

= Massospondylus =

Massospondylus (/ ˈmæsoʊspɒndɪlʊs / mas @-@ oh @-@ SPON @-@ di @-@ lʊs ; from Greek , ????? (masson , " longer ") and ????????? (spondylos , " vertebra ")) is a genus of sauropodomorph dinosaur from the Early Jurassic Period (Hettangian to Pliensbachian ages , ca . 200 ? 183 million years ago) . It was described by Sir Richard Owen in 1854 from remains discovered in South Africa , and is thus one of the first dinosaurs to have been named . Fossils have since been found at other locations in South Africa , Lesotho , and Zimbabwe . Material from Arizona 's Kayenta Formation , India , and Argentina has been assigned to this genus at various times , but the Arizonan and Argentinian material are now assigned to other genera .

The type species is *M. carinatus* ; seven other species have been named during the past 150 years , but only *M. kaalae* among these is still considered valid . Early sauropodomorphs systematics have undergone numerous revisions during the last several years , and many scientists disagree where exactly Massospondylus lies on the dinosaur evolutionary tree . The family name Massospondylidae was once coined for the genus , but because knowledge of early sauropodomorph relationships is in a state of flux , it is unclear which other dinosaurs ? if any ? belong in a natural grouping of massospondylids ; several 2007 papers support the family 's validity .

Although Massospondylus was long depicted as quadrupedal , a 2007 study found it to be bipedal . It was probably a plant eater (herbivore) , although it is speculated that the early sauropodomorphs may have been omnivorous . This animal , which was 4 ? 6 metres (13 ? 20 ft) long , had a long neck and tail , with a small head and slender body . On each of its forefeet , it bore a sharp thumb claw that was used in defense or feeding . Recent studies indicate that Massospondylus grew steadily throughout its lifespan , possessed air sacs similar to those of birds , and may have cared for its young .

= = Description = =

Massospondylus was a mid @-@ size sauropodomorph , around 4 metres (13 ft) in length and weighed approximately 1000 kilograms (2200 lb) , although a few sources have estimated its length at up to 6 metres (20 ft) . It was a typical early sauropodomorph , with a slender body , a long neck and a proportionally very small head . The vertebral column was composed of nine cervical (neck) vertebrae , 13 dorsal (back) vertebrae , three sacral (hip) vertebrae , and at least 40 caudal (tail) vertebrae . The pubis faced forward , as with most saurischians . It had a slighter build than that of Plateosaurus , an otherwise similar dinosaur . The neck was proportionally longer than in most other plateosaurids , with the foremost cervicals being four times the length of their width . The forelimbs were only half the length of the hindlimbs but quite powerful , as indicated by the broad upper end of the humerus that provided attachment areas for a large arm musculature . Like Plateosaurus , it had five digits on each hand and foot . The hand was short and wide , with a large sickle shaped thumb claw used for feeding or defense against predators . The thumb was the longest finger in the hand , while the fourth and fifth digits were tiny , giving the forepaws a lopsided look .

= = = Cranial anatomy = = =

The small head of Massospondylus was approximately half the length of the femur . Numerous openings , or fenestrae , in the skull reduced its weight and provided space for muscle attachment and sensory organs . These fenestrae were present in pairs , one on each side of the skull . At the front of the skull were two large , elliptical nares , which were roughly half the size of the orbits . The orbits were proportionally larger in Massospondylus than in related genera , such as Plateosaurus . The antorbital fenestrae , smaller than those seen in Plateosaurus , were situated between the eyes and the nose . At the rear of the skull were two more pairs of temporal fenestrae : the lateral temporal fenestrae immediately behind the eye sockets , which were shaped like an inverted " T " in Massospondylus , and the supratemporal fenestrae on top of the skull . Small fenestrae also

penetrated each mandible . The shape of the skull is traditionally restored as wider and shorter than that of Plateosaurus , but this appearance may be due just to differential crushing experienced by the various specimens . Some features of the skull are variable between individuals ; for example , the thickness of the upper border of the orbit and the height of the posterior maxilla . These differences may be due to sexual dimorphism or individual variation .

