= Majungasaurus =

Majungasaurus (/ m??d??????s??r?s / ; " Mahajanga lizard ") is a genus of abelisaurid theropod dinosaur that lived in Madagascar from 70 to 66 million years ago , at the end of the Cretaceous Period . The genus contains a single species , Majungasaurus crenatissimus . This dinosaur was briefly called Majungatholus , a name which is now considered a junior synonym of Majungasaurus .

Like other abelisaurids , Majungasaurus was a bipedal predator with a short snout . Although the forelimbs are not completely known , they were very short , while the hind limbs were longer and very stocky . It can be distinguished from other abelisaurids by its wider skull , the very rough texture and thickened bone on the top of its snout , and the single rounded horn on the roof of its skull , which was originally mistaken for the dome of a pachycephalosaur . It also had more teeth in both upper and lower jaws than most abelisaurids .

Known from several well @-@ preserved skulls and abundant skeletal material , Majungasaurus has recently become one of the best @-@ studied theropod dinosaurs from the Southern Hemisphere . It appears to be most closely related to abelisaurids from India rather than South America or continental Africa , a fact that has important biogeographical implications . Majungasaurus was the apex predator in its ecosystem , mainly preying on sauropods like Rapetosaurus , and is also one of the few dinosaurs for which there is direct evidence of cannibalism .

= = Description = =

Majungasaurus was a medium @-@ sized theropod that typically measured 6 ? 7 meters (20 ? 23 ft) in length , including its tail . Fragmentary remains of larger individuals indicate that some adults reached lengths of more than 8 meters (26 ft) . Sampson and Witmer estimated an average weight for an adult Majungasaurus of 1 @,@ 100 kilograms (2 @,@ 400 lb) . The specimen they based it on (FMNH PR 2100) was not the largest one discovered . Larger specimens of Majungasaurus crenatissimus could have been similar in size to its relative Carnotaurus , which has been estimated to weigh 1 @,@ 500 kilograms (3 @,@ 300 lb) .

The skull of Majungasaurus is exceptionally well @-@ known compared to most theropods and generally similar to that of other abelisaurids . Like other abelisaurid skulls , its length was proportionally short for its height , although not as short as in Carnotaurus . The skulls of large individuals measured 60 ? 70 centimeters (24 ? 28 in) long . The tall premaxilla (frontmost upper jaw bone) , which made the tip of the snout very blunt , was also typical of the family . However , the skull of Majungasaurus was markedly wider than in other abelisaurids . All abelisaurids had a rough , sculptured texture on the outside faces of the skull bones , and Majungasaurus was no exception . This was carried to an extreme on the nasal bones of Majungasaurus , which were extremely thick and fused together , with a low central ridge running along the half of the bone closest to the nostrils . A distinctive dome @-@ like horn protruded from the fused frontal bones on top of the skull as well . In life , these structures would have been covered with some sort of integument , possibly made of keratin . Computed tomography (CT scanning) of the skull shows that both the nasal structure and the frontal horn contained hollow sinus cavities , perhaps to reduce weight . The teeth were typical of abelisaurids in having short crowns , although Majungasaurus bore seventeen teeth in both the maxilla of the upper jaw and the dentary of the lower jaw , more than in any other abelisaurid except Rugops .

The postcranial skeleton of Majungasaurus closely resembles those of Carnotaurus and Aucasaurus , the only other abelisaurid genera for which complete skeletal material is known . Majungasaurus was bipedal , with a long tail to balance out the head and torso , putting the center of gravity over the hips . Although the cervical (neck) vertebrae had numerous cavities and excavations (pleurocoels) to reduce their weight , they were robust , with exaggerated muscle attachment sites and ribs that interlocked for strength . Ossified tendons attached to the cervical ribs , giving them a forked appearance , as seen in Carnotaurus . All of these features resulted in a very

strong and muscular neck . Uniquely , the cervical ribs of Majungasaurus had long depressions along the sides for weight reduction . The humerus (upper arm bone) was short and curved , closely resembling those of Aucasaurus and Carnotaurus . Also like related dinosaurs , Majungasaurus had very short forelimbs with four extremely reduced digits , first reported with only two very short external fingers and no claws . The hand and finger bones of Majungasaurus , like other majungasaurines , lacked the characteristic pits and grooves where claws and tendons would normally attach , and its finger bones were fused together , indicating that the hand was immobile . In 2012 , a better specimen was described , showing that the lower arm was robust , though short , and that the hand contained four metatarsals and four , probably inflexible and very reduced , fingers , with small claws on the second and third finger . The phalanx formula was 1 @-@ 2 @-@ 2 @-@ 1 @-@ 0 .

