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LITHOSTROTIA

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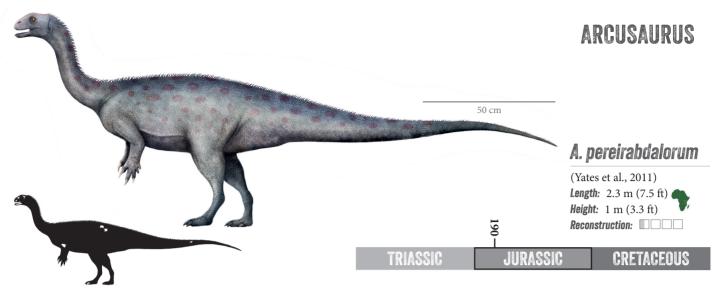
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SALTASAUROIDEA

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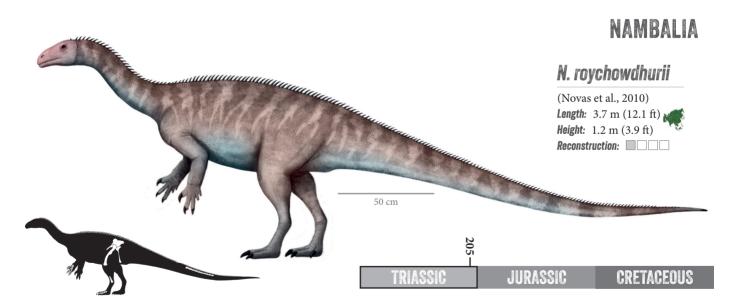
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Arcusaurus pereirabdalorum (meaning "Pereira's and Abdala's rainbow lizard") is an enigmatic sauropodomorph, one which is difficult to classify accurately because of the incompleteness of its known skeletal remains. With only some portions of the skull and a few other fragments, there is little information upon which to base a phylogenetic analysis. Further confounding the issue is that the individual was a juvenile at the time of its death—immature skeletal remains tend to skew phylogenetic results in the

basal direction. According to the describers, *Arcusaurus* is most likely a late-surviving example of a basal species, although it does also share traits with more contemporary *Plateosaurus*.

The generic name *Arcusaurus* combines the Latin "arcus" (meaning "rainbow") and the Greek "sauros" (meaning "lizard"), alluding to South Africa being known as the "rainbow nation." The specific name *pereirabdalorum* honors fossil discoverers Lucille Pereira and Fernando Abdala.

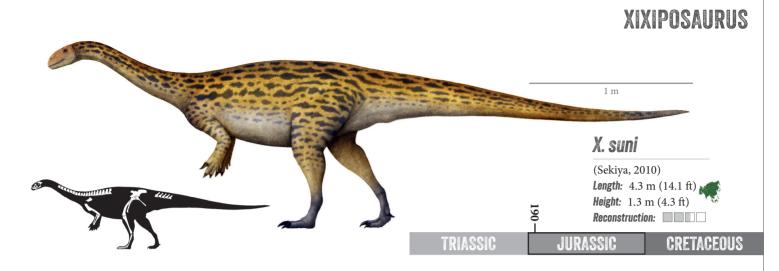


Nambalia roychowdhurii (meaning "Roy Chowdhuri's one from Nambal") is a little-studied genus that has thus far been closely examined only by the original study that described it. In this study, it was found to be a very basal sauropodomorph, closely related to *Thecodontosaurus* and *Efraasia*.

Nambalia is known from fossil elements that were gathered from a small erosion slope, representing the remains of at least three different individuals, judging by

overlapping elements including foot bones. Its hands have been described as gracile and similar to those of *Herrerasaurus* and *Guaibasaurus*. The femur is discernible from that of *Alwalkeria*, one of the only other Triassic dinosaurs known from India.

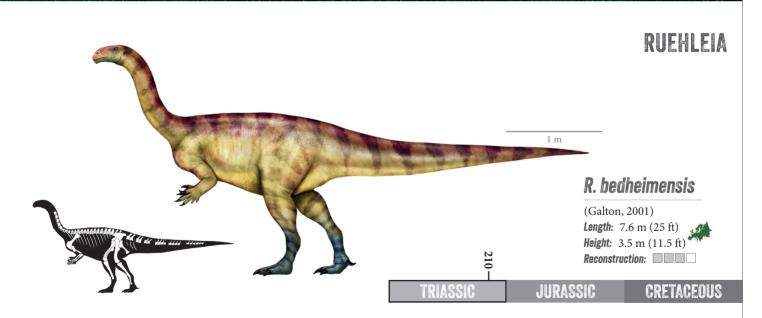
The generic name *Nambalia* refers to the town of Nambal, India, near where the fossils were located. The specific name *roychowdhurii* honors paleontologist Roy Chowdhuri.



Xixiposaurus suni (meaning "Sun's lizard from Xixipo") is a little-studied sauropodomorph. It was briefly described in a primarily Chinese-language journal, *Global Geology*, and the holotype specimen (ZLJ 01018, consisting of a skull, jaw, and partial skeleton) has not been examined by any subsequent works or included in phylogenetic analyses. This original paper concluded that *Xixiposaurus* was the sister taxon of

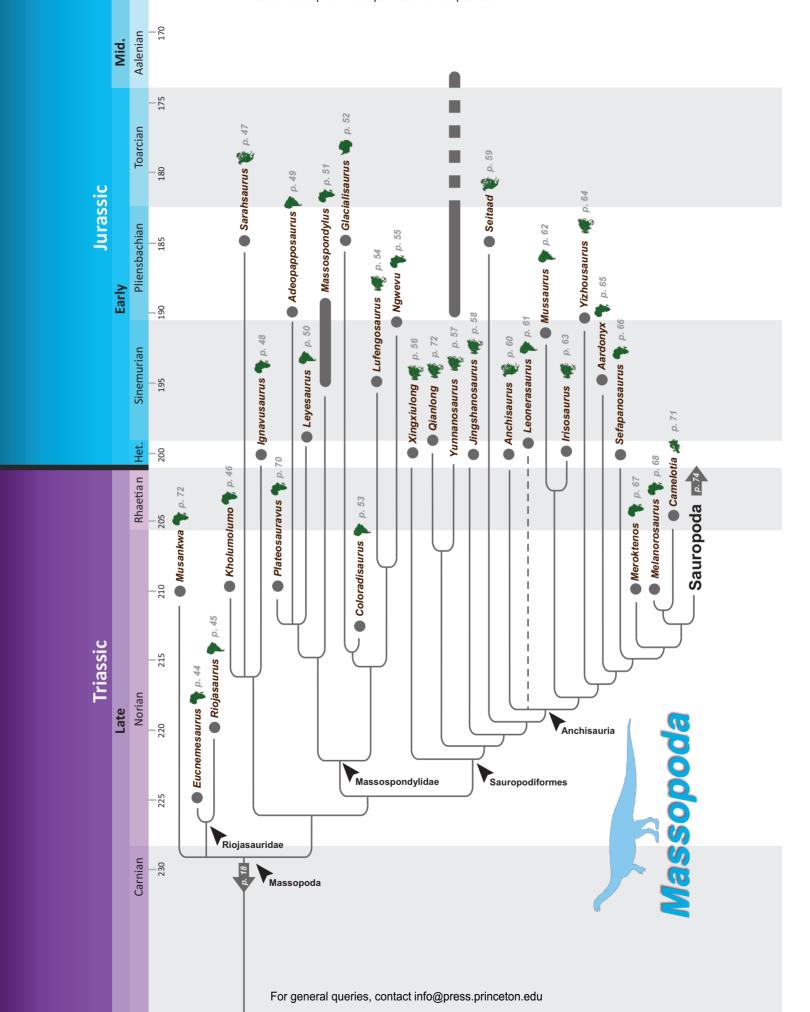
Mussaurus, both of which were considered to lie within Plateosauridae. The authors considered *Xixiposaurus* to be the "most derived taxon among Chinese prosauropod dinosaurs."

The generic name *Xixiposaurus* refers to the village of Xixipo in Lufeng County, China, where the holotype was discovered. The specific name *suni* honors Sun Ge, professor at Jilin University.



Ruehleia bedheimensis (meaning "Rühle's one from Bedheim"), a German sauropodomorph, was briefly described in the journal Revue de Paléobiologie in an addendum to an article about Plateosaurus. Differentiating the animal from Plateosaurus, which has 15 dorsal (back) vertebrae, Ruehleia has only 14. Additionally, the animal's sacrum (collection of fused hip vertebrae) is "dorsosacral" rather than "caudosacral," as seen in Plateosaurus.

According to *The Dinosauria* (Weishampel et al., 2004), the known remains of *Ruehleia* include one "nearly complete skeleton" as well as "2 incomplete skeletons, juvenile to adult." The holotype was originally referred to as an "unnumbered" specimen from the Berlin Museum of Nature; a later paper would refer to the remains as MB.R.4718–42 (Otero, 2018). The animal was named for the German paleontologist Hugo Rühle von Lilienstern of Bedheim.



The name Massopoda comes from the Latin "massa" (meaning "lump") and from the Greek "podi" (meaning "foot"). It is also a contraction of the names Massospondylidae (a family within the group) and Sauropoda.

The massopods include many animals that once fell within the umbrella of the "prosauropod" group. In the past, it was thought that the various genera within Plateosauridae, Riojasauridae, and Massospondylidae were all members of a monophyletic group—in other words, that they shared their own singular branch on the family tree, known as Prosauropoda. However, this view began falling out of favor in the 2000s, as it became clear that these various families were paraphyletic with respect to sauropods, branching off the family tree at numerous points along the way.

There is a high degree of variability regarding the exact placements of most species near the **Massopoda** node on the sauropodomorph family tree. One common thread, though, places *Eucnemesaurus* and *Riojasaurus* as sister taxa within their own group, **Riojasauridae**, at the very base of Massopoda (Wang et al., 2017b; Rauhut et al., 2020; Fernández and Werneburg, 2022), although they have been placed even more basally (Beccari et al., 2021) or in a more derived position (Peyre de Fabrègues et al., 2020; Zhang et al., 2020). The describers of *Musankwa* placed it as the basalmost massopod (Barrett et al., 2024).

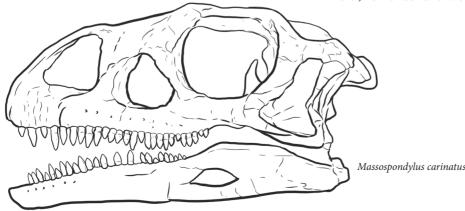
Sarahsaurus has variably been placed basal to Massospondylidae (Peyre de Fabrègues and Allain, 2020; Rauhut et al., 2020; Fernández and Werneburg, 2022), within that family (Chapelle et al., 2019), or more derived than it (Beccari et al., 2021). The description of Kholumolumo placed it as the sister taxon to Sarahsaurus (Peyre de Fabrègues and Allain, 2020). Ignavusaurus has not been included in as many analyses, but those that have included it tend to find it to be very closely related to Sarahsaurus as well (Apaldetti et al., 2011; Chapelle et al., 2019). Massospondylidae is currently accepted as being its own family and thus not being directly ancestral to the true sauropods; which species belong in the group, though, is unsurprisingly ambiguous. In addition to Massospondylus, Adeopapposaurus and Leyesaurus are regarded as definite members and as sister taxa (Peyre de Fabrègues et al., 2020; Zhang et al., 2020).