Tooth count is variable between individuals and increases with skull size . The premaxilla shows the constant number of four teeth per side in all known skulls ; however , in the maxilla , the tooth count ranges from 14 to 22 . There are 26 teeth in each side of the lower jaw in the largest known skull . The height of the teeth crowns decreases from front to back in the upper jaw , but was more or less constant in the lower jaw . The lack of pronounced tooth wear and the variable height of the crowns suggests that the teeth were replaced by succeeding new ones in relatively short time intervals . Notably , there was variation in the tooth morphology based on the position of the teeth in the jaw . The heterodonty present in Massospondylus is greater than that present in Plateosaurus , although not as pronounced as the specialization of teeth in Heterodontosaurus . Teeth closer to the front of the snout had round cross @-@ sections and tapered to points , unlike the back teeth , which were spatulate and had oval cross @-@ sections .

As with other early sauropodomorphs , it has been proposed that Massospondylus had cheeks . This theory was proposed because there are a few large holes for blood vessels on the surfaces of the jaw bones , unlike the numerous small holes present on the jaws of cheekless reptiles . The cheeks would have prevented food from spilling out when Massospondylus ate . Crompton and Attridge (1986) described skulls of Massospondylus as possessing pronounced overbites and suggested the presence of a horny beak on the tip of the lower jaw to make up the difference in length and account for tooth wear on the teeth at the tip of the snout . However , the difference in length may be a misinterpretation based on crushing in a top ? bottom plane , and the possession of a beak is considered unlikely in recent studies .

= = Discovery = =

The first fossils of Massospondylus were described by paleontologist Sir Richard Owen in 1854 . Originally , Owen did not recognize these finds as those of a dinosaur ; instead he attributed them to " large , extinct , carnivorous reptiles " that were related to today 's lizards , chameleons and iguanas . This material , a collection of 56 bones , was found in 1853 by the government surveyor Joseph Millard Orpen in the Upper Elliot Formation at Harrismith , South Africa and was donated to the Hunterian Museum at the Royal College of Surgeons in London . Among the remains were vertebrae from the neck , back , and tail ; a shoulder blade ; a humerus ; a partial pelvis ; a femur ; a tibia ; and bones of the hands and feet . All these bones were found disarticulated , making it difficult to determine if all material belongs to a single species or not . However , Owen was able to distinguish three different types of caudal vertebrae , which he attributed to three different genera : Pachyspondylus , Leptospondylus and Massospondylus . Massospondylus was separated from the other two genera on the basis of its much longer caudal vertebrae , which also lead to the scientific name that has been derived from the Greek terms masson / ?????? ' longer ' and sphondylos / ?????????? ' vertebra ' . However , later it was shown that the putative caudal vertebrae of Massospondylus were actually cervical vertebrae and that all the material probably belongs only to a single species . On May 10 , 1941 , the Hunterian Museum was demolished by a German bomb , destroying all the fossils ; only casts remain .

Possible Massospondylus remains have been found in the Upper Elliot Formation , the Clarens Formation , and the Bushveld Sandstone of South Africa and Lesotho ; the Forest Sandstone and the Upper Karroo Sandstone of Zimbabwe . These remains consist of at least 80 partial skeletons and four skulls , representing both juveniles and adults . The report of Massospondylus from Arizona 's Kayenta Formation is based on a skull described in 1985 . The skull of the Kayenta specimen from Arizona is 25 % larger than the largest skull from any African specimen . The Kayenta specimen possesses four teeth in the premaxilla and sixteen in the maxilla . Uniquely among dinosaurs , it also had tiny , one @-@ millimetre- (0 @.@ 04 in-) long palatal teeth . Recent

restudy of African *Massospondylus* skulls , however , indicates that the Kayenta specimen does not pertain to *Massospondylus* . This Kayenta skull and associated postcranial elements , identified collectively as MCZ 8893 , has been recently referred to the newly described genus *Sarawsaurus* .

