

# Additional skulls of *Talarurus plicatospineus* (Dinosauria: Ankylosauridae) and implications for paleobiogeography and paleoecology of armored dinosaurs

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## ABSTRACT

Three new additional skull specimens of *Talarurus plicatospineus* have been recovered from the Upper Cretaceous (Cenomanian–Santonian) Bayanshiree Formation, of Bayan Shiree cliffs, eastern Gobi Desert, Mongolia. The skulls feature unique characters such as an anteriorly protruded single internarial caputegulum, around 20 flat or concave nasal-area caputegulae surrounded by a wide sulcus, a vertically oriented elongate loreal caputegulum with a pitted surface, an elongate lacrimal caputegulum positioned above the posterodorsal border of the maxilla, two longitudinally arranged large frontoparietal caputegulae surrounded by smaller rhomboid caputegulae, small but elongate medial supraorbital caputegulae, a posterior supraorbital caputegulum that is four times larger than the anterior one, up to three transverse parallel grooves on the dorsal surface of the posterior supraorbital caputegulum, postocular caputegulae along the ventral to posterior rim of the orbit that extend almost to the anteroventral margin of the squamosal horn, a longitudinal furrow tapering towards the apex of the squamosal horn, a lateral nuchal caputegulum four to five times larger than other nuchal caputegulae, and a pterygomerine keel with a ventral margin that is dorsally positioned to the alveolar ridge. The phylogenetic analysis result showed that *Talarurus* is sister to the clade that includes the derived Asian ankylosaurines (*Saichania chulsanensis*, *Tarchia kielanae*, and *Zaraapelta nomadis*). It also shows that there was dispersal of ankylosaurines from Asia into western North America before the Cenomanian. Moreover, the rostral differences between *Talarurus* and *Tsagantegia*, another ankylosaur from the same formation, suggest possible niche partitioning between these taxa.

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## 1. Introduction

*Talarurus plicatospineus* (Maleev, 1952) is an armored dinosaur from the Upper Cretaceous Bayanshiree Formation of Mongolia. Since its initial discovery, numerous specimens have been

collected, including partial postcranial skeletons of six individuals from the Bayan Shiree cliffs and many fragmentary specimens from nearby localities (Tumanova, 1987, 2000; Arbour and Currie, 2016). However, cranial elements of *Talarurus* are rare, and only two incomplete skulls including the holotype have been described in the scientific literature (Maleev, 1952; Tumanova, 1987). The holotype skull (PIN 557-91) only includes the frontal, parietal, and occipital regions with partial squamosal horns (Maleev, 1952). Another partial cranium (PIN 3780/1) includes the skull roof, occipital regions, and a nearly complete braincase (Tumanova, 1987).

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Both specimens lack the premaxillae and maxillae, ventral rami of the jugals, the ventral postorbital regions (including the quadratojugal horns), most of the palatal elements, and the mandibles. Therefore, much of the cranial morphology of *Talarurus* has been unknown.

Here we present three new additional skulls of *Talarurus*, which are much more complete than the previously reported materials. They allow us to more accurately reconstruct the overall shape of the skull of *Talarurus*, and to understand detailed cranial anatomy of this taxon. Furthermore, they provide new information on ankylosaur phylogeny, intercontinental exchange of ankylosaurines between Asia and North America during the Cretaceous, and also have implications for understanding niche partitioning among armored dinosaurs.

### 1.1. Institutional abbreviations

MPC, Mongolian Paleontological and Geological Institute, Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; PIN, Paleontological Institute, Russian Academy of Sciences, Moscow, Russia.

## 2. Geological setting

The Bayanshiree Formation is a terrestrial sedimentary succession and is up to 300 m thick (Martinson, 1982; Jerzykiewicz and Russell, 1991; Hicks et al., 1999; Jerzykiewicz, 2000). The formation conformably overlies the Sainshand Formation and underlies the Javkhant Formation (Eberth et al., 2009). It is widely distributed in the eastern Gobi basins of Mongolia (Jerzykiewicz and Russell, 1991; Hicks et al., 1999), comprising multi-colored clays with fluvial fine-grained sandstones with calcareous concretions (Vasiliev et al., 1959), and conglomerates (Sochava, 1975; Martinson, 1982; Jerzykiewicz, 2000). A variety of fossils have been discovered from the Bayanshiree Formation, including freshwater ostracods and mollusks (Barsbold, 1972; Sochava, 1975; Hicks et al., 1999), fishes (Efremov, 1949), an abundance of turtles (Mlynarski and Narmandach, 1972; Sukhanov and Narmandach, 1975; Chkhikvadze and Shuvalov, 1980; Jerzykiewicz and Russell, 1991; Sukhanov, 2000; Danilov et al., 2014), neosuchian crocodyliforms (Efimov, 1983; Jerzykiewicz and Russell, 1991; Turner, 2015; Lee et al., 2019), and a wide range of dinosaurs such as ankylosaurs (Maleev, 1952; Tumanova, 1987, 1993; Arbour and Currie, 2016), ceratopsians (Maryańska and Osmólska, 1975; Jerzykiewicz

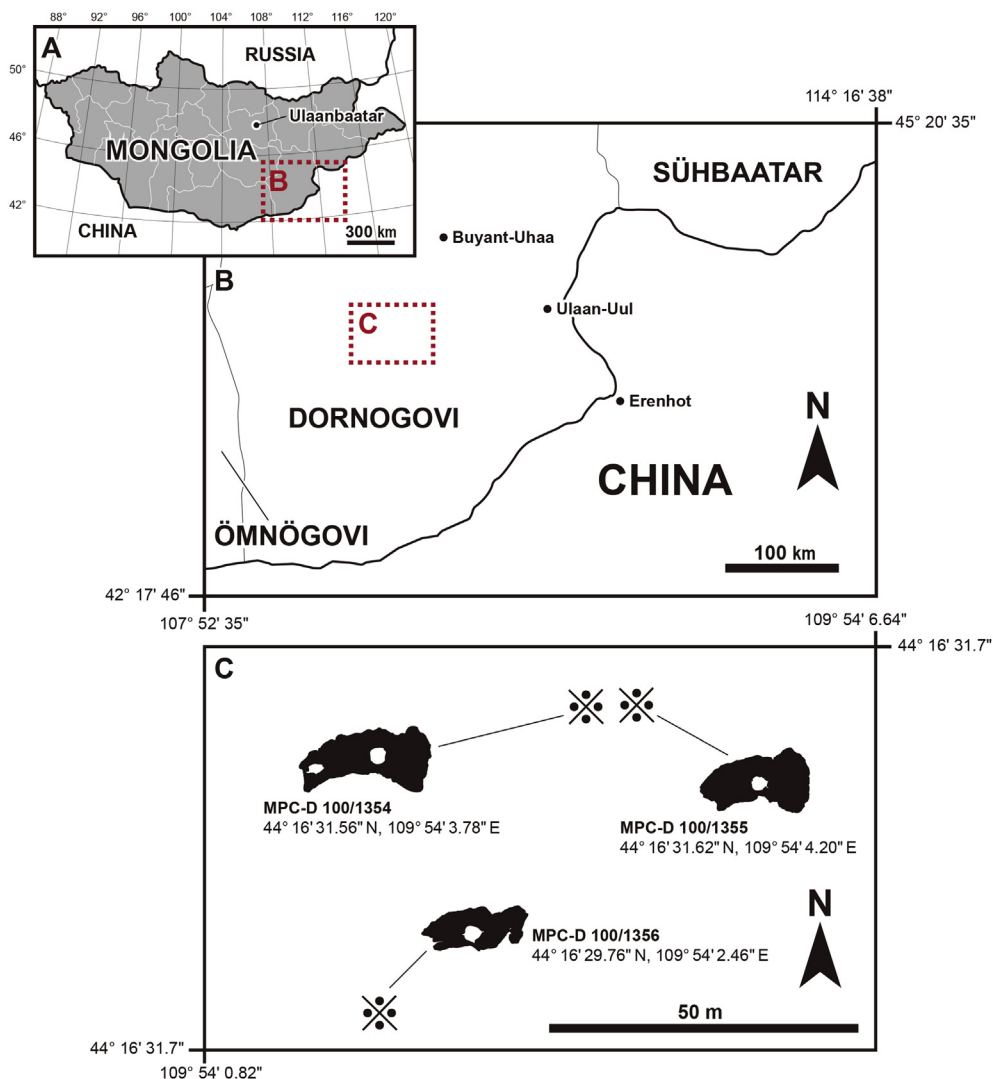
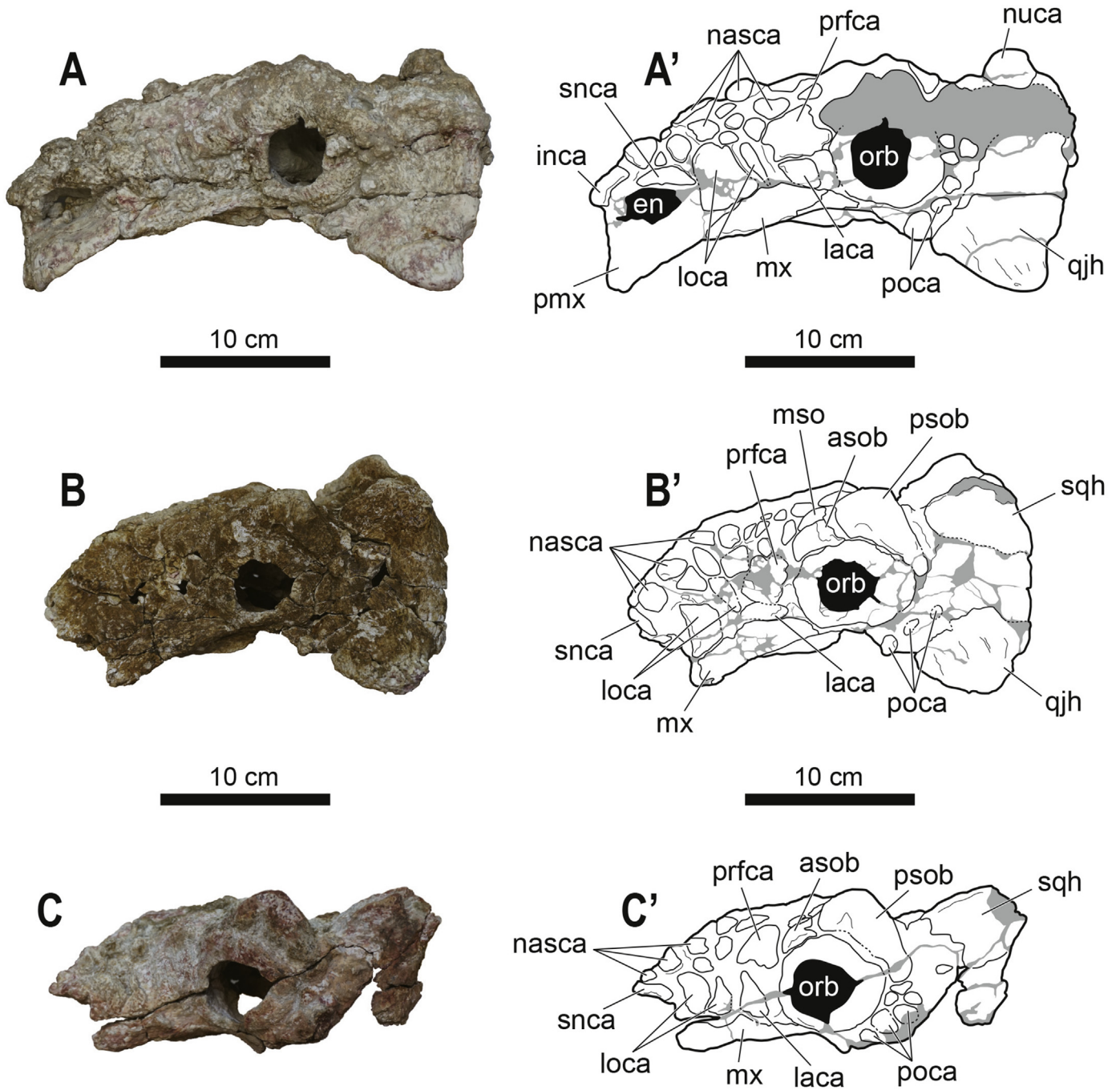