Additionally, *Glacialisaurus*, *Coloradisaurus*, and *Lufengosaurus* are most often grouped into their own clade within Massospondylidae (Rauhut et al., 2020; Beccari et al., 2021; Fernández and Werneburg, 2022). The description of the newer genus *Ngwevu* placed it as the sister taxa to *Lufengosaurus* (Chapelle et al., 2019). Although *Plateosauravus* has been depicted in almost any position imaginable among the early sauropodomorphs, the most recent comprehensive study on the genus identified it as a massospondylid (Krupandan, 2019).

Yunnanosaurus, Jingshanosaurus, and Seitaad have sometimes been placed as closely related genera within Massospondylidae (Rauhut et al., 2020; Beccari et al., 2021) but are more commonly shown (in various configurations) as being among the basalmost **Sauropodiformes** (Wang et al., 2017b; Zhang et al., 2020; Fernández and Werneburg, 2022). Xingxiulong has, at times, been placed as the very basalmost sauropodiform (Peyre de Fabrègues et al., 2020; Rauhut et al., 2020; Zhang et al., 2020), although it has also been placed as a massopod (Peyre de Fabrègues and Allain, 2020) and basally to the massospondylids (Fernández and Werneburg, 2022). Qianlong was placed by its describers as sister to Yunnanosaurus (Han et al., 2024).

Some analyses have placed *Anchisaurus* (and thus **Anchisauria**) basal to (and thus including) Massospondylidae (Peyre de Fabrègues et al., 2020; Zhang et al., 2020); however, this is not generally favored. *Mussaurus* and *Aardonyx* are often placed in the subsequent derived positions, along with *Sefapanosaurus* (Otero et al., 2015; Rauhut et al., 2020; Fernández and Werneburg, 2022). *Yizhousaurus* has been similarly placed by its describers (Zhang et al., 2020), and the describers of *Irisosaurus* placed it as the sister taxon of *Mussaurus* (Peyre de Fabrègues et al., 2020). Placement of the fragmentary *Leonerasaurus* is quite inconsistent between studies.

Hovering on the boundary of Sauropoda are *Melanoro-saurus* and the closely related *Meroktenos*, along with the enigmatic *Camelotia* (Apaldetti et al., 2018; Chapelle et al., 2019; Fernández and Werneburg, 2022).



EUCNEMESAURUS



Eucnemesaurus fortis (meaning "strong good tibia lizard") is a long-dormant genus that was recently revitalized.

Eucnemesaurus was originally described in 1920 by Egbert van Hoepen based on the specimen TrM 119, consisting of fragmentary vertebrae, leg bones, and hip bones. After that time, the genus was largely forgotten.

Starting in the 1860s, collections of fossils—mostly sauropodomorph bones—were sent by Alfred Brown to several European institutions. A distinctive femur (NMW 1889-XV-39) was identified by Friedrich von Huene in 1906 as belonging to the now-dubious "prosauropod" *Euskelosaurus browni*, although this was not to last. In 1985, the femur, along with a carnivorous upper-jaw bone, was reinterpreted by Peter Galton as the remains of a herrerasaurid-type theropod. Together, these fossils formed the holotype of the now-debunked chimera *Aliwalia rex*,

which, owing to the large size of the femur, was interpreted as a gargantuan *Herrerasaurus*-like carnivore.

Finally, in 2003, a new femur (BP/1/6111) was unearthed among other sauropodomorph remains, clarifying the nature of the aforementioned specimens: *Eucnemesaurus* was reestablished as a valid genus while *Aliwalia rex* was invalidated (Yates, 2007). This analysis also established that the genus was a close relation of *Riojasaurus*, which together form the family **Riojasauridae**.

In 2015, a new articulated set of remains (BP/1/6234) was identified as a second species, within the genus, *E. entaxonis* (McPhee et al., 2015).

The generic name *Eucnemesaurus* combines the Greek "eu" (meaning "good" or "true"), "kneme" (meaning "tibia"), and "sauros" (meaning "lizard"). The specific name *fortis* is Latin for "strong"; "entaxonic" is an anatomical term referring to the weight-bearing nature of the foot bones.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Riojasauridae

LOCATION South Africa

KNOWN REMAINS

Leg, hip, and fragments



44



Riojasaurus incertus (meaning "uncertain lizard from Rioja") was quite large for an early sauropodomorph; it also possessed dense leg bones, contrasted by its partially hollow, lightened vertebrae. This combination of traits could potentially indicate that *Riojasaurus* was something of a transitional form between the early, bipedal sauropodomorphs and the later, quadrupedal sauropods.

Whether or not *Riojasaurus* could actually walk on all four legs is a matter that is open for debate. On the one hand, the animal's forelimbs are longer, proportionately, than those of more basal sauropodomorphs, making it easier for those appendages to touch the ground. *Riojasaurus* also had four sacral (hip) vertebrae, similar to later sauropods and unlike the three sacral vertebrae found in bipedal sauropodomorphs. However, researcher Scott Hartman has pointed out aspects of the animal's shoulders and spine that disfavor the quadrupedal interpretation, and no detailed

analyses of these options have been carried out in the last two decades.

CRETACEOUS

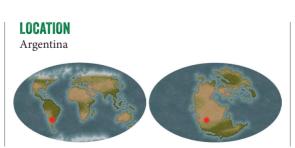
Some sources from the twentieth century suggested that *Riojasaurus* was most closely related to *Melanorosaurus*, but most modern analyses instead place *Riojasaurus* as one of the basalmost massopods (Müller et al., 2018), with one pushing its position even further back than that (Beccari et al., 2021). *Riojasaurus* is now thought to be most closely related to *Eucnemesaurus*, with these two genera being the only members of the family **Riojasauridae**.

A study of *Riojasaurus*'s scleral eye rings suggests that it was active at both day and night (Schmitz and Motani, 2011).

The generic name *Riojasaurus* refers to La Rioja Province in Argentina. The specific name *incertus* is Latin for "uncertain." The genus *Strenusaurus* (meaning "vigorous lizard") (Bonaparte, 1969) has been synonymized with *Riojasaurus* (Galton, 1985).

CLASSIFICATION

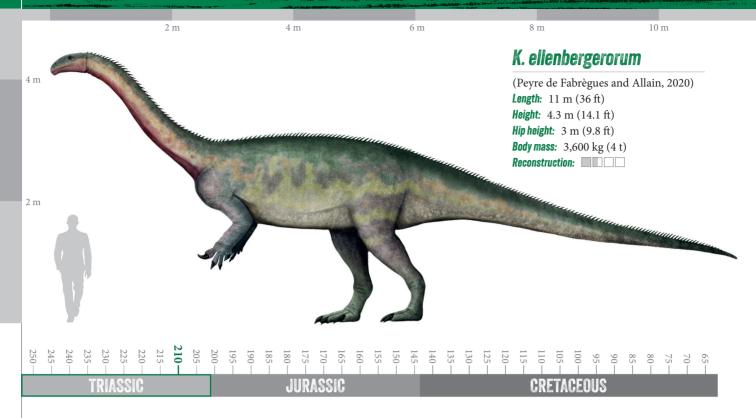
Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Riojasauridae



KNOWN REMAINS Nearly complete

45

KHOLUMOLUMO



Kholumolumo ellenbergerorum (meaning "Ellenbergers' dragon") is among the largest animals known to have lived during the Late Triassic. Despite its size, it was clearly a bipedal creature, not a quadruped.

Between the years of 1955 and 1970, a large quantity of dinosaur bones and trackways were discovered in Lesotho, in southern Africa. These discoveries were made adjacent to a large trash pile, known as a "thotobolo" in the indigenous Sotho language. A number of the fossils were initially attributed to *Euskelosaurus browni*; in 1970, the name "*Thotobolosaurus mabeatae*" was mentioned in literature as a suggested name but was never formally published. Similarly, an unpublished doctoral dissertation referred to the specimen by the name "*Kholumolumosaurus ellenbergerorum*" (Gauffre, 1996), but this too remained invalid. Finally, the total sum of the species' known remains (210 bones that

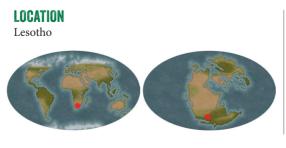
originate from at least five separate individuals) were described in 2020. Not every bone was thoroughly analyzed, though, and more material remains in museum collections.

The phylogenetic examination conducted on the *Kholumolumo* remains concluded that the animal was a member of the earliest-branching clade within **Massopoda**, sandwiched between Plateosauridae and Massospondylidae. The analysis showed that the creature's closest relatives (*Xingxiulong*, from China, and *Sarahsaurus*, from North America) were geographically widespread. This could suggest this particular lineage of sauropodomorphs originated in Gondwana before geographically dispersing.

The generic name *Kholumolumo* refers to a mythological dragon-like creature of indigenous Sotho folklore. The specific name *ellenbergerorum* honors paleontologists Paul and François Ellenberger.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda



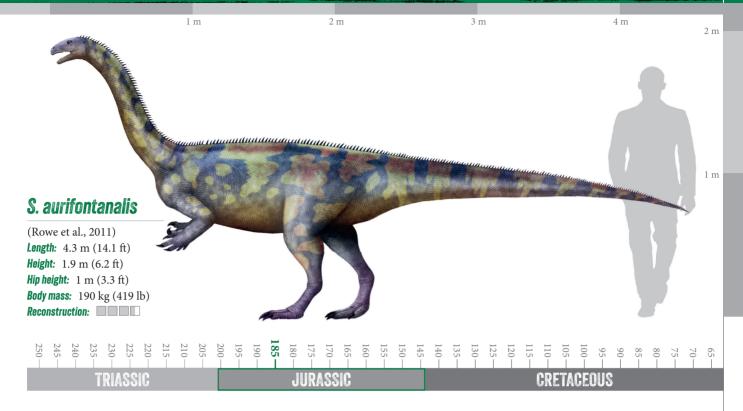
KNOWN REMAINS

Partial limbs, other fragments



46

SARAHSAURUS



Sarahsaurus aurifontanalis (meaning "Sarah's lizard from Gold Spring") is a possibly omnivorous North American sauropodomorph.

Sarahsaurus is known primarily from two specimens that were found at the same location (along with a juvenile *Dilophosaurus* and a handful of unidentified bones) in the 1970s. These remains include the majority of the skeleton but little skull material.