Massospondylus had also been reported from Argentina , but this has been reassessed as a closely related but distinct genus . The fossils included several partial skeletons and at least one skull , found in the Lower Jurassic Canon del Colorado Formation of San Juan , Argentina . This material was named *Adeopapposaurus* in 2009 .

= = = Species = = =

Many species have been named , although most are no longer considered valid . *M. carinatus* , named by Richard Owen , is the type species . Other named species include : *M. browni* Seeley , 1895 , *M. harriesi* Broom 1911 , *M. hislopi* Lydekker , 1890 , *M. huenei* Cooper , 1981 , *M. kaalae* Barrett 2009 , *M. rawesi* Lydekker , 1890 , and *M. schwarzi* Haughton , 1924 .

M. browni , *M. harriesi* , and *M. schwarzi* were all found in the Upper Elliot Formation of Cape Province , South Africa . All three are based on fragmentary material , and were regarded as indeterminate in the most recent review . *M. browni* is based on two cervical , two back , and three caudal vertebrae and miscellaneous hind limb elements . *M. harriesi* is known from a well @-@ preserved forelimb and parts of a hindlimb . *M. schwarzi* is known from an incomplete hind limb and sacrum . *M. hislopi* and *M. rawesi* were named from fossils found in India . *M. hislopi* is based on vertebrae from the Upper Triassic Maleri Formation of Andhra Pradesh , whereas *M. rawesi* is based on a tooth from the Upper Cretaceous Takli Formation of Maharashtra . *M. hislopi* was tentatively retained as an indeterminate sauropodomorph in the latest review , but *M. rawesi* may be a theropod or nondinosaur . *M. huenei* is a combination derived by Cooper for *Lufengosaurus huenei* , as he considered *Lufengosaurus* and *Massospondylus* to be synonyms . This synonymy is no longer accepted .

M. kaalae was described in 2009 on the basis of a partial skull from the Upper Elliot Formation in Eastern Cape of South Africa . This species is known from the same time and region as some specimens of *M. carinatus* . It differs from the type species in the morphology of the braincase , as well as in several other characters of the skull such as the proportions of the premaxilla .

= = = Dubious names = = =

Several dinosaurs are often considered synonymous with *Massospondylus* . These include the above @-@ mentioned *Leptospondylus* and *Pachyspondylus* , as well as *Aristosaurus* , *Dromicosaurus* , *Gryponyx taylori* and *Hortalotarsus* , which are dubious names of little scientific value . *Hortalotarsus skriptopodus* was named by Harry Seeley in 1894 . According to Broom (1911) , " Originally most of the skeleton was in the rock , and it was regarded by the farmers as the skeleton of a Bushman , but it is said to have been destroyed through fear that a Bushman skeleton in the rock might tend to weaken the religious belief of the rising generation . " Seeley however , states that most of the skeleton was lost by a failed attempt to free it from the rock by using gunpowder . Some partial leg bones were salvaged . Together with *Massospondylus carinatus* , Owen named *Leptospondylus capensis* and *Pachyspondylus orpenii* . *Aristosaurus erectus* was named by E.C.N. van Hoepen in 1920 based on a nearly complete skeleton . Hoepen also named *Dromicosaurus gracilis* , which consisted of a partial skeleton . *Gryponyx taylori* was named by Sidney H. Haughton in 1924 . It consists of hip bones . All of the above fossils come from the Hettangian or Sinemurian faunal stages of South Africa , where *Massospondylus* has been found . Under the rules of zoological nomenclature , these names are junior synonyms . They were named after *Massospondylus* was described in a scientific paper ; the name *Massospondylus* thus takes priority .

Ignavusaurus , known from a young specimen , may also be synonymous with *Massospondylus* .

