= Carnotaurus =

Carnotaurus / ?k??rno??t??r?s / is a genus of large theropod dinosaur that lived in South America during the Late Cretaceous period , between about 72 and 69 @.@ 9 million years ago . The only species is Carnotaurus sastrei . Known from a single well @-@ preserved skeleton , it is one of the best @-@ understood theropods from the Southern Hemisphere . The skeleton , found in 1984 , was uncovered in the Chubut Province of Argentina from rocks of the La Colonia Formation . Derived from the Latin carno [carnis] (" flesh ") and taurus (" bull ") , the name Carnotaurus means " meat @-@ eating bull " , alluding to its bull @-@ like horns . Carnotaurus is a derived member of the Abelisauridae , a group of large theropods that occupied the large predatorial niche in the southern Landmasses of Gondwana during the late Cretaceous . The phylogenetic relations of Carnotaurus are uncertain ; it may have been closer to either Majungasaurus or Aucasaurus .

Carnotaurus was a lightly built , bipedal predator , measuring 8 to 9 m (26 to 30 ft) in length and weighing at least 1 @.@ 35 metric tons (1 @.@ 33 long tons ; 1 @.@ 49 short tons) . As a theropod , Carnotaurus was highly specialized and distinctive . It had thick horns above the eyes , a feature unseen in all other carnivorous dinosaurs , and a very deep skull sitting on a muscular neck . Carnotaurus was further characterized by small , vestigial forelimbs and long and slender hindlimbs . The skeleton is preserved with extensive skin impressions , showing a mosaic of small , non @-@ overlapping scales measuring approximately 5 mm in diameter . The mosaic was interrupted by large bumps that lined the sides of the animal , and there are no hints of feathers .

The distinctive horns and the muscular neck may have been used in fighting conspecifics . According to separate studies , rivaling individuals may have combated each other with quick head blows , by slow pushes with the upper sides of their skulls , or by ramming each other head @-@ on , using their horns as shock absorbers . The feeding habits of Carnotaurus remain unclear : some studies suggest the animal was able to hunt down very large prey such as sauropods , while other studies find it preyed mainly on relatively small animals . Carnotaurus was well adapted for running and was possibly one of the fastest large theropods .

= = Description = =

Carnotaurus was a large but lightly built predator . The only known individual was about 8 ? 9 metres (26 ? 30 ft) in length , making Carnotaurus one of the largest abelisaurids . Only Ekrixinatosaurus and possibly Abelisaurus may have been similar or larger in size , though the incomplete remains of these genera make size estimations imprecise . Its mass is estimated to have been 1 @,@ 350 kg (1 @.@ 33 long tons ; 1 @.@ 49 short tons) 1 @,@ 500 kg (1 @.@ 5 long tons ; 1 @.@ 7 short tons) and 2 @,@ 100 kg (2 @.@ 1 long tons ; 2 @.@ 3 short tons) in separate studies that used different estimation methods . Carnotaurus was a highly specialized theropod , as seen especially in characteristics of the skull , the vertebrae and the forelimbs . The pelvis and hindlimbs , on the other hand , remained relatively conservative , resembling those of the more basal Ceratosaurus . Both the pelvis and hindlimb bones were long and slender . The left thigh bone of the individual measures 103 cm in length , but shows an average diameter of only 11 cm .

= = = Skull = = =

The skull , measuring 59 @.@ 6 cm (23 @.@ 5 in) in length , was proportionally shorter and deeper than in any other large carnivorous dinosaur . The snout was moderately broad , not as tapering as seen in more basal theropods like Ceratosaurus , and the jaws were curved upwards . As in other abelisaurids , the facial bones , especially the nasal bones , were sculptured with numerous small holes and spikes . In life , a wrinkled and possibly keratinous skin would have covered these bones . A prominent pair of horns protruded obliquely above the eyes . These horns , formed by the frontal bones , were thick , cone @-@ shaped but in cross @-@ section somewhat vertically flattened , and measured 15 cm (5 @.@ 9 in) in length . In life , they would probably have formed the bony cores of much longer keratinous horns . The proportionally small eyes were

situated in the upper part of the keyhole shaped orbita (eye sockets) . The upper part was slightly rotated forward , probably permitting some degree of binocular vision .

The teeth were long and slender , as opposed to the usually very short teeth seen in other abelisaurids . On each side of the upper jaws there were four premaxillary and twelve maxillary teeth , while the lower jaws were equipped with fifteen dentary teeth per side . In contrast to the robust @-@ looking skull , the lower jaw was shallow and weakly constructed , with the dentary (the foremost jaw bone) connected to the hindmost jaw bones by only two contact points . The lower jaw was found with hyoid bones , in the position they would be in if the animal was alive . These slender bones , supporting the tongue musculature and several other muscles , are rarely found in dinosaurs because they are not connected to other bones and therefore get lost easily .