Fig. 1. Map showing the locality where the new skull specimens of *Talarurus plicatospineus* were discovered. (A) Map of Mongolia. (B) Magnified map from A (surrounded by the dotted lined rectangle). (C) Magnified map from B (surrounded by the dotted lined rectangle) with the locality marked by the reference mark (⊗).



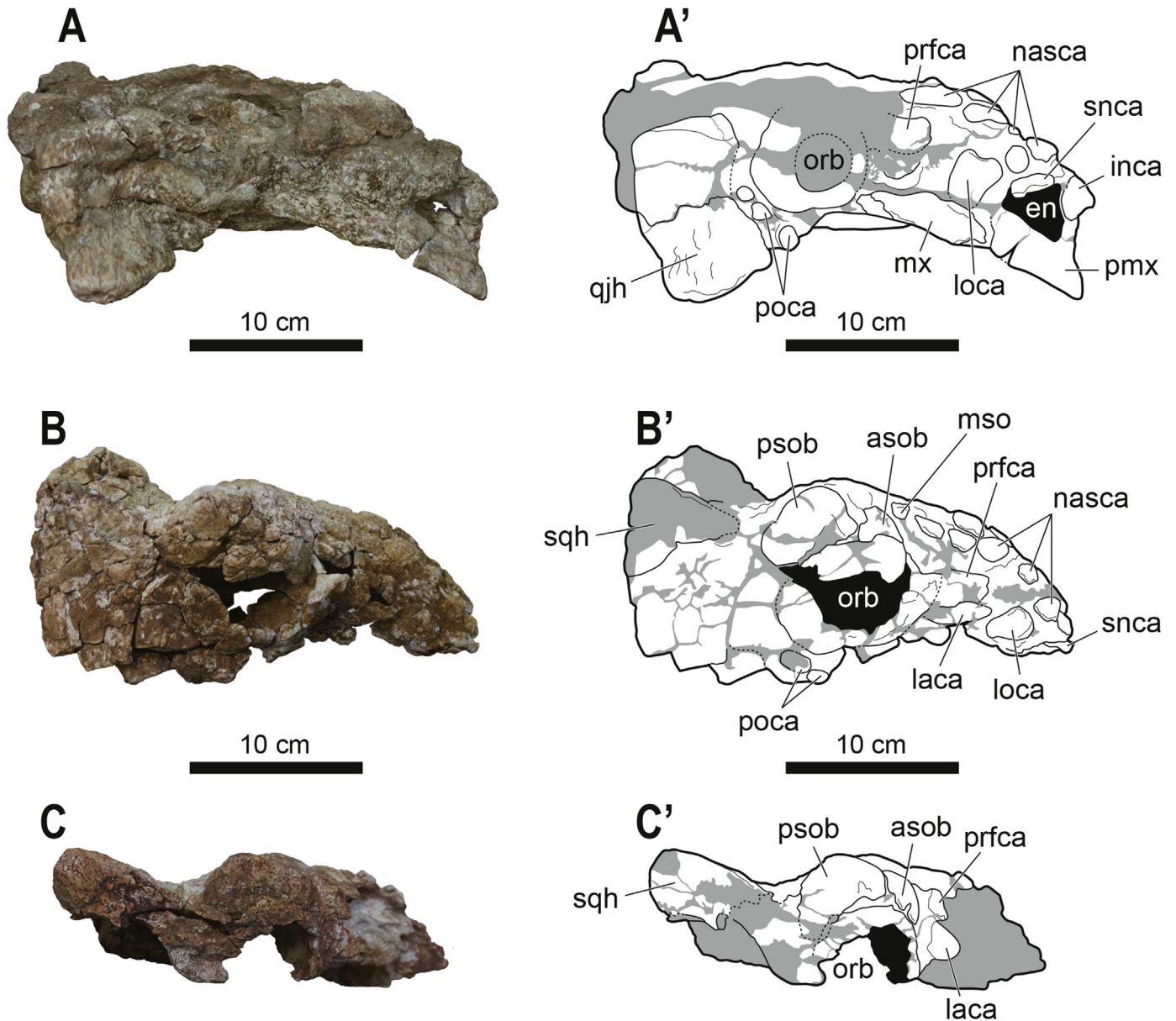
**Fig. 2.** Photographs (A–C) and line drawings (A'–C') of new skull specimens of *Talarurus plicatospineus* in left lateral view. (A–A') MPC-D 100/1354. (B–B') MPC-D 100/1355. (C–C') MPC-D 100/1356. Grey area indicates damaged surface. Abbreviations are as follows: asob, anterior supraorbital caputegulum; en, external naris; inca, internarial caputegulum; laca, lacrimal caputegulum; loca, loreal caputegulum; mso, middle supraorbital caputegulae; mx, maxilla; nasca, nasal caputegulum; nuca, nuchal caputegulum; orb, orbit; pmx, premaxilla; pocca, postocular caputegulum; prfca, prefrontal caputegulum; psob, posterior supraorbital caputegulum; qjh, quadratojugal horn; snca, supranarial caputegulum; sqh, squamosal horn.

and Russell, 1991), hadrosauroids (Maryńska and Osmólska, 1975, 1981; Tsogtbaatar et al., 2019), sauropods (Martinson, 1982), tyrannosaurids (Perle, 1977), ornithomimosaurids (Jerzykiewicz and Russell, 1991; Makovicky et al., 2004), therizinosaurids (Jerzykiewicz and Russell, 1991; Russell and Dong, 1993), and dromaeosaurids (Barsbold, 1983). Comparisons to vertebrate faunas of North American non-marine units, which are well confined by ammonite zonation and palynology, yield a late Cenomanian–Coniacian to early Santonian age (Jerzykiewicz and

Russell, 1991). However, magnetostratigraphical and palynological analysis suggests a deposit age between Cenomanian to no later than the Santonian (Hicks et al., 1999).

