

The Chinese colossus: an evaluation of the phylogeny of *Ruyangosaurus giganteus* and its implications for titanosaur evolution

Nima Sassani^{1*}, Gunnar Tyler Bivens²

¹28361 Millwood Rd., Trabuco Canyon, California, USA

²302 E Paradise Ln., Phoenix, Arizona, USA

*Email address: paleoking13@gmail.com

Abstract: For many years the precise taxonomy of Titanosauria has been a puzzle, and even today only certain segments of this vast clade are well-understood. The phylogenetic positions of many titanosaurs are murky, though specimens often still await rigorous analysis. One of the largest examples is the massive Chinese titanosaur *Ruyangosaurus giganteus* – though largely incomplete, the holotype is distinct enough to indicate strong phylogenetic affinities with a specific subgroup of titanosaurs. A review of previous literature on *Ruyangosaurus*, referred tentatively to Andosauridae, shows that this classification is based on three weak, non-diagnostic characters. *Ruyangosaurus* differs from taxa traditionally included in Andosauridae in at least 20 characters of the torso, femur, and tibia. Several plesiomorphies of *Ruyangosaurus* are extremely rare in titanosauria except for the clade Lognkosauria and its close relatives. The vertebra initially described as a posterior cervical is most likely an anterior dorsal, with a strong resemblance to that of *Puertasaurus*. The posterior dorsal of *Ruyangosaurus* shares synapomorphies with *Mendozasaurus* and *Dreadnoughtus*. The femur clusters close to the femora of *Malawisaurus*, *Traukutitan*, and *Pitekunsaurus*. *Ruyangosaurus* is here recovered as a lognkosaurian, with significant implications for the distribution and evolution of that group and the paleobiology of Mid-Cretaceous China.

Introduction

In recent years, China has yielded several new titanosauriform taxa, including five truly gigantic ones that rival many of the largest South American titanosaurs in size: “Huanghetitan” *ruyangensis* (Lü, *et. al.*, 2007), *Daxiatitan binglingi* (You, *et. al.*, 2008), *Yunmenglong ruyangensis* (Lü *et al.*, 2013), *Fusuisaurus zhaoi* (Mo, *et. al.*, 2006) and *Ruyangosaurus giganteus* (Lü, *et. al.* 2009). Possibly the largest of the five, *Ruyangosaurus* is also arguably the least understood. Whereas *Daxiatitan* was recovered as a basal somphospondyliian close to *Euhelopus* (Wiman, 1929) and “Huanghetitan” *ruyangensis* was recovered as a basal titanosauriform intermediate between *Brachiosaurus* (Riggs, 1903) and *Euhelopus*, *Ruyangosaurus* does not much resemble either of these two giant Chinese taxa, and is more derived in morphology. Known from fewer remains, *Ruyangosaurus* is also more difficult to place into a cladistic analysis. However many holotype plesiomorphies not analyzed in great detail by Lü, *et. al.* (2009) are shared with titanosaurs more derived than *Andesaurus* (Calvo and Bonaparte, 1991) and *Argentinosaurus* (Bonaparte and Coria, 1993), two of the three principal members of the weakly defined clade *Andesauridae* (*ibid*, 1993). The *Ruyangosaurus* material also differs in all comparable elements from the clades third member, *Epachthosaurus sciuttoi* (Powell, 1990). Lü, *et. al.* (2009) tentatively placed *Ruyangosaurus* in *Andesauridae* based on three weak characters which are present in titanosaurs outside that clade, and therefore polyphyletic. *Ruyangosaurus* shares many synapomorphies with non-andesaurid titanosaurs. Of particular note is the similarity in morphology between the “posterior cervical” of *Ruyangosaurus* and the anterior dorsal of *Puertasaurus reuili* (Novas, *et. al.*, 2005), a lognkosaur which it resembles in this region far more closely than any other species. Both described vertebrae of *Ruyangosaurus* share configurations of laminae and fossae in common with *Mendozasaurus* (Gonzalez-Riga, 2003), *Puertasaurus*, and *Pitekunsaurus* (Filippi and Garrido, 2008), as well as similarities in proportions of the centrum, neural canal, and neural arch, which are also found in the recently described lognkosaurs *Dreadnoughtus* (Lacovara *et al.*, 2014) and *Notocolossus* (González Riga *et al.*, 2016). The lateral laminae of the posterior dorsal show a pattern similar to *Elaltitan lilloi* (Mannion and Otero, 2012). Hindlimb elements show synapomorphies with *Malawisaurus* (Jacobs, *et. al.*, 1993), *Pitekunsaurus*, *Elaltitan*, *Traukutitan* (Juarez Valieri and Calvo, 2011), as well as a specimen referred by Swinton (1947) to *Titanosaurus indicus* (Lydekker, 1877) and two unnamed South American taxa. The femur and tibia are anomalous but strongly resemble a few titanosaur specimens and reflect extreme hindlimb morphology. The robust cervical and dorsal ribs indicate a massive animal but offer few clues to its phylogenetic relationships.

Anatomical Abbreviations: We use the classic “Romerian” anatomical terminology (anterior/posterior>cranial/caudal: chevrons>haemal arches). Laminae and fossae abbreviations are listed below.

Lamina

ACDL – anterior centrodiapophyseal lamina
PCDL – posterior centrodiapophyseal lamina
SPDL – spinodiapophyseal lamina
PPDL – paradiapophyseal lamina
CPRL – centroprezygapophyseal lamina
SPRL – spinoprezygapophyseal lamina
TPRL – intraprezygapophyseal lamina
CPOL – centropostzygapophyseal lamina
SPOL – spinopostzygapophyseal lamina
ACPL – anterior centroparapophyseal lamina
PCPL – posterior centroparapophyseal lamina
PRSL – prespinal lamina
POSL - postspinal lamina

Fossa

CDF - centrodiapophyseal fossa
PACDF - parapophyseal centrodiapophyseal fossa
CPAF - centroparapophyseal fossa
PODF - postdiapophyseal fossa
POPAF - Postparapophyseal fossa

Institutional Abbreviations

BIBE, Big Bend National Park, Texas, USA
FMNH, Field Museum of Natural History, Chicago, USA
GSLTZP03, Fossil Research and Development Center, Third Geology and Mineral Resources Exploration Academy of Gansu Province, Lanzhou, China
HGM, Henan Geological Museum, Zhengzhou, Henan, China. [including HIII as used for *Ruyangosaurus* and others]
HMN, Museum für Naturkunde Berlin, Berlin, Germany.
IANIGLA, Instituto Argentino de Nivología Glaciología y Ciencias Ambientales, Mendoza, Argentina
ISI or **ISIR**, Geology Museum, Indian Statistical Institute, Calcutta, India
MACN, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina
MAL, Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi
MAU, Museo Argentino Urquiza, Rincón de los Sauces, Neuquén, Argentina
MCF-PVPH, Museo ‘Carmen Funes’, Plaza Huincul, Neuquén, Argentina

MCT, Collection of the Earth Science Museum of the National Department of Mineral Production, Rio de Janeiro, Brazil.
MLP, Museo de La Plata, Argentina
MPM, Museo Padre Molina, Rio Gallegos, Santa Cruz, Argentina
MPZ, Museo Paleontológico de Zaragoza, Zaragoza, Spain
MUCPv, Museo de Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina
NHMUK, Natural History Museum, London, United Kingdom.
PMU, Paleontological Museum, Uppsala, Sweden
PVL, Colección de Paleontología de Vertebrados de la Fundación Instituto Miguel Lillo, Tucumán, Argentina
TMM, Texas Memorial Museum, Austin, Texas, USA
UNCUYO-LD, Universidad Nacional de Cuyo, Instituto de Ciencias Básicas, Laboratorio de Dinosaurios, Mendoza, Argentina
UNPSJB, Universidad Nacional de la Patagonia San Juan Bosco, Comodoro Rivadavia, Argentina
ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland

FOSSIL MATERIAL

Ruyangosaurus giganteus

Holotype: 41HIII -0002, consisting of six elements: an anterior dorsal vertebra (listed as a posterior cervical in Lü, *et. al.* 2009), a posterior dorsal vertebra, right femur, right tibia, proximal portion of a cervical rib, and proximal portion of a dorsal rib. The complex features of the holotype elements described in Lü, *et. al.* 2009 are detailed as follows.

Anterior dorsal vertebra (Fig. 1)

The widest element of the *Ruyangosaurus* holotype is a very large vertebra, provisionally described in Lü, *et. al.* 2009 as “a possible incomplete posterior cervical”, but which appears to be an anterior dorsal, due to its extreme short length, high diapophyses, and parapophyses situated laterally to the centrum’s dorsal margins rather than ventrally. The neural arch, as preserved, is roughly 88 cm across, and is missing large portions of the diapophyses, the right parapophysis, and some of the neural spine. With the extremely deep diapophyses reconstructed, the neural arch would be roughly 150-160cm across, slightly smaller than that of *Puertasaurus*. The centrum is heavily eroded on its right ventral surface, exposing a honeycomb-like structure of internal camellae (Lü, *et. al.* 2009; p. 2). The extreme width of the anterior dorsal is, nevertheless, apparent in what remains of the centrum and neural arch. The centrum is squat and oblate, and 51 cm wide, rivaling in width the anterior dorsal centra of *Argentinosaurus* (D2? 47

cm wide at the condyle, 60 cm at the cotyle) and *Puertasaurus* (D2, 56 cm wide at both condyle and cotyle). The *Ruyangosaurus* anterior dorsal centrum resembles that of *Puertasaurus* in being ventrally non-concave and extremely short relative to its breadth. The neural spine is damaged but appears to have been triangular or trapezoidal, moderately short, and wide. The shallow PRSL is partially split by a crack and intersected by the TPRL. The right prezygapophysis is destroyed, but the left is mostly intact and is separated from the PRSL by a distance roughly equal to its own articular width. It is robust, short, and medially sloping as in *Mendozasaurus*. The intraprezygapophyseal junction is a solid lamina high above the neural canal, with no hypantrum gap, and beneath it is a pair of laminae terminating above a shallow anterior neural fossa which is largely destroyed due to being intersected by both the prespinal crack and a massive diagonal fault which runs from the medial margin of the left parapophysis, over the centrum and up to the base of the destroyed right prezygapophysis. Both of these fractures run clean through the vertebra from the anterior to the posterior face. However, enough of the anterior neural fossa remains to indicate a roughly pentagonal shape. It is separated from the neural canal by a thin but distinct lamina. The neural canal is bordered laterally by a pair of shallow ovoid fossae, as in *Puertasaurus* and *Malawisaurus*. The anterior faces of the diapophyses contain a pair of very large *Puertasaurus*-like fossae, possibly with a second, smaller pair below them, just above the parapophyses.

The posterior face of the vertebra shows a similar pattern of a large pair of fossae above a smaller pair. Both pairs of fossae contain many small laminae and shallow foramina. There is also a large posterior neural fossa, which is partially destroyed in the center for the same reasons as the anterior neural fossa, and is also unusual in being pinched off from the neural canal itself by a thick bar of bone formed from two projections of its own laminae walls. The postzygapophyses form a wide V-shaped junction whose vertex has been twisted right as a result of geologic processes. It overhangs the neural fossa and does not form a hyposphene. The POSL is weak and short, ventrally bifurcated into two laminae which attach perpendicularly to the dorsal surfaces of the postzygapophyses, forming an inverted v-shape; the lamina is similarly forked on its dorsal end. The PCDL are the most massive laminae on the vertebra and contain an upward kink located roughly 30 cm from the vertebra's midline. The rim of the cotyle is thick and somewhat rugose, with small foramina on its upper margins. The center of the cotyle has a small elliptical depression, which is roughly concentric to the cotyle.

Posterior dorsal vertebra (Fig. 2)

The posterior dorsal of *Ruyangosaurus* is more complete than the anterior dorsal. The entire centrum and most of the left diapophysis are preserved. However as with the anterior dorsal, the right diapophysis and much of the neural spine is missing. The vertebra has many small foramina and laminae and several unusual structures associated with the major laminae and fossae.

The centrum is very large, and the cotyle is significantly larger than the condyle, a condition not observed in the anterior dorsal. Also considerably different from the anterior dorsal is the extremely concave ventral surface of the centrum. The centrum is riddled with small foramina around the edges of the condyle and nestled in depressions near the base of the neural arch. The vertebra also has a few poorly defined laminae on the ventral surface of the centrum. The pleurocoels are of average size relative to the vertebra, and moderately shallow. The right pleurocoel is larger and more rhomboid than the left. The cotyle has concentric stress fractures on the left, and a shallow but distinct central depression as well as several small foramina surrounding it. The dorsal surfaces of both the condyle and the cotyle are nearly horizontal and the margins of the condyle are nearly square. The neural canal is smaller anteriorly than posteriorly, and dorsally pinched at its triangular anterior end. Its posterior end is roughly trapezoidal.

The neural arch is somewhat damaged anteriorly, with some portions of the neural arch eroded and a large fracture through much of the right prezygapophysis. There is a very strong and pronounced TPRL, with no trace of a medial gap or hypantrum, indicating as with the anterior dorsal that there are no true hypantrum-hyposphene connections present. The TPRL forms a shallow V-shape (corresponding to the relatively shallow junction of the postzygapophyses) with a short vertical ridge below its center. The lower half of this ridge contains a sharp central foramen which is likely the uppermost vestige of a neural fossa. Beneath this, the neural arch is largely flat and featureless, including the portion surrounding the neural canal. The prespinal lamina is shallow, poorly preserved, and medially split by a large vertical fracture similar to that on the anterior dorsal. The SPRL are weak and damaged. The parapophyses are high on the neural arch, typical of titanosaur posterior dorsals, but unusually they are extremely close to the diapophyses, connected by a very short PPDL. The PCPL have several thin accessory laminae threading into the PACDF; these are huge and triangular, being the largest fossae on the vertebra containing many small laminae and foramina, those in the left fossa being more prominent. There are no CPRL (Lü, *et. al.*, 2009). The lateral base of the neural arch is fringed with foramina, and on the right side these form a rugose network of ridges and depressions near the base of the CPRL. The PODF are large and relatively shallow, taking up much of the posterior area of the diapophyses. The neural canal fills most of a shallow posterior neural fossa, which is surrounded by two pairs of weak “spider” laminae radiating down from below the intrapostzygapophyseal junction. The inner pair tightly borders a shallow neural fossa, a very different condition from the posterior neural fossa in the anterior dorsal, a far larger fossa whose bordering laminae are massive and well-defined.

The vertebra lacks a true POSL; instead there are two large subsidiary laminae which anchor perpendicularly to the dorsal surfaces of the postzygapophyses, and intersect above the intrapostzygapophyseal junction, then branch off again dorsally into two more laminae, forming

a postspinal X-shaped lamina complex. The fossae on either side of this “X” are asymmetric; the left fossa is largely open, while the right is crowded with additional thick laminae. Beneath the “X” is a fossa which borders the dorsal surface of the intrapostzygapophyseal junction, and itself contains a second, smaller X-shaped laminar feature. The upper portion of the neural spine, though missing, was likely short due to its antero-dorsal thinness at its center. The articular surfaces of both postzygapophyses are broken off, but their bases are massive. The CPOs are large and relatively flat, and are medially bordered by a pair of roughly elliptical fossae, which in turn border the intrapostzygapophyseal junction. The right portion of the neural arch is somewhat laterally displaced due to a stress fracture which runs 360 degrees around its base – the same fracture that splits the right prezygapophysis. The anterior and PCDL enclose very shallow CDF. The PCDL, as in the anterior dorsal, are the largest laminae on the vertebra.

Right femur (Fig. 3)

The right femur of *Ruyangosaurus* as depicted in Lü, *et. al.* (2009) is partially reconstructed; only the proximal half was recovered, but this is well-preserved enough to record some very peculiar features. The fourth trochanter is located high up on the femur, relative to the proportions of the extant proximal femur and the size of the femoral head. The femoral head itself is very bumpy and rugose on its proximal surface relative to most other titanosaurs; this texture does not appear to be an artifact of erosion. Despite the bumps, it is also unusually straight-edged on its proximal surface, lacking the rounded appearance of typical titanosaur femoral heads – a morphology found in only a handful of titanosaurian taxa. The femoral condyle is very short and the proximal end of the shaft is very straight, without much of the medial tilt that is often found in very derived titanosaurs like *Saltasaurus* (Bonaparte and Powell, 1980) and *Neuquensaurus* (Lydekker, 1893). There also appear to be three or four unusual small fossae located laterally from the fourth trochanter. The lateral protuberance is situated extremely high, near the femoral head, and bulges out considerably relative to the lateral surface of the proximal femur. It is also noticeably sharp and triangular relative to its state in most titanosaurs. In this regard it resembles *Traukutitan*, “*Titanosaurus indicus*” and *Pitekunsaurus*, but not *Dreadnoughtus*. Lü, *et. al.* (2009) mention that the preserved proximal element of the femur is 120 cm long, and speculate that the complete femur would have been approximately 200cm long. However, based on the scale bar included in the paper’s photograph of the reconstructed femur, it was restored to a length of 235 cm. The absence of fossil material for the distal portion of the femur makes it difficult to diagnose beyond what can be gleaned from these few facts.

Right tibia (Fig. 4)

The short tibia of *Ruyangosaurus* indicates that it had very unusual hindlimb proportions. The tibia is only 127cm long, a little over half the length of the reconstructed femur, and just barely longer than the femur’s preserved proximal element. Such an extreme length discrepancy between the tibia and femur is rare among sauropods, and seems to have evolved multiple times

in the macronaria; *Giraffatitan* (Janensch, 1914) is well known for its unusually short tibiae combined with very long femora, and *Europasaurus* (Sander *et. al.*, 2006) also exhibits a low tibia to femur length ratio. A short, compact tibia is also present in *Opisthocoelicaudia* (Borsuk-Bialynicka, 1977) and several other derived lithostrotians. The *Ruyangosaurus* tibia has a very large, deep cnemial crest which is partially broken. The tibia is 51cm wide at its greatest extent at the proximal end. It is also medio-posteriorly extremely concave relative to its ends, indicating unusually large calf muscles, and its distal end is notched and posteriorly elongated.

Cervical rib (Fig. 5)

The holotype includes the proximal portion of a left cervical rib, which is robust and massive. As pointed out by Lü, *et. al.* 2009, the tuberosity and the capitum of the cervical rib form a straight 90-degree angle. However, the angle between the capitum and the posterior portion of the rib is greater, around 120 degrees. As a result, the ventral surface of the rib is not perfectly level, with the tuberosity being angled downward relative to the posterior element of the rib. Assuming this is not the result of geological distortion or pathology, it is likely that when complete the cervical ribs of *Ruyangosaurus* were distally kinked to accommodate the ventral protrusion of the next cervical rib's tuberosity. The tuberosity itself is massive and club-shaped, and the connection between it and the capitum is buttressed by a large heavy lamina. The capitum is eroded at its proximal end, where the diapophyseal articular surface would be.

Dorsal rib (Fig. 6)

The proximal portion of a right anterior dorsal rib is preserved in the type material, and is 127 cm long (Lü, *et. al.* 2009). A shallow concavity is present near the proximal end, and the area around this is similarly concave, forming a depression between the parapophyseal condyle and the main body of the rib. The parapophyseal condyle is separated by only about 30 cm vertically from the level of the diapophyseal condyle. This corresponds perfectly to the 30 cm vertical difference between the level of the estimated end of the diapophysis of the anterior dorsal vertebra and that of its parapophysis – a further indication that the vertebra in question is indeed a dorsal, since a cervical vertebra from an animal this large would likely have far more distance between the two processes due to having the parapophysis located far lower, ventrally on the centrum. Indeed, the distance between the diapophyseal connection and the ventral surface of the preserved cervical rib is at least 60 cm long, as this is the length of the capitum, not accounting for erosion. The diapophyseal condyle of the dorsal rib is large and has an unusual protuberance on its posterior margin. The rib itself is very large, with a shaft width of 18 cm.

