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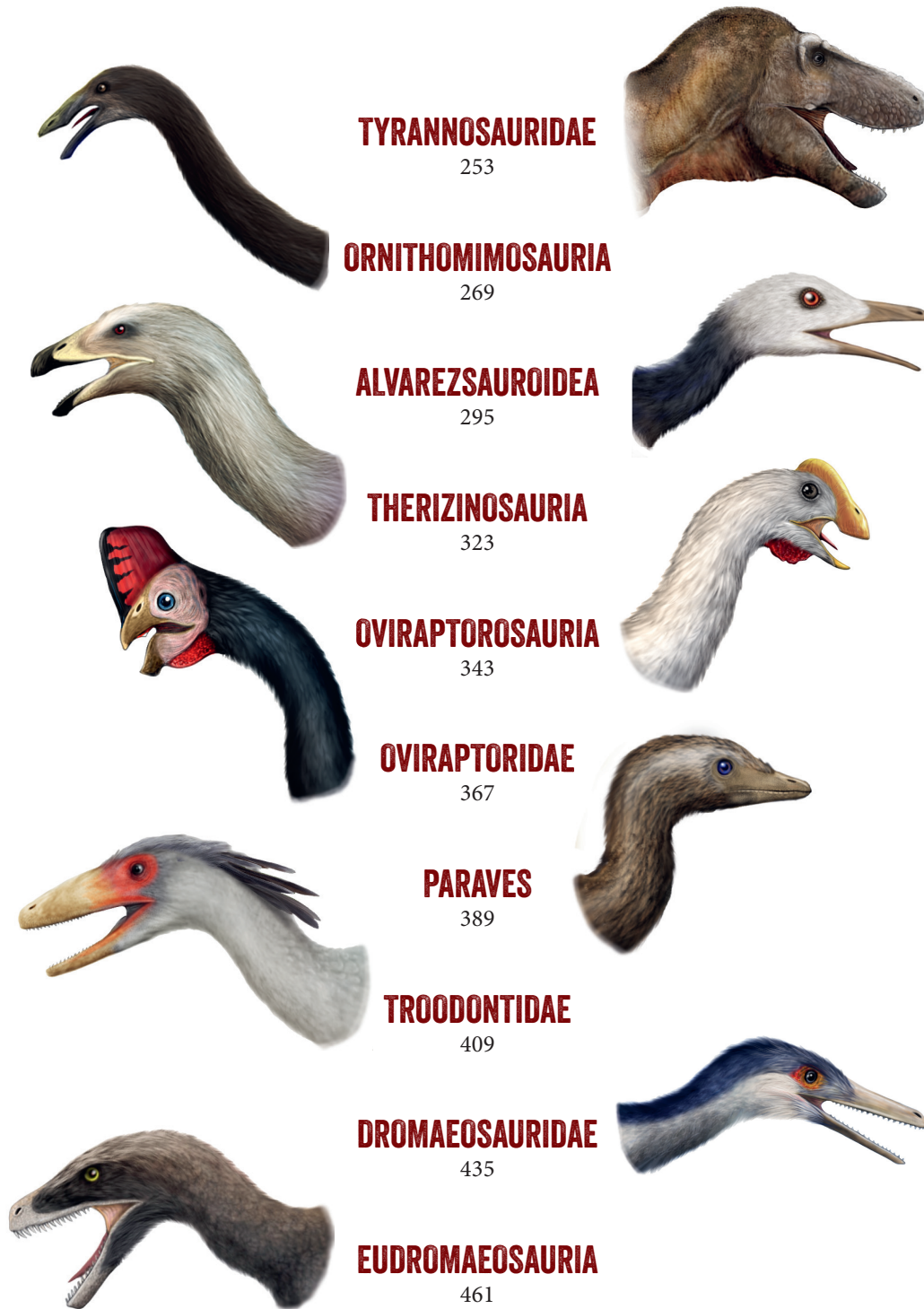
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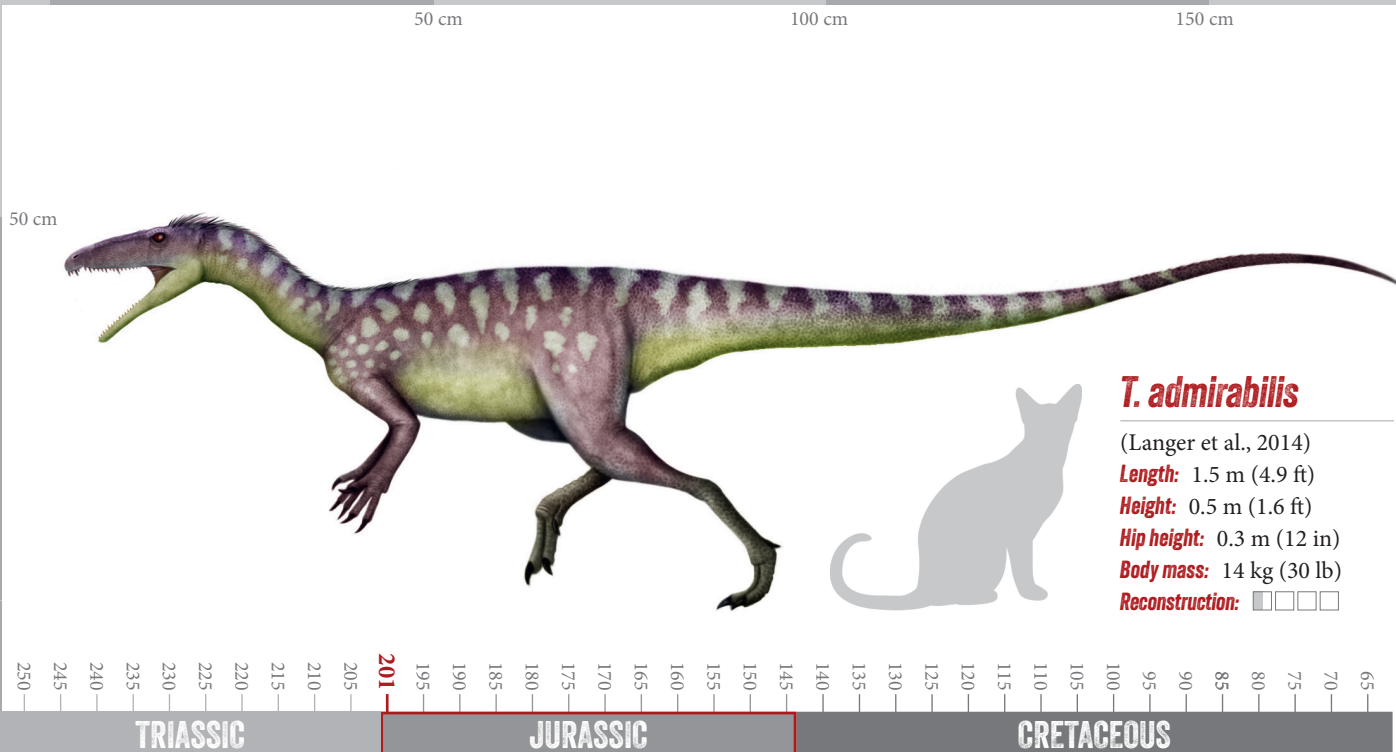
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TACHIRAPTOR



Tachiraptor admirabilis (meaning “admirable thief of Táchira”) is one of the few dinosaurs known from northern South America.

The fossil remains of *Tachiraptor* are sparse. The holotype (IVIC-P-2867) is a nearly complete lone tibia. A second specimen (IVIC-P-2868) consists of an upper portion of the ischium. The second specimen is assumed to belong to the same genus as the first, due to both its size and where it was found. Various theropod teeth had previously been recovered from the same area and could potentially belong to *Tachiraptor* as well.

Despite the fragmentary nature of the remains, a unique combination of traits suggests an interesting phylogenetic placement for *Tachiraptor* as a “stem-averostran,” part of the stem branch that leads directly to **Averostra** (the group that encompasses all of the theropods from the Middle Jurassic onward).

At the time of the initial description, there were no other known “stem-averostrans.” Thus, the description of *Tachiraptor* reduced the averostrans’ “ghost lineage” by approximately 25 million years. Later, in 2020, a reevaluation of *Sarcosaurus* would place it as a sister taxon of *Tachiraptor* (Ezcurra et al., 2020).

Tachiraptor also added to the greater knowledge of dinosaur evolution by implying that the environment of Pangea’s equatorial zone played a significant role in the diversification of early dinosaur species. Hence, future efforts to further expand this part of the dinosaur family tree might best be focused in this geographic area.

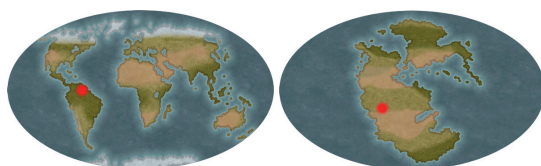
The generic name *Tachiraptor* is derived from the state of Táchira, where the holotype was discovered, combined with the Latin word “raptor” (meaning “thief”). The specific name *admirabilis* is in reference to the Admirable Campaign of 1813, a military action for which the region is historically known.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda

LOCATION

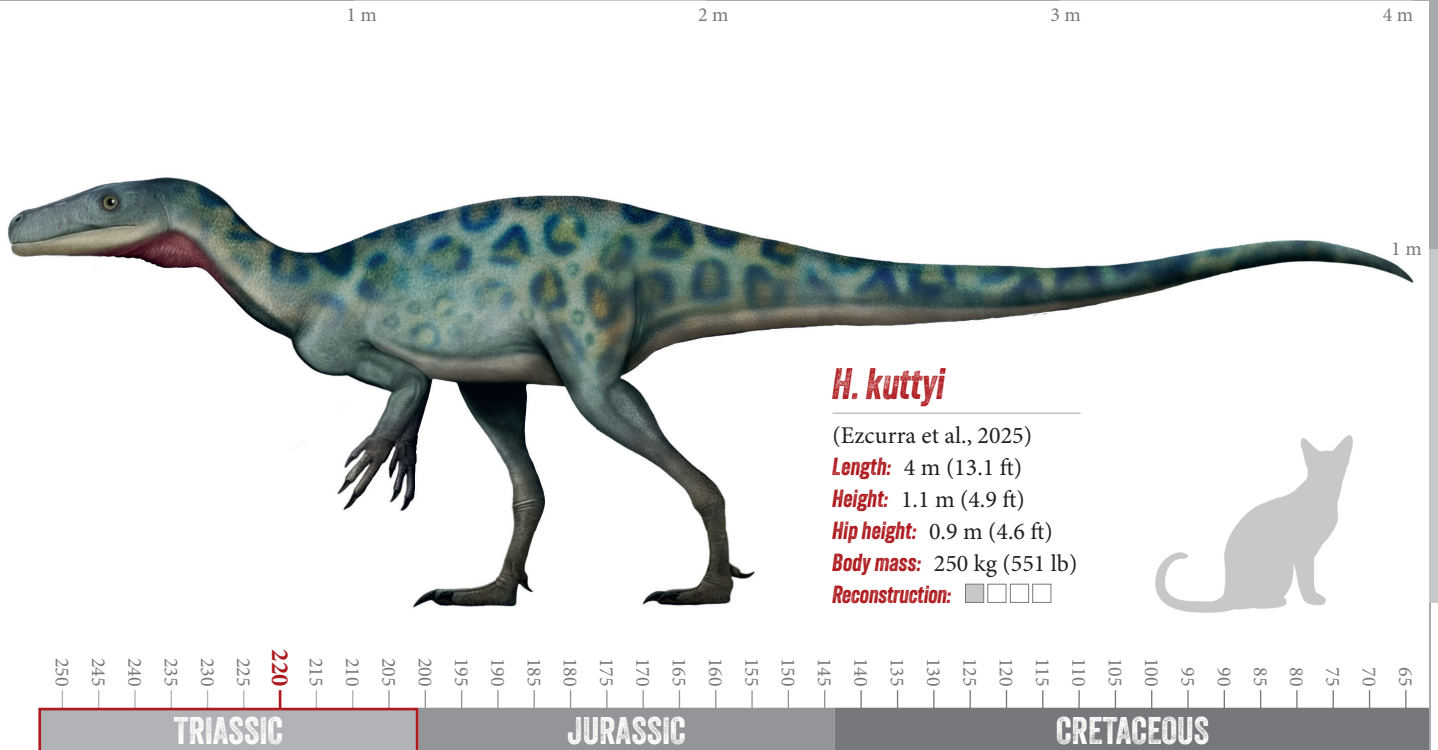
Venezuela



KNOWN REMAINS

Right tibia, partial left ischium





Maleriraptor kuttyi (meaning “Kutty’s raptor from Maleri”) is the first herrerasaurid from outside of South America to be described, and it lived several million years after all other known herrerasaurids.

Although possible fragments of herrerasaurids have been found in North America, Africa, and Europe, none of these specimens have been definitely identified, let alone named to a particular species. This makes *Maleriraptor*, unearthed in India, important for showing that herrerasaurids were not geographically limited to a single region.

It also shows that not all herrerasaurids went extinct at the same time. Previously, it had been hypothesized that herrerasaurids vanished around the same time as the rhynchosaurs, a type of reptilian archosaurs. But *Maleriraptor* most definitely lived after this event.

The fossils of *Maleriraptor* were discovered prior to 1985 and consist of fragmentary portions of the pelvis, along with a single tail vertebra. The specimen received a preliminary description in 2011 but was not definitively identified at that time; one reason for this is because the fossils could not be ruled out as possibly belonging to a closely related dinosaur known as *Alwalkeria*. Eventually, though, since *Alwalkeria* was significantly older and inhabited a different kind of ecosystem (one rife with rhynchosaurs,) it was decided that *Maleriraptor* was almost certainly different enough to warrant the erection of a new genus.

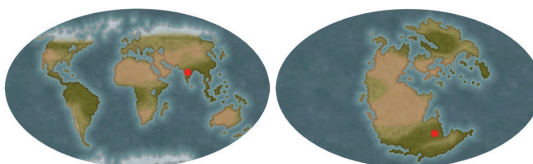
The generic name *Maleriraptor* combines the name of the geological formation in which the specimen was discovered, Maleri, with the Greek “raptor,” meaning “thief.” The specific name *kuttyi* honors fossil discoverer T. S. Kutty.

CLASSIFICATION

Dinosauria
Saurischia
Herrerasauridae

LOCATION

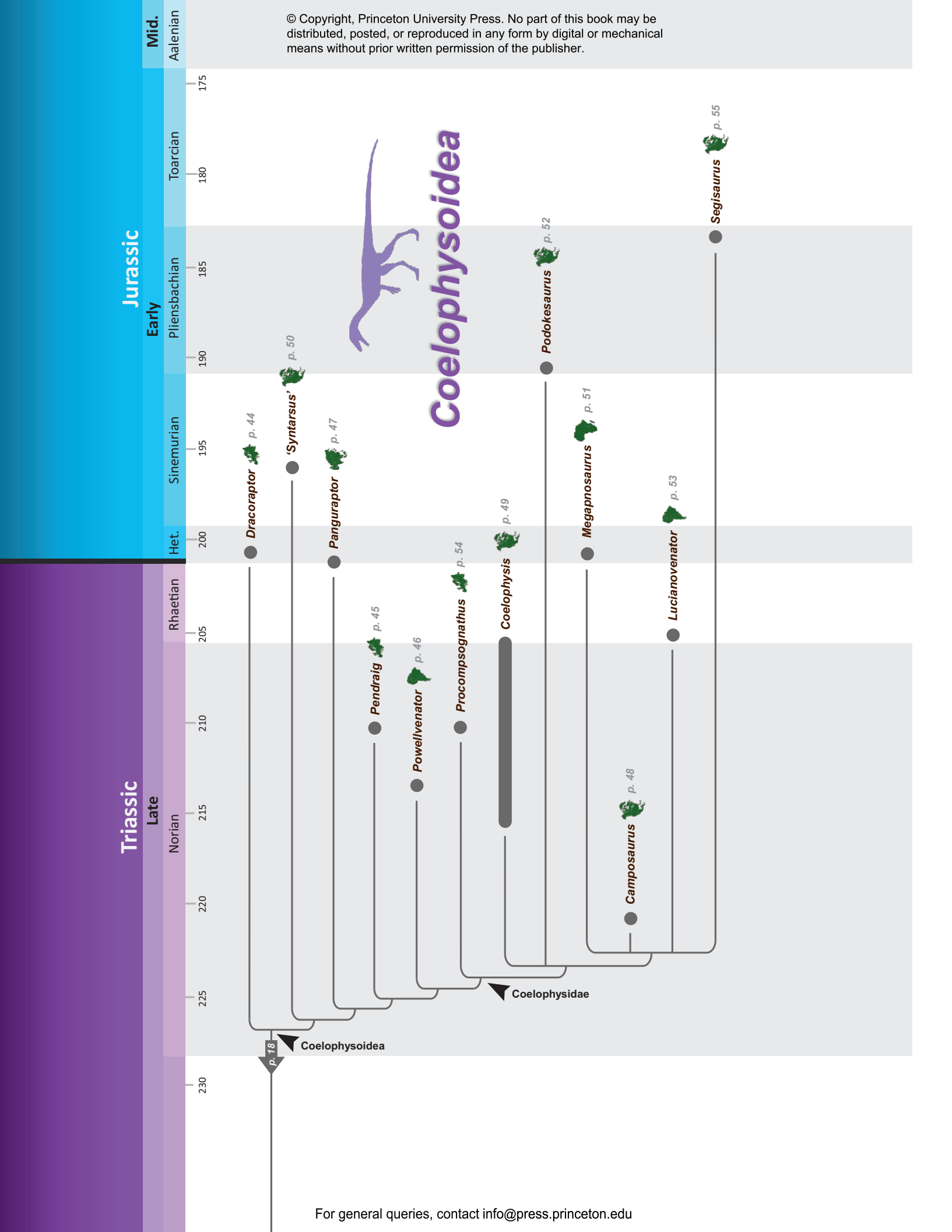
India



KNOWN REMAINS

Partial pelvis and fragments





Coelophysoid dinosaurs were tiny to medium-sized nimble bipedal carnivores that lived during the Late Triassic and Early Jurassic Periods across much of Pangaea (Tykoski, 2005). They are some of the oldest dinosaurs to be well known, and they constitute the first major neotheropod radiation.

Beginning with **Coelophysoidea**, *Dracoraptor* is placed in the most basal position, following Martill et al. (2016) and Ezcurra et al. (2020), despite Spiekman et al. (2021) placing it just outside Coelophysoidea among the “stem-averostrans.” “*Syntarsus*” and then *Panguraptor* are placed in the following derived positions, as seen in Martill et al. (2016), Martínez and Apaldetti (2017), and Ezcurra et al. (2020).

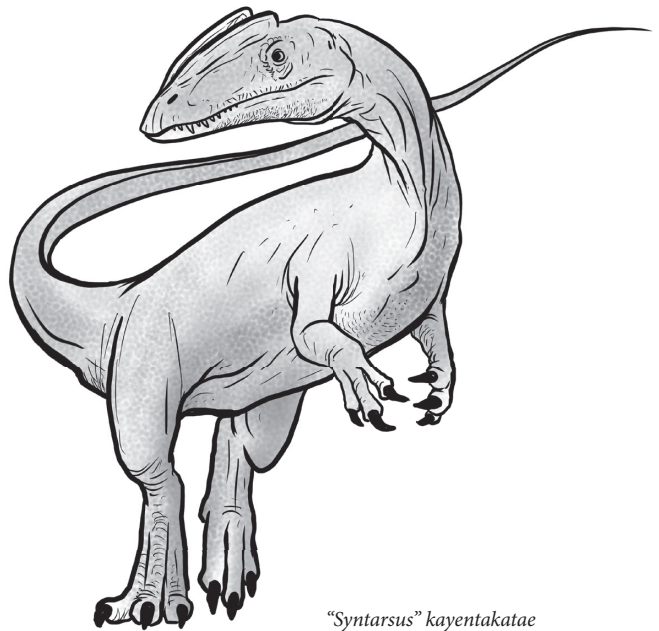
Pendraig, the most recent discovery on this list, was sandwiched by the describing authors between *Panguraptor* and *Powellvenator* (Spiekman et al., 2021). *Powellvenator* and *Procompsognathus* form the next branches, as seen in Ezcurra (2017) and Ezcurra et al. (2020).