Like other abelisaurids , the hindlimbs were stocky and short compared to body length . The tibia (lower leg bone) of Majungasaurus was even stockier than that of its relative Carnotaurus , with a prominent crest on the knee . The astragalus and calcaneum (ankle bones) were fused together , and the feet bore three functional digits , with a smaller first digit that did not contact the ground .

= = Classification and systematics = =

Majungasaurus is classified as a member of the theropod clade Abelisauridae , which is considered a family in Linnaean taxonomy . Along with the family Noasauridae , abelisaurids are included in the superfamily Abelisauroidea , which is in turn a subdivision of the infraorder Ceratosauria . Abelisaurids are known for their tall skulls with blunt snouts , extensive sculpturing on the outer surfaces of the facial bones (convergent with carcharodontosaurids) , very reduced (atrophied) forelimbs (convergent with tyrannosaurids) , and stocky hindlimb proportions , among other features .

As with many dinosaur families , the systematics (evolutionary relationships) within the family Abelisauridae are confused . Several cladistic studies have indicated that Majungasaurus shares a close relationship with Carnotaurus from South America , while others were unable to firmly place it in the phylogeny . The most recent analysis , using the most complete information , instead recovered Majungasaurus in a clade with Rajasaurus and Indosaurus from India , but excluding South American genera like Carnotaurus , Ilokelesia , Ekrixinatosaurus , Aucasaurus and Abelisaurus , as well as Rugops from mainland Africa . This leaves open the possibility of separate clades of abelisaurids in western and eastern Gondwana .

A cladogram by Tortosa et al . 2013 places Majungasaurus in a new subfamily , Majungasaurinae . A simplified version showing the taxa within the group is shown below .

= = Discovery and naming = =

French paleontologist Charles Depéret described the first theropod remains from northwestern Madagascar in 1896 . These included two teeth , a claw , and some vertebrae discovered along the Betsiboka River by a French army officer and deposited in the collection of what is now the Université Claude Bernard Lyon 1 . Depéret referred these fossils to the genus Megalosaurus , which at the time was a wastebasket taxon containing any number of unrelated large theropods , as the new species M. crenatissimus . This name is derived from the Latin word crenatus (" notched ") and the suffix -issimus (" most ") , in reference to the numerous serrations on both front and rear edges of the teeth . Depéret later reassigned the species to the North American genus Dryptosaurus , another poorly known taxon .

Numerous fragmentary remains from Mahajanga Province in northwestern Madagascar were recovered by French collectors over the next 100 years , many of which were deposited in the Muséum National d 'Histoire Naturelle in Paris . In 1955 , René Lavocat described a theropod dentary (MNHN.MAJ 1) with teeth from the Maevarano Formation in the same region where the original material was found . The teeth matched those first described by Depéret , but the strongly curved jaw bone was very different from both Megalosaurus and Dryptosaurus . Based on this

dentary , Lavocat created the new genus Majungasaurus , using an older spelling of Mahajanga as well as the Greek word ?????? / sauros (meaning " lizard ") . Hans @-@ Dieter Sues and Philippe Taquet described a dome @-@ shaped skull fragment (MNHN.MAJ 4) as a new genus of pachycephalosaur (Majungatholus atopus) in 1979 . This was the first report of a pachycephalosaur in the Southern Hemisphere .

In 1993 , scientists from the State University of New York at Stony Brook and the University of Antananarivo began the Mahajanga Basin Project , a series of expeditions to examine the fossils and geology of the Late Cretaceous sediments near the village of Berivotra , in Mahajanga Province . Among these scientists was paleontologist David W. Krause of Stony Brook . The first expedition turned up hundreds of theropod teeth identical to those of Majungasaurus , some of which were attached to an isolated premaxilla that was described in 1996 . The following seven expeditions would turn up tens of thousands of fossils , many of which belonged to species new to science . The Mahajanga Basin Project claims credit for quintupling the known diversity of fossil taxa in the region .