A third specimen, MCZ 8893 (consisting of a much more complete skull and jaw, but very little other skeletal material), was discovered in 1978 less than a kilometer away and was initially referred to *Massospondylus* (Attridge et al., 1985). Later works questioned this identification and referred to the specimen as the "undescribed Kayenta prosauropod" (Yates, 2003). When *Sarahsaurus* was first described, this specimen was referred to the new genus, based, in part, on the location of its discovery and that no characteristics that were shared between the specimens

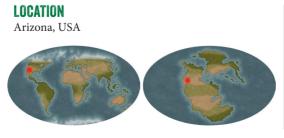
could clearly differentiate them. That being said, only one of the numerous tested characteristics could be used to unambiguously show their shared identity. The skull was also from an individual that was less mature than the other two specimens.

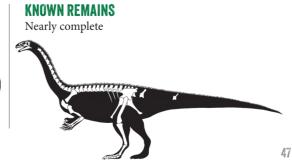
The exact phylogenetic positioning of *Sarahsaurus* depends on whether or not this third specimen is included in the analysis, as well as with which other genera it is being compared. A number of tested variations favored the interpretation of *Sarahsaurus* being a member of Massospondylidae, although some results show it placed in a more basal position (Apaldetti et al., 2011; Marsh and Rowe, 2018; Peyre de Fabrègues and Allain, 2020).

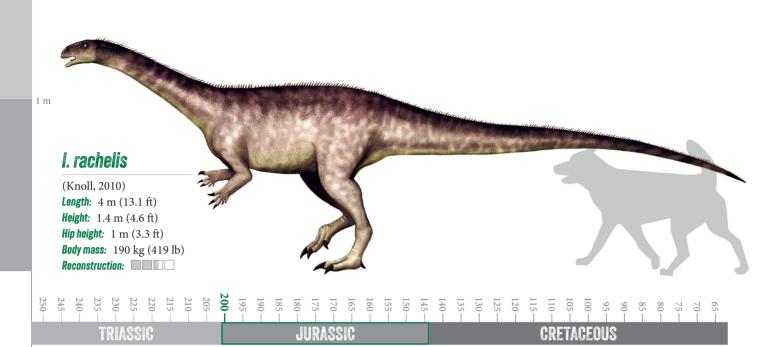
The generic name *Sarahsaurus* honors philanthropist Sarah "Mrs. Ernest" Butler. The specific name *aurifontanalis* combines the Latin "aurum" (meaning "gold") and "fontinalis" (meaning "of the spring"), in reference to where the holotype was discovered: Gold Spring, Arizona.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda







Ignavusaurus rachelis (meaning "Raquel's coward lizard") is known primarily from a partial yet well-preserved and mostly articulated specimen. Although the skull and jaw were fragmented into more than 100 pieces, numerous preserved teeth have shown that Ignavusaurus was likely more of a generalist or opportunist, as opposed to engaging primarily in herbivory. It had teeth of various shapes, with some being more pointed and less serrated than others, and the teeth generally lacked any of the overlapping placement seen in other early sauropodomorphs.

The holotype specimen (BM HR 20) is that of a juvenile, with an estimated body length measuring only 1.5 meters. This age determination was made based on the internal features of both the femur and humerus, which revealed that the individual was no more than one year of age. As such, the full size of an adult *Ignavusaurus* can only be estimated.

The immature nature of the skeletal remains has complicated the matter of determining the phylogenetic

placement of *Ignavusaurus*. The original description placed the animal quite basally, outside Massopoda, although a lack of certainty was emphatically expressed. Soon thereafter, another paper questioned the validity of the genus, suggesting that the specimen could actually be a juvenile *Massospondylus* (Yates et al., 2011). This notion, however, has not been universally accepted, with the two genera continuing to be considered separate and distinct by some studies. One more recent analysis placed the genus within Massospondylidae (Chapelle et al., 2019).

The generic name *Ignavusaurus* combines the Latin "ignavus" (meaning "coward") and the Greek "sauros" (meaning "lizard"); this refers to the name of the locality of the specimen's discovery, Ha Ralekoala, which literally translates as "the place of the father of the coward." The specific name *rachelis* honors paleontologist Raquel Lopez-Antonanzas.

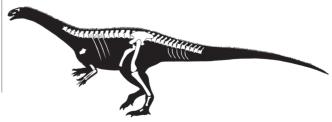
CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda

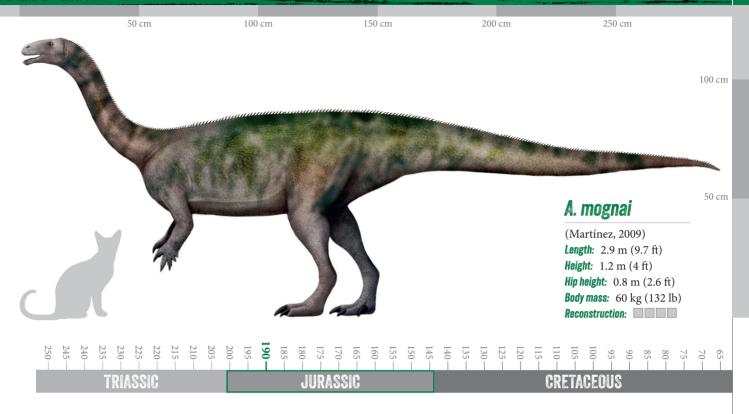
Location Lesotho

KNOWN REMAINS

Partial skeleton (juvenile)



ADEOPAPPOSAURUS



Adeopapposaurus mognai (meaning "far-eating lizard from Mogna") is based on several partial sets of remains that were initially speculated to represent *Massospondylus* (Martínez, 1999). In comparison with related species, the foremost dorsal vertebra of *Adeopapposaurus* has actually transitioned into being a cervical (neck) vertebra.

The researchers who initially described *Adeopapposaurus* proposed the idea that the animal actually had a bony, keratinous beak. This notion is based on a combination of distinctive traits, such as the animal's jaw being actually slightly shorter than its skull. The sides of the snout also host a pronounced "bony platform," and both the snout and jaw feature an increased number of openings meant for the passage of blood vessels and nerve connections.

Taken altogether, it would seem that *Adeopapposaurus* likely had some form of enhanced structure on its face.

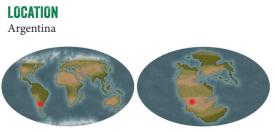
Given that limited archosaurian facial musculature would eliminate the possibility of *Adeopapposaurus* having fleshy, horse-like lips, the next most likely conclusion would be a beak. This beak would have widened the animal's selection of potential food sources by giving it the ability to snip and prune tougher vegetation, perhaps compensating for the animal's smaller size in comparison with other sauropodomorphs present at the time.

Phylogenetic analyses tend to agree that *Adeopapposaurus* is a close relative of *Massospondylus* (Rauhut et al., 2020).

The generic name *Adeopapposaurus* combines the Latin "adeo" (meaning "far"), "pappo" (meaning "eating"), and the Greek "saurus" (meaning "lizard"); this is in reference to the animal's long neck. The specific name *mognai* refers to the location, Mogna, in San Juan Province, Argentina.

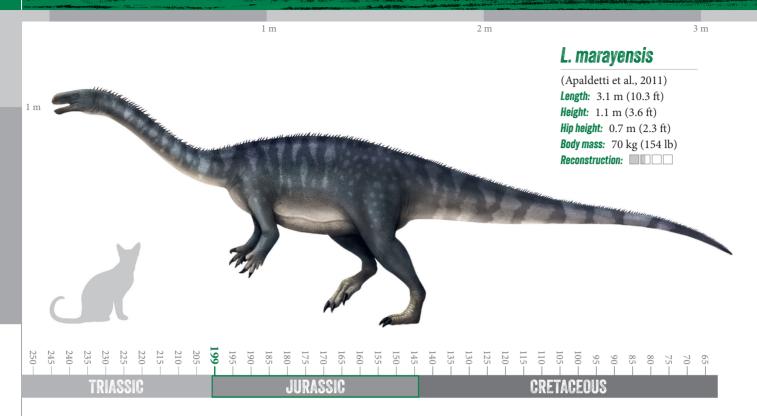
CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Massospondylidae



KNOWN REMAINS Complete

LEYESAURUS



Leyesaurus marayensis (meaning "Leyes's lizard from Marayes") represents an intermediate state within the sauropodomorph lineage. While it possessed an extended neck and leaf-shaped teeth that were suitable for an herbivorous diet, it lacked the huge sauropods' column-like extremities and likely walked on just two legs.

Leyesaurus was not an ancestor of the enormous quadrupedal sauropods that lived in the later portions of the Mesozoic. Instead, throughout the Late Triassic and Early Jurassic, the **massospondylids** were just one of several sauropodomorph lineages that dispersed over the globe (Rauhut et al., 2020).

The only known *Leyesaurus* specimen (PVSJ 706) was recovered from the Quebrada del Barro geological formation; the exact age of this strata has not been accurately determined and could range from the Late Triassic all the way through the Early Jurassic. Other

fragmentary sauropodomorph fossils that have been discovered from this formation have previously been speculated to be *Riojasaurus* remains, although this identification is ambiguous. The best-preserved portions of the *Leyesaurus* specimen are the skull and the first several neck vertebrae, although several other skeletal fragments are also present.

The incompleteness of the remains makes the animal's size difficult to gauge, but estimates put the animal's length somewhere near the 3 meter mark. This makes *Leyesaurus* one of the smallest sauropodomorphs of its time, as some genera—such as *Kholumolumo*—had already reached lengths greater than 10 meters.

The generic name *Leyesaurus* honors the finders of the fossils, the Leyes family from the town of Balde de Leyes. The specific name *marayensis* refers to Marayes-El Carrizal Basin, where the fossils were unearthed.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Massospondylidae

LOCATION Argentina

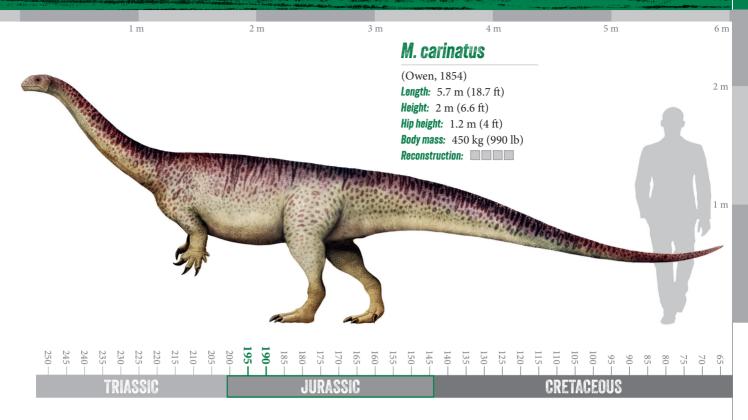
KNOWN REMAINS

Partial skull and skeleton



50

MASSOSPONDYLUS



Massospondylus carinatus (meaning "longer-keeled vertebrae") is a well-known, midsized sauropodomorph that had a proportionately small head. The presence of relatively large openings for blood vessels on the animal's jaws has been interpreted as evidence that *Massospondylus* had fleshy cheeks and, thus, chewed its food (Galton and Upchurch, 2004).

