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Rebbachisaurid sauropods in Asia? A re-evaluation of the phylogenetic position of *Dzharatitanis kingi* from the Late Cretaceous of Uzbekistan

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REBBACHISAURID SAUROPODS IN ASIA? A RE-EVALUATION OF THE PHYLOGENETIC POSITION OF *DZHARATITANIS KINGI* FROM THE LATE CRETACEOUS OF UZBEKISTAN

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Abstract. An isolated vertebra from the Late Cretaceous of Uzbekistan (Asia), previously interpreted as a titanosaur anterior caudal, was recently assigned as the holotype and unique specimen of a new rebbachisaurid taxon, *Dzharatitanis kingi*. This record would drastically impact both biogeographical and chronological aspects of the group. As some of the characters identified for such systematic assignment seem to have been incorrectly scored and/or have a more widespread distribution amongst Neosauropoda, we revised and discussed them in depth to verify the putative rebbachisaurid affinities of this taxon. The phylogenetic analyses carried out recovered *Dzharatitanis* as a titanosaur sauropod, most probably related to Lognkosauria. The extra steps needed to force *Dzharatitanis* within Rebbachisauridae confirms that its titanosaur affinity is not solely the most parsimonious hypothesis but also is well supported when the incompleteness of the material is considered. Given this new phylogenetic position, a new modified diagnosis is provided here. Although more complete evidence is needed, the reinterpretation of *Dzharatitanis* as a titanosaur with lognkosaurian affinities suggests a wider biogeographic distribution of this group of colossosaurs during the Cretaceous. At present, there is no reliable evidence to assume that rebbachisaurid sauropods have inhabited Asia.

Key words. *Dzharatitanis.* Titanosauria. Cretaceous. Rebbachisauridae. Dinosauria.

Resumen. ¿SAURÓPODOS REBBAQUISÁURIDOS EN ASIA? UNA RE-EVALUACIÓN DE LA POSICIÓN FILOGENÉTICA DE *DZHARATITANIS KINGI* DEL CRETÁCICO TARDÍO DE UZBEKISTÁN. Una vértebra caudal aislada del Cretácico Tardío de Uzbekistán (Asia), previamente interpretada como una caudal anterior de titanosaurio, fue asignada recientemente como el holotipo y único espécimen de un nuevo rebaquisáurido, *Dzharatitanis kingi*. Este registro impacta drásticamente tanto en los aspectos biogeográficos como cronológicos del grupo. Como algunos de los caracteres identificados para dicha asignación sistemática parecen estar codificados incorrectamente y/o tener una distribución más amplia entre Neosauropoda, los mismos son revisados y discutidos en este trabajo con el fin de verificar las afinidades de este taxón con los rebaquisáuridos. Los análisis filogenéticos llevados a cabo recuperan a *Dzharatitanis* como un saurópodo titanosaurio, probablemente más relacionado a Lognkosauria. Los pasos extras necesarios para forzar *Dzharatitanis* dentro de Rebbachisauridae confirman sus afinidades con los titanosaurios, siendo esta no solo la hipótesis más parsimoniosa, sino que también está bien soportada cuando se tiene en cuenta la escasez del material. Dada esta nueva posición filogenética, aquí se proporciona una nueva diagnosis modificada. Aunque se necesita evidencia más completa, la reinterpretación de *Dzharatitanis* como un titanosaurio con afinidades a los lognkosaurios sugiere una distribución biogeográfica más amplia de este grupo de colossosaurios durante el Cretácico. Actualmente, no hay evidencia confiable para suponer que los saurópodos rebaquisáuridos hayan habitado Asia.

Palabras clave. *Dzharatitanis.* Titanosauria. Cretácico. Rebbachisauridae. Dinosauria.

Cranial and postcranial remains from the Bissekty Formation (Turonian) at Dzharakuduk, Uzbekistan (Asia) were described and attributed to titanosaurian sauropods by Sues *et al.* (2015). Amongst that material, they described an isolated braincase, teeth, caudal vertebrae and manual and pedal bones. Because the remains were found isolated, they did not ascertain if the material represents one or more taxa. Recently, Averianov and Sues (2021) redescribed one of these elements (USNM 538127) which they interpreted as a first caudal vertebra of a new rebbachisaurid species, *Dzharatitanis kingi* Averianov & Sues, 2021. The systematic assignment made by Averianov and Sues (2021) was based on the phylogenetic analysis that they carried out including *Dzharatitanis* into the data matrix of Xu *et al.* (2018), which was mainly based on that of Rauhut *et al.* (2015), both of which were primarily designed to investigate the relationships of diplodocoids. Rebbachisauridae have two principal subclades, Limaysaurinae, which is exclusively South American (Calvo & Salgado, 1995; Gallina & Apesteguía, 2005) and Rebbachisaurinae, with a more cosmopolitan distribution comprising South America, Africa and Europe (Fernández-Baldor *et al.*, 2011; Wilson & Allain, 2015; Fanti *et al.*, 2015; Canudo *et al.*, 2018; Lindoso *et al.*, 2019). Within Rebachisauridae, *Dzharatitanis*, was closely related with the Rebbachisaurinae clade and could represent the first rebbachisaurid from Asia (Averianov & Sues, 2021). Until present, Rebbachisauridae is reliably known from the Cretaceous strata of South America, Africa and Europe. Although a record from the Late Jurassic of North America was recently proposed based on a picture of a lost material (Carpenter, 2018), this is a dubious interpretation that, as noted by Whitlock and Wilson-Mantilla (2020), should be taken carefully. In the same way, the presence of a rebbachisaurid in Asia would drastically impact both the biogeographical and chronological aspects of the group. Therefore, the systematic assignment of this isolated anterior caudal vertebra from Uzbekistan deserves to be critically analyzed in order to verify its putative rebbachisaurid affinities.