### 3. Materials and methods

All new *Talarurus* specimens (MPC-D 100/1354, MPC-D 100/1355, and MPC-D 100/1356) were collected from the sandstone layer at the type section of the Bayanshiree Formation, eastern Gobi

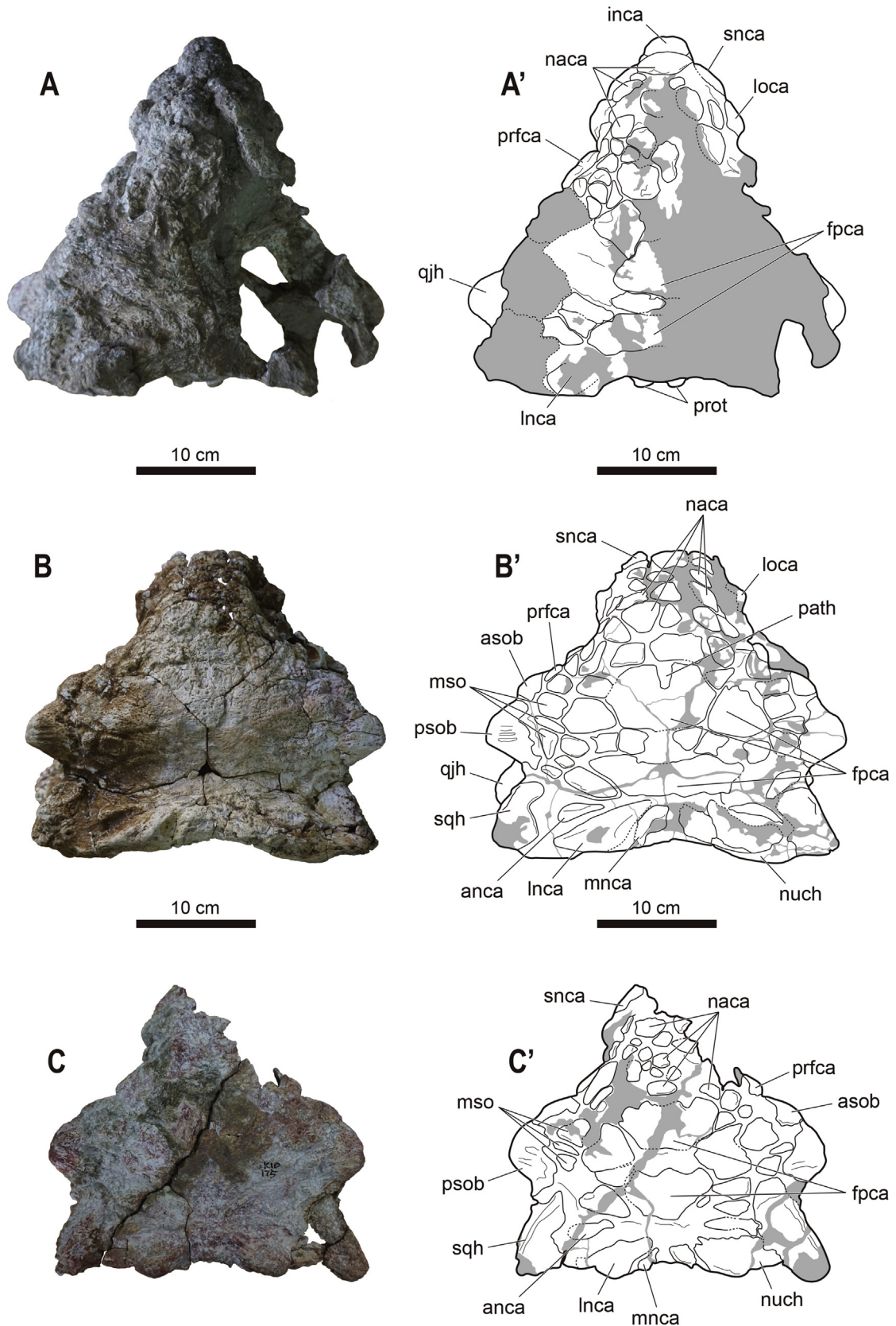


**Fig. 3.** Photographs (A–C) and line drawings (A'–C') of new skull specimens of *Talarurus plicatospineus* in right lateral view. (A–A') MPC-D 100/1354. (B–B') MPC-D 100/1355. (C–C') MPC-D 100/1356. Grey area indicates damaged surface. Abbreviations as in Fig. 2.

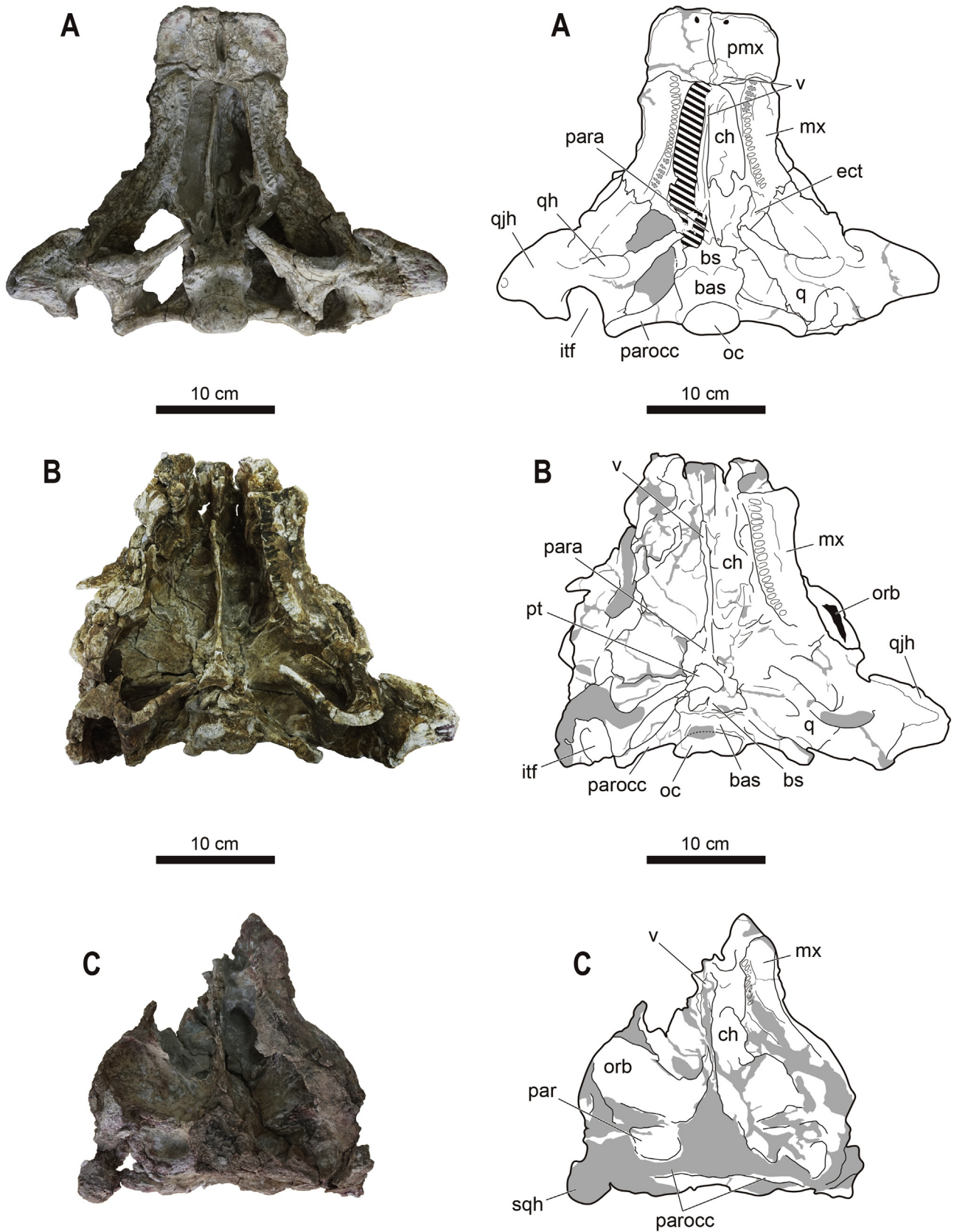
Desert, Mongolia during the Korea-Mongolia International Dinosaur Expedition in 2007 (Fig. 1). Fossil preparation was done at the Hwaseong City laboratory of South Korea in 2013, and the specimens are now permanently held in the Institute of Paleontology and Geology in Ulaanbaatar, Mongolia. All measurements were taken using a measuring tape and a digital caliper. Comparisons to other ankylosaurid taxa were made by examining some specimens in MPC and from published literature. The term 'caputegulum' (*sensu* Blows, 2001) is used herein to refer to cranial ornamentation.

To determine the phylogenetic position, the skull-related characters of *Talarurus* were re-coded into the data matrix of Zheng et al. (2018), with addition of *Akainacephalus* (Wiersma and Irmis, 2018). "*Zhejiangosaurus*" and all nodosaurids, with the exception of *Gargoyleosaurus* and *Nodosaurus*, were excluded for improved consistency index. We have also corrected one error in the data