The maximum size of *Massospondylus* adults seems to have been variable, with some reaching nearly 6 meters in length, while others only grew to about 4 meters. Its thumb claw was proportionately large and could have been used for defense or foliage manipulation. Although *Massospondylus* was long thought to be partially quadrupedal, it is now known to have been an obligate biped, as it was incapable of rotating its wrists enough to have walked quadrupedally (Bonnan and Senter, 2007).

Numerous *Massospondylus* specimens of varying age and completeness are known from locations across southern

Africa. The holotype remains were destroyed in a World War II bombing, necessitating the designation of a neotype, BP/1/4934 (Yates and Barrett, 2010). In the century and a half since its initial description, numerous *Massospondylus* species have been named, but only *M. carinatus* and *M. kaalae* are typically considered to be valid by modern researchers (Barrett, 2009). Various obsolete genera are now considered to be synonymous with *Massospondylus*, including *Leptospondylus*, *Pachyspondylus*, *Aristosaurus*, *Dromicosaurus*, and *Hortalotarsus*. Conversely, several specimens previously considered to be *Massospondylus* remains have since been reclassified as new genera, such as *Sarahsaurus* and *Ngwevu*.

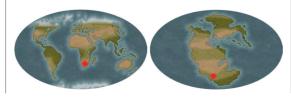
The generic name *Massospondylus* combines the Greek "masson" (meaning "longer") and "spondylos" (meaning "vertebra"). The specific name *carinatus* is Latin for "keeled"; *kaalae* honors museum worker Sheena Kaal.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Massospondylidae

LOCATION

South Africa, Lesotho, Zimbabwe

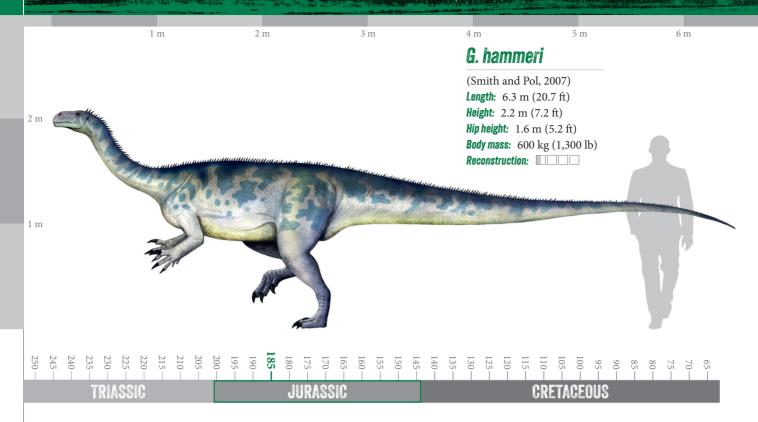


KNOWN REMAINS

Complete

51

GLACIALISAURUS



Glacialisaurus hammeri (meaning "Hammer's icy lizard") was the first sauropodomorph to be discovered from Antarctica. At the time of its literature debut, Antarctica represented the sixth continent on which sauropodomorph remains had been found (leaving out only Australia). This helped to show the nearglobal distribution that sauropodomorphs had achieved by the early stages of the Jurassic. During this time, Antarctica was located farther north, and its coastal regions were likely quite mild in temperature.

Only two fragmentary specimens of *Glacialisaurus* are currently known; they were found near to one another, although they are believed to have originated from two separate individuals. These fossils were recovered in 1990 and 1991, during the same expedition that discovered the theropod *Cryolophosaurus*. The *Glacialisaurus* material consists of fragments of the foot, ankle, and leg; some

vertebrae initially suspected to belong to the same animal were later attributed to *Cryolophosaurus* instead.

During a later expedition in 2003–2004, fossil material was discovered from the same geological formation that is thought to have belonged to a true sauropod dinosaur. If so, this would indicate that at least some Early Jurassic ecosystems hosted both the giant, derived sauropods, and the smaller, "primitive" sauropodomorphs at the same time. This state of affairs has been borne out by various phylogenetic analyses, which have shown that the group **Massospondylidae** was not directly ancestral to the true sauropods but rather was an earlier-diverging offshoot (Rauhut et al., 2020).

The generic name *Glacialisaurus* is derived from the Latin "glacialis" (meaning "icy" or "frozen"). The specific name *hammeri* honors paleontologist William R. Hammer, who led the expedition to Mt. Kirkpatrick that unearthed the fossils.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Massospondylidae

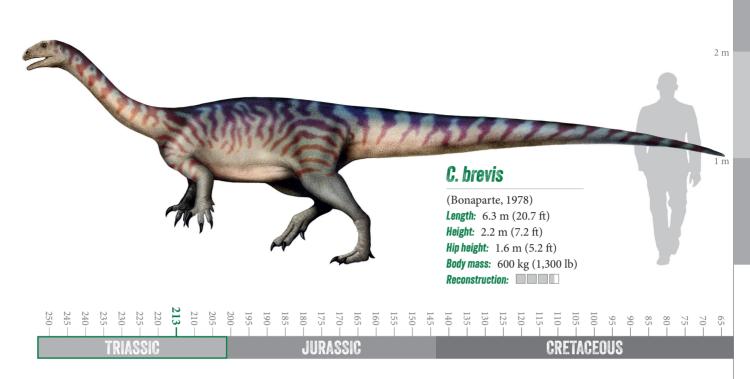
LOCATION Antarctica

KNOWN REMAINS

Leg fragments

52

COLORADISAURUS



Coloradisaurus brevis (meaning "short lizard from Colorados") is known from two partial specimens that were unearthed in 1971 by José Bonaparte. For many years, the skull of the holotype (PVL 3967) was the only portion of the remains to be well described. Later works would reexamine this material (Apaldetti et al., 2014) and finally provide adequate detail and analysis on the remainder of the skeleton (Apaldetti et al., 2013).

The rather gracile *Coloradisaurus* was only one of several sauropodomorphs to apparently share an ecosystem with one another. The presence of the robust *Riojasaurus* and the larger *Lessemsaurus*, along with at least one as-yet unidentified species (PULR 136; Ezcurra and Apaldetti, 2012), potentially demonstrates a case of niche partitioning.

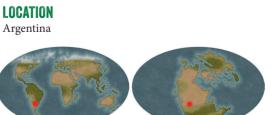
Along with the animal's closest known relative, *Lufengosaurus*, *Coloradisaurus* is considered to be a member of the family **Massospondylidae** (Müller, 2020).

It has also been noted, though, that *Coloradisaurus* shares some traits in common with the more "primitive" plateosaurids. These traits are thought to have evolved independently and is one of several examples of sauropodomorph traits that can be difficult to interpret and can easily muddy the waters of numerous phylogenetic interpretations (Apaldetti et al., 2014).

The name originally intended for the genus was *Coloradia*, but it was later found that this name was preoccupied by a type of moth. David Lambert, after communication with José Bonaparte, used the name *Coloradisaurus* in 1983, but this was not an official name until its proper use by Peter Galton in 1990. The generic name *Coloradisaurus* refers to the Los Colorados geological formation. The specific name *brevis* is Latin for "short," apparently in reference to the length of the animal's skull in relation to its height and width.

CLASSIFICATION

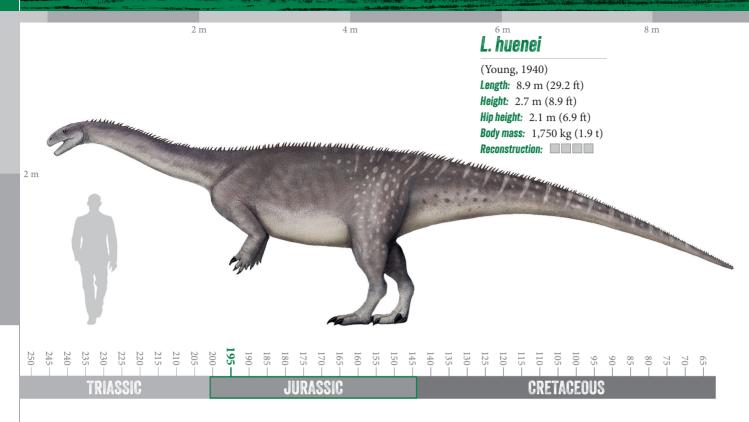
Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Massospondylidae



KNOWN REMAINS Nearly complete

53

LUFENGOSAURUS



Lufengosaurus huenei (meaning "Huene's lizard from Lufeng") was described by a pioneer of Chinese paleontology, Yang Zhongjian (also known as "C. C. Young"). He designated two species, first *L. huenei*, and then the larger *L. magnus* in 1947, although many modern sources consider the two to be one and the same. Judging only from specimens historically attributed to *L. huenei*, the animal's average adult length was once considered to be approximately 6 meters, but when *L. magnus* specimens are included in the calculations, this length increases to nearly 9 meters.

Numerous specimens of *Lufengosaurus* are currently known, many of which were cataloged more than half a century ago. The first dinosaur skeleton to ever be mounted and displayed in China was that of *Lufengosaurus*. These fossils were originally considered to be of Late Triassic origin but now are known to be from the Early Jurassic.

Known specimens include the remains of individuals of differing ages, allowing for the analysis of growth patterns and ontogenetic changes (Sekiya and Dong, 2010). The genus *Tawasaurus* and at least one species of *Gyposaurus* are often considered to be synonymous with *Lufengosaurus*.

Several bony bumps are present on the skull of *Lufengosaurus*, as well as a ridge of bone that has been interpreted as the anchoring location of substantial cheek muscles (Barrett et al., 2005).

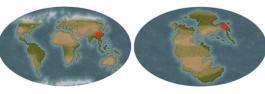
In 2015, researchers identified soft-tissue collagen proteins from a fragment of a *Lufengosaurus* rib bone, breaking the record for the oldest such discovery by more than 100 million years (Lee et al., 2017).

