

= Ankylosaurus =

Ankylosaurus (/ ˈæŋkɪləˈsɔːrəs / ANG @-@ k? @-@ lo @-@ SAWR @-@ ?s) is a genus of armored dinosaur . Fossils of Ankylosaurus have been found in geological formations dating to the very end of the Cretaceous Period , between about 68 ? 66 million years ago , in western North America , making it among the last of the non @-@ avian dinosaurs . It was named by Barnum Brown in 1908 , and the only species classified in the genus is *A. magniventris* . The genus name means " fused lizard " and the specific name means " great belly " . A handful of specimens have been excavated to date , but a complete skeleton has not been discovered . Though other members of Ankylosauria are represented by more extensive fossil material , Ankylosaurus is often considered the archetypal member of its group .

The largest known ankylosaurid , Ankylosaurus measured up to 6 @.@ 25 m (20 @.@ 5 feet) in length , 1 @.@ 7 m (5 @.@ 6 feet) in height , and weighed 6 tonnes (13 @,@ 000 lb) . It was a quadrupedal animal , with a broad , robust body . It had a wide , low skull , with two horns pointing backwards from the back of the head , and two horns below these that pointed backwards and down . The front part of the jaws were covered in a beak , with rows of small , leaf @-@ shaped teeth further behind it . It was covered in armor plates , or osteoderms , with bony half @-@ rings covering the neck , and had a large club on the end of its tail . Bones in the skull and other parts of the body were fused , increasing their strength , and this feature is the source of the genus name .

Ankylosaurus is a member of the family Ankylosauridae , and its closest relatives appear to be Anodontosaurus and Euoplocephalus . Ankylosaurus is thought to have been a slow moving animal , able to make quick movements when necessary . Its broad muzzle indicates it was a non @-@ selective browser . Sinuses and nasal chambers in the snout may have been for heat and water balance or played a role in vocalization . The tail club is thought to have been used in defense against predators or in intraspecific combat . Ankylosaurus has been found in the Hell Creek , Lance , and Scollard formations , but appears to have been rare in its environment . Although it lived alongside a nodosaurid ankylosaur , their ranges and ecological niches do not appear to have overlapped , and Ankylosaurus may have inhabited upland areas . Ankylosaurus also lived alongside dinosaurs such as Tyrannosaurus , Triceratops , and Edmontosaurus .

= = Description = =

Ankylosaurus is the largest known ankylosaurid dinosaur , estimated to have been up to 6 @.@ 25 m (20 @.@ 5 feet) long , 1 @.@ 5 m (4 @.@ 9 feet) wide , and 1 @.@ 7 m (5 @.@ 6 feet) tall at the hip . This length has been proposed by American palaeontologist Kenneth Carpenter , and is based on the largest known skull (specimen NMC 8880) , which is 64 @.@ 5 cm (25 @.@ 4 inches) long and 74 @.@ 5 cm (29 @.@ 3 inches) wide . The smallest known skull (specimen AMNH 5214) is 55 @.@ 5 cm (21 @.@ 9 inches) long and 64 @.@ 5 cm (25 @.@ 4 inches) wide , and this specimen is estimated to have been 5 @.@ 4 m (17 @.@ 7 feet) long and around 1 @.@ 4 m (4 @.@ 6 feet) tall . Other authors have proposed a body length of 7 m (23 feet) , 8 ? 9 m (26 @.@ 2 ? 29 @.@ 5 ft) , or more than 9 m (29 @.@ 5 feet) . The weight of the animal has been estimated at 6 tonnes (13 @,@ 000 lb) .

The structure of much of the skeleton of Ankylosaurus , including most of the pelvis , tail and feet , is still unknown . It was quadrupedal , and its hind limbs were longer than the forelimbs . The scapula (shoulder blade) and coracoid (a rectangular bone connected to the lower end of the scapula) of specimen AMNH 5895 were fused , and had entheses (connective tissue) for various muscle attachments . The scapula was 61 @.@ 5 cm (24 @.@ 2 inches) long . The humerus (upper arm bone) was short and very broad , and about 54 cm (21 inches) long in specimen AMNH 5214 . The femur (thigh bone) was very robust , and 67 cm (26 inches) long in AMNH 5214 . While the feet of Ankylosaurus are incompletely known , the hindfeet probably had three toes , as is the case in related animals .

