Velociraptor

Velociraptor (/vɪˈlɒsɪræptər/; meaning "swift seizer" in Latin)[1] is a genus of dromaeosaurid theropod dinosaur that lived approximately 75 to 71 million years ago during the latter part of the Cretaceous Period.[2] Two species are currently recognized, although others have been assigned in the past. The type species is *V. mongoliensis*; fossils of this species have been discovered in Mongolia. A second species, *V. osmolskae*, was named in 2008 for skull material from Inner Mongolia, China.

Smaller than other dromaeosaurids like *Deinonychus* and *Achillobator*, *Velociraptor* nevertheless shared many of the same anatomical features. It was a bipedal, feathered carnivore with a long tail and an enlarged sickle-shaped claw on each hindfoot, which is thought to have been used to tackle and tear into prey. *Velociraptor* can be distinguished from other dromaeosaurids by its long and low skull, with an upturned snout.

Velociraptor (commonly shortened to "**raptor**") is one of the dinosaur genera most familiar to the general public due to its prominent role in the *Jurassic Park* motion picture series. In real life, however, *Velociraptor* was roughly the size of a turkey, considerably smaller than the approximately 2 m ($6\frac{1}{2}$ ft) tall and 80 kg (180 lb) reptiles seen in the films (which were based on members of the related genus *Deinonychus*). Today, *Velociraptor* is well known to paleontologists, with over a dozen described fossil skeletons, the most of any dromaeosaurid. One particularly famous specimen preserves a *Velociraptor* locked in combat with a *Protoceratops*.

Contents

Velociraptor
Temporal range: Late Cretaceous (Campanian),

Mounted *V. mongoliensis* cast at Dinosaur Journey Museum
Scientific classification
Kingdom: Animalia
Phylum: Chordata
Clade: Dinosauria
Clade: Saurischia
Clade: Theropoda
Family: †Dromaeosauridae
Clade: †Eudromaeosauria
Subfamily: †Velociraptorinae
Genus: †*Velociraptor* Osborn, 1924
Type species
†***Velociraptor mongoliensis*** Osborn, 1924
Other species
▪ †***V. osmolskae*** Godefroit *et al.*, 2008

History of discovery

The type skull of *V. mongoliensis* on display at the American Museum of Natural History

During an American Museum of Natural History expedition to the Outer Mongolian Gobi Desert on 11 August 1923, Peter Kaisen discovered the first *Velociraptor* fossil known to science: a crushed but complete skull, associated with one of the raptorial second toe claws (AMNH 6515). In 1924, museum president Henry Fairfield Osborn designated the skull and claw (which he assumed to come from the hand) as the type specimen of his new genus, *Velociraptor*. This name is derived from the Latin words *velox* ('swift') and *raptor* ('robber' or 'plunderer') and refers to the animal's cursorial nature and carnivorous diet. Osborn named the type species *V. mongoliensis* after its country of origin.[1] Earlier that year, Osborn had mentioned the animal in a popular press article, under the name "Ovoraptor djadochtari" (not to be confused with the similarly named *Oviraptor*).[3] However, because the name "Ovoraptor" was not published in a scientific journal or accompanied by a formal description, the name *Velociraptor* retains priority.[4]

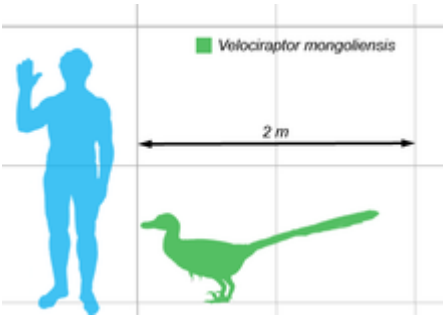
While North American teams were shut out of communist Mongolia during the Cold War, expeditions by Soviet and Polish scientists, in collaboration with Mongolian colleagues, recovered several more specimens of *Velociraptor*. The most famous is part of the "Fighting Dinosaurs" specimen (GIN 100/25), discovered by a Polish-Mongolian team in 1971. The fossil preserves a *Velociraptor* in battle against a *Protoceratops*.[5][6][7] It is considered a national treasure of Mongolia, and in 2000 it was loaned to the American Museum of Natural History in New York City for a temporary exhibition.[8]