The generic name *Lufengosaurus* refers to the city of Lufeng, China. The specific name *huenei* honors paleontologist Friedrich von Huene, while the name *magnus* means "large one" in Latin.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Massospondylidae

LOCATION China

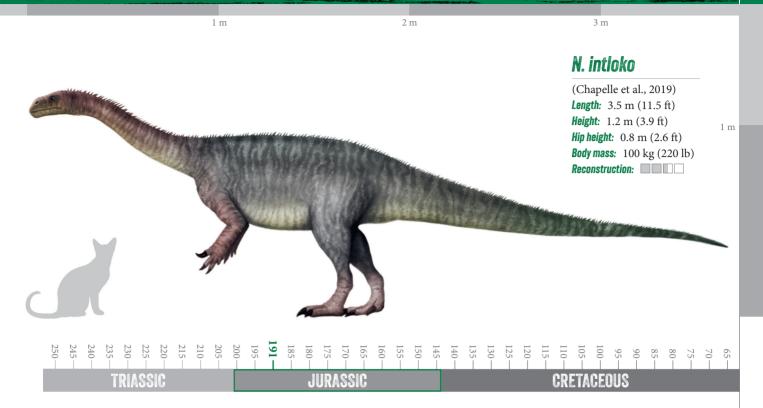


KNOWN REMAINS

Complete







Ngwevu intloko (meaning "gray skull," pronounced Ng-g'where-voo) is known from a single specimen (BP/1/4779) that was discovered 1978 and was long believed to represent *Massospondylus*. A more detailed analysis, though, would eventually reveal it to be its own, unique type of creature.

The skull of *Ngwevu* has quite a different shape than that of *Massospondylus*, but this was initially put down to taphonomic distortion—in other words, deformation of a geologic nature that had warped the shape of the fossil. It was also assumed that the individual had been a juvenile, which could possibly account for the shorter dimensions of the skull.

The researchers who described the genus, though, found that histological growth patterns within the specimen's bones indicated that the individual was nearly fully grown. Thus, different physical characteristics of the skull could not

be attributed to age-related development. Further, the skull bones were actually found to be quite intact and not nearly so distorted as originally reported. Analysis of the specimen's inner-ear structure also revealed marked differences between itself and specimens of *Massospondylus*.

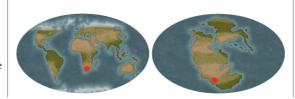
Consequently, *Ngwevu* was erected as a new genus. With a shorter and more robust skull, it was proposed that *Ngwevu* was able to develop tougher jaw musculature than *Massospondylus* and was thus able to base its diet upon sturdier types of foliage. The longer, narrower snout of *Massospondylus* would have been better suited for targeted, selective browsing. These differing feeding strategies could have allowed for niche partitioning, letting *Massospondylus* and *Ngwevu* share the same habitat without competition.

The binomial name is taken from the indigenous Xhosa language, meaning "gray skull".

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Massospondylidae

LOCATIONSouth Africa



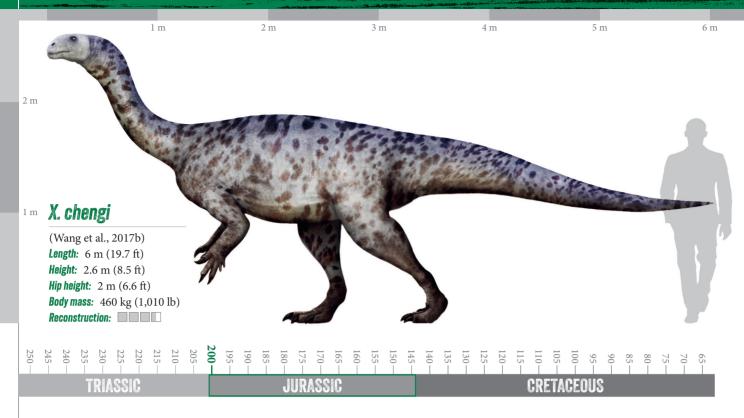
KNOWN REMAINS

Skull and partial skeleton



55

XINGXIULONG



Xingxiulong chengi (meaning "Cheng's bridge dragon") is just one of numerous sauropodomorph species that inhabited what is now the Lufeng geological formation. The remains of Lufengosaurus, Yunnanosaurus, Jingshanosaurus, and Chuxiongosaurus have also been unearthed from this Early Jurassic layer. These latter three, along with Xingxiulong, are among the most basal genera of Sauropodiformes currently known, perhaps suggesting that the clade first originated in China.

Despite its "primitive" positioning on the sauropod family tree, *Xingxiulong* possesses some traits that were common in the more derived "true" sauropods and less common in the basal sauropodomorph species. For instance, *Xingxiulong* had four sacral (hip) vertebrae, rather than three, and had comparatively robust leg bones. These adaptations are thought to have facilitated the development of an increased body mass and, in particular, a larger digestive system,

which was physically supported by a very sauropod-like pubis bone.

Despite its heavy weight, and despite its rather strong shoulder blades, *Xingxiulong* was likely a bipedal creature and was not partially quadrupedal. This conclusion is supported by the available range of motion and the relative proportions of the forearms. *Xingxiulong* was also not particularly long; two of the three known fossil specimens are known to have been fully grown adults, based on the fused nature of their cranial and vertebral bones, so the animal's maximum size is confidently known.

The generic name *Xingxiulong* refers to the ancient "Xingxiu Bridge" located in Lufeng County, China; the term "xingxiu" translates literally as "constellation," while "long" means "dragon." The specific name *chengi* honors Zheng-Wu Cheng.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Sauropodiformes

LOCATION China

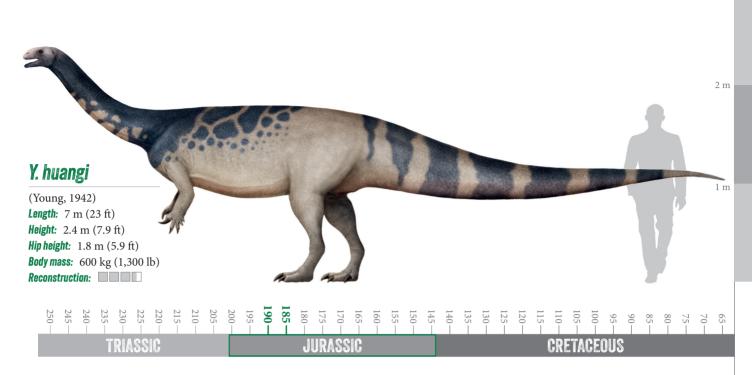
KNOWN REMAINS

Nearly complete



56

YUNNANOSAURUS



Yunnanosaurus huangi (meaning "lizard from Huangchiatien, Yunnan") is a long-studied animal known from numerous sets of fossil remains that include several skulls and individuals of varying ages and, thus, varying developmental states.

The *Y. huangi* holotype specimen was discovered by Yang Zhongjian (i.e., C. C. Young) in 1939, then fully described in 1942. In 1951, he erected a second species, *Y. robustus*; many subsequent analyses have concluded that the two species are synonymous, although the study of a juvenile specimen has led at least one group to continue differentiating the two, citing minor differences such as the presence of serrations on some of the animal's teeth (Sekiya et al., 2014).

A third species, *Y. youngi*, was described in 2007 based on material that was excavated in 2000. Whereas the adult length of *Y. huangi* is approximately 7 meters, the new *Y*.

youngi was significantly larger, reaching lengths of 13 meters. *Yunnanosaurus youngi* also lived several million years later than the previously known species, during the beginning stages of the mid-Jurassic (Lü et al., 2007).

Since 1942, *Yunnanosaurus* has been placed all over the messy and ever-changing "prosauropod" family tree. Most modern analyses, though, place the genus near the base of the **Sauropodiformes** (Wang et al., 2017b; Zhang et al., 2020). Although its teeth were very much akin to those of the true sauropods, this is likely a result of convergent evolution.

The animal's binomial name refers to the holotype's palace of discovery, the village of Huangchiatien in Yunnan Province, China. The specific name *robustus* refers to the comparative robustness of the specimen; *youngi* honors paleontologist C. C. Young.

CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Sauropodiformes

LOCATION China

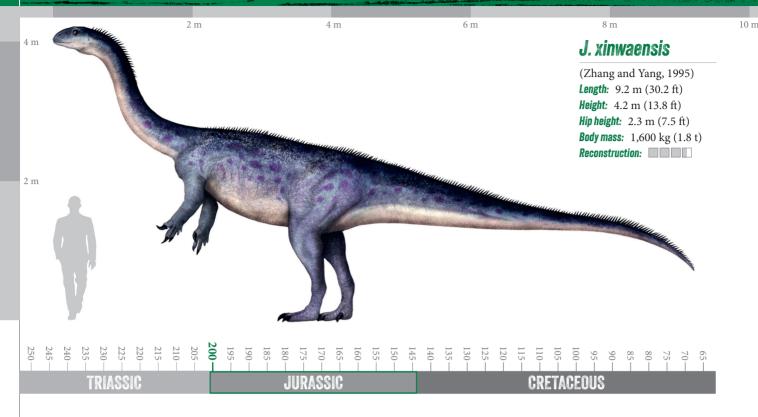
KNOWN REMAINS

Nearly complete



57

JINGSHANOSAURUS



Jingshanosaurus xinwaensis (meaning "lizard from Xinwa, Jinghsan") is the largest example out of numerous sauropodomorph species that inhabited the area that is now the Lufeng geological formation, outsizing Lufengosaurus, Yunnanosaurus, Xingxiulong, and Chuxiongosaurus.

The nearly complete holotype specimen of *Jingshanosaurus* (LFGT-ZLJ0113) was discovered in 1988 by paleontologist Zheng-Ju Wang in the area that has since been designated the Lufeng Dinosaur National Geopark. In 1995, *Jingshanosaurus* was described in the Chinese-language book *A New Complete Osteology of Prosauropoda in Lufeng Basin, Yunnan, China.* After this publication, *Jingshanosaurus* was included in various phylogenetic classification studies based on its stated measurements, but no other research material was produced that took any closer of a look at the remains until 2019 (Zhang et al., 2020).

This new analysis focused on the animal's skull, updating and clarifying the unique anatomical details of the cranium. This area of focus was chosen because the phylogenetic positions of several underdescribed early sauropodomorphs were very dependent on skull morphology; small changes in the stated characteristics of an animal's skull could lead to significantly different outcomes on models of the family tree. Thus, getting these exact details right is crucial to piecing together the precise nature of sauropodomorph evolution.

Although it was originally placed within Plateosauridae, the newer reanalysis of the skull has determined that *Jingshanosaurus* was one of the earliest-branching members of **Sauropodiformes**.

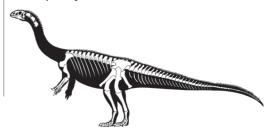
The creature's binomial name references the village of Xinwa and the town of Jinghsan in Yunnan Province, China.

