= Ampelosaurus =

Ampelosaurus (/ ?æmp?lo??s??r?s / AM @-@ pi @-@ lo @-@ SAWR @-@ ?s ; meaning " vine lizard ") is a titanosaurian sauropod dinosaur hailing from the Late Cretaceous Period of what is now Europe . Its type species is A. atacis , named by Le Loeuff in 1995 . A possible unnamed species has given Ampelosaurus an age reaching to the latest Cretaceous , from about 70 to 66 million years ago .

Like most sauropods , it would have had a long neck and tail but it also carried armor in the form of osteoderms . Over 500 bones have been assigned to Ampelosaurus and all but the braincase (assigned to A. sp .) has been assigned to A. atacis . They are assigned to the same species because all the differences in the limb proportions have been linked to individual variation . A. atacis is known from a few , well @-@ preserved teeth and some cranial material . A right scapula was discovered associated with a coracoid . The blade of the scapula , contrary to most titanosaurs , is triangular . The blade narrows at one end instead of showing an expansion like most other genera . A. atacis is also known from a pubis about 75 centimetres (30 in) long and an ilium . Aside from that , it is known from a partial forelimb , and many femora .

Titanosaurians were a flourishing group of sauropod dinosaurs during Cretaceous times . The Spanish locality from the latest Cretaceous of ? Lo Hueco ? yielded a relatively well preserved , titanosaurian braincase , which shares a number of unique features with A. atacis from France . However , it appeared to differ from A. atacis in some traits also . The specimen has been provisionally identified as Ampelosaurus sp .. A. sp. is most likely a mature titanosaurian since the bones of the braincase have largely fused together .

Ampelosaurus lived alongside many other animals . Over 8500 specimens have been found alongside it , including gastropods , bivalves , crocodiles , other sauropods , plants and invertebrates in the Villalba de la Sierra , Gres de Saint @-@ Chinian , Marnes Rouges Inférieures and Gres de Labarre formations . Recent attention has made Ampelosaurus one of the most well @-@ known dinosaurs known from France .

= = Description = =

Like most sauropods , Ampelosaurus would have had a long neck and tail , but it also carried armor in the form of osteoderms 25 to 28 centimetres (9 @.@ 8 to 11 @.@ 0 in) long . The four osteoderms found have three different morphologies , they are plate , bulb , and spine @-@ shaped . This dinosaur would have stretched up to about 15 metres (49 ft) from snout to tail . Ampelosaurus atacis is known from many unattached bones and teeth . It is one of the best @-@ known dinosaurs from France . It is considered to be a dwarf sauropod by Coria et al . (2005) because it has a smaller size in comparison with its ancestors .

= = = Skeleton = = =

Ampelosaurus is one of the most completely known titanosaurian sauropods from Europe . Since 1989 , over 500 bones discovered at the Upper Cretaceous Bellevue locality of southern France have been assigned to A. atacis . An abundant amount of well @-@ preserved elements have been uncovered at Bellevue . In the original description , only a tooth and some vertebrae were examined . In 2005 , a complete description was made by Le Loueff of all known material , allowing Ampelosaurus to be much better understood . All the material has been assigned to the species , and even though there are some differences in limb proportions , it has all been linked to individual variation .

A. atacis is known from a few , well @-@ preserved teeth and some cranial material , a tooth of which was described in its original description . The teeth differentiate Ampelosaurus from Magyarosaurus and Lirainosaurus , both of which are also from Europe . The teeth are different from the two later genera as Ampelosaurus has teeth that are roughly cylindrical in the top with thin expansions at the bottom . They are 21 millimetres (0 @.@ 83 in) high and about 6 millimetres (0

@.@ 24 in) wide . Those expansions give its teeth a slight constriction between the root and the crown . The teeth are also quite different from the peg @-@ like teeth of titanosaurids . The teeth , have a general morphology similar to titanosaurians Antarctosaurus and a braincase from Dongargaon . Another skull was described from southern France , but showed some differences , meaning there could have been at least two different titanosaurians in France during the Late Cretaceous .