Fieldwork in 1996 turned up a spectacularly complete theropod skull preserved in exquisite detail (FMNH PR 2100) . On top of this skull was a dome @-@ shaped swelling nearly identical to the one described by Sues and Taquet as Majungatholus atopus . Majungatholus was redescribed as an abelisaurid rather than a pachycephalosaur in 1998 . Although the name Majungasaurus crenatissimus was older than Majungatholus atopus , the authors judged the type dentary of Majungasaurus too fragmentary to confidently assign to the same species as the skull . Further fieldwork over the next decade turned up a series of less complete skulls , as well as dozens of partial skeletons of individuals ranging from juveniles to adults . Project members also collected hundreds of isolated bones and thousands of shed Majungasaurus teeth . Taken together , these remains represent nearly all the bones of the skeleton , although most of the forelimbs , most of the pelvis and the tip of the tail are still unknown . This fieldwork culminated in a 2007 monograph consisting of seven scientific papers on all aspects of the animal 's biology , published in the Society of Vertebrate Paleontology Memoirs . The papers are in English , although each has an abstract written in Malagasy . In this volume , the dentary described by Lavocat was re @-@ evaluated and determined to be diagnostic for this species . Therefore , the name Majungatholus was replaced by the older name Majungasaurus . Although the monograph is comprehensive , the editors noted that it describes only material recovered from 1993 through 2001 . A significant quantity of specimens , some very complete , were excavated in 2003 and 2005 and await preparation and description in future publications . The dentary was made the neotype specimen after a 2009 petition to the ICZN .

= = Paleobiology = =

= = = Skull ornamentation = = =

Majungasaurus is perhaps most distinctive for its skull ornamentation , including the swollen and fused nasals and the frontal horn . Other ceratosaurs , including Carnotaurus , Rajasaurus , and Ceratosaurus itself bore crests on the head . These structures are likely to have played a role in intraspecific competition , although their exact function within that context is unknown . The hollow cavity inside the frontal horn of Majungasaurus would have weakened the structure and probably precluded its use in direct physical combat , although the horn may have served a display purpose . While there is variation in the ornamentation of Majungasaurus individuals , there is no evidence for sexual dimorphism .

= = = Feeding = = =

Scientists have suggested that the unique skull shape of Majungasaurus and other abelisaurids indicate different predatory habits than other theropods . Whereas most theropods were

characterized by long , low skulls of narrow width , abelisaurid skulls were taller and wider , and often shorter in length as well . The narrow skulls of other theropods were well equipped to withstand the vertical stress of a powerful bite , but not as good at withstanding torsion (twisting) . In comparison to modern mammalian predators , most theropods may have used a strategy similar in some ways to that of long- and narrow @-@ snouted canids , with the delivery of many bites weakening the prey animal .

Abelisaurids , especially Majungasaurus , may instead have been adapted for a feeding strategy more similar to modern felids , with short and broad snouts , that bite once and hold on until the prey is subdued . Majungasaurus had an even broader snout than other abelisaurids , and other aspects of its anatomy may also support the bite @-@ and @-@ hold hypothesis . The neck was strengthened , with robust vertebrae , interlocking ribs and ossified tendons , as well as reinforced muscle attachment sites on the vertebrae and the back of the skull . These muscles would have been able to hold the head steady despite the struggles of its prey . Abelisaurid skulls were also strengthened in many areas by bone mineralized out of the skin , creating the characteristic rough texture of the bones . This is particularly true of Majungasaurus , where the nasal bones were fused and thickened for strength . On the other hand , the lower jaw of Majungasaurus sported a large fenestra (opening) on each side , as seen in other ceratosaurs , as well as synovial joints between certain bones that allowed a high degree of flexibility in the lower jaw , although not to the extent seen in snakes . This may have been an adaptation to prevent the fracture of the lower jaw when holding onto a struggling prey animal . The front teeth of the upper jaw were more robust than the rest , to provide an anchor point for the bite , while the low crown height of Majungasaurus teeth prevented them from breaking off during a struggle . Finally , unlike the teeth of Allosaurus and most other theropods , which were curved on both the front and back , abelisaurids like Majungasaurus had teeth curved on the front edge but straighter on the back (cutting) edge . This structure may have served to prevent slicing , and instead holding the teeth in place when biting .