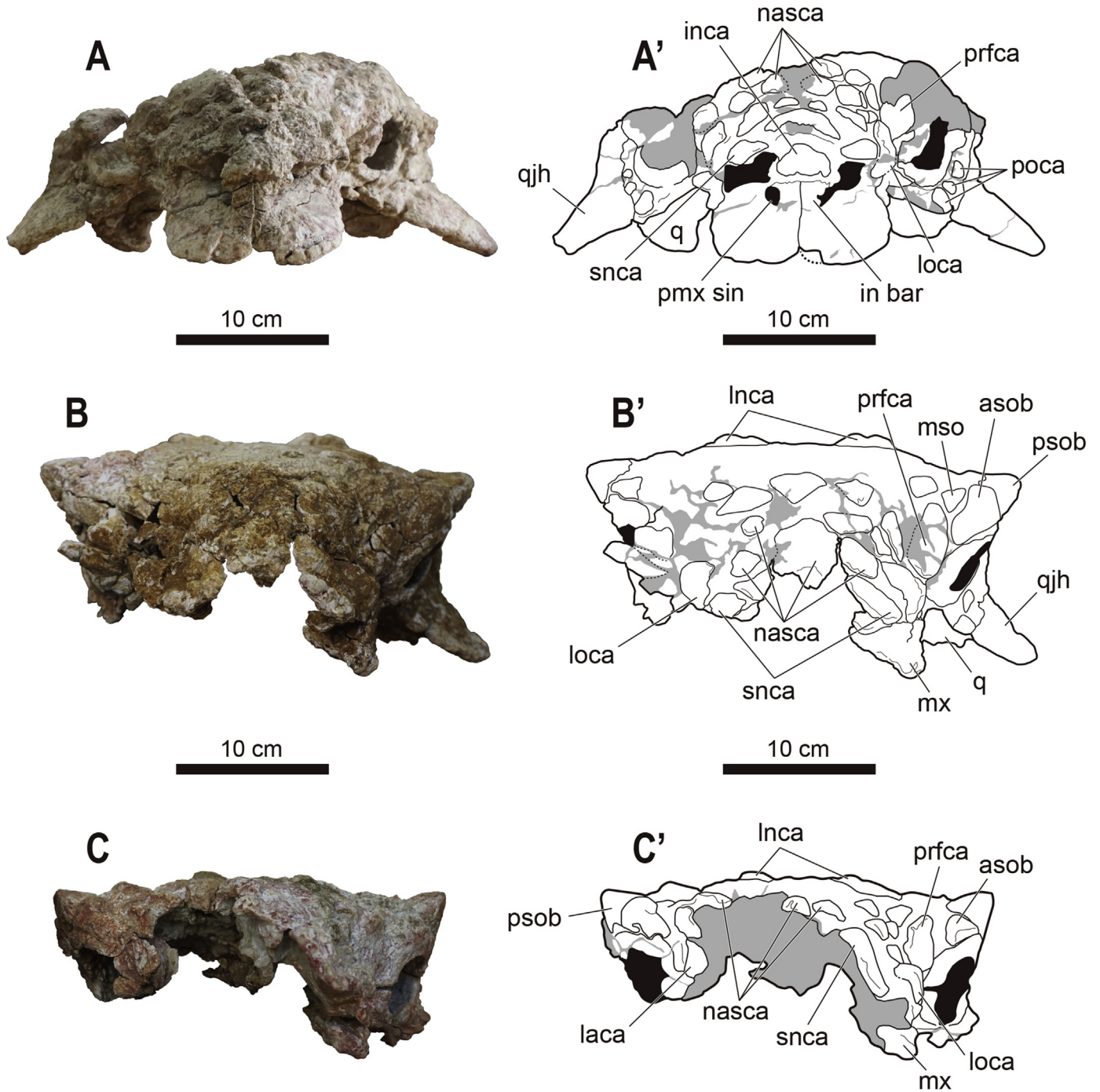
matrix of *Tsagantegia* (character state 15:1 was changed to 15:0). We should note that the data matrix of Zheng et al. (2018), which is based on Arbour and Currie (2016), includes *Minotaurasaurus ramachandrani* within *Tarchia kielanae*, *Tarchia teresae* within *Saichania chulsanensis*, and *Oohkotokia horneri* within *Scolosaurus cutleri*. The revised dataset of 177 characters and 27 taxa (25 ingroup and two outgroup taxa) were analyzed using TNT (Tree Analysis Using New Technology) version 1.1 (Goloboff et al., 2008). All characters were treated as unordered and of equal weight. A traditional search (Wagner trees; swapping algorithm: tree bisection-reconnection; random seeds: 1; replicates: 1000; trees to save per replication: 10) was performed, and the 'Bremer.run' script was used to calculate the Bremer support values on each node of the strict consensus tree.



**Fig. 4.** Photographs (A–C) and line drawings (A'–C') of new skull specimens of *Talarurus plicatospineus* in dorsal view. (A–A') MPC-D 100/1354. (B–B') MPC-D 100/1355. (C–C') MPC-D 100/1356. Grey area indicates damaged surface. Abbreviations are as follows: anca, anterolateral nuchal caputegulum; asob, anterior supraorbital caputegulum; fpca, frontoparietal caputegulum; inca, internarial caputegulum; Inca, lateral nuchal caputegulum; loca, loreal caputegulum; mnca, medial nuchal caputegulum; mso, middle supraorbital caputegulae; nasca, nasal caputegulum; nuch, nuchal shelf; path, pathology; prfca, prefrontal caputegulum; prot, protuberance; psob, posterior supraorbital caputegulum; q, quadrate; qjh, quadratojugal horn; snca, supranarial caputegulum; sqh, squamosal horn.



**Fig. 5.** Photographs (A–C) and line drawings (A'–C') of new skull specimens of *Talarurus plicatospineus* in palatal view. (A–A') MPC-D 100/1354. (B–B') MPC-D 100/1355. (C–C') MPC-D 100/1356. Grey area indicates damaged surface. Diagonal solid lines indicate unremoved matrix. Abbreviations are as follows: bas, basioccipital; bs, basisphenoid; ch, channel; ect, ectopterygoid; itf, infratemporal fenestra; mx, maxilla; oc, occipital condyle; orb, orbit; par, parietal; para, parasphenoid; parocc, paroccipital process; pmx, premaxilla; pt, pterygoid; qh, quadrate head; qjh, quadratojugal horn; sqh, squamosal horn; v, vomer.



**Fig. 6.** Photographs (A–C) and line drawings (A'–C') of new skull specimens of *Talarurus plicatospineus* in anterior view. Grey area indicates damaged surface. (A–A') MPC-D 100/1354. (B–B') MPC-D 100/1355. (C–C') MPC-D 100/1356. Abbreviations are as follows: asob, anterior supraorbital caputegulum; in bar, internarial bar; inca, internarial caputegulum; laca, lacrimal caputegulum; Inca, lateral nuchal caputegulum; loca, loreal caputegulum; mso, middle supraorbital caputegulae; mx, maxilla; nasca, nasal caputegulum; pmx sin, premaxillary sinus; poca, postocular caputegulum; prfca, prefrontal caputegulum; psob, posterior supraorbital caputegulum; q, quadrate; qjh, quadratojugal horn; snca, supranarial caputegulum.

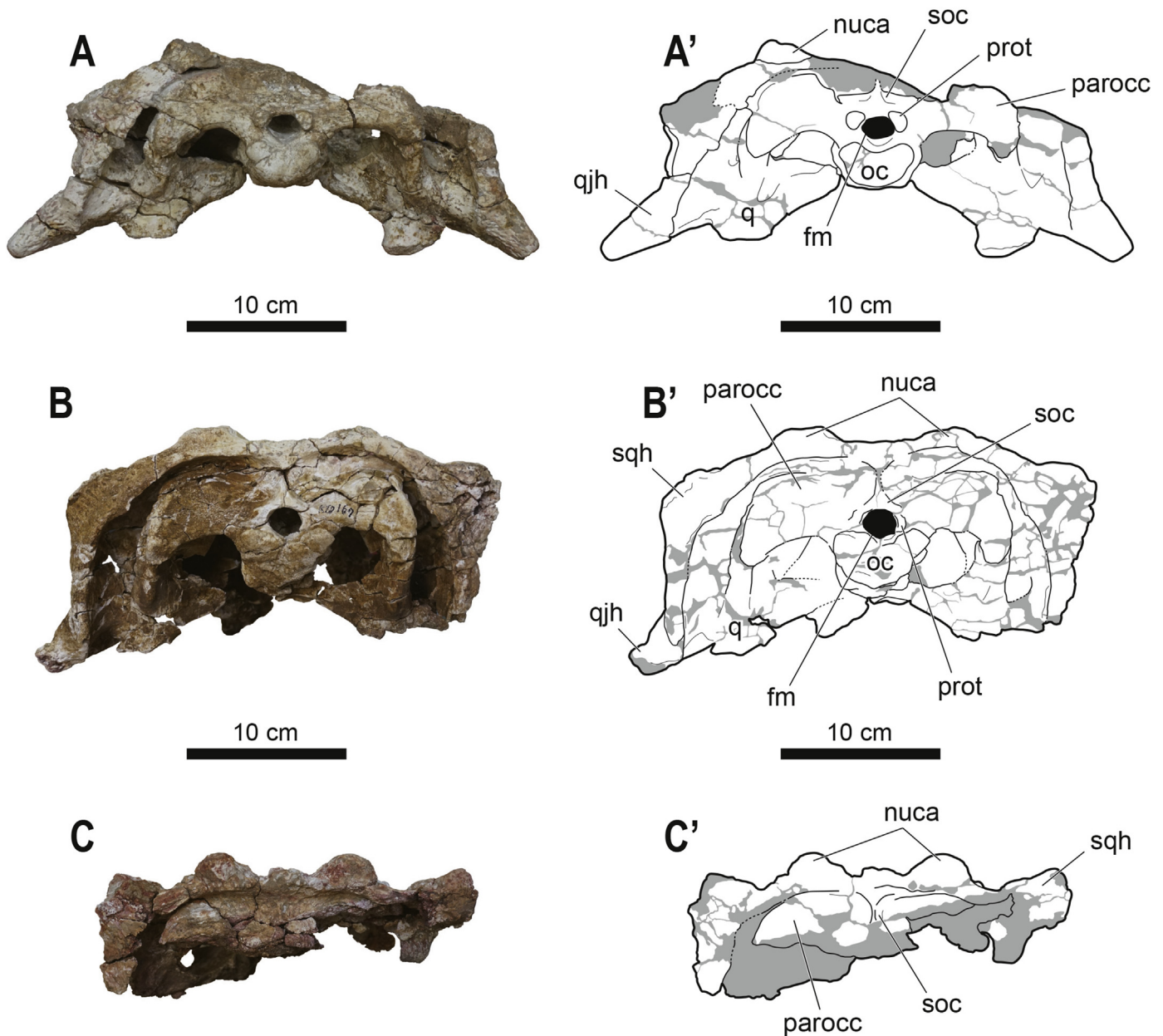
#### 4. Systematic paleontology

Dinosauria Owen, 1842.  
 Ornithischia Seeley, 1887.  
 Thyreophora Nopcsa, 1915 (sensu Norman, 1984).  
 Ankylosauria Osborn, 1923.  
 Ankylosauridae Brown, 1908.  
 Ankylosaurinae Nopcsa, 1918 (sensu Sereno, 1998).

*Talarurus plicatospineus* Maleev (1952).