COMPARISON WITH OTHER TITANOSAURS

Anterior dorsal vertebra (Fig. 7)

The centrum is squat and oblate, rivaling the anterior dorsal centra of *Argentinosaurus* and *Puertasaurus* in size as previously mentioned. The condyle is extremely convex laterally, much like the similarly oblate condyle of *Puertasaurus*. The centrum is very short antero-posteriorly, a trait also present in *Puertasaurus*. Though a significant right-ventral portion of the centrum is broken off, enough of the ventral surface remains to show that this centrum is even more proportionally squat than the dorsal centrum of *Puertasaurus*, and the parapophyses (only one of which is completely preserved) appear to have been more pronounced and less fused to the centrum, with notches separating them from it. The cotyle's central depression is far smaller than in *Puertasaurus*. As in *Mendozasaurus*, it appears to be centered slightly below the center of the cotyle itself. Very few titanosaurs outside of Lognkosauria exhibit a central cotyle depression, such as *Phuwiosaurus* (Martin, *et. al.*, 1994). *Pitekunsaurus* has a depression located dorsally in the cotyle. In saltosaurids and nemegtosaurids this feature is absent.

The neural canal is small and triangular as in *Puertasaurus* and *Mendozasaurus*, but not *Malawisaurus*, *Epachthosaurus*, *Pitekunsaurus*, *Saltasaurus* or *Argentinosaurus*. It is bordered at both ends by neural fossae, whose morphology is unique among titanosaurs. The presence of a large and boxy posterior neural fossa framed by large and non-intersecting CPOL and a pointed intrapostzygapophyseal junction is remarkably similar to the neural fossa of *Puertasaurus*, and unlike those of any other titanosauria. The fossa is roughly hexagonal in *Ruyangosaurus*, and more rectangular in *Puertasaurus*. The structure of the neural canal relative to this fossa is also different; in *Puertasaurus* it is within the fossa, whereas in *Ruyangosaurus* it is cut off from the fossa by a bar of bone formed from two medial projections of the CPOLs which border the fossa itself. The same is true of the far smaller anterior neural fossa, except that the lamina which separates it from the neural canal is a thinner, undivided structure. The anterior neural fossa is largely destroyed due to being at the intersection of the two large fractures on the vertebra, resulting in a hole through the center of the neural arch; what remains of the fossa indicates it was roughly pentagonal or hexagonal. *Ruyangosaurus* differs significantly from both *Puertasaurus* and *Pitekunsaurus* in having neural fossae separated from the neural canal by laminae, and having the TPRL located far higher above the neural canal.

The intrapostzygapophyseal junction is a single overhanging point, as in *Puertasaurus* – it totally lacks any lower accessory laminae and thus does not form even a trace of a hyposphene. A hyposphene is also absent in *Malawisaurus*, and *Mendozasaurus* and *Pitekunsaurus* preserve only a small semblance of a hyposphene in the form of an X-shaped lamina complex at the junction, which does not form an articular surface with the prezygapophyses of the next dorsal vertebra.

The PODFs are very large as in *Puertasaurus* though their margins are more complex, with several small fossae near the postzygapophyses. There are also large POPAF containing

complexes of small laminae, bordered dorsally by the massive PCDL and lateroventrally by the parapophyses themselves. By contrast, *Puertasaurus* has barely a trace of POPAF. The external structure of the *Puertasaurus* second dorsal is less excavated than that of the *Ruyangosaurus* anterior dorsal, a derived condition typical of its later age.

The general proportions of the two vertebrae are remarkably similar, particularly in their extremely low height/width ratios, at the bottom end of the lognkosaurian range. *Mendozasaurus* has a greater height/width ratio than the other lognkosaurs, though less than most basal somphospondyli except for *Ligabuesaurus* (Bonaparte, *et. al.*, 2006). Among nemegtosaurids the ratio is relatively low, though considerably higher in *Saltasaurus* and *Isisaurus* (Jain and Bandyopadhyay, 1997) (see table 1).

Posterior dorsal vertebra

As with the anterior dorsal vertebra, the posterior dorsal of *Ruyangosaurus* is unique among titanosaurs in its size, compact antero-posterior proportions, and the unusual patterns of laminae on its posterior surface.

The horizontal shape of dorsal margins of the condyle and cotyle seen in *Ruyangosaurus* is rare in titanosauria and does not occur in the posterior dorsals of either *Andesaurus*, *Phuwiangosaurus*, or *Argyrosaurus*. Horizontal dorsal condyle and cotyle margins are known from the anterior dorsals of *Puertasaurus* and *Mendozasaurus*, but not *Malawisaurus*. The presence of small fossae on either side of the intrapostzygapophyseal junction is similar to such structures in *Pitekunsaurus* and *Mendozasaurus* anterior dorsals. The centrum is not as expanded laterally as in derived lithostrotia like *Alamosaurus* (Gilmore, 1922) and *Opisthocoelicaudia*, though more so than in *Argentinosaurus*, *Elaltitan*, *Phuwiangosaurus*, *Tastavinsaurus* (Canudo, *et. al.*, 2008), or *Malawisaurus* and far more oblate than in *Andesaurus*. The centrum is anteroposteriorly short relative to the height of the vertebra (which was taller when complete). This sets it apart from *Epachthosaurus*, *Trigonosaurus* (Campos, *et. al.*, 2005) and *Malawisaurus*. Its relatively low length-to-height ratio (~4.5:5) is very different from the condition in *Phuwiangosaurus* and the three previously mentioned titanosaurs. The condyle of the centrum is covered in small pits and rugosities, similar to the condition in *Malawisaurus* and *Pitekunsaurus*, but very different from the heavily pitted condyle of the 9th (?) dorsal vertebra of *Elaltitan*. The *Elaltitan* condyle is also marked by a large concentric depression, a feature absent in the condyles of *Ruyangosaurus* and most other titanosaurs (though present in lognkosaurian cotyles).

The configuration of the lateral laminae of the neural arch roughly resembles that in the *Argyrosaurus* vertebra, though in *Ruyangosaurus* the margins of these laminae are well-defined and the fossae appear deep as in *Malawisaurus* but not *Elaltitan*. The ACDL and PCDL also lack the retrograde tilt found in *Elaltitan*. Since that specimen is immature (as is evident from the

scapula lacking a fused coracoid), its spinal morphology may have still been undergoing ontogenetic changes. The cotyle in *Ruyangosaurus* contains small pits and a concentric depression, partially marred on its right by what may be ossified cartilage. The cotyle's rim is narrow and radially expanded.

The four “spider laminae” beneath the intrapostzygapophyseal junction are unlike any other structure known in titanosauria, although the inner pair surrounding the posterior neural fossa do bear a rough resemblance to neural laminae in the anterior dorsals of other titanosaurs such as *Argentinosaurus*. Unlike *Argentinosaurus* however, the laminae do not form the lower portion of a hyposphene, as they are far too shallow and do not extend posteriorly to the apex of the shelf-like intrapostzygapophyseal junction. This junction forms a shallow v-shape, and would fit perfectly above the prezygapophyses of the next vertebra without need for a hyposphene. The posterior dorsal itself has no hypantrum to accept a hyposphene, making it unlikely that the next vertebra in the dorsal series had one. This sets it apart from *Andesaurus*, *Argentinosaurus*, and *Epachthosaurus*, and indicates a possible affinity with Lognkosauria or more derived clades rather than Andesauridae. Unfortunately the posterior dorsal of *Ruyangosaurus* is of limited use in phylogenetic analysis and diagnosis as there are very few posterior dorsal vertebrae from Lognkosauria proper to compare it to (the only true lognkosaur known from complete posterior dorsals, *Futalognkosaurus*, has never had photographs of the entire dorsal series published). Thus a phylogenetic analysis for *Ruyangosaurus* using posterior dorsals would not be robust across all clades of titanosauria.

Right femur (Figs. 8-9)

The femur is extremely unusual in its shape, particularly the short proximal condyle, the proximal positions of the fourth trochanter and the lateral protuberance, and the rugosity of the femoral head. These same features are markedly present in *Pitekunsaurus*, and to a lesser extent in *Malawisaurus*, indicating a possible lognkosaurian affinity. Also the relative narrowness and unexpanded form of the femoral head and the proportions and straightness of the proximal shaft make for an unusually slender femur relative to other titanosaurs. These characters are present to a similar degree in only a few titanosaurs, nearly all of which are either lognkosaurs or resemble lognkosaurs in both the axial and appendicular skeleton.

The absence of the distal portion of the femur makes its dimensions and full proportions difficult to calculate. Ironically the same problem is true of both *Malawisaurus* and *Pitekunsaurus*, making a comparison between the three femora possible, but limited at best. *Mendozasaurus* is known from a proximal femur, which Gonzalez-Riga (2003) described as having a lateral bulge on the lateral and proximal part of the shaft, as in *Brachiosaurus* (Riggs, 1903) and *Chubutisaurus* (Del Corro, 1975) – both of which have the lateral bulge in a very proximal position like *Ruyangosaurus*, but have the fourth trochanter far lower on the femur. The

mid-sized lognkosaur *Traukutitan eocaudata* has a proportionally wider femur than *Ruyangosaurus*, as well as having a more pronounced pelvic condyle, but it does share with *Ruyangosaurus* (as well as *Malawisaurus* and *Pitekunsaurus*) a weakly inclined proximal end relative to the shaft, lacking the substantial medial tilt found in derived lithostrotia. The fourth trochanter appears to be unusually high on the femur in *Traukutitan*, a further similarity to *Ruyangosaurus*. *Ruyangosaurus* and *Traukutitan* also have the fourth trochanter transversely compressed, so it does not form a large medial bulge as in *Aegyptosaurus baharijensis* (Stromer, 1932). The giant holotype of *Futalognkosaurus*, in many ways the defining member of the clade, was initially described in 2007 without limb elements, though two smaller specimens at the same site apparently included femurs. Recently a 1.56m humerus and a 1.98m femur were mentioned by Calvo (2014) as belonging to the same individual as the holotype, MUCPv-323.

Outside of Lognkosauria, the *Ruyangosaurus* femur bears no definite resemblances to holotype femora of any described titanosaur taxa. The femur of *Andesaurus* is too incomplete to use for reliable comparison. The expanded, smooth, and medially flared femoral heads found in derived lithostrotians like *Saltasaurus*, *Antarctosaurus*, *Neuquensaurus*, and *Elaltitan*, bear little resemblance to the compact, rough femoral head of *Ruyangosaurus*. In addition, the laterally wide and medio-proximally flared femora of *Argentinosaurus* and *Epachthosaurus* are unlike the more slender, proximally straight shaft in *Ruyangosaurus*. One non-lognkosaurian femur shaft which does seem to bear a resemblance in some superficial aspects, including a highly placed lateral bulge, is that of *Pellegrinisaurus* (Salgado, 1996). However its dorsal centra indicate a derived lithostrotian similar to *Opisthocoelicaudia* or *Alamosaurus*, and bear little resemblance to those of *Ruyangosaurus*. Powell (2003) records a small unnamed left femur from Argentina's Salta province, PVL 3670-4, whose unusual shape closely resembles the femur of *Ruyangosaurus*. This femur is extremely straight-shafted proximally and shows the same lack of medial expansion at its proximal end as the *Ruyangosaurus* femur. However the proximal end is eroded so a definitive comparison is difficult. The overall proportions of the Salta femur's proximal half are very similar to *Ruyangosaurus*, though the lateral bulge and the fourth trochanter are located more distally.

An additional titanosaurian femora bear a strong resemblance to *Ruyangosaurus* and the Lognkosauria. An undescribed Brazilian taxon known from a largely complete unpublished femur from Mangabeira, Minas Gerais state, discovered and illustrated by Llewellyn Ivor Price (Kellner and Campos, 2000, fig. 3) which is similar to both the *Ruyangosaurus* femur and the femora of previously known lognkosaurs. The unpublished femur is presently part of a large dinosaur collection housed at the Museu de Ciências da Terra (MCT) of the Departamento Nacional da Produção Mineral (DNPM, Rio de Janeiro). It is long and proximally straight compared to most titanosaur femora, roughly similar in proximal proportions to those of *Ruyangosaurus* and *Pitekunsaurus*. However the femoral head is smoother and more curved than

in either of those taxa. The medial surface of this femur's upper portion shows a gentle medial curve proximally, as in *Malawisaurus*, and what remains of the fourth trochanter indicates it was located proximally, less than halfway down the femur's length – a trait found in *Ruyangosaurus*, *Malawisaurus*, and *Pitekunsaurus*, and *Traukutitan*, but extremely rare in non-lognkosaurian titanosaurs, both basal and derived. Measurements for this femur are unknown as it was never described; Price passed away before he could finish his extensive monograph on this and other Brazilian specimens.

One useful ratio in comparing the *Ruyangosaurus* femur to other titanosaur femora is the percentage of the width of the femur's proximal end located *medially to the mid-shaft meridian*, here referred to as proximal MMM. A midline proximodistal meridian is drawn parallel to the femur at mid-shaft, extending up towards the femur's proximal end. The portion of the proximal ends transverse width located medial to this meridian (a raw figure), divided by the proximal ends total transverse width, and then multiplied by 100, is the proximal MMM. This is a good indicator of the femur's medial inclination at its proximal end regardless of how expanded the femoral head is. For many titanosaurs the proximal MMM ratio is extremely high as the femoral head is inclined medially even relative to the shaft of the femur, not just relative to the tibia. In *Petrobrasaurus puestohernandezii* (Filippi, *et. al.*, 2011) the MMM is nearly 100% (see Fig. 9 and table 2).

The proximal MMM percentages of titanosauriforms sort out into several ranges. Brachiosaurid and basal somphospondylid MMM values fall in the 70s and 80s. With *Chubutisaurus*, the percentage is in the 80s. In *Euhelopus* the ratio is just 80%, and it falls back into the 70s in other euhelopodids. In *Phuwiangosaurus*, it rises into the 80s range again, and appears to stay that way in basal titanosaurs, leading up to *Epachthosaurus* and the basal stem-lognkosaurs *Malawisaurus* and *Aegyptosaurus*. Lognkosaurs and putative lognkosaurs have MMM values in the 70s, perhaps reverting to the basal condition, with straighter femora than sister taxon *Malawisaurus*. *Petrobrasaurus*, which has relatively slim femora compared to saltasaurids, nevertheless has a more extreme medial tilt to the proximal end, with MMM percentages in the high 90s. In saltasaurids the MMM is typically in the 80s, though in opisthocoelicaudiines the value is back into the 70s. In *Rapetosaurus* the ratio is also in the 70s (see table 2).

Proximal MMM is an indicator of how much the proximal end of the femur is tilted inward relative to the midshaft, so this indicates a possible difference in hip design. Indeed, there is evidence of this in the fact that *Elaltitan*, which has a high MMM value, also has a pubis which is flared out laterally to a great extreme at its proximal end near the hip socket; whereas *Futalognkosaurus* has a straighter pubis which exhibits far less lateral flaring at its proximal end, as does the ischium. Most saltasaurids were wider in the ventral portion of the pelvis than lognkosaurs and may have “bottom-wide” hip sockets, and hence needed more bowed-out

femora with a higher MMM to clear the proximal pubis than lognkosaurs did. The reasons for this proximal widening of the pubis could range from larger sexual organs to a greater portion of the intestines being contained in the pelvic girdle. The extremely wide anterior ilia of *Futalognkosaurus*, more flared out than even in saltosaurids, indicate an extremely wide gut, perhaps meaning that the intestines were contained mostly in the belly and did not take up much pelvic space. The end result for lognkosaurs appears to be a pelvis that is anteriorly very wide, but rather narrower at the hip sockets, with a narrow ventral portion and thus straighter femora and more vertical hindlimbs.

Titanosaurs had two ways of widening the gait of their hindlimbs to accommodate wider proximal pubes over millions of years – increasing the medial tilt of the femur’s proximal end (and thus the MMM); and lengthening the fibular condyle to make the knee joint splay out laterally at a more bent articular angle. This latter approach is strongly manifested in *Opisthoceolicaudia* and *Saltasaurus*. Saltosaurids combine both a lengthened fibular condyle and high MMM, whereas nemegtosaurids exhibit a lengthened condyle but have relatively low MMM levels - but this is due to the proximal end of the femur being widened at its lateral margin, not to any reversal in the strong medial tilt of the femoral head. The femoral head in nemegtosaurids is still very medially inclined, and the pubes are still expanded proximolaterally as in saltosaurids. The lateral expansion of the femur’s proximal end in nemegtosaurids, which increases transverse width and deceptively skews the MMM percentage downwards, is indicative of a change in lateral femur structure totally unrelated to the medial tilt of the femoral head - most noticeably a larger greater trochanter. This is taken to its greatest extreme in *Alamosaurus*, and may indicate increased thigh strength for defensive kicks against predators. *Ruyangosaurus* has a low MMM value, in the lognkosaur range. Though its fibular condyle is not preserved, it was probably not elongated as in saltosaurids and nemegtosaurids, as the rest of the holotype indicates an animal far more basal than these two groups. Its greater trochanter is small, but the large lateral protuberance is another possible source of lateral leg strength. Unusually, high MMM values and bowed-out femora are found in taxa both more derived and more basal than lognkosauria, indicating that proximolaterally expanded pubes and medially bowed femoral heads were a basal trait of titanosauria, which lognkosaurs alone may have lost.

Right tibia (Fig. 10)

The right tibia of *Ruyangosaurus* is very unusually shaped, particularly in the posterior aspect. The extremely concave medio-posterior surface of the bone, relative to its proximal and distal ends, is not found in any other titanosauria. The calf muscles would have been quite large due to the medio-posterior concavity and the projection of the posterior proximal crest – the closest similarity to this extreme morphology is found in *Titanosaurus* (= *Neuquensaurus*?) *robustus* referred left tibia MLP CS 2064 (Von Huene, 1929; plate 19:4a), although its more compact proportions and the shape of the associated femur MLP CS 1480 indicate this obscure specimen

is most likely a saltosaurid rather than a lognkosaur. The proximal end of the tibia is far wider than in *Mendozasaurus*, with a far larger lateral process. There is a distinct notch between the two distal processes, as in the referred *Argyrosaurus* tibia. The tibia is short and compact relative to the femur and proximally expanded as in *Dreadnoughtus*, but less expanded distally.

Cervical rib

The heavy cervical rib is reminiscent of *Puertasaurus*, which has very expanded capita on its cervical ribs. However, *Puertasaurus* differs in lacking the massive tuberosity found in the *Ruyangosaurus* rib and having the capitum inclined distally forward rather than backward. The *Ruyangosaurus* cervical rib bears little resemblance to the slender, smooth cervical ribs of *Malawisaurus*. The ventrally deflected tuberosity is very unusual among titanosauria and may be pathological, although this seems unlikely as it is not significantly different in texture and thickness from that of the rest of the preserved portion of the rib. The only other titanosaur known to possess ventrally deflected cervical rib tuberosities is *Pitekunsaurus*.

Dorsal rib

Among titanosaurs, few can challenge the dorsal ribs of *Ruyangosaurus* for size. The preserved dorsal rib's shaft is 18 cm wide. The next biggest species known from described rib material, *Huanghetitan ruyangensis*, has an anterior dorsal rib with a maximum width of 17.2 cm (Lü, *et al.* 2007). Unlike the ribs of the *H. ruyangensis* holotype, the *Ruyangosaurus* rib is lacking the distal portion. However as the proximal portion of the shaft is the widest, it is possible to compare the ribs of the two animals at their widest point. The rib head also appears more laminate than that of *H. ruyangensis*. Until more *Ruyangosaurus* specimens are found, little more can be known about the dorsal ribs of this giant.