Majungasaurus was the largest predator in its environment , while the only known large herbivores at the time were sauropods like Rapetosaurus . Scientists have suggested that Majungasaurus , and perhaps other abelisaurids , specialized on hunting sauropods . Adaptations to strengthen the head and neck for a bite @-@ and @-@ hold type of attack might have been very useful against sauropods , which would have been tremendously powerful animals . This hypothesis may also be supported by the hindlegs of Majungasaurus , which were short and stocky , as opposed to the longer and more slender legs of most other theropods . While Majungasaurus would not have moved as fast as other similar @-@ sized theropods , it would have had no trouble keeping up with slow @-@ moving sauropods . The robust hindlimb bones suggest very powerful legs , and their shorter length would have lowered the animal 's center of gravity . Thus Majungasaurus may have sacrificed speed for power . Majungasaurus tooth marks on Rapetosaurus bones confirm that it at least fed on these sauropods , whether or not it actually killed them .

= = = Cannibalism = = =

Although sauropods may have been the prey of choice for Majungasaurus , discoveries published in 2007 detail finds in Madagascar that indicate the presence of other Majungasaurus in their diet . Numerous bones of Majungasaurus have been discovered bearing tooth marks identical to those found on sauropod bones from the same localities . These marks have the same spacing as teeth in Majungasaurus jaws , are of the same size as Majungasaurus teeth , and contain smaller notches consistent with the serrations on those teeth . As Majungasaurus is the only large theropod known from the area , the simplest explanation is that it was feeding on other members of its own species . Suggestions that the Triassic Coelophysis was a cannibal have been recently disproven , leaving Majungasaurus as the only non @-@ avian theropod with confirmed cannibalistic tendencies , although there is some evidence that cannibalism may have occurred in other species as well .

It is unknown if Majungasaurus actively hunted their own kind or only scavenged their carcasses . However , some researchers have noted that modern Komodo monitors sometimes kill each other when competing for access to carcasses . The lizards will then proceed to cannibalize the remains

of their rivals , which may suggest similar behavior in Majungasaurus and other theropods .

= = = Respiratory system = = =

Scientists have reconstructed the respiratory system of Majungasaurus based on a superbly preserved series of vertebrae (UA 8678) recovered from the Maevarano Formation . Most of these vertebrae and some of the ribs contained cavities (pneumatic foramina) that may have resulted from the infiltration of avian @-@ style lungs and air sacs . In birds , 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 . Similar features in Majungasaurus vertebrae imply the presence of these air sacs . These air sacs may have allowed for a basic form of avian @-@ style ' flow @-@ through ventilation , ' where air flow through the lungs is one @-@ way , so that oxygen @-@ rich air inhaled from outside the body is never mixed with exhaled air laden with carbon dioxide . This method of respiration , while complicated , is highly efficient .

The recognition of pneumatic foramina in Majungasaurus , besides providing an understanding of its respiratory biology , also has larger @-@ scale implications for evolutionary biology . The split between the ceratosaur line , which led to Majungasaurus , and the tetanuran line , to which birds belong , occurred very early in the history of theropods . The avian respiratory system , present in both lines , must therefore have evolved before the split , and well before the evolution of birds themselves . This provides further evidence of the dinosaurian origin of birds .

= = = Brain and inner ear structure = = =

Computed tomography , also known as CT scanning , of a complete Majungasaurus skull (FMNH PR 2100) allowed a rough reconstruction of its brain and inner ear structure . Overall , the brain was very small relative to body size , but otherwise similar to many other non @-@ coelurosaurian theropods , with a very conservative form closer to modern crocodilians than to birds . One difference between Majungasaurus and other theropods was its smaller flocculus , a region of the cerebellum that helps to coordinate movements of the eye with movements of the head . This suggests that Majungasaurus and other abelisaurids like Indosaurus , which also had a small flocculus , did not rely on quick head movements to sight and capture prey .

Inferences about behavior can also be drawn from examination of the inner ear . The semicircular canals within the inner ear aid in balance , and the lateral semicircular canal is usually parallel to the ground when the animal holds its head in an alert posture . When the skull of Majungasaurus is rotated so that its lateral canal is parallel to the ground , the entire skull is nearly horizontal . This contrasts with many other theropods , where the head was more strongly downturned when in the alert position . The lateral canal is also significantly longer in Majungasaurus than in its more basal relative Ceratosaurus , indicating a greater sensitivity to side @-@ to @-@ side motions of the head .

