= Kentrosaurus =

Kentrosaurus (/ ?k?ntro??s??r?s / KEN @-@ tro @-@ SAWR @-@ ?s) is a genus of stegosaurian dinosaur from the Late Jurassic of Tanzania . The type species is K. aethiopicus , named and described by German palaeontologist Edwin Hennig in 1915 . Often thought to be a " primitive " member of the Stegosauria , several recent cladistic analyses find it as more derived than many other stegosaurs , and a close relative of Stegosaurus from the North American Morrison Formation within the Stegosauridae .

Fossils of K. aethiopicus have been found only in the Tendaguru Formation , dated to the late Kimmeridgian and early Tithonian ages , about 152 million years ago . Hundreds of bones were unearthed by German expeditions to German East Africa between 1909 and 1912 . Although no complete skeletons are known , the remains provided a nearly complete picture of the build of the animal .

Kentrosaurus generally measured around 4 @.@ 5 metres (15 ft) in length as an adult , and weighed about one tonne (1 @.@ 1 tons) . It walked on all fours with straight hindlimbs . It had a small , elongated head with a beak used to bite off plant material that would be digested in a large gut . It had a , probably double , row of small plates running down its neck and back . These plates gradually merged into spikes on the hip and tail . The longest spikes were on the tail end and were used to actively defend the animal . There also was a long spine on each shoulder . The thigh bones come in two different types , suggesting that one sex was larger and more stout than the other .

= = Description = =

Kentrosaurus was a small stegosaur . It had the typical dinosaurian body bauplan , characterised by a small head , a long neck , short forelimbs and long hindlimbs , and a long , horizontal and muscular tail . Typical stegosaurid traits included the elongation and flatness of the head , the powerful build of the forelimbs , erect and pillar @-@ like hindlimbs and an array of plates and spikes running along both sides of the top mid @-@ line of the animal . Only a single complete tooth was known when Hennig published his monography in 1925 . Later , a part of a dentary , the tooth @-@ bearing bone of the front lower jaw , was found , which bears a just emerging tooth , and some tooth fragments were recovered from matrix sticking to other bones . The deep dentary is almost identical in shape to that of Stegosaurus , albeit much smaller . Similarly , the tooth is a typical stegosaurian tooth , small with a widened base and vertical grooves creating five ridges .

= = = Size and posture = = =

Kentrosaurus aethiopicus was smaller than Stegosaurus armatus , Hesperosaurus mjosi , Dacentrurus armatus and Tuojiangosaurus multispinus , and about as large as Huayangosaurus taibaii . The total length of a composite skeletal mount in the Museum für Naturkunde Berlin , Germany , from the tip of the snout to the tip of the tail is 4 @.@ 5 m (15 ft) . Slightly more than half of this length is made up by the tail . Larger single elements were found , so that the animal could probably attain a total length of 5 @.@ 5 m (18 ft) . In 2010 , Gregory S. Paul estimated the weight of a 4 @-@ metre @-@ long (13 ft) Kentrosaurus at seven hundred kilograms (1 @,@ 500 lb) . An estimate for the 4 @.@ 5 m long composite mount in the Museum für Naturkunde Berlin by Mallison , on the basis of a virtual 3D skeleton and 3D model , varied between 1073 L and 1267 L , and a body mass between 1 and 1 @.@ 5 tonnes (1 @.@ 1 and 1 @.@ 7 short tons) , depending on the amount of musculature reconstructed for the tail .

The long tail of Kentrosaurus results in a position of the center of mass that is unusually far back for a quadrupedal animal . It rests just in front of the hip , a position usually seen in bipedal dinosaurs . However , the femora are straight in Kentrosaurus , as opposed to typical bipeds , indicating a straight and vertical limb position . Thus , the hindlimbs , though powered by massive thigh muscles attached to a long ilium , did not support the animal alone , and the very robust forelimbs took up 10 to 15 % of the bodyweight .

= = = Distinguishing features = = =

Kentrosaurus can be distinguished from other members of the Stegosauria by a number of osteological characters . Mallison (2011) provided a revised diagnosis , an updated list of distinguishing traits or autapomorphies . Most notably , the neural spines , the blade @-@ like upper extensions of the vertebrae , in the tail do not run sub @-@ parallel , as in most dinosaurs . In the front third of the tail , they point backwards , the usual direction . In the middle tail , however , they are almost vertical , and further back they are hook @-@ shaped and point obliquely forward . Also typical is that the dorsal (back) vertebrae have a neural arch more than twice as high as the centrum , the vertebral body , and almost completely occupied by the extremely spacious neural canal . The preacetabular process , front blade , of the ilium widens laterally , to the front outer side , and does not taper .