= = = Vertebrae = = =

The vertebral column consisted of ten cervical (neck) , twelve dorsal , six fused sacral and an unknown number of caudal (tail) vertebrae . The neck was nearly straight , rather than having the S @-@ curve seen in other theropods , and also unusually wide , especially towards its base . The top of the neck 's spinal column featured a double row of enlarged , upwardly directed bony processes called epipophyses , creating a smooth trough on the top of the neck vertebrae . These processes were the highest points of the spine , towering above the unusually low spinous processes . The epipophyses probably provided attachment areas for a markedly strong neck musculature . A similar double row was also present in the tail , formed there by highly modified caudal ribs , in front view protruding upwards in a V @-@ shape , their inner sides creating a smooth , flat , top surface of the front tail vertebrae . The end of each caudal rib was furnished with a forward projecting hook @-@ shaped expansion that connected to the caudal rib of the preceding vertebra .

= = = Forelimbs = = =

The forelimbs were proportionally shorter than in any other large carnivorous dinosaurs , including Tyrannosaurus . The forearm was only a quarter the size of the upper arm . There were no carpalia in the hand , so that the metacarpals articulated directly with the forearm . The hand showed four basic digits , though apparently only the middle two of these ended in finger bones , while the fourth consisted of a single splint @-@ like metacarpal that may have represented an external ' spur ' . The fingers themselves were fused and immobile , and may have lacked claws . Carnotaurus differed from all other abelisaurids in having proportionally shorter and more robust forelimbs , and in having the fourth , splint @-@ like metacarpal as the longest bone in the hand . A 2009 study suggests that the arms were vestigial in abelisaurids , because nerve fibers responsible for stimulus transmission were reduced to an extent seen in today 's emus and kiwis , which also have vestigial forelimbs .

= = = Skin = = =

Carnotaurus was the first theropod dinosaur discovered with comprehensive fossil skin impressions . These impressions , found beneath the skeleton 's right side , come from different body parts , including the lower jaw , the front of the neck , the shoulder girdle , and the rib cage . The largest patch of skin corresponds to the anterior part of the tail . Originally , the right side of the skull also was covered with large patches of skin ? this was not recognized when the skull was prepared , and these patches were accidentally destroyed . Still , the surface texture of much of the right side of the skull is very different from that of the left side , and probably shows some features of the scalation pattern of the head .

The skin was built up of a mosaic of polygonal , non @-@ overlapping scales measuring approximately 5 mm (0 @.@ 20 in) in diameter . This mosaic was divided by thin , parallel grooves . Scalation was similar across different body parts with the exception of the head , which apparently showed a different , irregular pattern of scales . There is no evidence of feathers . Uniquely for

theropods , there were large knob @-@ like bumps running along the sides of the neck , back and tail in irregular rows . Each bump showed a low ridge and measured 4 to 5 cm (1 @.@ 6 to 2 @.@ 0 in) in diameter . They were set 8 to 10 cm (3 @.@ 1 to 3 @.@ 9 in) apart from each other and became larger towards the animal 's top . The bumps probably represent clusters of condensed scutes , similar to those seen on the soft frill running along the body midline in hadrosaurid (" duck @-@ billed ") dinosaurs . Stephen Czerkas (1997) suggested that these structures may have protected the animal 's sides while fighting members of the same species (conspecifics) and other theropods , arguing that similar structures can be found on the neck of the modern iguana where they provide limited protection in combat .

= = Classification = =

Carnotaurus is one of the best @-@ understood genera of the Abelisauridae , a family of large theropods restricted to the ancient southern supercontinent Gondwana . Abelisaurids were the dominant predators in the Late Cretaceous of Gondwana , replacing the carcharodontosaurids and occupying the ecological niche filled by the tyrannosaurids in the northern continents . Several notable traits that evolved within this family , including shortening of the skull and arms as well as peculiarities in the cervical and caudal vertebrae , were more pronounced in Carnotaurus than in any other abelisaurid .

Though relationships within the Abelisauridae are debated , Carnotaurus is consistently shown to be one of the most derived members of the family by cladistical analyses . Its nearest relative may have been either Aucasaurus or Majungasaurus ; this ambiguity is largely due to the incompleteness of the Aucasaurus skull material . A recent review suggests that Carnotaurus was not closely related with either Aucasaurus or Majungasaurus , and instead proposed Ilokelesia as its sister taxon .

Carnotaurus is eponymous for two subgroups of the Abelisauridae : the Carnotaurinae and the Carnotaurini . Paleontologists do not universally accept these groups . The Carnotaurinae was defined to include all derived abelisaurids with the exclusion of Abelisaurus , which is considered a basal member in most studies . However , a 2008 review suggested that Abelisaurus was a derived abelisaurid instead . Carnotaurini was proposed to name the clade formed by Carnotaurus and Aucasaurus ; only those paleontologists who consider Aucasaurus as the nearest relative of Carnotaurus use this group .