The group **Coelophysidae** is ill defined. Some authors have treated it as synonymous with Coelophysoidea, while others reserve Coelophysidae for all of the dinosaurs shown here and use Coelophysoidea to encompass a larger group that includes the likes of *Zupaysaurus* and *Liliensternus*.

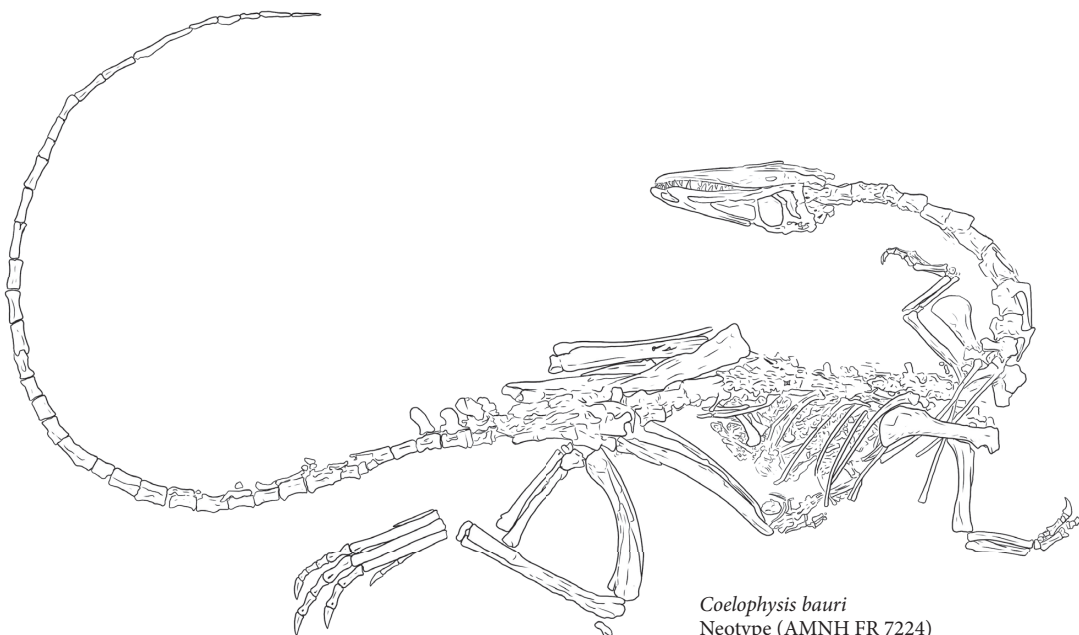
Since the fossil remains of *Podokesaurus* are now lost, and some argue that the genus is synonymous with *Coelophysis*, the two are very closely placed.

Megapnosaurus, *Camposaurus*, and *Segisaurus* are fairly consistently placed on the most derived branch of Coelophysoidea (Martill et al., 2016; Ezcurra et al., 2020; Spiekman et al., 2021). The more recent discovery, *Lucianovenator*, has

also been placed among this subgroup more than once (Martínez and Apaldetti, 2017; Ezcurra et al., 2020).



“Syntarsus” kayentakatae



Coelophysis bauri
Neotype (AMNH FR 7224)

DRACORAPTOR

1 m

2 m

3 m

1 m



D. hanigani

(Martill et al., 2016)

Length: 3 m (9.8 ft)

Height: 1 m (3.2 ft)

Hip height: 0.8 m (2.6 ft)

Body mass: 65 kg (143 lb)

Reconstruction: 



Dracoraptor hanigani (meaning “Hanigan’s dragon thief”) is one of the oldest known dinosaurs from the Jurassic. This means that *Dracoraptor* either survived the catastrophic Triassic–Jurassic mass extinction or was among the first dinosaurs to adapt after the fact.

Even though researchers have approximately 40% of the skeleton to work with, the phylogenetic placement of *Dracoraptor* is not certain. Multiple skeletal traits suggest a placement within **Neotheropoda**, although not all of the typical characteristics of this group are present in *Dracoraptor*. The analysis performed by the describing authors suggests that *Dracoraptor* may be a member of **Coelophysoidea**, even though some of the defining coelophysid characteristics are ambiguous or missing from the specimen. These missing traits could indicate that *Dracoraptor* occupies a very basal position within Coelophysoidea (Martill et al., 2016). Alternatively, Spiekman et al. (2021) place *Dracoraptor* just outside Coelophysoidea.

The holotype specimen (NMW 2015.5G.1–2015.5G.11), found in the Blue Lias Formation of the United Kingdom, is likely a juvenile, making the full size of an adult *Dracoraptor* uncertain. The fossils were discovered in 2014 by Rob and Nick Hanigan, two brothers and amateur paleontologists who donated the remains to the National Museum of Wales. A year later, a missing set of foot bones from the specimen was found by Sam Davies, a paleontology student.

The remains were deposited within marine strata. This could possibly indicate that *Dracoraptor* occupied a coastal environment, or perhaps the individual was simply swept out to sea by a river or stream.

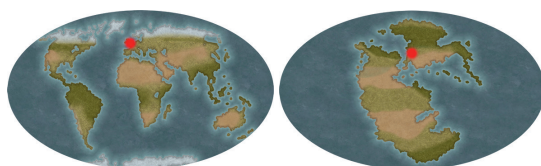
The generic name *Dracoraptor* is a combination of the Latin words “draco” (in reference to the dragon present on the Welsh flag) and “raptor” (meaning “thief”). The specific name *hanigani* is meant to honor the holotype’s discoverers, Rob and Nick Hanigan.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea

LOCATION

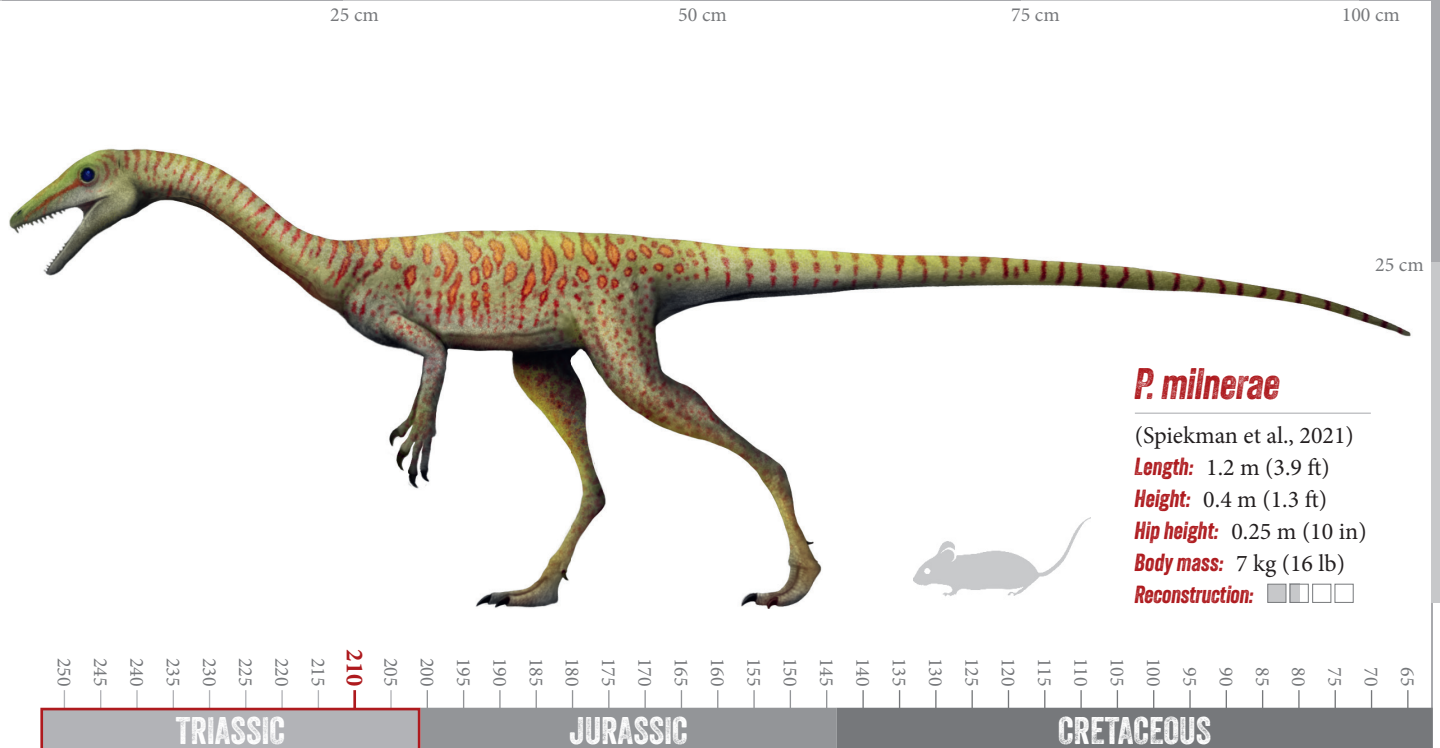
Wales, United Kingdom



KNOWN REMAINS

Partial skull and skeleton





Pendraig milnerae (meaning “Milner’s chief dragon”) is the oldest carnivorous dinosaur species to be discovered in the United Kingdom. Its exact age is uncertain and could be anywhere from 214 to 201 million years old.

The holotype specimen (NHMUK PV R 37591) is believed to be a subadult. It was collected in 1952 but was subsequently misplaced within the vast collections of the Natural History Museum, London. Much later, Dr. Angela Milner and Dr. Susannah Maidment rediscovered the specimen, which had been stored with some unrelated crocodilian fossils. The dinosaur’s fossils, while fragmentary, are notable for being very well preserved and undistorted.

Pendraig has been classified as a non-coelophysid coelophysoid. *Pendraig*’s small size is, in and of itself, not unexpected for a member of **Coelophysoidea**; however, it is telling that small size had been selected for so early in the

coelophysoid lineage, since the averostran-line theropods were rapidly increasing in size during the same period (Spiekman et al., 2021).

Pendraig lived in an archipelago, and species that live on small islands with limited resources have been known to shrink in size compared to mainland relatives, a process known as insular dwarfism. Other reptile fossils discovered from the area also tend to be smaller. Therefore, it is a possibility that *Pendraig* was subject to this effect.

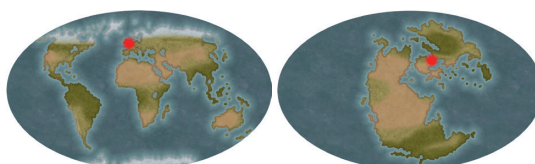
The generic name *Pendraig* combines Welsh words “pen” (meaning “head” or “chief”) and “draig” (meaning “dragon”), which literally means “chief dragon” but is a term used in Medieval Welsh to refer to the “chief warrior.” The specific name *milnerae* honors Dr. Angela C. Milner (1947–2021), a prominent expert on theropod fossils of the British Isles.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea

LOCATION

Wales, United Kingdom

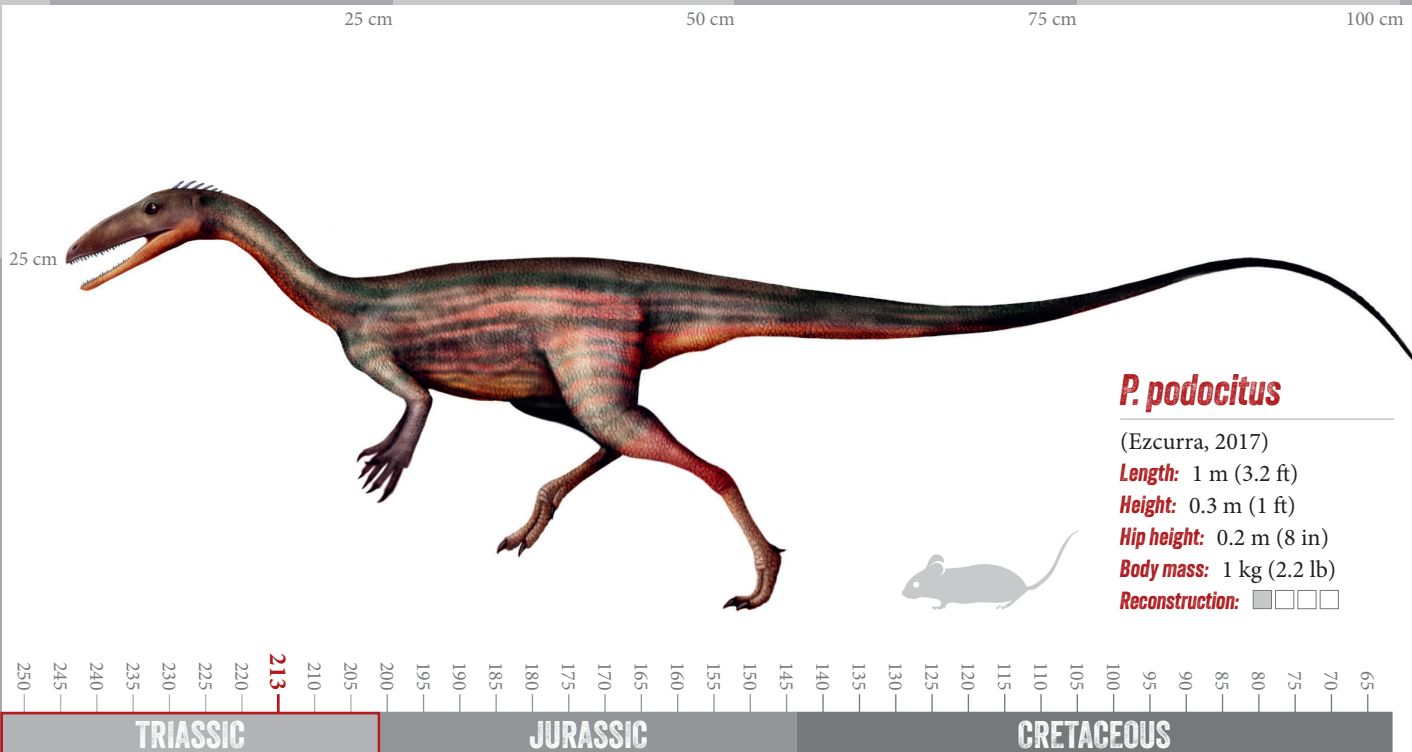


KNOWN REMAINS

Partial pelvic area



POWELLVENATOR



Powellvenator podocitus (meaning “Powell’s early foot hunter”) is an early coelophysoid known only from fragmentary remains.

The holotype material (PVL 4414–1) consists of partial hindlimbs and was originally collected by J. F. Bonaparte in the 1970s. The remains were labeled as “unrecognized elements [found] next to the holotype of *Riojasuchus*” and sat undescribed until 2017. Some of the bones in this set belonged to cynodonts (early mammal relatives) and archosaurs (reptilian cousins to dinosaurs), but several were determined to belong to a neotheropod. The determination was made that these various neotheropod bones belonged to the same creature. Further, an additional specimen of Bonaparte’s (also consisting only of leg bones), labeled only as “indeterminate coelurosaur (PVL 3848),” was likewise referred to the genus—although this fossil appears to have become lost, and only illustrations remain available for

study. Based on their sizes, PVL 3848 may have represented a mature individual, whereas PVL 4414–1 is likely a subadult (Ezcurra, 2017).

Various analyses of *Powellvenator*’s phylogenetic placement indicate that it likely fits in near the base of **Coelophysoidea**, although until more complete specimens are found, an exact placement is highly uncertain (Ezcurra, 2017; Spiekman et al., 2021).

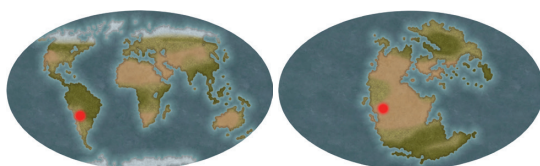
The first portion of the generic name *Powellvenator* honors the Argentinean paleontologist Dr. Jaime Powell (1953–2016), known for his work involving titanosaurs. The second portion of the name adds the Latin word “venator” (meaning “hunter”). The specific name *podocitus* is a combination of the ancient Greek word “podos” (meaning “foot”), in reference to the small size of the animal, and the Latin “citus” (meaning “early”), referring to the period in which the creature lived.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea

LOCATION

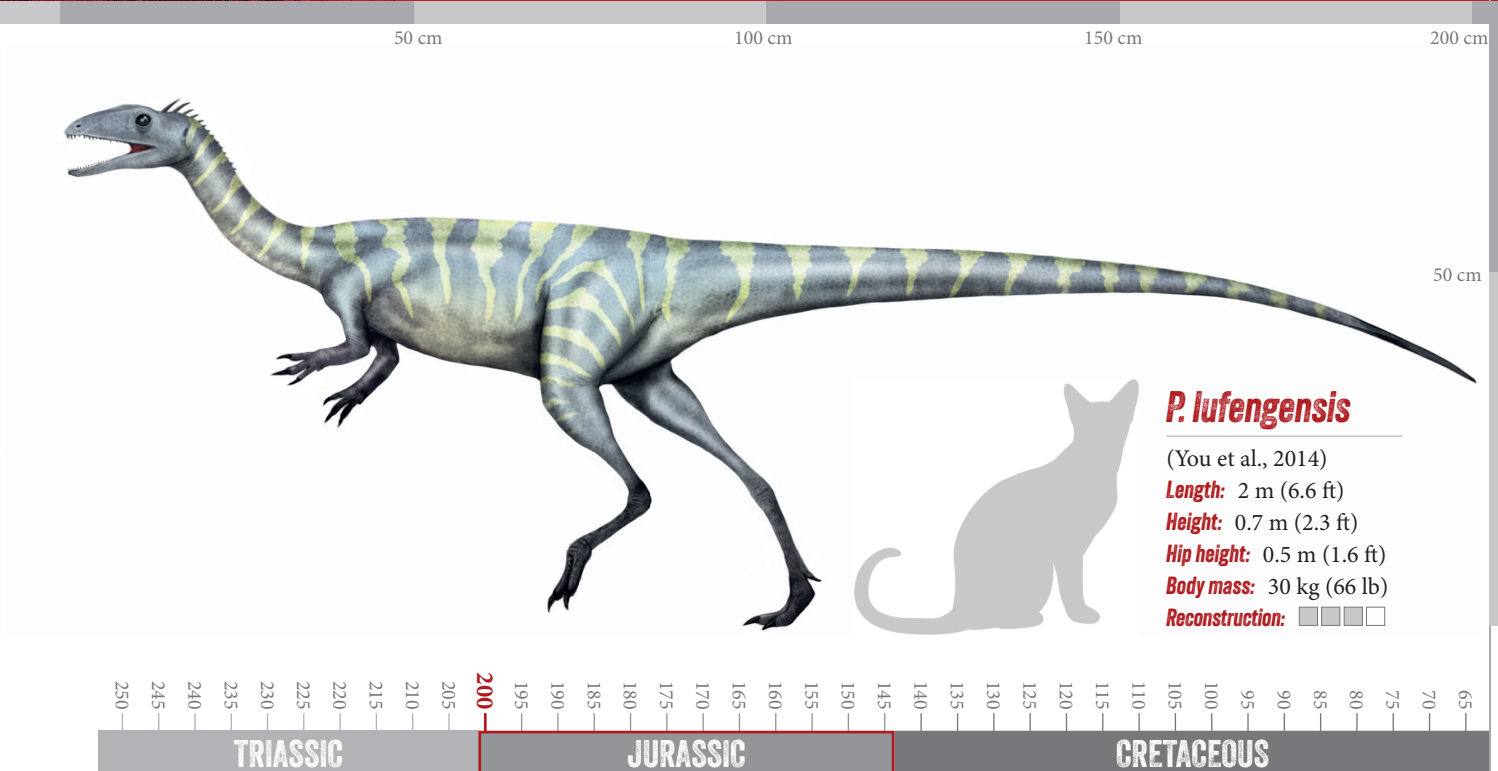
Argentina



KNOWN REMAINS

Portions of legs





Panguraptor lufengensis (meaning “Pangu’s thief from Lufeng”) is the first coelophysoid known from well-preserved remains found on the Asian continent, adding credence to the idea that theropod dinosaurs were already well distributed throughout the supercontinent Pangaea in the Late Triassic and the Early Jurassic, rather than being confined to a single latitude or region. Prior to this discovery, the only coelophysoid remains known from Asia were two limb fragments that are too poorly preserved to be confidently identified.