The cervical vertebrae of the neck had broad neural spines that increased in height towards the body . The front part of the neural spines had well developed entheses , which was common among

adult dinosaurs , and indicates the presence of large ligaments which helped support the massive head . The dorsal vertebrae of the back had centra (or bodies) that were short relative to their width , and their neural spines were short and narrow . The dorsal vertebrae were tightly spaced , which limited the downwards movement of the back . The neural spines had ossified (turned to bone) tendons , which also overlapped some of the vertebrae . The ribs of the last four back vertebrae were fused to them , and the ribcage was very broad in this part of the body . The ribs had scars that show where muscles attached to them . The caudal vertebrae of the tail had centra that were slightly amphicoelous , meaning they were concave on both sides . The interlocked zygapophyses (articular processes) of the caudal vertebrae formed a V @-@ shape when seen from above .

= = = Skull = = =

The three known Ankylosaurus skulls differ in various details , but this is thought to be the result of taphonomy (changes happening during fossilisation of the remains) and individual variation . The skull was low and triangular in shape , wider than it was long . It had a broad beak on the premaxillae . The orbits (eye sockets) were almost round to slightly oval and did not face directly sideways , because the skull tapered towards the front . Crests above the orbits merged into the upper squamosal horns (their shape has been described as " pyramidal ") , which pointed backwards to the sides from the back of the skull . The crest and horn were probably separate elements originally , as seen in the related Pinacosaurus and Euoplocephalus . Below the upper horns , jugal horns were present , which pointed backwards and down . The horns may have originally been osteoderms (armor plates) that fused to the skull . However , the scale pattern on the skull surface was instead the result of remodelling of the skull . This obliterated the sutures between skull elements , which is common for adult ankylosaurs . The scale pattern of the skull was variable between specimens , though some details are shared ; it had a diamond @-@ shaped scale (internarial scale) at the front of the snout , two squamosal osteoderms above the orbit , and a ridge of scales at the back of the skull .

The snout of Ankylosaurus was arched and truncated at the front , and the nostrils were ellipse @-@ shaped and faced sideways , unlike in many other ankylosaurids where they faced the front or upwards . This was because the sinuses were expanded to the sides of the premaxilla bone , to a larger extent than seen in other ankylosaurs . The nostrils also had an intranarial septum , which separated the nasal passage from the sinus . Each side of the snout had five sinuses , four of which expanded in to the maxilla bone . The nasal cavities or chambers of Ankylosaurus were elongated and separated by a septum at the midline , which divided the inside of the snout in two mirrored halves . The septum had two openings , including the choanae (internal nostrils) .

The maxillae expanded to the sides , giving the impression of a bulge , which may have been due to the sinuses inside . The maxillae had a ridge which may have been the attachment site for fleshy cheeks ; the presence of cheeks in ornithischians is controversial , but some nodosaurid ankylosaurs had armor plates that covered the cheek region , which may have been embedded in the flesh . Specimen AMNH 5214 has 34 @-@ 35 dental alveoli (tooth sockets) in the maxilla , which was more teeth than any other ankylosaurid . The tooth rows in the maxillae of this specimen are about 20 cm (8 inches) long . Each alveoli had a foramen (opening) near its side wherein a replacement tooth could be seen . The back of the skull was broad and low .

Compared to other ankylosaurs , the mandible of Ankylosaurus was low in proportion to its length , and the tooth row was almost straight instead of arched , when seen from the side . The mandibles are only completely preserved in the smallest specimen (AMNH 5214) and are about 41 cm (16 inches) long . The incomplete mandible of the largest specimen (NMC 8880) is the same length . AMNH 5214 has 35 dental alveoli in the left dentary and 36 in the right . The prementary bone of the tip of the mandibles has not yet been found . Like other ankylosaurs , Ankylosaurus had small , phylliform (leaf @-@ shaped) teeth , which were compressed sideways . The teeth were mostly taller than they were wide , and were very small in relation to the size of the skull . Some teeth from behind in the tooth row curved backwards , and tooth crowns were usually flatter on one side than

the other . Ankylosaurus teeth are diagnostic and can be distinguished from the teeth of other ankylosaurids based on their smooth sides . The denticles were large , their number ranging from six to eight on the front part of the tooth , and five to seven behind .

