**Kundurosaurus nagornyi**

*Kundurosaurus* est un saurolophiné du Maastrichtien supérieur de Russie. L’article qui suit contient la description ostéologique de ce nouveau genre (nouvelle espèce) et du moulage endocrânien. La découverte de ce dinosaure accroît encore la diversité des hadrosauridés en Asie à la fin du Crétacé. Les hadrosaures font preuve d’une spéciation élevée à ce moment-là en Asie, alors que le groupe a presque disparu en Amérique du Nord. Les découvertes en Asie permettent d’éclairer les relations paléogéographiques complexes entre les deux continents durant le Crétacé.

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A new saurolophine dinosaur from the latest Cretaceous of Far Eastern Russia

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Abstract

Background: Four main dinosaur sites have been investigated in latest Cretaceous deposits from the Amur/Heilongjiang Region: Jiayin and Wulaga in China (Yuliangze Formation), Blagoveschensk and Kundur in Russia (Udurchukan Formation). More than 90% of the bones discovered in these localities belong to hollow-crested lambeosaurine saurolophids, but flat-headed saurolophines are also represented: Kerberosaurus manakini at Blagoveschensk and Wulagasaurus dongi at Wulaga.

Methodology/Principal Findings: Herein we describe a new saurolophine dinosaur, Kundurosaurus nagornyi gen. et sp. nov., from the Udurchukan Formation (Maastrichtian) of Kundur, represented by disarticulated cranial and postcranial material. This new taxon is diagnosed by four synapomorphies.

Conclusions/Significance: A phylogenetic analysis of saurolophines indicates that Kundurosaurus nagornyi is nested within a rather robustly clade including Edmontosaurus spp., Saurolophus spp., and Prosauropodophus maximus, possibly as a sister-taxon for Kerberosaurus manakini also from the Udurchukan Formation of Far Eastern Russia. The high diversity and mosaic distribution of Maastrichtian hadrosaurid faunas in the Amur – Heilongjiang region are the result of a complex palaeogeographical history and imply that many independent hadrosaurid lineages dispersed without any problem between western America and eastern Asia at the end of the Cretaceous.
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**Introduction**

Four rich dinosaur localities have been discovered in the Amur/Heilongjiang region of eastern Asia (Fig. 1): Jiayin [1, 2] and Wulaga [3] in the Yuliangze Formation of northern Heilongjiang Province (China), Blagoveschensk [4, 5] and Kundur [6, 7], in the Udurchukan Formation of southern Amur Region (Russia). All these sites are located in south-eastern part (‘Lower Zeya depression’) of the Zeya-Bureya sedimentary basin, near its borders with the adjacent uplifted areas: the Lesser Khingang Mountains and the Turan uplift. In the four sites, the dinosaur bones form large bonebeds extending over several hundreds square metres [7, 8]. In each locality, the dinosaur fauna is largely dominated by lambeosaurine hadrosaurids [2-4, 6], but hadrosaurine (non-crested or solid-crested) hadrosaurids are also represented: *Kerberosaurus manakini* at Blagoveschensk [5] and *Wulagasaurus dongi* [3] at Wulaga.

The Kundur locality was discovered in 1990 by V.A. Nagorny (Far Eastern Institute of Mineral Resources, FEB RAS), who collected fossil bones in a road section along the Chita – Khabarovsk highway near the village of Kundur. He immediately sent his discoveries to Y. L. Bolotsky (Institute of Geology and Research Exploration, FEB RAS). Large-scale excavations started at Kundur in 1999. This dinosaur locality has yielded a nearly complete skeleton, several fragmentary skeletons and isolated bones of a new lambeosaurine hadrosaurid, *Olorotitan arharensis* [6], together with isolated bones and teeth belonging to theropods [9], nodosaurids [10], and lindholmemydid turtles [11]. The first multituberculate mammal fossil ever discovered in Russia was also described from Kundur locality [12].

The greatest part of the dinosaur material from Kundur, including the fossils described in the present paper, are included within massive, unsorted strata representing the deposits of ancient sediment gravity flows that originated from the uplifted areas at the borders of the
Zeya-Bureya Basin. These gravity flows assured the concentration of dinosaur bones and carcasses as well as their quick burial. Such taphonomic conditions allowed the preservation of sub-complete hadrosaurid skeletons unearthed at the Kundur site [7].

The age of the Kundur locality is still subject to debates. Although the three sites belong to the same *Wodehouseia spinata – Aquilapollenites subtilis* palynozone, Markevich & Bugdaeva [13] date the Kundur and Jiayin dinosaur localities as Early Maastrichtian, whereas Blagoveschensk is dated as ‘middle’ Maastrichtian. The proposed ages are based on comparisons with other palynological assemblages in neighbouring basins. They assert that both the vegetation change and dinosaur extinction in the Russian Far East took place at the locally defined ‘middle’-upper Maastrichtian boundary. Nevertheless, the pollen assemblage described in Kundur resembles the *Wodehouseia spinata* Assemblage Zone of the United States [7, 14], which is late Maastrichtian in age [15, 16]. Consequently, it may be hypothesized that the Udurchukan and Yuliangze Formations are late Maastrichtian in age, not early or ‘middle’ Maastrichtian and that the observed dinosaur extinction and vegetation changes mark the upper Maastrichtian – Paleocene boundary, not the ‘middle’ Maastrichtian – upper Maastrichtian boundary, as proposed by the Russian colleagues. To close this debate, independent indicators (palaeontologic, geochronologic, or magnetostratigraphic) are yet to be found in the Maastrichtian deposits of the Amur-Heilongjiang Region.

Besides the abundant *Olorotitan arharensis* material, the Kundur locality has also yielded a partially articulated skull, a well-preserved pelvic girdle and numerous isolated bones belonging to a new saurolophine saurolophid. Because of the homogeneity of the recovered material, there is no reason to believe that more than one single saurolophine taxon lived in the Kundur area by latest Cretaceous time. The present paper describes this new saurolophine and discusses its phylogenetic, biostratigraphic and palaeogeographical significance.

Institutional Abbreviations: AENM, Amur Natural History Museum of the Far Eastern Institute of Mineral Resources, FEB RAS, Blagoveschensk, Russia. AMNH, American Museum of Natural History, New York, USA; MOR, Museum of the Rockies, Bozeman, USA. PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia. ROM, Royal Ontario Museum, Toronto, Canada. TMM, Texas Memorial Museum, Austin, USA. TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Canada. USNM, United States National Museum, Washington D.C., USA. ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.
Results

**SYSTEMATIC PALEONTOLOGY**

Dinosauria Owen, 1842 [17]

Ornithischia Seeley, 1887 [18]

Saurolophidae Brown, 1914 [19] *sensu* Prieto-Márquez, 2010 [20]

Saurolophinae Brown, 1914 [19] *sensu* Prieto-Márquez, 2010 [20]

*Kundurosaurus nagornyi* gen. et sp. nov.

**ZooBank Life Science Identifier (LSID) for genus.**

**Zoobank LSID for species.**

**Holotype.** AENM 2/921, a partial, disarticulated skull.

**Referred specimens.** AENM 2/45, 2/46, jugals; AENM 2/83, 2/84, 2/86, maxillae; AENM 2/57, 2/58, nasals; AENM 2/48, postorbital; AENM 2/19, quadrate; AENM 2/121, 2/928 partial braincases; AENM 2/846, 2/902, dentaries; AENM 2/906, scapula; AENM 2/913, sternal; AENM 2/117, 2/903, 2/907, 2/908, humeri; AENM 2/905, ulna; AENM 2/904, radius; AENM 2/922, nearly complete pelvic girdle and associated sacral elements.

**Specific Diagnosis (as for genus by monotypy).** Saurolophinae characterized by the following autapomorphies: prominent and thick ridge on the lateral side of the nasal that borders caudally the circumnasal depression and invades the caudal plate of the nasal; caudal buttress of proximal head of scapula oriented quite laterally, parallel to the pseudoacromial process; preacetabular process of ilium straight and only moderately deflected ventrally (angle of ventral deflection: 160°): it does not reach the level of the plane formed by the bases of the iliac and pubic peduncles; axis of the postacetabular process strongly twisted along its length, so that its lateral side progressively faces dorsolaterally

**Locality and horizon.** Kundur (N49°04′57.5″/E130°51′34.1″), Amur Region, Far Eastern Russia. Udurchukan Formation (*Wodehouseia spinata* - *Aquilapollenites subtilis* palynozone), ?late Maastrichtian, Late Cretaceous.

**Etymology.** Kundurosaurus, from Kundur, the type-locality, and the transliterated Greek *sauros* (lizard); *nagornyi*, in honour of V.A. Nagorny (Far Eastern Institute of Mineral Resources, FEB RAS), who discovered the Kundur locality.
Figure 1. Map of the Amur/Heilongjiang Region indicating the main dinosaur sites (▲) in the Amur Region. The Kundur locality is indicated by an arrow. The grey zones indicate the uplifted areas.

OSTEOLOGICAL DESCRIPTION

Measurements on the holotype and referred specimens are available as online supplementary information (File S1). The description of the skull of *Kundurosaurus nagornyi* is partly based on the holotype AENM 2/921. It is completed by the description of bones found at the same level, but that maybe belong to other individuals. A reconstitution of the skull of *Kundurosaurus nagornyi* is proposed in Fig. 2. Disarticulated forelimb elements with typical saurolophine morphology have been found in the same layer as the *Kundurosaurus nagornyi* holotype skull. They can be easily distinguished from the equivalent bones of *Olorotitan arharensis* discovered in the same locality. Because there is no indication that more than one hadrosaurine taxon lived in the Kundur area by late Maastrichtian time, those fossils with hadrosaurine morphology are tentatively attributed to *Kundurosaurus nagornyi*. 
Figure 2. Reconstruction of the skull of *Kundurosaurus nagornyi* gen. et sp. nov. The dotted areas indicate the portions preserved in the Kundur fossil material.