The holotype specimen (LFGT-0103) consists of most of an articulated skeleton. The specimen is likely a subadult, rather than a juvenile or a fully grown individual, due to the combination of both fused and unfused bone joints. The teeth that are preserved with the skull and jaw are recurved but do not possess serrations. One of the only missing major components of the fossil is the tail; based on close relatives, it is assumed that the tail of *Panguraptor* would be long and

stiff. There are currently no other specimens of *Panguraptor* known, although previously discovered fragments may or may not belong to the genus.

A phylogenetic analysis performed by the describing authors placed *Panguraptor* as being closely related to *Camposaurus* and *Coelophysis*, which would make it a member of the more derived family **Coelophysidae** (You et al., 2014). However, a more recent analysis places *Panguraptor* in a more basal position, outside Coelophysidae, while still being within the broader **Coelophysoidea** (Spiekman et al., 2021).

The first portion of the generic name *Panguraptor* is named for “Pangu,” a well-known Chinese mythological figure who was said to be the first living being as well as the creator of all reality. The second portion is the Latin word “raptor” (meaning “thief” or “robber”). The specific name *lufengensis* references Lufeng County, a source of plentiful Early Jurassic fossils.

CLASSIFICATION

Dinosauria
 Saurischia
 Theropoda
 Neotheropoda
 Coelophysoidea

LOCATION

China

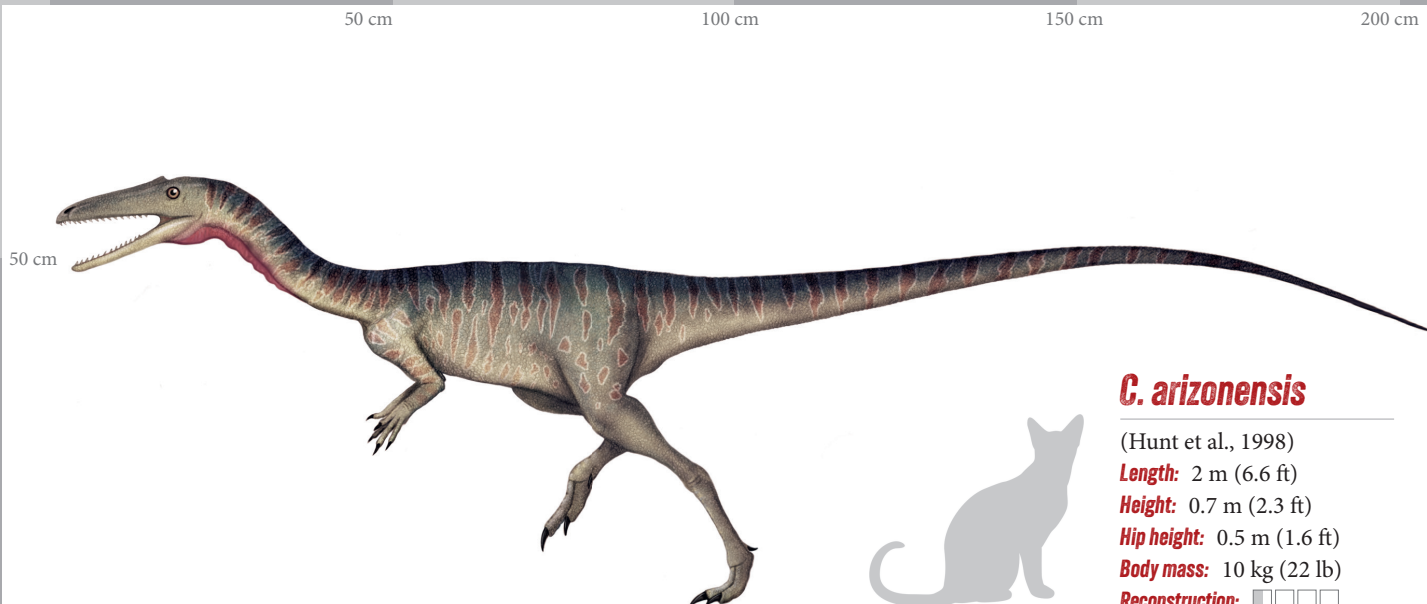


KNOWN REMAINS

Majority of skull and skeleton



CAMPOSOSAURUS



C. arizonensis

(Hunt et al., 1998)

Length: 2 m (6.6 ft)

Height: 0.7 m (2.3 ft)

Hip height: 0.5 m (1.6 ft)

Body mass: 10 kg (22 lb)

Reconstruction: ☐ ☐ ☐ ☐

Camposaurus arizonensis (meaning “Camp’s lizard from Arizona”) is a coelophysid that is regarded by some as the earliest known neotheropod.

The holotype material (UCMP 34498) consists only of the lower portions of a tibia and fibula and the upper portion of an ankle bone. It was discovered in 1934 in the Bluewater Creek Formation of Arizona, at the Placerias Quarry, but the fossils were not described and named until 1998.

These scant fossils bear a strong resemblance to those of *Coelophysis*. Consequently, many paleontologists considered *Camposaurus* to be just a junior synonym of *Coelophysis* (Downs, 2000; Heckert, 2002; Rauhut, 2003).

However, a reassessment of the material has since uncovered unique characteristics in the fossil, distinguishing

it as a valid and separate species after all (Ezcurra and Brusatte, 2011).

This analysis also shows *Camposaurus* to be very closely related to *Megapnosaurus rhodesiensis*, which lived much later, during the Early Jurassic. This relationship would necessitate a long ghost lineage, reinforcing just how patchy our knowledge of early theropod evolution actually is. On the other hand, it is possible that the fragmentary nature of the fossil might lead to incorrect “figments” in the data, with regard to these relationships (Ezcurra and Brusatte, 2011).

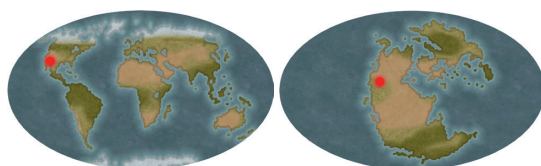
The generic name *Camposaurus* means “Camp’s lizard,” in honor of the paleontologist Charles Lewis Camp, who did extensive work at the Placerias Quarry. The specific name *arizonensis* refers to the discovery location of the holotype.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea
Coelophysidae

LOCATION

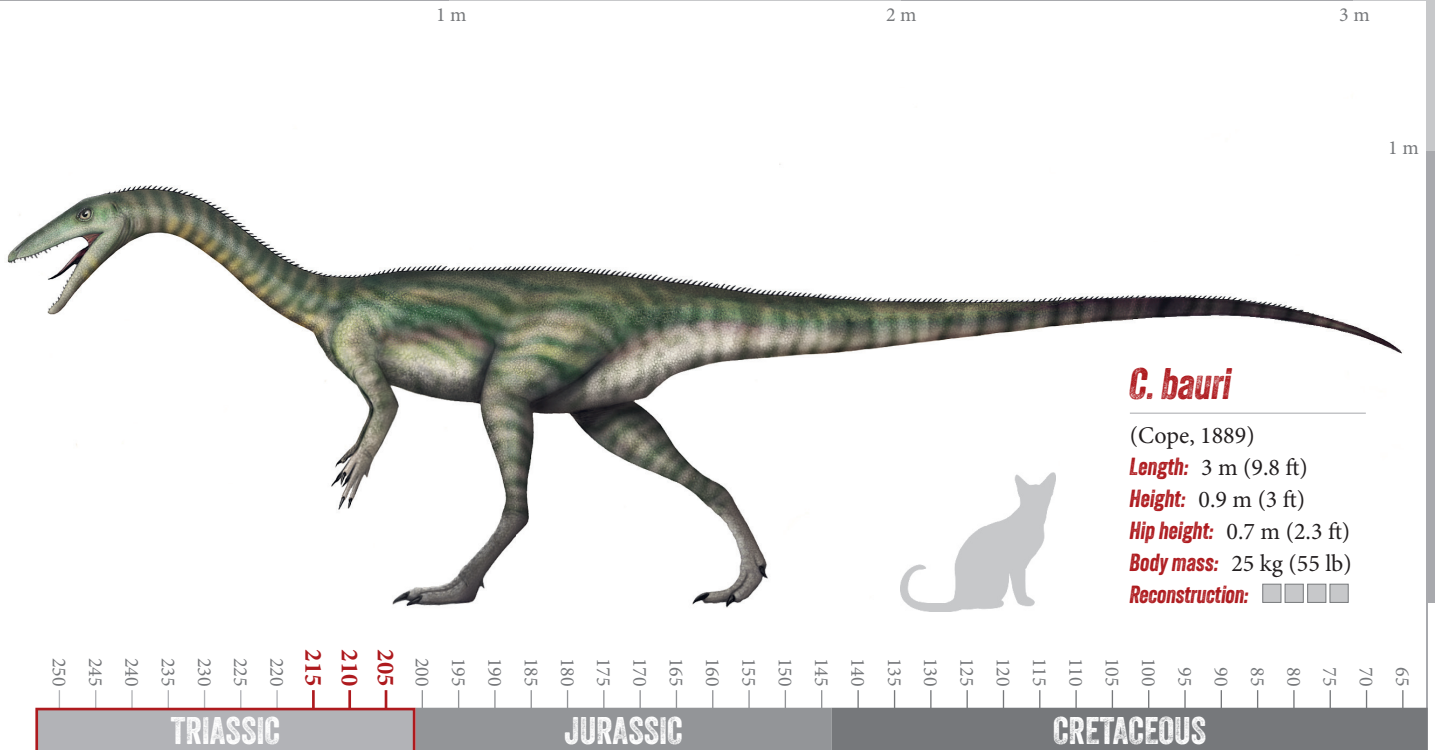
Arizona, USA



KNOWN REMAINS

Fragment of lower leg





Coelophysis bauri (meaning “Baur’s hollow form”) is among the most famous of dinosaurs and known from many hundreds of specimens.

The first fossils of *Coelophysis* were uncovered in 1881, but these remains were fragmentary. In 1947, a “graveyard” of skeletons—composed of more than a thousand individuals—was unearthed at Ghost Ranch in New Mexico, USA. One of several fully articulated specimens found here was actually named as a replacement for the poorly preserved original type specimen. Exactly how so many skeletons came to rest in one place is currently an unsettled matter.

With so many specimens available, detailed comparative assessments of *Coelophysis* have been conducted that would be impossible to attempt with most other species. Approximately half of the known specimens have a more “robust” form, while the rest are more “gracile.” This has led some researchers to believe that males and females were different and distinguishable, a trait known as sexual dimorphism (Rinehart et al., 2009). However, others argue

that these differences may just be due to a differential growth rate among different individuals (Griffin and Nesbitt, 2016).

Coelophysis had forward-facing eyes, giving it stereoscopic vision. Analysis of a complete sclerotic ring (a support structure within the eye) suggests that the animal was diurnal and had visual acuity comparable to that of a modern hawk. *Coelophysis* also possesses the earliest known wishbone in the dinosaur fossil record. The vertebrae of the tail feature an unusual interlocking pattern that would prevent the tail from moving vertically (Gay, 2001).

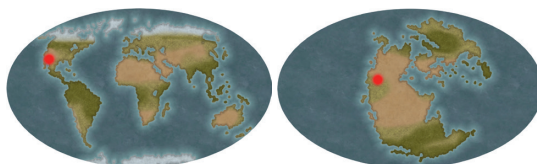
The generic name *Coelophysis* combines the Greek words “koilos” (meaning “hollow”) and “physis” (meaning “form”), in reference to the animal’s hollow bones. The specific name *bauri* honors the comparative anatomist Georg Baur. Many different species have been named in the literature over the years, but *C. bauri* is the only universally recognized species at this time. The generic names *Rioarribasaurus* and *Longosaurus* are considered to be synonymous with *Coelophysis*.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea
Coelophysidae

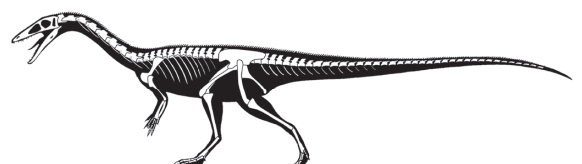
LOCATION

United States (various locations)

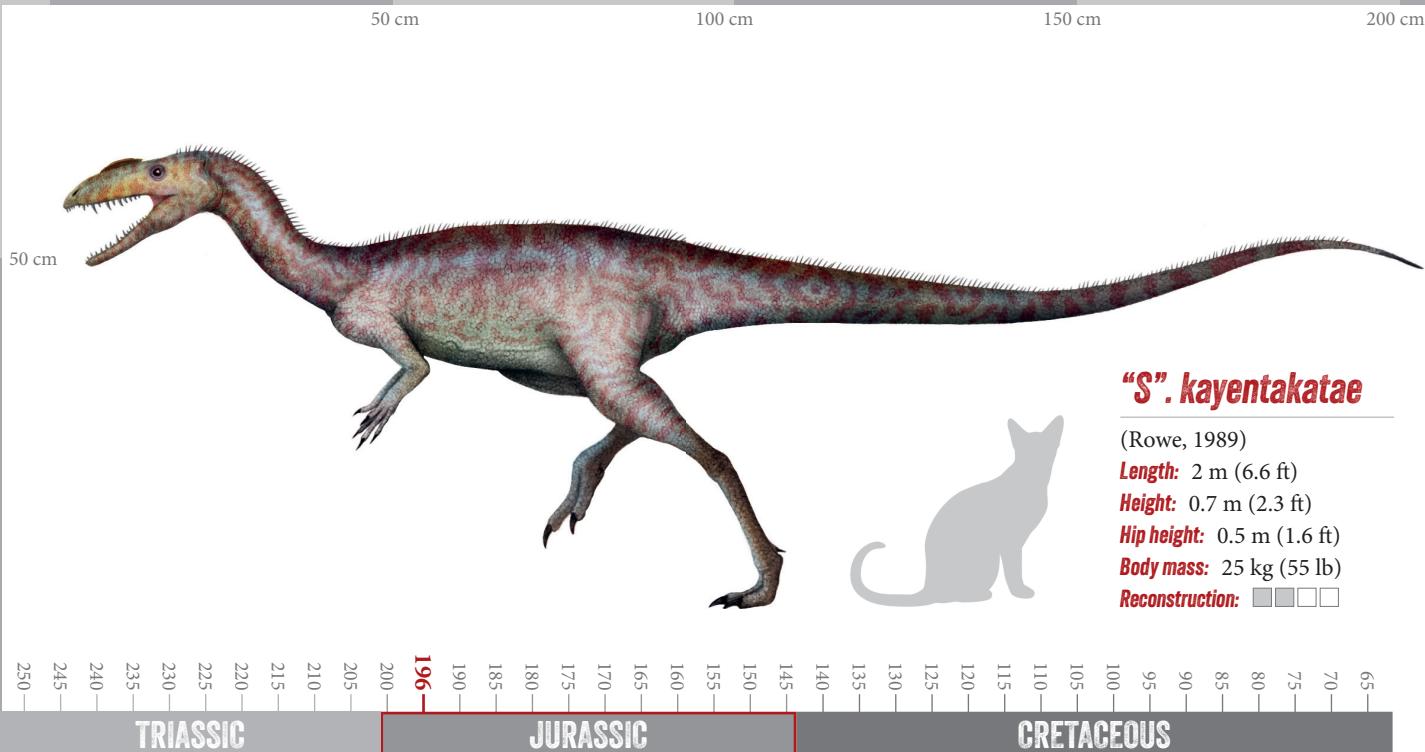


KNOWN REMAINS

Entire skeleton and skull



"SYNTARSUS"



The story of "*Syntarsus*" *kayentakatae* is both complicated and convoluted. The short version is that while the species is valid and distinct, the genus to which it belongs is undetermined, as of 2022.

The fossils were victim to significant surface erosion and were found in various states of preservation. (A number of referred specimens that were originally assigned to the species have now been reassigned; a large number of "juveniles" are now thought to belong to the as-yet-undescribed "Shake 'N Bake" coelophysid, and the original paratype is now identified as *Kayentavenator*.)

What makes this species stand out are two small crests on the top of the skull, which are unknown in other coelophysids (Tykoski and Rowe, 2004). Some paleontologists have interpreted these crests as a possible evolutionary link between this species and *Dilophosaurus*.

The story grows confusing because of the animal's assigned name. The coelophysid "*Syntarsus*" *rhodesiensis* was named in 1969, and this species, *Syntarsus kayentakatae*,

was added in 1989. The trouble is that the name "*Syntarsus*" was already in use, describing a genus of beetle. Therefore, the dinosaurs had to be moved to a new genus in 2001, which was called *Megapnosaurus* (Ivie et al., 2001).

So we would have been left with this species being named *Megapnosaurus kayentakatae* ... except, at one point in time, the type species, *Megapnosaurus rhodesiensis*, was thought to be synonymous with *Coelophysis*. Which meant that "*Megapnosaurus*" no longer existed and that *Megapnosaurus kayentakatae* had to be moved to *Coelophysis kayentakatae*. Except it is highly dubious that this species, which possesses skull crests, actually belongs in the same genus that features species that lacked crests and also lived much earlier.

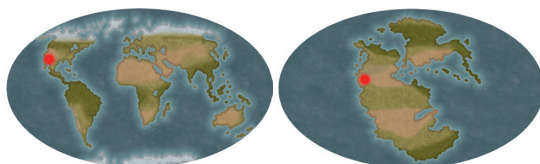
As it currently stands, most literature now refers to this dinosaur as quote-unquote "*Syntarsus*" *kayentakatae*, for lack of a better option. The specific name honors Dr. Kathleen Smith, nicknamed "Kayenta Kay" due to her extensive studies in the Kayenta Formation region.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea

LOCATION

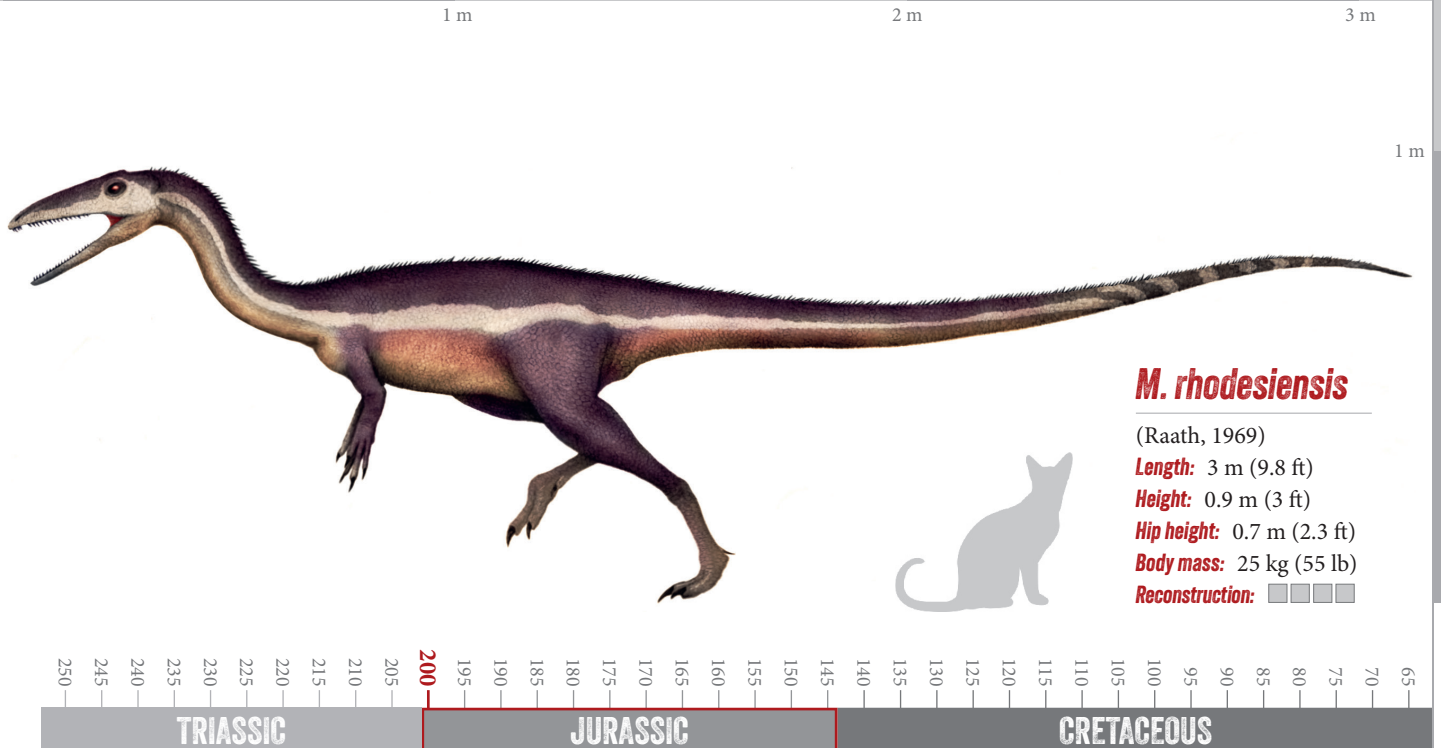
Arizona, USA



KNOWN REMAINS

Skull and jaw; additional fragments





Megapnosaurus rhodesiensis (meaning “big dead lizard from Rhodesia”) is a coelophysid that has, confusingly, been assigned several different names over time.