Averianov and Sues (2021) scored *Dzharatitanis* into the data set of Xu *et al.* (2018), which in turns results from a modification of that of Rauhut *et al.* (2015) with the inclusion of five characters (two from the skull and three from cervical vertebrae). Despite that the original data set used by Averianov and Sues (2021) has a wide taxon sampling, it includes a reduced sample of titanosaurs, in comparison to more actualized versions of the primary data set from which this analysis is based on (that of Rauhut *et al.*, 2015). In the recent description of the titanosaur *Patagotitan mayorum* Carballido *et al.*, 2017, several new characters and taxa were added to the original data set of Rauhut *et al.* (2015) which allowed to recognise a diverse lineage of Lognkosauria within Titanosauria. The presence of such taxa, and especially the inclusion of additional taxa (*e.g.*, *Dreadnoughtus* Lacovara *et al.*, 2014, *Puertasaurus* Novas *et al.*, 2005, *Quetecsaurus* González Riga & Ortiz David, 2014, *Notocolossus* González Riga *et al.*, 2016, *Patagotitan* Carballido *et al.*, 2017), could have a deep impact on the position of certain problematic taxa, especially those represented by fragmentary or isolated elements. In that sense, several of the characters referred by Averianov and Sues (2021) as typical for rebbachisaurids, need a re-evaluation, both in taxon sampling but also in their interpretation, as is the case of the "wing-like" transverse process of *Dzharatitanis*. Such a process is actually more reminiscent of that of some lognkosaur titanosaurs (*e.g.*, *Patagotitan*, *Futalognkosaurus* Calvo *et al.*, 2007) than that of diplodocoids. A similar situation occurred when Upchurch and Mannion (2009) described an anterior caudal vertebra (PMU R263) from Qingshan Formation of the Province of Shandong, China, as the first Diplodocidae of Asia. Taking into account that all Cretaceous Asian sauropods were members of the derived neosauropod subgroup Titanosauriformes, Whitlock *et al.* (2011) re-evaluated the character data nesting this vertebra within Diplodocidae, and concluded that PMU R263 most likely belongs to a titanosauriform than to a diplodocoid.

In order to further evaluate the phylogenetic position of *Dzharatitanis*, we performed a new phylogenetic analysis using an updated version (Gallina *et al.*, 2021) of the primary data set used by Averianov and Sues (2021). Given that Averianov and Sues (2021) provided a detailed description and figures from *Dzharatitanis*, we solely describe and discuss the characters scored and the results of our phylogenetic analysis. Additionally, a new modified diagnosis is proposed for *Dzharatitanis*.

Institutional abbreviations. MDS, Museo de Dinosaurios de Sala de los Infantes, Burgos, Spain; MNN, Musee National du Niger, Niamey, Niger; MPCA, Museo Provincial 'Carlos Ameghino', Cipolletti, Argentina; MPEF, Museo Paleontológico Egidio Feruglio, Trelew, Argentina; MUCPv, Museo de Geología y Paleontología de la Universidad Nacional de Comahue, Comahue, Argentina; PMU, Palaeontological Museum of the University of Uppsala, Uppsala, Sweden; USNM, United States National Museum, Washington, D.C., United States.

Anatomical abbreviations. PRSL, prespinal lamina; SPDL, spinodiapophyseal lamina; SPOL, spinopostzygapophyseal lamina; SPRL, spinoprezygapophyseal lamina.

SYSTEMATIC PALEONTOLOGY

SAUROPODA Marsh, 1878
NEOSAUROPODA Bonaparte, 1986
MACRONARIA Wilson & Sereno, 1998
TITANOSAURIA Bonaparte & Coria, 1993

Genus ***Dzharatitanis*** Averianov & Sues, 2021

Type species. *Dzharatitanis kingi* Averianov & Sues, 2021. Turonian (Late Cretaceous), Bissekty Formation of Dzharakuduk, Uzbekistan.

