

= Opisthocoelicaudia =

Opisthocoelicaudia / ˌɒpɪˈstɒkoʊliˈkɔːdiə / was a genus of sauropod dinosaur of the Late Cretaceous Period discovered in the Gobi Desert of Mongolia . The only species is Opisthocoelicaudia skarzynskii . A well @-@ preserved skeleton lacking only the head and neck was unearthed in 1965 by Polish and Mongolian scientists , making Opisthocoelicaudia one of the best known sauropods from the Late Cretaceous . Tooth marks on this skeleton indicate that large carnivorous dinosaurs had fed on the carcass and possibly had carried away the now @-@ missing parts . To date , only two additional , much less complete specimens are known , including a part of a shoulder and a fragmentary tail . A relatively small sauropod , Opisthocoelicaudia measured about 11 @.@ 4 metres (37 ft) in length . Like other sauropods , it would have been characterised by a small head sitting on a very long neck and a barrel shaped trunk carried by four column @-@ like legs . The name Opisthocoelicaudia means " posterior cavity tail " , alluding to the unusual , opisthocoel condition of the anterior tail vertebrae that were concave on their posterior sides . This and other skeletal features lead researchers to propose that Opisthocoelicaudia was able to rear on its hindlegs .

Named and described by Polish paleontologist Maria Magdalena Borsuk @-@ Białyńska in 1977 , Opisthocoelicaudia was first thought to be a new member of the Camarasauridae , but is currently considered a derived member of the Titanosauria . Its exact relationships within Titanosauria are contentious , but it may have been close to the North American Alamosaurus . All Opisthocoelicaudia fossils stem from the Nemegt Formation . Despite being rich in dinosaur fossils , the only other sauropod from this rock unit is Nemegtosaurus , which is known from a single skull . Since the skull of Opisthocoelicaudia remains unknown , several researchers have suggested that Nemegtosaurus and Opisthocoelicaudia may represent the same species . Sauropod footprints from the Nemegt Formation , which include skin impressions , can probably be referred to either Nemegtosaurus or Opisthocoelicaudia as these are the only known sauropods from this formation .

= = Description = =

Like other sauropods , Opisthocoelicaudia had a small head on a long neck , a barrel @-@ shaped body on four columnar limbs , and a long tail . It was relatively small for a sauropod ; the type specimen was estimated at 11 @.@ 4 m (37 ft) from the head to the tip of the tail . The body mass has been estimated at 8 @.@ 4 t (19 @,@ 000 lb) , 10 @.@ 5 t (23 @,@ 000 lb) , 22 t (49 @,@ 000 lb) , 13 t (29 @,@ 000 lb) and 25 @.@ 4 t (56 @,@ 000 lb) in separate studies .

The skull and neck are not preserved , but the reconstruction of the nuchal ligament indicates the possession of a neck of medium length of roughly 5 m (16 ft) . As in other titanosaurs , the back was quite flexible due to the lack of accessory vertebral joints (hyposphene @-@ hypantrum articulations) , while the pelvic region was strengthened by an additional sixth hip vertebra . The anterior vertebrae of the tail were opisthocoelous , which means they were convex on their anterior sides and concave on their back sides , forming ball @-@ and @-@ socket joints . These opisthocoelous tail vertebrae lend Opisthocoelicaudia its name and serve to distinguish the genus from all other titanosaurs . Other titanosaurs were usually characterised by strongly procoelous anterior tail vertebrae , which were concave on their anterior sides and convex on their back sides . Another unique feature can be found in the back vertebrae , which show bifurcated spinous processes , resulting in a double row of bony projections along the top of the spine . While unique in titanosaurs , this feature can be found in several other unrelated sauropods , including Diplodocus and Euhelopus , where it evolved independently .

As in the hips of other titanosaurs , the ischium was relatively short , measuring only two @-@ thirds the length of the pubis . The left and right ischium bones as well as the left and right pubis bones were ossified with each other over most of their length , closing the gap that in other sauropods is normally present between these bones . The limbs were proportionally short , as seen in other titanosaurs . The forelimbs measured 1 @.@ 87 m (6 @.@ 1 ft) in height in the nearly complete specimen , approximately two thirds the length of the hindlimbs , which were reconstructed

at 2 @. @ 46 m (8 @. @ 1 ft) height . As in other titanosaurs , the limbs were slightly spread outwards rather than standing vertically under the body , while the forelimbs were more flexible and mobile compared to other sauropods .

