

= Thescelosaurus =

Thescelosaurus (/ ˌθɛskəˈloʊsɔːrəs / THESS @-@ il @-@ ? @-@ SOR @-@ ?s ; ancient Greek ?????????- / theskelos- meaning " godlike " , " marvelous " , or " wondrous " and ??????? / sauros " lizard ") was a genus of small ornithomimid dinosaur that appeared at the very end of the Late Cretaceous period in North America . It was a member of the last dinosaurian fauna before the Cretaceous - Paleogene extinction event around 66 million years ago . The preservation and completeness of many of its specimens indicate that it may have preferred to live near streams .

This bipedal ornithomimid is known from several partial skeletons and skulls that indicate it grew to between 2 @. @ 5 and 4 @. @ 0 meters (8 @. @ 2 to 13 @. @ 1 ft) in length on average . It had sturdy hind limbs , small wide hands , and a head with an elongate pointed snout . The form of the teeth and jaws suggest a primarily herbivorous animal . This genus of dinosaur is regarded as a specialized basal ornithomimid , traditionally described as a hypsilophodont , but more recently recognized as distinct from Hypsilophodon . Several species have been suggested for this genus . Three currently are recognized as valid : the type species *T. neglectus* , *T. garbanii* and *T. assiniboensis* .

The genus attracted media attention in 2000 , when a specimen unearthed in 1993 in South Dakota , United States , was interpreted as including a fossilized heart . There was much discussion over whether the remains were of a heart . Many scientists now doubt the identification of the object and the implications of such an identification .

= = Description = =

Thescelosaurus was a heavily built bipedal animal , probably herbivorous , but potentially not . There was a prominent ridge along the length of both maxillae (the tooth @-@ bearing " cheek " bones) , and a ridge on both dentaries (tooth @-@ bearing bone of the lower jaw) . The ridges and position of the teeth , deeply internal to the outside surface of the skull , are interpreted as evidence for muscular cheeks . Aside from the long narrow beak , the skull also had teeth in the premaxilla , or upper beak (a primitive trait among ornithomimids) . Long rod @-@ like bones called palpebrals were present over the eyes , giving the animal heavy bony eyebrows . Its teeth were of two types : small pointed premaxillary teeth , and leaf @-@ shaped cheek teeth . Six small teeth were present in both premaxillae , with a toothless section at the tip of the beak .

Thescelosaurus had short , broad , five @-@ fingered hands , four @-@ toed feet with hoof @-@ like toe tips , and a long tail braced by ossified tendons from the middle to the tip , which would have reduced the flexibility of the tail . The rib cage was broad , giving it a wide back , and the limbs were robust . The animals may have been able to move on all fours , given its fairly long arms and wide hands , but this idea has not been widely discussed in the scientific literature , although it does appear in popular works . Charles M. Sternberg reconstructed it with the upper arm oriented almost perpendicular to the body , another idea that has gone by the wayside . As noted by Peter Galton , the upper arm bone of most ornithomimids articulated with the shoulder by an articular surface that consisted of the entire end of the bone , instead of a distinct ball and socket as in mammals . The orientation of the shoulder 's articular surface also indicates a vertical and not horizontal upper arm in dinosaurs .

Large thin flat mineralized plates have been found next to the ribs ' sides . Their function is unknown ; they may have played a role in respiration . However , muscle scars or other indications of attachment have not been found for the plates , which argues against a respiratory function . Recent histological study of layered plates from a probable subadult indicates that they may have started as cartilage and became bone as the animal aged . Such plates are known from several other ornithomimids and their ceratopsian relatives .

The nature of this genus ' integument , be it scales or something else , is currently unknown , although potential evidence exists : Charles Gilmore described patches of carbonized material near the shoulders as possible epidermis , with a " punctured " texture , but no regular pattern , and William J. Morris suggested that armor was present , in the form of small scutes he interpreted as

located at least along the midline of the neck of one specimen . Scutes have not been found with other articulated specimens of *Thescelosaurus* , though , and Morris 's scutes could be crocodilian in origin .

Overall , the skeletal anatomy of this genus is well documented , and restorations have been published in several papers , including skeletal restorations and models . The skeleton is known well enough that a detailed reconstruction of the hip and hindlimb muscles has been made . The animal 's size has been estimated in the 2 @. @ 5 ? 4 @. @ 0 m range for length (8 @. @ 2 ? 13 @. @ 1 ft) for various specimens , and a weight of 200 ? 300 kilograms (450 ? 660 pounds) , with the large type specimen of *T. garbanii* estimated at 4 ? 4 @. @ 5 meters (13 @. @ 1 ? 14 @. @ 8 feet) long . As discussed more fully under " Discovery , history , and species " , it may have been sexually dimorphic , with one sex larger than the other . Juvenile remains are known from several locations , mostly based on teeth .