Dzharatitanis kingi Averianov & Sues, 2021
Figure 1.1

Modified diagnosis. *Dzharatitanis kingi* is characterized by the following combination of characters: 1) Well developed and anterolaterally placed SPRLs that reach the dorsal edge of the neural spine (differing from lognkosaurs and convergently acquired in several non-lognkosaur titanosaurs such as *Bonitasaura* Apesteguía, 2004, *Baurutitan* Kellner *et al.*, 2005, *Rapetosaurus* Curry Rogers & Foster, 2001, and *Xianshanosaurus* Lü *et al.*, 2009). 2) Anterior caudal centra (perhaps the first) slightly opisthocoelous (convergently acquired in rebbachisaurids and *Opisthocoelicaudia* Borsuk-Bialynicka, 1977, although in the latter this character is much more developed). 3) Presence of a marked spinodiapophyseal lamina in the anterior caudal vertebra (character widespread amongst Lognkosauria and Rebbachisauridae). 4) Prespinal lamina of anterior caudal vertebra dorsally expanded, acquiring an inverted triangular shape (also observed in derived lognkosaurs).

Comments. The original diagnosis of *Dzharatitanis kingi* was solely based only on differences with others rebbachisaurids. Given the new phylogenetic position here proposed, we provide a revised diagnosis for the Asian taxon. As in Averianov and Sues (2021), no unique autapomorphic characters were detected, instead we proposed a modified diagnosis based on a new combination of characters. Nevertheless, it must be noted that further materials are needed to better clarify the validity of this species.

CHARACTER SCORES

Here we comment on several of the characters scored in our data set, starting from those already scored by Averianov and Sues (2021) (as numbered in that contribution) and following from those characters previously defined in augmented versions of the data set of Rauhut *et al.* (2015) (*e.g.*, Canudo *et al.*, 2018; Gallina *et al.*, 2021), plus one character taken from Calvo and Salgado (1995). Other characters not discussed here were scored following Averianov and Sues (2021), without modification. These authors considered the vertebra as the first caudal, based on the absence of chevron facets and its moderate opisthocoelous condition. Whereas the latter seems to be the condition of the first caudal vertebrae of rebbachisaurids (Fernández-Baldor *et al.*, 2011; Carballido *et al.*, 2012) the absence of chevron facets usually occurs between the first and the third caudal element. Thus, solely the unequivocal interpretation of *Dzharatitanis* as a rebbachisaurid will allow the assignment of this caudal as the first. The following discussion and the phylogenetic analyses carried out (see below) considered this element as the first (after Averianov and Sues, 2021) but also as an anterior one (most probably between the second or third caudal, given the absence of chevron facets).

All corresponding matrices and TNT files can be found in the Morphobank under the permalink P3973 (http://morphobank.org/permalink/?P3973; Lerzo *et al.*, 2021). Please see below for detailed information.

Characters scored by Averianov and Sues (2021)

Character 190. First caudal centrum or last sacral vertebra, articular face shape: flat (0); procoelous (1); opisthocoelous (2); biconvex (3). Averianov and Sues (2021) scored this character as opisthocoelous, given that the anterior articular surface is slightly convex and the posterior articular surface is more deeply concave. In the current data set, the articular surfaces of the first caudal vertebra were split into two characters by Carballido *et al.* (2017). Whereas one character refers to the anterior articular surface (character 224) with three states (flat, concave, or convex), a second character (225) refers to the posterior one, with four states (flat, concave, moderate convex, and strongly convex). Thus, we scored this element as having an anterior convex articular surface (character 224: state 2) and a posterior concave one (character 225: state 1).

Character 192. Anterior caudal vertebrae, transverse processes ventral surface: directed laterally or slightly ventrally (0); dorsally directed (1). Averianov and Sues (2021) scored *Dzharatitanis* as having a dorsally directed ventral surface of the transverse process, which is considered a synapomorphic character of rebbachisaurids (Whitlock, 2011). Nevertheless, we scored it as having the plesiomorphic state, *i.e.*, laterally directed ventral surface of the transverse process (character 230: state 0). The laterodorsal orientation of the ventral surface of the transverse process is not equal to that observed in rebbachisaurids, instead it resembles the slightly dorsal orientation of some titanosaurs (such as *Patagotitan*, *Futalognkosaurus*, *Bonitasaura*; Carballido *et al.*, 2017; Calvo *et al.*, 2007; Gallina & Apesteguía, 2015) (Fig. 1, character 230). On the contrary, the anterior caudal vertebrae of rebbachisaurids typically show a marked dorsal angle, such as that observed in *Limaysaurus* Salgado *et al.*, 2004; *Demandasaurus* Fernández-Baldor *et al.*, 2011, *Tataouinea* Fanti *et al.*, 2013, *Nigersaurus* Sereno *et al.*, 1999 (Calvo & Salgado, 1995; Pereda Suberbiola *et al.*, 2003; Fanti *et al.*, 2015).

Character 194. Anterior caudal centra, pleurocoels: absent (0); present (1). Although the state scored by Averianov and Sues (2021) was respected (absence of pleurocoels in anterior caudal vertebrae), the original character was modified and two characters referring to the presence of pleurocoels were included by Gallina *et al.* (2021). Whereas character 228 refers to the presence of lateral "pneumatic" foramen (absent or present), character 232 refers to the development of such foramen (absent or present as small foramen or well developed). Here, both characters were scored with the plesiomorphic state.