**Jugal** (AENM 2/45, 2/46, 2/921-2). The jugal (Fig. 3) is robust and rostrocaudally elongated. The morphology of its rostral process closely resembles that of *Gryposaurus notabilis* (TMP 80.22.1). In lateral view, it is asymmetrical and strongly upturned. It forms a short, robust and sharply-pointed triangular spur. Contrary to *Maiasaura peeblesorum* and *Brachylophosaurus canadensis*, this triangular spur is very asymmetrical and not centered, but set above mid-height of the rostral plate. The dorsal border of the triangular spur forms a laterally-everted lip, the lacrimal facet (Fig. 3A). Its ventral border is nearly horizontal, so that the rostral process looks notched in lateral view. The medial side of the rostral process forms a large and deeply excavated maxillary facet. An elevated vertical crest limits it caudally. The ventral part of this crest forms an elliptical and slightly concave plateau, the maxillary process. The dorsal part of the crest is widened to form the elliptical palatine facet. The postorbital process is long, very slender and elliptical in cross-section. It ascends at nearly a 90° angle. Its dorsal portion forms a flattened rostral facet for articulation with the postorbital. The quadratojugal process raises caudodorsally at nearly the same angle as the postorbital process. It is very thin mediolaterally and appears more robust dorsoventrally than in *Gryposaurus* spp. Its ventral margin is slightly concave. At the angle between the quadratojugal process and the main body of the jugal, a flange is developed, so that the
dorsoventral depth of the jugal from the ventral border of the infratemporal fenestra to the ventral edge of the flange is about 1.5 times as high as the minimum dorsoventral depth of the rostral segment of the jugal, between the rostral and postorbital processes. The quadratojugal facet forms a well-marked depressed area on the medial side of the quadratojugal process. The lateral side of AENM 2/45 forms an elliptical depression, probably of pathological origin, between the rostral and postorbital processes (Fig. 3C). It must also be noted that the ventral curvature is highly variable in the jugals referred to as Kundurosaurus nagornyi. It could therefore be argued that several saurolophine taxa are represented in the Kundur bonebed. However, the ventral curvature seems intraspecifically variable in saurolophine, directly depending on several factors such as the development of the rostral process, the ventral flange, and the rostral constriction. For that reason, we consider that the degree of curvature of the ventral margin of the jugal is not a good diagnostic character and that it must be cautiously considered in phylogenetic analyses.

![Figure 3](image3.jpg)

**Figure 3. Jugals of Kundurosaurus nagornyi gen. et sp. nov.** Left jugal (AENM 2/921-2) in medial (A) and lateral (B) views. Right jugal (AENM 2/45) in lateral (C) and medial (D) views.

Maxilla (AENM 2/83, 2/84, 2/86). Maxillae referred to as Kundurosaurus nagornyi are incompletely preserved, lacking their rostral and medial portions (Fig. 4). However, they display a characteristic saurolophine morphology: although it is broken, the dorsal process appears proportionally low and the caudal portion of the bone is particularly long and robust.
The dorsal process appears less rostrocaudally long and robust than in *Kerberosaurus manakini*, but it can also be interpreted as an ontogenetic character. Caudoventrally to the dorsal process, the lateral side of the maxilla forms a wide, prominent, and concave jugal process that faces slightly dorsally. The jugal process is prolonged rostrodorsally by a deep horizontal sulcus, which received the ventral border of the rostral spur of the jugal (Fig. 4A). Such sulcus is also figured in *Edmontosaurus* [21]. Below the jugal process, the ventral margin of the maxilla is very convex in lateral view. Caudally to the dorsal process, the palatine process forms an elongated concave facet along the dorsolateral border of the maxilla. This situation contrasts with the hook-like palatine process described in *Kerberosaurus manakini* [5]. Between the dorsal and palatine processes, an oblique groove communicates with the excavated caudomedial surface of the dorsal process. Ventrally to the jugal process, the lateral side of the maxilla is pierced by four large foramina. The ectopterygoid ridge is prominent and nearly horizontal; only its caudal part is deflected ventrally. The ectopterygoid shelf is long, wide and dorsoventrally concave. The caudal part of the dorsal border of the maxilla bears a large hook-like pterygoid process.

Figure 4. Right maxillae of *Kundurosaurus nagornyi* gen. et sp. nov., in lateral view. A: AENM 2/84. B: AENM 2/83.
Nasal (AENM 2/57, 2/58). The nasal of *Kundurosaurus nagornyi* is formed by a wide caudal plate and by a robust rostrodorsal process that forms the dorsal and caudal margins of the external nares (Fig. 5). It is much more robust and more curved downwards than in *Kerberosaurus manakini* [5]. However, it is not as strongly arched as in *Gryposaurus notabilis* (ROM 873) or in *Gryposaurus monumentensis* [22]. Its medial side is flat, where it contacted the paired process. The caudal part of its lateral side bears a strong flattened crest that marks the dorsal and caudal limits of the circumnarial depression. Contrary to *Kerberosaurus*, this crest does not closely follow the margin of the external naris, but it invades the caudal plate. The circumnarial depression is not invaginated at this level, as frequently observed in *Edmontosaurus* and *Saurolophus* adult specimens [20]. The caudal plate of the nasal is proportionally shorter than in *Kerberosaurus manakini* [5]: the distance between the rostral point of the articulation with the prefrontal and the caudal point of the external naris is shorter than the height of the plate. The caudal margin of the dorsoventrally convex lateral side of the caudal plate bears a large depressed triangular facet for articulation with the prefrontal. A similar prefrontal facet can also be observed in *Gryposaurus latidens* [23]. The ventral border is depressed along its whole length for articulation with the premaxilla and the lacrimal. The medial side of the caudal plate is very concave where it enclosed the nasal cavity. The rostroventral portion of the nasal plate is broken off, but it apparently participated in the caudoventral margin of the external naris, as e.g. observed in *Gryposaurus* spp. [22] and *Brachylophosaurus canadensis* [24].

![Figure 5. Right nasals of Kundurosaurus nagornyi gen. et sp. nov. AENM 2/57 in lateral (A) and medial (B) views. AENM 2/58 in lateral view (C).](image_url)
**Postorbital** (AENM 2/48, 2/921-6). The postorbital is a triradiate bone formed by a medial, a caudal and a ventral ramus oriented at about 90° from each other (Fig. 6). It is low and rostrocaudally elongated. In lateral view, the dorsal surface of the postorbital above the jugal process is markedly depressed, as also observed in *Saurolophus osborni* and *Saurolophus angustirostris* [20]. The medial ramus, which forms the rostral corner of the supratemporal fenestra, is particularly stout. The articular surface for the frontal forms a very large notch, with thick and persillate border for intimate contacts (Fig. 6A). The caudal ramus is elongated, mesiolaterally compressed and slightly convex upwards. It is distinctly longer than in *Gryposaurus monumentensis* [22], but more slender than in *Edmontosaurus* spp. [21]. On its medial side, a wide and elongated groove that progressively deepens rostrally marks the contact with the rostral ramus of the squamosal. The ventral ramus of the postorbital is broken off in the available specimens. The internal orbital surface does not form any enlarged pouch as in *Edmontosaurus* spp. At the junction between the three rami, a large pocket-like depression received the postorbital process of the laterosphenoid in a synovial joint (Fig. 6C). The dorsolateral orbital rim of the postorbital is very rugose. This feature suggests that the hadrosaurid postorbital results from the fusion of the ‘true’ postorbital with a small supraorbital II [25].

![Figure 6. Left postorbital (AENM 2/921-6) of *Kundurosaurus nagornyi* gen. et sp. nov., in dorsal (A), lateral (B), and medial (C) views.](image-url)
Frontal (AENM 2/921-7). The frontal of *Kundurosaurus nagornyi* is massive and particularly wide (Fig. 7). This condition contrasts with the narrow frontals of *Kerberosaurus manakini* [5]. Its dorsal surface is essentially flat; however, the bone is slightly more elevated medially, so that it looks slightly concave mediolaterally. The frontal is thick caudally and forms a persillate and interdigitate contact with the parietal. The caudolateral side of the frontal is also thickened and roughened for interdigitate contact with the postorbital. The rostromedial side of the frontal is deeply notched by the articular surface for the prefrontal. Between the articular surfaces for the prefrontal and the postorbital, the lateral margin of the frontal participated in the dorsal margin of the orbit. The rostromedial corner of the frontal forms a narrow depressed process that supported the dorsal part of the rostral plate of the nasal. Caudally to the nasal process, the medial margin of the frontal is slightly notched, suggesting that small medial processes of the paired nasals inserted between the midline of the frontals, as observed in *Gryposaurus* spp. [22, 23]. Caudally to this notch, the medial margin of the frontal is particularly thin: this is the place where a frontal-nasal fontanella was described in several juvenile hadrosaurines and basal hadrosauroids [25-28]. In ventral view, the caudomedial portion of the frontal is deeply excavated by the rostral part of the cerebrum. Around this area, strong rugosities mark the contact area with the laterosphenoid and orbitosphenoid portions of the braincase (Fig. 7B). Rostromedially, the ventral side of the frontal bears an elongate encephalic impression, probably for the olfactory lobe of the brain.

![Figure 7. Left frontal (AENM 2/921-7) of Kundurosaurus nagornyi gen. et sp. nov., in dorsal (A) and ventral (B) views.](image)
Squamosal (AENM 2/921-5). The squamosal of *Kundurosaurus nagornyi* has a typical saurolophine morphology, with a low lateral wall above the quadrate cotylus (Fig. 8). The rostral process of the squamosal is mediolaterally compressed and its lateral side is deeply excavated for reception of the caudal ramus of the postorbital. The precotyloid process is robust and triangular in cross-section. Although it is incomplete, it is strikingly longer than the rostrocaudal width of the quadrate cotylus or the dorsal head of quadrate; it is, in any case, proportionally longer than in *Maiasaura* and *Brachylophosaurus* [24]. The precotyloid fossa is poorly marked on the lateral side of the squamosal. The postcotyloid process is also robust and mediolaterally compressed. Both the pre- and postcotyloid processes limit a very deep quadrate cotylus.

![Figure 8. Left squamosal (AENM 2/921-5) of *Kundurosaurus nagornyi* gen. et sp. nov., in lateral view.](image)

Quadrat (AENM 2/19, 2/921-3, 2/921-4). The quadrate of *Kundurosaurus nagornyi* is high, moderately bowed caudally, and relatively narrow in lateral view (Fig. 9). It is more robust than in *Kerberosaurus manakini* [5]. The ratio ‘height of the quadrate / length of the jugal’ = 1.2 in the holotype, suggesting that the skull was proportionally high dorsoventrally, like in *Gryposaurus* spp. [22]. The proximal quadrate head of AENM 2/921-3 is rounded, sub-triangular in cross-section and mediolaterally flattened. The quadrate notch appears proportionally shorter, but deeper than in *Kerberosaurus*. As it is usual in saurolophines, the midpoint of the quadrate notch is located ventral to the mid-height of the quadrate: the ratio
between the distance from the mid-height of the notch to the quadrate height and the height of the bone is 0.7, similar to the condition observed in *Edmontosaurus* ssp. [20]. The lateral border around the quadrate notch is depressed around its whole height, indicating that it was completely closed in life by the quadraatojugal. As it is usual in saurolophids, the distal head of the quadrate is composed of a large rounded lateral condyle that articulated in the surangular part of the mandibular glenoid, and of a smaller medial condyle, set more dorsally and that fitted into the articular component of the mandibular glenoid. The greatest part of the pterygoid wing in destroyed on both quadrates of the holotype specimen. On the left specimen (AENM 2/921-4), the quadrate ramus of the pterygoid is partly preserved and pathologically fused to the rostral part of the pterygoid wing and to the medial part of the quadrate body, so that the respective limits of the bones cannot be discerned (Fig. 9C).