= = = Armor = = =

A prominent feature of Ankylosaurus was its armor , consisting of knobs and plates of bone known as osteoderms or scutes embedded in the skin . These have not been found in articulation , so their exact placement on the body is unknown , though inferences can be made based on related animals . The osteoderms ranged from 1 cm (0 @. @ 4 inches) in diameter to 35 @. @ 5 cm (14 @. @ 0 inches) in length , and also varied in shape . The osteoderms of Ankylosaurus were generally thin walled and hollowed on the underside . Compared to Euoplocephalus , the osteoderms of Ankylosaurus were smoother in texture . The osteoderms covering the body were very flat , though with a low keel at one margin . In contrast , the nodosaurid Edmontonia had high keels , stretching from one margin to the other on the midline of its osteoderms . Ankylosaurus had some smaller osteoderms with a keel across the midline . Some osteoderms without keels may have been placed above the hip region , as in Euoplocephalus . Flattened , pointed plates resemble those on the sides of the tail of Saichania . Osteoderms with oval keels could have been placed on the upper side of the tail or the side of the limbs . Small osteoderms and ossicles likely occupied the space between the larger ones .

Like other ankylosaurids , Ankylosaurus had cervical half @-@ rings (armor plates on the neck) , but these are only known from fragments , making their exact arrangement uncertain . Carpenter suggested that when seen from above , the plates would have been paired , and created an inverted V @-@ shape across the neck , with the midline gap probably being filled with small ossicles (round bony scutes) to allow for movement . He believed the width of this armor belt was too wide to have fitted solely on the neck , and that it covered the base of the neck and continued onto the shoulder region . Paleontologists Victoria M. Arbour and Philip J. Currie disagreed with Carpenter 's interpretation , and pointed out that the cervical half @-@ ring fragments of specimen AMNH 5895 did not fit together in the way proposed by Carpenter (though this could be due to breakage) . They instead suggested that the fragments represented the remains of two cervical half @-@ rings , which formed two semi @-@ circular plates of armor around the upper part of the neck , as in the closely related Anodontosaurus and Euoplocephalus .

The tail club of Ankylosaurus was composed of two large osteoderms , with a row of small osteoderms at the midline , and two small osteoderms at the tip . As only the tail club of specimen AMNH 5214 is known , the range of variation between individuals is unknown . The tail club of AMNH 5214 is 450 mm (18 in) wide . The last seven tail vertebrae formed the " handle " of the tail club . These vertebrae were in contact , with no cartilage between them , and sometimes co @-@ ossified , which made them immobile . Ossified tendons attached to the vertebrae in front of the tail club , and these features together helped strengthen it .

= = History of discovery = =

In 1906 , an American Museum of Natural History expedition led by paleontologist Barnum Brown discovered the type specimen of Ankylosaurus magniventris (AMNH 5895) in the Hell Creek Formation , near Gilbert Creek , Montana . The specimen (found by collector Peter Kaisen) consisted of the upper part of a skull , two teeth , part of the shoulder girdle , cervical , dorsal , and caudal vertebrae , ribs , and more than thirty osteoderms . Brown scientifically described the animal in 1908 ; the genus name is derived from the Greek words ' ??????? / ankulos (' bent ' or ' crooked ') , referring to the medical term ankylosis , the stiffness produced by the fusion of bones in the skull and body , and ?????? / sauros (' lizard ') . The name can be translated as " fused lizard " , " stiff lizard " , or " curved lizard " . The type species name magniventris is derived from the Latin magnus (' great ') and venter (' belly ') , referring to the great width of the animal 's body .

The skeletal reconstruction accompanying the 1908 description restored the missing parts in a

fashion similar to Stegosaurus , and Brown likened the result to the extinct armored mammal Glyptodon . Contrary to modern depictions , Brown 's reconstruction showed a strongly arched back , while the tail club was missing as it was unknown at the time . Brown also reconstructed the armor plates in parallel rows running down the back ; this arrangement , however , was purely hypothetical . In a 1908 review of Brown 's Ankylosaurus description , American palaeontologist Samuel Wendell Williston criticised the skeletal reconstruction as being based on too scanty remains , and claimed that Ankylosaurus was merely a synonym of the genus Stegopelta , which Williston had named in 1905 . Williston also stated that a skeletal reconstruction of the related Polacanthus by Hungarian palaeontologist Franz Nopcsa was a better example of how ankylosaurs would have appeared in life . The claim of synonymy was not accepted by other researchers , and the two genera are now considered distinct .