A group of students discovered the first *Megapnosaurus* fossils in 1963. The original specimen (QG 1) was excavated by Michael A. Raath and consists of a well-preserved postcranial skeleton, with only the skull and some cervical vertebrae missing. In 1969, Raath named the animal *Syntarsus rhodesiensis*, referring to the joined tarsal bones in its foot. Raath maintained his hunt for complete *Megapnosaurus* specimens in the Jurassic stratum of Zimbabwe until 1972, when he discovered the most productive *Megapnosaurus*-bearing site to date, close to the Chitake River. Hundreds of bones from at least 26 specimens representing various stages of development were found in the quarry. Gastralia, sexual dimorphism, and stomach contents were also retained in some specimens.

In 2001, entomologists noticed that the name “*Syntarsus*” had already been in use, describing a type of beetle, so the

dinosaur had to be moved to a new genus, *Megapnosaurus* (Ivrie et al., 2001).

Since that time, numerous researchers have argued that this species should actually fall within the genus *Coelophysis*, naming it *Coelophysis rhodesiensis*. This is due to the similar anatomy of the two animals, even though they were separated by millions of years and hundreds of miles of latitude. However, a recent comprehensive analysis has suggested that the two species are so distantly related that *Megapnosaurus* is indeed a valid taxon (Ezcurra et al., 2021).

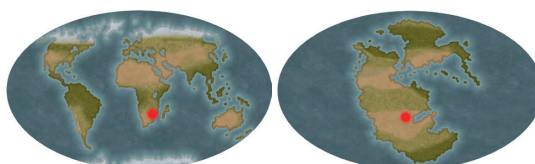
The generic name *Megapnosaurus* combines the Greek words “me-gas” (meaning “big”), “ap-noos” (meaning “dead”), and “sau-ro” (meaning “lizard”). This tongue-in-cheek description was given to the dinosaur by the entomologists who removed it from “*Syntarsus*.” The specific name *rhodesiensis* refers to the location of the holotype’s discovery; the area known today as Zimbabwe was, at the time, known as Rhodesia.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea
Coelophysidae

LOCATION

Zimbabwe



KNOWN REMAINS

Entire skeleton and skull



► **PODOKESAURUS**

25 cm

50 cm

75 cm

100 cm

25 cm



P. holyokensis

(Talbot, 1911)

Length: 1 m (3.2 ft)

Height: 0.3 m (1 ft)

Hip height: 0.2 m (8 in)

Body mass: 1 kg (2.2 lb)

Reconstruction: ☐ ☐ ☐ ☐



Podokesaurus holyokensis (meaning “swift-footed lizard from Holyoke”) is a coelophysid that is known only from destroyed remains.

The holotype material was both discovered and described by the geologist Mignon Talbot, which gave her the distinction of being the first woman to accomplish such a feat for a nonavian dinosaur. The affinities of *Podokesaurus* were not initially clear, because it was one of the few tiny theropods known when it was described. Thus, it was initially grouped with other small theropods, such as *Compsognathus*, in the family known as Podokesauridae (an outdated term that is no longer used).

Sadly, during the winter of 1917, the building in which the specimen was kept burned to the ground, and the fossil material was lost. All that now remains are illustrations and poor-quality casts.

When a trove of *Coelophysis* remains were found in 1947, *Podokesaurus* began to receive renewed interest.

As early as the 1960s, some researchers suggested that *Coelophysis* and *Podokesaurus* were in fact so similar that the genera should be considered synonymous. A litany of agreements and disagreements on this issue have ensued over the years, and the animal is sometimes referred to as *Coelophysis holyokensis*. While some researchers conclude that *Podokesaurus* lacks any specific traits that would unite it with *Coelophysis* (Tykoski and Rowe, 2004), that there are no modern detailed descriptions of the remains precludes *Podokesaurus* from being used in detailed phylogenetic analyses of the relationships within **Coelophysoidea**.

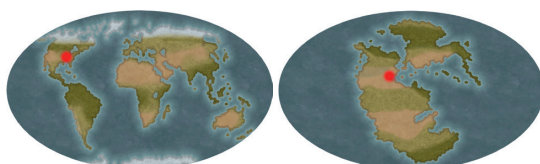
The generic name *Podokesaurus* comes from the ancient Greek words “podokes” (meaning “swift” or “fleet-footed”) and “sauros” (meaning “lizard”). The specific name *holyokensis* refers to the discovery location of the holotype, near Mt. Holyoke, Massachusetts. In 2021, *Podokesaurus* became the state dinosaur of Massachusetts.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea
Coelophysidae

LOCATION

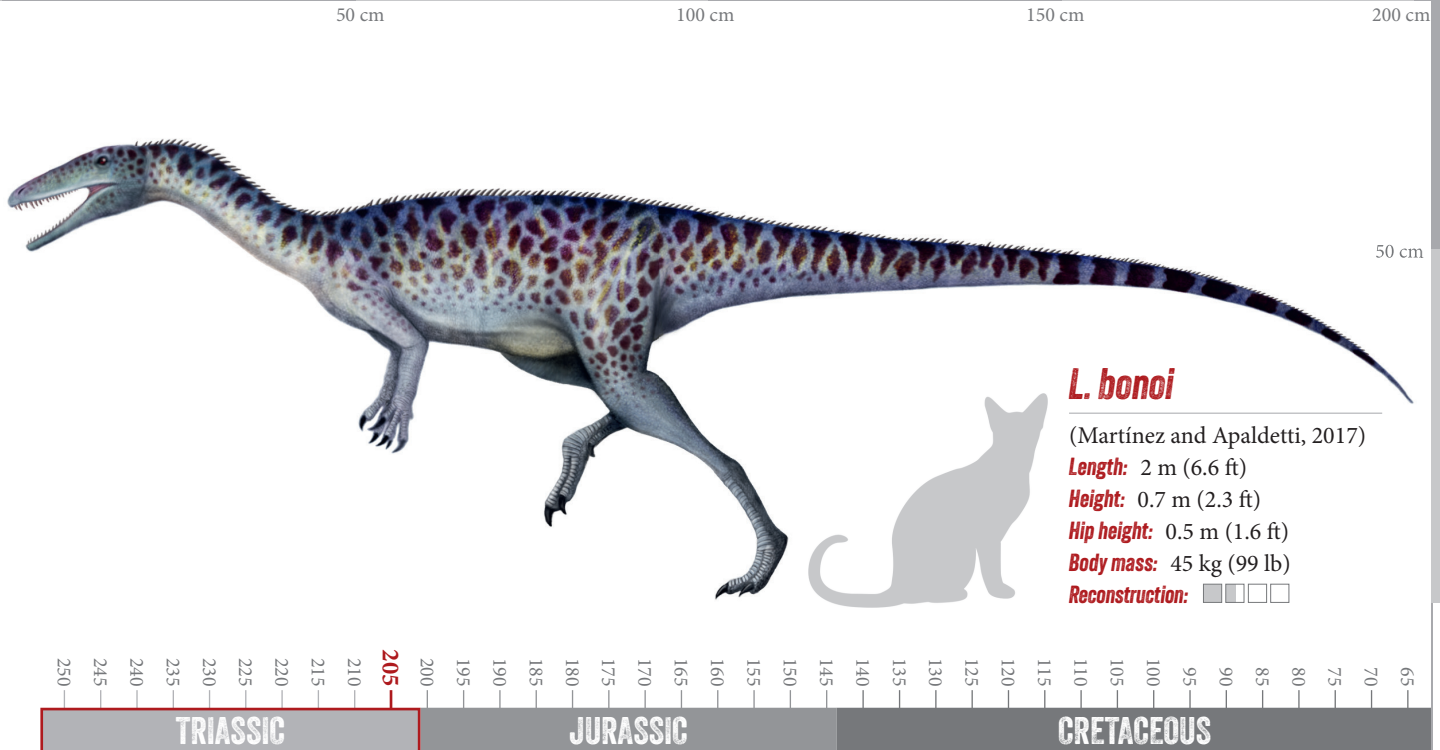
Massachusetts, USA



KNOWN REMAINS

Partial skeleton





Lucianovenator bonoi (meaning “Luciano’s and Bono’s hunter”) is one of the few coelophysids known from South America.

Much like *Coelophysis*, *Lucianovenator* is a small, gracile carnivore with a long, slender neck. Similarly, the neck vertebrae possess cavities for “air sacs” to pass through, which are part of the respiratory system of modern birds. In fact, within **Coelophysoidea**, *Lucianovenator* is likely most closely related to *Coelophysis* and *Camposaurus* (Martínez and Apaldetti, 2017).

The holotype of *Lucianovenator* (PVSJ 906) was unearthed in the Quebrada del Barro Formation of Argentina, a location that had previously yielded hundreds of reptilian fossils. Researchers from the Institute and Museum of Natural Sciences (IMCN) of the National University of San Juan (UNSJ) conducted the excavation. Three other partial specimens, mostly consisting of pelvic-region remains, were also found.

The age of these specimens could be anywhere from 205 to 210 million years, placing them in the final age of the Triassic Period, known as the Rhaetian. The fossil record of theropods is sparse throughout the Rhaetian, in comparison to the earlier Norian age. The presence of *Lucianovenator* could suggest that the paucity of Rhaetian theropods is due to either a bias in the formation of fossils at the time or a stratigraphic bias in the rock layers that are available for scientists to research, rather than an actual dip in theropod diversity or abundance during the time (Martínez and Apaldetti, 2017).

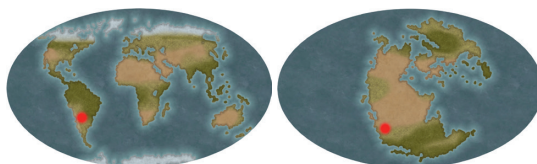
The generic name *Lucianovenator* means “Luciano’s hunter,” in honor of Don Luciano Leyes, who was the first to discover the animal’s remains. The specific name *bonoi* refers to Tulio del Bono, a local scientific leader who helped with the describers’ research.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea
Coelophysidae

LOCATION

Argentina

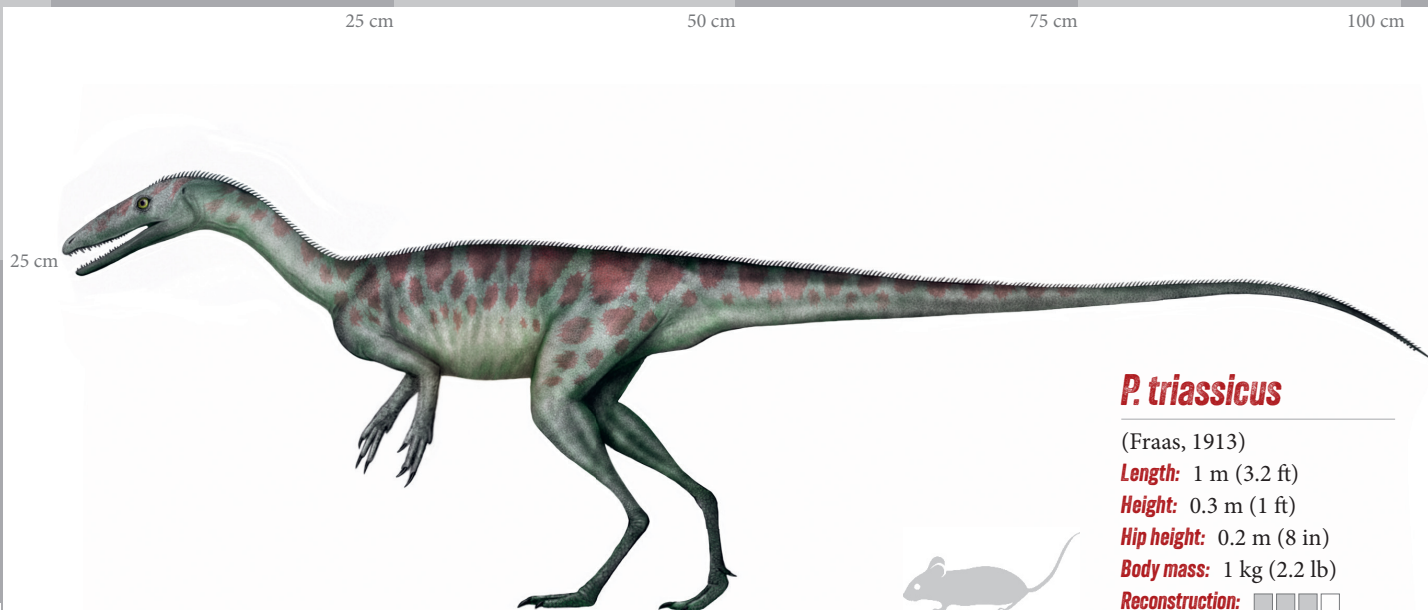


KNOWN REMAINS

Partial vertebrae and pelvis



► PROCOMPSOGNATHUS



Procompsognathus triassicus (meaning “ancestor of the elegant jaw of the Triassic”) is a famous dinosaur, although its fossil remains have been the subject of much controversy.

In 1909, Albert Burrer discovered the holotype of *Procompsognathus* (SMNS 12591) in his quarry, distributed across three slabs of rock. In 1913, Professor Eberhard Fraas named and described the genus. Friedrich von Huene assigned two more specimens to *Procompsognathus* in 1921: SMNS 12352, a fragmentary skull and lower jaws, and SMNS 12352a, an isolated left hand; however, both have been found to be from a crocodylomorph (Knoll and Schoch, 2006).

Somewhat predictably, nearly all of these remains have had their validity called into question. The skull material assigned to the holotype has been claimed by authors to belong to a different creature entirely. Some suggest that the skull belongs to some sort of crocodylomorph (Sereni and Wild, 1992), while others state that it belongs to a

different, indeterminate theropod (Knoll and Schoch, 2006; Chatterjee, 1993, 1998). The two referred specimens are now generally agreed to be crocodylomorph in origin (Knoll and Rohrberg, 2012).

While *Procompsognathus* is still considered a valid genus, its future in the scientific literature is uncertain. With only one fragmentary postcranial skeleton to use as a baseline, many paleontologists are reluctant to definitively assign any new finds to this genus.

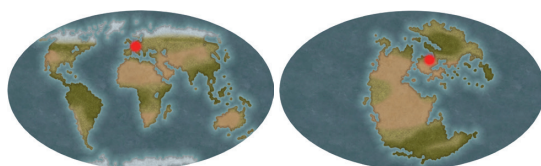
The generic name *Procompsognathus* combines the Greek words “kopsos” (meaning “elegant” or “dainty”) and “gnathos” (meaning “jaw”) with the prefix “pro” (meaning “before” or “ancestor of”). However, rather than a literal meaning, the name is in reference to the Jurassic theropod *Compsognathus*, which had been discovered previously and is also characterized by its diminutive size. (The two dinosaurs are not very closely related, as it turns out.) The specific name *triassicus* refers to when the animal lived.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Coelophysoidea

LOCATION

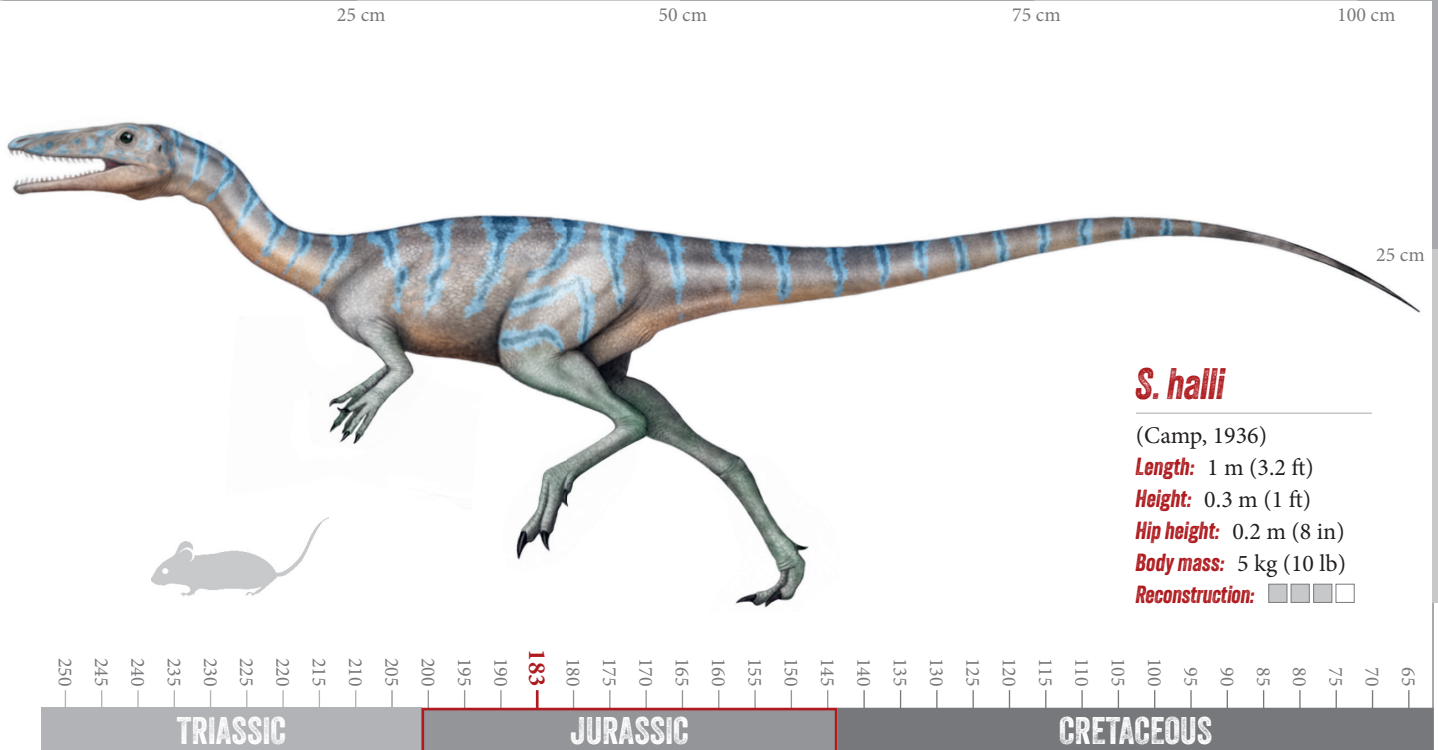
Germany



KNOWN REMAINS

Skull (?) and partial skeleton





Segisaurus halli (meaning “Hall’s lizard from Segi”) is the latest-surviving coelophysid currently known, likely making it one of the last of its kind.