**Figure 9. Quadrates of Kundurosaurus nagornyi gen. et sp. nov.** Right quadrate (AENM 2/921-3) in lateral (A) and medial (B) views. C: left quadrate (AENM 2/921-3) in caudal view.
**Parietal** (AENM 2/121, 2/921-8). The parietal of *Kundurosaurus nagornyi* is long and transversely narrow, with a ‘length / minimal width’ ratio > 3 (Fig. 10-11). Along nearly its whole length, the parietal has a strong sagittal crest. Far rostrally, this crest flattens and widens to form a lozenge-shaped surface. Although it is incompletely preserved, the rostral margin of the parietal is apparently not depressed around the contact area with the frontals as in *Kerberosaurus manakini* [5]. In ventral view, the impression area for the cerebellum is narrow, but deep. The rostral impression for the distal part of the cerebrum is wider, but shallower.

![Figure 10. Parietal (AENM 2/921-8) of Kundurosaurus nagornyi gen. et sp. nov., in dorsal (A) and ventral (B) views.](image)

**Prootic** (AENM 2/121, 2/921-1). The prootic of *Kundurosaurus nagornyi* is particularly massive (Fig. 11A-D). Its caudodorsal ramus, which covered the rostral part of the exoccipital-opisthotic, is wide and stout. The rostral margin of the auditory foramen notches the caudoventral portion of the prootic, whereas the caudal margin of the trigeminal nerve (V) notches its rostral part. Below this latter foramen, the ventral part of the prootic is deeply excavated by a pocket-like depression. This pocket is separated from the trigeminal foramen by a horizontal ridge. This is the situation observed in *Kerberosaurus manakini* [5], but also in *Brachylophosaurus canadensis* (pers. obs.). In *Edmontosaurus* spp. and *Saurolophus* spp., on the other hand, this pocket is not developed, but a vertical groove, which probably transmitted the ramus mandibularis (V3), runs from this foramen along the lateral surface of the prootic. Between the notches for the auditory foramen and the trigeminal nerve, the lateral wall of the prootic is pierced by two smaller foramina. The caudodorsal foramen
transmitted hyomandibularis and the cranioventral, ramus palatinus of the facial nerve (VII). A long and narrow groove runs from the latter foramen along the lateral side of the prootic. The prootic forms a ventrally directed flange that covers the lateral side of the basisphenoid. This flange has a strong vertical ridge, in continuity with the alar process of the basisphenoid.

**Laterosphenoid** (AENM 2/121, 2/921-1). The laterosphenoid of *Kundurosaurus nagornyi* (Fig. 11A-D) is a stout bone formed by three processes. The prootic process, which contacts the parietal dorsally and covers the prootic ventrally, forms a wide, triangular and caudally-directed wing. The basisphenoid process forms a ventrally-directed foot that covers the basisphenoid and the rostrodorsal part of the ventral flange of the prootic. The angle between the prootic and the basisphenoid processes forms the rostral margin of the foramen for the trigeminal foramen. From this notch, a wide and deep groove extends rostrally along the lateral side of the laterosphenoid, indicating the rostral passage of the deep *ramus ophthalmicus* of the trigeminal nerve (V₁). The postorbital process of the laterosphenoid is elongated and stout. From the tip of the postorbital process to the basisphenoid process, the lateral side of the laterosphenoid has a regularly rounded crest marking the separation between the orbit and the supratemporal fenestra.

**Orbitosphenoid** (AENM 2/121, 2/921-1). This bone participates in the rostral part of the lateral wall of the braincase and in the greatest part of the incomplete interorbital septum (Fig. 11 A-D). Its dorsal border contacts the frontal, its caudal border the laterosphenoid, its ventral border the parasphenoid, and its rostral border the presphenoid. A common foramen for the oculomotor (III) and abducens (VI) nerves is located between the parasphenoid and the orbitosphenoid, at the caudoventral corner of the latter.

**Presphenoid** (AENM 2/121, 2/921-1). Only a portion of the presphenoid is preserved in these specimens (Fig. 11A-D), but it does not provide any valuable information.

**Basioccipital** (AENM 2/121, 2/921-1, 2/928). In caudal view, the basioccipital is kidney-shaped (Fig. 11F). It appears rostrocaudally elongated, when compared with other advanced hadrosaurids (Fig. 11A-D). Two prominent tubercles, projecting lateroventrally from the basioccipital, form the caudal half of the sphenooccipital tubercles.
Figure 11. Braincase (AENM 2/121) of *Kundurosaurus nagornyi* gen. et sp. nov., in right (A, B) and left (C, D) lateral views, close-up of the hypophyseal cavity (E). F: caudal view of the braincase (AENM 2/928).
Basisphenoid (AENM 2/121, 2/921-1, 2/928). The caudal part of the basisphenoid is developed into a pair of large processes, separated by a wide and deep fossa; these processes form the rostral part of the sphenoccipital tubercles. More rostrally, the stout basipterygoid processes diverge caudolaterally from the base of the basisphenoid at an angle of about 45° from the horizontal. A small median process projects caudoventrally from the caudal junction between both basipterygoid processes (Fig. 11F). The deep carotid canal extends obliquely along the dorsal part of the basipterygoid process. The alar process that concealed rostrally the carotid canal is broken off (Fig.11 A-D). The rostroventral surface of the basisphenoid is deeply excavated by the hypophyseal cavity. Two large foramina, which correspond to the entrance of the internal carotid arteries, open in the ventrocaudal part of the hypophyseal cavity (Fig. 11E). Two pairs of foramina are visible on the caudodorsal wall of this cavity: the ventrolateral pair corresponds to the passage for the abducens (VI) nerves, whereas the dorsomedial pair corresponds to the passage for ramus caudalis of the internal carotid artery [29].

Exoccipital (AENM 2/121, 2/928). The exoccipitals are much eroded and damaged and the main interesting characters cannot be adequately distinguished. The exoccipital condylloid is large and is pierced by three foramina, successively. The oval vagus foramen (CN X) is the largest and is bordered ventrally by two smaller foramina interpreted as opening conducting branches of the hypoglossal nerve (CN XII) [30]. Rostrally to these foramina, a strong ridge extends obliquely along the lateral side of the condylloid. This crest is not developed in Kerberosaurus manakini [5]. In caudal view, the exoccipitals apparently formed an extended shelf that roofed the foramen magnum (Fig.11F), contrasting with the shorter shelf in Maiasaura peeblesorum, Brachylophosaurus canadensis, and Wulagasaurus dongi [3, 23].

Parasphenoid (AENM 2/921-1). The parasphenoid is poorly preserved. It participates in the ventral margin of the large common opening for the occulomotor (III) and abducens (VI) nerves (Fig. 11A-D).

Dentary (AENM 2/846, 2/902). Two incomplete dentaries discovered in Kundur locality display significant differences with Olorotitan specimens from the same site, more closely resembling typival saurolophine dentaries (Fig. 12). They are therefore tentatively referred to as Kundurosaurus nagornyi. Unfortunately the diastema and the symphysis are not preserved in both specimens, and the dental battery is completely dissociated. The lateral side of the dentary is proportionally high and moderately convex dorsoventrally, and pierced by 5 or 6 sparsely distributed foramina. In AENM 2/846, the largest specimen, the dental battery
fitted into more than 41 narrow parallel-sided alveolar grooves, visible in medial view (Fig. 12B). Viewed from above, the dentary ramus is perfectly straight. In lateral view, the ventral border of the dentary is also perfectly straight along the whole length of the dental battery area. The coronoid process is proportionally high and slender. The height of the coronoid process, taken between the apex of the process and the dorsal border the dentary ramus, is greater than the maximal height of the dentary ramus. This character can of course be correlated with the important height of the quadrate and with the high proportions of the skull as a whole. The apex of the coronoid process is slightly inclined rostrally as usually observed in saurolophids. Its lateral side is convex both rostro-caudally and dorso-ventrally, whereas its medial side is slightly concave. In AENM 2/846, the dental battery extends caudally well beyond the level of the caudal border of the apex of the coronoid process (Fig. 12B). Under the coronoid process, the dentary is deeply excavated by the rostral portion of the adductor fossa; it extends rostrally as a deep mandibular groove (Fig. 12D).

Figure 12. Dentaries of Kundurosaurus nagornyi gen. et sp. nov. A-B: AENM 2/846 in lateral (A) and medial (B) views. C-D: AENM 2/902 in lateral (C) and medial (D) views.
Neuroanatomy (AENM 2/121). The braincase of *Kundurosaurus nagornyi* was scanned in the coronal plane, in three millimeter slice thickness with 1.5 millimeter overlap using Siemens Emition scanner in the Amur Region Hospital in Blagoveschensk. Selection and reconstruction were made in transverse plane using ArteCore from the VisiCore Suite. Different views of the reconstruction are presented in Fig. 13. The purpose of this work is not to describe the cranial nerves but the overall brain morphology of *Kundurosaurus nagornyi*. The resolution of the scanner did not allow reconstructing finite features like nerve foramina or semi-circular canals. The braincase was incomplete and therefore endocranial reconstruction was restricted to the posterior part of the brain, just behind the cerebral hemispheres.

The endocranial reconstitution is 115.29 mm long and 72.03 mm high at its largest dimensions. It is 63.58 mm at his largest point but due to the lack of cerebral hemispheres we can assess that the complete brain was larger. The volume of the reconstruction is 151 cm³. The major divisions are distinct, although the precise limits are not discernible. The midbrain is constricted and slightly triangular in transverse section. The cerebellum was tight in transverse section and marks the highest point of the brain. The upper limit of the brain decreases rapidly after this point. The pituitary body is incomplete but large. Large internal carotid arteries enter it posterolaterally. The constriction behind the cerebellum is particularly visible in a dorsal view (Fig. 13C). This constriction is formed by the otic mass marking the position of the semi-circular canals. The cast of the medulla region is oval in transverse section, being slightly higher than wide. The brain shows no sign of pontine flexure.