Brown had collected seventy @-@ seven osteoderms while excavating a Tyrannosaurus specimen in the Lance Formation of Wyoming in 1900 . He mentioned these osteoderms (specimen AMNH 5866) in his description of Ankylosaurus , but thought they belonged to the Tyrannosaurus instead . Palaeontologist Henry Fairfield Osborn also expressed this view when he described the Tyrannosaurus specimen as the now invalid genus Dynamosaurus in 1905 . Later examination has shown them to be similar to those of Ankylosaurus , and that Brown had compared them with some Euoplocephalus osteoderms , which had been erroneously catalogued as belonging to Ankylosaurus at the AMNH .

In 1910 , another AMNH expedition led by Brown discovered an Ankylosaurus specimen (AMNH 5214) in the Scollard Formation by the Red Deer River in Alberta , Canada . This specimen included a complete skull , mandibles , the first and only tail club known of this genus , as well as ribs , vertebrae , limb bones , and armor . In 1947 , fossil collectors Charles M. Sternberg and T.P. Channey collected a skull and mandible (specimen NMC 8880) , a kilometre (0 @.@ 6 miles) north of where the 1910 specimen was found . This is the largest known Ankylosaurus skull , but is badly preserved . A section of caudal vertebrae (specimen CCM V03) was discovered in the 1960s , in the Powder River drainage , Montana , also part of the Hell Creek Formation . In addition to these five incomplete specimens , many other isolated osteoderms and teeth have been found .

In 1990 , American palaeontologist Walter P. Coombs pointed out that the teeth of two skulls referred to *A. magniventris* differed from those of the holotype specimen in some details , and though he expressed a " considerate temptation " to name a new species of Ankylosaurus for these , he refrained from doing so , as the range of variation in the species was not completely documented . He also raised the possibility that the two teeth associated with the holotype specimen perhaps did not belong to it , as they were found in matrix within the nasal chambers . Kenneth Carpenter accepted the teeth as belonging to *A. magniventris* and that all specimens belonged to the same species , noting that the teeth of other ankylosaurs are highly variable .

Most of the known Ankylosaurus specimens were not scientifically described at length , though several palaeontologists planned to do so , until Carpenter redescribed the genus in 2004 . Carpenter noted that Ankylosaurus has become the archetypal member of its group , and the best known ankylosaur in popular culture , perhaps due to a life @-@ sized reconstruction of the animal being featured at the 1964 World 's Fair in New York City . Many traditional popular depictions show Ankylosaurus in a squatting posture and with a huge tail club being dragged over the ground . Modern reconstructions , however , show the animal with a more upright limb posture and with the tail being held clear off the ground . Likewise , large spines projecting sideways from the body are present in many traditional depictions , but are actually only known in nodosaurids while being unknown in ankylosaurids .

= = Classification = =

Brown considered Ankylosaurus so distinct that he made it the type genus of a new family , Ankylosauridae (members of which are called ankylosaurids) , typified by massive , triangular skulls , short necks , stiff backs , broad bodies , and osteoderms . He also classified *Palaeoscincus* (only known from teeth) , and *Euoplocephalus* (then only known from a partial skull and osteoderms

) as part of the family . Due to the fragmentary remains , Brown was unable to fully distinguish between Euoplocephalus and Ankylosaurus . Only having few , incomplete members of the family to compare with , he believed the group was part of the suborder Stegosauria . In 1923 , Osborn coined the name Ankylosauria (members of which are called ankylosaurs or ankylosaurians) , thereby placing the ankylosaurids in their own suborder .