Furthermore , there is a unique combination of traits not in themselves unique . The transverse processes , the side extensions , of the tail are present up to the twenty @-@ eighth vertebra of the series . The transverse processes of the front tail vertebrae are rod @-@ shaped with narrow bases and do not touch the plate formed by the fusion of the processes of the sacral vertebrae . The chevrons , bones pointing to below from the bottom side of the tail vertebrae , have the shape of an inverted T. The length of the ilium equals , or is greater than , that of the thighbone .

= = = Armour = = =

Typically for a stegosaur , Kentrosaurus had extensive osteoderm (bony structures in the skin) covering , including small plates (probably located on the neck and anterior trunk) , and spikes of various shapes . The spikes of Kentrosaurus are very elongated , with one specimen having a bone core length of 731 millimetres . The plates have a thickened section in the middle , as if they were modified spines . The spikes and plates were likely covered by horn . Aside from a few exceptions they were not found in close association with other skeletal remains . Thus , the exact position of most osteoderms is uncertain . A pair of closely spaced spikes was found articulated with a tail tip , and a number of spikes were found apparently regularly spaced in pairs along the path of an articulated tail .

Hennig and Janensch , while grouping the dermal armour elements into four distinct types , recognised an apparently continuous change of shape among them , shorter and flatter plates at the front gradually merging into longer and more pointed spikes towards the rear , suggesting an uninterrupted distribution along the entire body , in fifteen pairs . Because each type of osteoderm was found in mirrored left and right versions , it seems probable that all types of osteoderms were distributed in two rows along the back of the animal , a marked contrast to the better @-@ known North American Stegosaurus , which had one row of plates on the neck , trunk and tail , and two rows of spikes on the tail tip . There is one type of spike that differs from all others in being strongly , and not only slightly , asymmetrical , and having a very broad base . Because of bone morphology classic reconstructions placed it on the hips , at the iliac blade , while many recent reconstructions place it on the shoulder , because a similarly shaped spike is known to have existed on the shoulder in the Chinese stegosaurs Gigantspinosaurus and Huayangosaurus .

= = Discovery and species = =

The first fossils of Kentrosaurus were discovered by the German Tendaguru Expedition in 1909 , recognised as belonging to a stegosaur by expedition leader Werner Janensch on 24 July 1910 , and described by German palaeontologist Edwin Hennig in 1915 . The name Kentrosaurus was coined by Henning and comes from the Greek kentron / ??????? , meaning " sharp point " or " prickle " , and sauros / ?????? meaning " lizard " , Hennig added the specific name aethiopicus to denote the provenance from Africa .

From 1909 onwards , Kentrosaurus remains were uncovered in four quarries in the Mittlere

Saurierschichten (Middle Saurian Beds) and one quarry in the Obere Saurierschichten (Upper Saurian Beds) . During four field seasons , the German Expedition found over 1200 bones of Kentrosaurus , belonging to about fifty individuals , many of which were destroyed during the Second World War . Today , almost all remaining material is housed in the Museum für Naturkunde Berlin (roughly 350 remaining specimens) , while the museum of the Institute for Geosciences of the Eberhard @-@ Karls @-@ University Tübingen houses a composite mount , roughly 50 % of it being original bones .

Although no complete individuals were found , some material was discovered in association , including a nearly complete tail , hip , several dorsal vertebrae and some limb elements of one individual . These form the core of a mount in the Museum für Naturkunde by Janensch . The mount was dismantled during the museum renovation in 2006 / 2007 , and re @-@ mounted in an improved pose by Research Casting International . Some other material , including a braincase and spine , was thought to have been misplaced or destroyed during World War II . However , all the supposedly lost cranial material was later found in a drawer of a basement cupboard .

The type and sole accepted species of Kentrosaurus is Kentrosaurus aethiopicus , named by Hennig in 1915 . Fragmentary fossil material from Wyoming , named Stegosaurus longispinus by Charles Gilmore in 1914 , was in 1993 classified as a North American species of Kentrosaurus , as K. longispinus . However , this action was not accepted by the paleontological community , and S. longispinus has been assigned to its own genus , Alcovasaurus , differing from Kentrosaurus in having more elongated tail spikes and the structure of the pelvis and vertebrae .