**Type specimen.** PIN 557, an incomplete posterior portion of skull (Maryańska, 1977). Postcranial materials from at least three different individuals were originally included by Maleev (1956) as part of the holotype, but were subsequently excluded by Maryańska (1977).

**Studied specimens.** MPC-D 100/1354 (Figs. 2–8), a nearly complete cranium except for the damaged right dorsal surface. MPC-D



**Fig. 7.** Photographs (A–C) and line drawings (A'–C') of new skull specimens of *Talarurus plicatospineus* in occipital view. Grey area indicates damaged surface. (A–A') MPC-D 100/1354. (B–B') MPC-D 100/1355. (C–C') MPC-D 100/1356. Abbreviations are as follows: fm, foramen magnum; nuca, nuchal caputegulum; oc, occipital condyle; parocc, paroccipital process; prot, protuberance; q, quadrate; qjh, quadratojugal horn; soc, supraoccipital; sqh, squamosal horn.

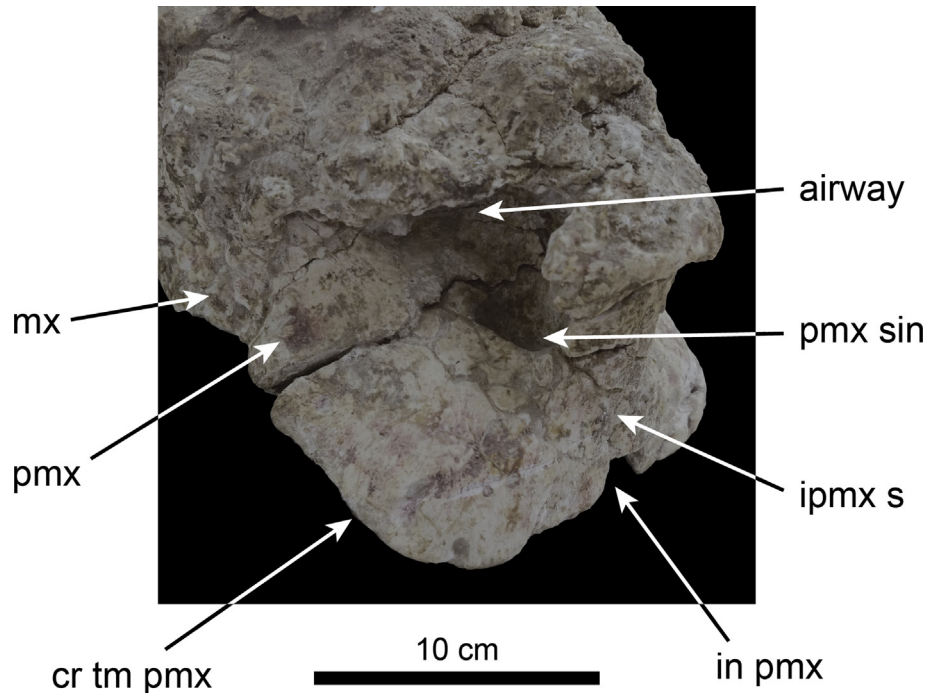
100/1355 (Figs. 2–7 and 9), a skull (lacking the nasal area) plus one partial left mandible, and one partial cervical half ring, one dorsal vertebra, one dorsal rib piece and other postcranial fragments. MPC-D 100/1356 (Figs. 2–7), a cranium lacking the nasal area.

**Locality and horizon.** Holotype and all other materials are from the Upper Cretaceous (Cenomanian–Santonian) Bayanshiree Formation, Bayan Shiree cliffs, eastern Gobi Desert, Mongolia.

**Revised diagnosis.** An ankylosaurid distinguished by the following unique set of characters (autapomorphies with an asterisk): an anteriorly protruded single internarial caputegulum\*; around 20 flat or concave caputegulae surrounded by a wide sulcus present in the nasal region\*; a vertically oriented, elongate loreal caputegulum with pitted surface\*; an elongate lacrimal caputegulum positioned above the posterodorsal border of the

maxilla\*; two longitudinally arranged large frontoparietal caputegulae surrounded by smaller rhomboid caputegulae\*; small but elongate medial supraorbital caputegulae\*; a posterior supraorbital caputegulum that is four times larger than the anterior one\*; up to three transverse parallel grooves on the dorsal surface of the posterior supraorbital caputegulum\*; a “neck” present at the base of the quadratojugal horn (shared with *Pinacosaurus mephistocephalus* and *Minotaurasaurus*); postocular caputegulae ventral to the posterior rim of the orbit extend almost to the anteroventral margin of the squamosal horn\*; a longitudinal furrow tapering towards the apex of the squamosal horn\*; a lateral nuchal caputegulum four to five times larger than surrounding nuchal caputegulae\*; ventral margin of the pterygovomerine keel positioned dorsal to the alveolar ridge\*; paired basal tubera of basisphenoid medially divided (shared with *Akainacephalus* and *Gobisaurus*);





**Fig. 8.** Rostrum of *Talarurus plicatospineus*, MPC-D 100/1354, in right oblique rostradorsolateral view. Abbreviations are as follows: cr tm pmx, premaxillary tomial crest; in pmx, premaxillary notch; ipmx s, interpremaxillary suture; mx, maxilla; pmx, premaxilla; pmx sin, premaxillary sinus.

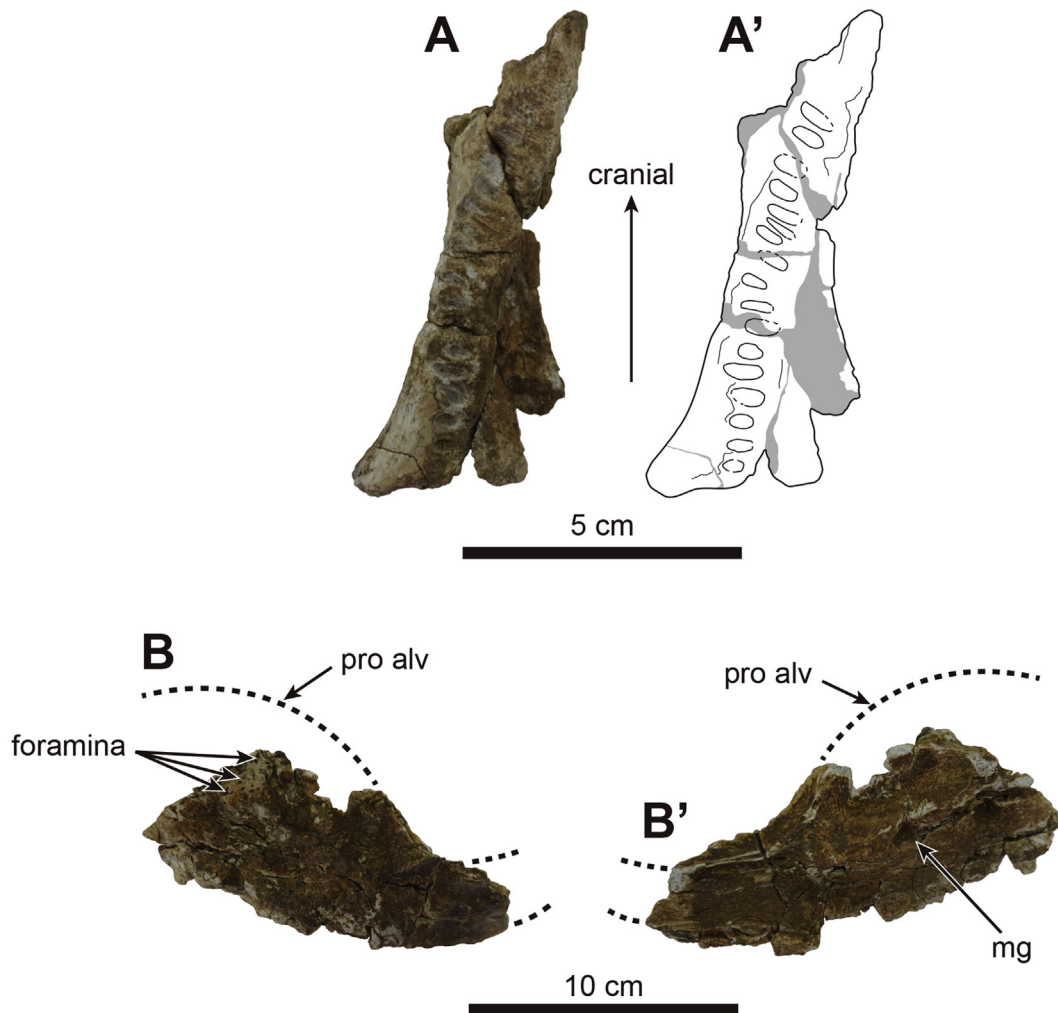
short paroccipital span that does not reach the squamosal horns (shared with *Akainacephalus* and *Minotaurasaurus*).

**Remarks.** All skull materials of *Talarurus* (PIN 557, 3780/1 and MPC-D 100/1354, 100/1355, 100/1356) share the following characters: polygonal nasal and frontal caputegulae with wide sulci between each; no lacrimal incisure (*sensu* Arbour et al., 2014b); large frontoparietal caputegulae surrounded by smaller caputegulae; small but elongate medial supraorbital caputegulae; laterally protruding large posterior supraorbital caputegulae; no overlap between the posterior border of the supraorbital caputegulum and the anterior border of squamosal horn in lateral view; transverse frontoparietal depression (*sensu* Godefroit et al., 1999); large lateral nuchal caputegulum that is four to five times larger than the medial ones; nuchal caputegulae slightly overhang the posterior margin of the skull; nuchal shelf ventrally fused with the supraoccipital and the paroccipital processes; anterolaterally projected short and stout basiptyergoid processes; medially divided and rounded rugose basal tubera on basisphenoid; posteroventrally directed reniform occipital condyle; foramen magnum wider than high; sagittal nuchal ridge on supraoccipital that increases in transverse width ventrally and dorsally; short paroccipital span that does not reach the squamosal horns; paroccipital process tapers in height towards the lateral terminus and curves ventrally. Among these features, the overall morphology of the caputegulae in general and the supraorbital and nuchal caputegulae in particular are considered to be diagnostic. Therefore, it is apparent that all three new specimens are *Talarurus*.