CLASSIFICATION

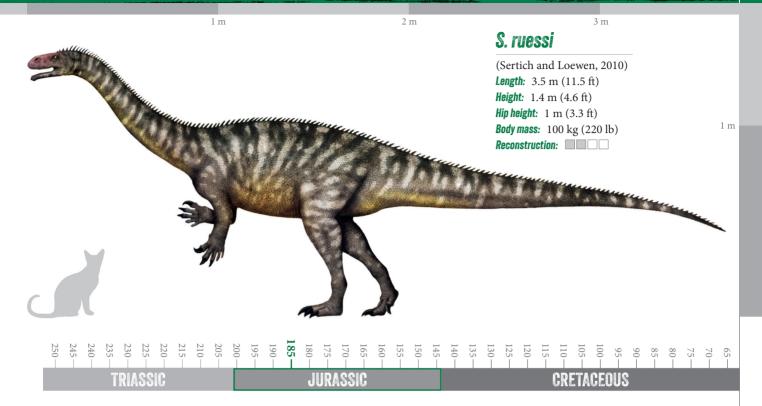
Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Sauropodiformes

LOCATION China

KNOWN REMAINS Nearly complete



58



Seitaad ruessi (meaning "Ruess's sand-monster") is one of the few sauropodomorphs to be described from North America. Although sauropodomorphs from the Late Triassic and Early Jurassic were common and widespread, thanks to the connections that existed between the modern continents, North American remains have proven to be curiously elusive, especially from the American West. Although scattered fragments from the region had been previously found, the remains of Seitaad proved to be among the first that were complete enough to diagnose and identify accurately.

The only known specimen (UMNH VP 18040) appears to have been buried in sand, likely by a collapsing dune, after the individual was already dead. Thus, the recovered remains (which consisted of portions of the animal's trunk and limbs) were preserved three-dimensionally and in articulation. With no skull, neck, or tail being preserved, the length of

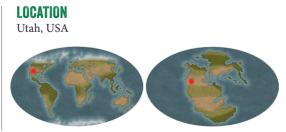
Seitaad is difficult to accurately surmise, but estimates place the value between 3 and 4 meters total. It is also not known for certain whether or not the individual was a juvenile or a fully grown adult.

The original description of the genus was unable to determine the genus's phylogenetic position confidently, suggesting several possibilities and leaning toward the conclusion that Seitaad was a massospondylid. However, subsequent studies have favored a more derived position, with Seitaad being among the Sauropodiformes (Apaldetti et al., 2011; McPhee et al., 2015).

The generic name Seitaad is taken from the Navajo term "séít'áád," the name of a mythological creature from Diné folklore that is said to bury its victims in sand dunes, just as the dinosaur specimen appears to have been. The specific name ruessi honors the American artist and naturalist Everett Ruess, who went missing in Utah in 1934.

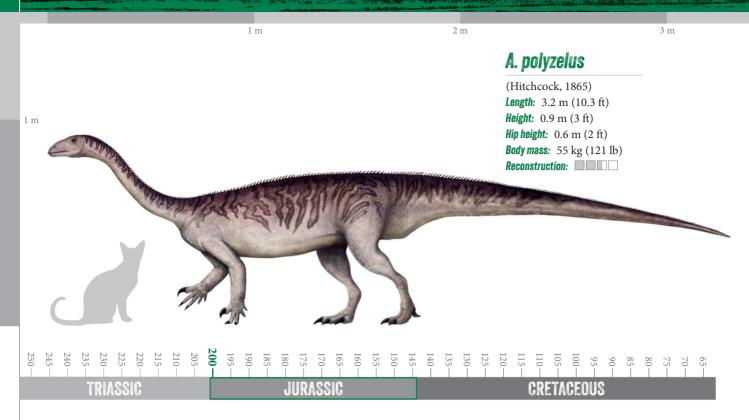
CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Sauropodiformes



KNOWN REMAINS Partial skeleton 59

ANCHISAURUS



Anchisaurus polyzelus (meaning "much sought for nearlizard") was once considered to be the "smallest sauropod" but is now thought to be more basally placed on the family tree, outside Sauropoda. It had narrow feet and an elongated midsection, which would have allowed for more effective digestion of plants.

Anchisaurus is known from four established sets of partial remains, discovered throughout the 1800s. The original type specimen (ACM 41/109) was unearthed during a blast excavation, and was quite damaged as a result; in 2012, it was proposed that a more complete and diagnostic specimen be given neotype status (YPM 1883; Galton, 2012). Additional partial remains from Arizona and Canada have been tentatively suggested but remain unconfirmed (Galton, 1971; Fedak, 2007).

The various specimens now attributed to *A. polyzelus* have been known by many names over time, including *A. colurus*,

A. major, Yaleosaurus, Ammosaurus, Amphisaurus, and Megadactylus. The latter two names were replaced because they turned out to already be occupied by other organisms.

Some of the specimens were not recognized as being attributable to the same species because of their different states of growth. Some are clearly of juvenile status, while at least one is thought to have been fully grown, being approximately 3.2 meters in length. However, the size of some footprints suggests individuals of at least 6 meters in length (Weems, 2019).

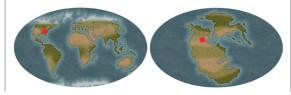
The generic name *Anchisaurus* combines the Greek "anchi" (meaning "near") and "sauros" (meaning "lizard"). The specific name *polyzelus* means "much sought for" in Greek; Edward Hitchcock Jr. gave the animal this name because his father had spent much time and effort in finding the identity of the mysterious reptile that had created certain fossilized trackways.

CLASSIFICATION

Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria

LOCATION

Eastern United States

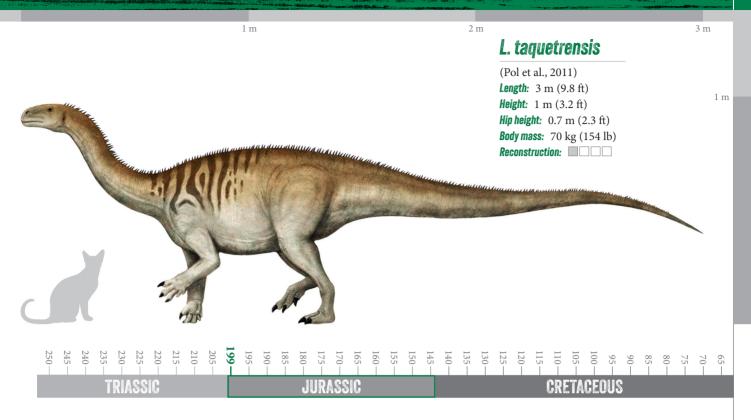


KNOWN REMAINS

Skull and majority of skeleton



LEONERASAURUS



Leonerasaurus taquetrensis (meaning "lizard from Leoneras, Taquetrén") is a relatively small animal that has many skeletal traits that mark it as a non-sauropod sauropodomorph. However, one very sauropod-like trait stands out as significant, which is that Leonerasaurus possesses four sacral (i.e., pelvic) vertebrae rather than just three.

Paleontologists have long debated how and why the four-element sacrum developed among the sauropods. Many had hypothesized that incorporating a fourth vertebra into the sacrum was necessary to help support the increased weight of the huge sauropod species as well as their increased gut volume; as a consequence, the presence of four vertebrae in the sacrum was often considered a diagnostic trait of Sauropoda.

However, the discovery of certain *Melanorosaurus* specimens cast doubt onto the notion that the larger sacrum was present only within Sauropoda, and *Leonerasaurus* has

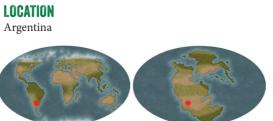
further muddied the waters by showing that this condition evolved even earlier in the sauropodomorph lineage, counterintuitively within small species that did not have enormous bodies to support.

The lone *Leonerasaurus* specimen (MPEF-PV 1663) is quite partial, and comes from an individual that was not fully grown. The animal is thought to have been roughly six years of age at the time of its death, which means it was not particularly young, nor was it an adult. Some of the remains were found in articulation, and all were unearthed from a small area. The lower limbs were almost entirely missing, but based on its phylogenetic position, *Leonerasaurus* was probably bipedal, at least to some degree.

The generic name *Leonerasaurus* refers to the Las Leoneras geological formation from which the fossils were unearthed. The specific name *taquetrensis* refers to the Sierras de Taquetrén, the region where the excavation took place.

CLASSIFICATION

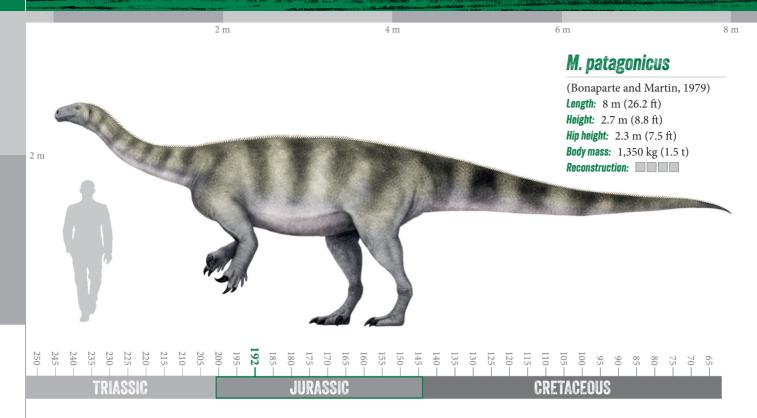
Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria



KNOWN REMAINS Partial skeleton and jaw

61

MUSSAURUS



Mussaurus patagonicus (meaning "mouse lizard from Patagonia") was originally known only from the remains of hatchlings, but more recent finds have been able to illuminate the animal's entire lifespan.

Several adult specimens, which had originally been misidentified as representing Plateosaurus, were reinterpreted in 2013; this analysis provided the first true glimpse of how non-sauropod sauropodiforms developed as they aged by allowing the comparison of the two age groups (Otero and Pol, 2013).

In 2021, an analysis of several rich fossil sites (from the original type locality where the first hatchlings were found) described dozens of substantial, articulated sets of remains representing six different ontogenetic stages (i.e., developmental growth states) that illuminated two key pieces of information. First, the Mussaurus individuals were mostly clustered in groups of similarly aged individuals;

this grouping was interpreted as clear evidence of herdforming social behavior being present 40 million years prior to the next-oldest evidence of such an occurrence (Pol et al., 2021).

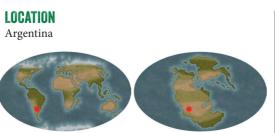
Second, it became clear that as hatchlings, Mussaurus were quadrupedal, but that as they aged, they shifted their stance until they were entirely bipedal as adults; this adds another piece to the puzzle of how the sauropods transitioned into their later, giant forms (Otero et al., 2019).

The site of these discoveries, the Laguna Colorada Formation, was once thought to be Late Triassic in age but is now known to be Early Jurassic (Pol et al., 2021).

The generic name Mussaurus combines the Latin "mus" (meaning "mouse") with the Greek "sauros" (meaning "lizard"), referring to the initial hatchlings' size. The specific name patagonicus refers to the animal's discovery in the Patagonia region of Argentina.