Character 197. Anterior and middle caudal vertebrae, triangular lateral process on the neural spine: absent (0); present (1). Despite that the neural spine is laterally expanded, such expansion is not the same observed in rebbachisaurids. Conversely, the development of such lateral expansion resembles that observed in some titanosaurs such as *Patagotitan*, which is scored with the plesiomorphic state (absence) in our character 235. The triangular lateral process observed in rebbachisaurids is much more developed and has marked laterally oriented tips (Fig. 1, character 235).

Character 198. Anterior caudal transverse processes shape: triangular, tapering distally (0); wing-like, not tapering distally (1). Averianov and Sues (2021) scored *Dzharatitanis* as having a wing-like transverse process, instead, we scored it with a different state, as was recently incorporated by Gallina *et al.* (2021). A complete discussion on the differences in the wing-like processes of diplodocoids can be found in Gallina and Otero (2009), who portrayed the differences in the morphology of the anterior caudal transverse processes of sauropods, and in Whitlock *et al.* (2011) regarding PMU R263 and particularly that of diplodocoids. As these latter authors noted, the wing-like transverse process has a dorsolaterally oriented dorsal margin that meets the subvertical lateral margin to form a right-angled at the dorsolateral corner (Whitlock *et al.*, 2011, fig. 3). As this is clearly not the morphology registered in *Dzharatitanis* nor in PMU R263 or some titanosaurs which morphology is either included under the distally tapering transverse process, Gallina *et al.* (2021) added a new state to their character 236 to include the dorsoventrally elongated transverse process of lognkosaurs sauropods. The transverse process of the lognkosaurs *Patagotitan*, *Drusilasaura* Navarrete *et al.*, 2011 or *Futalognkosaurus* (as well as that of *Dzharatitanis* and PMU R263) is formed by a laterally expanded ventral margin, that contacts to the high laterodorsal edge, which is dorsomedially oriented instead of vertical, resulting in a laterally unexpanded dorsal margin (Fig. 1, character 236).

Character 199. Anterior caudal neural spines, transverse breadth: approximately 50% of (0); or greater than anteroposterior length (1). We scored this morphology following Averianov and Sues (2021) in our character 237 (neural spine wider lateromedially than long anteroposteriorly). Nevertheless, the current states of this character were modified concerning the version used by Averianov and Sues (2021). Actually, there are four states under character 237: anterior caudal neural spines, transverse breadth: approximately 50% the anteroposterior length (0); square (1); lateral expanded (2); and + shaped (3). Whereas the laterally expanded neural spines (state 2) are