= = = Type specimens and type locality = = =

In the original description , Hennig did not designate a holotype specimen . However , in a detailed monography on the osteology , systematic position and palaeobiology of Kentrosaurus in 1925 , Hennig picked the most complete partial skeleton , today inventorised as MB.R.4800.1 through MB.R.4800.37 , as a lectotype (see syntype) . This material includes a nearly complete series of tail vertebrae , several vertebrae of the back , a sacrum with five sacral vertebrae and both ilia , both femora and an ulna , and is included in the mounted skeleton at the Museum für Naturkunde in Berlin , Germany . The type locality is Kindope , Tanzania , near the Tendaguru hill .

Unaware that Hennig had already defined a lectotype , Peter Galton selected two dorsal vertebrae , specimens MB.R.1930 and MB.R.1931 , from the material figured in Hennig 's 1915 description , as ' holotypes ' . This definition of a holotype is not valid , because Hennig 's selection has priority . In 2011 , Heinrich Mallison clarified that all the material known to Hennig in 1915 , i.e. all the bones discovered before 1912 , when Hermann Heck concluded the last German excavations , are paralectotypes , and that MB.R.4800 is the correct lectotype .

= = = Naming controversy = = =

Soon after its description , a controversy arose over the stegosaur 's name , which is very similar to the ceratopsian Centrosaurus . Under the rules of biological nomenclature , forbidding homonymy , two animals may not be given the same name . Hennig renamed his stegosaur Kentrurosaurus , " pointed @-@ tail saurian " , in 1916 , while Hungarian paleontologist Franz Nopcsa renamed the genus Doryphorosaurus , " lance @-@ bearing saurian " , the same year . If a renaming had been necessary , Hennig 's would have had priority . However , because both the spellings and the pronunciations are different (Centrosaurus is pronounced with a soft C) , both Doryphorosaurus and Kentrurosaurus are unneeded replacement names ; Kentrosaurus remains the valid name for the genus with Kentrurosaurus and Doryphorosaurus being its junior objective synonyms .

= = Phylogeny = =

Kentrosaurus was by Hennig assigned to the Stegosauridae in 1915 . This is confirmed by modern cladistic analyses , although it should be noted that in 1915 Stegosauridae was a far more inclusive

concept . A consecutive narrowing down of this concept caused Kentrosaurus , until the 1980s to be seen as a typical " primitive " stegosaurian , to be placed in a more derived , higher , position in the stegosaur evolutionary tree . Derived traits include a sacral yoke , a long prepubic process , a long thighbone and two rows of plates or spikes . A study by Octávio Mateus e.a. in 2009 recovered Kentrosaurus in a basal position in the Stegosauridae as shown by this cladogram :

Earlier analyses had shown Kentrosaurus closer in the tree to Stegosaurus . Basal traits include a prominent paraquadratic foramen at the quadrate in the skull ; maxillary teeth with only seven denticles at the margin ; and a shoulder spine .

= = Paleobiology = =

= = = Feeding = = =

Like all ornithischians , Kentrosaurus was a herbivore . The fodder was barely chewed and swallowed in large chunks . One theory on stegosaurid diet holds that they were low @-@ level browsers , eating foliage and low @-@ growing fruit from various non @-@ flowering plants . Kentrosaurus was capable of eating at heights of up to 1 @.@ 7 m (5 ft 7 in) when on all fours . It may also have been possible for it to rear up on its hindlegs to reach vegetation higher in trees . With its centre of mass close to the hind @-@ limbs , the animal could potentially support itself as it stood up . The hips were likely capable of allowing a vertical trunk rotation of about 60 degrees and the tail probably would either have been fully lifted , not blocking this movement or have enough curvature to rest on the ground ; thus it could have provided additional support , though precisely because of this flexibility it is not certain whether much support was actually provided : it was not stiff enough to function as a " third leg " as had been suggested by Robert Thomas Bakker . In this pose , Kentrosaurus could have fed at heights of 3 @.@ 3 m (11 ft) .

= = = Defense = = =

Because the tail had at least forty caudal vertebrae , it was highly mobile . It could possibly swing at an arc of 180 degrees , covering the entire half circle behind it . Swing speeds at the tail end may have been as high as 50 km / h . Continuous rapid swings would have allowed the spikes to slash open the skin of its attacker or to stab the soft tissues and break the ribs or facial bones . More directed blows would have resulted in the sides of the spikes fracturing even sturdy longbones of the legs by blunt trauma . These attacks would have crippled small and medium @-@ sized theropods and may even have done some damage to large ones . Earlier interpretations of the defensive behaviour of Kentrosaurus included the suggestion that the animal might have charged to the rear , to run through attackers with its spines , in the way of modern porcupines .