The scapula was found attached to a coracoid . In the longer direction , the bone is 72 centimetres (28 in) long . The blade of the scapula , contrary to titanosaurs , is triangular , larger closer to the base . The blade narrows distally instead of showing an expansion . Differing from Magyarosaurus and Saltasaurus , the scapula does not have the dorsal crest at the base of the scapular blade . The shape of the coracoid is quadrangular , and the coracoid has a thickened cranial margin .

Ampelosaurus is also known from a pubis , about 75 centimetres (30 in) long . It has a strong distal expansion , that is similar to a titanosaur from Brazil , and a large foramen . Contrary to the South American titanosaurs , the ilium does not have an expansion on the side . The ischium , known from a shaft , is unexpanded distally and very well developed . It is also very flat . An incomplete radius is also known . It lacks the proximal and distal ends , and possesses a very prominent ridge along it . The largest and best @-@ preserved specimens are both ulnas . The right ulna has a total length of 395 millimetres (15 @.@ 6 in) . The right ulna is small and slender , is missing an olecranon , and has a well @-@ marked ridge . The left ulna is larger , with a length of 725 millimetres (28 @.@ 5 in) . The ulna has a deep radial fossa .

About 27 femora are known from Bellevue , making them the most common bone , most of them more @-@ or @-@ less complete . They are very flat craniocaudally but otherwise , lack any unusual features . In a study of its bone physiology , it was found that the maximum known femur length was 1 @,@ 100 millimetres (43 in) , which is much larger than previously known (802 millimetres (31 @.@ 6 in)) . That means , that the ancestors Ampelosaurus were slightly smaller than itself . 18 humeri are also known , but none of them approach the size of the largest femur . The humeri do not have a free medullary cavity . The humeri are robust , about 63 centimetres (25 in) long , with very expanded distal and proximal ends .

Three different types of osteoderms have been recovered at Bellevue . Two with large spines have been uncovered . At the base of each spine , which is about 12 centimetres (4 @.@ 7 in) tall , are two large foramina . The internal faces are all concavo @-@ convex and have a ridge opposite the spine . In side view , they have two sections , a low half that progressively thickens , and a spine .

= = = = Vertebrae = = = =

The holotype specimen of A. atacis is a group of three connected dorsal vertebrae . Cervical vertebrae are uncommon from Bellevue and most of them are poorly preserved . The vertebrae are opisthocoelous , with centra that lengthen toward the rear . Neural spines have been preserved on the vertebrae , and they face toward the rear . Two dorsal vertebrae were preserved with a complete , but very crushed neural arch , a neural spine with a characteristic shape : it is very widened distally and narrows downwards . The vertebrae also have an internal structure that is spongy , with very large cells . The caudal vertebrae are all strongly procoelous and are compressed on the sides . The neural spines of the caudal vertebrae are very narrow and very tall and point toward the rear . The middle caudal vertebrae are more compressed on the sides that the others . Also , the centrum of middle caudal vertebrae is longer proportionally . Two sacral vertebrae were known from Bellevue . They are poorly preserved , and are thought to belong to a juvenile . A complete sacrum was also found in 2002 .

= = = Distinguishing anatomical features = = =

This set of characters was identified by Le Loeuff in his description of Ampelosaurus to distinguish it from all other genera : teeth that weakly spatulate ; a laterally widening distal extremity of neural spines on the dorsal vertebrae ; neural arch of the dorsal vertebrae inclining strongly towards the

rear ; the lack of a distal expansion on the scapular blade ; the presence of a light , ventral crest on top of the scapula ; the presence of plate , bulb , and spine shaped osteoderms ; and , in 2005 , Le Loeuff added that the constriction of the neural spine on the dorsal and cervical vertebrae was also probably a characteristic of Ampelosaurus .

= = = Ampelosaurus sp . = = =

A fossil braincase from Lo Hueco was tentatively assigned to an unnamed species of Ampelosaurus , A. sp . , in a 2013 article in the journal PLoS ONE . The braincase was found to share many features with A. atacis , such as a back of the skull that is flat . The braincase , MCCM @-@ HUE @-@ 8741 , is small in size overall , with a front @-@ to @-@ back length of 100 @.@ 8 millimetres (3 @.@ 97 in) , and the maximum width of the left half being 64 @.@ 3 millimetres (2 @.@ 53 in) . Parts of the bottom half of the braincase are missing . Even though section are missing , the specimen does not appear to have been deformed much , as the left and right halves are not very different .