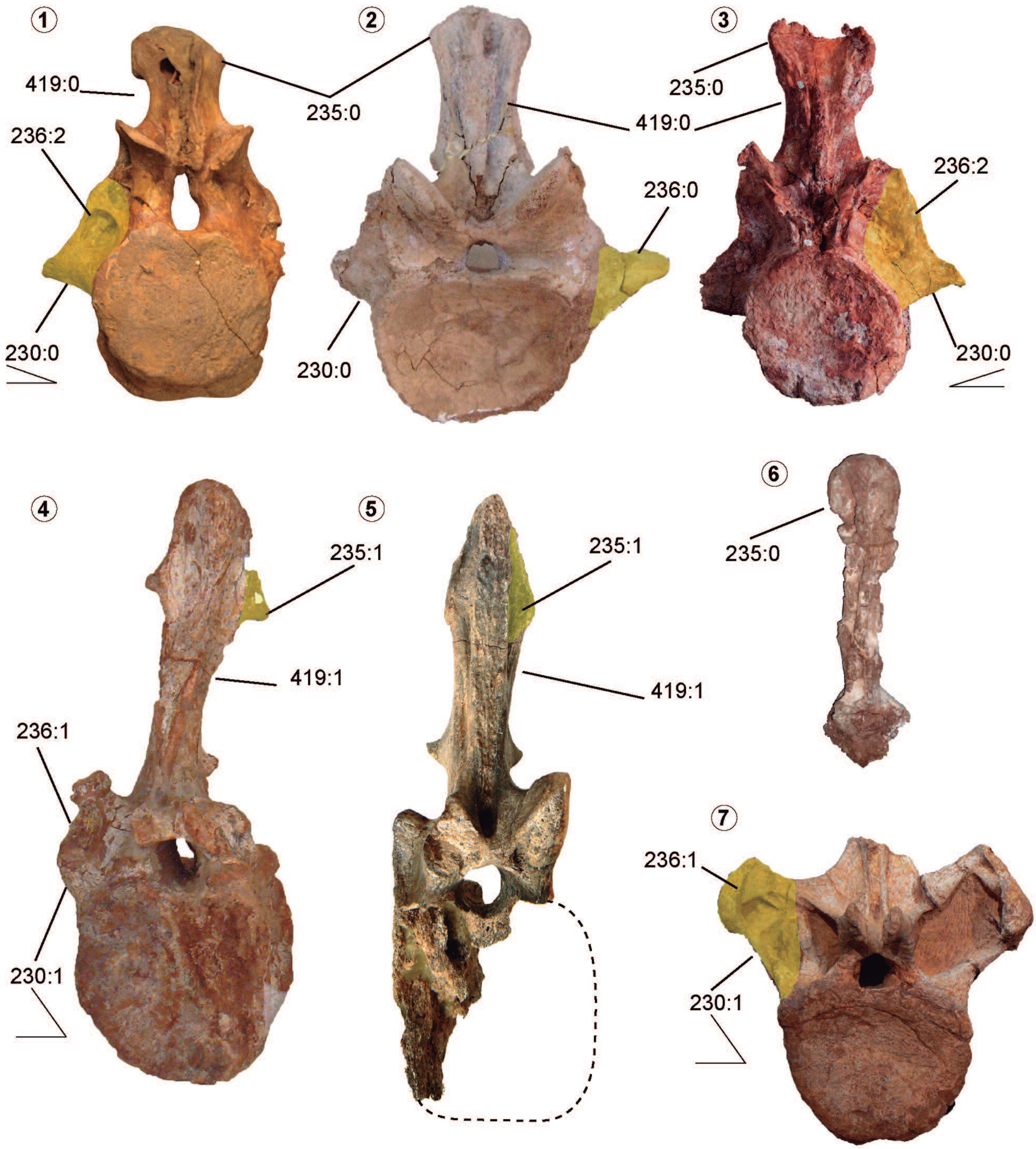

Figure 1. Anterior caudal vertebrae of titanosaur and rebbachisaurid sauropods in anterior view (not in scale). **1,** *Dzharatitanis*, modified from Averianov and Sues (2021, fig. 1). **2,** *Bonitasaura* (MPCA 460). **3,** *Patagotitan* first caudal (MPEF-PV 3400). **4,** *Demandasaurus* (MPS-RV II-15). **5,** *Nigersaurus* (MNN GAD 517). **6,** *Limaysaurus* neural spine (MUCPv-153). **7,** *Demandasaurus* (MDS-RV II-153). Note the wing-like transverse process of the rebbachisaurid *Demandasaurus* (character 236: state 1), the high but not wing-like process of the titanosaur *Patagotitan* and its similarity with *Dzharatitanis* (character 236: state 2), and the distally tapered transverse process of *Bonitasaura* (character 236: state 0). The ventral edge of the transverse process is slightly inclined in *Dzharatitanis*, *Bonitasaurua* and *Patagotitan* (character 230: state 0), whereas it is heavily inclined dorsally in *Demandasaurus* (character 230: state 1). The development of a triangular process is well marked in the neural spine of *Demandasaurus* and *Nigersaurus* (character 235: state 1), whereas it is absent in *Dzharatitanis*, *Bonitasaura*, *Patagotitan* and *Limaysaurus* (character 235: state 0). The neural spine total height is around the same as the height of the centrum in *Dzharatitanis*, *Bonitasaura* and *Patagotitan* (character 419: state 0), whereas it is around 1.5 times in *Demandasaurus* and *Nigersaurus* (character 419: state 1).

widespread amongst colossosaurs, those of rebbachisaurids are + shaped, as a result of the great development of the prespinal, postspinal, and spinodiapophyseal laminae (see Wilson & Allain, 2015, fig. 12). In contrast to *Rebbachisaurus* Lavocat, 1954 and other rebbachisaurids, the prespinal and postspinal laminae of *Dzharatitanis* are laterally tapered by the SPOL and SPRL, which are not laminar but rough inverted triangular-shaped.

Character 205. Anterior caudal neural arches, SPRL: absent, or present as small short ridges that rapidly fade out into the anterolateral margin of the spine (0); present, extending onto the lateral aspect of neural spine (1). Averianov and Sues (2021) scored this character with the plesiomorphic state. Nevertheless, well developed SPRL can be traced throughout the anterior surface of the neural spine of this taxon (Averianov & Sues, 2021, fig. 2). The current version of the data set includes a third state in the character 243 that includes the morphology of a SPRL anterolaterally placed, as is the morphology of *Dzharatitanis* and several titanosaurs. On the contrary, the SPRL of most diplodocoids is, under this modification of the character (see Canudo *et al.*, 2018), extended onto the lateral aspect of the neural spine.

Additional scored characters here included

The numbering of characters corresponds to the data set here used (nexus and TNT files can be downloaded from the Morphobank; Lerzo *et al.*, 2021).

Character 231. Anterior caudal centra (excluding the first), articular face shape: amphiplatyan or amphicoelous (0); procoelous/distoplatyan (1); slightly procoelous (2); procoelous (3); and those with posterior surface markedly more concave than the anterior one (4). This character was scored in the present analysis considering this caudal vertebra as an anterior one but not the first. Given the opisthocoelous condition of this centrum, we incorporate a sixth state, which corresponds to opisthocoelous anterior caudal vertebra and that, in the current taxonomic sample, can be scored solely for *Dzharatitanis* and the Asian titanosaur *Opisthocoelicaudia*.