REVISED SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

SAURISCHIA Seeley, 1888

SAUROPODA Marsh, 1878

NEOSAUROPODA Bonaparte, 1986

MACRONARIA Wilson and Sereno, 1998

TITANOSAURIFORMES Salgado, Coria and Calvo, 1997

TITANOSAURIA Bonaparte and Coria, 1993

LOGNKOSAURIA Calvo, Porfiri, González Riga and Kellner, 2007

Diagnosis: 13-14 or more cervical vertebrae; posterior cervical neural spines massive, unbifurcated, pyramidal, and vertically to posteriorly directed; cervical ribs massive and widely arched; squat posterior cervical and anterior dorsal centra; anterior dorsal vertebrae extremely

wide, with expanded diapophyses; prezygapophyses short, wide, and connected together via a strong intraprezygapophyseal junction; absence of true hypantrum-hyposphene connections; neural canal small and occasionally triangular; anterior dorsal diapophyses extremely wide deep with strong CDLs; anterior dorsal centra short; anterior dorsal parapophyses low, large, and closely attached to centrum; anterior dorsal neural spines triangular and antero-posteriorly flattened; SPDLs large and prominent; PRSLs narrow; intrapostzygapophyseal junctions sunken relative to postzygapophyses and bordered by small fossae; prominent CPOLs bordered laterally by large fossae; cotyles marked by a central depression; proximal femoral ends rugose; fourth trochanter situated more proximally on femur than in other titanosaurs; tibia short and compact relative to femur; anterior caudals procoelous; and anteriormost caudal vertebrae with neural spines transversely expanded.

Ruyangosaurus giganteus Lü, Xu, Jia, Zhang, Zhang, Yang, You and Ji, 2009

Revised diagnosis (autapomorphies marked by an asterisk): Cervical ribs massive and anteriorly laminate with ventrally deflected club-shaped tuberosities; anterior dorsal vertebrae squat, wide, and anteroposteriorly flattened; anterior dorsal centra short, wide, and ventrally level; posterior dorsal centra narrower, slightly longer, and ventrally very concave; neural arches massive and wide; neural spines short, triangular, and generally vertically directed; diapophyses of anterior dorsal vertebrae highly laminate, much deeper and wider than those of posterior dorsals; PCDL very stout; neural canal small and dorsally pinched; posterior surfaces of neural arches largely flat; anterior dorsal parapophyses large, low, and adjacent to centrum; dorsal ribs wide, massive, and proximally laminate; femoral head and condyle less expanded than in most titanosaurs; femur long, slender, and proximally rugose with fourth trochanter and lateral protuberance more proximally placed than in other titanosaurs; small, rugose pits on posterior face of femur adjacent to fourth trochanter*; tibia very short and medially concave; distal breadth of tibia compared to midshaft width exactly 15%*.

PHYLOGENETIC ANALYSIS (figs. 11-12)

Ruyangosaurus giganteus is characterized by several distinct plesiomorphies rare among titanosaurs which point to a lognkosaurian affinity, but it also shares enough basal traits to be well within titanosauria.

For this analysis, we used the data matrix as present in González-Riga, *et al.* (2016), with additional characters new to this analysis and characters from Wilson (2002) considered synapomorphies of Somphospondyli. As for new taxa, we added all lognkosaurs and putative lognkosaurs (*Austroposeidon* [Baneirido, *et al.* 2016], *Drusilasaura*, *Pitekunsaurus*, *Puertasaurus*, *Ruyangosaurus*, and *Traukutitan*) to test their phylogenetic affinities as well. The *Apatosaurus* spp. OTU was removed, so as to not create a chimeric taxon (as the original OTU

uses scores from *Apatosaurus ajax* as well as *Brontosaurus excelsus* and *B. louisae* [Tschopp, Giovanardi, and Maidment, 2016]). For re-codings, *Alamosaurus sanjuanensis* C16 was recoded as unknown (as there is no skull material for *Alamosaurus* besides teeth). In OTU *Diplodocus spp.*, C179 was recoded to 0, while in *Giraffatitan brancai* it was recoded to 1. The *Brachiosaurus spp.* OTU was re-coded for the sacrum, ilium, and coracoid. *Argentinosaurus* was re-coded for the sacrum, ilium, femur, and fibula. *Tapuiasaurus*' skull was recoded based on Wilson, *et. al.* (2016). *Chubutisaurus*, *Euhelopus* and *Diamantinasaurus* were recoded for C273 (all recoded to 1), *Diamantinasaurus* skull, cervical, sacral, and pelvic characters were rescored based on Poropat, *et. al.* (2014, 2016). C136 was modified to include a new state (coded as 4) for taxa with 11 dorsal vertebrae (*Opisthocoelicaudia* was scored as such), and C130 includes a new state for taxa with steeply sloped posterior faces and less steeply sloped anterior margins of the posterior cervical neural spines (as in *Diamantinasaurus*). C138 includes a new state for taxa with ventrally directed diapophyses (as in *Austroposeidon* and *Bonitasaura*). C212 includes a new state (coded as 4) for taxa with opisthoplatyan middle caudals (*Traukutitan*). A spreadsheet with all the codings and characters is available in the supplementary information (S1).

The present analysis (including characters novel to this study) features 400 characters, and 38 taxa. The outgroup taxon is *Plateosaurus*. The analysis was run in PAUP* v. 4.0a152 (Swofford, 1998). The matrix was analyzed the same way as González-Riga, *et. al.*, including treating 24 of the multistate characters as ordered (12, 58, 95, 96, 102, 106, 108, 115, 116, 119, 120, 156, 166, 215, 218, 234-237, 260, 271, 302, 303, and 305 for González-Riga, *et. al.*).

In the 50% majority rule tree (fig. 11), the most basal taxa are *Plateosaurus*, *Shunosaurus*, *Omeisaurus*, *Diplodocus*, *Camarasaurus*, and *Europasaurus*. Within titanosauriformes, Brachiosauridae was recovered in 100% of trees, with two separate branches of *Brachiosaurus*+*Giraffatitan* and *Cedarosaurus*+*Venenosaurus*. Up the somphospondyli, *Euhelopus* was recovered as the most basal taxon, with a grouping of *Chubutisaurus*+*Ligabuesaurus* following. *Phuwiangosaurus* lies in between the previous node and Titanosauria. Within Titanosauria, *Andesaurus* is the most basal, followed by *Wintonotitan* and *Argentinosaurus*. *Epachthosaurus* lies next, and the remainder of the taxa are recovered as lithostrotians. A branch is recovered of the groupings, Lognkosauria on one side and advanced lithostrotians on the other side. In the derived lithostrotians branch, there are two separate subclades. In the first, *Trigonosaurus* is recovered as basal to a clade of *Rapetosaurus*+(*Tapuiasaurus*+*Isisaurus*) (effectively a Nemegtosauridae plus *Trigonosaurus*). On the other branch, Saltosaurinae and Opisthocoelicaudiinae are recovered as monophyletic clades. In Opisthocoelicaudiinae, *Alamosaurus* is recovered basal to a *Diamantinasaurus*+*Opisthocoelicaudia* grouping. In Saltosaurinae, *Neuquensaurus* and *Saltasaurus* are recovered as sister taxa.

Malawisaurus is the most basal lognkosaur, followed by a branch of all taxa that have been considered lognkosaurs or similar. *Drusilasaura* is recovered as the most basal of these,

followed in ascending order by *Traukutitan*+*Dreadnoughtus*, and *Notocolossus*+*Pitekunsaurus*. A well supported node comprises the remaining lognkosaurs. *Mendozasaurus* and *Futalognkosaurus* is recovered in most trees, and this is sister taxon to a grouping of *Austroposeidon*+(*Puertasaurus*+*Ruyangosaurus*), recovered in ~69% of trees.

In the strict consensus tree (fig. 12), all taxa up to *Europasaurus* lie in the same position. From there, *Euhelopus* and *Phuwiangosaurus* are in a dichotomy together, followed by the grouping of *Ligabuesaurus*+*Chubutisaurus*. For Brachiosauridae, *Cedarosaurus* and *Venenosaurus* are sister taxa, next to a *Brachiosaurus*-*Giraffatitan* dichotomy. Above this is a polytomy of *Andesaurus*, *Wintonotitan*, *Argentinosaurus*, and *Epachthosaurus*, and this is sister taxa to the remaining titanosaurs. Here, there are several diverging branches. *Trigonosaurus* lies basal to *Neuquensaurus*+*Saltasaurus*, *Rapetosaurus* is basal to *Tapuiasaurus*+*Isisaurus*, *Alamosaurus* is outside the *Diamantinasaurus*+*Opisthocoelicaudia* grouping, and the final branch holds all the remaining taxa. In this branch, *Malawisaurus* is basal to a polytomy comprising all remaining lognkosaurian taxa, and this includes *Drusilasaura*, *Traukutitan*, *Dreadnoughtus*, *Pitekunsaurus*, *Notocolossus*, *Mendozasaurus*, *Futalognkosaurus*, *Austroposeidon*, *Puertasaurus*, and finally *Ruyangosaurus*.

DISCUSSION

Ruyangosaurus giganteus is the largest dinosaur found in Cretaceous China, and among the largest in the entire eastern hemisphere. Along with *Daxiatitan binglingi* and both species of *Huanghetitan*, it indicates several diverse radiations of titanosauriforms in China over millions of years. *Ruyangosaurus* is unfortunately also among the most poorly preserved of China's giant sauropods, known only from six bones, nearly all of them incomplete. Yet the surviving elements preserve many important clues that aid in its identification. Most of these point toward a lognkosaurian affinity, particularly with *Puertasaurus* and the possible lognkosaur *Pitekunsaurus*. The overall squat and extremely wide proportions of the anterior dorsal centrum, neural arch, and deep diapophyses present a stark similarity with *Puertasaurus*, and other unusual features such as the small fossae surrounding the intrapostzygapophyseal junction resemble *Mendozasaurus* and *Pitekunsaurus*. Another feature of note is the presence of a central, well-defined and roughly concentric depression in the cotyles of the dorsal vertebrae, a feature found in both *Puertasaurus* and *Mendozasaurus* (and to a lesser extent in *Pitekunsaurus*) but very rare outside of Lognkosauria. The absence of true hypantrum-hyposphene connections, contrary to the preliminary analysis in Lü, *et. al.* 2009, also makes a lognkosaurian affinity more likely than previously thought.

The original diagnosis revisited

Lü, *et. al.* 2009 posited that *Ruyangosaurus* may be assigned to Andesauridae based on the following three characteristics: its large size, the presence of a supposed hypantrum-hyposphene

complex, and the network of two or three deep depressions on the lateral sides of the neural arch. However Lü, *et. al.* also conceded: “Ruyangosaurus is not the typical andesaurids [sic] in the lower neural spine, weakly developed hyposphene-hypantra and large deep fossa present on the lateral surface of the neural arch. Thus is it only tentatively assigned to Andesauridae and further finds may suggest an alternative systematic relationship.” (Lü, *et. al.* 2009; p.9) So far, an alternative systematic relationship may not only be indicated by the type material, but necessitated by the taxonomy and phylogeny of titanosauria as well.

The size justification used by Lü, *et. al.* for assigning a new taxon to Andesauridae is not valid, unless *Argentinosaurus* is classed as an andesaurid, as it was (along with the far smaller *Epachthosaurus*) by Bonaparte and Coria (1993) - a grouping that was found to be paraphyletic and invalid (Salgado, *et. al.* 1997; Wilson and Upchurch, 2003 and 2006). *Andesaurus* itself is a medium-sized sauropod at best, with dorsal centrum diameters of around 20 cm, as opposed to the gigantic 50 cm range for *Argentinosaurus*.

Additionally, the claim of a hypantrum-hyposphene complex in Lü, *et. al.* 2009 appears to be based solely on a single-sentence misdiagnosis of inner of the two pairs of thin “spider laminae” on the posterior dorsal as the lower portion of a “weakly developed hyposphene between the neural canal and the postzygapophyses.” (Lü, *et. al.*, 2009; p. 2) However in lateral view it is apparent these laminae are far too low to form any such structure. The posterior dorsal also exhibits no hypantrum for a hyposphene from the previous vertebra to fit into, nor do the authors assert that a hypantrum is present. In fact, their findings on the same page state the opposite: “A distinct ridge is present above the neural canal, connecting to the base of the prezygapophyses” (Lü, *et. al.*, 2009; p.2). Instead of a hypantrum above the anterior neural canal, there is a solid ridge of bone. The authors’ paradox is that a creature should have hyposphenes but no hypantra to accept them. The function of hypantra and hyposphenes is to stiffen the spine; thus they are always found together in several consecutive vertebrae in the same animal, not one without the other or only in one isolated vertebra. The lack of a hypantrum therefore makes a hypantrum-hyposphene connection with the previous vertebra impossible, such a connection with the next vertebra extremely unlikely, and the presence of hyposphenes altogether unnecessary and physically impossible to accommodate. The “spider laminae”, even had they been more elevated, could not form the lower part of a hyposphene at all – there would have been no space for one. Instead, the intrapostzygapophyseal junction would fit shelf-like above the solid TPRL of the next vertebra, as in many titanosaurs which lack a hypantrum-hyposphene complex (Fig. 13).

The presence of two or three deep depressions in the lateral face of the posterior dorsal’s neural arch has not been attributed exclusively to Andesauridae as a defining character, nor is it a defining character in the description of the clade’s previous taxonomic incarnation,

“Andesaurinae” (Calvo and Bonaparte, 1991). Therefore this is not a strong basis for referring *Ruyangosaurus* to “Andesauridae”. In addition, *Andesaurus* lacks a complex of deep depressions on the anterior lateral face of the lower neural arch, where *Ruyangosaurus* has its rugose system of depressions.

Aside from the ambiguity of the above-mentioned characters, an andesaurid classification currently also poses significant phylogenetic problems since Andesauridae may not actually be a valid family. The family Andesauridae was originally erected by Bonaparte and Coria (1993) as the more basal of two proposed families within titanosauria – the other being Titanosauridae. However, Andesauridae was defined based on characteristics such as a hypantrum-hyposphene complex and non-procoelous caudals, which are primitive features not unique to Andesauridae – indeed they are also found in many dinosaur taxa outside of titanosauria and even sauropoda altogether. Furthermore, Salgado and Martinez (1993), Salgado and Bonaparte (2007), Novas and Ezcurra (2006), and Salgado and Powell (2010) call into question whether *Argentinosaurus*, initially considered an andesaurid on the basis of hypantrum-hyposphene connections, actually had them at all. Thus Andesauridae was judged as paraphyletic by Salgado *et. al.* (1997) and was abandoned by Wilson and Upchurch (2003): “Andesauridae is based on primitive characters that by definition specify a paraphyletic group. Until taxa are found sharing synapomorphies with *Andesaurus*, ‘Andesauridae’ will remain an informal name.” Titanosauridae has likewise been found to be an invalid grouping (Wilson and Upchurch, 2003), making Bonaparte and Coria’s original 1993 familial dichotomy an unnatural system.

Paleoecology and time horizon

Lü, *et. al.* 2009 labeled the time horizon of the *Ruyangosaurus* strata as “early Late Cretaceous”. Its stratigraphic position in the “Mangchuan” formation (Lü, *et. al.* 2006) makes it difficult to date precisely for the time being; however by definition it can be no older than Cenomanian in age. The same applies to *Huanghetitan ruyangensis*, which is also from the Ruyang basin region of the “Mangchuan” formation, though whether it is from the same strata as *Ruyangosaurus* has not yet been demonstrated. Other dinosaurs from the Ruyang basin include the oviraptorid *Luoyanggia liudianensis* and the basal titanosauriform sauropod *Xianshanosaurus shijiagouensis*, both of which were originally dated to the Cenomanian (Lu, Ming, *et. al.* 2009). These two species were unearthed near the town of Liudian in Ruyang County, Henan province – as were *Ruyangosaurus* and *Huanghetitan ruyangensis* (Fig. 14). Finally, the newly discovered *Yunmenglong* (Lü, *et. al.* 2013) adds another giant titanosauriform. The stratigraphy of the “Mangchuan” formation was heavily revised (Xu, *et. al.* 2012), and found that the “Mangchuan” is actually divisible into three units (listed in ascending order): the Xiahedong, Haoling, and Shangdonggou formations. All of the species listed above come from the Haoling formation, which is dated to the Aptian-Albian epochs in age. Thus it appears the Aptian-Albian-aged fauna in the Liudian locale was dominated by very large macronarian sauropods. The nodosaurid

Zhongyuansaurus luoyangensis (Xu, *et. al.* 2007) is also present in this fauna. Lu, Ming, *et. al.* 2009 also discuss the presence of various theropods in the Ruyang basin, including ornithomimids, oviraptorids, dromaeosaurids, spinosaurids, and carcharodontosaurids. The last two groups are mainly known from the Albian and Cenomanian in Africa and South America, making it likely that they spread into Asia as a consequence of Africa's break from South America and subsequent eastward continental drift in the mid-Cretaceous, also a plausible scenario for *Ruyangosaurus* considering its lognkosaurian (and thus Gondwanan) affinities.

Despite being only recently explored, the Ruyang basin fauna has already proven to have been extremely diverse and comparable to Albian and Cenomanian assemblages in both Patagonia and northern Africa in the types of dinosaurs which filled its major niches. Further discoveries in upcoming years will likely reveal an extremely detailed picture of China's largest Cretaceous megafauna.

Body proportions and anatomy

Ruyangosaurus exhibits a number of unusual plesiomorphies not found in many titanosaurs which provide critical clues to understanding its anatomy and possible appearance, despite the scarcity of fossil material; particularly the proportionally short centra in both known vertebrae, the extremely wide neural arch of the anterior dorsal, the long femur and short tibia, and the heavily laminate cervical and dorsal ribs.

The lack of hypantrum-hyposphene connections further makes it possible that *Ruyangosaurus* was a longkosaur. They are absent in the defining members of Lognkosauria, *Futalognkosaurus* and *Mendozasaurus*, as well as the late-stage lognkosaur *Puertasaurus*, the basal sister taxon *Malawisaurus*, the recently described lognkosaurs *Dreadnoughtus* and *Notocolossus*, and the possible lognkosaur taxon *Pitekunsaurus*. However Calvo, *et. al.*, (2008) did not include lack of hypantrum-hyposphene as one of the defining synapomorphies of Lognkosauria. There is a possibility that basal lognkosaurs retained small vestiges of hyposphenes. *Mendozasaurus* and *Pitekunsaurus* dorsals only have traces of a hyposphene-like structure, in the form of two converging laminae beneath the intrapostzygapophyseal junction which join with it, giving it an X-shaped appearance. These X-junctions do not protrude far beyond the posterior face of the neural arch, unlike a true hyposphene (such as that of *Andesaurus*), and owe their unusual shape to the presence of small fossae surrounding the laminae which form the "X". They do not form an articulation with the prezygapophyses of the next vertebra in *Pitekunsaurus* or (presumably) *Mendozasaurus*, as the prezygapophyses in these two genera are too widely spaced apart to permit it, and are joined together by a solid lamina entirely devoid of a hypantrum. The X-configurations may have evolved independently of hyposphenes, since the closest relative of the longkosauria, *Malawisaurus*, lacks them. The "spider laminae" on the posterior dorsal of *Ruyangosaurus* are too weak and shallow relative to the intrapostzygapophyseal junction even to

form the lower part of something like these X-shaped structures, which are nearly symmetrical in depth, width, and protrusion both above and below the junction. *Ruyangosaurus*' odd quartet of ventro-laterally sloping laminae is unknown in any other titanosaur, and the outer pair has no analogue on any species with hyposphenes.

Rib cage dimensions and form are nearly impossible to approximate for *Ruyangosaurus*. However, the torso was probably shorter and more compact than in *Argentinosaurus* based on centrum length, though its width may have been equal or greater. Complete ribs are known from neither animal, so the best indication of rib cage width available is the size of the diapophyses. They are extremely deep and laminate in *Ruyangosaurus*, as in *Puertasaurus*, indicating a similarly expanded configuration which likely supported a wide, tank-like rib cage as in more derived titanosaurs also known for long diapophyses and wide neural arches (i.e. *Saltasaurus*, *Alamosaurus*, *Opisthocoelicaudia*). By contrast the diapophyses of *Argentinosaurus* are not unusually large relative to the overall size of its dorsal vertebrae, and are not buttressed by large laminae as in *Puertasaurus*; their more primitive cruciform appearance is common throughout sauropods, particularly in deep, slab-sided basal macronarians.