The holotype and only known specimen (UCMP 32101) was discovered in 1933 entombed in sediment known as the Navajo Sandstone. This type of sedimentary rock is much more likely to preserve trackways than it is to preserve bones, so to find a partially articulated skeleton in this location was an extraordinary discovery.

Although it was largely overlooked at the time, the skeleton of *Segisaurus* held an important evolutionary clue. *Segisaurus* possessed clavicles that were fused, forming a furcula—also known as a wishbone. At the time, the debate about the link between birds and dinosaurs was in full swing. One point against the notion that dinosaurs were ancestral to birds, though, was the lack of any known furcula among theropods. However, this detail about *Segisaurus* would be overlooked for some time.

Another important hint about the link between dinosaurs and birds can be seen in the position in which the fossilized remains were found. *Segisaurus* appears to have been in a “roosting” position when it died, perhaps in an attempt to hunker down against a sandstorm. The significance of this bird-like positioning was, again, unnoticed for a long time (Carrano et al., 2005).

In addition to these overlooked truths, there was, for a time, also a popular falsehood about the specimen—namely, that it possessed solid bones, rather than hollow ones. This has since been discounted (Carrano et al., 2005).

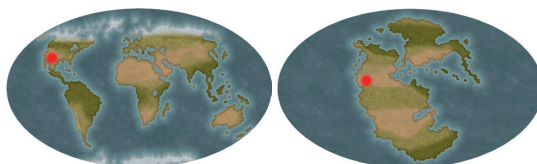
The first portion of the generic name *Segisaurus* refers to Tsegi Canyon, Arizona, where the fossil was discovered. The second portion adds the Greek word “sauros” (meaning “lizard”). The specific name *halli* is meant to honor A. Hall, a colleague of Charles Lewis Camp, the paleontologist who formally described the specimen.

CLASSIFICATION

Dinosauria
 Saurischia
 Theropoda
 Neotheropoda
 Coelophysoidea
 Coelophysidae

LOCATION

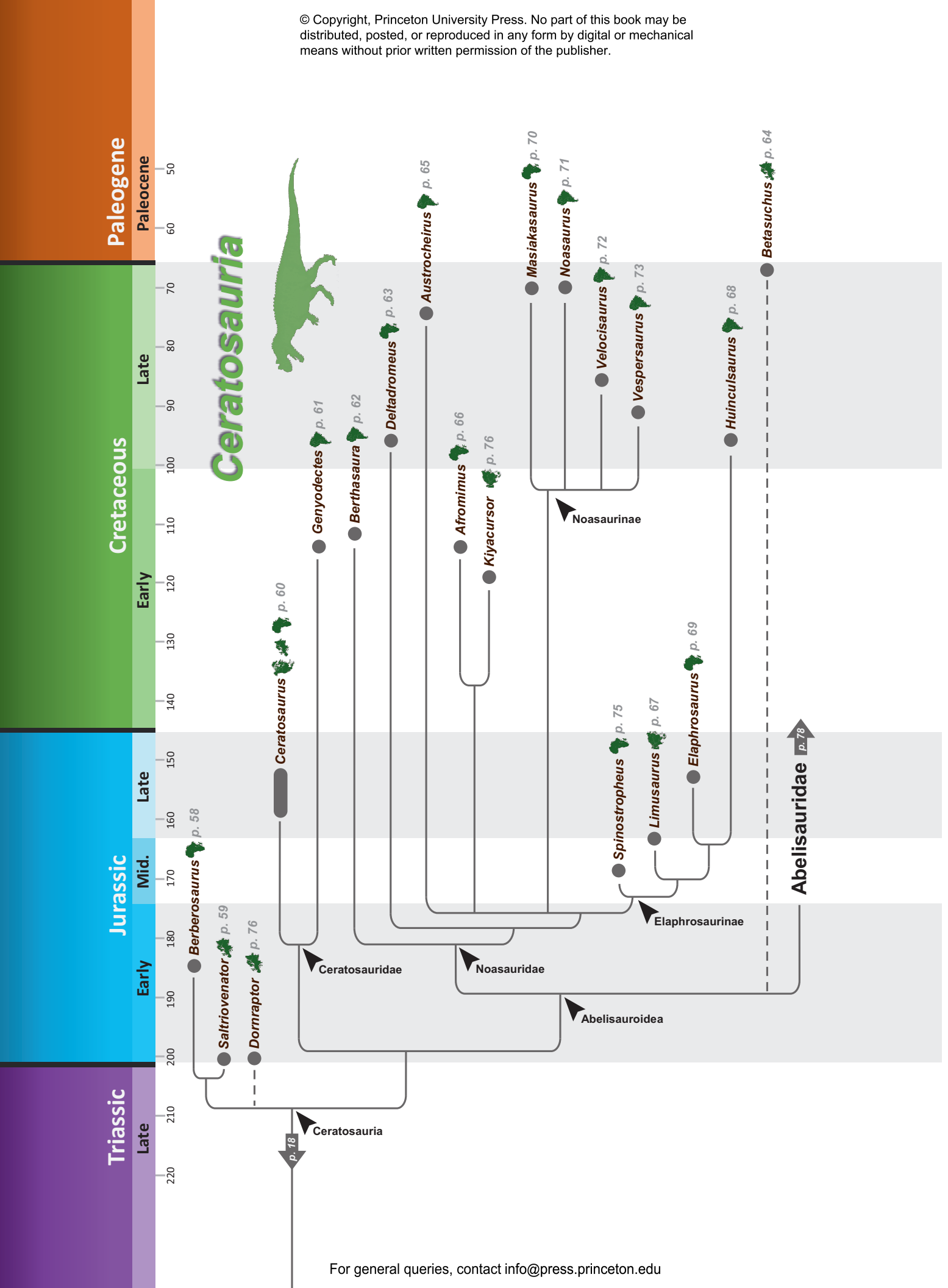
Arizona, USA



KNOWN REMAINS

Partial postcranial skeleton

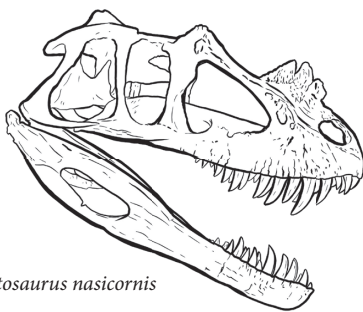




Ceratosauria is a diverse clade, including not only the likes of the ubiquitous *Ceratosaurus* but also many other theropods that do not bear much of an outward similarity to that nose-crested specimen. These include the enigmatic and gracile noasaurids, as well as the short-faced abelisaurids.

Berberosaurus is most often placed as the most basal member of Ceratosauria (Ezcurra et al., 2010; Dal Sasso et al., 2018; de Souza et al., 2021). This is what has been depicted here, although occasionally *Berberosaurus* is shown in a slightly more derived position, either as a part of Ceratosauridae (Zaher et al., 2020) or slightly closer to Abelisauridae (Tortosa et al., 2014). To date, the only phylogenetic examination of *Saltriovenator* conducted was in the initial description of the genus, which placed it as the sister taxon to *Berberosaurus* (Dal Sasso et al., 2018).

The earliest major branching point separates Ceratosauridae from Abelisauroidae. **Ceratosauridae** contains only two genera with confidence, *Ceratosaurus* and *Genyodectes* (Rauhut and Carrano, 2016; Dal Sasso et al., 2018; de Souza et al., 2021).



Ceratosaurus nasicornis

Most commonly, **Abelisauroidae** is interpreted as then diverging into two groups, Abelisauridae and Noasauridae, with each group being separate and monophyletic (descending from a single ancestor not shared by another group) (Rauhut and Carrano, 2016; Langer et al., 2019; Cerroni et al., 2019; de Souza et al., 2021). This is the arrangement that has been reproduced here, although, notably, Dal Sasso et al. (2018) show Noasauridae to be paraphyletic.

As depicted here, the most basal member of **Noasauridae** is the recently described *Berthasaura* (de Souza et al., 2021), followed by *Deltadromeus* (Rauhut and Carrano, 2016; Zaher et al., 2020; de Souza et al., 2021). However, the position of *Deltadromeus* is uncertain; in one instance, that of Cerroni et al. (2019), it has been placed in an even more basal position outside Noasauridae.

Several studies have also placed the dinosaur *Camarillasaurus* as a basal ceratosaur or noasaurid (Tortosa et al., 2014; Zaher et al., 2020); this is not depicted here, as the most recent analysis places *Camarillasaurus* within Spinosauridae (Samathi et al., 2021).

Afromimus and *Austrocheirus*, along with other noasaurids, are known from such scant remains that many analyses are unable even to estimate the exact placement of each genus relative to the others and simply place most or all of the non-elaphrosaur noasaurids into one large undifferentiated group (Ezcurra et al., 2010; Tortosa et al., 2014; Baiano et al., 2020; de Souza et al., 2021). The taxon **Noasaurinae** was coined to encompass “all noasaurids more closely related to *Noasaurus* than to *Elaphrosaurus*, *Abelisaurus*, *Ceratosaurus*, or *Allosaurus*” (Rauhut and Carrano, 2016). As mentioned above, it is unclear whether *Afromimus* and *Austrocheirus* would fall into this group. Several analyses, though, show that *Velocisaurus*, *Masiakasaurus*, *Noasaurus*, and (most recently) *Vespersaurus* would fall within this grouping (Rauhut and Carrano, 2016; Langer et al., 2019; Zaher et al., 2020).

Perhaps the most uncertain placement here regards **Elaphrosaurinae**. Multiple studies have placed the group outside and basal to Noasauridae (Tortosa et al., 2014; Brissón Egli et al., 2016; Cerroni, 2019). Contrastingly, multiple studies have placed it *within* Noasauridae (Rauhut and Carrano, 2016; Langer et al., 2019; de Souza et al., 2021). The latter arrangement is depicted here, although, again, this is highly uncertain.

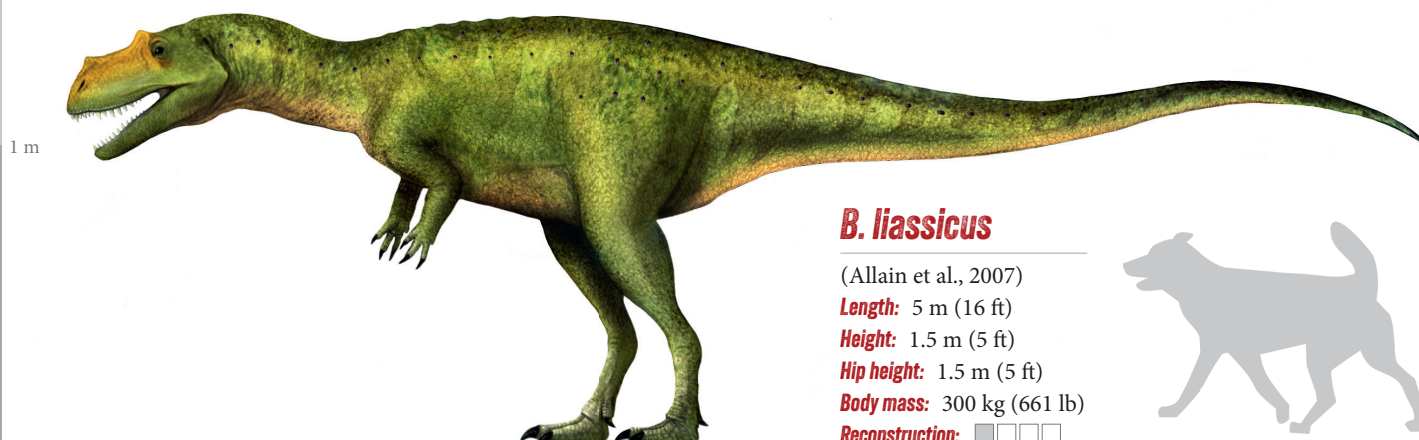
Despite the confusion surrounding the family’s overall placement, though, the question of which dinosaurs belong *within* the family Elaphrosaurinae stands on slightly firmer ground. Most studies that include *Spinostropheus* place it as the basalmost member of the group (Wang et al., 2017; Cerroni et al., 2019; Baiano et al., 2020). *Limusaurus* and *Elaphrosaurus* are consistently resolved as very closely related (Zaher et al., 2020; de Souza et al., 2021). The recently described *Huinculsaurus* was assigned as the most derived member of this group, according to its original description (Baiano et al., 2020). *Betasuchus*, known from a single bone, can be assigned only to Abelisauria *incertae sedis* (“uncertain placement”) (Tykoski and Rowe, 2004). As stated previously, **Abelisauridae** is then shown as the sister clade of Noasauridae.



Masiakasaurus knopfleri

▶ BERBEROSAURUS

1 m 2 m 3 m 4 m 5 m



B. liassicus

(Allain et al., 2007)

Length: 5 m (16 ft)

Height: 1.5 m (5 ft)

Hip height: 1.5 m (5 ft)

Body mass: 300 kg (661 lb)

Reconstruction: ☐ ☐ ☐ ☐



Berberosaurus liassicus (meaning “Berber lizard of the Lias”) may be the most basal ceratosaur known, coming from a period for which the fossil record of theropods is very sparse. Only a small number of theropods have been identified from the latter half of the Early Jurassic, so any new data regarding this part of the theropod family tree is considered invaluable.

The holotype material was discovered in the early 2000s in Morocco’s High Atlas Mountains, as part of a series of bone beds that have yielded numerous discoveries, such as early sauropods. It consists of a cervical vertebra, part of the sacrum, a metacarpal, a right femur, and portions of the tibia and fibula. (An additional partial femur has also been referred to *Berberosaurus*.)

At the time of its initial description, *Berberosaurus* was phylogenetically placed as the basalmost abelisauroid (Allain et al., 2007), while a subsequent analysis placed it as a dilophosaurid (Xu et al., 2009). However, the current

majority consensus seems to place *Berberosaurus* as the most basal member of Ceratosauria (Carrano and Sampson, 2008; Ezcurra et al., 2010; Dal Sasso et al., 2018).

This is a more stratigraphically compatible placement; if *Berberosaurus* were an abelisauroid, it would essentially increase the total stratigraphic debt by pushing the origins of the more primitive ceratosaur taxa further backward in time. Furthermore, whereas *Berberosaurus* does indeed bridge the gap between Ceratosauria and Coelophysoidea, it essentially closes the gap separating Ceratosauria and Tetanurae, a group that is also known only beginning from the Early Jurassic but not from any time prior (Carrano and Sampson, 2008).

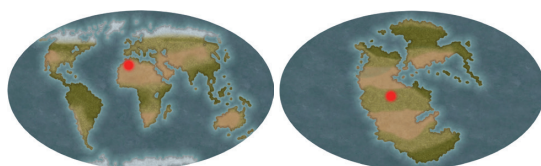
The first part of the generic name *Berberosaurus* refers to the Berber people who live mainly in Morocco; the remainder of the name, “sauros,” is Greek for “lizard.” The specific name *liassicus* refers to the Lias stratigraphic epoch in which the specimen was located.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Averostra
Ceratosauria

LOCATION

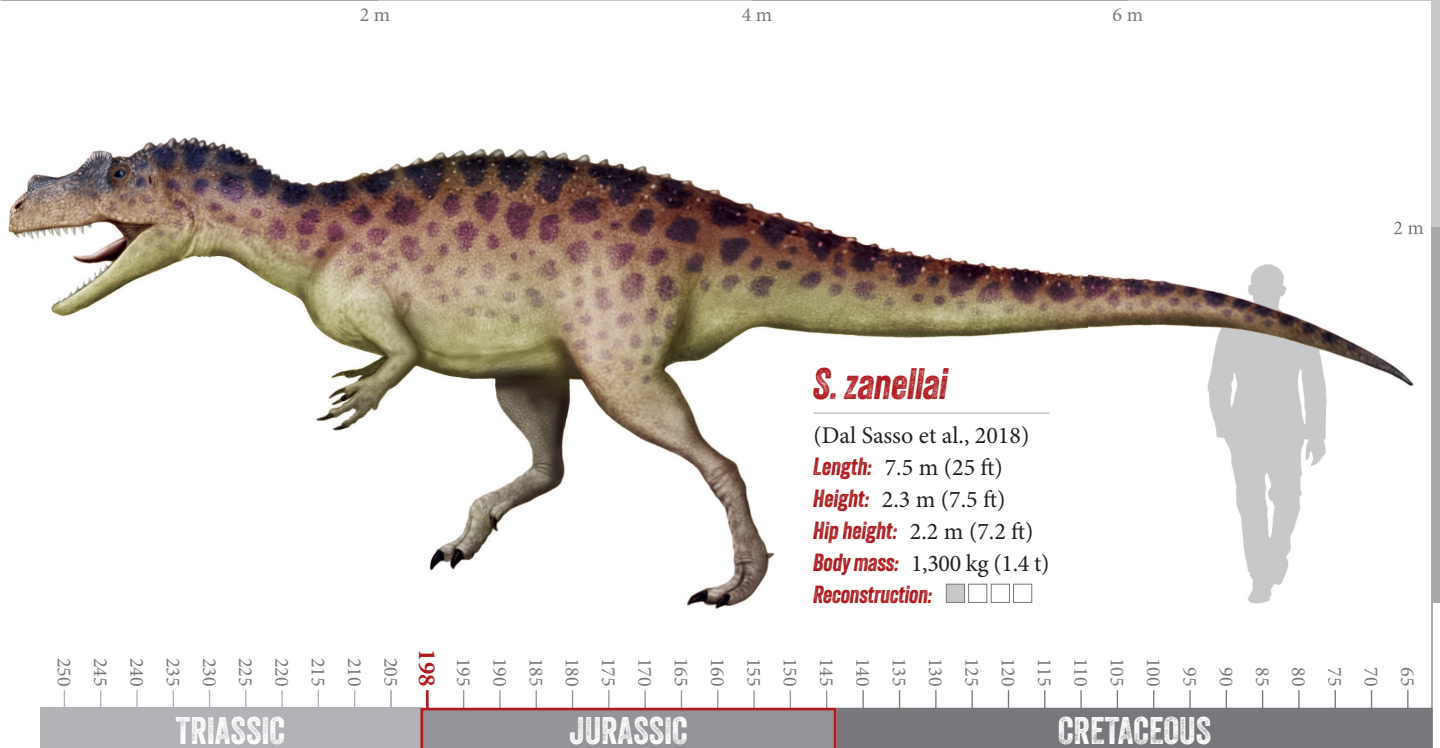
Morocco



KNOWN REMAINS

Fragmentary remains





Saltriovenator zanellai (meaning “Zanella’s hunter from Saltrio”) is only the third nonavian dinosaur ever discovered from Italy and the largest theropod known from the Early Jurassic.

The holotype material (MSNM V3664) was discovered unexpectedly in the 1990s in a quarry, after an excavation explosion exposed the fossils. The fragments that survived were embedded in chalky material, and extensive baths of formic acid were needed to free the bones completely. Many of the remains were too damaged or fragmentary to be identified, but roughly 10% of the total skeleton was eventually accounted for.

The specimen was found in marine deposits alongside ammonites and crinoids, so it has been speculated that *Saltriovenator* could have occupied a coastal environment and was swept out to sea after its death. This is likely, as much of Europe consisted of island-like landmasses during the Early Jurassic. There were also signs that the remains had been scavenged by aquatic animals.

Before the specimen was formally described, there were opinions that *Saltriovenator* was a tetanuran or coelophysoid, but the describing authors determined that it was most likely a basal member of **Ceratosauria**. By sharing several traits of both ceratosaurs and tetanurans, *Saltriovenator* is shown to occupy a placement near the divergence of these two primary lineages of **Averostra** (Dal Sasso et al., 2018).