Specimen IGM 100/982

Between 1988 and 1990, a joint Chinese-Canadian team discovered *Velociraptor* remains in northern China.[9] American scientists returned to Mongolia in 1990, and a joint Mongolian-American expedition to the Gobi, led by the American Museum of Natural History and the Mongolian Academy of Sciences, turned up several well-preserved skeletons.[10][11] One such specimen, IGM 100/980, was nicknamed "Ichabodcraniosaurus" by Norell's team because the fairly complete specimen was found without its skull (an allusion to the Washington Irving character Ichabod Crane).[12] While Norell and Makovicky provisionally considered it a specimen of *Velociraptor mongoliensis*,[10] it was named as a new species *Shri devi* in 2021.[13]

Maxillae and a lacrimal (the main tooth-bearing bones of the upper jaw, and the bone that forms the anterior margin of the eye socket, respectively) recovered in 1999 by the Sino-Belgian Dinosaur Expeditions were found to pertain to *Velociraptor*, but not to the type species *V. mongoliensis*. Pascal Godefroit and colleagues named these bones *V. osmolskae* (for Polish paleontologist Halszka Osmólska) in 2008.[2]

Description



V. mongoliensis compared in size to a human

Velociraptor was a mid-sized dromaeosaurid, with adults measuring up to 2.07 m (6 ft 9½ in) long, 0.5 m (1 ft 7½ in) high at the hip, and weighing up to 15 kg (33 lb), though there is a higher estimate of 19.7 kg (43½ lb),[14][15] and an even higher estimate suggesting a length of 2.5 m (8.2 ft) and a body mass of 25 kg (55 lb).[16] The skull, which grew up to 25 cm (10 in) long, was uniquely up-curved, concave on the upper surface and convex on the lower. The jaws were lined with 26–28 widely spaced teeth on each side, each more strongly serrated on the back edge than the front.[1][17]

Velociraptor, like other dromaeosaurids, had a large manus ('hand') with three strongly curved claws, which were similar in construction and flexibility to the wing bones of modern birds. The second digit was the longest of the three digits present, while the first was shortest. The structure of the carpal (wrist) bones prevented pronation of the wrist and forced the 'hands' to be held with the palmar surface facing inward (medially), not downward.[18] The first digit of the foot, as in other theropods, was a small dewclaw. However, whereas most theropods had feet with three digits contacting the ground, dromaeosaurids like *Velociraptor* walked on only their third and fourth digits. The second digit, for which *Velociraptor* is most famous, was highly modified and held retracted off the ground. It bore a relatively large, sickle-shaped claw, typical of dromaeosaurid and troodontid dinosaurs. This enlarged claw, which could grow to over 6.5 cm (2½ in) long around its outer edge, was most likely a predatory device used to tear into or restrain struggling prey.[10][19]


Skeletal restoration of *V. mongoliensis*

As in other dromaeosaurs, *Velociraptor* tails had long bony projections (prezygapophyses) on the upper surfaces of the vertebrae, as well as ossified tendons underneath. The prezygapophyses began on the tenth tail (caudal) vertebra and extended forward to brace four to ten additional vertebrae, depending on position in the tail. These were once thought to fully stiffen the tail, forcing the entire tail to act as a single rod-like unit. However, at least one specimen has preserved a series of intact tail vertebrae curved sideways into an *S*-shape, suggesting that there was considerably more horizontal flexibility than once thought.[10][5]