*Talarurus* was previously diagnosed by Arbour and Currie (2016) based on a single autapomorphy, which is the presence of a unique V-shaped upraised area, anteromedial to the transverse frontoparietal depression. This V-shaped area is observable in PIN 557-91. Although Penkalski (2018) considered this as a possible result of taphonomic alteration, it is obvious that it is the anterior boundary of the posteriorly situated large frontoparietal caputegulum. However, this boundary is transversely linear in PIN 3780/1 and MPC-D 100/1355. It also appears to be W-shaped in MPC-D 100/1356 (Fig. 4). We consider this to be intraspecific variation.

**Description.** All of three skulls are similar in size (Table 1). MPC-D 100/1354 is 301 mm in length and 372 mm in greatest width across the two quadratojugal horns. The preserved portion of MPC-D 100/1355 is 262 mm in length and 333 mm in greatest width. The preserved mandibular element of MPC-D 100/1355 is 137 mm in length and 75 mm in greatest height. The preserved portion of MPC-D 100/1356 is 249 mm in length and 265 mm in greatest width. In dorsal view, all skulls are trapezoidal in shape and wider than long (Fig. 4). Although MPC-D 100/1355 includes a few isolated postcranial elements, in this paper only the skull materials of *Talarurus* are being considered and the postcranial elements of MPC-D 100/1355 will be presented elsewhere. The neuroanatomy of MPC-D 100/1354 was already fully described (Paulina-Carabajal et al., 2018). For more detailed comparative description of MPC-D 100/1354, 100/1355, and 100/1356, see supplementary text 1.

**Rostral region:** The premaxillae (Figs. 2–6 and 8) are fused although an interpremaxillary suture (*sensu* Vickaryous and Russell, 2003) is present. A premaxillary notch can be observed on the anterior tip. The anterior boundary of the combined premaxillae is straight transversely and the broad internarial bar is oriented vertically. The exposed premaxilla-maxilla suture inclines posterodorsally. The palatal surfaces of the premaxillae are broad and rectangular. There are no premaxillary teeth. The external nares are triangular and face anterolaterally. A single paranasal aperture is present behind the internarial bar (Fig. 8). The external nares are rimmed dorsally by the elongate supranarial caputegulae. A single large internarial caputegulum protrudes anteriorly over the premaxillae (Figs. 2–4 and 8). Around 20 caputegulae are present in the nasal region (Fig. 4). These caputegulae are relatively small, mostly irregular, flat or concave, and are surrounded by a wide sulcus. The exposed maxillae are anteroposteriorly elongate and extend below the orbits. In palatal view (Fig. 5), the convex maxillary tooth row is situated medial to the buccal emargination. At least 23 alveoli are present in each maxilla, but no maxillary teeth are preserved. Two loreal caputegulae are present on each side (Figs. 2 and 3). The most anterior loreal caputegulum is large and rhomboid, whereas the posteriormost loreal caputegulum is



**Fig. 9.** New maxilla and dentary specimens of *Talarurus plicatospineus*, MPC-D 100/1355. (A–A') Photograph (A) and line drawing (A') of isolated right maxilla in palatal view. (B–B') Partially preserved right dentary in external (B) and medial (B') views. Grey area indicates damaged surface. Abbreviations are as follows: mg, Meckalian groove; pro alv, alveolar border.

**Table 1**

Measurements (mm) of the new skull specimens of *Talarurus plicatospineus* referred to in the text. Tilde symbol (~) indicates that the measurement is given in terms of the specimen as preserved. 'L' refers to a structure from the left side, 'R' to a structure from the right side.

Specimens	Skull dimension				Orbit dimension	
	Craniocaudal length	Transverse width across:			Width	Height
		Supraorbitals	Squamosal horns	Quadratojugal horns		
MPC-D 100/1354	301	~194	~306	372	L: 34 R: ~33	L: 35 R: ~34
MPC-D 100/1355	~262	302	290	~333	L: 34 R: 49	L: 31 R: 34
MPC-D 100/1356	~249	265	263	~234	L: 38 R: 45	L: 33 R: ~35

elongate. Only one lacrimal caputegulum is present on each sides (Figs. 2 and 3). This small, elongate ornament is located above the posterodorsal border of the maxilla. A large rhomboid “prefrontal” caputegulum is behind the loreal caputegulae, and an additional small prefrontal caputegulae is present along the anteromedial border of the anterior supraorbital caputegulum (Fig. 4).

**Temporal region:** The frontoparietal caputegulae (Fig. 4) form a mosaic pattern. Two large frontoparietal caputegulae are medially positioned on the skull roof. These ornamentations are transversely wide, mostly hexagonal, and are surrounded by smaller

caputegulae. In the holotype, only the posteriormost large frontoparietal caputegulum is preserved, and it is triangular. Three small medial supraorbital caputegulae (Fig. 4) are longitudinally arranged along the medial border of the supraorbital caputegulae. The keeled supraorbital caputegulae (Figs. 2–4) have distinct apices. The posterior supraorbital caputegulum is about four times larger in area than the anterior one. Shallow transverse grooves can be observed on the dorsal surface of the posterior supraorbital caputegulum. The orbits (Figs. 2, 3 and 6) face anterolaterally and tilt somewhat ventrally. The orbital rim thickens posteriorly. The

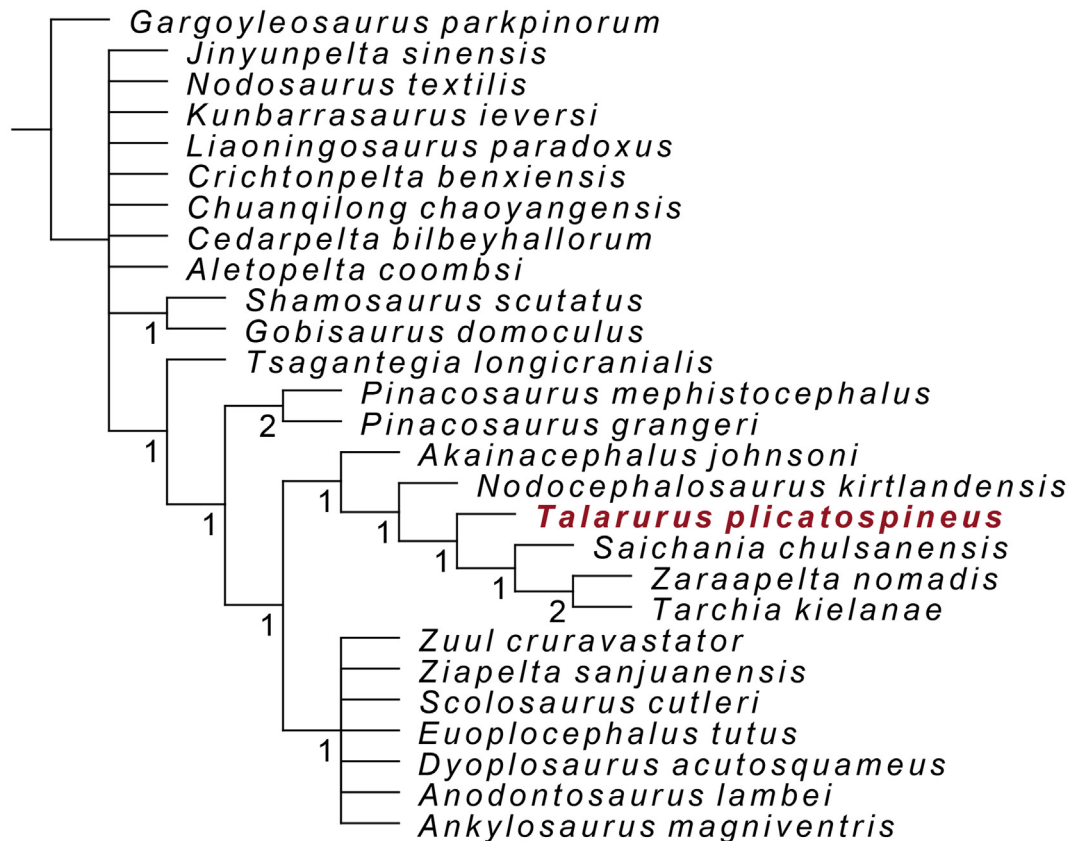


Fig. 10. Strict consensus of 60 most parsimonious trees. Values beneath nodes indicate Bremer support.

triangular quadratojugal horns (Figs. 2, 3 and 5–7) project lateroventrally. Proximally and anteriorly, each horn ends behind the orbit and does not contact the jugal, which results in a quadratojugal “neck” (*sensu* Arbour and Currie, 2016). Up to seven postocular caputegulae (*sensu* Arbour and Currie, 2016) (Figs. 2 and 3) are situated behind the orbit. A wide transverse frontoparietal depression (Figs. 2, 3 and 4) is present posteromedial to the posterior supraorbital caputegulae. The rounded, triangular squamosal horns (Figs. 2–4) project posterolaterally, have dorso-lateral keels, and have triangular bases. A longitudinal furrow can be observed on the keel. Three caputegulae are present on each side of the dorsally raised nuchal shelf (Fig. 4). The high-relief lateral nuchal caputegulum is four to five times larger than the surrounding nuchal ornamentations. The nuchal shelf is fused with the supraoccipital and the paroccipital processes in occipital view (Fig. 7).