Comparison with other endocranial casts from the literature reveals that the brain of *Kundurosaurus nagornyi* resembles that of other saurolophines [29-31]. It shares a lot of similarities with North American *Gryposaurus* endocasts [29]. It is distinguished from non-hadrosaurian ornithopod by the enlarged cerebrum and the absence of the pontine flexure [30]. Unfortunately the incompleteness of the braincase did not allow us to observe some characteristics like the expansion of the cerebrum or the size of the olfactory tracts.
Figure 13. Endocranial reconstruction of *Kundurosaurus nagornyi* gen. et sp. nov. (AENM 2/121). A: drawing of the left lateral view. B: rear 3/4 view, reconstructed from CT scan. C: dorsal view, reconstructed from CT scan.

**Scapula** (AENM 2/906). The scapula of *Kundurosaurus nagornyi* closely resembles that of *Gryposaurus notabilis* [32]. The proximal head is dorsoventrally low, but mediolaterally thick (Fig. 14C). The coracoid suture is broad, sub-triangular, slightly concave and very rough. The pseudoacromial process is strongly developed and oriented quite laterally, as usually observed in saurolophines [20]. It extends caudally as a rounded deltoid ridge that progressively fuses with the dorsolateral aspect of the scapular blade (Fig. 14A). Ventrally to the coracoid suture, the glenoid forms a large crescent-like depression, supported caudally by a prominent buttress from the ventral border of the scapula. Like the pseudoacromial process, this protuberance is oriented quite laterally. Consequently, the deltoid fossa, limited by the parallel pseudoacromial process and the caudal buttress, appears narrow but very deep and U-shaped (Fig. 14C). This lateral orientation of the caudal buttress is unusual in saurolophids: the caudal
buttress is usually oriented ventrally to ventrolaterally. Although it is not completely preserved, the scapular blade appears mediolaterally thick and dorsoventrally low (Fig. 14A-B).

**Figure 14.** Right scapula (AENM 2/906) of *Kundurosaurus nagornyi* gen. et sp. nov., in lateral (A), medial (B), and ventral (C) views.

**Sternal** (AENM 2/911, 2/913). As it is usual in saurolophids, the sternal is formed by a paddle-like expanded proximal region located at the end of an elongated handle-like segment (Fig. 15). The proximal ‘paddle’ is much shorter than the distal ‘handle’, as in other saurolophines [33]. The ‘paddle’ is fan-like. Its dorsal side is slightly concave, whereas its ventral side is markedly convex. Its cranial border is very rough, indicating the presence of a cartilaginous cap in life. From its dorsal border, the ventral side of the paddle bears a prominent buttress, also figured in *Edmontosaurus annectens* [31]. The dorsal side of the paddle has numerous longitudinal striations, starting from the cranial border of the bone. The
‘handle’ is long and robust. Its ventral side is convex, whereas its dorsal side is flat. Its distal end is slightly expanded and has longitudinal striations on both sides.

Figure 15. Right sternal (AENM 2/913) of *Kundurosaurus nagornyi* gen. et sp. nov., in ventral (A) and dorsal (B) views.

**Humerus** (AENM 2/117, 2/903, 2/907, 2/908). Humeri tentatively referred to as *Kundurosaurus nagornyi* are rather robust when compared with those of other saurolophines such as *Edmontosaurus* spp. (Fig. 16). The articular head is globular and supported by a short buttress on the caudal side of the bone; it is separated from the outer tuberosity by a sulcus, but appears to be continuous with the inner tuberosity. The cranial side of the humerus forms a regularly concave bicipital sulcus. From the inner tuberosity, the medial side of the humerus is regularly concave. From the outer tuberosity, the deltopectoral crest extends craniolaterally down below the mid-point of the bone. It is not particularly wide and its border is straight to slightly concave. The distal portion of the humerus is slightly twisted outwards. The ulnar condyle is more prominent and extends more distally than the radial condyle. The intercondylar groove is equally developed along both sides of the bone.
Ulna (AENM 2/905). Two ulna and radius morphotypes, a robust one and a gracile one, can be distinguished within the Kundur material. A very gracile ulna was found associated with Olorotitan holotype. Although the size of this ulna corresponds with the general size of the holotype, it cannot be definitely asserted that it belongs to this specimen, because it was not find in connection with the humerus, but close to the head. On the other hand, associated robust right radius and ulna were found close to the Kundurosaurus nagornyi holotype skull. Here also, in spite of corresponding size and preservation, it cannot be definitely asserted that they belong to the same specimen. However, we have decided to tentatively assign those robust ulna and radius to Kundurosaurus nagornyi, pending the discovery of more complete specimen that would confirm or infirm this association.
The ulna of *Kundurosaurus nagornyi* is robust, like that of *Gryposaurus incurvimanus* [32] and that of *Gryposaurus notabilis* [34]. In cranial view, this bone is distinctly curved medially. It is slightly sigmoid in medial or lateral view: the proximal end is convex caudally, whereas the distal part is convex cranially (Fig. 17 A-B). The olecranon process is prominent, more developed, in any case than in the gracile morphotype. The medial proximal process is particularly high and robust, whereas the lateral one is distinctly lower and thinner. Between both processes, the cranial border of the ulna forms a deep and wide U-shaped triangular depression against which the proximal part of the radius articulated; longitudinal striations indicate strong ligamentous attachment with the radius. Under this area, the body of the ulna is craniocaudally high. It remains triangular in cross section along its whole length. The ulna progressively tapers distally. Its distal end is rounded and laterally compressed. The large triangular articular surface for the distal end of the radius faces cranio-medially; a well-developed crest along the distal end of the ulna borders it laterally and it also bears strong longitudinal striations.

Figure 17. Forearm of *Kundurosaurus nagornyi* gen. et sp. nov. A-B: right ulna (AENM 2/905) in cranial (A) and medial (B) views. C-D: right radius (AENM 2/904) in caudal (C) and cranial (D) views.
**Radius (AENM 2/904).** The radius referred to as *Kundurosaurus nagornyi* is robust, as also observed in *Gryposaurus incurvimanus* [32] and that of *Gryposaurus notabilis* [34]. It is nearly perfectly straight (Fig. 17 C-D). The proximal end of the radius is well expanded, resembling the top of a Doric column in cranial view; its cranial side is slightly convex, whereas its caudal side is flattened where it articulated with the proximal part of the ulna. At some distance from the proximal end, the caudal side of the radius forms a strong keel-like prominence that fits into the U-shaped depression on the cranial side of the ulna. Longitudinal striations indicate strong ligamentous attachment of the proximal head of the radius with the ulna. The distal end of the radius is mediolaterally much expanded, as also observed in *Gryposaurus notabilis* [34]. Its flattened caudolateral side forms a wide, strongly striated, triangular surface, which fitted against the distal part of the ulna. A strong lateral ridge limits this surface.

*Figure 18. Pelvic girdle of Kundurosaurus nagornyi* gen. et sp. nov. A: left pubis (AENM 2/922-5L) in lateral view. B: left ischium (AENM 2/922-3L) in lateral view. C: left ilium (AENM 2/922-7L) in lateral view.
**Ilium** (AENM 2/922-6R, 2/922-7L). The following description is based on a nearly complete pelvic girdle, in connection with sacral elements, found a few metres from the holotype skull. However, although it is tentatively referred to as *Kundurosaurus nagornyi*, there is no direct evidence that it belongs to the same individual as the holotype skull.

The preacetabular process of the ilium of *Kundurosaurus nagornyi* forms a long and tapering projection from the craniodorsal edge of the iliac blade. It is straight and only moderately deflected ventrally. With an angle of ventral deflection of 160°, it does not reach the level of the plane formed by the bases of the iliac and pubic peduncles (Fig. 18C). In other saurolophines, on the other hand, the rostral point of preacetabular process is usually located at the level or below this plane and the angle of ventral deflection is less than 150° (Fig. 19). The lateral side of the preacetabular process is perfectly flat. Its dorsal edge is very thickened and rounded, whereas its ventral edge is sharper. The caudal half of its medial side has, at about the dorsal third of its height, a strong carina. The main blade of the ilium is not very high. Its dorsal edge is sigmoid and thickened. At the level of the ischial peduncle, its dorsolateral border is folded laterally to form a prominent and roughened antitrochanter, nearly symmetrical in lateral view. The ventral extension of the antitrochanter is different on the left and right ilia, although they clearly belong to the same individual: although it extends projects lateroventrally between half and three quarters of the dorsoventral depth of the right ilium, it remains limited on the dorsal quarter of the dorsoventral depth of the left ilium. The supraacetabular process is also longer on the right ilium, although it is extremely difficult to quantify this character because the cranial and caudal ends of the process gradually merge with the dorsal margin of the ilium. It means that characters related to the development of the supraacetabular process must be cautiously considered in phylogenetic analyses. A strong ridge thickens medially the dorsal part of the main blade of the ilium, in continuity with that on the medial side of the preacetabular process. It fuses caudally with the dorsal border of the ilium, at the level of the ischial peduncle. The preacetabular notch is well developed and rather open, because of the slight ventral deflection of the preacetabular process. The pubic peduncle is relatively short, not very massive. The iliac portion of the acetabulum is rather deep and slightly asymmetrical. The ischial peduncle is elongated craniocaudally and laterally prominent. Its articular surface faces caudoventrally and is formed by two sub-rectangular protrusions separated by a well-marked depression. The postacetabular notch is only slightly marked. The postacetabular process is particularly long (around 90% of the length of the
preacetabular process) and sub-rectangular in shape. Its dorsal border is thick mediolaterally, whereas its ventral border is sharp. Whereas the lateral side of the postacetabular process is perfectly flat, its medial side bears a strong rounded oblique ridge. The postacetabular process consequently looks triangular in cross-section. The axis of the postacetabular process is strongly twisted along its length, so that its lateral side progressively faces dorsolaterally. It is usually more vertical in other saurolophines. The dorsal margin of the postacetabular process is caudodorsally oriented, as it is usual in saurolophids, rising dorsally relative to the acetabular margin.