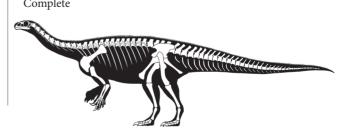
CLASSIFICATION

Dinosauria Sauropodomorpha Bagualosauria Plateosauria Massopoda Sauropodiformes Anchisauria



KNOWN REMAINS

Complete



| 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m | 1 m

Irisosaurus yimenensis (meaning "iridescent lizard from Yimen") is a medium-sized sauropodomorph that can be distinguished from other species by a unique combination of character traits that, in and of themselves, are not individually unique.

The partial holotype skeleton (CVEB 21901) was discovered in 2018 in the Fengjiahe geological formation, near the village of Zhanmatian, China. This Chinese formation, and others of a similar age (such as the Lufeng Formation) have proven to be remarkably diverse in non-sauropodan sauropodomorph genera; indeed, over half of the described Laurasian species have come from Chinese strata.

The phylogenetic analysis conducted by the describers placed *Irisosaurus* within **Sauropodiformes**. This placement was an unexpectedly derived result, as the animal shares

several traits in common with more "primitive" sauropodomorphs (such as having elongated cervical vertebrae) and also appears to have been entirely bipedal, with the forelimbs being fairly gracile and not well adapted for locomotion. The claw on the first finger was definitely quite mobile and is speculated to have been important for the browsing of vegetation.

The analysis also concluded that *Irisosaurus* was the sister taxon of *Mussaurus*, even though the two genera have some significant differences: the latter hails from Gondwana rather than from Laurasia, and *Irisosaurus* is approximately 15–20 million years more recent. The two animals also have more than a few anatomical differences.

The generic name *Irisosaurus* refers to the famous "iridescent clouds" of its discovery location. The specific name *yimenensis* refers to Yimen County, China.

CLASSIFICATION

Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria

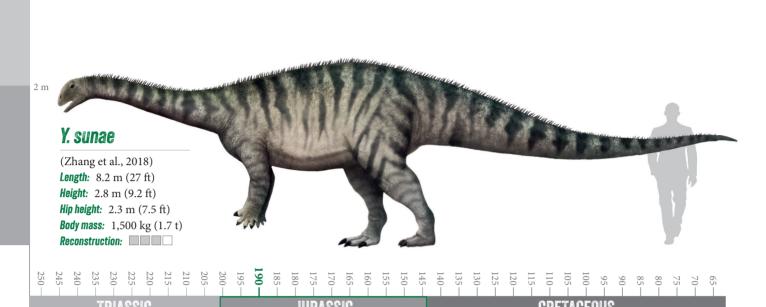


KNOWN REMAINS

Partial skeleton and skull fragments



63



Yizhousaurus sunae (meaning "Sun's lizard from Chuxiong Yi") is possibly a transitional form of sauropodomorph, as it bears a curious mixture of traits—some that resemble ancestral forms (particularly in the skeleton) and others that are similar to more derived species (especially in the skull).

Skeletally, *Yizhousaurus* does not differ greatly from related species: the animal's forearm and femur suggest that it was bipedal, like the more basal sauropodomorphs were. However, the skull of *Yizhousaurus* is notably short and wide as opposed to the moderately elongated forms that were common for plateosaurids and massospondylids; this condition would instead be common for the true sauropods, which would soon come to dominate the biosphere. Additionally, the skull was also relatively small in comparison with the animal's body and had developed more robust bones and reinforcement structures that are consistent with those found in true sauropods.

These traits might make it seem possible that *Yizhousaurus* was a direct ancestor of the true sauropods;

however, cladistic analysis suggests that it was more likely that *Yizhousaurus* was on a side branch of the family tree, among the **Sauropodiformes**. This would mean that its sauropod-like features were a result of convergent evolution rather than being the progenitor of directly inherited traits.

The remains of *Yizhousaurus* (consisting of a three-dimensionally preserved skull and the majority of the skeleton, lacking just the lower legs and tail) were first discovered in 2002 and were introduced to the scientific community in a preliminary fashion at a conference in 2010 (Chatterjee et al., 2010). One noteworthy aspect of the remains is simply that the skeleton and skull were found together, as this allowed for comparisons to be made between both the cranial and skeletal traits of other related species.

The generic name *Yizhousaurus* makes reference to the Chinese region Chuxiong Yi. The specific name *sunae* honors paleontologist Ai-Ling Sun.

CLASSIFICATION

Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria

LOCATION China



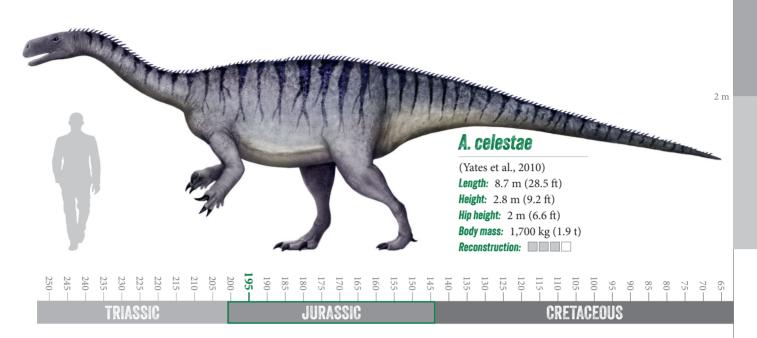
KNOWN REMAINS

Skull and partial skeleton



64

2 m 4 m 6 m



Aardonyx celestae (meaning "Celeste's Earth-claw") is notable because its anatomy seems to be truly intermediate between bipedality and quadrupedality. This transitionary form of locomotion is a valuable clue for understanding how the bipedal sauropodomorphs gave rise to the quadrupedal sauropods.

Full quadrupedality was beyond the ability of *Aardonyx*, as its hands could not fully rotate to the degree that would allow them to be placed flat on the ground. The convex shape of the animal's femur is also a trait seen in bipedal sauropodomorphs. However, regions for muscle attachment along the femur indicate that *Aardonyx* was stronger and slower than other bipedal sauropodomorphs, and the arrangement of the radius and ulna show that they could support one another in order to bear increased weight.

Taken altogether, it seems that *Aardonyx* was a habitual, but not an obligatory, quadruped—an animal that spent some time on all fours but still relied on its hindlimbs for the

majority of its locomotory movement. Having such traits appear so early in the Jurassic was surprising to the fossil's describers, as these characteristics had been thought to have appeared only much later in the Sauropodiformes' lineage.

The jaws of *Aardonyx* also bear an intriguing mixture of traits. Its jaws are narrow, as opposed to the broad mandibles of the later true sauropods. However, *Aardonyx* seems to have lacked fleshy cheeks, which would help its mouth open wide, enabling the broad-grazing style of herbivory that was ubiquitous among the colossal sauropods.

The most studied *Aardonyx* specimens are two subadults that imply an animal roughly 10 meters in length. Certain isolated elements, though, tantalizingly suggest a potential maximum size of roughly twice that (Yates et al., 2012).

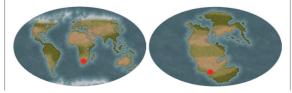
The generic name *Aardonyx* combines the Afrikaans "aard" (meaning "Earth") and the Greek "onyx" (meaning "claw"). The specific name *celestae* honors fossil preparator Celeste Yates.

CLASSIFICATION

Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria

LOCATION

South Africa



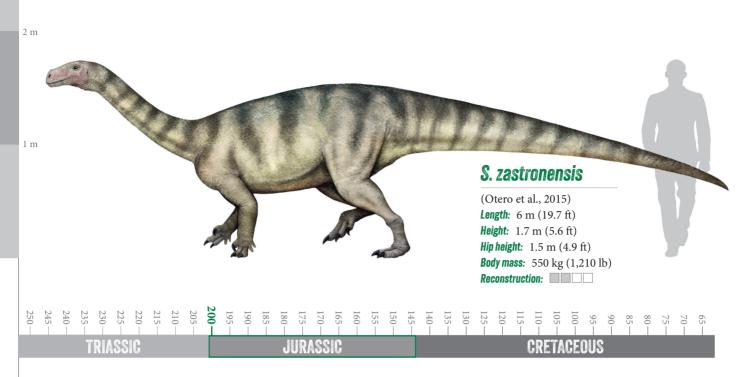
KNOWN REMAINS

Partial skull and skeleton



65

SEFAPANOSAURUS



Sefapanosaurus zastronensis (meaning "cross lizard from Zastron") is another potential "transitional form" of sauropodomorph, displaying some traits that seem intermediate compared with the smaller and clearly bipedal early sauropodomorphs and the quadrupedal true sauropods.

The remains now attributed to *Sefapanosaurus* were collected by A. W. Keyser in the late 1930s; they were designated *Euskelosaurus* and essentially remained hidden and unstudied among many half-forgotten university specimens until 2010, when they were attributed to the closely related sauropodomorph *Aardonyx* (Yates et al., 2010). Closer scrutiny by researcher Emil Krupandan, however, would reveal that some of these fragments—originating from at least four individual animals—were from a separate species entirely. In particular, it was the subtle

differences in the bones of the ankle and upper foot that first became apparent.

It has become clear, particularly with the addition of *Sefapanosaurus*, that southern Gondwanan localities were hotspots for sauropodiform diversity. To date, the vast majority of Sauropodiformes species originating near the Triassic-Jurassic boundary have been unearthed from either southern Africa or South America. In order to gain a clearer understanding of the evolutionary trends which gave rise to the true sauropods, further discoveries from these regions will continue to be paramount.

The generic name *Sefapanosaurus* incorporates the Sesotho word "sefapano" (meaning "cross"), which refers to the distinctive cross-shaped structure of the animal's astragalus bone. The specific name *zastronensis* refers to the Zastron locality where the specimen was discovered.

CLASSIFICATION

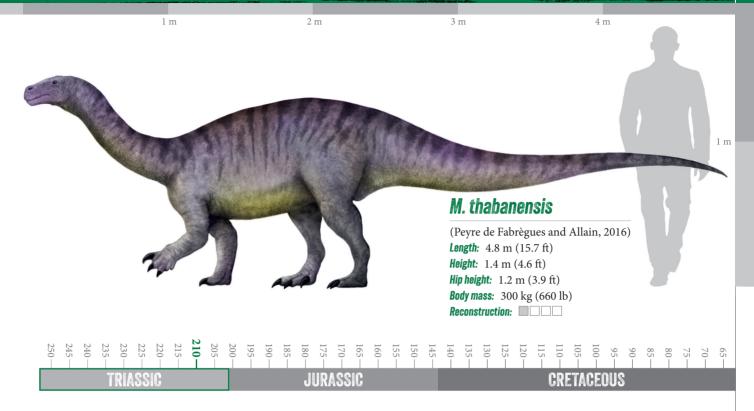
Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria

Lesotho Control Contro

KNOWN REMAINS

Fragments





Meroktenos thabanensis (meaning "femur beast from Thaban") is based on a very partial set of remains that were originally attributed to *Melanorosaurus*, specifically to the non–type species *M. thabanensis*. These remains were unearthed in 1959 and briefly described in 1962, although it was not until 1993 that they were properly assigned to a genus and species (Gauffre, 1993). Further description came just a few years later (van Heerden and Galton, 1997).