Feathers

Fossils of dromaeosaurids more primitive than *Velociraptor* are known to have had feathers covering their bodies and fully developed feathered wings.[20] The fact that the ancestors of *Velociraptor* were feathered and possibly capable of flight had long suggested to paleontologists that *Velociraptor* bore feathers as well, since even flightless birds today retain most of their feathers. In September 2007, researchers found quill knobs on the forearm of a *Velociraptor* found in Mongolia.[21] These bumps on bird wing bones show where feathers anchor, and their presence on *Velociraptor* indicate it too had feathers. According to paleontologist Alan Turner,

> A lack of quill knobs does not necessarily mean that a dinosaur did not have feathers. Finding quill knobs on *Velociraptor*, though, means that it definitely had feathers. This is something we'd long suspected, but no one had been able to prove.[22]

Co-author Mark Norell, Curator-in-Charge of fossil reptiles, amphibians and birds at the American Museum of Natural History, also weighed in on the discovery, saying:

> The more that we learn about these animals the more we find that there is basically no difference between birds and their closely related dinosaur ancestors like velociraptor. Both have wishbones, brooded their nests, possess hollow bones, and were covered in feathers. If animals like velociraptor were alive today our first impression would be that they were just very unusual looking birds.[22]

V. mongoliensis, showing large wing feathers as evidenced by the discovery of quill knobs

According to Turner and co-authors Norell and Peter Makovicky, quill knobs are not found in all prehistoric birds, and their absence does not mean that an animal was not feathered, flamingos, for example, have no quill knobs. However, their presence confirms that *Velociraptor* bore modern-style wing feathers, with a rachis and vane formed by barbs. The forearm specimen on which the quill knobs were found (specimen number IGM 100/981) represents an animal 1.5 meters (4 feet 11 inches) in length and 15 kilograms (33 pounds) in weight. Based on the spacing of the six preserved knobs in this specimen, the authors suggested that *Velociraptor* bore 14 secondaries (wing feathers stemming from the forearm), compared with 12 or more in *Archaeopteryx*, 18 in *Microraptor*, and 10 in *Rahonavis*. This type of variation in the number of wing feathers between closely related species, the authors asserted, is to be expected, given similar variation among modern birds.[21]

Turner and colleagues interpreted the presence of feathers on *Velociraptor* as evidence against the idea that the larger, flightless maniraptorans lost their feathers secondarily due to larger body size. Furthermore, they noted that quill knobs are almost never found in flightless bird species today, and that their presence in *Velociraptor* (presumed to have been flightless due to its relatively large size and short forelimbs) is evidence that the ancestors of dromaeosaurids could fly, making *Velociraptor* and other large members of this family secondarily flightless, though it is possible the large wing feathers inferred in the ancestors of *Velociraptor* had a purpose other than flight. The feathers of the flightless *Velociraptor* may have been used for display, for covering their nests while brooding, or for added speed and thrust when running up inclined slopes.[21]

Classification

Mounted *V. mongoliensis* cast at Wyoming Dinosaur Center

Velociraptor is a member of the group Eudromaeosauria, a derived sub-group of the larger family Dromaeosauridae. It is often placed within its own subfamily, Velociraptorinae. In phylogenetic taxonomy, Velociraptorinae is usually defined as "all dromaeosaurs more closely related to *Velociraptor* than to *Dromaeosaurus*." However, dromaeosaurid classification is highly variable. Originally, the subfamily Velociraptorinae was erected solely to contain *Velociraptor*.[5] Other analyses have often included other genera, usually *Deinonychus* and *Saurornitholestes*,[23] and more recently *Tsaagan*.[24] Several studies published during the 2010s, including expanded versions of the analyses that found support for Velociraptorinae, have failed to resolve it as a distinct group, but rather have suggested it is a paraphyletic grade which gave rise to the Dromaeosaurinae.[25][26]