Ruyangosaurus is characterized by a long, slender femur and a very short, proximally robust tibia, in addition to a wide dorsal column with expanded diapophyses possibly indicative of a wide rib cage. The dorsal centra are short for an animal with such a large femur, but very wide, indicating a rather compact and stout torso as in *Malawisaurus*. Nothing is known from the forelimbs, though two recently discovered probable lognkosaurs (*Dreadnoughtus* and *Notocolossus*) have forelimb material. It is possible that the forelimbs of *Ruyangosaurus* had more extreme proportions as in the hindlimbs, with a long humerus and much shorter radius and ulna, as in *Argyrosaurus* (Lydekker, 1893). Since sauropod forelimbs are less robust than their hindlimbs, even in species with the most pronounced forelimbs (Paul, 1988a), it is logical to infer that *Ruyangosaurus* also had forelimbs more gracile than its hindlimbs, which given the slenderness of the femur, would make all four limbs relatively slender for their length, at least in the proximal segments.

The lack of good cervical material makes neck proportions very difficult to estimate, but based on the anterior dorsal it seems to resemble *Puertasaurus*, which has a large squat mid-cervical vertebra, indicating a substantial neck with a dorsoventrally flattened cross-section. The same unusual neck design could also be present in *Ruyangosaurus*, since it has a very squat anterior dorsal centrum, which in *Puertasaurus* corresponds in condyle proportions to the cervical centrum. The somewhat ventrally deflected capitum of the preserved cervical rib of *Ruyangosaurus* indicates a kinked network of cervical ribs, potentially resulting in a bumpy appearance to the outer margins of the neck's ventral surface.

The overall appearance of *Ruyangosaurus*, though difficult to restore by any standards, seems to be highly unusual. The animal had a robust, short, and possibly very wide torso, limbs with an elongated femur shaft and short tibia, and a hefty neck with massive cervical ribs. This combination of features is comparable to *Puertasaurus* in the axial skeleton, and to *Malawisaurus* and *Pitekunsaurus* in the appendicular. The lengths of the neck and tail are unknown, but for a sauropod of such great size and with such a massive cervical rib, it is likely that both were very long. A full skeletal embodying these proportions is seen in fig. 15.

Implications for titanosaur evolution

The unusual plethora of features present in the mere six bones that make up what is currently described from *Ruyangosaurus*, carries vast implications for the history of titanosauria. The majority of identifiable skeletal features in the type material indicate a lognkosaurian identity, which would mean that lognkosaurians were present in Asia in the Late Cretaceous. The transcontinental spread of this mostly South American clade probably occurred in the Aptian or Albian, before the final severing of all land connection between South America and Africa. *Malawisaurus*, the sister group of Lognkosauria, is their closest African relative, and dates back to the Aptian epoch. *Futalognkosaurus* and *Mendozasaurus* appear to herald an age of lognkosaurian dominance in Patagonia in the Turonian and Coniacian epochs. In the time gap between the Aptian and Turonian, there is almost nothing known of lognkosaurs, and their migration and diversification patterns are not known. Around the middle of the Cretaceous period South America and Africa completely severed, and Africa moved toward Asia, narrowing the Tethys sea and forming a number of small archipelagos and shallow tidal zones in what is now the Middle East. At this time the Iranian plate was beginning its formation, and the Zagros mountains were gradually being pushed up from the seafloor by the collision with the larger plates. Migration of African lognkosaurs as well as more derived titanosaur groups across such shallow areas was likely, and their reaching the eastern Asian mainland is a plausible scenario. If *Ruyangosaurus* is a lognkosaur, it is the first to be found beyond Gondwana, and evidence that Asia was inhabited by multiple waves of migrating titanosauriforms throughout the Cretaceous. The presence of the euhelopodids *Euhelopus*, *Daxiatitan*, *Erketu* (Ksepka and Norell, 2006), *Qiaowanlong* (You and Li, 2009), *Gannansaurus* (Lü, *et. al.* 2013b) and *Yunmenglong* (Lü, *et. al.* 2013a), as well as *Huanghetitan* and “*Huanghetitan*” *ruyangensis*, the tall-arched basal forms such as *Phuwiangosaurus*, *Sonidosaurus* (Xu, *et. al.* 2006) and *Baotianmansaurus* (Zhang, *et. al.*, 2009), and finally saltasaurids and nemegtosaurids, already points to a high diversity of titanosaurs and titanosauriforms in a region that was largely isolated before the Cretaceous. The presence of a lognkosaur in China indicates that large titanosaurs, from basal to intermediate and derived, were widespread in Asia as well as the southern continents. The presence of the possible nemegtosaurid *Tapuiasaurus* (Zaher, *et. al.*, 2011) in Brazil in the Albian epoch, provides an example of how a lineage originated in the Early Cretaceous, and by the end of the Late

Cretaceous was common everywhere from Madagascar to Mongolia. *Ruyangosaurus* illustrates how a similar global migration pattern may have occurred in Lognkosauria (Fig. 16).

In the process of lognkosaurian evolution, the features characteristic of the clade became more pronounced and exaggerated. The wide anterior dorsal diapophyses of *Mendozasaurus* and *Pitekunsaurus* are nevertheless roughly rectangular in anterior or posterior view, and do not show a great degree of proximal deepening relative to distal depth. *Puertasaurus* was originally dated to the Maastrichtian (Novas, *et. al.* 2005), but later research suggests that the Pari Aike formation is actually Cenomanian in age, and is part of the Mata Amarilla formation (Varela, *et. al.* 2012). The base of the *Puertasaurus* diapophyses had become considerably deepened relative to their terminal surfaces and the diapophyses themselves became triangular or wedge-shaped due to the enlargement of the CDLs. *Ruyangosaurus* appears to show these proximally deep *Puertasaurus*-like diapophyses as well. *Ruyangosaurus*, being Aptian-Albian in age, existed slightly earlier than *Puertasaurus*. At the same time of *Ruyangosaurus*, in the Cerro Barcino formation is the new “Chubut Monster” titanosaur, which appears to have close affinities to other giant patagonian titanosaurs such as *Futalognkosaurus*, *Notocolossus*, and *Puertasaurus* (Carballido, *et. al.* 2016). The presence of two different lognkosaur vertebral morphologies coexisting at around the same time (and the presence of the later species *Notocolossus* and *Pitekunsaurus*) point to the possibility of two sub-clades within Lognkosauria – one with highly laminate and buttressed wedge-shaped diapophyses (Puertasaurinae), the other with more rectangular, less laminate ones (Futalognkosaurinae). Puertasaurinae appears to be able to trace its origins back to the Barremian epoch in the form of a cervical and some mid-caudals from the Wessex formation (Bivens, Sassani, and Reid, In prep), which looks nearly identical to the described cervical of *Puertasaurus* (despite being slightly further back in the series). Puertasaurinae seemingly lasted all the way up to the Campanian epoch (with *Pitekunsaurus*), and may have persisted into the Maastrichtian as well. Futalognkosaurinae lasted up until the very end, with a near complete cervical series from Big Bend National Park, Texas likely being referable to Lognkosauria (Bivens, Sassani, and Reid, In Prep).

The lack of true hypantra and hyposphenes in *Ruyangosaurus* and other lognkosaurs further begs the question as to whether lognkosaurs categorically lacked a hypantrum-hyposphene complex as a defining basal character of the clade, or if the clade lost it during its evolution. The complex is found outside “Andesauridae” in basal titanosauriforms like *Tastavinsaurus* as well as more derived ones closer to the base of titanosauria, like *Phuwiangosaurus*. It also exists in yet more primitive groups including diplodocids, camarasaurids, brachiosaurids, basal eusauropods, and even basal sauropodomorphs (Salgado, *et. al.* 1997, p. 20). They disappear in *Malawisaurus*, the lognkosaurs, and are also absent in derived lithostrotians, though they are present in *Epachthosaurus*, which appears to occupy an intermediate position between *Argentinosaurus*

and *Malawisaurus* (González Riga *et. al.*, 2016). Why hypantra and hyposphenes are absent or reduced to a non-functional X-shaped rudiment in lognkosaurs is not fully understood.

It is not clear what caused hypantrum-hyposphene connections to disappear from intermediate and derived titanosaur lineages, after sauropods had retained them for so many millions of years. It has been suggested that as titanosaurs developed armor, the back may have become reinforced by external scutes and its mobility thus restricted, to the extent that hypantrum-hyposphene connections were no longer necessary to stiffen it (Le Loeuff, *et. al.*, 1994). However this explanation suffers from a major flaw: titanosaur armor was made of non-interlocking plates separated by skin, which in some of the more derived species contained small hard nodules as well – but it was not a stiff, immovable structure. The plates were incapable of forming any sort of solid carapace. Armor is primarily for defense rather than external bracing, and the mostly conical osteoderms found with many titanosaurs do not appear suited to the latter purpose. Titanosaurs lacking hypantrum-hyposphene connections had proportionally wider vertebrae with more oblate centra and longer diapophyses than basal forms, and thus a far reduced range of lateral flexion for the dorsal column even without a hypantrum-hyposphene system. Furthermore the extreme backward-sloping neural spines of derived lithostrotians like *Saltasaurus* result in a high degree of passive interlocking with posteriorly tilted pre-postzygapophyseal connections and spinal overlap, the neural spine of one vertebra fitting between the diapophyses of the next, reducing dorsal column flexibility regardless of armor. Though lognkosaurs may not have had the extreme degree of spinal overlap present in more derived titanosaurs (the anterior dorsals of *Mendozasaurus*, *Ruyangosaurus*, and *Puertasaurus* all have relatively vertical neural spines), it is possible that the oblate centra and unusually wide, antero-posteriorly compressed vertebrae of lognkosaurs already formed a dorsal column that had enough stiffness in its design to lack a need for hypantrum-hyposphene connections, passive interlocking of neural spines, or external bracing. Nevertheless osteoderms have been found in association with *Malawisaurus* and *Mendozasaurus*. Whether larger forms like *Ruyangosaurus* also possessed them is unknown.

Sizes of *Ruyangosaurus* and the largest asian titanosauriformes

The enormous size of *Ruyangosaurus* remains places it in a rare class of titanosaurs which likely exceeded 30 meters in length. Along with “Huanghetitan” *ruyangensis* and *Daxiatitan binglingi*, *Ruyangosaurus giganteus* was a giant worthy of the name. Its dorsal vertebrae rival those of *Argentinosaurus*, *Notocolossus* and *Puertasaurus* for sheer size, and at an approximate length somewhere between 2 and 2.4 meters, its femur is comparable to those of “Antarctosaurus” *giganteus* and the largest referred “Argyrosaurus” specimens. As the type material for *Ruyangosaurus* and for these other giants is so scarce, estimating the dimensions of the complete animal is problematic. *Futalognkosaurus* is known from the entire precaudal series, but there are difficulties in using most of it to scale other lognkosaurs due to some measurement discrepancies in Calvo, *et. al.* (2008). *Malawisaurus*, the most complete relative of Lognkosauria, measures

roughly 11.5 meters long, and has a relatively short neck and long tail for a sauropod. Scaling up from such small relatives poses its own problems, but assuming similar body proportions, and accepting the consistency of the scale bars for *Ruyangosaurus* in Lü, *et. al.* 2009 in the absence of full measurement tables, the scaling based on more complete titanosaurs is as follows:

1. Scaling conservatively based on the length of the shortest centrum among the anterior dorsals of *Malawisaurus* (that of the third dorsal, MAL-236) yields the following result: the *Malawisaurus* centrum is 121 mm long, while that of the *Ruyangosaurus* anterior dorsal is 300 mm, or 2.4793 times as long. Scaling based on this ratio results in a length of 28.5 m (94 ft.) for *Ruyangosaurus*. However this is based on three assumptions: that the *Malawisaurus* dorsals are from an animal 11.5 m long, a figure which includes a few interpolated bones; that *Ruyangosaurus* had similar proportions to *Malawisaurus*, a far smaller and relatively short-necked titanosaur; and that anterior dorsal centra scale isometrically across clades, an unstable proposition for *Malawisaurus*, whose centrum lengths do not follow a simple pattern.

2. Scaling based on posterior centrum length is not as reliable since the posterior centra of *Malawisaurus* are proportionally far more elongated than the centrum of the posterior dorsal of *Ruyangosaurus*. However, the height of the centrum in the ninth *Malawisaurus* dorsal, MAL-182, seems to follow similar proportions to the posterior dorsal centrum of *Ruyangosaurus*, relative to approximate total vertebra height. The height of this *Malawisaurus* centrum is 111 mm, as opposed to 300 mm for the posterior *Ruyangosaurus* centrum at the condyle, and 370 mm at the cotyle. Scaling conservatively based on the condyle height, *Ruyangosaurus* is 2.7 times larger. Once again assuming a length of 11.5 meters for *Malawisaurus*, *Ruyangosaurus*' length is calculated at 31.08 meters (~102.6 ft.)

3. Limb elements do not scale isometrically as consistently as vertebrae in large animals even within the same clade (Paul, 1988a), but their widths may provide useful clues to their size. *Malawisaurus*' femur, like that of *Ruyangosaurus*, is incomplete, so in any case an accurate length comparison is out of the question. However the remnants of both femora are the proximal portions, so the medio-lateral width of the femoral heads can be compared. That of *Malawisaurus* is 280 mm wide. That of *Ruyangosaurus* is 600 mm wide (Lü, *et. al.*, 2009, p.9). Scaling based on *Malawisaurus* proximal femur width yields a length of only 24.6 meters for *Ruyangosaurus*. The radical differences in cross-scaling results indicate that *Ruyangosaurus*, even conservatively, had very different body proportions from *Malawisaurus*.

4. In Calvo *et. al.* 2008, the dorsals of *Futalognkosaurus* are mentioned as having a neural arch width of 100 cm, a measurement which corresponds well with the scale photograph of the anterior dorsals (all of roughly equal width, around 100cm wide at the diapophyses). The neural arch of the anterior *Ruyangosaurus* dorsal is estimated at 160 cm wide when complete, assuming

Puertasaurus-like proportions. Thus *Ruyangosaurus* seems to have anterior dorsals that are ~60% wider than those of *Futalognkosaurus*. Calvo, *et. al.* (2007) gave a length estimate of 32 to 34 meters for *Futalognkosaurus*, but according to Calvo, *et. al.*, (2008) its largest dorsal centra are 43 cm, unusually short to yield such *Argentinosaurus*-like lengths, and Paul (2010) estimates its length at only 30 meters. Scaling up this figure by 60% based on maximum neural arch width, *Ruyangosaurus* comes out at 48 meters (~160 ft.), a radical length for any titanosaur. To scale it more conservatively, assuming a length of 26 meters (85.3 ft.) for *Futalognkosaurus* (as suggested by Calvo, *et. al.* In press), one gets a *Ruyangosaurus* that still measures 41.6 m (~136.5 ft.) long! If this estimate is excessive (and assuming similar anterior dorsal proportions to *Puertasaurus*) both of these giants may have been far wider in their neural arches (and possibly their rib cages) relative to body length than *Futalognkosaurus*.

5. A comparison with a largely complete and more derived giant titanosaur produces an interesting result: *Alamosaurus sanjuanensis* has a short dorsal column of only 10 vertebrae, as in both *Malawisaurus* and *Futalognkosaurus*. Its neck and tail proportions are moderate for a large sauropod and its posterior dorsal centra have similar height-to-length proportions to *Ruyangosaurus*. The juvenile *Alamosaurus* specimen TMM 43621-1 (Lehman and Coulson, 2002) has a very squat mid-dorsal centrum 11.5 cm wide. The anterior dorsal centrum of *Ruyangosaurus* is 51 cm wide (a factor of 4.4), with similar squat proportions in anterior view. Assuming similar proportions, *Ruyangosaurus* seems therefore to scale to about 4.4 times the size of the juvenile *Alamosaurus*, which was roughly 8 m (~26 ft.) long. *Ruyangosaurus* scales up at 35.2 m (~116 ft.), a gigantic though credible length given a creature whose bones rival *Puertasaurus* and *Argentinosaurus*.

An average of all five methods yields a length of ~33.5 m (~110 ft.), comparable with length estimates for *Argentinosaurus* (Paul, 1994; Carpenter, 2006), though given the difficulty of cross-scaling from such incomplete remains, even this average is not a highly reliable indication of the animal's true size. Estimating the volume and mass of *Ruyangosaurus* is currently impractical regardless of the method used, given the scarcity of fossil material. However based on the gigantic size of the vertebrae it probably was in the same general mass range as *Argentinosaurus* and *Puertasaurus*.

Notocolossus (González-Riga, *et. al.* 2016) is another recently described giant lognkosaur close to the same total length as *Ruyangosaurus* (given the similar dorsal vertebra widths: 150 cm for *N. gonzalezparejasi* versus ~160 cm for *R. giganteus*). In *Notocolossus*, the humerus is 179 cm long. To make it 6.667% larger (the difference between *Notocolossus* and *Ruyangosaurus* anterior dorsals) makes the humerus 190.9 cm long. Compared to the femur of *Ruyangosaurus*, which is 235 cm, gives us a humerus:femur ratio of 0.81. This is slightly higher than the ratio for *Futalognkosaurus*, which is 0.78.

A giant femur (MPM-Pv-39) was mentioned in Lacovara, *et. al.* (2004) from the “Pari Aike” (now Mata Amarilla) formation. Based on the massive size (222cm long), provenance, and characters mentioned in Lacovara, *et. al.*, we tentatively refer this femur to *Cf. Puertasaurus reuili*. This potentially being the first case of material for *Puertasaurus* outside of the holotype.

Because of the incomplete nature of all the species here tentatively referred to “Puertasaurinae”, proportions are extremely difficult to estimate. However, there is just enough overlap between the various specimens to scale them all with reasonable accuracy (assuming they all have similar proportions). Cross-scaling of each element was determined by first comparing the size differences in overlapping material, finding the difference in percentage, and scaling the various elements up or down, we were able to assemble a full table of measurements for the overlapping material of several elements of puertasaurines. Table 4 gives this full list of measurements.

Scaling the speculative ulna size for *Ruyangosaurus* (based on cross-scaling with the anterior dorsal vertebra of *Pitekunsaurus*) gives a total length of 924mm. Dividing this by the speculative humerus length (cross-scaled with *Notocolossus*) gives us a ratio of 0.48. This is much lower than the ratio for *Futalognkosaurus*, which is 0.60.

So how does *Ruyangosaurus* compare with the other giant Asian titanosauriforms? Its rib material is wider than that of the already robust “Huanghaiitan” *ruyangensis*, and its posterior dorsal centrum is also larger than the sacral centra of “H.” *ruyangensis*, indicating a more robust if not overall larger animal. Unfortunately, there is little overlap of remains between the two specimens, so a good size comparison is not possible. However considering “H.” *ruyangensis* has among the deepest body cavities on record, with the longest rib measuring 2.93m. it must truly be immense. The anterior caudals’ centra maintain a consistent anterior diameter of 32cm for the first four (whereas for *Brachiosaurus* they are 33cm wide for the first caudal and shrink to 31cm for the second), and a gigantic referable anterior dorsal found at Wanggou Village (41HIII-0008) is 1.13m wide at the diapophyses and has a posterior centrum diameter of 43cm. This vertebra is short lengthwise and the posterior dorsals likely were as well, though given its similarity to euhelopodid anterior dorsals in terms of spine bifurcation and overall shape, this could indicate that the neck may have had a high vertebra count, making up for the short length of the vertebrae. The very long ribs and cavernous torso of this animal recall that of *Brachiosaurus altithorax*, and the more constant anterior caudal dimensions indicate a slightly more elongated tail, though with similar base diameter. The sacrum of “H.” *ruyangensis* measures roughly 125cm wide at the last pair of sacral ribs, versus 98cm for *Brachiosaurus altithorax*, around 27% larger (and having similar proportions). The *B. altithorax* holotype FMNH PR 25107 was from an individual roughly 24m in length, based on cross-scaling with

referred specimens, so scaling based sacrum length yields a length of 30.6m for “H.” *ruyangensis* assuming similar proportions.