The exact location from which these remains originated was never properly documented. For a time, it was thought that they came from the Upper Elliot geological formation, which would have made them 20 million years younger than the type species of *Melanorosaurus*, *M. readi*. In part, for this reason, they were assigned to a new, second species in the genus. However, later work would suggest that they had instead come from the Lower Elliot (Gauffre, 1996).

In 2016, the specimen (MNHN.F.LES16) was reexamined and compared with all other known

specimens of *Melanorosaurus*; it was found to be sufficiently unique to justify its reassignment to a new genus, *Meroktenos*. Additional remains, which were previously overlooked but are suspected to have come from the same animal, were also included in this analysis. The specimen's relatively small size suggests that it might not have been fully grown, but its ontogenetic status has not actually been determined.

The femur of *Meroktenos* is shaped similarly to those of the true sauropods, despite the creature's small size and Triassic provenance. This means that it could have been among the first sauropodomorphs to develop this particular trait, which the later, larger sauropods would retain.

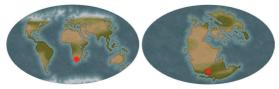
The generic name *Meroktenos* combines the Greek "meros" (meaning "femur") and "ktenos" (meaning "animal" or "beast"). The specific name *thabanensis* refers to the village near where the specimens were found, Thabana-Morena.

CLASSIFICATION

Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria

LOCATION

Lesotho



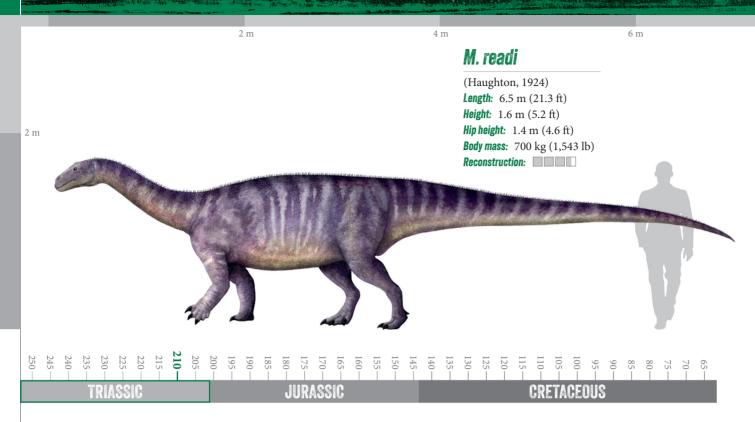
KNOWN REMAINS

Fragments



67

MELANOROSAURUS



Melanorosaurus readi (meaning "Read's Black Mountain lizard") was one of the largest animals of its time, and despite its early appearance, seems to have already been at least partially quadrupedal.

The original syntype specimens (SAM 3449 and SAM 3450) were discovered and described in 1924 by Sidney H. Haughton. Regrettably, even then it was unclear whether or not all of these bones actually belonged to the same creature, with Haughton noting that many were "lying isolated" and that the femur, in particular, was "in doubtful association with the other remains." Many of these fossils were later reassigned to *Euskelosaurus* instead (van Heerden, 1979), but that genus is now largely considered a *nomen dubium* wastebasket taxon. Currently, it is believed that selected material from the syntype specimens is indeed diagnostically relevant and is attributable to *Melanorosaurus* instead (Galton et al., 2005).

Some bones from SAM 3532 were also referred to the genus by Haughton but have thus far remained relatively

unstudied. The most complete sets of remains often referred to *Melanorosaurus* are NM QR3314 (Welman, 1998; Bonnan and Yates, 2007) and NM QR1551 (Galton et al., 2005). However, a later review cast doubt on whether or not these specimens were of the same species as one another (citing differences in the feet and sacral vertebrae) or even attributable to *M. readi* at all (noting a lack of overlapping, comparable elements with the syntype specimens) (McPhee et al., 2015, 2017).

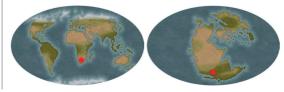
The generic name *Melanorosaurus* combines the Greek "melas" (meaning "back"), "oros" (meaning "mountain"), and "sauros" (meaning "lizard"). This refers to the location of the holotype's discovery, on the slope of Thaba 'Nyama (meaning "Black Mountain" in the indigenous Nyanja language) in South Africa. The specific name *readi* is meant to honor B. Read of the Bensonvale Training School.

CLASSIFICATION

Dinosauria
Sauropodomorpha
Bagualosauria
Plateosauria
Massopoda
Sauropodiformes
Anchisauria

LOCATION

South Africa

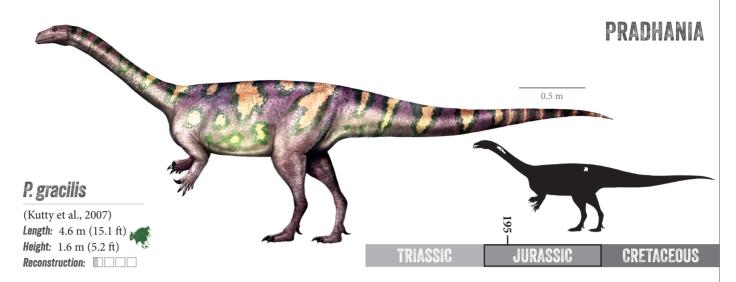


KNOWN REMAINS

Nearly complete

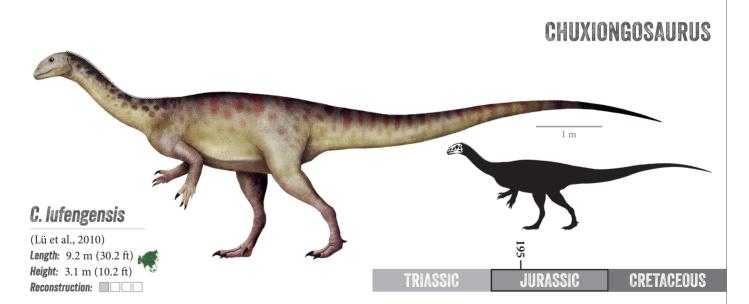


68



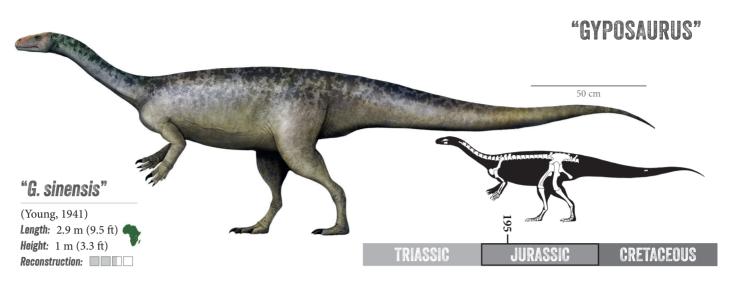
Pradhania gracilis (meaning "Pradhan's slender one") is known from a single set of very fragmentary remains (ISI R265) that were unearthed in India. Its most distinguishing characteristic, which prompted the erection of this genus, is the presence of a prominent ridge along the inside of the upper jaw bone.

Owing to the paucity of the remains, the original description of the genus was unable to determine its phylogenetic placement accurately; a later study concluded that *Pradhania* was likely a **massospondylid** (Novas et al., 2010). The generic name honors fossil collector Dhuiya Pradhan.



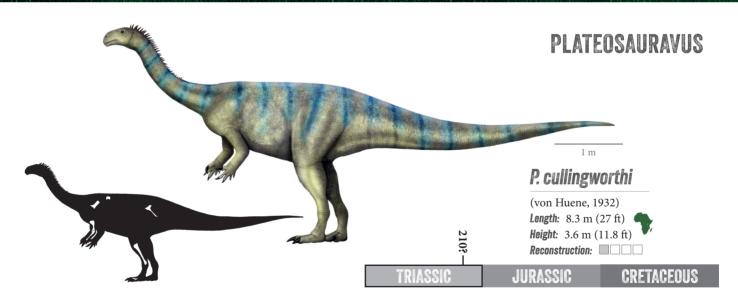
Chuxiongosaurus lufengensis (meaning "lizard from Chuxion, Lufeng") was described on the basis of a single specimen (CMY LT9401) consisting of a mostly complete skull and jaw. It was compared with *Thecodontosaurus* and was phylogenetically placed as a basal sauropodiform. It was distinguished from similar animals, such as *Jingshanosaurus*, based on several characteristics, including the number of teeth it had.

This same Chinese specimen had been previously reported as representing *Jingshanosaurus*. After the description of *Chuxiongosaurus*, a reanalysis of *Jingshanosaurus* disputed the validity of the genus and questioned the accuracy of the criteria that had been used to erect it; it was then concluded that *Chuxiongosaurus* was merely a synonym of *Jingshanosaurus* (Zhang et al., 2020).



The original (and, technically, current) type species of the genus *Gyposaurus* (meaning "vulture lizard") is *G. capensis*, named in 1911 from South Africa. However, this species was later determined to be the same animal as *Massospondylus* (Barrett et al., 2007), rendering the generic name invalid and undescriptive. But it seems that a second species within the genus, "*G. sinensis*", may actually be distinct from *Massospondylus* (Cooper,1981). This Chinese species was named by C. C. Young in 1941.

If "G. sinensis" is indeed distinct from other known genera, it would not be proper to refer to it as Gyposaurus, since that name was invalidated. It could be renamed to a new genus, or the type species of the genus could formally be recategorized. More analyses are needed in order to determine the uniqueness of the species, as some researchers have suggested a synonymy with Lufengosaurus instead (Wang et al., 2017a).



In 1924, a smattering of dinosaur bones discovered in South Africa were named to a new species of *Plateosaurus*, *P. cullingworthi*, by Sidney Haughton. In 1932, though, Friedrich von Huene reassessed the remains and decided that they actually represented an all-new genus, which he dubbed *Plateosauravus cullingworthi* (meaning "Cullingworth's grandfather of *Plateosaurus*"). In 1979, the fossils were once again reassigned by Jacques van Heerden, being lumped together with other remains as belonging to

the genus *Euskelosaurus*. However, this genus has now largely been recognized as a wastebasket taxon and is often treated as *nomen dubium*. Throughout the 2000s, paleontologist Adam Yates advocated that the name *Plateosauravus* once again be adopted. In 2019, work done by Emil Darius Krupandan reassessed each of the supposed *Plateosauravus* fossils, reevaluating which fossils could actually be confidently assigned as coming from the same animal and revalidating the establishment of the genus.



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