Two frontals are preserved . They are each 57 @.@ 3 millimetres (2 @.@ 26 in) long and 64 @.@ 3 millimetres (2 @.@ 53 in) wide . The upper surface of each frontal is not smooth . One crest runs along the each frontal , and the together the two crests make up the orbital roof . Both parietals have also been found . The connection between them is marked by a ? @-@ shaped crest . Viewed from the side , the parietal has two extensions . These extensions are not fully preserved , but they would have been on the border of the upper temporal fenestrae in their middle . Each parietal was preserved as 79 @.@ 6 millimetres (3 @.@ 13 in) wide . The basioccipital of the specimen from Lo Hueco is unique as it has an occipital condyle that is much wider than tall . The occipital condyle has an irregular surface that was probably caused by the loss of the original cartilaginous covering . The complete braincase was especially low in the skull , and was oriented to the side . The occipital condyle is 28 @.@ 6 millimetres (1 @.@ 13 in) wide and 15 @.@ 8 millimetres (0 @.@ 62 in) tall . The braincase floor is made by the parabasisphenoid . The prootic is a tall but not long bone . The basisphenoid is mostly on the side of it , along with the laterosphenoid , the parietal , and the otoccipital . The length of the prootic from the front to the back is around 10 @.@ 6 millimetres (0 @.@ 42 in) .

= = = = Neuroanatomy = = = =

Compared with the Giraffititan , the inner ear of A. sp. shows a more basal morphology . That feature is possibly related to a restricted range of possible movements that involve head @-@ turning .

Like in Jainosaurus and most other non @-@ avian archosaurs , the hindbrain and midbrain of A. sp. is relatively poorly preserved in the endocast . In contrast with TMM 40435 and a few other taxa such as cf . Cetiosaurus oxoniensis and Giraffatitan , no characteristic " nub " of the cerebellum can be seen . As in TMM 40435 and many other archosaurs , the back of the brain is especially narrow in A. sp .

The cerebral region of the brain is separated from the rest of the brain by a distinct compression caused in the endocranial cavity . The rearmost part of the cerebral region of the braincase has a top with a small expansion . This is different from Jainosaurus . However , relatively much larger expansions are known in the diplodocoid sauropods Dicraeosaurus and Diplodocus . In MCCM @-@ HUE @-@ 8741 , the small opening in the skull roof middle is responsible for a swelling on the endocast that is suggestive of a pineal system . It is in the exact position where the pineal gland is expected to have been , between the forebrain and the midbrain .

The semicircular canals are contracted , and they are highly curved . The semicircular system of MCCM @-@ HUE @-@ 8741 shows also a basal morphology , because the semicircular canals do not attach to each other .

= = Discovery and naming = =

Ampelosaurus was originally found near the commune of Campagne @-@ sur @-@ Aude in the Aude département of France . It was recovered in the lower levels of the Marnes Rouges Inférieures Formation , which belong to the early Maastrichtian epoch of the Late Cretaceous Period , ~ 70 million years ago . These sediments represent an ancient floodplain with numerous river channels . French paleontologist Jean Le Loeuff first described and named this dinosaur in 1995 . Ampelosaurus is derived from the Greek ???????? , " the vineyard " and the Latin saurus , " reptile " . Therefore , Ampelosaurus means " vineyard lizard " after the Blanquette de Limoux vineyard . The vineyard is located on the south side of the region Ampelosaurus was found in . The specific name is based on the Latin ajax , the " Aude river " .

The first remains were found in a bonebed discovered in 1989 , which produced numerous ribs and vertebrae from the back and tail , as well as many limb bones , but no skull material aside from one tooth . Four osteoderms of different sizes and shapes were also recovered from this bonebed . This material comes from several different individuals . Since 1989 , more material has been uncovered in the same region of France , including a relatively complete skeleton with some elements of the skull and lower jaw .