![Figure 19. Ilium of Kundurosaurus nagornyi gen. et sp. nov., compared to other hadrosaurine ilia. Modified from [47].](image)
**Pubis** (AENM 2/922-4R, 2/922-5L). The prepubic blade is ellipsoidal and craniocaudally longer than dorsoventrally high, resembling the condition encountered in *Maiasaura peeblesorum* and *Brachylophosaurus canadensis* [35]. It is less strongly deflected ventrally than in *Gryposaurus notabilis* (ROM 764). The prebubic neck is more contracted in *Kundurosaurus nagornyi* than in *Brachylophosaurus* [35]. The prepubic neck is longer than the prepubic blade, as in *Edmontosaurus* spp., but it remains more robust than in the latter [31]. The iliac peduncle is prominent and robust; a strong, vertical and roughened ridge along its lateral side limits rostrally the acetabular surface of the bone. A well-marked, triangular and striated surface on the medial side of the iliac peduncle reveals a close contact with one of the cranialmost sacral ribs. The ischial peduncle is long and its articular surface with the ischium is expanded and rounded. The proximal part of the ischial peduncle bears a well-marked ventrolateral boss, also described in *Brachylophosaurus* [35]. The development of this protuberance appears highly variable in the *Amurosaurus riabinini* specimens discovered in Blagoveschensk locality, probably reflecting ontogenetic variation. For that reason, the presence or absence of this character is not retained in the phylogenetic analysis presented herein (contra [20]). The postpubic rod is short, robust, mediolaterally compressed and gently curved. Together with the ischial peduncle, it limits a deep obturator foramen.

**Iscium** (AENM 2/922-2R, 2/922-3L). The ischial shaft is slender, slightly curved and rod-like; the distal end tapers in a rounded point (Fig. 18B). The expanded cranial region of the ischium is not parallel to the parasagittal plane, but tilts a few degrees laterally. The iliac ramus is subrectangular and projects craniodorsally; its dorsal articular end process is slightly expanded both mediolaterally and dorsoventrally and sub-ellipsoidal in cross section. The pubic ramus is more slender and less differentiated than the iliac ramus. It projects anteriorly and is very compressed mediolaterally. The articular facet for the pubis is sub-rectangular in cross section. The pubic ramus is slightly concave laterally and convex medially. Numerous striations are found extending craniocaudally across the lateral side of the pubic ramus, especially on its ventral portion. The obturator process is well developed, projecting ventrally lower than the pubic ramus. Its ventral border is expanded and closely contacted the pubic bar. It is prolonged caudally as a carina along the medioventral side of the ischial shaft. The obturator process and the pubic ramus limit an ovoid and ventrally-open obturator gutter. This gutter is closed ventrally, thus forming a foramen in *Saurolophus osborni* [36], in several specimens of *Saurolophus angustirostris* (ZPAL MgDI/159 and MgDI/169) and
in *Brachylophosaurus canadensis* (MOR 794). However, it cannot be excluded that this character is ontogenetic amongst hadrosaurines.

**Sacral vertebrae (AENM 2/922-1).** Between the pelvic elements described above, one very fragmentary and disarticulated sacrum was found. The centra are proportionally short, low and wide. Both proximal and distal articular surfaces are flat and very rough, indicating strong connections between adjacent centra. Between the articular surfaces, the centra are strongly constricted. On the dorsal side of the centra, the neural canal is very wide. The ventral side of the sacrum is neither grooved nor keeled. Sacral ribs were also found disarticulated between the pelvic elements.

### Discussion

**Phylogenetic Analysis**

A phylogenetic analysis was conducted in order to assess the relationships of *Kundurosaurus nagornyi* within Saurolophinae. Although several phylogenies of saurolophines have recently been proposed [3, 22, 37, 38], our analysis is based on the data matrix published by Prieto-Márquez [20]. Indeed, this paper is the most comprehensive phylogenetic analysis of Hadrosauroida to date. However, because of the large size of the original matrix (286 characters and 41 ingroup taxa), it is sometimes difficult to interpret the resulting cladogram. We have therefore decided to concentrate our own analysis on the saurolophines, because it is a priori clear that *Kundurosaurus nagornyi* is not a basal Hadrosauroida or a Lambeosaurinae. We have also decided to exclude the OTUs that are not formally published yet and also *Shantungosaurus giganteus*, which clearly requires a systematic revision. Our data matrix is therefore limited to 21 OTUs. *Probactrosaurus gobiensis* and *Bactrosaurus johnsoni* have been chosen as successive outgroups, because they are fairly complete and familiar to the authors of the present paper. The number of characters considered in our analysis is consequently reduced too, because many of them became non-informative. We have also excluded several characters when we considered that their intraspecific variability was too important, that the preservation of the fossils could too easily influence the polarity of the character (this is particularly the case for characters based on angulations, which can easily be influenced by post-mortem crushing), or when the polarity was problematic (polarity unknown in outgroup taxa). The final matrix is consequently
reduced to 176 characters. The character description (file S2) and character-taxon matrix (file S3) are presented as online supplementary information.

The 176 characters were equally weighted and analysed with TNT 1.1 [39]. A heuristic search of 10000 replicates using random addition sequences, followed by branch swapping by tree-bisection-reconnection (TBR; holding ten trees per replicate) was conducted. The trees were subsequently analysed using Winclada ver.1.00.08 [40] with fast and slow optimizations. To assess the repeatability of tree topologies, a bootstrap analysis was performed (1000 replicates with the heuristic algorithm in Winclada). Bremer support was assessed by computing decay indices with TNT 1.1.

The maximum parsimony analysis resulted in a single tree of 354 steps (Fig. 23). The consistency index (CI) is 0.68 and the retention index (RI) is 0.75. The tree description is presented as supplementary online information (file S4). This analysis confirms that both *Lophorhothon atopus* and *Hadrosaurus foulkii* occupy a basal position, outside the clade Sauropodidae (defined as the last common ancestor of *Saurolophus osborni* and *Lambeosaurus lambei* and all of its descendants [20]). *Kundurosaurus nagorny*i is placed as the sister-taxon of *Kerberosaurus manakini*, also from the Maastrichtian of the Amur Region. However, this clade is particularly weakly supported, and synapomorphies uniting both genera can only been found under fast optimization. It means that the polarity of these characters is unknown in at least one of these two taxa. It reflects the fact that both taxa are represented by fragmentary specimens and that many characters usually regarded important from a phylogenetic point of view are lacking. *Kundurosaurus nagorny*i and *Kerberosaurus manakini* are placed with the clade Edmontosaurini, characterized by three unambiguous (characters that do not change placement under both fast and slow optimizations) synapomorphies: supracranial crest absent (character 114 [0]), postacetabular process of ilium nearly as long as the central plate, ratio greater than 0.8 but less than 1.1 (character 154 [1], convergent in the brachylophosaurine clade), and proximal constriction of the prepubic process of the pubis longer than the dorsoventral expansion (character 160 [2]). However, this clade is also weakly supported (Bremer decay value = 1; bootstrap proportion < 50). In this cladogram, the Edmontosaurini and Saurolophini clades form a rather well-supported (Bremer decay value = 3; bootstrap proportion= 76) monophyletic group, supported by the following unambiguous and unequivocal (CI = 1) synapomorphies: more than 42 tooth position in the dentary dental battery (character 1 [2]), the medial or lateral profile of the dorsal margin of the rostral edentulous region of the dentary for articulation with the predentary has a very subtle
concavity or is straight (character 23 [1]), margin of the dentary with a wide and well-developed ventral bulge rostral to the coronoid process (character 24 [1]), rostral end of the nasal at the contact with the dorsal process of the premaxilla long and subrectangular process, with slightly rounded corners (character 50 [2]), the nasal forms a greatly shortened and dorsoventrally narrow hook-like rostroventral process, exposed dorsal to the premaxillary caudoventral process (character 51 [2]), the triangular caudoventral expansion of the rostral process of the jugal forms a shallow and rostrocaudally wide prominence (wider than deep) (character 68 [1]), circumnarial fossa deeply incised (character 113 [1]) and sometimes invaginated in adults (character 113 [2]), and relatively long iliac peduncle of the ischium, ratio between the proximodistal length and the craniocaudal width of the distal margin greater than 2 (character 164 [1]). *Gryposaurus* is the sister-taxon of this this Saurolophini + Edmontosaurini clade; however this monophyly is weakly supported supported by a single unambiguous and unequivocal synapomorphy: at least five teeth per alveoli arranged dorsoventrally at mid length of the dental battery (character 2 [2]).

Although they are basically based on the same data matrix, the ckadogram of Saurolophinae presented here is clearly different from published by Prieto-Márquez [20], more closely resembling the phylogenies previously published by Godefroit et al. [3], Bolotsky and Godefroit [5], and Bell [38]. The most important difference is the position of *Gryposaurus* and *Edmontosaurus*. According to Prieto-Márquez, *Edmontosaurus* is the sister-taxon of the monophyletic clade formed by Saurolophini + gryposaurs (including *Wulagasaurus dongi* and *Kritosaurus navajovius*). It is notable that both phylogenies are weakly supported, because only a few clades have a Bremer decay value greater than 1 and a bootstrap proportion greater than 50.

We have therefore decided to test the influence of missing data on the topology and robustness of the resulting cladogram and we have eliminated from the analysis taxa that are represented by too fragmentary specimens. However, we have kept *Kundurosaurus nagornyi*, keeping in mind that the ultimate aim of this analysis is to clarify its phylogenetic affinities within Saurolophinae. The maximum parsimony analysis resulted in two most parsimonious trees of 315 steps each with a consistency index of 0.74 and a retention index of 0.78. The consensus tree (Fig.21; tree description in online supplementary information, File S5) shows that the general topology of the cladogram is kept (compare with Fig. 20), but that the robustness of the nodes is significantly increased. *Kundurosaurus nagoryi* is nested within an unresolved polytomy with *Edmontosaurus* and Saurolophini. This clade is rather robustly
supported (Bremer decay value = 5, bootstrap proportion = 79). An additional analysis was constrained to produce a monophyletic group comprising *Gryposaurus* ssp and Saurolophini, as hypothesized by Prieto-Márquez [20]. This analysis shows that this later hypothesis requires seven additional steps and is therefore less parsimonious.