The giant euhelopodid *Daxiatitan binglingi* is known from more complete material, including most of the cervical and dorsal vertebrae, and a femur 1.77m long, so a size comparison to *Ruyangosaurus* is simpler. Its femur and dorsals suggest a *Euhelopus*-shaped animal about 75-80% as large as *Ruyangosaurus*, not taking into account the possibly huge difference in rib cage volume and the extremely long neck of *Daxiatitan*. After calculating the tail length based on related species (such a *Huabeisaurus*), its total length was roughly 27m.

Yunmenglong ruyangensis (Lü *et al.*, 2013) another giant euhelopodid more robust than *Daxiatitan*, is known from a partial cervical series, a partial dorsal, caudals, rib, and a femur 1.92m long, which makes it perhaps the largest known euhelopodid, perhaps reaching 30m given the high cervical counts and extreme neck length common to all euhelopodids, but still falls short of *Ruyangosaurus* and other wide-bodied titanosaurs in dorsal size and likely volume. Based on centrum size alone, *Ruyangosaurus* appears to be larger than both *Daxiatitan* and *Yunmenglong* as well as “Huanghetitan” *ruyangensis*.

The only other titanosauriform from Asia that rivals these giants is the poorly known Early Cretaceous taxon *Fusuisaurus zhaoi*, an animal so basal in terms of its ilium and caudal morphology and lack of rib pneumatization, that it may actually form an unusually late-surviving offshoot of Brachiosauridae more basal than *Brachiosaurus* itself. Its ilium is roughly 1.45m long (though it has been anteroposteriorly crushed and likely measured closer to 165cm in life) and its pubis 1.1m, with one of the anterior caudals having a posterior centrum diameter of 40cm, comparable to 42cm for the first caudal of *Yunmenglong* and well exceeding the 31cm diameter for that of the *Brachiosaurus altithorax* holotype FMNH PR 25107. Since the similar-shaped ilium of the *B. altithorax* holotype is 1.24m long, and the entire individual was ~24m in length, a rough scaling from ilium length provides a length of 31m for *Fusuisaurus*. Thus “Huanghetitan” *ruyangensis*, *Yunmenglong* and *Fusuisaurus* were all extremely large sauropods in the range of 30m lengths, though they differed in morphology and none of them appear to have matched the dimensions of *Ruyangosaurus*, which likely measured 33m or more and had a wider and more massive torso than any of them.

All of these animals are considerably larger than the Late Cretaceous euhelopodid *Huabeisaurus allocotus* (Pang and Cheng, 2000), which has a femur only about 156cm long and a dorsal centrum just 28.6cm wide (D’Emic, *et al.* 2013). Claims that other Asian titanosauriforms such as *Phuwiosaurus* reached lengths of 30m or more are so far unsubstantiated. Interestingly, the all of the truly gigantic Asian forms other than *Ruyangosaurus* are basal titanosauriforms, with the true titanosaurs of Asia mostly being small *Saltasaurus*-like animals - whereas

Ruyangosaurus itself has the morphology of a lognkosaurian titanosaur. As with these far smaller titanosaurs, *Ruyangosaurus* likely evolved from gondwanan ancestors that reached east Asia through the rising archipelagos and land bridges which would later become the Zagros Range. Although the Mangchuan formation in Henan is still largely unexplored, it is likely that in the future more true titanosaurs may be found there. Currently the other titanosaurs known from China and Mongolia are all derived lithostrotians such as *Opisthocoelicaudia*, *Borealosaurus* (You, *et. al.*, 2004), *Qingxiusaurus* (Mo, *et. al.*, 2008), *Yongjinglong* (Li, *et. al.*, 2014), and *Dongbeititan* (Wang, *et. al.*, 2007), which shares the same heavily canted femur morphology with *Opisthocoelicaudia*, as well as with the Australian taxon *Diamantinasaurus* (Hocknull, *et. al.*, 2009). These are all small animals, not much longer than 10m, and all with very stocky and short limbs relative to both lognkosaurs and more basal titanosaurs and titanosauriforms. Whether these sorts of titanosaurs turn up in the Mangchuan formation, or whether lognkosaur taxa may be found elsewhere in China, is one of the still-unknown frontiers of titanosaur research.

CONCLUSION

Ruyangosaurus giganteus represents a new and unusual radiation of Lognkosauria in Asia in the early part of the Late cretaceous period, coinciding with a time of Africa's final separation from South America and gradual collision with Asia. Its unique morphology implies a close relationship to *Puertasaurus*, and it is possible it may form a subclade within Lognkosauria with *Notocolossus*, *Pitekunsaurus*, and *Puertasaurus*, with *Mendozasaurus*, *Dreadnoughtus* and *Futalognkosaurus* forming another sub-clade. However, *Ruyangosaurus* differs from all other lognkosaurs and the rest of titanosauria in having neural fossae separated from the neural canal by laminae, in having a strange quartet of nearly flat "spider laminae" on the posterior neural arch of the posterior dorsal, and in having the intraprezygapophyseal lamina located far higher on the neural arch in the anterior dorsal. As there is a paucity of *Ruyangosaurus* material, diagnosis of many features is not possible, though it shows a particularly strong affinity with *Puertasaurus* in anterior dorsal morphology and with Lognkosauria and Lithostrotia in general as it lacks defined hypantra and hyposphenes. Based on the dorsal material, the *Ruyangosaurus* holotype is a very large sauropod, exceeding *Futalognkosaurus* and *Dreadnoughtus* in size. Based on the dimensions of the anterior dorsal, it likely also exceeded *Notocolossus*, though was probably smaller than *Puertasaurus* and the recently discovered titanosaur species in the MPEF collections still awaiting description. This newly excavated taxon from Argentina's Chubut province is known from multiple specimens in an excellent state of preservation, which appear strongly lognkosaurian in morphology, among which the largest femur appears to be roughly 2.6m in length

(<https://svpow.com/2014/05/19/the-new-argentine-titanosaur-was-about-the-same-size-as-the-big-gest-argentinosauros/>), though no formal lengths have been published. With the *Ruyangosaurus* femur estimated at 2.35m when complete, this makes it the third largest lognkosaur yet

discovered, the largest Cretaceous dinosaur in Asia, and currently the fifth largest titanosaur after *Argentinosaurus*, *Puertasaurus*, the new gigantic *Alamosaurus* specimens (Rivera-Sylva, Guzman-Gutierrez, and Palomino-Sanchez, 2006; Fowler and Sullivan, 2011), and the undescribed Chubut titanosaur.

ACKNOWLEDGEMENTS:

Special thanks go to Mathew J. Wedel and Michael P. Taylor of SV-POW! and the Open Dinosaur Project, for their massive store of information on sauropods and expert advice on all practical aspects of vertebrate paleontology. Many thanks also to Lü Junchang of the Chinese Academy of Geological Sciences and Xu Li of the Henan Geological Museum for their time and dedication in preparing and presenting the *Ruyangosaurus* holotype, without whose hard work this paper would not have been possible. Many thanks also to You Hailou and Peter Dodson and all their colleagues, for introducing us to the wonderful cretaceous sauropods of Gansu and Henan, and for inspiring much of the research that went into this paper.

Works Cited:

Bandeira, K.L.N.; Medeiros Simbras, F.; Batista Machado, E.; de Almeida Campos, D.; Oliveira, G.R.; Kellner, A.W.A., 2016. A New Giant Titanosauria (Dinosauria: Sauropoda) from the Late Cretaceous Bauru Group, Brazil.. *PLoS ONE*. 11 (10): e0163373.
doi:10.1371/journal.pone.0163373.

Bonaparte, J.F. and Coria, R.A., 1993. Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniano) de la provincia del Neuquén, Argentina. *Ameghiniana*, 30:271-282.

Bonaparte, J. F., González Riga, B. J., and Apesteguía, S., 2006. *Ligabuesaurus leanzai* gen. et sp. nov. (Dinosauria, Sauropoda), a new titanosaur from the Lohan Cura Formation (Aptian, Lower Cretaceous) of Neuquén, Patagonia, Argentina. *Cretaceous Research* 27(3): 364-376.

Bonaparte, J.F. and Powell, J.E., 1980. A continental assemblage of tetrapods from the Upper Cretaceous beds of El Brete, north-western Argentina (Sauropoda–Coelurosauria–Carnosauria–Aves). *Mémoires de la Société Géologique de France, Nouvelle Série* 139: 19–28.

Borsuk-Bialynicka, M. 1977. A new camarasaurid sauropod *Opisthocoelicaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologica Polonica* 37: 1–64.

Calvo, J.O., Porfiri, J.D., González-Riga, B.J., and Kellner, A.W., 2007. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais Academia Brasileira Ciência*, 79(3): 529-41.

Calvo, J. O.; Porfiri, J. D.; González Riga, B. J.; Kellner, A. W. A., 2007. Anatomy of *Futalognkosaurus dukei* Calvo, Porfiri, González Riga, and Kellner, 2007 (Dinosauria, Titanosauridae) from the Neuquen Group, Late Cretaceous, Patagonia, Argentina (PDF). *Arquivos do Museu Nacional* 65 (4): 511–526.

Calvo, J. O. New fossil remains of *Futalognkosaurus dukei* (Sauropoda, Titanosauria) from the Late Cretaceous of Neuquén, Argentina in 4th International Palaeontological Congress, The History of Life: A View from the Southern Hemisphere abstract volume (ed Cerdeño, E.) 325 (International Palaeontological Association, 2014).

Campos, D., Kellner, A.W.A., Bertini, R.J., and Santucci, R.M., 2005. On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional, Rio de Janeiro*, v.63 n.3, 565-593

Canudo, J. I., Royo-Torres, R. and Cuenca-Bescós, G., 2008. A new sauropod: *Tastavinsaurus sanzi* gen. et sp. nov. from the Early Cretaceous (Aptian) of Spain. *Journal of Vertebrate Paleontol.* 28 (3): 712–731.

Carballido, J. L., Pol, D., Otero, A., Cerda, I., Salgado, L., Garrido, A., Ramezzani, J., Cúneo, N. R., Krause, M., 2016. A new giant titanosaur from the late early Cretaceous of Patagonia yields light into titanosaur body size evolution. *SVP 2016 Meeting Program and Abstracts*. 109-110.

Del Corro, G., 1975. Un Nuevo sauropodo del Cretácico Superior: *Chubutisaurus insignis* gen. et sp. nov. (Saurischia-Chubutisauridae nov.) del Cretácico Superior (Chubutiano), Chubut, Argentina. *Actas I Congreso Argentino de Paleontología y Bioestratigrafía*, 229-240.

D'Emic, M.D.; Mannion, P.D.; Upchurch, P.; Benson, R.B.J.; Pang, Q.; Cheng, Z., 2013. Osteology of *Huabeisaurus allocotus* (Sauropoda: Titanosauriformes) from the Upper Cretaceous of China. *PLoS ONE*. 8 (8): e69375. doi:10.1371/journal.pone.0069375.

Filippi, L.S. and Garrido, A.C., 2008. *Pitekunsaurus macayai* gen. et sp. nov., new titanosaur (Saurischia, Sauropoda) from Upper Cretaceous Neuquén Basin, Argentina. *Ameghiniana*, 45 (3): 575–590.

Filippi, L.S., Canudo, J.I., Salgado, J.L., Garrido, A., Garcia, R., Cerda, I., and Otero, A., 2011. A new sauropod titanosaur from the Plottier Formation (Upper Cretaceous) of Patagonia (Argentina). *Geologica Acta*, vol.9 n.1, 1-23

Fowler, D. W.; Sullivan, R. M., 2011. The First Giant Titanosaurian Sauropod from the Upper Cretaceous of North America. *Acta Palaeontologica Polonica*. 56 (4): 685.
doi:10.4202/app.2010.0105.

Gilmore, C.W., 1922. A new sauropod dinosaur from the Ojo Alamo Formation of New Mexico. *Smithsonian Miscellaneous Collections*. 72(14): 1-9.

Gomani, E.M., 2005. Sauropod Dinosaurs from the Early Cretaceous of Malawi, Africa. *Palaeontologia Electronica* 8 (1); 27A

González Riga, B.J., 2003. A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza, Argentina. *Ameghiniana*, 40: 155-172.

González Riga, Bernardo J.; Lamanna, Matthew C.; Ortiz David, Leonardo D.; Calvo, Jorge O.; Coria, Juan P., 2016. A gigantic new dinosaur from Argentina and the evolution of the sauropod hind foot. *Scientific Reports*. 6: 19165.

Hocknull, Scott A.; White, Matt A.; Tischler, Travis R.; Cook, Alex G.; Calleja, Naomi D.; Sloan, Trish; Elliott, David A., 2009. Sereno, Paul, ed. New Mid-Cretaceous (Latest Albian) Dinosaurs from Winton, Queensland, Australia. *PLoS ONE*. 4 (7): e6190.

Jacobs, L.L., Winkler, D.A., Downs, W.R. and Gomani, E.M., 1993. New material of an early Cretaceous titanosaurid sauropod dinosaur from Malawi. *Palaeontology*, 36: 523-534.

Jain, S.L., Bandyopadhyay, S., 1997. New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of Central India. *Journal of Vertebrate Paleontology*, 17 (1): 114-136.

Juarez Valieri, R.D. and Calvo, J.O., 2011. Revision of MUCPv 204, a Senonian Basal Titanosaur from Northern Patagonia. *Paleontología y dinosaurios desde América Latina*: 143–152.

Kellner, A.W.A. and Campos, D. A., 2000. Brief Review of Dinosaur Studies and Perspectives in Brazil *Anais da Academia Brasileira de Ciências*, 72 (4): 509-538.

- Ksepka, D.T. and Norell, M.A., 2006. *Erketu ellisoni*, a long-necked sauropod from Bor Guvé (Dornogov Aimag, Mongolia). *American Museum Novitates* 3508: 1-16.
- Lacovara, K.J.; Harris, J.; Lamanna, M.C.; Novas, F.E.; Martinez, R.; Ambrosio, A., 2004. An enormous sauropod from the Maastrichtian Pari Aike formation of southernmost Patagonia. *Society of Vertebrate Paleontology Abstracts of Papers*. 81A.
- Lacovara, K.J.; Ibiricu, L.M.; Lamanna, M.C.; Poole, J.C.; Schroeter, E.R.; Ullmann, P.V.; Voegelé, K.K.; Boles, Z.M.; Egerton, V.M.; Harris, J.D.; Martínez, R.D.; Novas, F.E., 2014. A Gigantic, Exceptionally Complete Titanosaurian Sauropod Dinosaur from Southern Patagonia, Argentina. *Scientific Reports*. 4: 6196.
- Lehman, T.M. and Coulson, A.B., 2002. A juvenile specimen of the sauropod dinosaur from the Upper Cretaceous of Big Bend National Park, Texas. *Journal of Paleontology*, 76: 156-172.
- Le Loeuff, J., Buffetaut, E., Cavin, L., Martin, M., Martin, V., and Tong, H., 1994. An armoured titanosaurid sauropod from the Late Cretaceous of southern France and the occurrence of osteoderms in the Titanosauridae; 153–159 in Lockley, M. G., Santos, V. F. d., Meyer, C. A., and Hunt, A. (eds.), *Aspects of Sauropod Paleobiology, Gaia 10*. Universidade de Lisboa, Lisbon.
- Li, L. G.; Li, D. Q.; You, H. L.; Dodson, P. (2014). Butler, Richard J, ed. A New Titanosaurian Sauropod from the Hekou Group (Lower Cretaceous) of the Lanzhou-Minhe Basin, Gansu Province, China. *PLoS ONE*. 9: e85979.
- Lü, J., Xu, L., Jiang, X., Jia, S., Li, M., Yuan, C., Zhang, X. and Ji, Q., 2009. A preliminary report on the new dinosaurian fauna from the Cretaceous of the Ruyang Basin, Henan Province of central China. *Journal of the Palaeontological Society of Korea*, 25: 43-56.
- Lü, J.; Xu, L.; Pu, H.; Zhang, X.; Zhang, Y.; Jia, S.; Chang, H.; Zhang, J.; Wei, X. (2013). A new sauropod dinosaur (Dinosauria, Sauropoda) from the late Early Cretaceous of the Ruyang Basin (central China). *Cretaceous Research*. 44: 202.
- Lü, J.; Yi, L.; Zhong, H.; Wei, X., 2013. A New Somphospondylan Sauropod (Dinosauria, Titanosauriformes) from the Late Cretaceous of Ganzhou, Jiangxi Province of Southern China. *Acta Geologica Sinica (English Edition)*. 87 (3): 678–685. doi:10.1111/1755-6724.12079.
- Lydekker, R., 1893. Contributions to the study of the fossil vertebrates of Argentina. I: The dinosaurs of Patagonia. *Anales del Museo de la Plata, Seccion de Paleontologia* 2: 1-14

Martin, V., Buffetaut, E., and Suteethorn, V., 1994. A new genus of sauropod dinosaur from the Sao Khua Formation (Late Jurassic or Early Cretaceous) of northeastern Thailand. *C. R. Acad. Sci. Paris*, 319, Series II 1085–1092.

Martin, V., Suteethorn, V. and Buffetaut, E., 1999. Description of the type and referred material of *Phuwiangosaurus sirindhornae* Martin, Buffetaut, and Suteethorn, 1994, a sauropod from the lower Cretaceous of Thailand. *Oryctos*, 2: 39-91.

Mo, J., Wang W., Huang Z., Huang X., Xu X., 2006. A Basal Titanosauriform from the Early Cretaceous of Guangxi, China. *Acta Geologica Sinica*, 80 (4): 486-489

Mo Jin-You; Huang Chuo-Lin; Zhao Zhong-Ru; Wang Wei; Xu X., 2008. A new titanosaur (Dinosauria: Sauropoda) from the Late Cretaceous of Guangxi, China. *Vertebrata Palasiatica*. 46 (2): 147–156.

Novas, F.E.; Salgado, L.; Calvo, J.O. and Agnolin, F., 2005. Giant titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia. *Revista del Museo de Ciencias Naturales*, 7(1):37-41.

Novas, F.E. and Ezcurra, M., 2006. Reinterpretation of the dorsal vertebrae of *Argentinosaurus huinculensis* (Sauropoda, Titanosauridae). *Ameghiniana* 43 (4, Supplement): 48R–49R.

Pang, Q. and Cheng, Z., 2000. A new family of sauropod dinosaur from the Upper Cretaceous of Tianzhen, Shanxi Province, China. *Acta Geologica Sinica* (English edition), 74 (2): 117–125.

Paul, G.S., 1988. The brachiosaur giants of the Morrison and Tendaguru with a description of a new subgenus, *Giraffatitan*, and a comparison of the world's largest dinosaurs. *Hunteria* 2: 1–14.

Paul, G.S., 2010. *The Princeton Field Guide to Dinosaurs*. Princeton University Press.

Poropat, S.F.; Upchurch, P.; Mannion, P.D.; Hocknull, S.A.; Kear, B.P.; Sloan, T.; Sinapius, G.H.K.; Elliott, D.A., 2014. Revision of the sauropod dinosaur *Diamantinasaurus matildae* Hocknull et al. 2009 from the mid-Cretaceous of Australia: Implications for Gondwanan titanosauriform dispersal. *Gondwana Research*. doi:10.1016/j.gr.2014.03.014.