Saltriovenator is also noteworthy due to the anatomy of its hands. While modern avians possess a tridactyl (three-fingered) hand, the details of how this trait evolved have remained elusive. *Saltriovenator* possesses a combination of various traits seen in other four-fingered theropods, which indicates that the loss of different digits was not a straightforward evolutionary process.

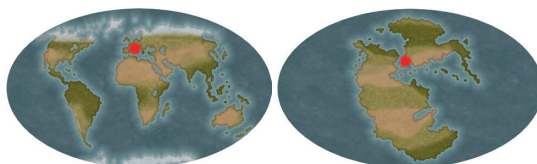
The first part of the generic name *Saltriovenator* refers to Saltrio, the location in Italy where the fossils were found. The second portion, “venator,” is Latin for “hunter.” The specific name *zanellai* honors fossil discoverer Angelo Zanella.

CLASSIFICATION

Dinosauria
 Saurischia
 Theropoda
 Neotheropoda
 Averostra
 Ceratosauria

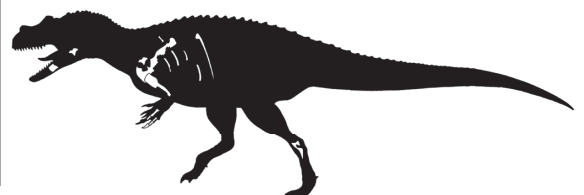
LOCATION

Italy

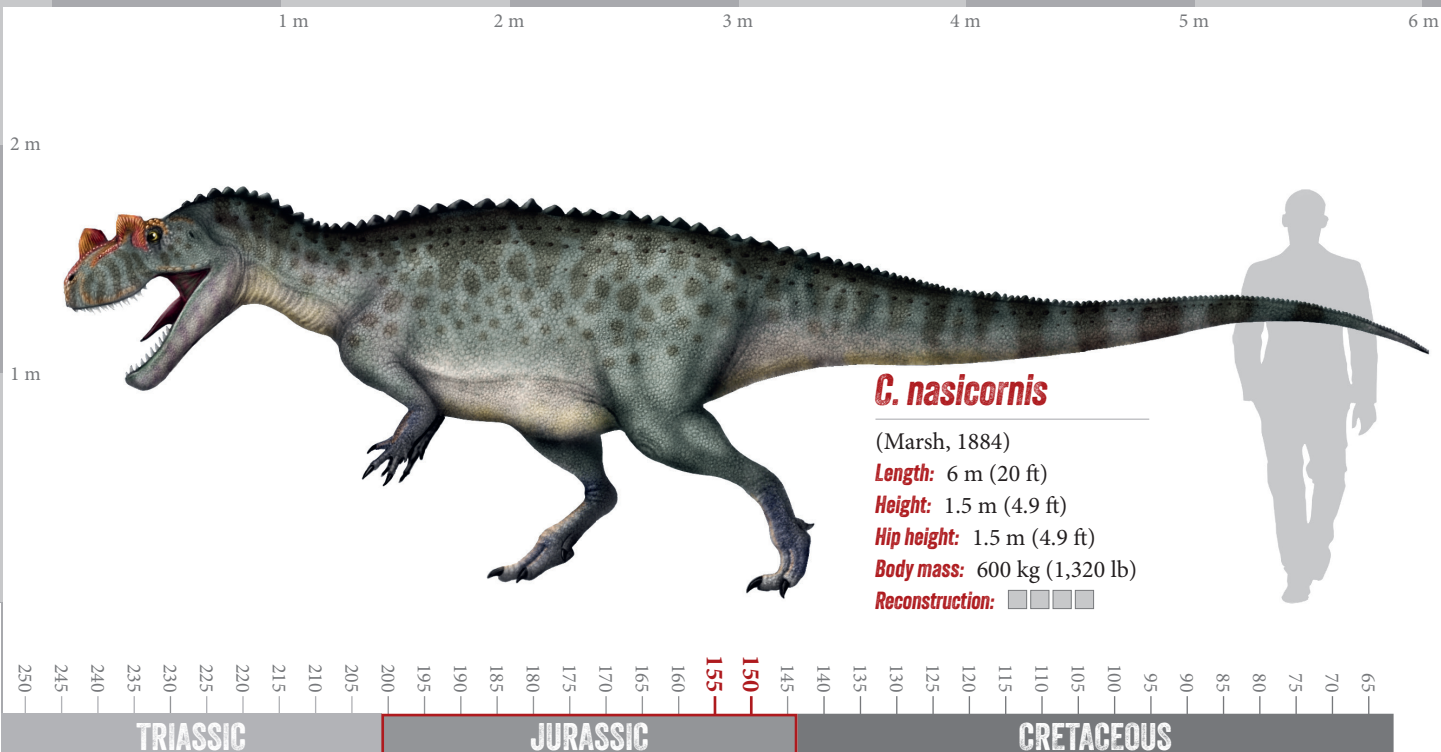


KNOWN REMAINS

Fragmentary remains



CERATOSAURUS



Ceratosaurus nasicornis (meaning “horned lizard bearing a nose horn”) is one of the most famous theropods, although its depiction in various media is often inaccurate. It is easily recognizable because of the distinctive “horn” on its skull, near the nose. Unlike the horns of dinosaurs such as *Triceratops*, however, this was not a robust appendage, but a rather thin protrusion of nasal bone. Nevertheless, the idea that this horn was used as an offensive weapon was accepted without question for many decades, and numerous depictions have subsequently shown *Ceratosaurus* with a menacing, sharp, spike-like horn. The modern consensus, however, is that this protrusion was likely too fragile for use in this way and most likely served a display purpose only, acting akin to a short crest (Rowe and Gauthier, 1990).

Ceratosaurus is also the only theropod known to possess osteoderms—small bony protrusions embedded in the skin. These sorts of features, as seen in other animals, usually serve a defensive purpose, suggesting either that

Ceratosaurus was preyed upon by even larger theropods or that individuals fought among themselves. Alternatively, the osteoderms could also have been purely ornamental (Madsen and Welles, 2000).

The tail vertebrae of *Ceratosaurus* were straight and tall, and the chevron bones located on the tail’s underside were unusually long. Some paleontologists have interpreted this as a “crocodile-like” tail that aided in swimming (Bakker and Bir, 2004). *Ceratosaurus* is also distinguished by having teeth that were exceptionally long, compared to other theropods (Henderson, 1998).

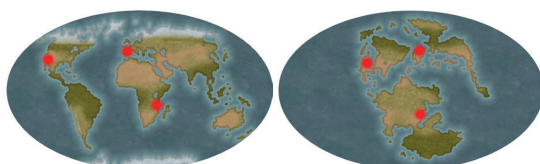
Ceratosaurus is known from numerous specimens. Multiple species have been assigned to the genus over the years, but currently *C. nasicornis* is the only uncontested example. The generic name is derived from the Greek “keratos” (meaning “horn”) and “sauros” (meaning “lizard”). The specific name combines the Latin word “nasus” (meaning “nose”) and “cornu” (meaning “horn”).

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Averostra
Ceratosauria
Ceratosauridae

LOCATION

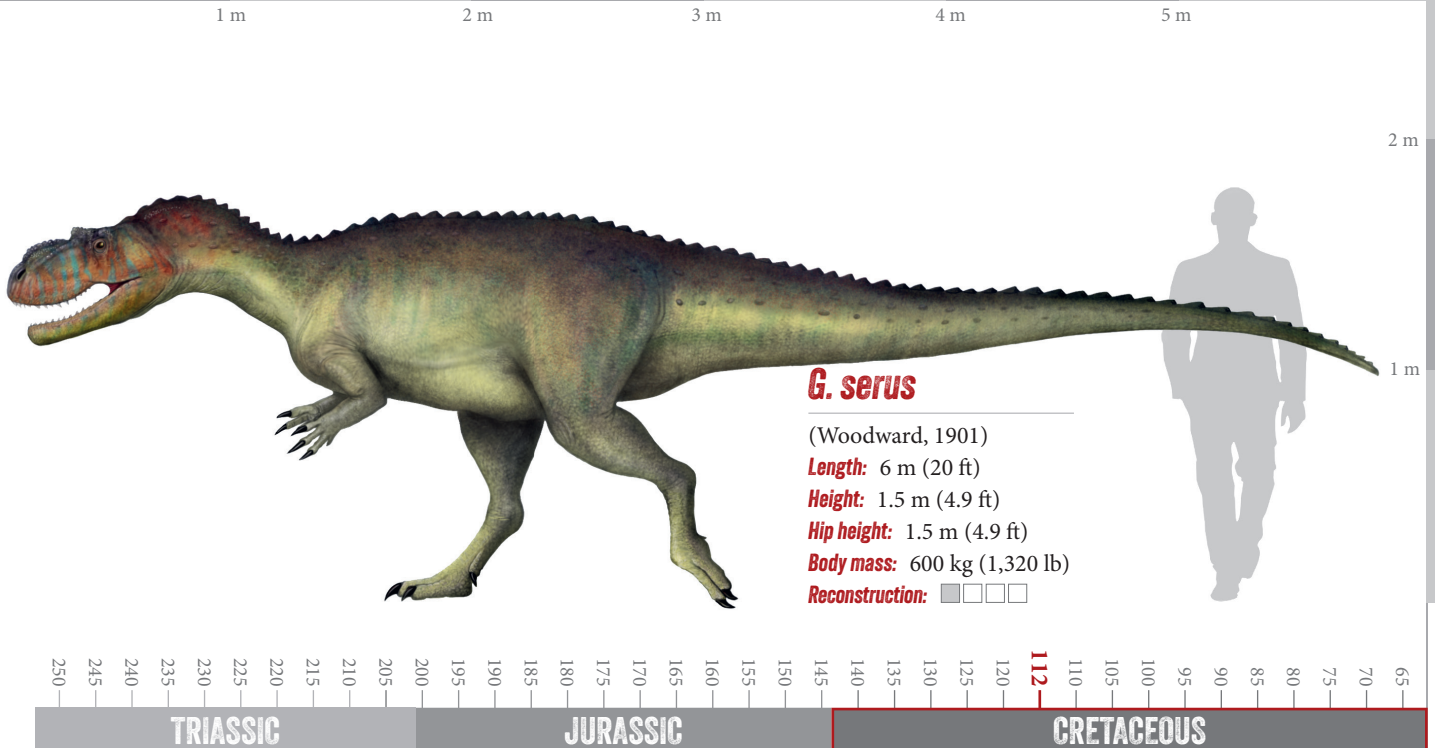
United States, Portugal, Tanzania



KNOWN REMAINS

Most of skull and skeleton





Genyodectes serus (meaning “late biting jaw”) was unearthed in 1901 by A. S. Woodward and is essentially the first theropod fossil known from South America. The specimen (MLP 26–39) consists of the snout of a single individual. For more than a century, the specimen received little in the way of attention and was considered by many to be *nomen dubium* (a dubious genus). While obviously belonging to a theropod, the specimen’s exact affinities were left ambiguous until 2004, when the fossil received a detailed reevaluation (Rauhut, 2004).

It was determined that *Genyodectes* was a distinct and valid genus and most closely related to *Ceratosaurus*, placing the genus within the family **Ceratosauridae**. While the bones are not in pristine condition, the anatomical features of the teeth (particularly their shape and unusual length) revealed compelling similarities between the two dinosaurs.

The exact location of the holotype’s discovery was not well documented, which meant that determining the fossil’s exact age took some detective work. Based on original notes and geological details of the rock material still attached to the fossil, it has been surmised that the fossil originated in the Cretaceous stone of Cañadón Grande. This is noteworthy, as all specimens of the related *Ceratosaurus* are from a much earlier time, nearly 40 million years prior, in the Jurassic. Thus, *Genyodectes* indicates that members of Ceratosauridae survived well into the latter part of the Mesozoic. Hopefully, new specimens will shed light on these missing years of the Ceratosauridae lineage.

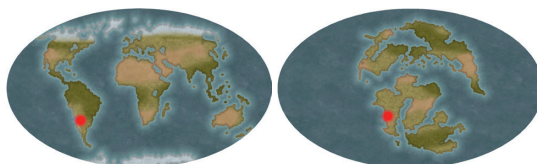
The generic name *Genyodectes* combines the Greek words “genys” (meaning “jaw”) and “dektēs” (meaning “bite”). The specific name *serus* means “late,” as Woodward believed that the species represented “one of the latest and most specialized members of its race.”

CLASSIFICATION

Dinosauria
 Saurischia
 Theropoda
 Neotheropoda
 Averostra
 Ceratosauria
 Ceratosauridae

LOCATION

Argentina

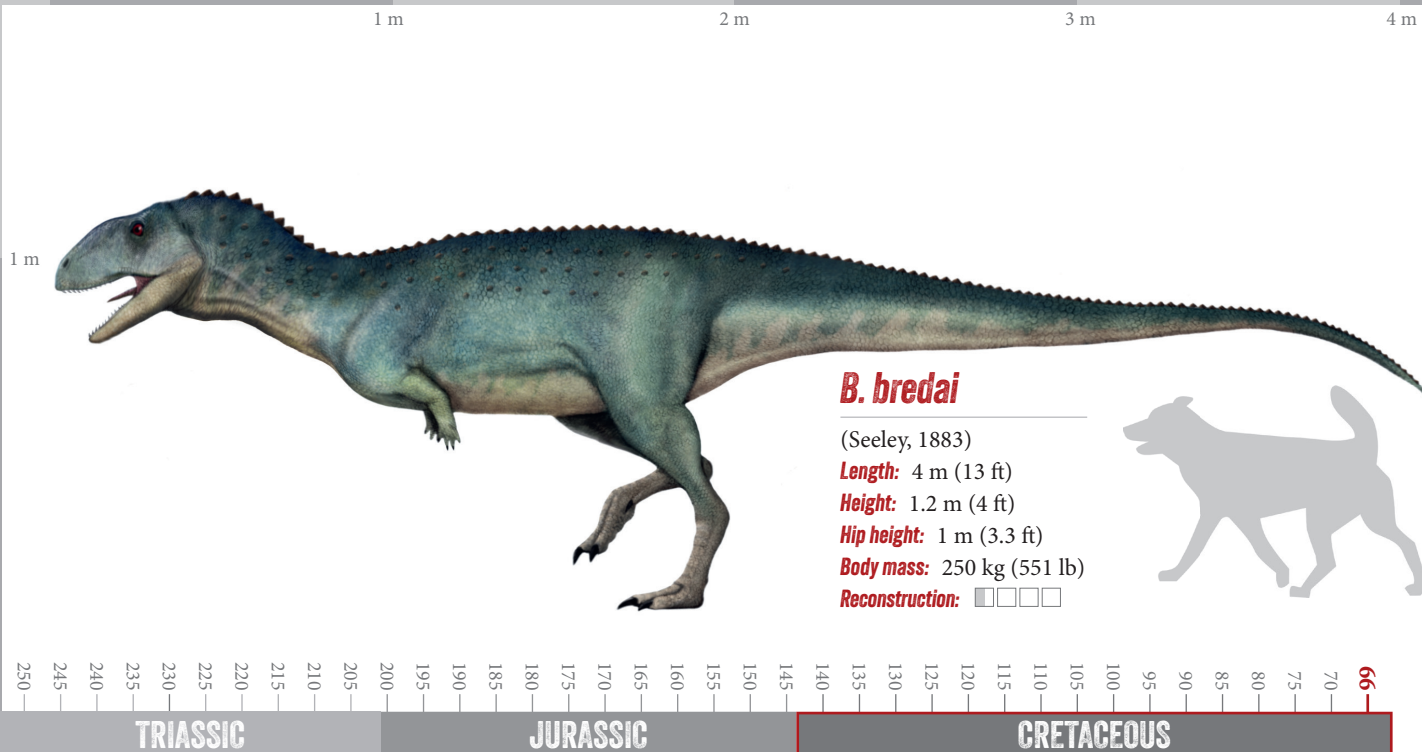


KNOWN REMAINS

Partial skull and jaw



BETASUCHUS



Betasuchus bredai (meaning “Breda’s ‘B’ crocodile”) is one of only two nonavian dinosaurs to be named from the Netherlands.

The holotype and only known material (NHMUK 42997), a fragment of a right femur, was discovered in the Netherlands in 1883 and named *Megalosaurus bredai* after the late Dutch scientist Jacob Gijsbertus Samuel van Breda, who had acquired the fossil sometime between 1820 and 1860. He did not unearth the remains personally, but purchased them from workers of a chalkstone quarry who had excavated various sites; thus, it is not possible to pinpoint the location of its discovery. Based on other fossils found in the general region, however, *Betasuchus* can be estimated to be about 67–66 million years old.

The top portion of the femur is the only material that was preserved; a portion of the distal end was lost when the bone was sawed cleanly in half by quarry workers, and the head of the bone was marred by other saw-borne cuts.

In 1926, Friedrich von Huene reevaluated the fossil and revealed that it belonged to a different genus than *Megalosaurus* (which had become a “wastebin taxon,” where numerous unrelated carnivorous dinosaurs were thrown together). Von Huene considered the specimen to belong to an ornithomimosaurian and formally renamed *M. bredai* as *Betasuchus* in 1932.

Because the genus is known from only a single poorly preserved bone from an indeterminate location, many researchers have dubbed it as *nomen dubium* (a doubtful or invalid name). Some, however, have argued that the fossil shows enough unique features to be considered valid. *Betasuchus* is generally thought to have been an abelisaurid, but an alternative view is that it is a relative of *Dryptosaurus* (Le Loeuff and Buffetaut, 1991; Carpenter et al., 1997).

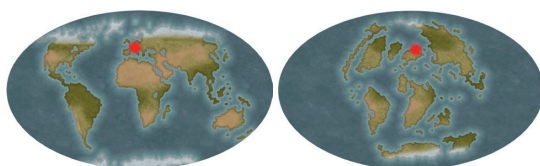
The generic name literally means “B-crocodile,” while the specific name honors the fossil’s first owner, Jacob van Breda.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Neotheropoda
Averostra
Ceratosauria
Abelisauroidae

LOCATION

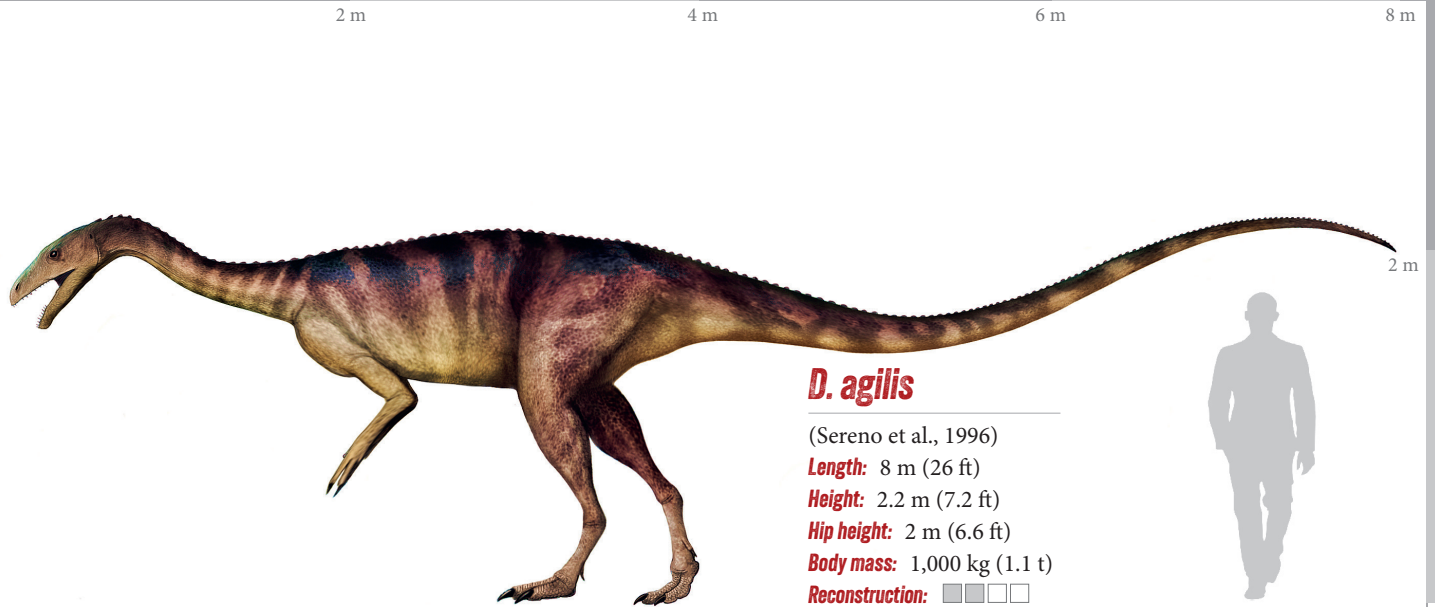
Netherlands



KNOWN REMAINS

Partial right femur





Deltadromeus agilis (meaning “agile delta runner”) is an unusual dinosaur whose taxonomic placement has been debated for years. Various interpretations have placed *Deltadromeus* as a coelurosaur, allosaur, or megaraptoran. The most common interpretation, however, places the animal as a ceratosaur—specifically, as a member of the **Noasauridae** (Rauhut and Carrano, 2016; Ibrahim et al., 2020). Confounding the matter, though, *Deltadromeus* shares many features with *Gualicho shinyae*, which may be a carnosaur or megaraptoran (Apesteguía et al., 2016).