**Palaeogeography**

So far, four main dinosaur localities are known along the borders of the Zeya-Bureya Basin. The distances between these localities are not important (see Fig. 1) and the saurolophid fossils have been discovered in the same *Wodehouseia spinata-Aquila pollenites subtilis* palynozone, suggesting that these hadrosaurs are roughly synchronous, from a geological point of view. *Kundurosaurus nagornyi* is the third saurolophine discovered in the Zeya-Bureya Basin. *Kerberosaurus manakini* is known from disarticulated skull material from the Udurchukan Formation at Blagoveshensk [7] and *Wulagasaurus dongi*, from disarticulated bones from the coeval Yuliangze Formation at Wulaga in China [3]. *Mandschurosaurus amurensis* and *Saurolophus kryshtofovici*, both from the Yuliangze Formation at Jiayin (China) are now unanimously regarded as *nomina dubia* [41]. Although the holotype specimen of *Mandschurosaurus amurensis* is clearly a chimera, reconstructed from several individuals, several of its bones (humerus, part of the mandible) apparently belong to saurolophines. A partial left dentary with dozens teeth from Jiayin [42] clearly belongs to a saurolophine and probably to 'Node J' in Figures 20-21, like *Kundurosaurus nagornyi* and *Kerberosaurus manakini*. Indeed, at least five teeth per alveoli are dorsoventrally arranged at mid length of the dental battery (character 2 [2]), which is an unambiguous and unequivocal synapomorphy for this clade. The dentary crowns of this specimen are characterized by the presence of well-developed secondary and tertiary ridges, an unusual character in saurolophines. Dentary teeth are unfortunately not associated with *Kundurosaurus nagornyi* dentaries, so it is not possible to know whether the saurolophine dentary from Jiayin belongs or not to the new taxon. The same apparent patchy distribution can also be observed in lambeosaurine saurolophids from the Amur region: *Charonosaurus jiayinensis* is limited to Jiayin locality, *Sahaliyania elunchunorum* to Wulaga, *Amurosaurus riabinini* to Blagoveshensk, and *Olorotitan arharensis* to Kundur locality. Ecological factors, which still have to be investigated, therefore probably lead to an important habitat partitioning of hadrosaurid faunas in eastern Asia during the Maastrichtian. Similar habitat
partitioning has also been observed in North American hadrosaurids [37]. Important habitat partitioning between species that have a great potential for dispersion suggests that competition for food resources was very important between hadrosaurid populations that lived in the Amur-Heilongjiang region at the end of the Cretaceous. In modern large vertebrates, important habitat partitioning usually implies an elaborated social life. It has been postulated that hadrosaurid circumnasal and supracranial features may have been used for both visual and vocal communication, and were implied in species recognition, intraspecific combat, ritualised display, courtship display, parent-offspring communication and social ranking. They would have promoted successful matings within species that live close from each other by acting as premating genetic isolating mechanisms [37, 43].

Figure 20. Phylogenetic analysis of Saurolophinae. Tree length = 354 stps, CI = 0.68; RI = 0.75. Character list modified from [20], see Online Supplementary Information, File S2 for the list of characters, File S3 for the data matrix, and File S4 for the tree description. bd, Bremer decay value; bs, bootstrap proportion. Bootstrap proportions lower than 50 are indicated by a hyphen.
**Figure 21. Simplified phylogenetic analysis of Saurolophinae.** Strict consensus tree resulting from the parsimony analysis of 15 hadrosaurid taxa. Tree length = 315 stps, CI = 0.74; RI = 0.78. Character list modified from [20], see Online Supplementary Information, File S2 for the list of characters, File S3 for the data matrix, and File S5 for the tree description. **bd**, Bremer decay value; **bs**, bootstrap proportion.

Figure 20 suggests that *Kundurosaurus nagornyi* and *Kerberosaurus manakini* belong to a single clade and that their presence in Maastrichtian deposits from Far Eastern Russia may be explained by the local evolution of a single saurolophine lineage. However, *Wulagasaurus dongi* is here regarded as the most basal Saurolophine (*contra* [20]). If this interpretation is correct, its presence in Maastrichtian deposits from Eastern Asia implies a long ghost lineage for basal saurolophines in Asia. Lambeosaurines from the Amur region also belong to well separated lineages: *Amurosaurus riabinini* is a basal lambeosaurine [4], *Sahaliyania elunchunorum* is a more advanced lambeosaurine [3], *Charonosaurus jiayinensis* is regarded as the sister-taxon of the North-American genus *Parasaurolophus* [41], and *Olorotitan arharensis* belongs to the same clade as the North-American genera *Hypacrosaurus* and *Corythosaurus* [44]. Such a diversity and mosaic distribution of Maastrichtian saurolophid faunas in the Amur-Heilongjiang region is the result of a complex paleogeographical history and implies that many independent hadrosaurid lineages dispersed without any problem between western America and eastern Asia at the end of the Cretaceous. Fiorillo [45] recently demonstrated that the concept of Beringia, an entity
encompassing northeastern Asia, northwestern North America and the surmised land connection between the two regions, should be formally extended back in time to the Cretaceous and is rooted in its accretionary rather than its climatic history. Godefroit et al. [46] showed that the late Maastrichtian Kakanaut dinosaur fauna in Chukotka (northeastern Russia) more closely resembles the Hell Creek fauna of western North America than the synchronous Amur-Heilongjiang fauna. All this partial data suggest that the evolutionary history and palaeogeography of dinosaur faunas in eastern Asia is still very partially understood. The huge territories of Far Eastern Russia, which have been poorly explored so far, have a great potential for new discoveries that would bring clues to clarify this complex situation.

NOMENCLATURAL ACTS

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File S1: Measurements

Jugal (AEHM 2/921), left

Length: 325 mm

Height of rostral process: 136 mm

Minimum depth of rostral constriction: 66 mm

Dorsoventral depth of the flange: 101 mm

Minimum depth of the caudal constriction: 77.5 mm

Distance between the point of maximum curvature of the infratemporal margin and the caudal margin of the lacrimal process: 125 mm

Quadrate (AEHM 2/723), right

Height: 408 mm
Distance from mid-height of quadrate notch to quadrate head: 285 mm

Length of distal surface: 57 mm

Width of distal surface: 64.5 mm

Frontal (AEHM 2/723), left

Length: 172 mm

Maximal width: 110 mm

Sternal (AEHM 2/913), right

Total length: 445 mm

Length of craniomedial plate: 180 mm

Length of caudoventral process: 300 mm

Scapula (AEHM 2/913), right

Dorsoventral depth of the proximal region: 109 mm

Dorsoventral depth of the distal end: +/- 95 mm

Dorsoventral depth of proximal constriction: +/- 77 mm

Distance from the coracoid joint and the cranial end of the acromion process: 76 mm

Height between the cranial end of the acromion process and the ventral apex of the glenoidal facet: 83 mm

Humerus (AEHM 2/203), right

Length: 303 mm

Length of deltopectoral crest: 156 mm

Width of deltopectoral crest: 71 mm

Width of distal shaft at the point of maximum curvature: 41 mm

Width of the lateral surface of the proximal end: 78 mm

Ulna (AEHM 2/905), right

Length: 710 mm
Mesiolateral width of proximal end: 138 mm

Dorsoventral thickness (measured at mid-shaft): 61 mm

Radius (AEHM 2/904), right

Length: 607 mm

Mesiolateral width of proximal end: 79 mm

Dorsoventral thickness (measured at mid-shaft): 51 mm

Ilium (AEHM 2/922), right

Length: +/- 930 mm

Length of preacetabular process: +/- 400 mm

Dorsoventral distance between the pubic peduncle and the dorsal margin of the ilium: 193 mm

Depth of the proximal region of the preacetabular process: 117 mm

Distance between the pubic peduncle and the caudodorsal prominence of the ischial peduncle: 275 mm

Length of the central plate: 283 mm

Depth of the central plate: 187 mm

Length of postacetabular process: 265 mm

Pubis (AEHM 2/922), left

Craniocaudal length of the pubis (distance from the acetabular margin to the distal margin of the prepubic process): +/- 530 mm

Distance from the dorsal margin of the iliac peduncle to the ventral margin of the proximal postpubic shaft: 153.5 mm

Width of the acetabular margin of the pubis: 154 mm

Depth of the dorsoventral expansion of the distal region of the prepubic process: +/- 184 mm

Length of proximal constriction of prepubic process: 310 mm
Length of the dorsoventral expansion of the prepubic process: +/- 220 mm

Length of ischial peduncle: 74.5 mm

Width of ischial peduncle: 32 mm

Length of iliac peduncle: 87 mm

Ischium (AEHM 2/922), left

Length: 792 mm

Length of iliac peduncle: +/- 140 mm

Width of iliac peduncle: 66 mm

Length of pubic peduncle: 38 mm

Width of pubic peduncle: 77 mm

Length of the ischial shaft: 590 mm

Dorsoventral thickness of the midshaft: 29 mm

File S2: List of characters used in the phylogenetic analysis (based on [20])

Dental characters:

1. Maximum number of tooth positions in the dentary dental battery: 30 or less (0); 31–42 (1); more than 42 (2). ([20], character 1). Character treated as ordered.
2. Minimum number of teeth per alveoli arranged dorsoventrally at mid length of the dental battery: maximum three (0); four (1); five (2). ([20], character 2, modified).
3. Maximum number of functional teeth exposed on the dentary occlusal plane: one or two (0); three functional teeth throughout most of the dental battery, gradually decreasing to two near the rostral and caudal ends of the dentary (1). ([20], character 2, modified).
4. Maximum number of ridges on the enamelled lingual side of dentary tooth crowns: presence of primary, secondary, and one or two tertiary ridges (0); presence of a primary ridge and one or two faint and shorter ridges (1); loss of all but primary ridge (2). ([20], character 5, modified). Character treated as ordered.
5. Dentary tooth crowns, position of primary ridge: well offset caudally from the midline (0); median for most teeth, although some teeth within the same dental battery may display a slight caudal offset of the primary ridge (1). ([20], character 6).

6. Shape of the primary ridge of dentary tooth crowns: straight in all teeth within the same dentition (0); straight for some crowns and sinuous for others. ([20], character 7).

7. Angle between the crown and the root of dentary teeth: more than 135° (0); up to 135° (1). ([20], character 8, modified).

8. Overall morphology of dentary marginal denticles: wedge to tongue-shaped (0); curved and mammillated asymmetrical ledge (1); absent or very reduced to small papillae along the apical half of the crown (2). ([20], character 9).

9. Maximum number of tooth positions in the maxillary dental battery: up to 32 tooth positions (0); from 33 to 44 tooth positions (1); 45 or more tooth positions (2). ([20], character 15). Character treated as ordered.