Ankylosauria and Stegosauria are now grouped together within the clade Thyreophora . This group first appeared in the Sinemurian age , and survived for 135 million years , until disappearing in the Maastrichtian . They were widespread and inhabited a broad range of environments . As more complete specimens and new genera have been discovered , theories about ankylosaurian interrelatedness have become more complex , and hypotheses have often changed between studies . In addition to Ankylosauridae , Ankylosauria has been divided into the families Nodosauridae , and sometimes Polacanthidae (these families lacked tail clubs) . Ankylosaurus is considered part of the subfamily Ankylosaurinae (members of which are called ankylosaurines) within Ankylosauridae . Ankylosaurus appears to be most closely related to Anodontosaurus and Euoplocephalus . The following cladogram is based on a 2015 phylogenetic analysis of the Ankylosaurinae conducted by Arbour and Currie :

Since Ankylosaurus and other Late Cretaceous North American ankylosaurids grouped with Asian genera (in a tribe the authors named Ankylosaurini) , Arbour and Currie suggested that earlier North American ankylosaurids had gone extinct by the late Albian or Cenomanian ages of the Middle Cretaceous . Ankylosaurids thereafter recolonised North America from Asia during the Campanian or Turonian ages of the Late Cretaceous , and diversified there again , leading to genera such as Ankylosaurus , Anodontosaurus , and Euoplocephalus . This explains a 30 million year gap in the fossil record of North American ankylosaurids between these ages .

= = Palaeobiology = =

= = = Feeding = = =

Like other ornithischians , Ankylosaurus was herbivorous . Its wide muzzle was adapted for non selective low browse cropping . The teeth of Ankylosaurus were worn on the face of the crowns , rather than on the tip of the crowns , as in nodosaurid ankylosaurs . In 1982 , Carpenter ascribed two very small teeth to baby Ankylosaurus , which originate from the Lance and Hell Creek Formations and measure 3 @.@ 2 to 3 @.@ 3 mm in length , respectively . The smaller tooth is heavily worn , leading Carpenter to suggest that ankylosaurids in general or at least the babies did not swallow their food whole but employed some sort of chewing .

A specimen of Pinacosaurus preserves large paraglossalia (triangular bones or cartilages located in the tongue) which show signs of muscular stress , and it is thought this was a common feature of ankylosaurs . Some researchers have suggested that ankylosaurs relied heavily on muscular tongues and hyobranchia (tongue bones) when feeding , since their teeth were fairly small and were replaced at a relatively slow rate . Some modern salamanders have similar tongue bones , and use prehensile tongues to pick up food .

In 1969 , Austrian paleontologist Georg Haas concluded that despite the large size of ankylosaur skulls , the associated musculature was relatively weak . He also thought jaw movement was limited to up and down movements . Extrapolating from this , Haas suggested that ankylosaurs ate relatively soft non @-@ abrasive vegetation . However , later research on Euoplocephalus indicates that forward and sideways jaw movement was possible in these animals , the skull being able to withstand considerable forces . Though ankylosaurs may not have fed on fibrous and woody plants , they may have had a more varied diet , including tough leaves and pulpy fruits . Based on the broadness of the ribcage , Ankylosaurus may have digested through a hindgut fermentation system like modern herbivorous lizards , which have several chambers in their enlarged colon .

= = = Airspaces and senses = = =

In 1977 , Polish paleontologist Teresa Maryańska proposed that the complex sinuses and nasal cavities of ankylosaurs may have lightened the weight of the skull , housed a nasal gland , or acted as a chamber for vocal resonance . Carpenter rejected these hypotheses , arguing that tetrapod animals make sounds through the larynx , not the nostrils , and that reduction in weight was minimal , as the spaces only accounted for a small percent of the skull volume . He also considered a gland unlikely , and noted that the sinuses may not have had any specific function .

A 2011 study of the nasal passages of *Euoplocephalus* supported their function as a heat and water balancing system , noting the extensive blood vessel system and an increased surface area for the mucosa membrane (used for heat and water exchange in modern animals) . The researchers also supported the loops acting as a resonance chamber , comparable to the elongated nasal passages of saiga antelope and looping trachea of cranes and swans . Reconstructions of the inner ear suggest adaptation to hearing at low frequencies , such as the low @-@ toned resonant sounds possibly produced by the nasal passages . They disputed the possibility that the looping is related to olfaction (sense of smell) as the olfactory region is pushed to the sides of the main airway .

The shape of the nasal chambers of *Ankylosaurus* indicate that airflow was unidirectional , (looping through the lungs during inhalation and exhalation) , although it may also have been bidirectional in the posterior nasal chamber , which directed air past the olfactory lobes . The enlarged olfactory region of ankylosaurids indicates a well @-@ developed sense of smell , and the position of the orbits of *Ankylosaurus* suggest some stereoscopic vision .