**Palatal region:** The dorsoventrally thin rostral extension of the vomer (Fig. 5) is splayed and fused over the posteromedial region of the premaxillae. The laterally thin osseous nasal septum (*sensu* Vickaryous and Russell, 2003) meets the skull roof dorsally and sagittally divides the rostrum. Posterolateral to the vomer is the pterygoid, but only a fragmentary right element is preserved in MPC-D 100/1355 (Fig. 5). A small, wedge-shaped left ectopterygoid is preserved in MPC-D 100/1354 (Fig. 5), which contributes to the anteromedial border of the supratemporal fenestra.

**Occipital/Basicranial region:** The parasphenoid (Fig. 5) tapers anteriorly into a triangular rostrum (*sensu* Vickaryous and Russell, 2003). The anteroposterior length of the basisphenoid and basioccipital are similar. Short, stout basipterygoid processes are present on the basisphenoid (Fig. 5). Posterior to these processes are medially divided, rounded basal tubera. The ventral surface of

the basioccipital (Fig. 5) is convex. Only the basioccipital contributes the occipital condyle in MPC-D 100/1354 and 100/1355. However, the exoccipitals also form part of the condyle in the holotype (Maleev, 1956). The reniform occipital condyle is oriented posteroventrally. The ovoid foramen magnum is wider than high. A dorsoventral, sagittal nuchal ridge (*sensu* Vickaryous et al., 2001) is present in between the foramen magnum and nuchal shelf. This medial ridge divides the supraoccipital region into two shallow fossae. Two small exoccipital protuberances project posteroventrally. The paraoccipital span does not reach the squamosal horns (Fig. 5). The lateral terminus of the paroccipital process is not fused to the squamosal condyle of the quadrates. Each quadrate (Figs. 5 and 6) is transversely broad and the pterygoid flange extends from the quadrate body more ventrally than in other ankylosaurids. In lateral aspect, the quadrate curves anteriorly but is obscured by the quadratojugal horn (Figs. 2 and 3).

**Mandibles:** Only the partial right dentary is preserved in MPC-D 100/1355 (Fig. 9). This represents the first mandibular element ever found for *Talarurus*. The ramus tapers anteriorly and curves ventromedially. A prementary sulcus is present on the anterodorsal edge. No alveoli are preserved. The rugose lateral surface has a few foramina on the posterodorsal region. A shallow shelf is present along the dorsomedial portion of the mandibular ramus. The Meckelian groove (*sensu* Vickaryous and Russell, 2003) can also be observed on the medial surface.

## 5. Phylogenetic analysis

The phylogenetic analysis resulted in 60 most parsimonious trees (tree length = 276 steps, consistency index = 0.547, and retention index = 0.56). The strict consensus tree shows that

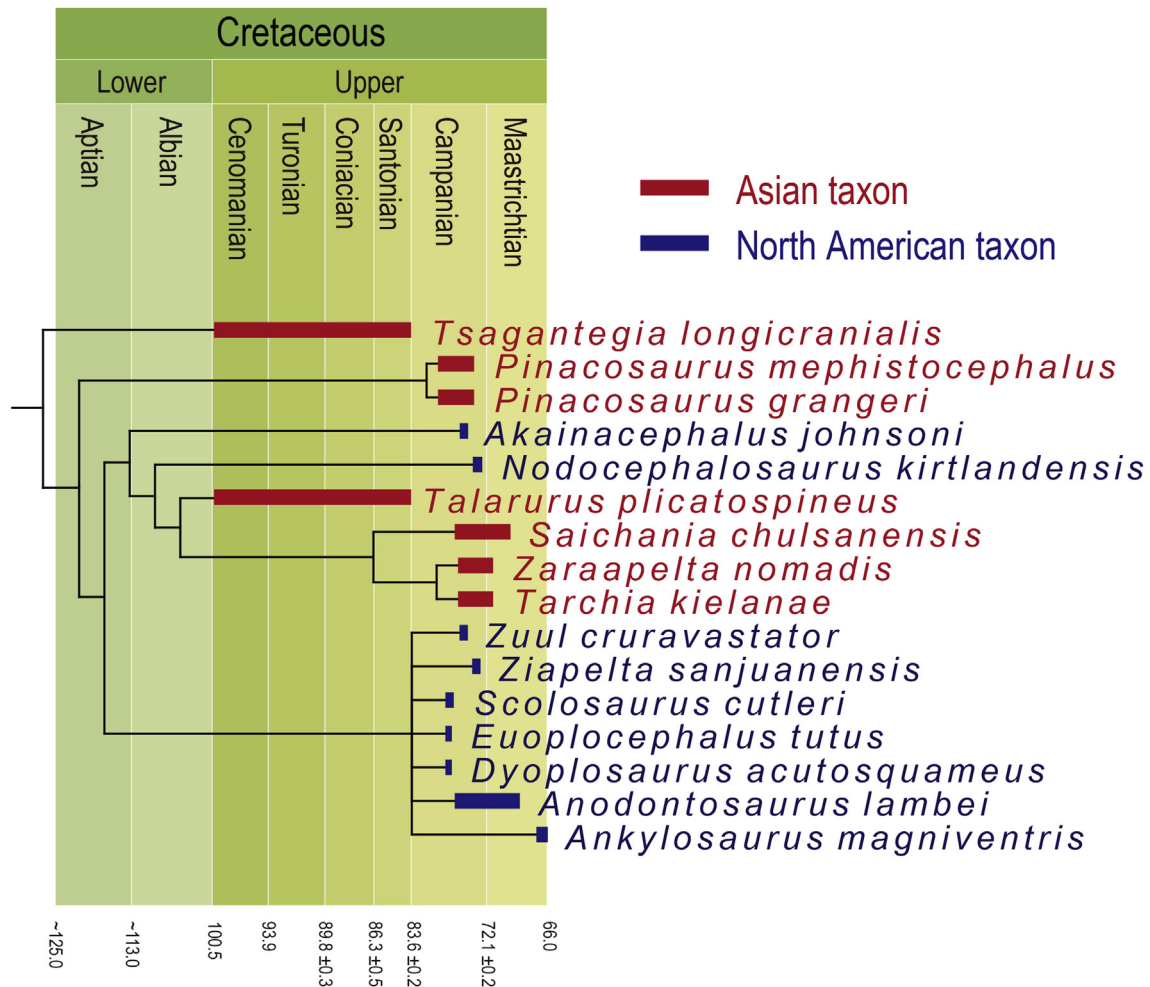


Fig. 11. Time-scaled strict consensus tree of the 60 most parsimonious trees.

*Talarurus* is sister to the clade that includes derived Asian taxa, such as *Saichania* (including *Tar. teresae*), *Tar. kielanae* (including *Mino- taurasaurus*) and *Zaraapelta*. The clade that includes *Talarurus*, *Saichania*, *Tar. kielanae*, and *Zaraapelta* shares only one synapomorphy: the presence of small postocular caputegulae posterolateral to the orbit (character 50, state 1). Two North American taxa *Akainacephalus* and *Nodocephalosaurus* appear to be basal to this clade.

## 6. Discussion

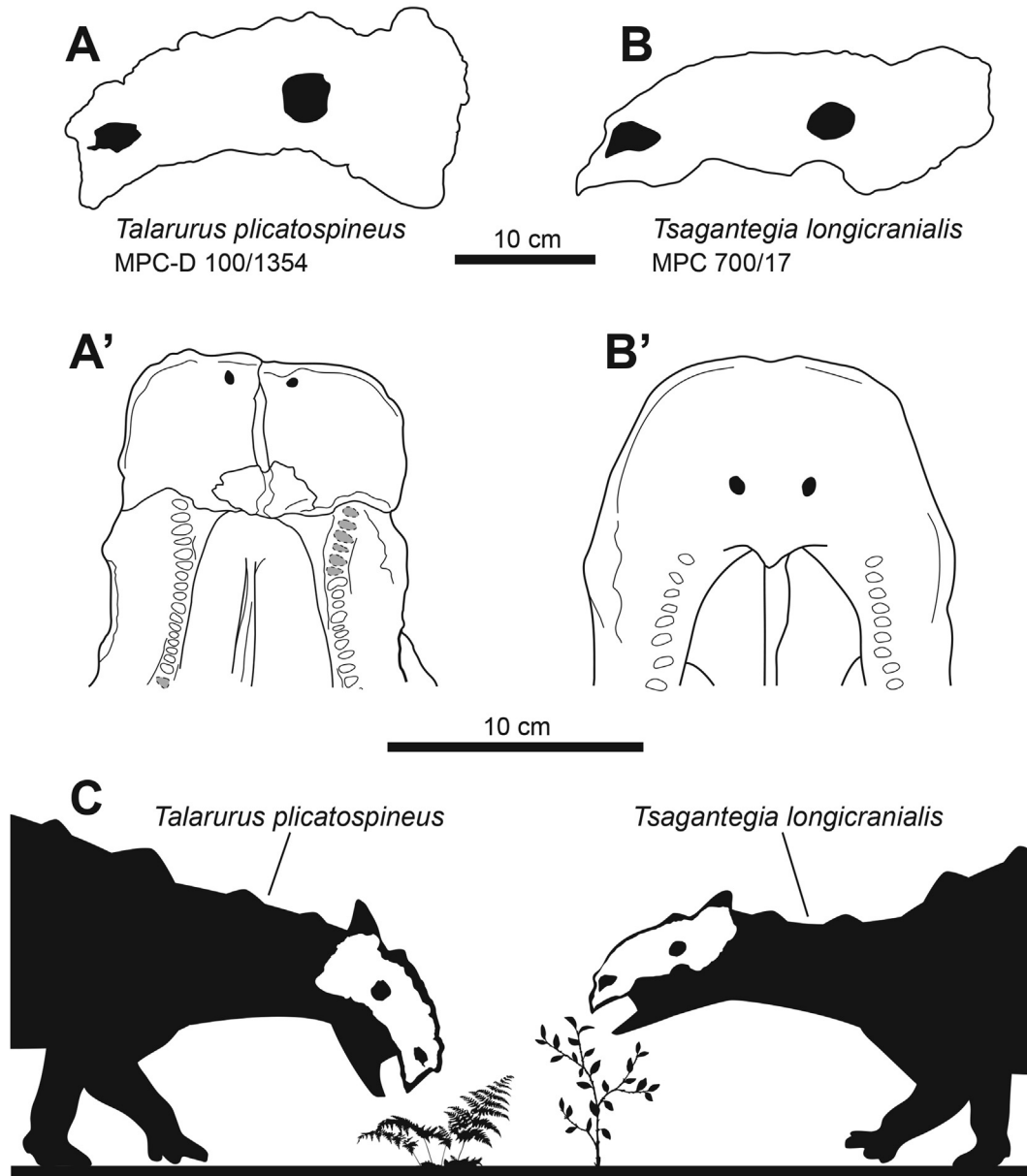
### 6.1. Phylogenetic placement of *Talarurus plicatospineus*