- Powell, J.E., 1990. *Epachthosaurus sciuttoi* (gen. et sp. nov.) un dinosaurio sauropodo del Cretácico de Patagonia (provincia de Chubut, Argentina). *Actas del Congreso Argentino de Paleontología y Bioestratigrafía* 5: 125-128
- Powell, J.E., 2003. Revision of South American Titanosaurid dinosaurs; palaeobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum*, 111: 1-173.
- Riggs, E.S. 1904. Structure and relationships of opisthocoelian dinosaurs. Part II. The Brachiosauridae. *Geological Series (Field Columbian Museum)*. 2 (6): 229–247.
- Rivera-Sylva, H. E., Guzman-Gutierrez, J. R., and Palomino-Sanchez, F. R., 2006. Preliminary Report on a vertebrate fossil assemblage from the Late Cretaceous of Chihuahua, Mexico. *Hantkeniana*, 5: 66-68
- Rose, P. J., 2007. A new titanosauriform sauropod (Dinosauria: Saurischia) from the Early Cretaceous of central Texas and its phylogenetic relationships. *Paleontologica Electronica*. 10: 1-65.
- Salgado, L., 1996. *Pellegrinisaurus powelli* nov. gen. et sp. (Sauropoda, Titanosauridae) from the Upper Cretaceous of Lago Pellegrini, northwestern Patagonia, Argentina. *Ameghiniana*, 33(4): 355-365
- Salgado, L. and Bonaparte, J.F., 2007. Sauropodomorpha. In Gasparini, Z., Salgado, L. and Coria, R.A., (eds.) *Patagonian Mesozoic Reptiles*. Indiana University Press, 188-228.
- Salgado, L., Coria, R.A., and Calvo, J.O., 1997. Evolution of titanosaurid sauropods. I: Phylogenetic analysis based on the postcranial evidence. *Ameghiniana*, 34: 3-32.
- Salgado, L. and Martínez, R., 1993. Phylogenetic relationships of the basal titanosaurids *Andesaurus delgadoi* and *Epachthosaurus* sp. *Ameghiniana*, 30: 339.
- Salgado, L. and Powell, J., 2010. Reassessment of the vertebral laminae in some South American titanosaurian sauropods, *Journal of Vertebrate Paleontology*, 30:6, 1760-1772, DOI: 10.1080/02724634.2010.520783
- Sander, P.M., Mateus, O., Laven, T., Knötschke, N., 2006. Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature*, 441: 739-741.

Stromer, E., 1932a. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 11. Sauropoda. *Abhandlungen der Bayerischen Akademie der Wissenschaften Mathematisch-naturwissenschaftliche Abteilung, Neue Folge*, 10: 1-21.

Swofford, D. L. (1998). "PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4." *Sinauer Associates*, Sunderland.

Taylor M. P. 2009. A re-evaluation of *Brachiosaurus altithorax* Riggs 1903 (Dinosauria, Sauropoda) and its generic separation from *Giraffatitan brancai* (Janensch, 1914). *Journal of Vertebrate Paleontology* 29:787-806

Tschopp, E., Giovanardi, S., Maidment, S. C., 2016. Temporal distribution of diplodocid sauropods across the upper Jurassic Morrison formation (USA). *SVP Program Meeting and Abstracts*. 239.

Tschopp, E.; Mateus, O. V.; Benson, R. B. J., 2015. A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda). *PeerJ*. 3: e857. doi:10.7717/peerj.857. PMC 4393826. PMID 25870766.

Vidal, D.; Ortega, F.; Sanz, J.L., 2014. Titanosaur Osteoderms from the Upper Cretaceous of Lo Hueco (Spain) and Their Implications on the Armor of Laurasian Titanosaurs. *PLoS ONE* 9(8): e102488. <https://doi.org/10.1371/journal.pone.0102488>

Von Huene, F., 1929. Los Saurisquios y ornithisquios de Cretacéo Argentino. *Anales del Museo de La Plata*, 3: 1-196.

Wang, X.; You, H.; Meng, Q.; Gao, C.; Chang, X.; Liu, J. (2007). *Dongbeititan dongi*, the first sauropod dinosaur from the Lower Cretaceous Jehol Group of western Liaoning Province, China. *Acta Geologica Sinica (English Edition)*. 81 (6): 911–916.

Wick, S.L., Lehman, T.M., 2014. A complete titanosaur femur from West Texas with comments regarding hindlimb posture. *Cretaceous Research*, 49: 39-44

Wilson, J.A., 2002. Sauropod dinosaur phylogeny: critique and cladistics analysis. *Zoological Journal of the Linnean Society*, 136: 217-276.

Wilson, J.A., and Upchurch, P., 2003. A Revision of Titanosaurus, Lydekker (Dinosauria-Sauropoda), the first dinosaur genus with a 'Gondwana' distribution. *Journal of Systematic Paleontology*, 1(3): 125-60

Wilson, J. A., Pol, D., Carvalho, A. B., Zaher, H., 2016. The skull of the titanosaur *Tapuiasaurus macedoi* (Dinosauria: Sauropoda), a basal titanosaur from the lower Cretaceous of Brazil. *Zoological Journal of the Linnean Society*, doi: 10.1111/zoj.12420

Wiman, C., 1929. Die Kreide-Dinosaurier aus Shantung. *Palaeontologia Sinica*, Series C 6(1): 1-67.

Xu, X., Zhang, X., Tan, Q., Zhao, X. and Tan, L., 2006. A new titanosaurian sauropod from Late Cretaceous of Nei Mongol, China. *Acta Geologica Sinica*, 80 (1): 20–26.

Xu, L., Pan, Z.C., Wang, Z.H., Zhang, X.L., Jia, S.H., Lü, J.C., Jiang, B.L., 2012. Discovery and significance of the Cretaceous system in Ruyang Basin, Henan Province. *Geological Review* 58, 601e613.

You, H.; Ji, Q.; Lamanna, M. C.; Li, J.; Li, Y., 2004. A titanosaurian sauropod dinosaur with opisthocoelous caudal vertebrae from the early Late Cretaceous of Liaoning province, China. *Acta Geologica Sinica*. 78 (4): 907–911.

You, H.-L.; Li, D.-Q.; Zhou, L.-Q.; Ji, Q., 2008. *Daxiatitan binglingi*: a giant sauropod dinosaur from the Early Cretaceous of China. *Gansu Geology*. 17 (4): 1–10.

You, H.-L.; Li, D.-Q., 2009. The first well-preserved Early Cretaceous brachiosaurid dinosaur in Asia. *Proceedings of the Royal Society B: Biological Sciences*. 276 (1695): 4077–4082. doi:10.1098/rspb.2009.1278. PMC 2825791. PMID 19734188.

Zaher, H., Pol, D., Carvalho, A.B., Nascimento, P.M., Riccomini, C., *et al.*, 2011. A Complete Skull of an Early Cretaceous Sauropod and the Evolution of Advanced Titanosaurians. *PLoS ONE* 6(2): e16663.

Zhang, X., Xu, L., Li, J., Yang, L., Hu, W., Jia, S., Ji, Q., *et al.*, 2009. A New Sauropod Dinosaur from the Late Cretaceous Gaogou Formation of Nanyang, Henan Province. *Acta Geologica Sinica*, 83: 212.

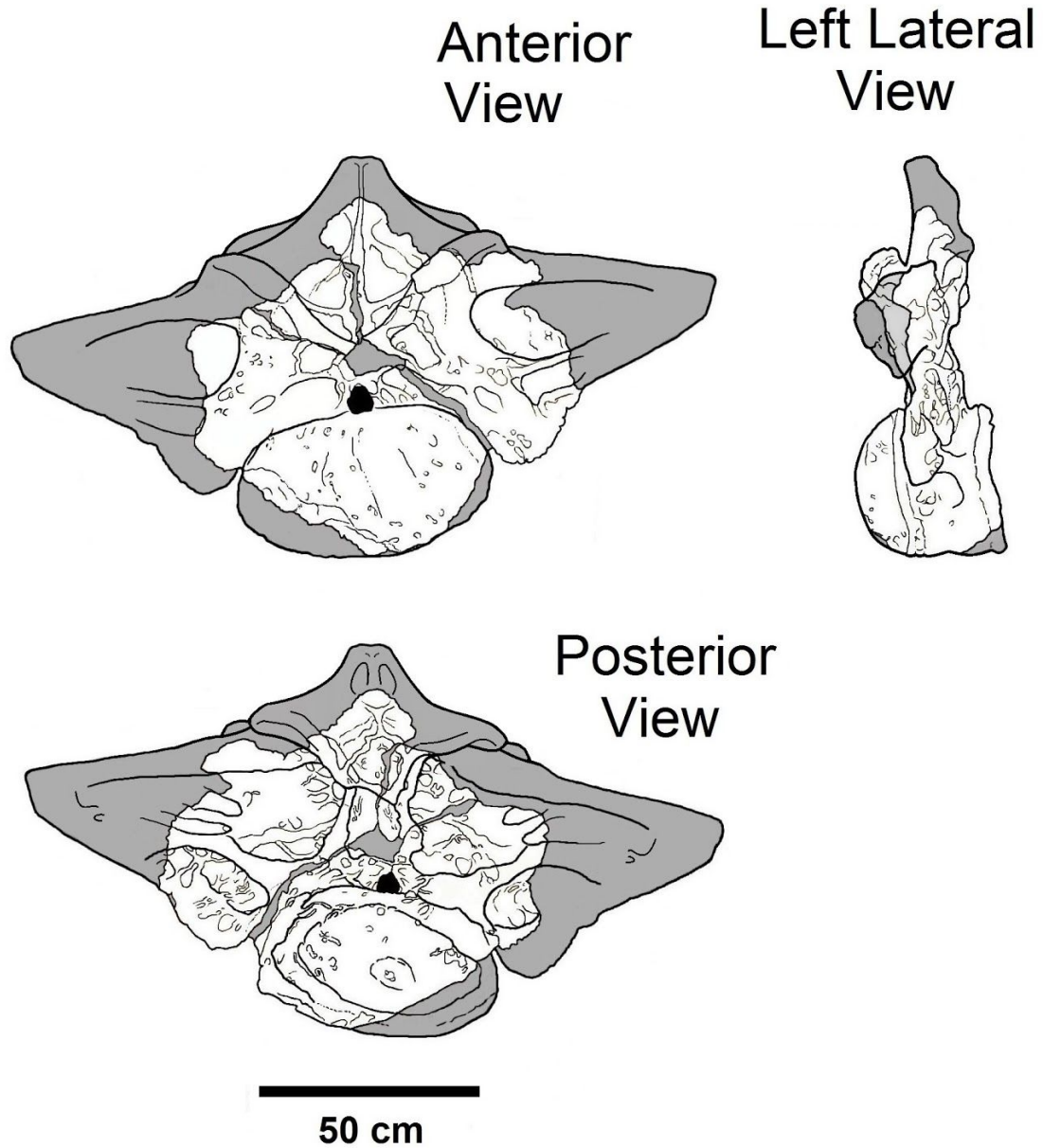


Fig. 1. Anterior dorsal (D2?) of *Ruyangosaurus giganteus*.

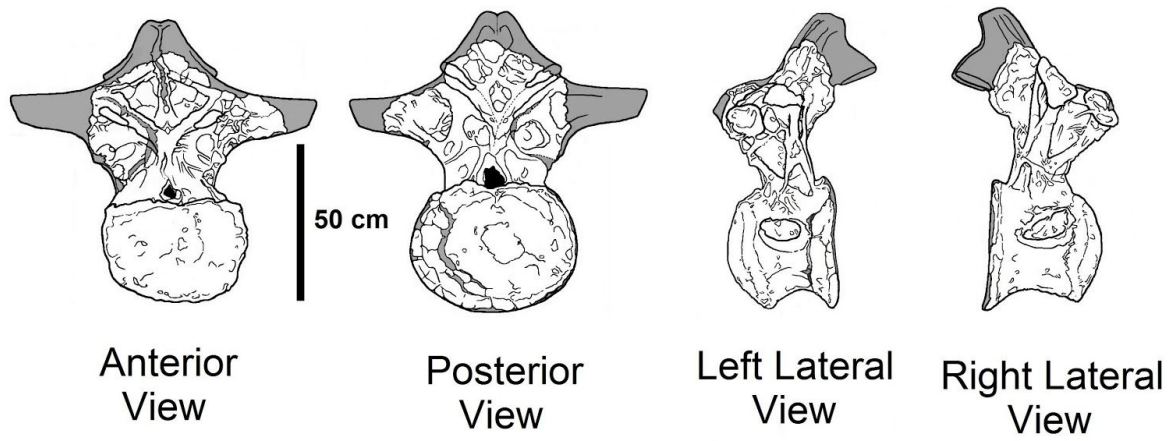


Fig. 2. Posterior dorsal (D10?) of *Ruyangosaurus giganteus*.

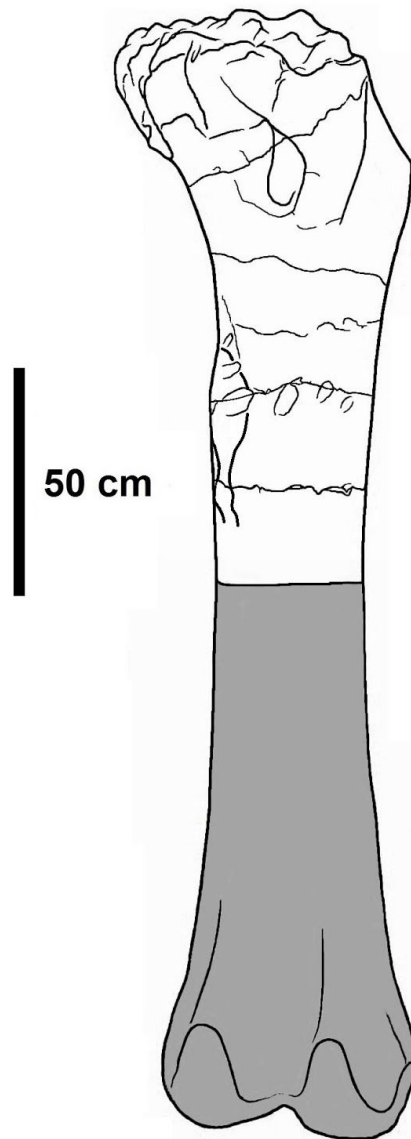


Fig. 3. Right femur of *Ruyangosaurus giganteus* in posterior view.

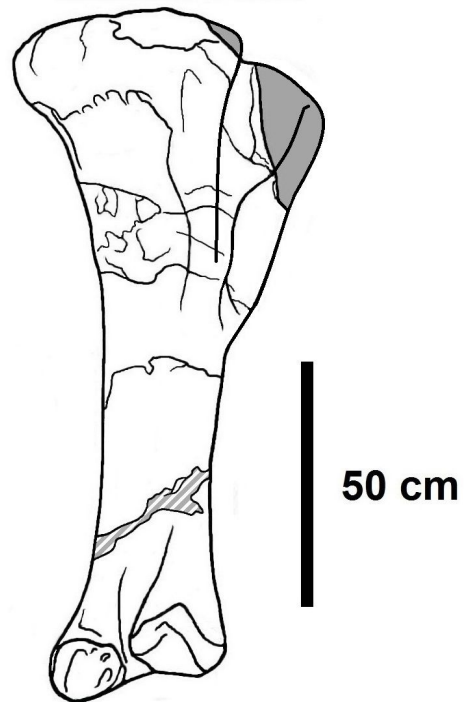


Fig. 4. Right tibia of *Ruyangosaurus giganteus* in right lateral view.

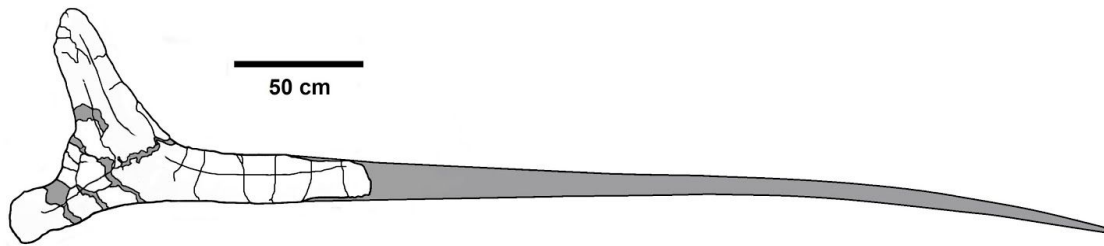


Fig. 5. Left cervical rib of *Ruyangosaurus giganteus* in left lateral view. Length of restored distal portion based on more complete titanosaurian taxa.

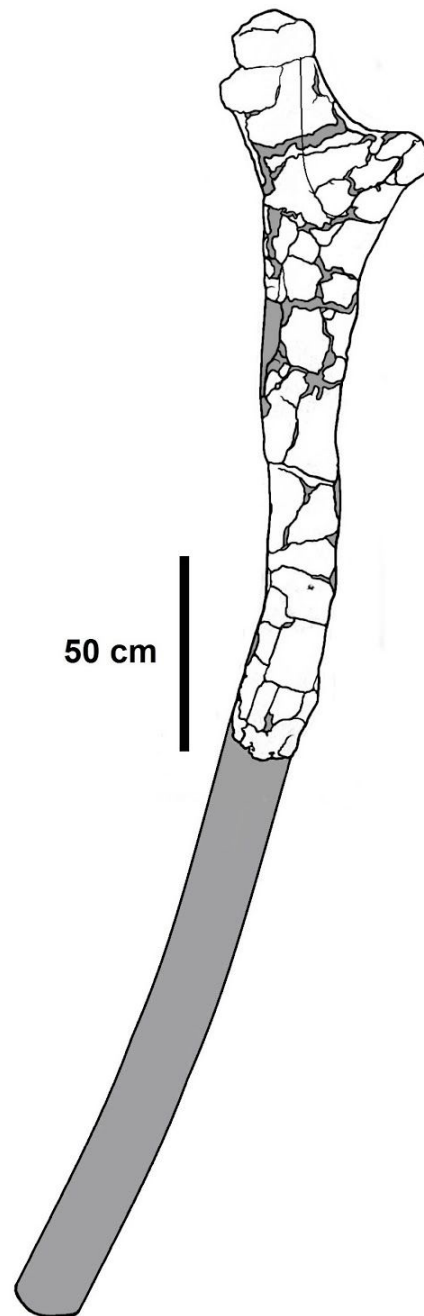


Fig. 6. Right dorsal rib of *Ruyangosaurus giganteus* in lateral view. Length of restored distal portion based on more complete titanosaurian taxa.

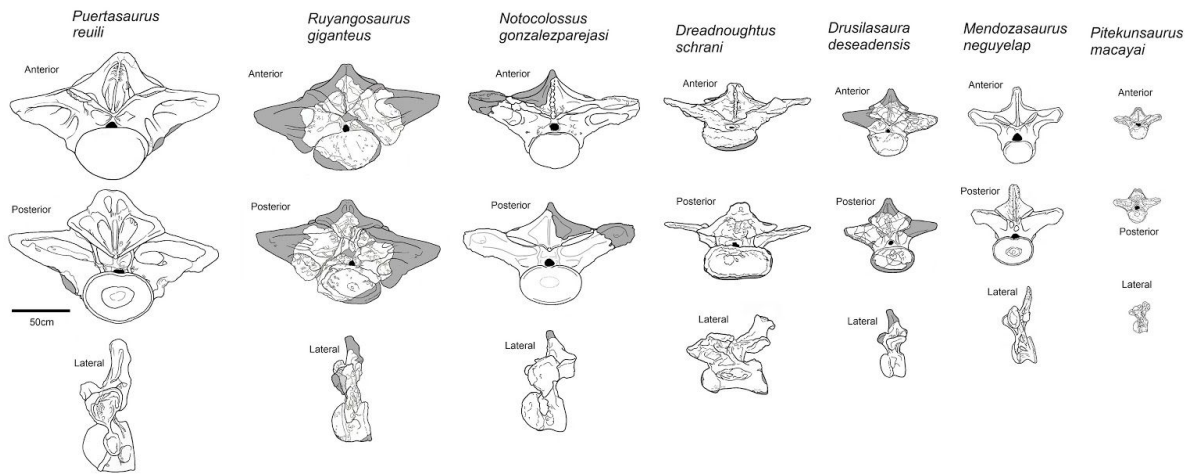


Fig. 7. Comparison between the anterior dorsals of several longosaurian titanosaurs. Some crushing has been removed from these specimens.