The holotype of *Deltadromeus* (UCRC PV11) is the only confirmed skeletal material belonging to the genus. Several other fragmentary specimens were initially referred to the genus, but they have since been questioned, because many originate from different localities (Mortimer, 2014).

It has also been noted that the holotype material of *Deltadromeus* bears a striking resemblance to a different dinosaur, *Bahariasaurus ingens*. *Bahariasaurus* was named

in 1934 from specimens discovered in Egypt. Sadly, all of the specimens of *Bahariasaurus* were destroyed in World War II, so a detailed comparison of the two sets of fossils cannot be conducted. Some have still suggested, though, that the two genera may be synonymous. If so, then the estimated 8-meter length of *Deltadromeus* would not represent a fully grown individual, as the *Bahariasaurus* specimen is estimated to have been 10–12 meters in length (Holtz, 2007).

No skull is known from the specimen, so the diet of *Deltadromeus* is unknown. The most striking feature of the skeleton, its long and slender legs, suggest the animal was fast and agile.

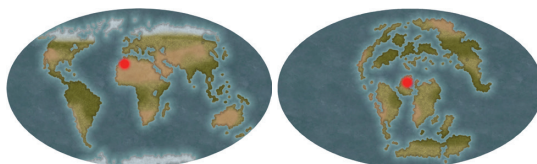
The first portion of the generic name *Deltadromeus* refers to the dinosaur’s suspected habitat of a river delta; the holotype material was found alongside the teeth of sawfish and crocodyliforms. This is attached to “dromeus,” the Greek word for “runner,” in reference to the animal’s perceived agility; the specific name *agilis* is Latin for “agile” or “quick.”

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Averostra
Ceratosauria
Abelisauroidae
Noasauridae

LOCATION

Morocco



KNOWN REMAINS

Partial skeleton



BERTHASAURA



B. leopoldinae

(de Souza et al., 2021)

Length: 1 m (3.3 ft)

Height: 0.4 m (1.3 ft)

Hip height: 0.25 m (10 in)

Body mass: 10 kg (22 lb)

Reconstruction:



Berthasaura leopoldinae (meaning “Bertha’s and Leopoldina’s lizard”) is one of the only ceratosaurs known to be edentulous (lacking in teeth). The only other example, *Limusaurus*, is known to have possessed teeth early in its life and then lost them after maturity. *Berthasaura*, on the other hand, might have possessed no teeth at any point of its life cycle. This conclusion was reached because the only known specimen is a juvenile, and it was already toothless—as confirmed by a CT scan of the remains. Regardless, *Berthasaura* and *Limusaurus* are not thought to be very closely related; this could suggest that toothlessness evolved more than once among **Noasauridae**.

As modern birds demonstrate, simply possessing a toothless beak does not necessarily mean that a creature is herbivorous. Indeed, certain features of the skull suggest that *Limusaurus*’s parrot-like beak possessed a “cutting

edge.” Lacking in any other evidence, such as gastroliths, it is speculated that *Berthasaura* had an omnivorous diet.

The holotype material (MN 7821-V) was unearthed in the Cemitério dos Pterossauros Quarry, a site that became famous in 2011 for being a bone bed of plentiful pterosaur remains. Another noasaurid from the same location, *Vespersaurus*, was previously described in 2019. The exact age of the stratum from the discovery site is unknown, with estimates ranging between 110 and 70 million years of age.

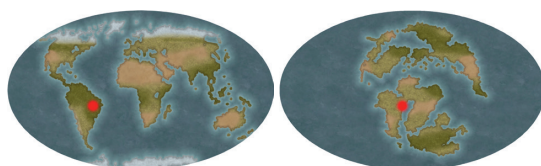
The generic name honors Bertha Maria Júlia Lutz (1894–1976), a scientist and women’s rights activist from Brazil. Instead of the typical suffix “saurus,” the term was feminized here as “saura.” The specific name refers to Maria Leopoldina, the first Brazilian empress (1797–1826); this was meant to reference the country’s upcoming (at the time of naming) bicentennial in 2022.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Averostra
Ceratosauria
Abelisauroidae
Noasauridae

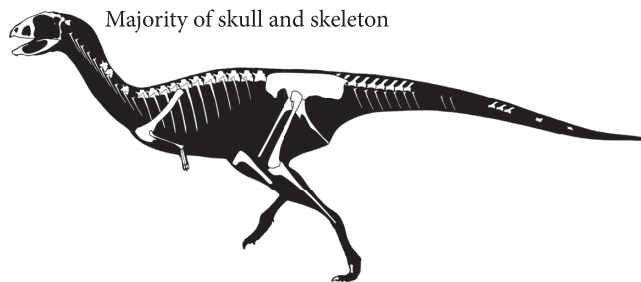
LOCATION

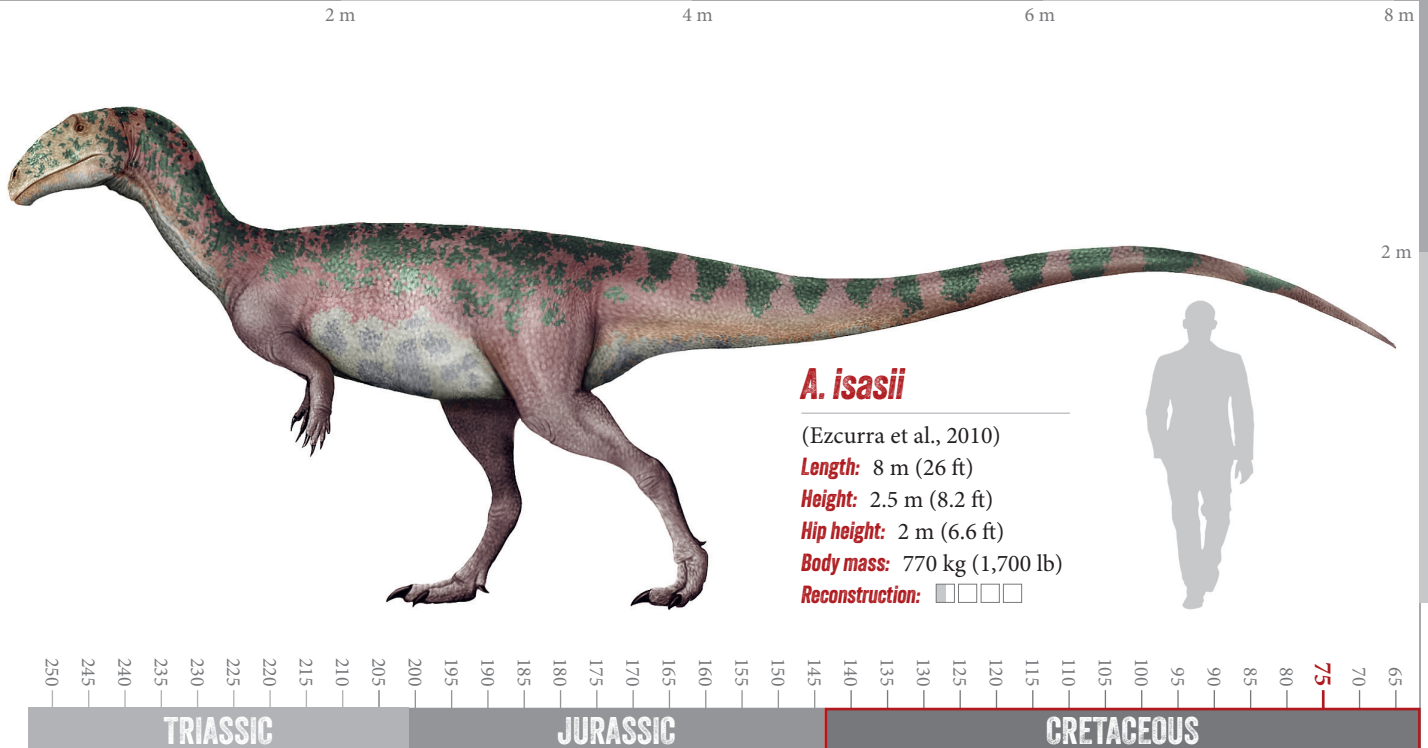
Brazil



KNOWN REMAINS

Majority of skull and skeleton





Austrocheirus isasii (meaning “Isasi’s southern hand”) is an intriguing specimen known only from fragmentary remains.

One of the most remarkable evolutionary changes seen as **Abelisauroidea** moved into the Cretaceous has been the reduction of the forelimb, as seen in species such as *Carnotaurus* and *Majungasaurus*. *Austrocheirus* is the first medium-sized abelisauroid from the Late Cretaceous discovered with nonatrophied hands. This suggests that the evolutionary pressures that reduced the forelimbs of more derived abelisaurids may not have been directly tied to their large size.

The holotype (MPM-PV 10003) was discovered in the Pari Aike Formation; the exact age of this formation has been adjusted several times based on various measurements. It is currently believed to date to the Middle Campanian of the Late Cretaceous (Novas et al., 2019).

Since the remains include such a small number of bones, the phylogenetic placement of *Austrocheirus* has been

contentious. It was originally assigned to the basal region of Abelisauroidea. Shortly thereafter, another analysis challenged this idea, suggesting that the remains could not be identified any more specifically than “indeterminate theropod,” partially because the set of data used in the original description did not include a wide enough variety of theropods for comparison (Rauhut, 2012). However, an expanded version of the original analysis still placed *Austrocheirus* within Abelisauroidea (Cau, 2010). Additionally, a subsequent analysis went further, placing the genus within **Noasauridae** (Tortosa et al., 2014).

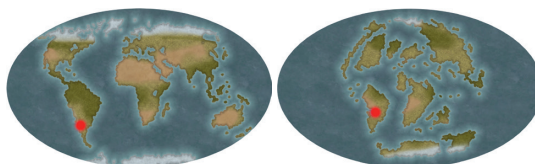
The generic name *Austrocheirus* combines the Greek words “austros” (meaning “south”) and “cheirus” (meaning “hand”), in reference to the dinosaur’s distinctive hands. The specific name *isasii* honors Marcelo Isasi, the discoverer of the holotype specimen.

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Averostra
Ceratosauria
Abelisauroidea
Noasauridae

LOCATION

Argentina

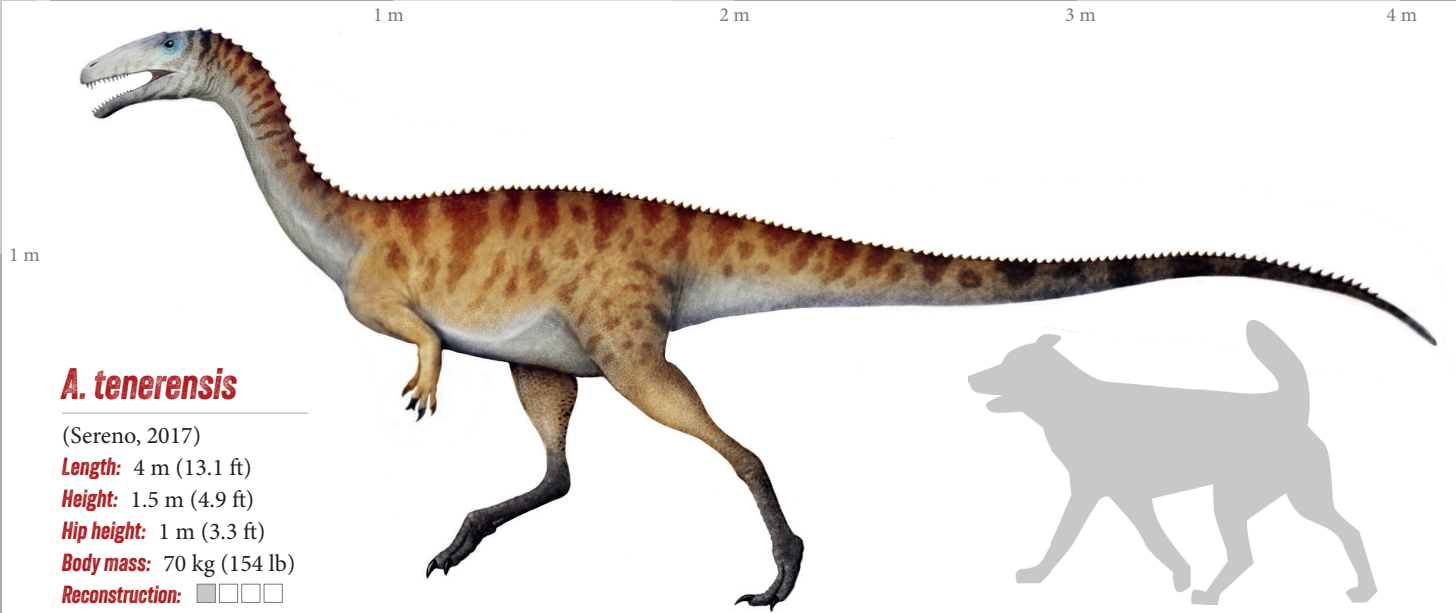


KNOWN REMAINS

Fragmentary elements



▶ AFROMIMUS



A. tenerensis

(Serenó, 2017)

Length: 4 m (13.1 ft)

Height: 1.5 m (4.9 ft)

Hip height: 1 m (3.3 ft)

Body mass: 70 kg (154 lb)

Reconstruction: ☐ ☐ ☐ ☐

Afromimus tenerensis (meaning “Africa mimic from Ténéré”) is an enigmatic noasaurid whose peculiar traits have made it the subject of much debate regarding its exact evolutionary placement.

The holotype and only known specimen (MNBH GAD112) was unearthed in 1997 in the Ténéré Desert. During the Cretaceous, this region sported numerous rivers and plentiful greenery. Many of the *Afromimus* fragments were exposed and weathered when discovered, suggesting that more of the skeleton may have been present at one time before being eroded away. Based on vertebral fusing, the specimen is believed to have been fully grown.

In the original scientific description of the fossils, the author assigned *Afromimus* to the group Ornithomimosauria, the same group that includes the famous *Gallimimus*, despite noticing certain similarities between *Afromimus* and the abelisauroids (Serenó, 2017).

Subsequent analyses have challenged this classification, noting that many of the diagnostic traits used to assign *Afromimus* to Ornithomimosauria can be found within Ceratosauria as well. Ensuing phylogenetic examinations have placed *Afromimus* within at least Abelisauroidea, or possibly even **Noasauridae** (Cerroni et al., 2019; Baiano et al., 2020).

This phylogenetic debate is not unique to *Afromimus*; many of the noasaurids present a confusing suite of traits, some of which bear striking similarity (at least superficially) to the ornithomimids.

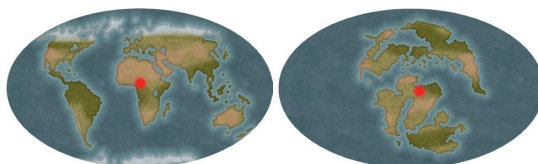
The generic name *Afromimus* combines the Latin word “Afro” (referring to “Africa”) and the Greek “mimos” (meaning “mimic,” a common suffix for the names of ornithomimosaurids). The specific name *tenerensis* refers to the fossil’s location of discovery, meaning “from the Ténéré Desert.”

CLASSIFICATION

Dinosauria
Saurischia
Theropoda
Averostra
Ceratosauria
Abelisauroidea
Noasauridae

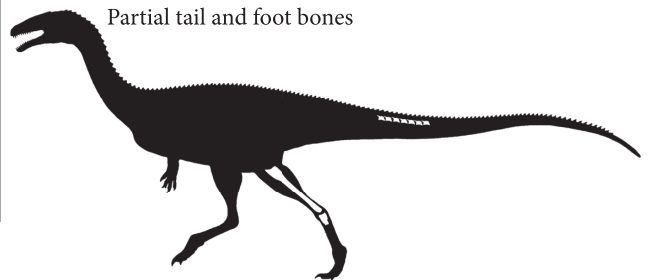
LOCATION

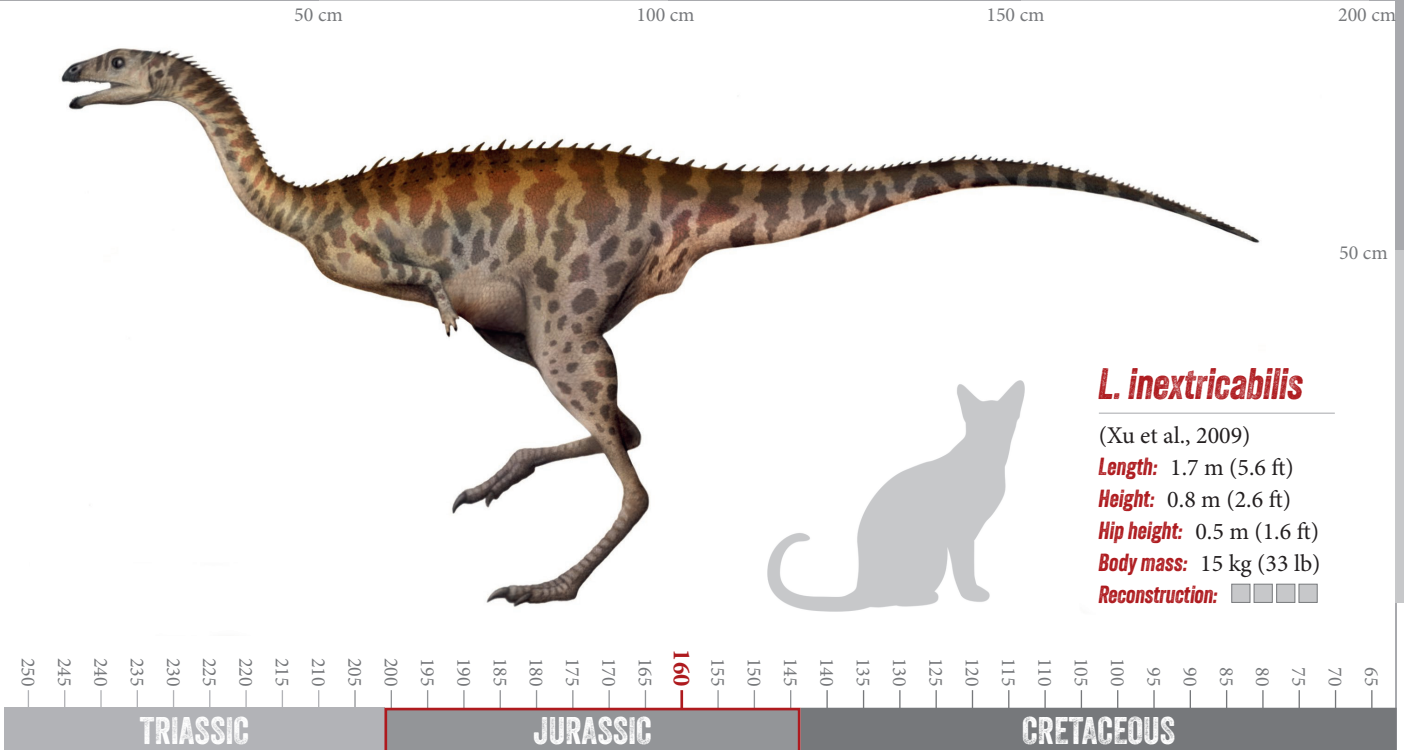
Niger



KNOWN REMAINS

Partial tail and foot bones





Limusaurus inextricabilis (meaning “mud lizard who could not escape”) is an intriguing dinosaur, possessing unusual traits that are important for understanding a variety of evolutionary topics.