= = = Pathology = = =

A 2007 report described pathologies in the bones of Majungasaurus . Scientists examined the remains of at least 21 individuals and discovered four with noticeable pathologies . While pathology had been studied in large tetanuran theropods like allosaurids and tyrannosaurids , this was the first time an abelisauroid had been examined in this manner . No wounds were found on any skull elements , in contrast to tyrannosaurids where sometimes gruesome facial bites were common . One of the specimens was a phalanx (toe bone) of the foot , which had apparently been broken and subsequently healed .

Most of the pathologies occurred on the vertebrae . For example , a dorsal (back) vertebra from a juvenile animal showed an exostosis (bony growth) on its underside . The growth probably resulted from the conversion of cartilage or a ligament to bone during development , but the cause of the ossification was not determined . Hypervitaminosis A and bone spurs were ruled out , and an

osteoma (benign bone tumor) was deemed unlikely . Another specimen , a small caudal (tail) vertebra , was also found to have an abnormal growth , this time on the top of its neural spine , which projects upwards from the vertebrae , allowing muscle attachment . Similar growths from the neural spine have been found in specimens of Allosaurus and Masiakasaurus , probably resulting from the ossification of a ligament running either between the neural spines (interspinal ligament) or along their tops (supraspinal ligament) .

The most serious pathology discovered was in a series of five large tail vertebrae . The first two vertebrae showed only minor abnormalities with the exception of a large groove that extended along the left side of both bones . However , the next three vertebrae were completely fused together at many different points , forming a solid bony mass . There is no sign of any other vertebrae after the fifth in the series , indicating that the tail ended there prematurely . From the size of the last vertebrae , scientists judged that about ten vertebrae were lost . One explanation for this pathology is severe physical trauma resulting in the loss of the tail tip , followed by osteomyelitis (infection) of the last remaining vertebrae . Alternatively , the infection may have come first and led to the end of the tail becoming necrotic and falling off . This is the first example of tail truncation known in a non @-@ avian theropod dinosaur .

= = Paleoecology = =

All specimens of Majungasaurus have been recovered from the Maevarano Formation in the Mahajanga Province in northwestern Madagascar . Most of these , including all of the most complete material , came from the Anembalemba Member , although Majungasaurus teeth have also been found in the underlying Masorobe Member and the overlying Miadana Member . While these sediments have not been dated radiometrically , evidence from biostratigraphy and paleomagnetism suggest that they were deposited during the Maastrichtian stage , which lasted from 70 to 66 Ma (million years ago) . Majungasaurus teeth are found up until the very end of the Maastrichtian , when all non @-@ avian dinosaurs became extinct .

Then as now , Madagascar was an island , having separated from the Indian subcontinent less than 20 million years earlier . It was drifting northwards but still 10 ? 15 ° more southerly in latitude than it is today . The prevailing climate of the time was semi @-@ arid , with pronounced seasonality in temperature and rainfall . Majungasaurus inhabited a coastal flood plain cut by many sandy river channels . Strong geological evidence suggests the occurrence of periodic debris flows through these channels at the beginning of the wet season , burying the carcasses of organisms killed during the preceding dry season and providing for their exceptional preservation as fossils . Sea levels in the area were rising throughout the Maastrichtian , and would continue to do so into the Paleocene Epoch , so Majungasaurus may have roamed coastal environments like tidal flats as well . The neighboring Berivotra Formation represents the contemporaneous marine environment .

Besides Majungasaurus , fossil taxa recovered from the Maevarano include fish , frogs , lizards , snakes , seven distinct species of crocodylomorphs , five or six species of mammals , Vorona and several other birds , the possibly flighted dromaeosaurid Rahonavis , the noasaurid Masiakasaurus and two titanosaurian sauropods , including Rapetosaurus . Majungasaurus was by far the largest carnivore and probably the dominant predator on land , although large crocodylomorphs like Mahajangasuchus and Trematochampsa might have competed with it closer to water .

= = Documentaries = =

Majungasaurus was a main focus of the fifth episode of the mini @-@ series When Dinosaurs Ruled hosted by Jeff Goldblum . It also featured in the pilot episode of Jurassic Fight Club , in which its cannibalistic behavior was explored . In both series , the animal was referred to as Majungatholus . It was properly referred to as Majungasaurus in the third episode of BBC 's Planet Dinosaur , in which its killing technique as well as its cannibalistic nature were explored .