Later , in 2001 , the Campagne @-@ sur @-@ Aude site was explored again , this time by Gerard Chauvet , Jean @-@ Luc Le Douarec , Colette Rives and Yvonne Vidoux . After 13 years of searching , they had uncovered a mostly complete skeleton that contained much more material , including bones unknown from the holotype . The material all went to the Musee des Dinosaures , and together took about 10 years to assemble .

The A. sp. was discovered in 2007 . It was found in the course of the construction of a high @-@ speed rail track connecting Madrid with Valencia , in a fossil site that many animals were found in , in the Villalba de la Sierra Formation . The site was at a locality named ? Lo Hueco , ? near the village of Fuentes , Castile @-@ La Mancha , Spain . Over the course of several months , a large @-@ scale emergency excavation by over 60 paleontologists and 100 manual workers allowed thousands of specimens of plants , invertebrates , and vertebrates of late Campanian @-@ early Maastrichtian age to be saved , including A. sp .

= = Classification = =

Characteristics of the tail vertebrae and the presence of osteoderms indicate that Ampelosaurus belongs to Lithostrotia , a group of derived titanosaurians which also includes Alamosaurus and Saltasaurus . Many other paleotologists have classified Ampelosaurus as belonging to Titanosauria , Saltasauridae , and Titanosauridae . Ampelosaurus may have an uncertain classification , but it is clearly a titanosaur , with many features found in titanosaurs .

Below is a cladogram by Klein et al. in 2012 , placing Ampelosaurus as a derived titanosaur :

= = Paleobiology = =

= = = Growth = = =

Ampelosaurus seems to have grown in a way similar to more basal sauropods . After a certain point in its development , the microscopic material of the bone became very different from more basal Sauropoda . Ampelosaurus grew more slowly once the bone microstructure became unique among sauropods . Although Diplodocoidea and basal Macronaria also show an increase in bone growth and a decrease in growth rate around the presumed onset of sexual maturity , it is much more gradual than Ampelosaurus . The process of growing , which in other sauropods started around sexual maturity , was clearly delayed in Ampelosaurus . The period of growth after sexual maturity seems to be shortened in Ampelosaurus and is dominated by slow bone building instead of fast growth . Growth marks are generally rare in sauropods or appearing only late in ontogeny , if at all . The lack of growth marks is suggestive of fast and continuous growth in sauropods , which supports

the hypothesis that they achieved large body size through because of fast growth . Ampelosaurus does not show growth marks on any bone sample . This is unusual to be found with the apparently reduced growth rate and high level of bone growth seen in it , as those features are often associated with the occurrence of growth marks .

= = = Histology = = =

EFS , a system found on the surface of bones , is thought to show a growth plateau which indicates that maximum body size and skeletal maturity is reached in an individual . Ampelosaurus has not been known to have EFS , found on most non @-@ titanosaurian sauropods . Magyarosaurus , a closely related titanosaur , Lirainosaurus , a titanosaur related to saltasaurids , Alamosaurus , a saltasaurid , and Phuwiangosaurus , a very basal titanosaur , were also found to have lacked EFS . However , the basal macronarian Europasaurus has been shown to have had EFS , so it was likely just titanosaurians that did not have them . The outer edge of the bones , were EFS would have been found , was well @-@ preserved , and still lacked any fossilized proof of them being present for Ampelosaurus . However , in the PLoS ONE study that found the lack of EFS , the larger specimens were not tested , so Ampelosaurus might have had EFS . This is characteristic of titanosaurs , as diplodocoids and basal macronarians seem to have EFS . A majority of all Ampelosaurus specimens have been found with secondary osteons placed densely in the inner regions of bones , and lightly in outer regions . The osteon orientation found in Ampelosaurus of osteons not only facing across the bone is not typical of Neosauropoda . Also , there is no medullary cavity in any bones of Ampelosaurus . Ampelosaurus seems to have had many ontogenetic stages in its life based on its bone histology .

= = Paleoecology = =

Ampelosaurus atacis is known from a specimen from the Marnes Rouges Inférieures Formation . More specifically , it is known from the Bellevue layer , which has produced many vertebrate fossils . Even though it produced many vertebrates , the formation only has a few elements of plants and invertebrates . The vertebrates consist of numerous remains of Ampelosaurus , scales of Lepisosteus , shell fragments of an indeterminate turtle , cranial fragments and teeth of a crocodile , isolated theropod teeth , classified as Dromaeosauridae indet . , an indeterminate ankylosaur , and a dentary and many postcranial elements of Rhabdodon priscus . The bird Gargantuavis philoinos , and dinosaur eggs have also been recovered .