Limusaurus is known from at least 19 individuals of various ages, which gives paleontologists a unique glimpse into the ontogeny (developmental growth) of the species. The most surprising discovery concerning the dinosaur’s growth was that young individuals possessed a full set of teeth, whereas adults had a toothless beak. Using CT scan data, it was determined that this process of tooth loss was a slow and complex development. Based on this, it is likely that *Limusaurus* of different ages had different diets. The presence of gastroliths suggests that adults had a mostly herbivorous diet, and it is speculated that the juveniles therefore required a more omnivorous diet (Wang et al., 2017).

The digits present on the hands of *Limusaurus* also raise interesting questions. In modern birds, it can be seen from embryological development that digits II, III, and IV go on to form the bones of the fully formed wing. However, many theropods possess tridactyl hands that feature digits I, II, and III. *Limusaurus*, by contrast, has digits II, III, and IV but also a small, vestigial digit I. This has prompted some scientists to speculate that the digits of various tridactyl theropods have been misidentified all along—they do not have digits I, II, and III, but digits II, III, and IV. This is a controversial opinion, and debate rages on (Vargas et al., 2009).

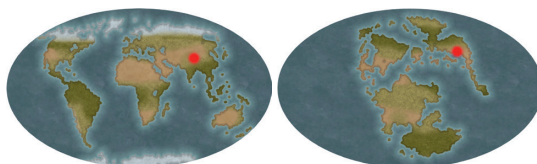
The generic name *Limusaurus* combines the Latin word “limus” (meaning “mud” or “mire”) and the Greek word “saurus” (meaning “lizard”). The specific epithet *inextricabilis* means “unable to extricate”; both names refer to the entombment of the specimens in mudstone from a marsh environment.

CLASSIFICATION

Dinosauria
Theropoda
Averostra
Ceratosauria
Abelisauroidea
Noasauridae
Elaphrosaurinae

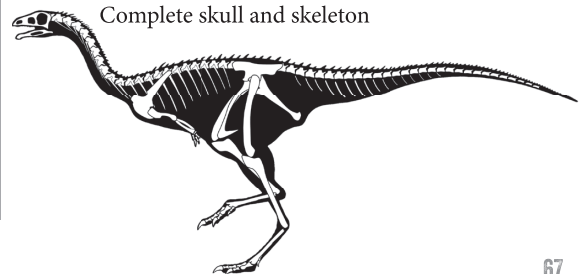
LOCATION

China

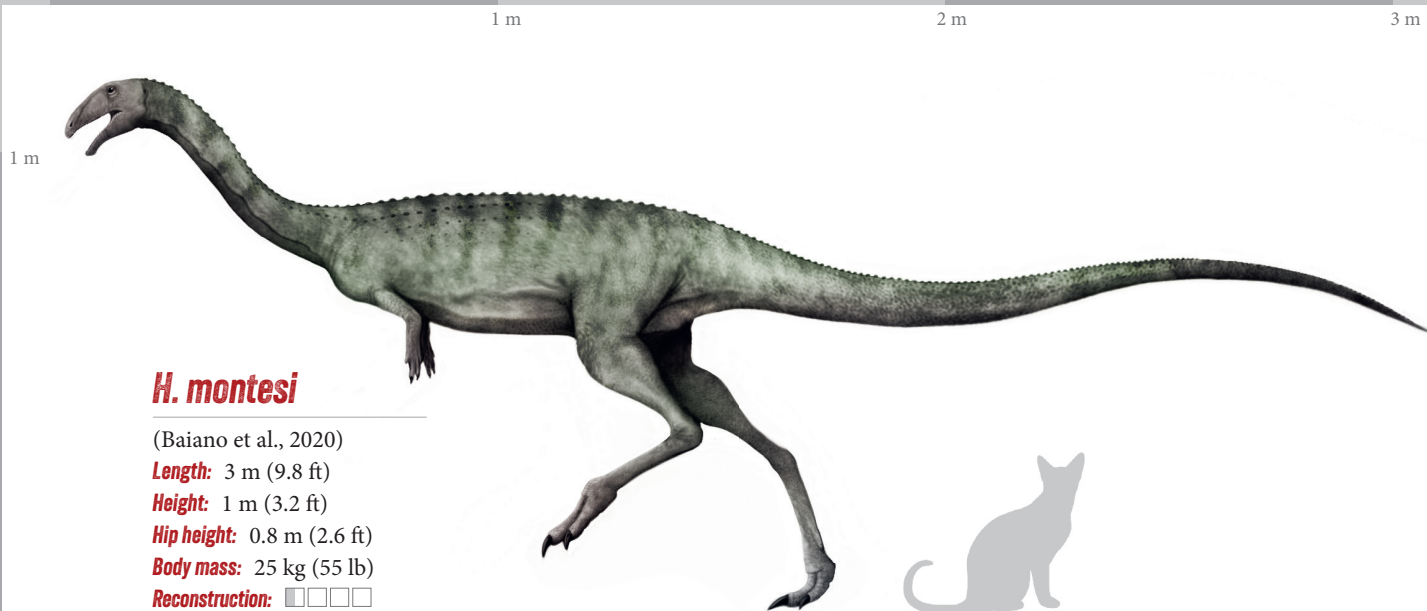


KNOWN REMAINS

Complete skull and skeleton



HUINCULSAURUS



H. montesi

(Baiano et al., 2020)

Length: 3 m (9.8 ft)

Height: 1 m (3.2 ft)

Hip height: 0.8 m (2.6 ft)

Body mass: 25 kg (55 lb)

Reconstruction: ☐ ☐ ☐ ☐



Huinculsaurus montesi (meaning “Montes’s lizard from Huincul”) is known from only a few bones, but these are distinctive enough to place the animal within the group **Elaphrosaurinae**.

The holotype and only known specimen (MCF-PVPH-36) was unearthed in the early 1990s but went undescribed until 2020. It was discovered in the Huincul Formation, which is thought to have been an arid environment with seasonal streams during the Late Cretaceous. Fossils from this locality tend to be rare, but several prominent specimens have been unearthed from the formation, such as *Argentinosaurus*. Approximately 10 meters from the *Huinculsaurus* discovery site, the holotype material for the abelisaurid *Ilokelesia* was also discovered.

The total absence of fusion between the fossil’s vertebral arches indicates that the specimen is in an early stage of development. As a result, the individual was most likely still a long way from attaining the size of a mature adult.

Huinculsaurus, along with *Afromimus*, *Limusaurus*, and *Elaphrosaurus*, are helping paleontologists paint a picture of the members of **Noasauridae** as “ornithomimosaur-mimics.” While ornithomimosaurs such as *Struthiomimus* occupied certain ecological niches in the Northern Hemisphere, it seems that these long-legged abelisauroids were filling similar roles in other areas, such as Western Gondwana. If these noasaurids were indeed prevalent in the Southern Hemisphere, it could help explain why certain kinds of maniraptoriforms have scarcely been found in Africa or South America (Baiano et al., 2020).

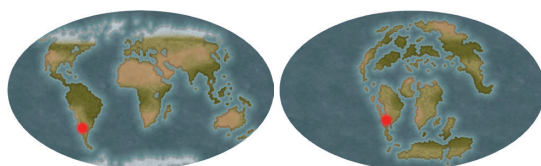
The first portion of the generic name *Huinculsaurus* refers to the Huincul Formation, where the fossil material was discovered; the second portion affixes the Greek word “saurus” (meaning “lizard”). The specific name *montesi*, honors the late Eduardo Montes, the technician who prepared the holotype specimen.

CLASSIFICATION

Dinosauria
Theropoda
Averostra
Ceratosauria
Abelisauroidea
Noasauridae
Elaphrosaurinae

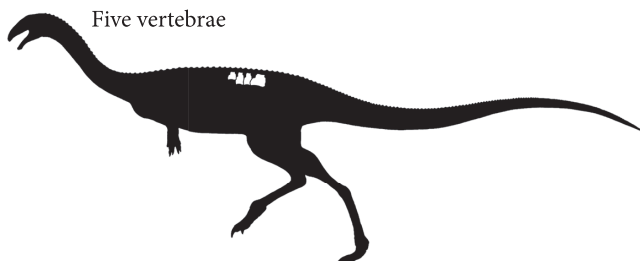
LOCATION

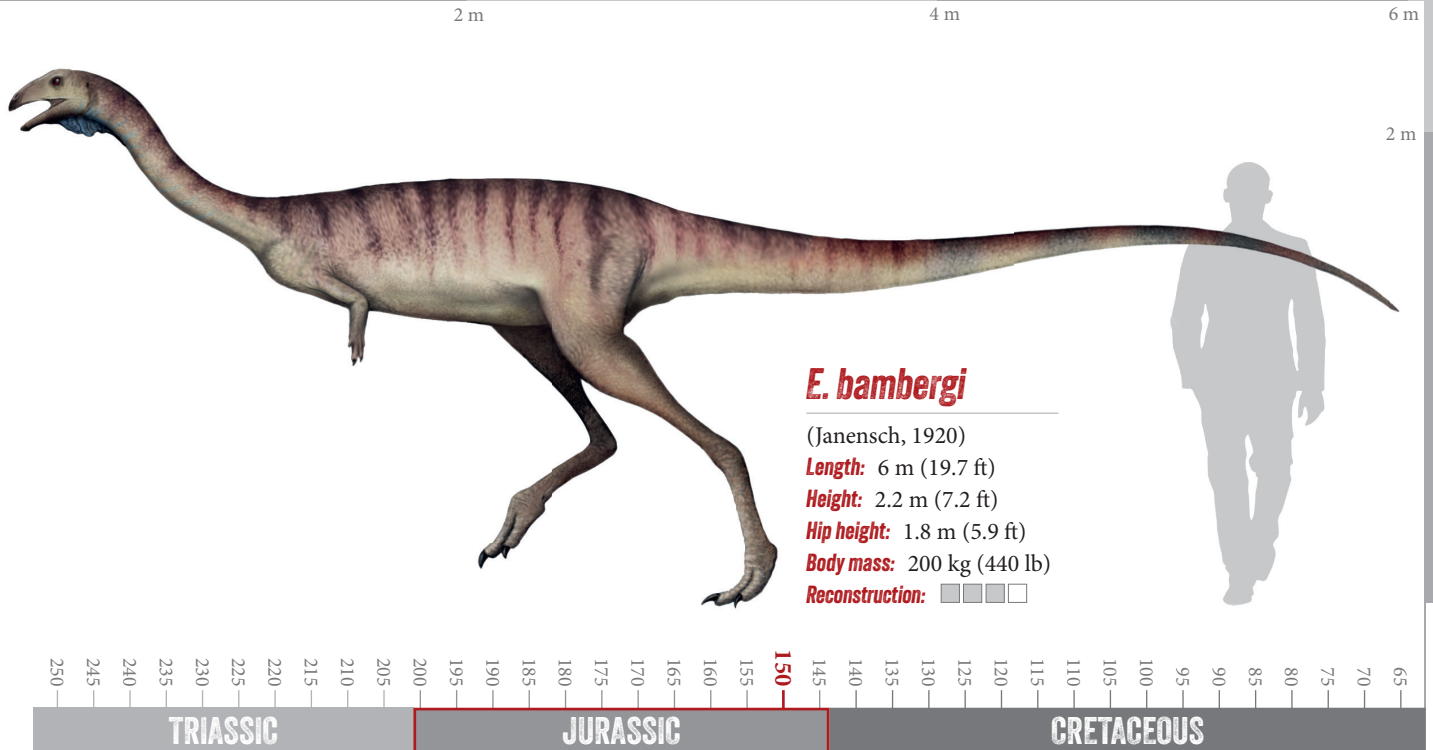
Argentina



KNOWN REMAINS

Five vertebrae





Elaphrosaurus bambergi (meaning “Bamberg’s light-footed lizard”) was unearthed by Werner Janensch in 1910 in the Tendaguru Formation in Tanzania. This specimen (HMN Gr.S. 38–44) is currently the only undisputed example of *Elaphrosaurus*; various fragmentary and scattered remains have also been assigned to the genus—many by Janensch—but most have had their validity or accuracy disputed over the years. Numerous other species have also been assigned to the genus, although all have since been disputed or reassigned to new genera, leaving *E. bambergi* as the only widely accepted valid example.

Janensch recognized that *Elaphrosaurus* was a peculiar animal that did not fit neatly within any known family of theropods, and thus he assigned it as a coelurosaurian (which at the time was used as a catchall group). As recently as 1990, it had been classified by some as an ornithomimid. More recently, however, careful reanalysis has revealed

that *Elaphrosaurus* is a **ceratosaur** (Carrano and Sampson, 2008) and, more specifically, a member of the **Noasauridae** (Rauhut and Carrano, 2016).

With no known skull material, it is difficult to determine what sort of diet or niche best fits *Elaphrosaurus*. Modern reconstructions, like the illustration here, base their appearance on *Limusaurus*, the closest known relative of *Elaphrosaurus* that features preserved skull material. Janensch referred a great many fossilized teeth to the genus, but their validity is doubtful.

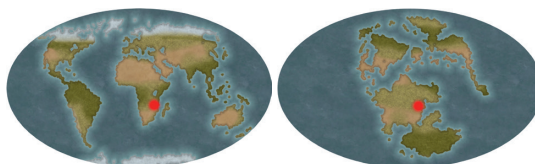
The generic name *Elaphrosaurus* combines the Greek words “elaphros” (meaning “light-footed,” referring to the animal’s presumed speed) and “sauros” (meaning “lizard”). The specific name *bambergi* is meant to honor Paul Bamberg, a businessman who financially supported various Tendaguru paleontological expeditions.

CLASSIFICATION

Dinosauria
 Theropoda
 Averostra
 Ceratosauria
 Abelisauroidae
 Noasauridae
 Elaphrosaurinae

LOCATION

Tanzania

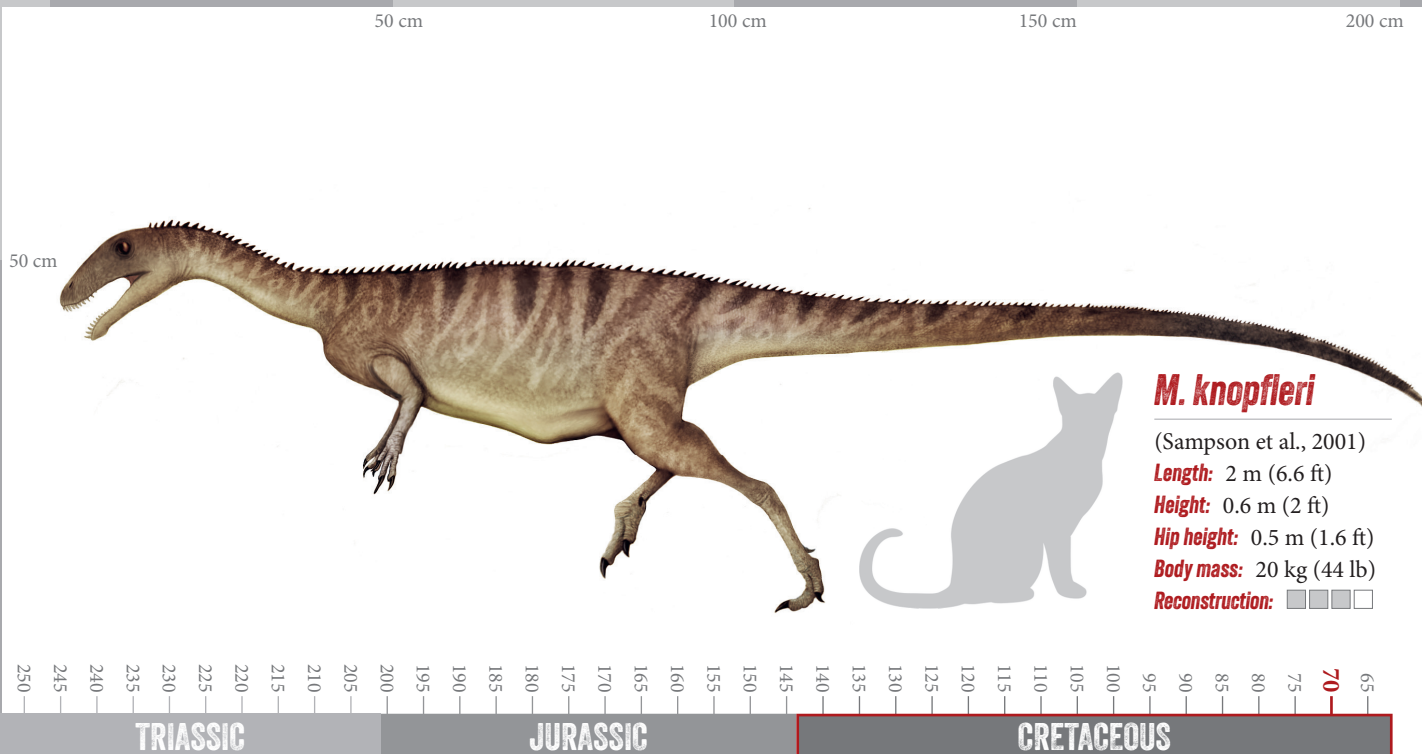


KNOWN REMAINS

Majority of skeleton



MASIAKASAURUS



Masiakasaurus knopfleri (meaning “Knopfler’s vicious lizard”) is a unique dinosaur that offers tantalizing clues into the obscure group of theropods known as the **noasaurids**.

The original specimen, described in 2001, comprised about 40% of the animal’s total skeleton. Numerous specimens from multiple localities were unearthed in the following years and were collectively described in 2011. Now known from most of the skeleton and skull, *Masiakasaurus* is among the most complete noasaurid dinosaurs known to science (Carrano et al., 2011).

The most striking feature of *Masiakasaurus* is its forward-projecting front teeth (see illustration in the introduction to the Ceratosauria). The first set of teeth in the upper and lower jaw are so procumbent that they are nearly horizontal. This adaptation was most probably utilized for grasping small prey items; hypothesized feeding behaviors for *Masiakasaurus* include a piscivorous diet, snatching fish

from the water’s edge, or a specialization in seizing small reptiles or mammals.

The original 2001 specimen did not preserve the skull’s snout region, so early reconstructions of *Masiakasaurus* often depicted an incorrect orientation of the upper front teeth. Additionally, based on a misinterpretation of a related species, *Noasaurus*, *Masiakasaurus* was once thought to possess a recurved raptor-like foot claw, but this has since been determined to be a misidentified hand claw.

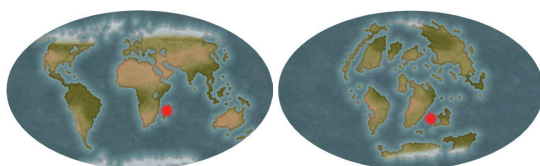
The generic name *Masiakasaurus* combines the Malagasy word “masiaka” (meaning “vicious”) and the Greek “sauros” (meaning “lizard”). Malagasy is the national language of Madagascar. The specific name *knopfleri* references the musician Mark Knopfler, since the expedition crew frequently listened to his music while unearthing the original material.

CLASSIFICATION

Dinosauria
Theropoda
Averostra
Ceratosauria
Abelisauroidae
Noasauridae
Noasaurinae

LOCATION

Madagascar



KNOWN REMAINS

Majority of skeleton and skull



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