Character 244. Anteriormost caudal neural arches, SPDL: absent (0); present (1). This one was scored as present.

Character 247. Anterior caudal vertebrae, ventral and medially placed SPRL, usually described as bifurcated PRSL: absent (0); present (1). Presence of a ventral SPRL (sometimes called divided PRSL), was scored as absent in *Dzharatitanis*.

Character 248. Anterior caudal PRSL, triangular shaped product of a dorsal expansion of it: absent (0); present (1). It describes the morphology of the PRSL, differentiating those taxa with dorsally unexpanded PRSL from those with a dorsally expanded PRSL as *Dzharatitanis* and some titanosaurs such as *Patagotitan*, *Mendozasaurus* González Riga, 2003 and *Futalognkosaurus*.

Character 249. Anterior caudal vertebrae, pair thin laminae that are bounding the prespinal laminae and that diverge dorsally: absent (0); present (1). This character describes the presence of a paired lamina that bounds the PRSL and POSL in few taxa such as *Bonitasaura* (Gallina, 2011; Gallina & Apesteguía, 2015) and *Patagotitan* (Carballido *et al.*, 2017). Although it was scored as absent, based on figure 2f of Averianov and Sues (2021), paired laminae similar to those of *Patagotitan* are bounding the dorsally expanded POSL of this taxon.

Character 254. Anterior caudal vertebrae, anterior face of the centrum strongly inclined anteriorly: absent (0); present (1). This character was scored as absent.

Character 419. Anterior caudal neural spine height: 1.5 centrum height or less (0); 1.5 centrum height or more (1). This character was added here from Calvo and Salgado (1995). Contrary to the morphology of the relatively short neural spine of *Dzharatitanis*, the neural spines of diplodocoids are markedly higher than the caudal centrum (Whitlock, 2011; Tschopp *et al.*, 2015)

PHYLOGENETIC ANALYSIS

In order to better evaluate the phylogenetic position of *Dzharatitanis kingi* and the robustness of this position, we conducted two different phylogenetic analyses. At the first one, we used an augmented version of the data set from Rauhut *et al.* (2015) and Gallina *et al.* (2021), with the addition of one character (character 419) and with two different sets of scores for *Dzharatitanis* (considering the caudal vertebra as the first one, or as an anterior one). The second analysis is a revised version of that of Averianov and Sues (2021) rescoring *Dzharatitanis*. As noted above, these authors scored *Dzharatitanis* into the data set of Xu *et al.*

(2018), which is a revised version of that published by Rauhut *et al.* (2015), and besides the inclusion of the caudal vertebra of *Dzharatitanis*, no other modifications were introduced by them. The data set here presented is an augmented version of that of Rauhut *et al.* (2015) and therefore, almost identical to that of Xu *et al.* (2018) but with a wider taxon and character sampling. The data set is composed of 419 characters and 95 taxa (including 13 rebbachisaurids and 27 titanosaurs). Nexus and TNT files can be downloaded from the Morphobank (Lerzo *et al.*, 2021).

The tree search was performed under an equally weighted analysis using New Technologies and conducting replicates up to find 50 hits (replicates that obtained the minimum number of steps). The memory was augmented for saving up to 400.000 trees, and after the initial tree search, the MPTs were subjected to a round of TBR branch swapping. Two different versions of the data set were performed, scoring the vertebra of *Dzharatitanis* as the first caudal, and scoring it as an anterior caudal (not the first). Both analyses recover *Dzharatitanis* as a titanosaur (Fig. 2). Scoring the vertebra as the first caudal resulted in more than 400.000 MPTs of 1457 steps. The strict consensus shows a major polytomy amongst titanosaurs, which can be much improved if *Ninjatitan* Gallina *et al.*, 2021 and *Dzharatitanis* are excluded from the consensus tree, as these taxa can be placed in different positions. Whereas *Ninjatitan* shows the same possible positions as those informed by Gallina *et al.* (2021), *Dzharatitanis* is recovered as a basal lognkosaur or as the sister taxon to *Baurutitan* (Fig. 2). If *Dzharatitanis* is forced as a basal rebbachisaurid two extra steps are needed, whereas an additional one is needed if it is forced as the sister taxon of Khebbashia or in basal positions amongst Rebbachisaurinae and Limaysaurinae. Additional steps are needed if *Dzharatitanis* is placed as a derived Rebbachisaurine.

Analyzing the data set considering the holotype of *Dzharatitanis* as an anterior caudal vertebra resulted in more than 400.000 MPTs of 1455 steps. Forcing *Dzharatitanis* as a basal rebbachisaurid needs 4 extra steps, five if it is placed as the sister taxon to Khebbashia or basal Rebbachisaurine or Limaysaurine, and two extra steps if is nested within more derived rebbachisaurines. Forcing *Dzharatitanis* as a non-titanosaur somphospondylan in both analyses requires the same number of steps as those obtained to place it as a basal rebbachisaurid. Therefore, although the position of *Dzharatitanis* amongst titanosaurs cannot be clearly established, the extra number of steps required to force it into different positions (either as a rebbachisaurid or as a basal somphospondylan) indicates that such positions are much less parsimonious. This is especially obvious when the low number of possible scores (0.95 missing data) for *Dzharatitanis* are taken into account, and when the vertebra is scored as an anterior caudal, which, based on our criterion, is the position in which this element has to be considered (see above).