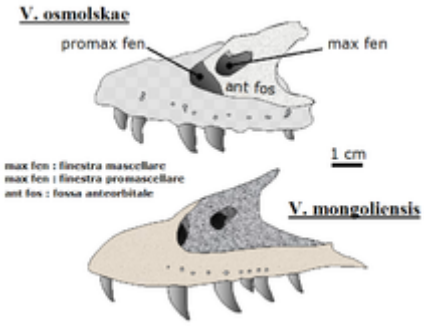
In the past, other dromaeosaurid species, including *Deinonychus antirrhopus* and *Saurornitholestes langstoni*, have sometimes been classified in the genus *Velociraptor*. Since *Velociraptor* was the first to be named, these species were renamed *Velociraptor antirrhopus* and *V. langstoni*.[14] As of 2008, the only currently recognized species of *Velociraptor* are *V. mongoliensis*[17][18][27] and *V. osmolskae*.[2] However, several studies have found "*V.*" *osmolskae* to be distantly related to *V. mongoliensis*.[28][29]

A 2020 thesis by Mark Powers considered the specimen MPC-D 100/982 to represent a third species,[30] although his conclusions have not yet been recognized by other researchers.

When first described in 1924, *Velociraptor* was placed in the family Megalosauridae, as was the case with most carnivorous dinosaurs at the time (Megalosauridae, like *Megalosaurus*, functioned as a sort of 'wastebin' taxon, where many unrelated species were grouped together).[1] As dinosaur discoveries multiplied, *Velociraptor* was later recognized as a dromaeosaurid. All dromaeosaurids have also been referred to the family Archaeopterygidae by at least one author (which would, in effect, make *Velociraptor* a flightless bird).[18]

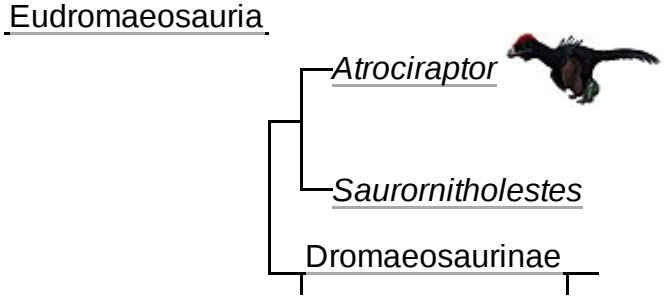
Size of *Velociraptor* (2) compared with other dromaeosaurs