Another formation A. atacis is known from is Gres de Saint @-@ Chinian . Along with Ampelosaurus , Rhabdodon priscus , Rhabdodon septimanicus , dinosaur eggs , a Nodosauridae indet . (previously known as Rhodanosaurus lugdunensis) , " Megalosaurus " pannoniensis , Variraptor mechinorum , an Avialae indet . , an Enantiornithes indet . , and a possible Abelisauridae indet. are known from this formation .

A. atacis is one of few vertebrates known from the Gres de Labarre Formation . The only other fossils from the formation belong to Rhabdodon priscus and a Nososauridae indet .

= = = Villalba de la Sierra Formation = = =

The A. sp. is from the latest Cretaceous aged Lo Hueco region in the Villalba de la Sierra Formation . A study shows that the area around Lo Hueco dates to the late Campanian and early Maastrichtian , although a more recent study revised the later date to the latest Maastrichtian . The study showed that Lo Hueco was near the coast of the Tethys Sea , a large seaway through southern Europe and northern Africa . The area directly on the coast was shown to be a brackish @-@ freshwater aquatic environment , with a muddy flood @-@ plain beside it . Lo Hueco was found to be inside the flood @-@ plain . The flood plain was found to have distributary channels of sand and terrigenous material .

About 8500 different marcoremains have been found in Lo Hueco . Sauropods make up the largest

amount of the remains with many articulated individuals , caudal vertebrae and teeth . The caudal vertebrae have been identified as being from a titanosaur closely related to Lirainsaurus , but with some differences . The teeth , were assigned to Ampelosaurus atacis . Apart from sauropods , the Villalba de la Sierra Formation has a good representation of carbonized plants , mostly known from branches and leaves , and invertebrates , mostly bivalves and gastropods . Fishes from the formation include lepisosteid , which have plenty of material , and unidentified actinopterygians and teleosteans . Turtle fossils are very common , even more common than fishes . Of all this material , only two different groups have been identified , the bothremydids Polysternon and Rosasia , along with an uncommon undetermined Pancryptodiran . Squamate lizards are known only from a few undetermined specimens , and eusuchian crocodiles are known from a specimen with similarities to Allodaposuchus and Musturzabalsuchus . Ornithischias and theropod dinosaurs are not as common as sauropods but still consist of much material . Basal euornithopods and probable ankylosaurians are known from Lo Hueco . The ankylosaurian remains consist of a few vertebrae . Rhabdodon sp. is known from the formation , and is known from a fair amount of elements . Only two theropods have been identified , both Dromaeosauridae indet . , one dromaeosaurine and one velociraptorine .

= = = Biogeography = = =

Titanosaurians were a flourishing group of sauropod dinosaurs during Cretaceous times . Fossils of titanosaurians have been found on all continents and their remains are abundant in a number of Late Cretaceous sites . Nonetheless , the cranial anatomy of titanosaurians is still very poorly known . Ampelosaurus is now the best known sauropod from Europe . Others include Magyarosaurus from Hungary and an unnamed species from Catalonia , Spain . Numerous other fragments and isolated bones may or may not belong to any of these forms . While most titanosaurs are found in the southern continents of Gondwana , several derived species are known from Maastrichtian sediments in the Northern Hemisphere , including Alamosaurus in North America and Opisthocoelicaudia in Asia , indicating that there must have been at least intermittent connections between the northern and southern continents . This seems to be corroborated by the European find of Tarascosaurus , a Late Cretaceous theropod dinosaur similar to the abelisaurids , otherwise known only from the southern continents .

Ampelosaurus sp. is a distinct sauropod as it is known from just a braincase . Although the number of sauropod braincases from the Late Cretaceous European archipelago found to date is limited , it shows a significant diversity . The specimen from Lo Hueco resembles the braincase of A. atacis MDE C3 ? 761 .