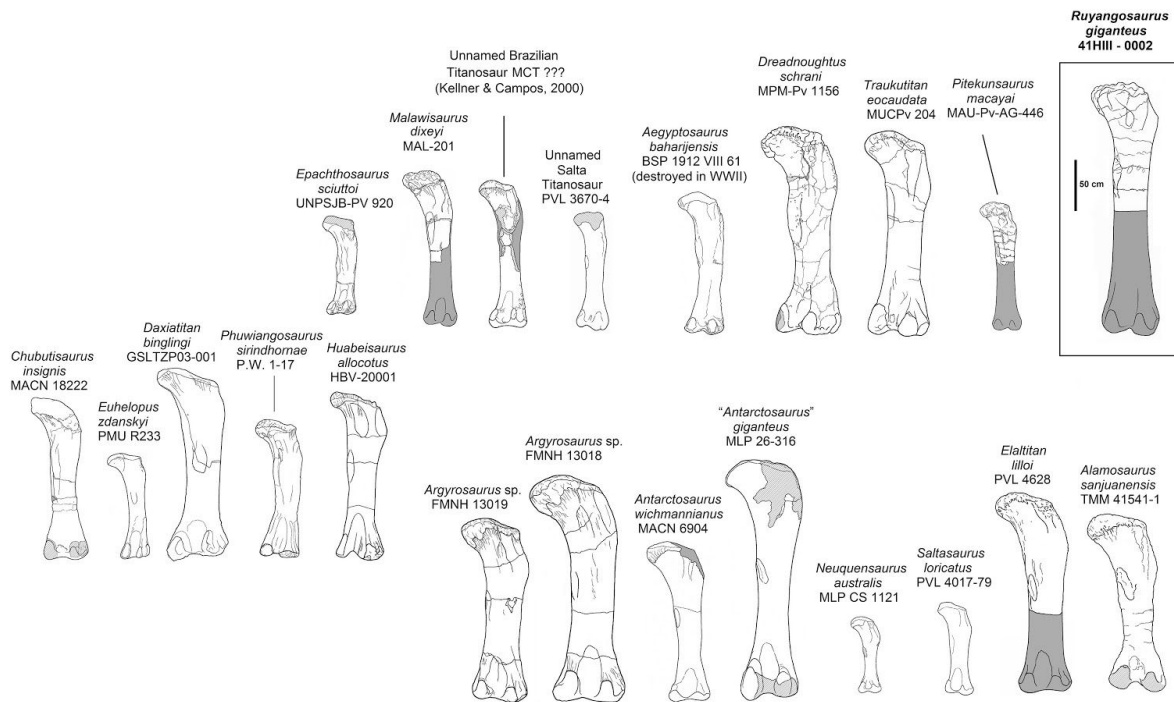


Fig. 8. Comparison between the right femur of *Ruyangosaurus* and femora of several other titanosaurs and titanosauriforms. Left femora reversed. to same scale.

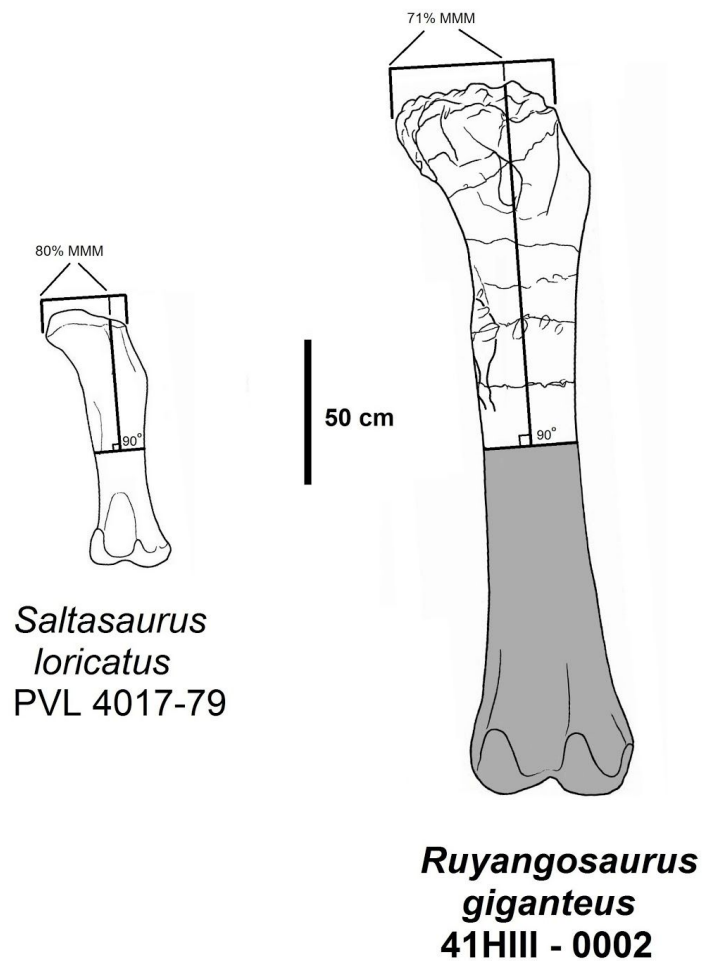


Fig. 9. Example of comparative proximal MMM ratios between *Saltasaurus* and *Ruyangosaurus*. To scale.

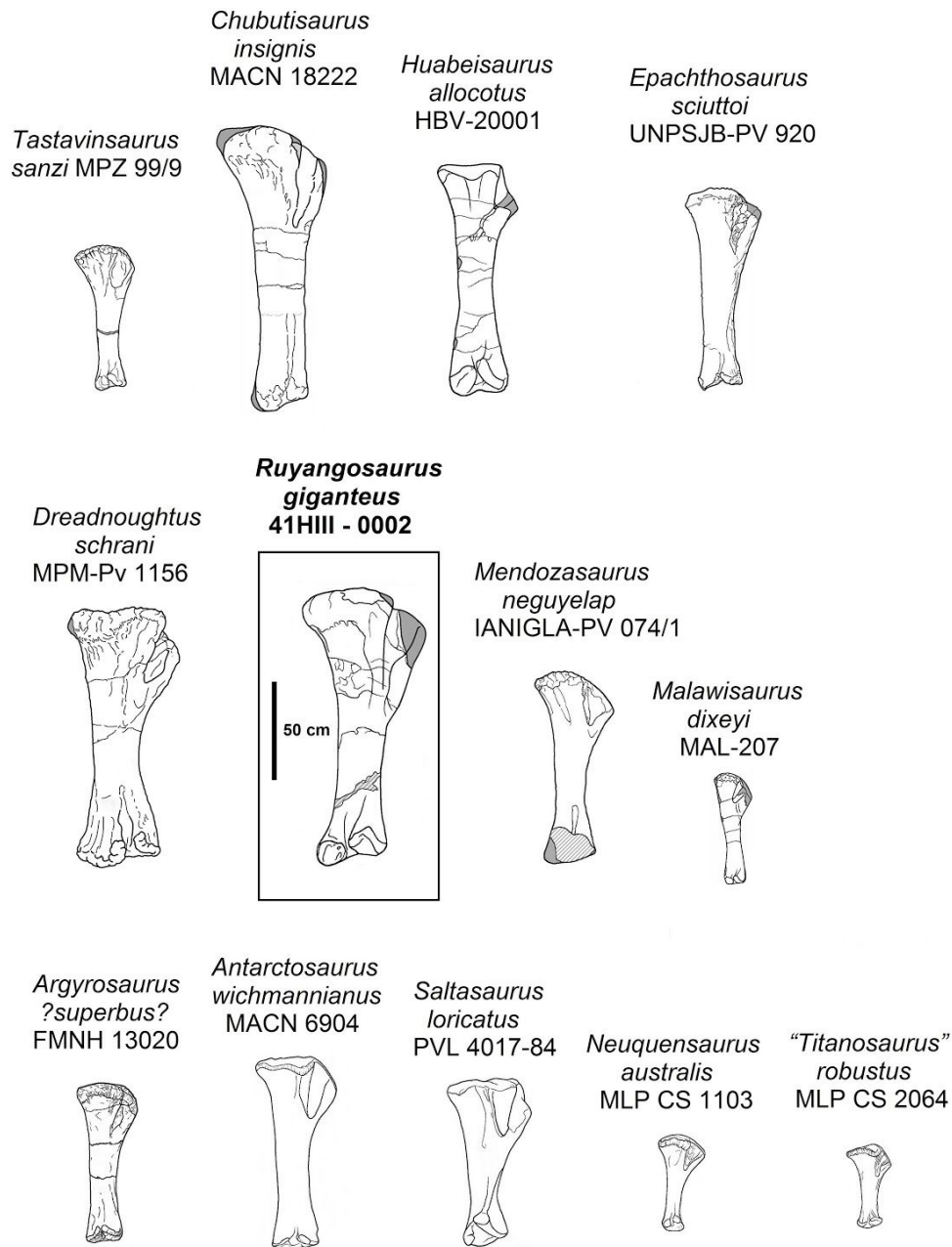


Fig. 10. Comparison of the right tibia of *Ruyangosaurus* to tibiae of several other titanosaurs and titanosauriforms. Left tibiae reversed. To same scale.

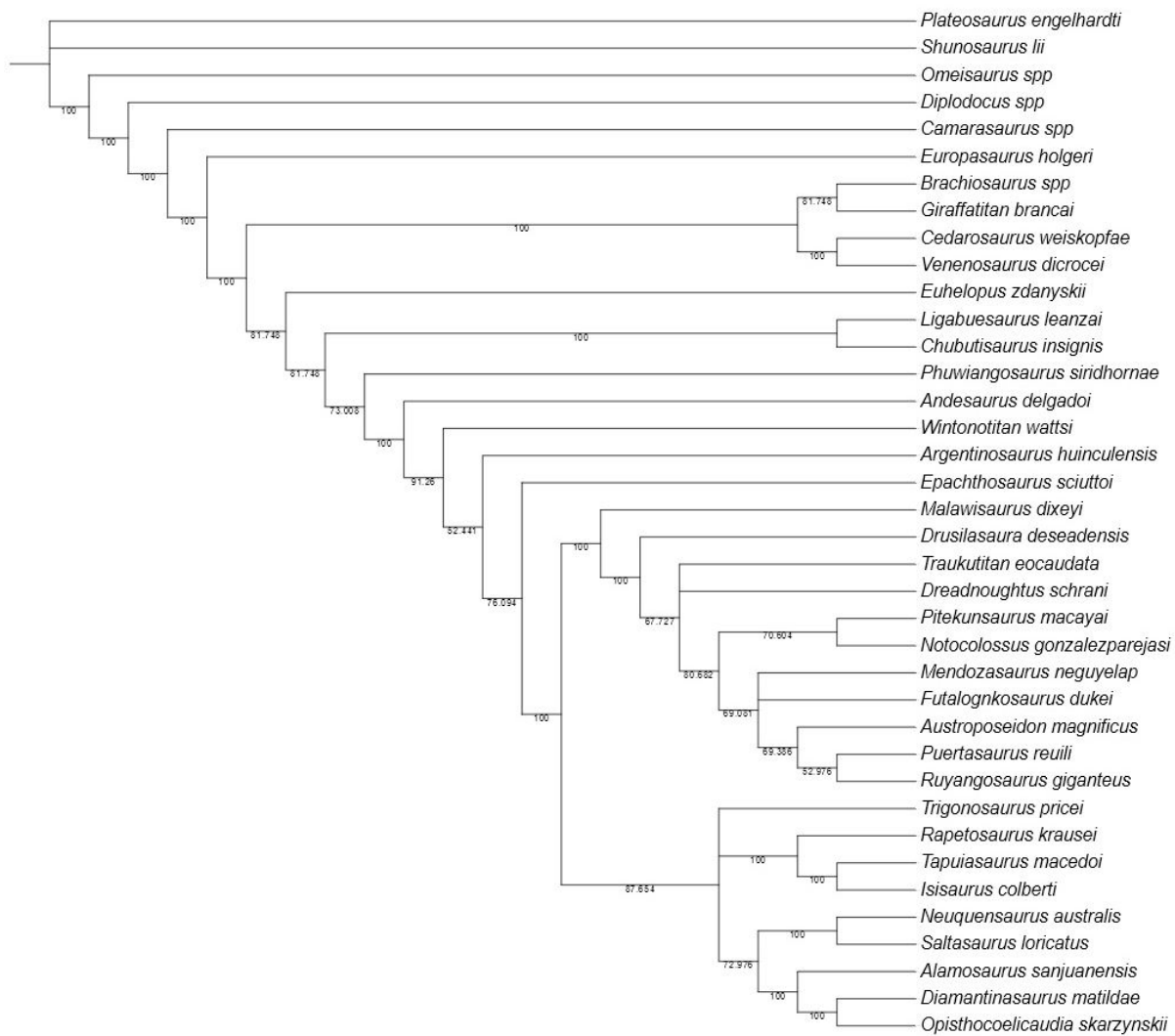


Fig. 11. 50% majority rule tree. Node support values listed.

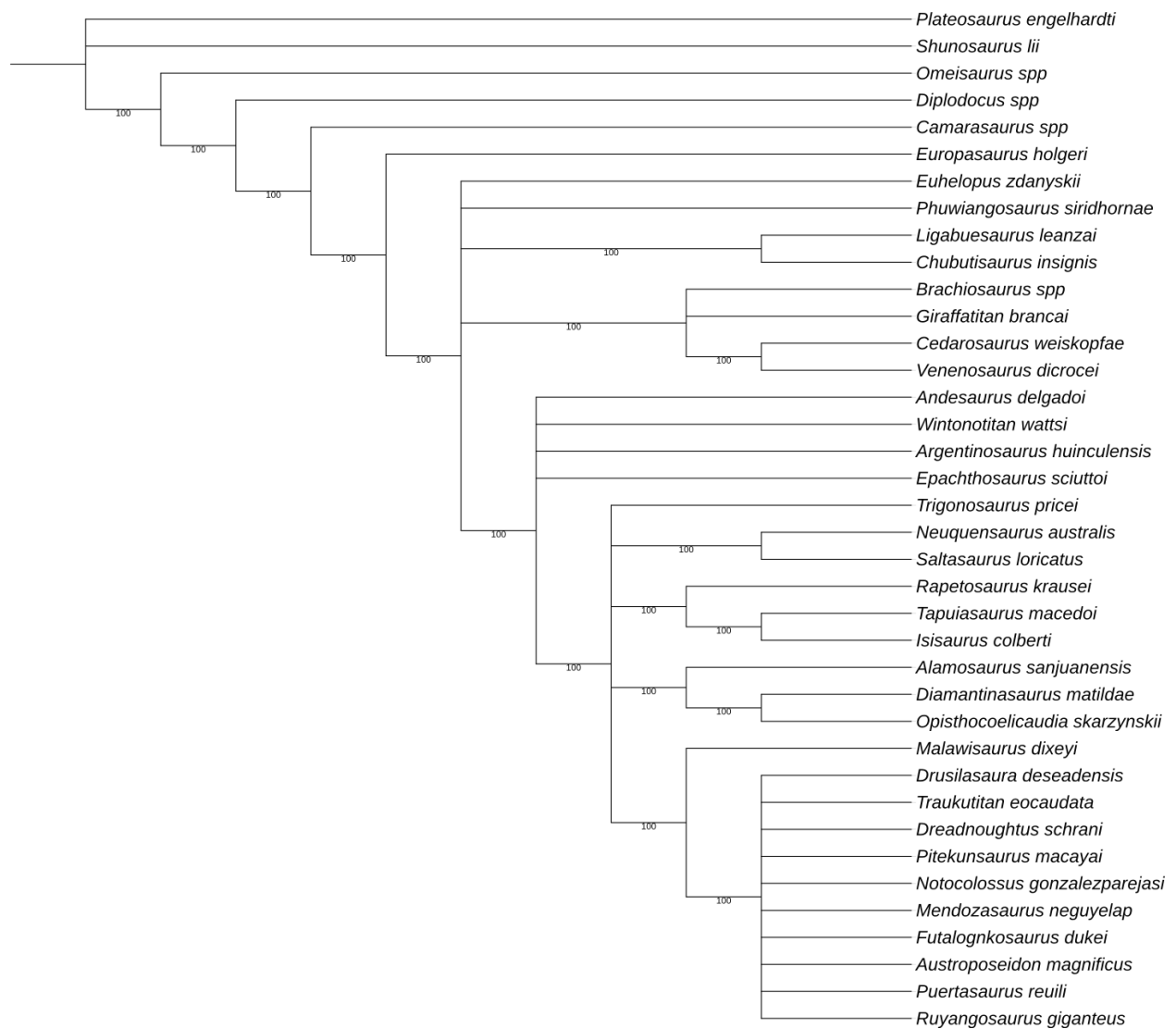


Fig. 12. Strict consensus tree. Node support values listed.

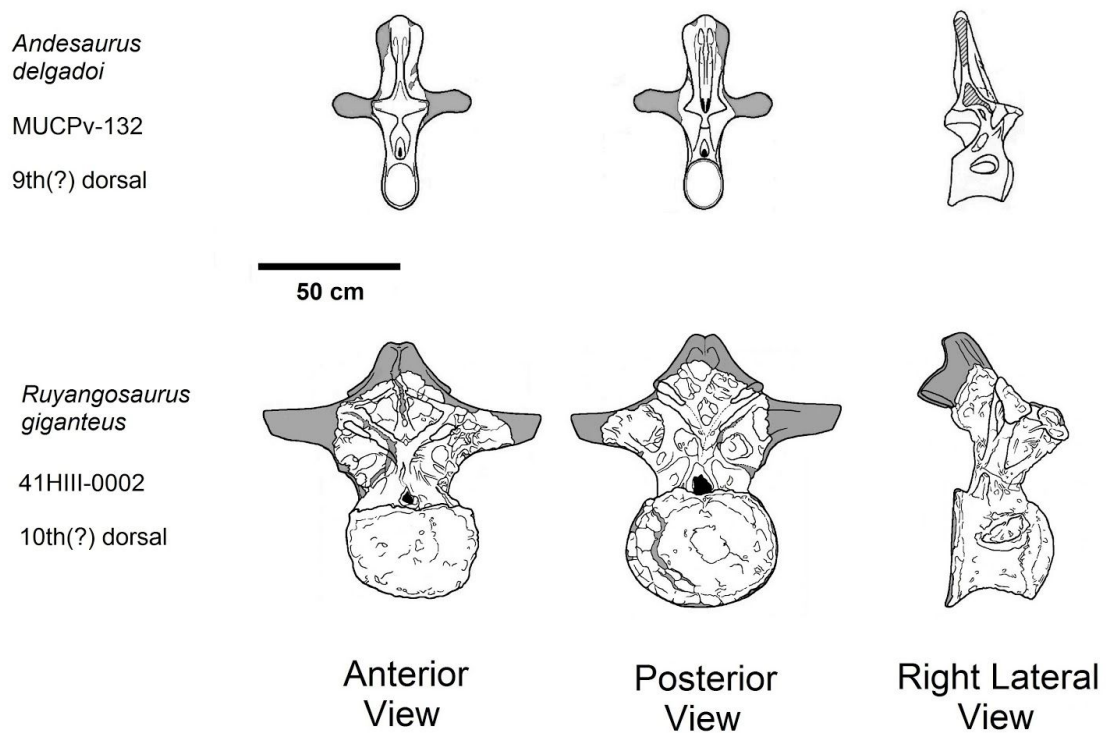


Fig. 13. Comparison between the posterior dorsals of *Andesaurus* (top) and *Ruyangosaurus* (bottom). Note the well-defined hypantrum and hyposphene in *Andesaurus*, and the lack of them in *Ruyangosaurus*.