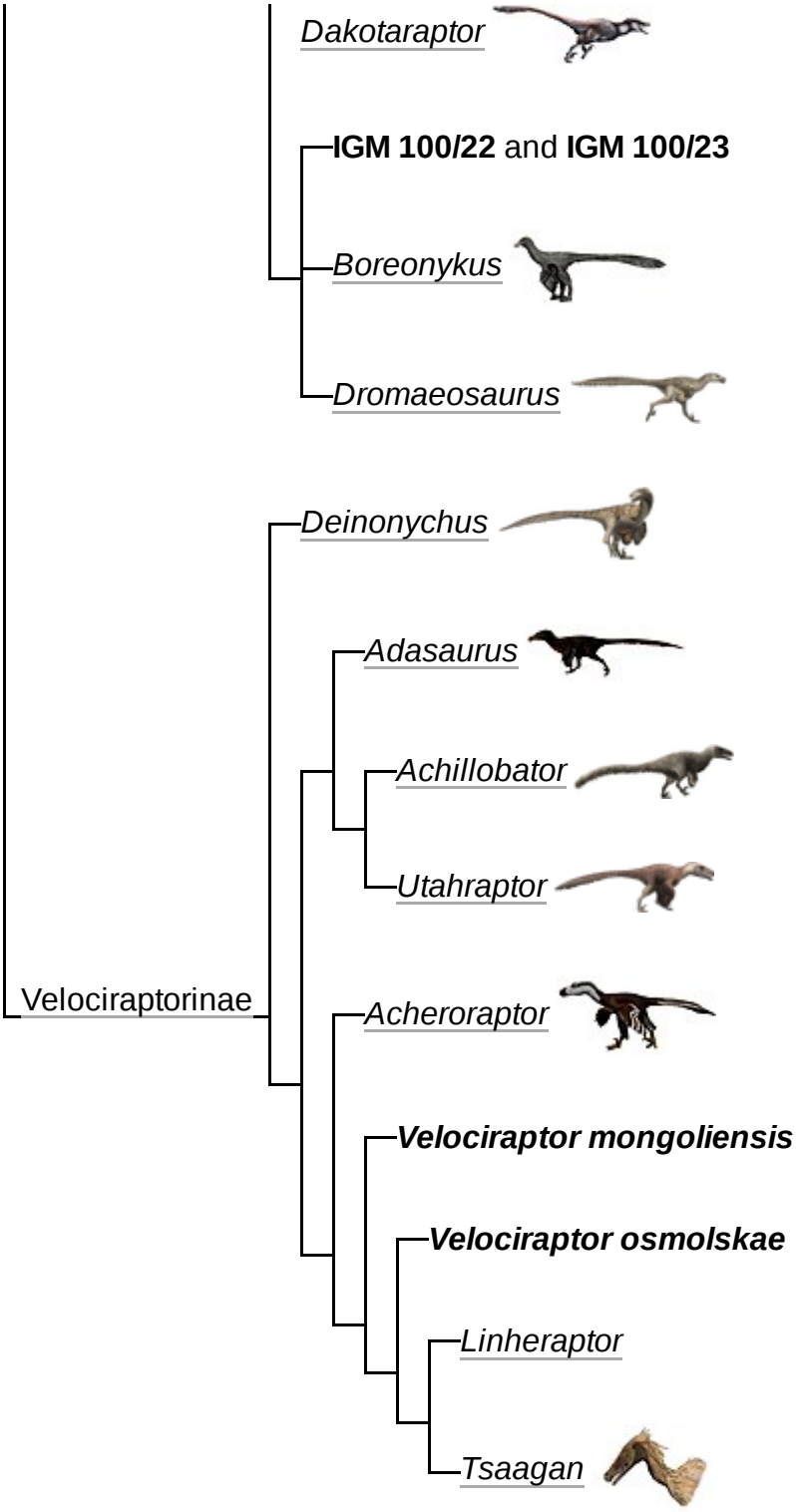
Below are the results for the Eudromaeosauria phylogeny based on the phylogenetic analysis conducted by Currie and Evans in 2019. Surprisingly enough, heavy built animals such as *Achillobator* and *Utahraptor* were recovered in the Velociraptorinae:[28]



Maxillae of *V. osmolskae* and *V. mongoliensis* compared

Diagram of the *V. mongoliensis* type skull and the associated claw from 1924





Paleobiology

Predatory behavior

The "Fighting Dinosaurs" specimen, found in 1971, preserves a *Velociraptor mongoliensis* and *Protoceratops andrewsi* in combat and provides direct evidence of predatory behavior. When originally reported, it was hypothesized that the two animals drowned.[7] However, as the animals were preserved in ancient sand dune deposits, it is now thought that the animals were buried in sand, either from a collapsing dune or in a sandstorm. Burial must have been extremely fast, judging from the lifelike poses in which the

animals were preserved. Parts of the *Protoceratops* are missing, which has been seen as evidence of scavenging by other animals.[31] Comparisons between the scleral rings of *Velociraptor*, *Protoceratops*, and modern birds and reptiles indicates that *Velociraptor* may have been nocturnal, while *Protoceratops* may have been cathemeral, active throughout the day during short intervals, suggesting that the fight may have occurred at twilight or during low-light conditions.[32]

The "Fighting Dinosaurs" specimen of *V. mongoliensis* and *Protoceratops andrewsi*