The manus was composed merely of the five metacarpalia , which were orientated vertically and arranged in a semicircle . Carpal bones were missing , as in other titanosaurs . Finger bones and claws were also completely absent ? in most other titanosaurs , these bones were still present though extremely reduced in size . In the foot , the talus bone was strongly reduced as in other titanosaurs , while the calcaneus was probably completely absent in Opisthocoelicaudia . In contrast to the manus , the foot showed well developed digits and claws . The phalangeal formula , which states the number of phalanges (digit bones) beginning with the innermost digit , is 2 @- @ 2 @- @ 2 @- @ 1 @- @ 0 . Foot skeletons of titanosaurs are rarely found , and besides Opisthocoelicaudia , completely preserved examples are known only from Epachthosaurus and the unnamed La Invernada titanosaur , whose phalangeal formulas are 2 @- @ 2 @- @ 3 @- @ 2 @- @ 0 and 2 @- @ 2 @- @ 2 @- @ 2 @- @ 0 , respectively . Of these three titanosaurs , Ophistocoelicaudia was the most derived while showing the fewest phalanges , indicating a progressive reduction in the phalangeal count during titanosaur evolution .

Osteoderms (bony plates formed in the skin) have been found with at least 10 titanosaur genera . The lack of osteoderms in the nearly complete Opisthocoelicaudia skeleton might indicate that they are absent in this genus . However the closeley related Alamosaurus was found to have osteoderms nearly a century after its discovery , this combined with basal forms like Malawisaurus and a number of closely related titanosaurs also bearing osteoderms it 's possible that Ophistocoelicaudia had them as well .

= = Discovery and specimens = =

The type specimen (ZPAL MgD @- @ Ij48) was discovered between the 10th and 23 June 1965 , during a joint Polish @- @ Mongolian paleontological expedition led by Polish paleontologist Zofia Kielan @- @ Jaworowska . The largest of a series of expeditions carried out in 1963 ? 1971 , this expedition involved 21 members , which at times were supported by additional hired Mongolian workers . The site of discovery is located in Ömnögovi Province in southern Mongolia in the Altan Uul area , which exposes some 100 km ² of badlands . The sediments exposed at Altan Uul belong to the Nemegt Formation , the youngest of the three geological formations of the Nemegt Basin . Opisthocoelicaudia was the first of several important dinosaur discoveries made by the 1965 expedition . The other finds , made at different localities , include several skeletons of the tyrannosaurid Tarbosaurus as well as the type specimens of the giant ornithomimosaur Deinocoelurus , the sauropod Nemegtosaurus , and the pachycephalosaur Homalocephale .

On the fifth day of fieldwork , Ryszard Gradzinski , the geologist of the expedition , found a concretion of well @- @ preserved bones which promised to belong to a fairly complete skeleton . Excavation started on the next day , revealing a nearly complete skeleton lacking only the head and neck . Until today , this specimen remains by far the most complete find of this dinosaur . The transport of the specimen out of rough terrain caused major technical problems . Stone blocks containing the fossils had to be moved some 580 m on improvised metal sledges made out of petrol drums before they could be loaded onto trucks . Because the skeleton was embedded in very hard sandstone layers , several blocks weighed over a ton . On the 9th of July , the packing of the skeleton into 35 crates started for transportation to Dalanzadgad ; together , the crates weighed about 12 tons .

The type specimen belonged to an aged individual . Its taphonomy is unusual as it was found lying on its back ? in contrast , most other nearly complete dinosaur skeletons of the Nemegt Formation usually are found lying on their sides . The specimen was found encased in cross @- @ bedded sandstone deposited by a river . Most of the discovered vertebrae were still connected together , forming a continuous series that consisted of 8 dorsal , 6 sacral and 34 caudal vertebrae . An additional 3 vertebrae were found isolated from the series and may belong to the transitional area between back and neck . The remaining parts of the skeleton were shifted slightly out of their

original anatomical position . Both the left limb and rib bones were found on the right side of the body , while conversely the right limb and rib bones were found on the left side . Bite marks have been identified on the skeleton , particularly in the pelvis and the thigh bone , showing that predators had fed on the carcass . The skull and neck are missing , indicating that the carnivores might have carried away these body parts . The completeness of the remains indicate that the individual had died near the discovery site . A flooding event might have transported the carcass a short distance and subsequently covered it with sediment , even before the soft tissue had decayed entirely .

In 1977 , Polish paleontologist Maria Magdalena Borsuk @-@ Bia?ynicka published her comprehensive description of the skeleton and named *Opisthocoelicaudia skarzynskii* as a new genus and species . The genus name , hinting at the unusual opisthocoel condition of the tail vertebrae , means " posterior cavity tail " . It is derived from the Greek ?????? , opisthe [back] , ?????? , koilos [hollow] , and Latin cauda [tail] . The specific name honors Wojciech Skar?y?ski , the person who prepared the type specimen . *Opisthocoelicaudia* was only the third sauropod from Asia known from a postcranial skeleton , after *Euhelopus* and *Mamenchisaurus* . Today , the skeleton is part of the collection of the Institute of Geology of the Mongolian Academy of Sciences in Ulaanbaatar .