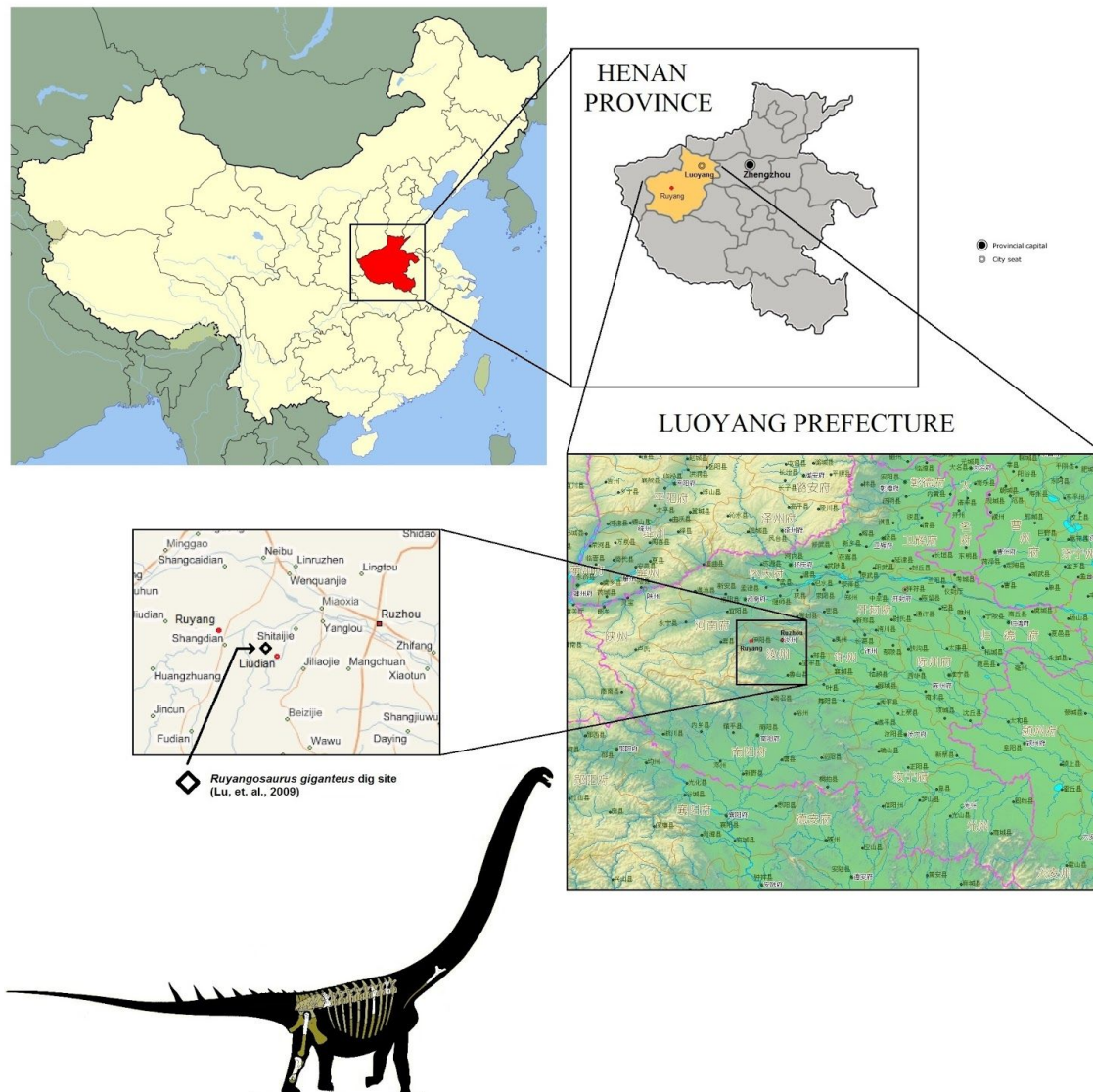


Fig. 14. Map showing locale where *Ruyangosaurus* was found, with skeletal of *Ruyangosaurus* below (see fig. 15 for high resolution version).

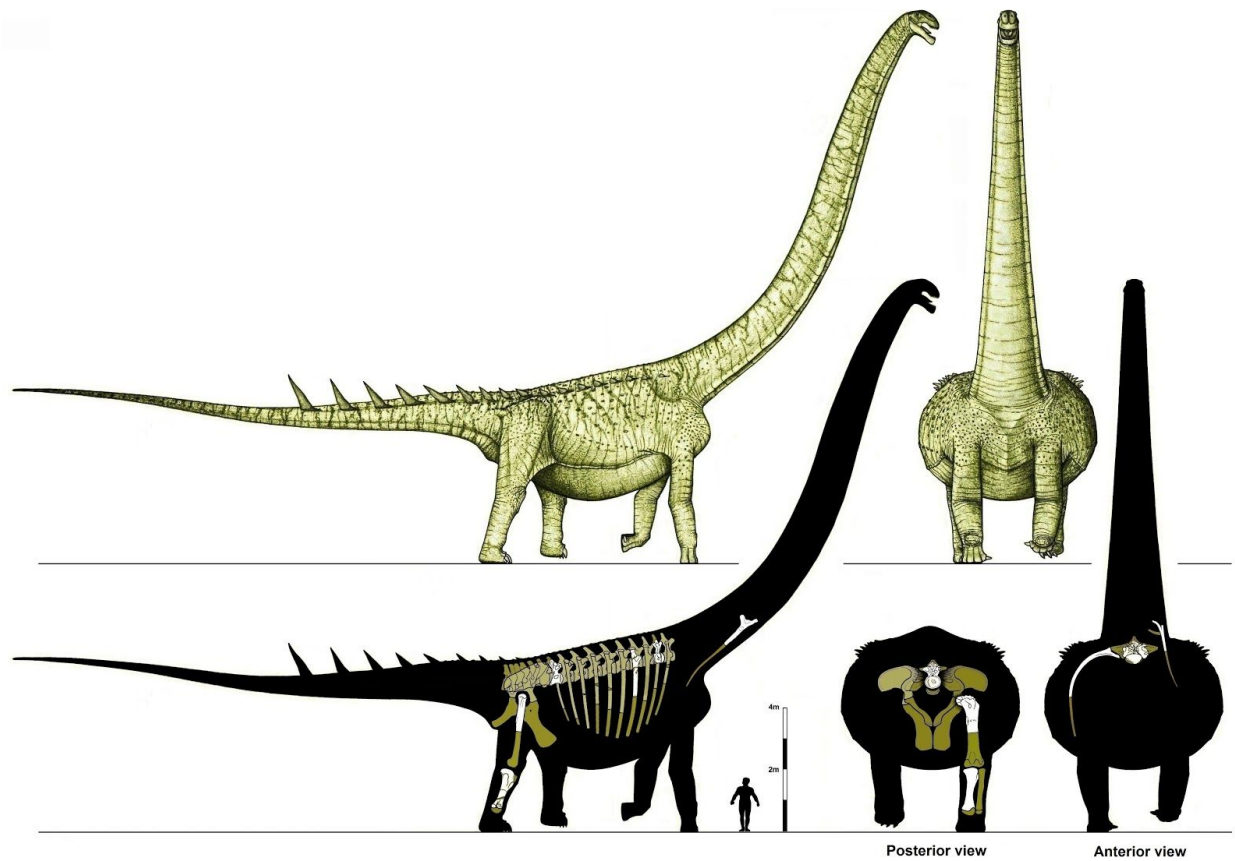


Fig. 15. Skeletal and life restorations of the *Ruyangosaurus giganteus* holotype by Nima Sassani. Osteoderms hypothesized based on Vidal, Ortega, and Sanz (2014). Beige elements are based on undescribed material likely referable to the holotype specimen. Scale bar equals 4m.

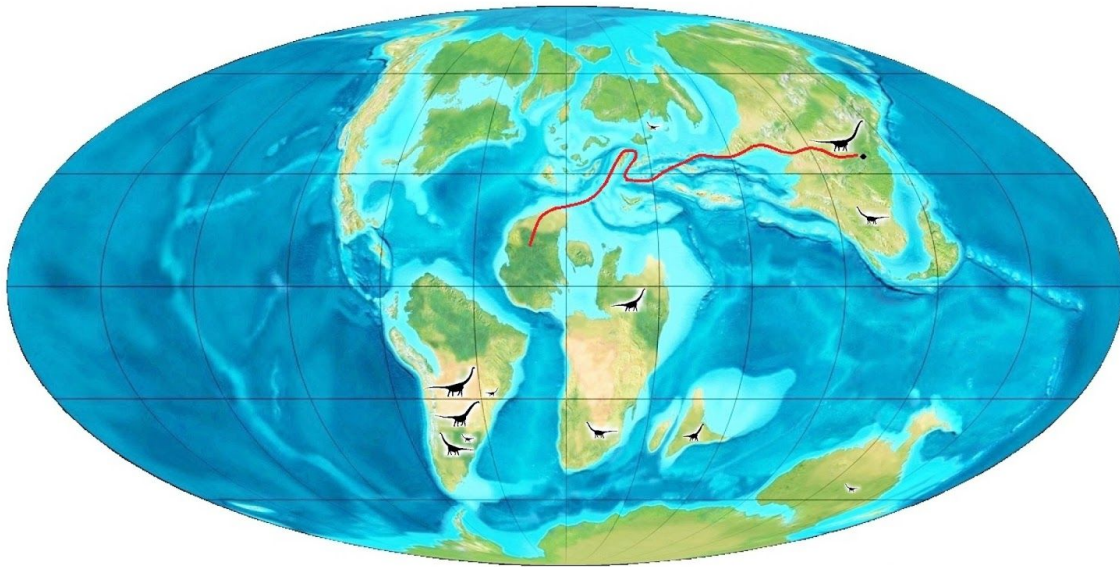


Fig. 16. Map of the Cretaceous, with red line showing likely migration path of Lognkosauria to Asia.

SPECIES	SPECIMEN	POSITION	WIDTH	HEIGHT	H/W ratio
<i>Brachiosaurus altithorax</i>	FMNH P 25107	D6?	759	910	1.197
<i>Giraffatitan brancai</i>	HMN SII	D4	1198	1170	.9766
<i>Ligabuesaurus leanzai</i>	MCF-PVPH-233/3	D2?	1000 (est.)	800	.8000
<i>Tastavinsaurus sanzi</i>	MPZ 99/9 (Ars1-78)	D5?	340	650	1.912
cf. "Huanghetitan" <i>ruyangensis</i>	4IHIII-0008	D2?	1126	820	.7282
<i>Argentinosaurus huinculensis</i>	MCF-PVPH-1	D3	1227 (est.)	~1273 (est.)	1.037
<i>Epachthosaurus sciutoi</i>	UNPSJB-PV 920	D5/D6	270/389	332/321	1.230/.8250
<i>Malawisaurus dixeyi</i>	Mal-236	D3	458	~385 (est.)	~.8400 (est.)
* <i>Mendozasaurus neguyelap</i>	IANIGLA-PV 066	D2?	760	615	.8092
* <i>Futalognkosaurus dukei</i>	MUCPv-323	D2	~1000	?700?	?.7000?
** <i>Dreadnoughtus schrani</i>	MPM-Pv 1156	D4	1100	440	.4000
** <i>Ruyangosaurus giganteus</i>	4IHIII-0002	D2?	~1600 (est.)	~864 (est.)	~.5400 (est.)
** <i>Puertasaurus reuili</i>	MPM 10002	D2	1680	1060	.6310
** <i>Notocolossus gonzalezparejasi</i>	UNCUYO-LD 301	D2/D3	1500 (est.)	780 (est.)	.5200 (est.)
** <i>Pitekunsaurus macayai</i>	MAU-Pv-AG-446/8	D2?	389	239+ (277 est.)	.61 (.71 est.)
<i>Trigonosaurus pricei</i>	MCT 1488-R	D4	~365 (est.)	243	.6658
<i>Alamosaurus sanjuanensis</i>	TMM 43621-1 (juvenile)	D1?	500	~320	~.6400
<i>Opisthocoelicaudia skarzynskii</i>	ZPAL MgD-I/48	D4	610	440	.7200
<i>Isisaurus colberti</i>	ISIR335/11	D2	600	600	1.000
<i>Saltasaurus loricatus</i>	PVL 4017-11	D3?	~300 (est.)	270	~.9000 (est.)

Table 1. Comparison of anterior dorsal vertebrae of *Ruyangosaurus* and other titanosauriforms, and their height/width ratios. Dimensions are estimated for incomplete vertebrae as reconstructed here. Data from Paul (1988a), Powell (2003) and cited descriptions of listed specimens. Measurements are in mm. Asterisks indicate lognkosaurs, and two asterisks indicate putative lognkosaurs.

SPECIES	SPECIMEN	LEFT/ RIGHT FEMUR	FEMUR LENGTH	PROXIMAL TRANSVERSE WIDTH	PROXIMAL MMM %
<i>Brachiosaurus altithorax</i>	FMNH P 25107	R	2030	602	72
<i>Giraffatitan brancai</i>	HMN XV1	R	2140	560	88
<i>Tastavinsaurus sanzi</i>	MPZ 99/9	L/R	1310/1300	360/360	62/62
<i>Chubutisaurus insignis</i>	MACN 18222	R	1680	350	80
“Huanghetitan” <i>ruyangensis</i>	41HIII-0001-1	R	~2350	~650?	?
<i>Euhelopus zdanskyi</i>	PMU R233, 234	R	955	285	80
<i>Daxiatitan binglingi</i>	GSLTZP03-001	R	1770	580	75
<i>Yunmenglong ruyangensis</i>	41HIII-0006	R	1920	650	71
<i>Huabeisaurus allocotus</i>	HBV-20001	L	1560	430	70
<i>Phuwianosaurus sirindhornae</i>	P.W. 1-16/1-17	L/R	~1263/1263	~394/394	82/82
<i>Argentinosaurus huinculensis</i>	MLP-DP 46-VIII-21-3 MCF-PVPH #?	R L	~2557 (est.) 2500	? ?	? ?
<i>Epachthosaurus sciuttoi</i>	UNPSJB-PV 920	R	1095	340	81
** <i>Malawisaurus dixeyi</i>	MAL-201	R	~1300 (est.)	280	~83
** <i>Aegyptosaurus baharijensis</i>	BSP 1912 VIII 61 (destroyed)	L/R	1290/1250+	330/330	83(?)
* <i>Futalognkosaurus dukei</i>	MUCPv-323	?	1980	?	?
** <i>Ruyangosaurus giganteus</i>	41HIII -0002	R	~2350 (est.)	600	71
* <i>Traukutitan eocaudata</i>	MUCPv 204	L	~1870	~540	71
** <i>Dreadnoughtus schrani</i>	MPM-Pv 1156	L	1910	~550	73
** <i>Pitekunsaurus macayai</i>	MAU-Pv-AG-446	L	~1222 (est.)	273	72
**Unnamed Salta titanosaur	PVL 3670-4	L	1157	289	71
**Unnamed Brazilian titanosaur	MCT ???	R	????	???	78
“Argyrosaurus” <i>sp.</i>	FMNH 13018 FMNH 13019	R R	2110 1770	640 (~690 est.) 570	94 (~88 est.) 83
<i>Antarctosaurus wichmannianus</i>	MACN 6904	L	1390	~450 (est.)	~75 (est.)
“Antarctosaurus” <i>giganteus</i>	MLP 26-316	L/R	2310/2220	600/650	84/78
“MLP giant”	MLP #?	N/A	~2400 (est.)	~600 (est.)	?
<i>Petrobrasaurus puestohernandezii</i>	MAU-PvPH-449	L/R	1575/1572	320/340	99/98
<i>Elaltitan lilloi</i>	PVL 4628	R	~1968 (est.)	~533	88
<i>Neuquensaurus australis</i>	MLP CS 1121	L	700	200	83
<i>Saltasaurus loricatus</i>	PVL 4017-79	L	~790	~230	80
<i>Alamosaurus sanjuanensis</i>	TMM 41541-1	R	~1730	523	75
<i>Rapetosaurus krausei</i>	FMNH PR 2209	L	657		71
<i>Opisthocoelicaudia skarzynskii</i>	ZPAL MgD-I/48	R	1395	470	73

Table 2. Rounded proximal MMM percentages for *Ruyangosaurus giganteus* as compared to other titanosaurs and titanosauriforms. Lengths for partial femurs are estimated total lengths. Data from Paul (1988a), Powell (2003), Taylor (2009) and cited description papers of listed specimens. Measurements are in mm. Asterisks indicate lognkosaurs, and two asterisks indicate putative lognkosaurs.

SPECIES	SPECIMEN	L/R TIBIA	LENGTH	MAX. PROX. DIAMETER	LENGTH/PROX. DIAMETER ratio
<i>Ligabuesaurus leanzai</i>	MCF-PVPH-233	R	1040	270	3.852
<i>Huabeisaurus allocotus</i>	HBV-20001	R	1170	~287	3.171
<i>Tastavinsaurus sanzi</i>	MPZ 99/9	R	735	251	2.928
<i>Epachthosaurus sciuttoii</i>	UNPSJB-PV 920	L/R	662/700	?/~383	1.828
<i>Malawisaurus dixeyi</i>	Mal-207	R	540	141	3.830
* <i>Mendozasaurus neguyelap</i>	IANIGLA-PV 074/1	R	990	375	2.640
	IANIGLA-PV 073/2	L	840	320	2.625
** <i>Dreadnoughtus schrani</i>	MPM-Pv-1156	R	1200	490	2.448
** <i>Ruyangosaurus giganteus</i>	41HIII -0002	R	1270	510	2.490
**“Titanosaurus indicus”	NHM R 5903	L	825	~268	~3.078
“Argyrosaurus” <i>sp.</i>	FMNH 13020	L	1240	~485	2.557
<i>Antarctosaurus wichmannianus</i>	MACN 6904	L	930	38	2.44
<i>Saltasaurus loricatus</i>	PVL 4017-84	R	~813	~400	2.033
<i>Neuquensaurus australis</i>	MLP CS 1103	L	460	250	1.840
“Titanosaurus” <i>robustus</i>	MLP CS 2064	L	400	230	1.739
<i>Alamosaurus sanjuanensis</i>	TMM 42495-4		?	?	~2.222?
<i>Opisthocoelicaudia skarzynskii</i>	ZPAL MgD-I/48	L/R	810/810	~390/~390	2.077

Table 3. Tibiae of titanosaurs including *Ruyangosaurus*. Max. proximal diameter includes cnemial crest. Data from Von Huene (1929), Powell (2003) and cited descriptions of listed specimens. Measurements in mm. Asterisks indicate lognkosaurs, and two asterisks indicate putative lognkosaurs.

Element	<i>Notocolossus gonzalezparejasi</i> (UNCUYO-LD 301)	<i>Pitekunsaurus macayai</i> (MAU-Pv-AG-446/6)	(NHMUK PV R173)	<i>Puertasaurus reuili</i> (MPM 10002)	<i>Cf. Puertasaurus reuili</i> (MPM-Pv-39)	<i>Ruyangosaurus giganteus</i> (41HIII-0001)
Cv9	1053 ?	583 ?	500-667 ?	1180	1061 ?	1123?
Cv12	631 ?	350	300-400	704 ?	635 ?	673?
D2	1500	389	334-445 ?	1680	1512 ?	1600
D10	938 ?	520 ?	446-595 ?	1047 ?	945 ?	1000
Scapula	1245 ?	690	592-790 ?	1391?	1254 ?	1328 ?
Humerus	1790	992 ?	852-1135 ?	1999 ?	1804 ?	1909 ?
Ulna	86 ?	480	412-549 ?	967 ?	873 ?	924 ?
Femur	2204 ?	1222	1049-1399 ?	2461 ?	2220	2350
Tibia	1191 ?	309 ?	265-353 ?	1330 ?	1200 ?	1270

Table 4. Comparative measurements between “puertasaurine” lognkosaurs to determine the sizes of missing elements in each species. Found fossils are bolded. All measurements are in mm.