= = Classification = =

Thescelosaurus has generally been allied to *Hypsilophodon* and other small ornithomimids as a hypsilophodontid , although recognized as being distinct among them for its robust build , unusual hindlimbs , and , more recently , its unusually long skull . Peter Galton in 1974 presented one twist to the classic arrangement , suggesting that because of its hindlimb structure and heavy build (not cursorial , or built for running , by his definition) , it should be included in the *Iguanodontidae* . This has not been followed , with Morris arguing strongly against Galton 's classification scheme . At any rate , Galton 's *Iguanodontidae* was polyphyletic and not a natural group , and so would not be recognized under modern cladistic usage .

Although *Hypsilophodontidae* was interpreted as a natural group in the early 1990s , this hypothesis has fallen out of favor and *Hypsilophodontidae* has been found to be an unnatural family composed of a variety of animals more or less closely related to *Iguanodontia* (paraphyly) , with various small clades of closely related taxa . " *Hypsilophodontidae* " and " hypsilophodont " are better understood as informal terms for an evolutionary grade , not a true clade . *Thescelosaurus* has been regarded as both very basal and very derived among the hypsilophodonts . One issue that has potentially interfered with classifying *Thescelosaurus* is that not all of the remains assigned to *T. neglectus* necessarily belong to it . Clint Boyd and colleagues found that while the clade *Thescelosaurus* included the genus *Bugenasaura* and the species that had been assigned to that genus , there were at least two and possibly three species within *Thescelosaurus* , and several specimens previously assigned to *T. neglectus* could not yet be assigned to a species within the genus . It appears to be closely related to *Parksosaurus* .

The dissolution of *Hypsilophodontidae* has been followed by the recognition of the distinct family *Thescelosauridae* . This area of the dinosaur family tree has historically been complicated by a lack of research , but papers by Clint Boyd and colleagues and Caleb Brown and colleagues have specifically addressed these dinosaurs . Boyd et al . (2009) and Brown et al . (2011) found North American " hypsilophodonts " of Cretaceous age to sort into two related clusters , one consisting of *Orodromeus* , *Oryctodromeus* , and *Zephyrosaurus* , and the other consisting of *Parksosaurus* and *Thescelosaurus* . Brown et al . (2013) recovered similar results , with the addition of the new genus *Albertadromeus* to the *Orodromeus* clade and several long @-@ snouted Asian forms (previously described under *Jeholosauridae*) to the *Thescelosaurus* clade . They also formally defined *Thescelosauridae* (*Thescelosaurus neglectus* , *Orodromeus makelai* , their most recent common ancestor , and all descendants) and the smaller clades *Orodrominae* and *Thescelosaurinae* . The below cladogram is that of Brown et al ..

= = Discovery , history , and species = =

The type specimen of *Thescelosaurus* (USNM 7757) was discovered in 1891 by paleontologists John Bell Hatcher and William H. Utterback , from beds of the late Maastrichtian @-@ age Upper Cretaceous Lance Formation of Niobrara County (at the time part of Converse County) , Wyoming ,

USA . The skeleton , however , remained in its shipping crates for years until Charles W. Gilmore of the Smithsonian Institution 's National Museum of Natural History had it prepared and described it in a short paper in 1913 , naming it *T. neglectus* (*neglectus* : " neglected ") . At the time , he thought it was related to *Camptosaurus* . He provided a detailed monograph in 1915 , describing the well @-@ preserved skeleton . The type specimen was found largely in natural articulation and was missing only the head and neck , which were lost due to erosion . The name comes from the surprise Gilmore felt at finding such a good specimen that had been unattended to for so long . He considered it to be a light , agile creature , and assigned it to the *Hypsilophodontidae* , a family of small bipedal dinosaurs .

Other remains of similar animals were found throughout the late 19th century and 20th century . Another well @-@ preserved skeleton from the slightly older Horseshoe Canyon Formation , in Alberta , Canada , was named *T. warreni* by William Parks in 1926 . This skeleton had notable differences from *T. neglectus* , and so Charles M. Sternberg placed it in a new genus , *Parksosaurus* , in 1937 . Sternberg also named an additional species , *T. edmontonensis* , based on another articulated skeleton , this time including a partial skull (NMC 8537) , and drew attention to the genus ' heavy build and thick bones . Due to these differences from the regular light *hypsilophodont* build , he suggested that the genus warranted its own subfamily , *Thescelosaurinae* . *T. edmontonensis* has , since Peter Galton 's 1974 review , generally been considered a more robust individual (possibly the opposite sex of the type individual) of *T. neglectus* . However , Boyd and colleagues found that they could not assign it to either of their valid species of *Thescelosaurus* and regarded the specimen as of uncertain placement within the genus . The other point of contention regarding *T. edmontonensis* is its ankle , which Galton claimed was damaged and misinterpreted , but which was regarded by William J. Morris (1976) as truly different from *T. neglectus* .