= = Classification = =

Basal sauropodomorph systematics continue to undergo revision , and many genera once considered classic " prosauropods " have recently been removed from the group in phylogenetic nomenclature , on the grounds that their inclusion would not constitute a clade (a natural grouping containing all descendants of a single common ancestor) . Yates and Kitching (2003) published a clade consisting of Riojasaurus , Plateosaurus , Coloradisaurus , Massospondylus , and Lufengosaurus . Galton and Upchurch (2004) included Ammosaurus , Anchisaurus , Azendohsaurus , Camelotia , Coloradisaurus , Euskelosaurus , Jingshanosaurus , Lessemsaurus , Lufengosaurus , Massospondylus , Melanorosaurus , Mussaurus , Plateosaurus , Riojasaurus , Ruehleia , Saturnalia , Sellosaurus , Thecodontosaurus , Yimenosaurus and Yunnanosaurus in a monophyletic Prosauropoda . Wilson (2005) considered Massospondylus , Jingshanosaurus , Plateosaurus , and Lufengosaurus a natural group , with Blikanasaurus and Antetonitrus possible sauropods . Bonnan and Yates (2007) considered Camelotia , Blikanasaurus and Melanorosaurus possible sauropods . Yates (2007) placed Antetonitrus , Melanorosaurus , and Blikanasaurus as basal sauropods and declined to use the term Prosauropoda , as he considered it synonymous with Plateosauridae . However , he did not rule out the possibility that a small group of prosauropods consisting of Plateosaurus , Riojasaurus , Massospondylus and their closest kin were monophyletic .

Massospondylus is the type genus of the proposed family Massospondylidae , to which it gives its name . The Massospondylidae family may also include Yunnanosaurus , although Lu et al . (2007) placed Yunnanosaurus in its own family . Yates (2007) considered Massospondylus , Coloradisaurus , and Lufengosaurus massospondylids , with Yunnanosaurus in Anchisauria . Smith and Pol (2007) also found a Massospondylidae in their phylogenetic analysis , including Massospondylus , Coloradisaurus , and Lufengosaurus , as well as their new genus , Glacialisaurus . Adeopapposaurus , based on the fossils once thought to belong to a South American form of Massospondylus , was also classified as a massospondylid , as was Leyesaurus , another South American genus that was named in 2011 . Pradhania was originally regarded as a more basal sauropodomorph but new cladistic analysis performed by Novas et al . , 2011 suggests that Pradhania is a massospondylid . Pradhania presents two shared traits of the Massospondylidae recovered in their phylogenetic analysis , and the fossils of Pradhania were discovered from the same region and basin in India as M. hislopi .

= = Paleoecology = =

The faunas and floras of the Early Jurassic were similar worldwide , with conifers adapted for hot weather becoming the common plants ; basal sauropodomorphs and theropods were the main constituents of a worldwide dinosaur fauna . The environment of early Jurassic southern Africa has been described as a desert . African Massospondylus was a contemporary of temnospondyli ; turtles ; a sphenodontia ; rauisuchids ; early crocodylomorphs ; tritylodontid and trithelodontid therapsids ; morganucodontid mammals ; and dinosaurs including the small theropod Megapnosaurus rhodesiensis and several genera of early ornithischians , such as Lesothosaurus and the heterodontosaurids Abriotosaurus , Heterodontosaurus , Lycorhinus and Pegomastax . Until recently , Massospondylus was regarded as the only known sauropodomorph from the Upper Elliot Formation . However , newer finds revealed a diverse contemporary sauropodomorph fauna with six additional species , including Ignavusaurus , Arcusaurus and two unnamed taxa as well as two unnamed sauropods .

It is not clear which carnivores may have preyed on Massospondylus . Most of the theropods that have been discovered in rocks of Early Jurassic age in southern Africa , such as Megapnosaurus , were smaller than mid @-@ sized sauropodomorphs like Massospondylus . These smaller predators have been postulated as using fast slashing attacks to wear down sauropodomorphs , which could have defended themselves with their large hand and foot claws . The 6 @-@ metre- (20 ft-) long carnivorous theropod Dracovenator lived during the same period (Hettangian to Sinemurian stages) as Massospondylus and has also been found in the Elliot Formation of South

Africa .