The distinctive claw, on the second digit of dromaeosaurids, has traditionally been depicted as a slashing weapon; its assumed use being to cut and disembowel prey.[33] In the "Fighting Dinosaurs" specimen, the *Velociraptor* lies underneath, with one of its sickle claws apparently embedded in the throat of its prey, while the beak of *Protoceratops* is clamped down upon the right forelimb of its attacker. This suggests *Velociraptor* may have used its sickle claw to pierce vital organs of the throat, such as the jugular vein, carotid artery, or trachea (windpipe), rather than slashing the abdomen. The inside edge of the claw was rounded and not unusually sharp, which may have precluded any sort of cutting or slashing action, although only the bony core of the claw is preserved. The thick abdominal wall of skin and muscle of large prey species would have been difficult to slash without a specialized cutting surface.[31] The slashing hypothesis was tested during a 2005 BBC documentary, *The Truth About Killer Dinosaurs*. The producers of the program created an artificial *Velociraptor* leg with a sickle claw and used a pork belly to simulate the dinosaur's prey. Though the sickle claw did penetrate the abdominal wall, it was unable to tear it open, indicating that the claw was not used to disembowel prey.[34]

V. mongoliensis restraining an oviraptorosaur with its sickle claws

Remains of *Deinonychus*, a closely related dromaeosaurid, have commonly been found in aggregations of several individuals. *Deinonychus* has also been found in association with the large ornithopod *Tenontosaurus*, which has been cited as evidence of cooperative (pack) hunting.[35][36] However, the only solid evidence for social behavior of any kind among dromaeosaurids comes from a Chinese trackway which shows six individuals of a large species moving as a group.[37] Although many isolated fossils of *Velociraptor* have been found in Mongolia, none were closely associated with other individuals.[27] Therefore, while *Velociraptor* is commonly depicted as a pack hunter, as in *Jurassic Park*, there is only limited fossil evidence to support this theory for dromaeosaurids in general and none specific to *Velociraptor* itself. Dromeosaur footprints in China suggest that a few other raptor genera may have hunted in packs, but there have been no conclusive examples of pack behavior found.[38][39]

In 2011, Denver Fowler and colleagues suggested a new method by which dromaeosaurs like *Velociraptor* and similar dromaeosaurs may have captured and restrained prey. This model, known as the "raptor prey restraint" (RPR) model of predation, proposes that dromaeosaurs killed their prey in a manner very similar to extant accipitrid birds of prey: by leaping onto their quarry, pinning it under their body weight, and gripping it tightly with the large, sickle-shaped claws. These researchers proposed that, like accipitrids, the dromaeosaur would then begin to feed on the animal while it was still alive, and prey death would eventually result from blood loss and organ failure. This proposal is based primarily on comparisons between the morphology and proportions of the feet and legs of dromaeosaurs to several groups of extant birds of prey with known predatory behaviors. Fowler found that the feet and legs of dromaeosaurs most closely resemble those of eagles and hawks, especially in terms of having an enlarged second claw and a similar range of grasping motion. The short metatarsus and foot strength, however, would have been more

similar to that of owls. The RPR method of predation would be consistent with other aspects of *Velociraptor*'s anatomy, such as their unusual jaw and arm morphology. The arms, which could exert a lot of force but were likely covered in long feathers, may have been used as flapping stabilizers for balance while atop a struggling prey animal, along with the stiff counterbalancing tail. The jaws, thought by Fowler and colleagues to be comparatively weak, would have been useful for row saw motion bites like the modern day Komodo dragon, which also has a weak bite, to finish off its prey if the kicks weren't powerful enough. These predatory adaptations working together may also have implications for the origin of flapping in paravians.[19]

Skull of the *V. mongoliensis* "Fighting Dinosaurs" specimen

Examinations of the endocranium of *Velociraptor* indicate that it was able to detect and hear a wide range of sound frequencies (2,368–3,965 Hz) and could track prey with ease as a result. The endocranium examinations also further cemented the theory that the dromaeosaur was an agile, swift predator. Fossil evidence suggesting *Velociraptor* scavenged also indicates that it was an opportunistic and actively predatory animal, feeding on carrion during times of drought or famine, if in poor health, or depending on the animal's age.[40]