== Limb movements ==

Reconstructions of ankylosaur forelimb musculature made by Coombs in 1978 suggest that the forelimbs bore the majority of the animal 's weight , and were adapted for high force delivery on the front feet , possibly for food gathering . In addition , Coombs suggested that ankylosaurs may have been capable diggers , though the hoof @-@ like structure of the manus would have limited fossorial activity . Ankylosaurs were likely to have been slow @-@ moving and sluggish animals , though they may have been capable of quick movements when necessary .

== Defense ==

The osteoderms of ankylosaurids were thin in comparison to those of other ankylosaurs , and appear to have been strengthened by randomly distributed cushions of collagen fibers . These were structurally similar to Sharpey 's fibers , and were embedded directly into the bone tissue , a feature unique to ankylosaurids . This would have provided the ankylosaurids with an armor covering which was both lightweight and highly durable , being resistant to breakage and penetration by the teeth of predators . In addition to protection , Carpenter suggested in 1982 that the heavily @-@ vascularized armor may have had a role in thermoregulation as in modern crocodilians .

The tail club of *Ankylosaurus* seems to have been an active defensive weapon , capable of producing enough of an impact to break the bones of an assailant . The tendons of the tail were partially ossified and were not very elastic , allowing great force to be transmitted to the club when it was used as a weapon . Coombs suggested in 1979 that several hindlimb muscles would have controlled the swinging of the tail , and that violent thrusts of the club would have been able to break the metatarsal bones of large theropods .

A 2009 study estimated that ankylosaurids could swing their tails at 100 degrees laterally and the mainly cancellous clubs would have a lowered moment of inertia and been effective weapons . However , the study also found that while large ankylosaurid tail clubs were capable of breaking bones , medium and small clubs were not . Despite the feasibility of tail swinging , the researchers could not determine whether ankylosaurids used their clubs for defense against potential predators , in intraspecific combat or both . In 1993 , Tony Thulborn proposed that the tail club of ankylosaurids primarily acted as a decoy for the head , as he thought the tail too short and inflexible to have an

effective reach ; the " dummy head " would lure a predator close to the tail , where it could be stricken . Carpenter has rejected this idea , as tail club shape is highly variable among ankylosaurids , even in the same genus .

= = Palaeoecology = =

Ankylosaurus existed between 68 and 66 million years ago , in the final , or Maastrichtian , stage of the Late Cretaceous Period . It was among the last dinosaur genera that appeared before the Cretaceous ? Paleogene extinction event . The type specimen is from the Hell Creek Formation of Montana , while other specimens have been found in the Lance Formation of Wyoming and the Scollard Formation in Alberta , Canada , all of which date to the end of the Cretaceous . Fossils of Ankylosaurus are rare in these sediments , and the distribution of its remains suggest that it was restricted to the uplands of the formations , rather than the coastal lowlands . Another ankylosaur , an indeterminate nodosaur (formerly referred to as Edmontonia sp .) , is also found in the same formations , but the range of the two genera does not seem to have overlapped . Their remains have so far not been found in the same localities , and the nodosaur appears to have inhabited the lowlands . The narrow muzzle of the nodosaur suggests it had a more selective diet than Ankylosaurus , further indicating ecological separation .

The Hell Creek , Lance and Scollard Formations represent different sections of the western shore of the Western Interior Seaway that divided western and eastern North America during the Cretaceous . They represent a broad coastal plain , extending westward from the seaway to the newly formed Rocky Mountains . These formations are composed largely of sandstone and mudstone , which have been attributed to floodplain environments . The Hell Creek is the best studied of these ancient environments . At the time , this region was subtropical , with a warm and humid climate . Many plant species were supported , primarily angiosperms , with less common conifers , ferns and cycads . An abundance of fossil leaves found at dozens of different sites indicates that the area was largely forested by small trees . Ankylosaurus shared its environment with dinosaurs including the ceratopsids Triceratops and Torosaurus , the hypsilophodont Thescelosaurus , the hadrosaurid Edmontosaurus , an indeterminate nodosaur , the pachycephalosaurian Pachycephalosaurus , and the theropods Struthiomimus , Ornithomimus , Troodon , and Tyrannosaurus .