10. Maximum number of functional teeth per alveolus in the maxillary occlusal plane: one tooth for most of the dental battery, with the sporadic presence of a second tooth forming the occlusal plane (0); two functional teeth throughout most of dental battery length, gradually changing to one near the rostral and caudal ends of the maxilla (1). ([20], character 16, modified).

11. Overall morphology of the maxillary marginal denticles: curved and mammillated asymmetrical ledge (0); absent or reduced to small papillae along the apical half of the dorsal half of the crown (1). ([20], character 21, modified).

Predentary

12. Ratio between the predentary maximum mediolateral width and the maximum rostrocaudal length along the lateral process: less than 1.2 (0); between 1.2 and 1.75 (1); more than 1.75 (2). ([20], character 22).

13. Shape of the denticles of the predentary oral margin: triangular and pointed (0); subtriangular to subrectangular (1). ([20], character 25, modified).

14. Number of predentary denticles in adults lateral to the median denticle (not included in the count: maximum of five (0); six or more (1). ([20], character 27, modified).

15. Extension of predentary denticulate margin: denticles extending on lateral process (0); denticles limited to the rostral margin (1). ([20], character 28).

16. Morphology of predentary rostrolateral corner: gently rounded and continuous with the lateral process, giving the predentary an arculate dorsal profile (0); subsquared rostrolateral corner (1); subsquared, very broad, and rostrolaterally projected (2). ([20], character 29).
Development of a lateral shelf on the dorsal side of the predentary lateral process: short and shallow shelf, limited to the laterocaudal region of the lateral process (0); short and well-incised shelf that is wider near the rostrolateral corner of the predentary (1); shelf extremely narrow mediolaterally and very long rostrocaudally (2); shelf rostrocaudally long, deeply incised and mediolaterally broad, forming half of the mediolateral breadth of the lateral process and becoming wider distally (3). ([20], character 30, modified).

Ridge on the dorsal lingual, keel-like process of the predentary: the process lacks a prominent median ridge on the lingual side of the rostral region of the predentary, and, if present, the former forms and projects caudally from the caudal margin of the predentary rostral region (0); the process has a well-developed ridge on the lingual surface of the rostral segment of the predentary, from which the former extends further caudally to lie dorsal to the dentary symphysis (1). ([20], character 31).

Degree of ondentation of the split of the predentary ventral median processes into two distinct lobes: short indentation and deep undivided portion (0); long indentation and shallow undivided portion (1). ([20], character 32).

**Dentary**

20. Ratio between the length of the proximal edentulous slope of the dentary and the distance between the rostralmost tooth position and the caudal margin of the coronoid process: less than 0.20 (0); ratio between 0.20 and 0.31 (1); ratio between 0.32 and 0.45 (2); ratio greater than 0.45 (3). ([20], character 33).

21. Lingual projection of the symphyseal region of the dentary: (measured as a ratio between the labiolingual extension of the symphyseal region and the maximum labiolingual width of the dentary): ratio greater than 1.65 and up to 2.85 (0); ratio up to 1.65 (1). ([20], character 38, modified).

22. Orientation of the dentary symphysis (measured as the angle formed by this surface and the lateral side of the rostral half of the dentary): angle greater than 15°; angle up to 15° (1). ([20], character 39).

23. Medial or lateral profile of the dorsal margin of the rostral edentulous region of the dentary for articulation with the predentary: having a well-pronounced concavity (0); ranging from having a very subtle concavity to straight (1). Prieto-Márquez ([20], character 40, modified).

24. Bulging of the ventral margin of the dentary: margin straight or slightly bowed rostral to coronoid process (0); margin with a wide and well-developed ventral bulge rostral to the coronoid process (1). ([20], character 41, modified).
25. Orientation of coronoid process: subvertical or caudally inclined (0); rostrally inclined (1). ([20], character 42, modified).

26. Morphology of the apex of the coronoid process: slightly expanded rostrocaudally, with very limited development of rostral and caudal expansions resulting in an apex that is taller than wider (0); well-developed expansion of both the caudal and, especially, the rostral margins (1). ([20], character 43).

27. Caudodorsal margin of the coronoid process projected dorsally into a sharp point: absent (0); present (1). ([20], character 43).

28. Thick and dorsoventrally elongated ridge on the medial side of the coronoid process: absent, presence of fine striations (0); present, the ridge forms the rostral boundary of a depressed facet for attachment of the rostrodorsal process of the surangular; coarse striations present rostral to the ridge (1). ([20], character 45).

29. Lateral expansion of the caudal region of the dentary, ventral to the base of the coronoid process (measured as the angle between the lateral surface of the dentary and that of the region caudoventral to the coronoid process): the lateral side of the dentary is only slightly expanded laterally ventral to the coronoid process, with an angle greater than 165° (0); well-developed expansion of the lateral side of the dentary ventral to the coronoid process, with an angle of up to 165° (1). ([20], character 46).

30. Orientation of the longitudinal axis of the dentary occlusal plane relative to the lateral side of the bone: diagonal axis, directed rostrolaterally and forming approximately 15° with the lateral side of the dentary (0); axis parallel to the lateral side of the dentary (1). ([20], character 47).

31. Lingual arching of the occlusal plane: present, lingually convex occlusal plane (0); absent, rostrocaudally straight occlusal plane (1). ([20], character 48).

32. Caudal extension of the dental battery: flush with the caudal margin of the coronoid process (0); caudal to the caudal margin of the coronoid process (1). ([20], character 49, modified).

33. Separation between the dentary tooth row and the coronoid process: the coronoid process is laterally offset (but nearly in contact) with the tooth row, lacking a platform in between the tooth row and the base of the process (0); the coronoid process is laterally offset relative to the tooth row, with the presence of a concave platform or, in some cases, a laterodorsal concave slope separating the base of the process from the dental battery (1). ([20], character 50).
Surangular

34. Morphology of the rostrodorsal process of the surangular: rostrocaudally thick process extensively exposed in lateral view (0); rostrocaudally reduced in thickness, strap-like and wedging dorsally into a thin sliver that becomes concealed in lateral view by the dorsal half of the caudal margin of the coronoid process (1). ([20], character 51).

35. Surangular foramen: present (0); absent (1). ([20], character 52).

36. Orientation of the convex side of the lateral lap and the lateroventral surface of the main body of the surangular: facing more laterally than ventrally (0); facing more ventrally than laterally (1). ([20], character 52).

37. Lateral curvature of the caudal process of the surangular: present, process laterally recurved (0); absent, process nearly straight rostrocaudally (1). ([20], character 55, modified).

Angular

38. Position of the angular in the mandible: positioned ventrally and slightly medially, exposed in lateral view (0); positioned medially, not exposed in lateral view (1). ([20], character 57).

Premaxilla

39. Mediolateral expansion of the premaxillary oral margin (measured as the ratio between the maximum mediolateral width of the premaxilla and the minimum width at the narrowest point or post-oral constriction): relatively narrow, ratio less than 1.65 (0); ratio between 1.65 and 2 (1); very wide, with a ratio greater than 2 (2). ([20], character 60). Character treated as ordered.

40. Position of the premaxillary oral margin relative to the occlusal plane of the dentition: premaxillary margin slightly ventrally offset from occlusal plane (approximately, the dorsoventral distance between the occlusal plane and the level of the premaxillary oral margin is less than the mean depth of the dentary) (0); very strongly deflected ventrally (approximately, the dorsoventral distance between the occlusal plane and the level of the premaxillary oral margin is equal to or larger than the mean depth of the dentary) (1). ([20], character 61).

41. Degree of expansion and folding of the oral margin of the premaxilla: moderately expanded border, becoming thinner towards the parasagittal plane of the snout (0); folded caudodorsally into a thin recurved margin (1); ventrally deflected and dorsoventrally expanded, forming a very thick 'lip-like' margin (2). ([20], character 62, modified).
42. Premaxillary oral margin with a double layer morphology consisting of an external denticle-bearing layer and an internal layer of thickened bone, set back slightly from the oral margin, and separated from the denticular layer by a deep sulcus bearing vascular foramina: absent (0); present (1). ([20], character 63).

43. Premaxillary foramen located rostrally and ventrolaterally to the rostral margin of the external naris: absent (0); present (1). ([20], character 64).

44. Premaxillary accessory foramen entering rostrally through the outer (rostral) narial fossa, located rostral to the premaxillary foramen: absent (0); present, empties into a common chamber with the premaxillary foramen (1). ([20], character 65).

45. Premaxillary accessory narial fossa located rostral to the circumnarial depression: absent (0); present, separated from circumnarial depression by a rostrocaudally wide ridge (1). ([20], character 66).

46. Premaxillary additional accessory fossa located lateral to the rostral accessory fossa and rostrolateral to the circumnarial depression, parallel with the lateral border of the oral margin: absent (0); present (1). ([20], character 67).

47. Elongation of premaxillary caudodorsal process: the premaxillary caudodorsal process does not meet the caudoventral process caudally (0); elongate caudodorsal process that extends caudally to meet the caudoventral process, forming the caudal margin of the external naris (1). ([20], character 68).

48. Dorsolateral flange at approximately mid-length of the caudoventral process of the premaxilla: absent (0); present (1). ([20], character 74).

Nasal

49. Location of the nasal bone and nasal cavity in the adult skull: the nasal extends from the rostral region of the skull to the rostroventral region of the snout with the nasal cavity rostromedial to the orbit (0); nasal retracted caudal to the rostrum, resulting in a supracranial hollow crest (1). ([20], character 75, modified).

50. Morphology of the rostral end of the nasal at the contact with the dorsal process of the premaxilla: long and wedge-shaped rostral process, gradually decreasing in width rostrally to a sharp point (0); hook-like process, it becomes abruptly deep near the rostral end and then wedges rostrally (1); long and subrectangular process, with slightly rounded corners (2). ([20], character 77, modified).

51. Morphology of the nasal contact with the caudodorsal region of the caudoventral premaxillary process at the caudal margin of the narial foramen: the nasal forms a subrectangular flange exposed dorsal to the premaxillary caudoventral process (0); the nasal
forms a large hook-like rostroventral process, exposed dorsal to the premaxillary caudoventral process (1); the nasal forms a greatly shortened and dorsoventrally narrow hook-like rostroventral process, exposed dorsal to the premaxillary caudoventral process (2). ([20], character 78).

52. Location of the rostral end of the dorsal process of the nasal relative to the rostral margin of the external naris: the rostral end of the rostrodorsal process of the nasal does not reach the rostral margin of the narial foramen (0); the rostral end of the rostrodorsal process of the nasal reaches the rostral margin of the narial foramen (1). ([20], character 79).