Scavenging behavior

In 2010, Hone and colleagues published a paper on their 2008 discovery of shed teeth of what they believed to be a *Velociraptor* near a tooth-marked jaw bone of what they believed to be a *Protoceratops* in the Bayan Mandahu Formation. The authors concluded that the find represented "late-stage carcass consumption by *Velociraptor*" as the predator would have eaten other parts of a freshly killed *Protoceratops* before biting in the jaw area.[41] The evidence was seen as supporting the inference from the "Fighting Dinosaurs" fossil that *Protoceratops* was part of the diet of *Velociraptor*.[42] In 2012, Hone and colleagues published a paper that described a *Velociraptor* specimen with a long bone of an azhdarchid pterosaur in its gut. This was interpreted as showing scavenging behaviour.[43]

Metabolism

Velociraptor was warm-blooded to some degree, as it required a significant amount of energy to hunt. Modern animals that possess feathery or furry coats, like *Velociraptor* did, tend to be warm-blooded, since these coverings function as insulation. However, bone growth rates in dromaeosaurids and some early birds suggest a more moderate metabolism, compared with most modern warm-blooded mammals and birds. The kiwi is similar to dromaeosaurids in anatomy, feather type, bone structure and even the narrow anatomy of the nasal passages (usually a key indicator of metabolism). The kiwi is a highly active, if specialized, flightless bird, with a stable body temperature and a fairly low resting metabolic rate, making it a good model for the metabolism of primitive birds and dromaeosaurids.[18]

Pathology

One *Velociraptor mongoliensis* skull bears two parallel rows of small punctures that match the spacing and size of *Velociraptor* teeth. Scientists believe that the wound was likely inflicted by another *Velociraptor* during a fight. Further, because the fossil bone shows no sign of healing near the bite wounds, the injury probably killed it.[44] Another specimen, found with the bones of an azhdarchid pterosaur within its

stomach cavity, was carrying or recovering from an injury sustained to its ribs. From evidence on the pterosaur bones, which were devoid of pitting or deformations from digestion, the *Velociraptor* died shortly after, possibly from the earlier injury.[43]

Paleoecology

V. mongoliensis in environment

All known specimens of *Velociraptor mongoliensis* were discovered in the Djadochta Formation (also spelled Djadokhta), in the Mongolian province of Ömnögovi. Species of *Velociraptor* have also been reported from the slightly younger Barun Goyot Formation of Mongolia,[45] though these are indeterminate and may belong to a related genus instead.[46] These geologic formations are estimated to date back to the Campanian stage (between 83 and 70 million years ago[47]) of the Late Cretaceous Epoch.[48]

V. mongoliensis has been found at many of the most famous and prolific Djadochta localities. The type specimen was discovered at the Flaming Cliffs site (also known as Bayn Dzak and Shabarakh Usu),[1] while the "Fighting Dinosaurs" were found at the Tugrig locality (also known as Tugrugeen Shireh).[7] The well-known Barun Goyot localities of Khulsan and Khermeen Tsav have also produced remains which may belong to *Velociraptor* or a related genus.[49] Teeth and partial remains attributed to juvenile *V. mongoliensis* have also been reported from the Bayan Mandahu Formation, a prolific site in Inner Mongolia, China that is contemporaneous with the Djadochta Formation.[9] However, these fossils had not been prepared or studied as of 2008.[2] A partial adult skull from the Bayan Mandahu Formation has been assigned to a distinct species, *Velociraptor osmolskae*.[2]

All of the fossil sites that have yielded *Velociraptor* remains preserve an arid environment with fields of sand dunes and only intermittent streams, although the younger Barun Goyot environment seems to have been slightly wetter than the older Djadochta.[48] The posture of some complete fossils, as well as the mode of preservation most show within structureless sandstone deposits, may show that a number of specimens were buried alive during sandstorm events common to the three environments.[2]

