the closely related *Syntarsus*. A Lower Jurassic trackway site at Holyoke (Massachusetts) shows evidence of 20 theropods moving as a group (see CONNECTICUT RIVER VALLEY). Possibly, these theropods formed large packs only for short periods of time for breeding or migration. In Upper Jurassic rocks of the Cleveland–Lloyd Quarry in Utah, the remains of as many as 50 individuals of *Allosaurus* were found in a single bone bed (Miller *et al.*, 1996), and it has been suggested that the site may have been a predator trap. Lower Cretaceous footprint sites in British Columbia suggest that small theropods were moving in packs of a half dozen or so individuals, whereas large theropods were moving in smaller groups of 2 or 3 animals. In Montana, the associated skeletal remains of *Deinonychus* and *Tenontosaurus* have been used to show packing behavior in dromaeosaurids (Maxwell and Ostrom, 1995). A bone bed of articulated *Albertosaurus* remains from Alberta, and the association of a large *Tyrannosaurus* skeleton in South Dakota with the remains of several smaller individuals, suggests that tyrannosaurids were also packing animals.

See also the following related entries:

CERATOSAURIA • HERRERASAURIDAE • SAURISCHIA
• SAUROPODOMORPHA • TETANURAE

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