= = Paleobiology = =

As with all dinosaurs , much of the biology of Massospondylus , including its behavior , coloration , and physiology , remains unknown . However , recent studies have allowed for informed speculation on subjects such as growth patterns , diet , posture , reproduction , and respiration .

A 2007 study suggested that Massospondylus may have used its short arms for defense against predators (" defensive swats ") , in intraspecies combat , or in feeding , although its arms were too short to reach its mouth . Scientists speculate that Massospondylus could have used its large pollex (thumb) claw in combat , to strip plant material from trees , digging , or for grooming .

= = = Growth = = =

A 2005 study indicated that Massospondylus ' sister taxon , Plateosaurus , exhibited growth patterns affected by environmental factors . The study indicated that , when food was plentiful or when the climate was favorable , Plateosaurus exhibited accelerated growth . This pattern of growth is called " developmental plasticity " . It is unseen in other dinosaurs , including Massospondylus , despite the close relationship between the two . The study indicated that Massospondylus grew along a specific growth trajectory , with little variation in the growth rate and ultimate size of an individual . Another study of age determination indicated that Massospondylus grew at a maximum rate of 34 @. @ 6 kg (76 @. @ 3 lb) per year and was still growing at around 15 years of age .

= = = Diet = = =

Early sauropodomorphs such as Massospondylus may have been herbivorous or omnivorous . As recently as the 1980s , paleontologists debated the possibility of carnivory in the " prosauropods " . However , the hypothesis of carnivorous " prosauropods " has been discredited , and all recent studies favor a herbivorous or omnivorous lifestyle for these animals . Galton and Upchurch (2004) found that cranial characteristics (such as jaw articulation) of most basal sauropodomorphs are closer to those of herbivorous reptiles than those of carnivorous ones , and the shape of the tooth crown is similar to those of modern herbivorous or omnivorous iguanas . The maximum width of the crown was greater than that of the root , resulting in a cutting edge similar to those of extant herbivorous or omnivorous reptiles . Barrett (2000) proposed that basal sauropodomorphs supplemented their herbivorous diets with small prey or carrion . Gastroliths (gizzard stones) have been found in association with three Massospondylus fossils from the Forest @-@ Sandstone in Zimbabwe , and with a Massospondylus @-@ like animal from the Late Triassic of Virginia . Until recently , scientists believed that these stones functioned as a gastric mill to aid ingestion of plant material , compensating for its inability to chew , as it is the case in many modern birds . However , Wings and Sander (2007) showed that the polished nature and the abundance of those stones precluded a use as an effective gastric mill in most non @-@ theropod dinosaurs , including Massospondylus .

= = = Gait and range of motion = = =

Although long assumed to have been quadrupedal , a 2007 anatomical study of the forelimbs has questioned this , arguing that their limited range of motion precluded effective habitual quadrupedal gait . Neither could the forelimbs swing fore and behind in a fashion similar to the hindlimbs , nor could the hand be rotated with the palmar surfaces facing downwards . This inability to pronate the hand is also supported by in @-@ situ finds of articulated (still @-@ connected) arms that always show unrotated hands with palmar faces facing each other . The study also ruled out the possibility of " knuckle @-@ walking " and other forms of locomotion that would make an effective locomotion possible without the need to pronate the hand . Although its mass suggests a quadrupedal nature ,

Massospondylus would have been restricted to its hind legs for locomotion .

Since the discovery of rudimentary and nonfunctional clavicles in ceratopsians , it was assumed that these shoulder bones were reduced in all dinosaurs that did not have true furculae . Robert Bakker (1987) suggested that this would have allowed the shoulder blades to swing with the forelimbs in quadrupedal dinosaurs , increasing their functional forelimb length . This would have reduced the discrepancy of length between fore- and hindlimbs in a quadrupedal Massospondylus . However , a recent discovery shows that Massospondylus possessed well developed clavicles that were joined in a furcula like arrangement , acting like a clasp between the right and left shoulder blades and prohibiting any rotation of these bones . This discovery indicates that the clavicle reduction is limited to the evolutionary line leading to the ceratopsians . It also indicates that the furcula of birds is derived from clavicles .