Derived characters supporting the positions of *Dzharatitanis* amongst Lognkosauria are listed and briefly discussed below. 1) *Dzharatitanis* shares with Colossosauria the presence of a laterally expanded neural spine (character 237), a character convergently acquired in *Baurutitan* (Kellner *et al.*, 2005, fig. 6) and *Xianshanosaurus* (Lü *et al.*, 2009, fig. 7). 2) *Dzharatitanis* shares with *Bonitasaura* and more derived titanosaurs, a dorsally expanded PRSL (character 248). 3) *Dzharatitanis* shares with Lognkosauria the presence of a marked SPDL, which is convergently present in rebbachisaurids (character 244; the lateral lamina that runs from the dorsal edge of the transverse process up to the summit of the neural spine). 4) *Dzharatitanis* shares with lognkosaurs more derived than *Mendozasaurus* a markedly developed transverse process (character 236), which is either the typical wing-like process nor the one tapering distally, as discussed above and in the discussion section (see below).

On the contrary, when the vertebra is scored as the first caudal, one of the positions retrieved for *Dzharatitanis* is as the sister taxon to *Baurutitan*, at the base of the stem conducting to *Saltasaurus* Bonaparte & Powell, 1980. This position is supported by the following character recovered as synapomorphy of *Dreadnoughtus* and more derived titanosaurs: 1) Convex anterior articular surface of the first caudal centrum (character 224). Such distribution of this character is related to the biconvex caudal vertebrae of several titanosaurs recovered in this clades such as *Dreadnoughtus*, *Baurutitan*, *Alamosaurus* Gilmore, 1922, and although the "first'' caudal vertebra of *Dzharatitanis* is not biconvex, it

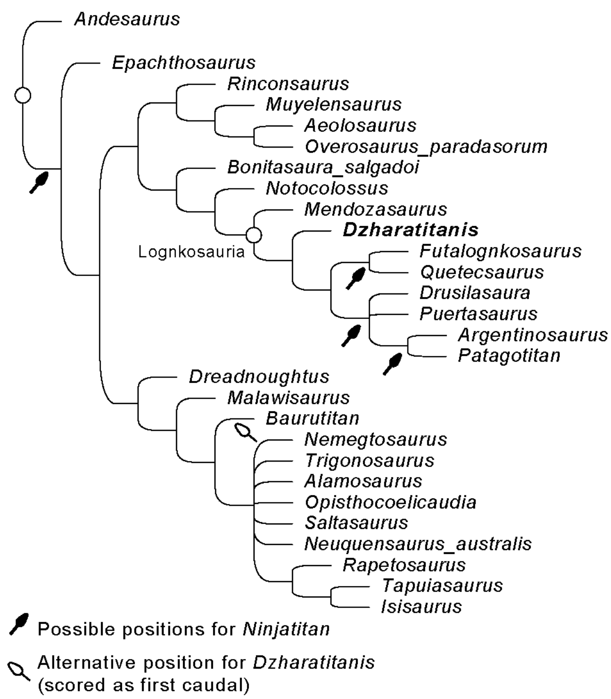

Figure 2. Reduced consensus tree (after pruning *Ninjatitan*) showing the position of *Dzharatitanis kingi* when the vertebra is scored as an anterior caudal. If the vertebra is scored as the first caudal, an alternative position of *Dzharatitanis* as the sister taxon to *Baurutitan* is recovered (white arrow). Possible positions for *Ninjatitan* are shown with black arrows.

shares with them the anterior convexity. Additionally, two characters are recovered as synapomorphies of *Baurutitan*+ *Dreadnougthus*: 1) The markedly developed transverse process (convergently acquired in derived lognkosaurs; see above) and 2) the laterally expanded neural spine (convergently acquired in Colossosauria; see above).

Rescoring into the data set of Averianov and Sues (2021), based on the different interpretation of the characters discussed above, and following the same search criteria used in previous analyses, resulted in 2232 MPTs of 1101 steps (TNT file available in the Morphobank; Lerzo *et al.*, 2021). In this analysis, *Dzharatitanis* is recovered as a somphospondylan titanosauriform. Therefore, both analyses resulted in a similar most parsimonious hypothesis, excluding *Dzharatitanis* from Rebbachisauridae and placing it amongst somphospondylans macronarians.

DISCUSSION

As noted by Whitlock *et al.* (2011), fragmentary specimens are limited in the amount of information that they can provide, which could preclude testing their phylogenetic position especially when they are represented by non-informative elements. Despite that *Dzharatitanis* is represented by a single anterior caudal vertebra, the amount of information provided from this element is enough to broadly test its phylogenetic position. After revising the character scorings for *Dzharatitanis*, the Asian taxon was here recovered as a titanosaur sauropod. In this section, we extended the discussion to the most important characters that differ *Dzharatitanis kingi* from rebbachisaurids sauropods.