= = Discovery = =

The only skeleton (holotype MACN @-@ CH 894) was unearthed in 1984 by an expedition led by Argentinian paleontologist José Bonaparte . This expedition also recovered the peculiar spiny sauropod Amargasaurus . It was the eighth expedition within the project named " Jurassic and Cretaceous Terrestrial Vertebrates of South America " , which started in 1976 and which was sponsored by the National Geographic Society . The skeleton is well @-@ preserved and articulated (still connected together) , with only the posterior two thirds of the tail , much of the lower leg , and the hind feet being destroyed by weathering . During fossilization , the skull and especially the muzzle were crushed laterally , while the premaxilla were pushed upwards onto the nasal bones . As a result , the upward curvature of the upper jaw is artificially exaggerated in the holotype . The skeleton belonged to an adult individual , as indicated by the fused sutures in the braincase . It was found lying on its right side , showing a typical death pose with the neck bent back over the torso . Unusually , it is preserved with extensive skin impressions . In view of the significance of these impressions , a second expedition was started to reinvestigate the original excavation site , leading to the recovery of several additional skin patches .

The skeleton was collected on a farm named " Pocho Sastre " near Bajada Moreno in the Telsen Department of Chubut Province , Argentina . Because it was embedded in a large hematite concretion , a very hard kind of rock , preparation was complicated and progressed slowly . In 1985 , Bonaparte published a note presenting Carnotaurus sastrei as a new genus and species and briefly describing the skull and lower jaw . The generic name (Latin carno [carnis] ? " flesh " and taurus ?

" bull ") refers to the bull @-@ like horns , while the specific name sastrei honors Angel Sastre , the owner of the ranch where the skeleton was found . A comprehensive description of the whole skeleton followed in 1990 . After Abelisaurus , Carnotaurus was the second member of the family Abelisauridae that was discovered . For years , it was by far the best @-@ understood member of its family , and also the best @-@ understood theropod from the Southern Hemisphere . It was not until the 21st century that similar well @-@ preserved abelisaurids were described , including Aucasaurus , Majungasaurus and Skorpiovenator , allowing scientists to re @-@ evaluate certain aspects of the anatomy of Carnotaurus . The holotype skeleton is displayed in the Argentine Museum of Natural Sciences , Bernardino Rivadavia ; replicas can be seen in this and other museums around the world . Sculptors Stephen and Sylvia Czerkas manufactured a life @-@ sized sculpture of Carnotaurus that is now on display in the Natural History Museum of Los Angeles County . This sculpture , ordered by the museum during the mid @-@ 1980s , is probably the first life restoration of a theropod showing accurate skin .

= = Age and paleoecology = =

Originally , the rocks in which Carnotaurus was found were assigned to the upper part of the Gorro Frigio Formation , which was considered to be approximately 100 million years old (Albian or Cenomanian stage) . Later they were realized to pertain to the much younger La Colonia Formation , dating 72 to 69 @.@ 9 million years ago (Late Cretaceous , Lower Maastrichtian stage) . Thus , Carnotaurus was the latest South American abelisaurid known . By the Late Cretaceous , South America was already isolated from both Africa and North America .

The La Colonia Formation is exposed over the southern slope of the North Patagonian Massif . Most vertebrate fossils , including Carnotaurus , come from the formation 's middle section (called the middle facies association) . This part likely represents the deposits of an environment of estuaries , tidal flats or coastal plains . The climate would have been seasonal with both dry and humid periods . The most common vertebrates collected include ceratodontid lungfish , turtles , crocodiles , plesiosaurs , dinosaurs , lizards , snakes and mammals . Some of the snakes that have been found belong to the families Boidae and Madtsoidae , such as Alamitophis argentinus . Turtles are represented by at least five taxa , four from Chelidae (Pleurodira) and one from Meiolaniidae (Cryptodira) . Among the marine reptiles is the plesiosaur Sulcusuchus erraini of the family Polycotylidae . Mammals are represented with Reigitherium bunodontum , which was considered the first record of a South American docodont , and Argentodites coloniensis , possibly of Multituberculata . In 2011 , the discovery of a new enantiornithine bird from the La Colonia Formation was announced .

= = Paleobiology = =

= = = Function of the horns = = =

Carnotaurus is the only known carnivorous bipedal animal with a pair of horns on the frontal bone . The use of these horns is not entirely clear ; several interpretations have revolved around use in fighting conspecifics , in display , or in killing prey .