Michael Cooper (1981) noted that the zygapophyses of the neck vertebrae were inclined , prohibiting significant horizontal movement of the neck , so that " consequently any significant movement in this direction must have been accomplished by a change in the position of the entire body " . This was contradicted in a recent study , noting that only the basalmost cervicals show inclined zygapophyses , allowing sufficient horizontal movement of the neck as a whole .

= = = Reproduction = = =

In 1976 , a clutch of seven 190 million year old Massospondylus eggs was found in Golden Gate Highlands National Park in South Africa by James Kitching , who identified them as most likely belonging to Massospondylus . It was nearly 30 years before extraction was started on the fossils of the 15 centimetre- (6 in-) long embryos . They remain the oldest dinosaur embryos ever found . By early 2012 , at least 10 egg clutches from at least four fossiliferous horizons had been found , with up to 34 eggs per clutch . This indicates that this nesting site may have been used repeatedly (site fidelity) , by groups of animals (colonial nesting) ; in both cases , these represent the oldest evidence of this behaviour . Sedimentary structures indicate that the nesting area was in the vicinity of a lake . The eggshells were very thin (about 0.1 mm) , allowing gas exchange even in a low oxygen and carbon dioxide rich environment , which indicates that the eggs were at least partly buried in the substrate . There are no hints that Massospondylus constructed nests ; however , the arrangement of the eggs in tight rows indicates that the eggs were pushed in this position by the adults .

The embryos probably represented near hatchlings . While the skeletal features were similar to those of the adults , the body proportions were very dissimilar . The head was big with a short snout and very large orbits , whose diameter amounts 39 % of the entire skull length . The neck was short , contrasting to the very long neck in the adults . Girdle bones and caudals were relatively tiny . The forelimbs were of equal length to the hindlimbs , indicating that newly hatched Massospondylus were quadrupedal , unlike the bipedal adults . The discovery of hatching footprints with manus impressions confirmed their quadrupedality . These impressions show that the hand was not pronated , with palm faces facing each other and the thumb facing forwards . The unpronated manus and the big head indicate that an effective locomotion was not possible for newly hatched Massospondylus . Notably , the near hatchlings had no teeth , suggesting they had no way of feeding themselves . Based on the lack of teeth and the ineffective locomotion , scientists speculate that postnatal care might have been necessary . This is further supported by evidence that the hatchlings remained at the nest sites until they had doubled in size .

Newly hatched juveniles are known from a second sauropodomorph , Mussaurus ; these remains resemble those of the embryonic Massospondylus , suggesting that quadrupedality was present in newly hatched Mussaurus and presumably other basal sauropodomorphs as well . The quadrupedality of the hatchlings suggests that the quadrupedal posture of later sauropods may have evolved from retention of juvenile characteristics in adult animals , an evolutionary phenomenon known as pedomorphosis . This discovery therefore " sheds some light in the evolutionary pathways through which the peculiar adaptations of giant dinosaurs were attained " , stated French paleontologist Eric Buffetaut .

=== Respiratory system ===

Many saurischian dinosaurs possessed vertebrae and ribs that contained hollowed out cavities (pneumatic foramina) , which reduced the weight of the bones and may have served as a basic ' flow @-@ through ventilation ' system similar to that of modern birds . In such a system , the neck vertebrae and ribs are hollowed out by the cervical air sac ; the upper back vertebrae , by the lung ; and the lower back and sacral (hip) vertebrae , by the abdominal air sac . These organs constitute a complex and very efficient method of respiration . " Prosauropods " are the only major group of saurischians without an extensive system of pneumatic foramina . Although possible pneumatic indentations have been found in Plateosaurus and Thecodontosaurus , the indentations were very small . One study in 2007 concluded that basal sauropodomorphs like Massospondylus likely had abdominal and cervical air sacs , based on the evidence for them in sister taxa (theropods and sauropods) . The study concluded that it was impossible to determine whether basal sauropodomorphs had a bird @-@ like flow @-@ through lung , but that the air sacs were almost certainly present .