In his paper , Morris described a specimen (SDSM 7210) consisting of a partial skull with heavy ridges on the lower jaw and cheek , four partial vertebrae , and two finger bones as an unidentified species of *Thescelosaurus* , from the late Maastrichtian @-@ age Hell Creek Formation of Harding County , South Dakota , USA . He drew attention to its premaxillary teeth and deeply inset toothline which he interpreted as supporting the presence of muscular cheeks . Morris also pointed out the outwardly flaring premaxilla (which would have given it a wide beak) and large palpebrals . This skull was recognized as an unnamed *hypsilophodont* for many years , until Galton made it the type specimen of new genus and species *Bugenasaura infernalis* (" large @-@ cheeked lizard belonging to the lower regions " , *infernalis* being a reference to the Hell Creek Formation) . Morris also named a new possible species of *Thescelosaurus* for specimen LACM 33542 : ? *T. garbanii* (with a question mark because he was uncertain that it belonged to the genus) . LACM 33542 comprised a large partial hindlimb (" a third larger than described specimens of *T. neglectus* and *Parksosaurus* or nearly twice as large as *Hypsilophodon* ") including a foot , tarsus , shin bones , and partial thigh bone , along with five cervical (neck) and eleven dorsal (back) vertebrae , from the Hell Creek Formation of Garfield County , Montana , USA . The specimen was discovered by amateur paleontologist Harley Garbani , hence the name . *T. garbanii* would have been about 4 @. 5 meters (15 feet) long , greater than average specimens of *T. neglectus* . Aside from the size , Morris drew attention to the way the ankle was constructed , which he considered to be unique except in comparison with *Thescelosaurus edmontonensis* , which he regarded as a separate species . Because Morris believed that the ankles of *T. garbanii* compared favorably to those of *T. edmontonensis* , he tentatively assigned it to *Thescelosaurus* . However , the scientific literature has favored Galton 's view that *T. edmontonensis* was not different from *T. neglectus* (see above) . In the same paper that he described *Bugenasaura* , Galton demonstrated that the features Morris had thought connected *T. garbanii* and *T. edmontonensis* were the result of damage to the latter 's ankle , so *T. garbanii* could also be considered distinct from *Thescelosaurus* . To better accommodate this species , Galton suggested that it belonged to his new genus *Bugenasaura* as *B. garbanii* , although he also noted that it could be belong to the similarly sized pachycephalosaurid *Stygimoloch* , or be part of a third , unknown dinosaur .

Clint Boyd and colleagues published a reassessment of *Thescelosaurus* , *Bugenasaura* , and

Parksosaurus in 2009 , using new cranial material as a starting point . They found that Parksosaurus was indeed distinct from Thescelosaurus , and that the skull of Bugenasaura infernalis was essentially the same as a skull found with a postcranial skeleton that matched Thescelosaurus . Because B infernalis could not be differentiated from Thescelosaurus , they regarded the genus as a synonym of Thescelosaurus , the species as dubious , and SDSM 7210 as an example of T. sp . They found that LACM 33542 , although fragmentary , was a specimen of Thescelosaurus , and agreed with Morris that the ankle structure was distinct , returning it to T. garbanii . Finally , they noted that another specimen , RSM P.1225.1 , differed from T. neglectus in some anatomical details , and may represent a new species . Thus , Thescelosaurus per Boyd et al . (2009) is represented by at least two , and possibly three valid species : type species T. neglectus , T. garbanii , and a possible unnamed species . In December 2011 , RSM P.1225.1 was assigned to its own species , Thescelosaurus assiniboiensis . It was named by Caleb M. Brown , Clint A. Boyd and Anthony P. Russell and is known only from its holotype , a small , articulated and almost complete skeleton from the Frenchman Formation (late Maastrichtian stage) of Saskatchewan .

= = Paleobiology = =

Thescelosaurus would have browsed in the first meter or so from the ground , feeding selectively , with food held in the mouth by cheeks while chewing . Thescelosaurus was probably slower than other hypsilophodonts , because of its heavier build and leg structure . Compared to them , it had unusual hindlimbs , because the upper leg was longer than the shin , the opposite of Hypsilophodon and running animals in general . One specimen is known to have had a bone pathology , with the long bones of the right foot fused at their tops , hindering swift movement .

= = = " Heart of stone " = = =

In 2000 , a skeleton of this genus (specimen NCSM 15728) informally known as " Willo " , now on display at the North Carolina Museum of Natural Sciences , was described as including the remnants of a four @-@ chambered heart and an aorta . It had been originally unearthed in 1993 in northwestern South Dakota . The authors had found the internal detail through computed tomography (CT) imagery . They suggested that the heart had been saponified (turned to grave wax) under airless burial conditions , and then changed to goethite , an iron mineral , by replacement of the original material . The authors interpreted the structure of the heart as indicating an elevated metabolic rate for Thescelosaurus , not reptilian cold @-@ bloodedness .