The centrum of the anterior caudal vertebrae of *Dzharatitanis* is opisthocoelous with the anterior articular surface of the centrum slightly convex, similar to the first caudal vertebra of *Comahuesaurus windhauseni* Carballido *et al.*, 2012 and *Demandasaurus darwini* Fernández-Baldor *et al.*, 2011. However, within Titanosauria, the opisthocoelic condition is present only in *Opisthocoelicaudia skarzynskii* Borsuk-Bialynicka, 1977 (in titanosaurs, the common feature is procoelous caudals centra). So, this feature probably seems to be more widespread within Titanosauria than previously assumed. Besides, taking into account that probably this caudal vertebra is not the first caudal vertebrae, this condition also differs from Rebbachisauridae, which do not present opisthocoelic anterior caudal vertebrae.

Averianov and Sues (2021) described the transverse processes of *Dzharatitanis kingi* as 'wing-like' such as in *Cathartesaura anaerobica* Gallina & Apesteguía, 2005, *Demandasaurus darwini*, *Itapeuasaurus cajapionensis* Lindoso *et al.*, 2019, *Katepensaurus goicoecheai* Ibiricu *et al.*, 2013, the Bajo Barreal rebbachisaurid (Ibiricu *et al.*, 2012), the Kem Kem rebbachisaruidae (Mannion & Barrett, 2013) and the Wessex rebbachisaurid (Mannion *et al.*, 2011). However, the general morphology resembles those of the Colossosauria sauropods such as *Mendozasaurus neguyelap* González Riga, 2003, *Futalognkosaurus dukei* Calvo *et al.*, 2007, *Patagotitan mayorum* and *Bonitasaura salgadoi* Apesteguía, 2004 (Gallina & Apesteguía, 2015), and the Lithostrotian *Baurutitan britoi* Kellner *et al.*, 2005, as mentioned above (Fig. 2).

The triangular lateral process of the anterior caudal neural spine of *Dzharatitanis* was originally described as present as in the Rebbachisaurine sauropods (Averianov & Sues, 2021) but this process is more developed and has marked lateral tips in that family, here proposed as a probable synapomorphy of Nigersaurinae/Rebbachisaurinae (Whitlock, 2011; Canudo *et al.*, 2018). We consider that this process is absent in this anterior caudal vertebra, in a similar condition observed in some titanosaurs (González Riga, 2003; Carballido *et al.*, 2017; Gallina & Apesteguía, 2015).

The neural spine of the anterior caudal vertebrae of Rebbachisauridae present a characteristic tetralaminated pattern (Pereda Suberbiola *et al.*, 2003; Wilson & Allain, 2015). In some rebbachisaurids, a lateral expansion of the upper third of the lateral lamina results in a 'petal'-shaped morphology that can be seen in *Amazonsaurus maranhensis* Carvalho *et al.*, 2003, *Limaysaurus tessonei* (Calvo & Salgado, 1995), *Katepensaurus* Ibiricu *et al.*, 2013, *Cathartesaura anaerobica* and *Itapeuasaurus cajapioensis*. In *Dzharatitanis* the neural spine does not present the tetralaminated pattern characteristic of Rebbachisauridae, resembling more the neural spine of the lognkosaurian sauropods such as *Futalognkosaurus* or *Patagotitan*. Additionally, the neural spine of *Dzharatitanis* is proportionally short with respect to the centrum height as its total dorsoventral height is less than 1.5 times the centrum height. In that sense, it is similar to those of non-diplodocoid sauropods and different from that of most diplodocoids, including rebbachisaurids.

CONCLUSIONS

The recently described sauropod from Uzbekistan, *Dzharatitanis kingi* is re-evaluated with the scope of better testing its phylogenetic position within Neosauropoda. Through two different phylogenetic analyses (including the rescoring of the taxon in the data set of Averianov and Sues, 2021) the Asian taxon was recovered within somphospondylans. When the most actualized data set is analyzed (both in taxon and character sampling), *Dzharatitanis* is recovered within Titanosauria. Scoring the vertebra as the first caudal retrieves *Dzharatitanis* as related to the Brazilian lithostrotian *Baurutitan* and lognkosaurian colossosaurs. When it is scored as an anterior caudal vertebra, this taxon is recovered well nesting within Lognkosauria. Based mainly on the morphology of the high but not wing-like transverse processes, the poor developed triangular lateral process of the neural spine, the absence of a tetralaminated pattern in the caudal neural spine, and the relatively short caudal neural spine, the exclusion of this Asian sauropod from the family Rebbachisauridae is well supported. Although more complete evidence is needed, the reinterpretation of *Dzharatitanis* as a titanosaur with lognkosaurian affinities suggests a wider biogeographic distribution of this group of colossosaurs during the Cretaceous, not restricted to Patagonia, as previously thought (*contra* Carballido *et al.*, 2017). Finally, at present, there is no reliable evidence to assume that rebbachisaurid sauropods have inhabited Asia.

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