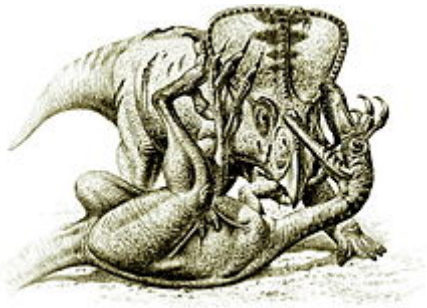
Undescribed *V. mongoliensis* skull

Many of the same genera were present across these formations, though they varied at the species level. For example, the Djadochta was inhabited by *Velociraptor mongoliensis*, *Protoceratops andrewsi*, and *Pinacosaurus grangeri*, while the Bayan Mandahu was home to *Velociraptor osmolskae*, *Protoceratops hellenikorhinus*, and *Pinacosaurus mephistocephalus*. These differences in species composition may be due a natural barrier separating the two formations, which are relatively close to each other geographically.[2] However, given the lack of any known barrier which would cause the specific faunal compositions found in these areas, it is more likely that those differences indicate a slight time difference.[46]

Other dinosaurs known from the same locality as *V. mongoliensis* include the troodontid *Saurornithoides mongoliensis*, the oviraptorid *Oviraptor philoceratops*, and the dromaeosaurid *Mahakala omnogovae*. *V. osmolskae* lived alongside the ceratopsian species *Magnirostris dodsoni*, as well as the oviraptorid *Machairasaurus leptonychus* and the dromaeosaurid *Linheraptor exquisitus*.[46]

Cultural significance

Velociraptor is commonly perceived as a vicious and cunning killer thanks to their portrayal in the 1990 novel *Jurassic Park* by Michael Crichton and its 1993 film adaptation, directed by Steven Spielberg. The "raptors" portrayed in *Jurassic Park* were actually modeled after the closely related dromaeosaurid *Deinonychus*. Paleontologists in both the novel and film excavate a skeleton in Montana, far from the central Asian range of *Velociraptor* but characteristic of the *Deinonychus* range.[50] Crichton met with the discoverer of *Deinonychus*, John Ostrom, several times at Yale University to discuss details of the animal's possible range of behaviors and appearance. Crichton at one point apologetically told Ostrom that he had decided to use the name *Velociraptor* in place of *Deinonychus* because the former name was "more dramatic." According to Ostrom, Crichton stated that the *Velociraptor* of the novel was based on *Deinonychus* in almost every detail, and that only the name had been changed. The *Jurassic Park* film-makers also requested all of Ostrom's published papers on *Deinonychus* during production.[51] They portrayed the animals with the size, proportions, and snout shape of *Deinonychus* rather than *Velociraptor*.[52][53]



2003 restoration by Raúl Martín showing a featherless *Velociraptor* battling *Protoceratops*. The creature continues to be rendered in this outdated way in many popular images.

Production on *Jurassic Park* began before the discovery of the large dromaeosaurid *Utahraptor* was made public in 1991, but as Jody Duncan wrote about this discovery: "Later, after we had designed and built the raptor, there was a discovery of a raptor skeleton in Utah, which they labeled 'super-slasher.' They had uncovered the largest Velociraptor to date and it measured five-and-a-half-feet tall, just like ours. So we designed it, we built it, and then they discovered it. That still boggles my mind."[52] Spielberg was particularly pleased with the discovery of the *Utahraptor* because of the boost it gave to the velociraptors in his film. Spielberg's name was briefly considered for naming of the new dinosaur.[54] In reality, *Velociraptor*, like many other maniraptoran theropods, was covered in feathers.[21]

See also

- Dinosaurs portal
- Timeline of dromaeosaurid research
- dromaeosaurid
- Velociraptorinae

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