Besides the type specimen , Borsuk @-@ Bia?ynicka described a shoulder blade and coracoid (ZPAL MgD @-@ I / 25c) from the same locality . These bones were not yet fused to each other , indicating a juvenile individual . Philip Currie and colleagues in 2003 mentioned a fragmentary tail (MPD 100 / 406) from the Nemegt locality that can be attributed to *Opisthocoelicaudia* .

= = Age and paleoenvironment = =

The Nemegt Formation was deposited within the Late Cretaceous , although its exact age is unknown as it has never been dated radiometrically . According to different authors , the formation is late Campanian to early Maastrichtian , early Maastrichtian , or middle Maastrichtian in age . The sediments of the Nemegt Formation were deposited in a plain crossed by rivers . The climate was warm and subhumid with seasonal droughts , and the soils were relatively dry . Nevertheless , the Nemegt Formation was more humid than the underlying (and thus older) Barun Goyot and Djadochta Formations , which show a semiarid climate .

The fauna of the Nemegt Formation includes aquatic or amphibious animals such as fish , turtles , and crocodiles as well as birds and the abundant medium to large sized dinosaurs , while smaller terrestrial vertebrates like lizards and mammals are rare . Theropod dinosaurs are very diverse in the Nemegt and include the abundant tyrannosaur *Tarbosaurus* , which might have preyed upon *Opisthocoelicaudia* . The only other known sauropod is *Nemegtosaurus* , which is known from a single skull . Ornithischians are represented by the " duck @-@ billed " hadrosaurids (including the very common *Saurolophus*) , the thick @-@ skulled pachycephalosaurs , and the heavily armored ankylosaurs . Neoceratopsians are absent , despite being present in the older Barun Goyot and Djadochta formations . Other important dinosaur finds from the same locality as *Opisthocoelicaudia* include the troodontid *Borogovia* and the ankylosaur *Tarchia* .

= = Classification = =

Originally , *Opisthocoelicaudia* was classified as a member of the family *Camarasauridae* , together with *Camarasaurus* and *Euhelopus* . This classification was based on several shared features of the skeleton , most importantly the forked neural spines of the back vertebrae . In 1977 , Borsuk @-@ Bia?ynicka considered *Opisthocoelicaudia* closer to *Euhelopus* than to *Camarasaurus* , placing it in the subfamily *Euhelopodinae* . A 1981 study by Walter Coombs and Ralph Molnar , on the other hand , considered it a member of the subfamily *Camarasaurinae* and therefore a close relative of *Camarasaurus* . Today , both *Euhelopus* and *Opisthocoelicaudia* are classified outside the *Camarasauridae* . In 1993 , Leonardo Salgado and Rodolfo Coria showed *Opisthocoelicaudia* to represent a titanosaur and classified it within the family *Titanosauridae* . The name *Titanosauridae* is currently considered invalid by many scientists ; instead , the name *Lithostrotia* is often used as an

equivalent .

Within the Lithostrotia , Opisthocoelicaudia has been found to be closely related to the genera Alamosaurus , Neuquensaurus , Rocasaurus and Saltasaurus , together forming the family Saltosauridae . Interrelationships of these genera are contested . Many scientists considered Opisthocoelicaudia to be most closely related to Alamosaurus , with both genera forming a monophyletic group , the Opisthocoelicaudiinae . Other scientists came to the conclusion that the Opisthocoelicaudiinae is paraphyletic (not forming a natural group) . Contradicting most other studies , Upchurch and colleagues in 2004 argued that Alamosaurus has to be placed outside the Saltosauridae as a close relative of Pellegrinisaurus , and therefore is not related to Opisthocoelicaudia at all .

The following cladogram is based on Calvo and colleagues (2007) , showing a monophyletic Opisthocoelicaudiinae :

== Relationship to Nemegtosaurus ==

Another sauropod of the Nemegt Formation , Nemegtosaurus , is known only from a skull . Opisthocoelicaudia , on the other hand , lacks both the skull and neck , precluding a direct comparison and leading to suspicions that it may represent a synonym of Nemegtosaurus . According to the International Code of Zoological Nomenclature (ICZN) , the oldest name has priority over younger synonyms ? if Opisthocoelicaudia would be shown to be a synonym of Nemegtosaurus , the name Nemegtosaurus would remain valid while Opisthocoelicaudia would become invalid .