Though Kentrosaurus likely stood with forelimbs erect like in other dinosaurs , it is hypothesised that the animal adopted a sprawling posture when defending itself . Its neck was flexible enough to allow it to keep sight of predators , as it could reach the sides of its body with its snout and look over the back . In addition , the posterior position of the center of mass may not have been advantageous for rapid locomotion , but meant that the animal could quickly rotate around the hips by pushing sideways with the arms , keeping the tail pointed at the attacker . Kentrosaurus was nevertheless not invulnerable . A quick predator could have made it to the tail base (where the impact speed would be much lower) when the tail passed and the neck and upper @-@ part of the body would have been unprotected by the tail swings . A successful predation of Kentrosaurus may have required group hunting . Compared to the more robust spikes of Stegosaurus , the thinner spikes of Kentrosaurus were at greater risk of bending .

= = = Growth = = =

In 2013 , a study by Ragna Redelstorff e.a. concluded that the bone histology of Kentrosaurus

indicated that it had a higher growth rate than reported for Stegosaurus and Scutellosaurus , in view of the relatively rapid deposition of highly vascularised fibrolamellar bone . As Stegosaurus was larger than Kentrosaurus , this contradicts the general rule that larger dinosaurs grew quicker than smaller ones .

= = = Sexual dimorphism = = =

Differences in the proportions , not the size , of the femurs (thighbones) led Holly Barden and Susannah Maidment to realize that Kentrosaurus probably showed sexual dimorphism . This dimorphism of the femurs consisted in them being either more or less robust than the other . The occurrence ratio of the robust morph to the gracile one was 2 : 1 , and it is likely that the higher percentage of animals were females . Because of this ratio , it was considered reasonable to assume that in their society , Kentrosaurus males mated with more than one female , a behaviour also found in other vertebrates .

The problem posed by the ratio is that the multiple specimens studied , died in the same place , but probably not in a sudden mass @-@ death and so do not represent a single herd or contemporary population . The results may have been distorted by a greater chance for robust animals of getting fossilised or discovered . In an earlier study by Galton in 1982 , it was suggested that individual difference in the sacral rib count of both Kentrosaurus and Dacentrurus might be an indication of dimorphism : females would have had an extra pair of sacral ribs , having also the first sacral vertebra connected to the ilium , in addition to the subsequent four sacrals .

= = Paleoecology = =

Kentrosaurus lived in what is now Tanzania in the Late Jurassic Tendaguru Formation . The main Kentrosaurus quarries were located in the Middle Saurian Beds dating from the upper Kimmeridgian . Some remains were found in the Upper Saurian Beds dating from the Tithonian . Since 2012 , the boundary between the Kimmeridgian and Tithonian is dated at 152 @.@ 1 million year ago . The Tendaguru ecosystem primarily consisted of three types of environment : shallow , lagoon @-@ like marine environments , tidal flats and low coastal environments ; and vegetated inland environments . The marine environment existed above the fair weather wave base and behind siliciclastic and ooid barriers . It appeared to have had little change in salinity levels and experienced tides and storms . The coastal environments consisted of brackish coastal lakes , ponds and pools . These environments had little vegetation and were probably visited by herbivorous dinosaurs mostly during droughts . The well vegetated inlands were dominated by conifers . Overall , the Late Jurassic Tendaguru climate was subtropical to tropical with seasonal rains and pronounced dry periods . During the Early Cretaceous , the Tendaguru became more humid . The Tendaguru Beds are similar to the Morrison Formation of North America except in its marine interbeds .

Kentrosaurus would have coexisted with fellow ornithischians like Dysalotosaurus lettowvorbecki ; the sauropods Giraffatitan brancai , Dicraeosaurus hansemanni and D. sattleri , Janenschia africana , Tendaguria tanzaniensis and Tornieria africanus ; theropods " Allosaurus " tendagurensis , " Ceratosaurus " roechlingi , " Ceratosaurus " ingens , Elaphrosaurus bambergi , Veterupristisaurus milneri and Ostafrikasaurus crassiserratus ; and the pterosaur Tendaguripterus recki . Other organisms that inhabited the Tendaguru included corals , echinoderms , cephalopods , bivalves , gastropods , decapods , sharks , neopterygian fish , crocodilians and small mammals like Brancatherulum tendagurensis .