The phylogenetic placement of *Talarurus* has always been problematic. In Hill et al. (2003), *Talarurus* was recovered as a sister taxon to the clade that includes derived ankylosaurines such as *Ankylosaurus*, *Euoplocephalus*, *Nodocephalosaurus*, *Saichania*, “*Shanxia*” (synonym of *Saichania*), “*Tarchia gigantea*” (now partially *Tar. teresae*), and “*Tianzhenosaurus*” (synonym of *Saichania*). A similar result was also obtained in a more recent analysis of Arbour and Evans (2017), which placed *Talarurus* outside of the clade that includes the derived ankylosaurines, such as *Ankylosaurus*, *Ano. lambei*, *Dyoplosaurus*, *Euoplocephalus*, *Saichania*, *Sc. Cutleri*, *Tar. kielanae*, *Ziapelta*, and *Zuul*. Vickaryous et al. (2004) placed *Talarurus* within the derived clade of Asian ankylosaurines, which includes *Pinacosaurus*, *Saichania*, and “*Tianzhenosaurus*”. The result of

Thompson et al. (2012) is similar to that of Vickaryous et al. (2004), and placed *Talarurus* within the clade that includes *Saichania*, “*Tar. gigantea*” and “*Tianzhenosaurus*”. In more recent analyses (Arbour and Currie, 2016; Zheng et al., 2018), however, *Talarurus* was positioned within the derived clade of North American Ankylosaurini. Our results (Fig. 10) are somewhat similar to those of Vickaryous et al. (2004) and Thompson et al. (2012).

### 6.2. Paleobiogeographic dispersal of ankylosaurines from Asia to North America

North American ankylosaurines are known from the middle to late Campanian to Late Maastrichtian (Arbour and Currie, 2016; Penkalski and Tumanova, 2017; Penkalski, 2018; Wiersma and Irmis, 2018). Because the temporal range of these taxa does not go below the Santonian-Campanian boundary, earlier researchers speculated that the paleobiogeographic dispersal of derived ankylosaurines between Asia and western North America must have occurred during or earlier than the Campanian (Sullivan, 1999; Arbour et al., 2014a; Wiersma and Irmis, 2018). However, the placement of two North American taxa, *Akainacephalus* and *Nodocephalosaurus*, basal to *Talarurus* in our cladogram suggests that a migration occurred before the Cenomanian (Fig. 11). We hypothesize that the paleobiogeographic dispersal of ankylosaurines happened at least twice, one earlier than the Cenomanian and the other during or before the Campanian. The migration of



**Fig. 12.** Skull (in left lateral view) and muzzle (in palatal view) comparisons of *Talarurus plicatospineus* (A–A') to *Tsagantegia longicranialis* (B–B'), and a hypothesized illustration for the different feeding heights between the two taxa (C).

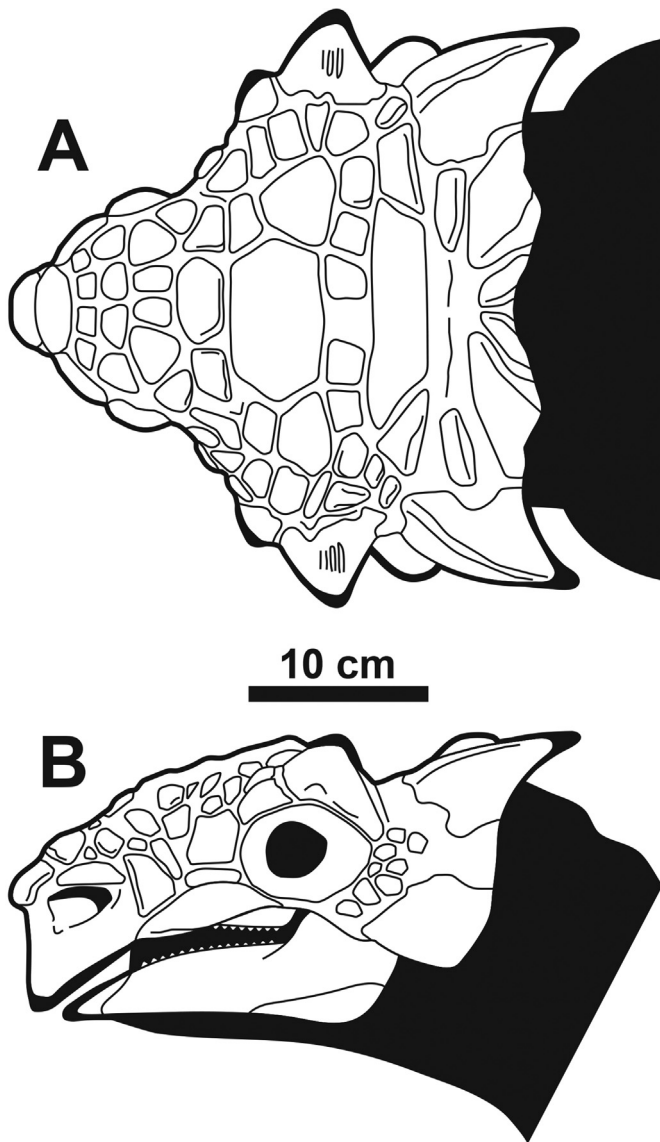
ankylosaurines from Asia to western North America may be concordant with the records of other dinosaurs such as tyrannosauroids (Loewen et al., 2013), therizinosaurids (Zanno, 2010), caenagnathids (Funston et al., 2018), and hadrosauroids (Prieto-Márquez, 2010).

### 6.3. Paleocology of armored dinosaurs in the Bayanshiree Formation

Only two ankylosaur taxa, *Talarurus* and *Tsagantegia*, are known from the Bayanshiree Formation (Maleev, 1952; Tumanova, 1987, 1993). The skulls of the two taxa are similar in size (up to 301 mm and 300 mm in length, respectively). Nevertheless, the rostra of both taxa are quite different from each other in shape (Fig. 12). In lateral view, the palatal surface of the premaxilla slopes down anteriorly in *Talarurus*, resulting in a ventrally pointing rostral tip. In *Tsagantegia*, however, it is horizontal like the skull

roof, and the rostral tip protrudes anteroventrally. In palatal view, the palatal surface of the premaxilla of *Talarurus* is broad and sub-rectangular, with a transversely straight anterior boundary. In contrast, the snout of *Tsagantegia* is somewhat shovel-shaped, with a rounded anterior boundary.

The rostral differences between these two taxa may be evidence of niche partitioning. A similar case can be observed in modern mammals such as the white (*Ceratotherium*) and black rhinoceros (*Diceros*). Both genera are distributed in central to southern Africa, and are similar in size measuring up to 4 m in length and weighing up to 3500 kg (Steele, 1960; Nowak, 1991). The white rhinoceros has a broad rectangular muzzle, whereas the muzzle of the black rhinoceros protrudes and is rounded (Groves, 1972; Hillman-Smith and Groves, 1994). The rostral differences provide a direct clue to the feeding habits of these two rhinocerotid taxa. The white rhinoceros, being a grazer, consumes low-lying vegetation (Groves, 1972). In contrast, the black rhinoceros, being a browser, prefers



**Fig. 13.** Skull reconstruction of *Talarurus plicatospineus* in dorsal (A) and left lateral (B) views.

high-growing shrubs (Hillman-Smith and Groves, 1994). The white rhinoceros might be the modern equivalent of *Talarurus*, with the black rhinoceros analogous to *Tsagantegia*. Like the white rhinoceros, the wide muzzle of *Talarurus* would have enhanced cropping vegetation along a flat surface. Similar niche-related rostral morphologies are also known in ungulates and ground sloths (Janis and Ehrhardt, 1988; Solounias et al., 1988; Solounias and Moelleken, 1993; Susana Bargo et al., 2006).

## 7. Conclusions

The three new specimens provide detailed and nearly complete anatomical information on the skull of *Talarurus* (Fig. 13). Our cladistic analysis suggests that *Talarurus* is sister to the clade that includes *Saichania chulsanensis* (including *Tarchia teresae*), *Tarchia kielanae* (including *Minotaurasaurus*) and *Zaraapelta nomadis*. A dispersal event of ankylosaurines from Asia to western North America occurred before the Cenomanian. The rostral morphology of *Talarurus* is different from that of *Tsagantegia*, another ankylosaurine from the Bayanshiree Formation, suggesting possible niche

partitioning among these taxa. The former was probably a grazer whereas the latter was a browser.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2019.104340>.