Both Opisthocoelicaudia and Nemegtosaurus were discovered during the 1965 joint Polish Mongolian expedition . Before the remains were prepared and described , the expedition crew believed both finds to belong to the same species of sauropod . In 1977 , Borsuk-Bianowska deemed Opisthocoelicaudia and Nemegtosaurus to represent separate genera because Nemegtosaurus was at this time considered to be a member of the Dicraeosauridae , while Opisthocoelicaudia seemed to be a representative of a different group , the Camarasauridae . Furthermore , she argued that different sauropod genera sharing the same habitat is nothing unusual ; this is most obvious in the North American Morrison Formation , which contains more than five contemporary sauropod species .

Currently , both Opisthocoelicaudia and Nemegtosaurus are classified within the Titanosauria , and Jeffrey Wilson stated in 2005 that synonymy cannot be ruled out . In a 2003 study , Currie and colleagues argued that a synonymy is very probable and reported a fragmentary tail referable to Opisthocoelicaudia that was discovered in the same locality where the Nemegtosaurus skull was found . Nevertheless , Kielan-Jaworowska stated in 2013 that the question of a possible synonymy may not be resolved until a skull is found in association with postcranial remains .

== Paleobiology ==

== Posture ==

Originally , Borsuk-Bianowska assumed that in standard position the neck was horizontal or slanted slightly downward . This was based on the reconstruction of the nuchal ligament , which runs atop of the cervical and dorsal vertebrae and serves to support the weight of the head and neck . Although an S-curved , swan-like ascending neck was envisaged in several subsequent reconstructions following similar depictions of better known sauropods , recent studies argue that sauropod necks were relatively straight and were carried more horizontally .

The back was also reconstructed in a more or less horizontal orientation by Borsuk-Bianowska , which was followed by most subsequent depictions . In a 2007 study , Daniela Schwarz and colleagues suggested that the back dipped towards the rear . According to these researchers , the shoulder blade would have been inclined at a horizontal angle of 55 ? 65 ° , much steeper than

previously thought , resulting in an elevated shoulder region . With the vertebral column of the trunk and neck held in a relatively straight line , this would result in an elevated position of the head .

== Rearing stance ==

Opisthocoelicaudia may have been able to rear up on its hindlimbs for foraging , using its tail as a third leg . In 1977 , Borsuk-Bianicka cited several skeletal features that might have been related to rearing , including the opisthocoelous vertebrae of the anterior part of the tail , which , according to this author , would have made the tail more flexible than in other sauropods . Features of the pelvis , such as the thickened shelf of the acetabulum , the flaring ilia , and the fused pubic symphysis , may have allowed the pelvis to withstand the stress of rearing .

Heinrich Mallison in 2011 argued that Opisthocoelicaudia was able to angle the anterior part of the tail against the posterior part , producing a buckle in midsection . Thus , the anterior part would have been more straight during rearing than in other sauropods . In 2005 , Wilson assumed that rearing was an innovation not only of Opisthocoelicaudia but also of related genera within the subfamily Saltasaurinae . Common features of these genera , such as the shortened tail , may have evolved as adaptations to rearing .

== Footprints ==

Footprints from the Nemegt Formation were unknown until 2003 , when Currie and colleagues described several examples from the Nemegt locality . Most of these footprints belonged to hadrosaurids (probably Saurolophus) , while two have been left by a large theropod (probably Tarbosaurus) and yet another two by the hindfoot of a sauropod . The sauropod tracks were assigned to Opisthocoelicaudia , which showed a matching hind foot morphology . The researchers argued that Opisthocoelicaudia was probably the only known sauropod from the Nemegt Formation when Nemegtosaurus is regarded a synonym , making it unlikely that the tracks were left by another , similar titanosaur . The tracks were left in the soft and wet mud of shallow or freshly dried up points along a river and subsequently filled up with sand . Today only the sand infill remains , with the encasing mudstone having been eroded away .

The best preserved footprint measures 63 cm (25 in) across , so it was probably created by an individual larger than the type specimen . Although the surface of the underside is hard to obtain , the vertical surfaces are very well preserved , making this track one of the best preserved sauropod tracks known . Four digital impressions can be distinguished , with two or three showing claw impressions . The toes were almost perpendicular . Even a skin impression has been preserved above the impression of the first toe , which shows the non overlapping scales , each with an average diameter of 14 mm (0.55 in) . The foot of the track creator was probably a little longer than wide . The second track is much shallower than the first , but shows well preserved digit impressions with a high degree of detail , including at least two deep claw impressions that are rotated outwards , and a well preserved impression of a fleshy toe pad behind the middle claw .