Their conclusions have been disputed ; soon after the initial description , other researchers published a paper where they asserted that the heart is really a concretion . As they noted , the anatomy given for the object is incorrect (for example , the " aorta " narrows coming into the " heart " and lacks arteries coming from it) , it partially engulfs one of the ribs and has an internal structure of concentric layers in some places , and another concretion is preserved behind the right leg . The original authors defended their position ; they agreed that it was a type of concretion , but one that had formed around and partially preserved the more muscular portions of the heart and aorta .

A study published in 2011 applied multiple lines of inquiry to the question of the object 's identity , including more advanced CT scanning , histology , X @-@ ray diffraction , X @-@ ray photoelectron spectroscopy , and scanning electron microscopy . From these methods , the authors found the following : the object 's internal structure does not include chambers but is made up of three unconnected areas of lower density material , and is not comparable to the structure of an ostrich 's heart ; the " walls " are composed of sedimentary minerals not known to be produced in biological systems , such as goethite , feldspar minerals , quartz , and gypsum , as well as some plant fragments ; carbon , nitrogen , and phosphorus , chemical elements important to life , were lacking in their samples ; and cardiac cellular structures were absent . There was one possible patch with animal cellular structures . The authors found their data supported identification as a concretion of sand from the burial environment , not the heart , with the possibility that isolated areas of tissues were preserved .

The question of how this find reflects metabolic rate and dinosaur internal anatomy is moot , though , regardless of the object 's identity . Both modern crocodilians and birds , the closest living relatives of dinosaurs , have four @-@ chambered hearts (albeit modified in crocodilians) , so dinosaurs probably had them as well ; the structure is not necessarily tied to metabolic rate .

= = Paleoecology = =

= = = Temporal and geographic range = = =

True *Thescelosaurus* remains are known definitely only from late Maastrichtian @-@ age rocks , from Alberta (Scollard Formation) and Saskatchewan (Frenchman Formation) , Canada , and Wyoming (Lance Formation) , South Dakota (Hell Creek Formation) , Montana (Hell Creek) , and Colorado (Laramie Formation) , USA . With the exception of birds , it was one of the last genera of dinosaurs , its remains being found as close as 3 meters to the boundary clay containing the iridium layer that closes the Cretaceous . There are reports of teeth from older , Campanian @-@ age rocks , particularly from the Dinosaur Park Formation of Alberta , but these specimens are not from *Thescelosaurus* and are much more likely those of *Orodromeus* . More specimens are known than have been officially described for this genus , such as the Triebold specimen , which has been the source of several skeletal casts for museums .

When Galton revisited *Thescelosaurus* and *Bugenasaura* in 1999 , he described the dentary tooth UCMP 46911 from the Upper Jurassic of Weymouth , England as cf . *Bugenasaura* . If it is indeed a tooth from a thescelosaur @-@ like animal , this would significantly extend the stratigraphic range of the group .

= = = Habitat = = =

Conflicting reports have been made as to its preferred habitat ; two papers suggest it preferred channels to floodplains , but another suggests it preferred the opposite . The possible preference for channels is based on the relative abundance of thescelosaur fossils in sandstones , representing channel environments , in comparison to mudstones , representing floodplain environments . No bonebeds or accumulations of multiple individuals have yet been reported . Dale Russell , in a popular work , noted that *Thescelosaurus* was the most common small herbivore in the Hell Creek Formation of the Fort Peck area . He described the environment of the time as a flat floodplain , with a relatively dry subtropical climate that supported a variety of plants ranging from angiosperm trees , to bald cypress , to ferns and ginkgos . Although most dinosaur skeletons from this area are incomplete , possibly due to the low preservation potential of forests , *Thescelosaurus* skeletons are much more complete , suggesting that this genus frequented stream channels . Thus when a *Thescelosaurus* died , it may have been in or near a river , making it easier to bury and preserve for later fossilization . Russell tentatively compared it to the capybaras and tapirs . Other dinosaurs that shared its time and place include the ceratopsids *Triceratops* and *Torosaurus* , hadrosaurid *Edmontosaurus* , ankylosaurid *Ankylosaurus* , pachycephalosaurian *Pachycephalosaurus* , and the theropods *Ornithomimus* , *Troodon* , and *Tyrannosaurus* . *Thescelosaurus* was also abundant in the Lance Formation . Toe bones from this genus are the most common finds after fossils of *Triceratops* and *Edmontosaurus* , and it may have been the most common dinosaur there in life , if the Lance Formation had a preservational bias against small animals .