Greg Paul (1988) proposed that the horns were butting weapons and that the small orbita would have minimized the possibility of hurting the eyes while fighting . Gerardo Mazzetta and colleagues (1998) suggested that Carnotaurus used its horns in a way similar to rams . They calculated that the neck musculature was strong enough to absorb the force of two individuals colliding with their heads frontally at a speed of 5 @.@ 7 m / s each . Fernando Novas (2009) interpreted several skeletal features as adaptations for delivering blows with the head . He suggested that the shortness of the skull might have made head movements quicker by reducing the moment of inertia , while the muscular neck would have allowed strong head blows . He also noted an enhanced rigidity and strength of the spinal column that may have evolved to withstand shocks conducted by the head

and neck .

Other studies suggest that rivaling Carnotaurus did not deliver rapid head blows , but pushed slowly against each other with the upper sides of their skulls . Thus , the horns may have been a device for the distribution of compression forces without damage to the brain . This is supported by the flattened upper sides of the horns , the strongly fused bones of the top of the skull , and the inability of the skull to survive rapid head blows .

Gerardo Mazzetta and colleagues (1998) propose that the horns might also have been used to injure or kill small prey . Though horn cores are blunt , they may have had a similar form to modern bovid horns if there was a keratinous covering . However , this would be the only reported example of horns being used as hunting weapons in animals .

= = = Jaw function and diet = = =

Analysis of the jaw design of Carnotaurus by Mazzetta and colleagues (1998 , 2004 , 2009) suggests that the animal was capable of quick bites , but not strong ones . Quick bites are more important than strong bites when capturing small prey , as shown by studies of modern @-@ day crocodiles . Furthermore , these researchers noted a high degree of flexibility (kinesis) within the skull and especially the lower jaw , somewhat similar to modern snakes . Elasticity of the jaw would have allowed Carnotaurus to swallow small prey items whole . In addition , the front part of the lower jaw was hinged , and thus able to move up and down . When pressed downwards , the teeth would have projected forward , allowing Carnotaurus to spike small prey items ; when the teeth were curved upwards , the now backward projecting teeth would have hindered the caught prey from escaping . Mazzetta and colleagues also found that the skull was able to withstand forces that appear when tugging on large prey items . Carnotaurus may therefore have fed mainly on relatively small prey , but also was able to hunt large dinosaurs .

This interpretation was questioned by François Therrien and colleagues (2005) , who found that the biting force of Carnotaurus was twice as high as that of the American alligator , which may have the strongest bite of any living tetrapod . These researchers also noted analogies with modern Komodo dragons : the flexural strength of the lower jaw decreases towards the tip linearly , indicating that the jaws were not suited for high precision catching of small prey but for delivering slashing wounds to weaken big prey . As a consequence , according to this study , Carnotaurus must have mainly preyed upon large animals , possibly by ambush .

Robert Bakker (1998) found that Carnotaurus mainly fed upon very large prey , especially sauropods . As he noted , several adaptations of the skull ? the short snout , the relatively small teeth and the strong back of the skull (occiput) ? had independently evolved in Allosaurus . These features suggest that the upper jaw was used like a serrated club to inflict wounds ; big sauropods would have been weakened by repeated attacks .

= = = Locomotion = = =

Mazzetta and colleagues (1998 , 1999) presumed that Carnotaurus was a swift runner , arguing that the thigh bone was adapted to withstand high bending moments while running . The ability of an animal 's leg to withstand those forces limits its top speed . The running adaptations of Carnotaurus would have been better than those of a human , although not nearly as good as those of an ostrich . Scientists calculate that Carnotaurus had a top speed of up to 48 ? 56 km (30 ? 35 mi) per hour .

In dinosaurs , the most important locomotor muscle was located in the tail . This muscle , called caudofemoralis , attaches to the fourth trochanter , a prominent ridge on the thigh bone , and pulls the thigh bone backwards when contracted . Scott Persons and Phil Currie (2011) note that in the tail vertebrae of Carnotaurus the caudal ribs did not protrude horizontally (" T @-@ shaped ") , but were angled against the vertical axis of the vertebrae , forming a " V " . This would have provided additional space for a caudofemoralis muscle larger than in any other theropod ? the muscle mass was calculated at 111 to 137 kilograms (245 to 302 lb) per leg . Therefore , Carnotaurus could have been one of the fastest large theropods . While the caudofemoralis muscle was enlarged , the

epaxial muscles situated above the caudal ribs would have been proportionally smaller . These muscles , called the longissimus and spinalis muscle , were responsible for tail movement and stability . To maintain tail stability in spite of reduction of these muscles , the caudal ribs bear forward projecting processes interlocking the vertebrae with each other and with the pelvis , stiffening the tail . As a consequence , the ability to make tight turns would have been diminished , because the hip and tail had to be turned simultaneously , unlike in other theropods .