53. Caudal processes of the nasals: absent (0); forming a pair of finger-like processes on top of the frontals and centered around the sagittal plane of the skull roof (1); forming a pair of small and short processes that insert between the frontals at the sagittal plane of the skull roof (2). ([20], characters 81-82, modified).

54. Nasal arch: absent, dorsal border of the rostral process of nasal at about the same level as the caudal plate (0); present, summit located dorsal to the caudal margin of the narial foramen (1); present, summit located caudodorsal to the caudal margin of the narial foramen (2). ([20], characters 83, modified).

Maxilla

55. Rostrodorsal process that is medially offset from the body of the maxilla, and also extends medial to the caudovenventral process of the premaxilla to form part of the medial floor of the external naris: present (0); absent, the rostral end of the maxilla forms a ventrally sloping rostrodorsal shelf that underlies the premaxilla (1). ([20], character 84).

56. Position of the base of the dorsal process: base of dorsal process positioned caudal to the mid-length of the maxilla (0); base of dorsal process centered around the mid-length of the maxilla (1); base of dorsal process located rostral to the mid-length of the maxilla (2). ([20], characters 90, modified).

57. Morphology of the apex of the dorsal process of the maxilla: subtriangular, not dorsoventrally taller than rostrocaudally wide (0); dorsoventrally taller than it is wide, with a peaked and caudally inclined apex (1). ([20], character 91).

58. Morphology of the jugal articulation surface: finger-like process (0); dorsolaterally-facing joint surface for the jugal with a caudolaterally directed corner (1); laterally-facing joint surface with a lateroventrally-directed pointed corner (2). ([20], characters 92, modified).

59. Arrangement of maxillary foramina ventral and rostral to the jugal articulation (excluding large rostrodorsal or rostrolateral foramen): positioned rostrocaudally and scattered
throughout the lateral side of the maxilla (0); forming either a row or cluster that is oriented rostromedially (1). ([20], character 93).

60. Number of maxillary foramina ventral and rostral to the jugal articulation (excluding large rostroventral or rostral lateral foramen): seven or more (0); six or less (1). ([20], character 94).

61. Large rostral maxillary foramen: opening on the rostralateral body of the maxilla, within the rostral half of the rostroventral margin of the element, and exposed in lateral view (0); opening on the rostralateral body of the maxilla, within the dorsal half of the rostroventral margin of the element, and exposed in lateral view (1); opening on the dorsal surface of the maxilla along the maxilla-premaxilla contact, not exposed laterally (2). ([20], character 95).

62. Maxilla-lacrimal contact: present externally (0); largely covered externally by the jugal-premaxilla contact (1). ([20], character 96).

63. Length of the ectopterygoid shelf relative to the total rostrocaudal length of the alveolar margin of the maxilla: ratio greater than 0.25 and up to 0.35 (0); ratio greater than 0.35 (1). ([20], character 97, modified).

64. Slope of the ectopterygoid shelf, measured as angle between this and the rostrocaudal axis of the caudal portion of the tooth row: steeply inclined caudoventrally, with an angle greater than 21° (0); slightly inclined (angle less than 20°) or nearly horizontal (1). ([20], character 98, modified).

65. Morphology of the lateral emargination of the ectopterygoid shelf: dorsoventrally thin ridge (0); faint or dorsoventrally thin rostrally, then abruptly becoming dorsoventrally thick along the caudal segment of the margin (1); dorsoventrally thick continuous ridge, gradually thicker caudally than rostrally (2). ([20], character 99).

Jugal

66. Rostral apex of the rostral process: present, wedge-shaped, elongated and sharply pointed, positioned at mid-distance along the dorsoventral depth of the rostral process (0); present, wedge-shaped, pointed and less elongated than in (0), positioned within the dorsal half of the rostral process of the jugal; the dorsal magin of the apex forms a steeper angle with the horizontal than in state (0) (1); reduced to a blunt convexity or straight (2). ([20], character 103, modified).

67. Dorsoventral expansion of the caudodorsal margin of the rostral process: dorsoventrally narrow, rostroventrally directed and forming little of the rostroventral margin of the orbital rim (0); dorsoventrally deep (about 60-90% as deep as the rostral jugal constriction), dorsally or slightly recurved caudodorsally, forming the rostroventral corner of the orbital rim (1). ([20], character 104).
68. Morphology of the triangular caudoventral expansion of the rostral process of the jugal: no expansion (0); shallow and rostrocaudally wide prominence (wider than deep) (1); ventrally pointed, approximately as deep as or slightly deeper as its proximal end is wide (2); ventrally projected triangular narrow process, at least twice as deep as it is wide, shapely pointed and often recurved caudally (3). ([20], character 105, modified).

69. Location of the caudoventral apex of the rostral process relative to the caudodorsal articulation with the lacrimal (with longitudinal axis of the rostral process oriented horizontally): apex located ventral to the caudal margin of the lacrimal process (0); apex located ventral to the caudal margin of the lacrimal process (1). ([20], character 106).

70. Orientation of the medial articular surface of the rostral process of the jugal: facing medioventrally, the articular surface forms a deep concavity bounded dorsally and caudally by a laterally offset rim (0); facing medially, the articular surface is bounded only caudally by a rim of bone (1). ([20], character 107).

71. Ventral expansion of the caudoventral jugal flange (measured as the ratio between the dorsoventral depth of the flange and the minimum depth of the caudal constriction of the jugal): slightly expanded flange, ratio of 1.55 or less; greatly expanded flange, ratio greater than 1.55 (1). ([20], character 110, modified).

72. Lateral profile of the quadratojugal flange: auricular in shape, with subparallel concave to nearly straight dorsal and convex ventral margins that converge dorsally into a short, subconical point (0); fanlike, with dorsal and ventral margins that are subparallel and diverge caudodorsally, dorsal and ventral margins can be straight or slightly bowed dorsally (1); auricular in shape, with subparallel concave to nearly straight dorsal and convex ventral margins that converge dorsally into a recurved or dorsally-directed tall subconical extension [this state is similar to (1), but the dorsal region of the flange is rostrocaudally narrower and taller] (2). ([20], character 111, modified).

73. Relative depth of the caudal and rostral constrictions (in adults) (rostral constriction: region located between the rostral and postorbital processes; caudal constriction: region located between the postorbital process and the caudoventral flange): deeper rostral constriction, ratio of the depth of the caudal constriction relative to the rostral of 1 or less (0); deeper caudal constriction, with a ratio greater than 1 and less than 1.35 (1); much deeper caudal constriction, with a ratio greater than 1.35 (2). ([20], character 113).

74. Jugal overall robustness (in adults), measured as the ratio between the minimum depth of the caudal constriction and distance between the point of maximum curvature of the infratemporal margin and the caudal margin of the lacrimal process: relatively gracile jugal, ratio less than 0.60 (0); relatively robust jugal, ratio of 0.60 or greater (1). ([20], character 114).
75. Relative width and lateral profiles of the orbital and infratemporal margins of the jugal: wider infratemporal margin (0); orbital and infratemporal margins are nearly equally wide (1); wider orbital margin (2). ([20], character 115, modified).

Quadrate

76. Development of the squamosal buttress on the caudal margin of the dorsal end of the quadrate: present, the squamosal buttress is a sharp protuberance hanging from the caudal side of the dorsal fourth of the quadrate, near the head of the element (0); absent or poorly developed as a gentle convexity (1). ([20], character 120, modified).

77. Morphology of the ventral surface of the quadrate: mediolaterally broad and rostrocaudally compressed, lateral condyle slightly larger than the medial one; the ventral surface of the lateral condyle is only slightly offset ventrally relative to the ventral surface of the medial condyle (0); subtriangular in ventral view, lateral condyle rostrocaudally expanded and much larger than the medial one; the ventral surface of the lateral condyle is well offset ventrally relative to the ventral surface of the medial condyle (1). ([20], character 121).

Prefrontal

78. Dorsomedial margin of the prefrontal developed into a caudodorsally-oriented crest: absent (0); present (1). ([20], character 122).

79. Lateral profile of the rostrodorsal margin of the prefrontal: subarcuate to smoothly curved, the rostral margin is rostroventrally oriented and forming an obtuse angle with the dorsal orbital margin (0); rostromedially broad with subsquared rostrodorsal corner, the rostral margin is ventrally oriented and forms a 90° angle with the dorsal orbital margin (1). ([20], character 123).

80. Inclusion of the prefrontal in the circumnarial fossa: absent (0); present (1). ([20], character 125).

81. Outward flaring of the rostrodorsal orbital margin of the prefrontal: absent, the prefrontal lies flush with the surrounding lacrimal and postorbital (0); present, the prefrontal flares dorsolaterally forming a thin and everted wing-like rim around the rostrodorsal margin of the orbit (1). ([20], character 126).
Postorbital

82. Dorsal surface of the postorbital above the jugal process: horizontal or slightly concave (0); deeply depressed (1). ([20], character 128, modified).

83. Rostrocaudal constriction of the dorsal region of the infratemporal fenestra: absent, caudal (squamosal) process of the postorbital elongate over the infratemporal fenestra (broad and subrectangular dorsal region of the fenestra) (0); present and caused by the presence of a nearly straight and oblique caudoventral margin of the caudodorsal region of the postorbital (dorsal region of infratemporal fenestra typically subtriangular) (1); present and caused by rostrocaudal shortening of the caudal process of the postorbital (dorsal region of infratemporal fenestra typically oval) (2). ([20], character 129).

84. Morphology of the central body of the postorbital: triangular, craniocaudally broad, expanded rostroventrally to form a straight and obliquely oriented caudodorsal orbital margin (0); triangular, with a caudodorsal orbital margin that ranges in lateral profile from semicircular to subsquared (1); rostrocaudally expanded, rostrally excavated and and bulging laterally ('inflated'), containing a hollow inner cavity (in adults) (2). ([20], character 130).

85. Length of the jugal process of the postorbital: relatively short, approximately as long as the craniocaudal width of the orbit, hook-like in lateral profile (0); relatively long, longer than the craniocaudal width of the orbit, nearly straight, only slightly recurved rostrally (1). ([20], character 131).

86. Caudal extension of the caudal ramus of the postorbital that overlaps the laterodorsal surface of the squamosal: the caudal end of the postorbital caudal ramus extends caudodorsal to the precotyloid process, and over as much as the rostral half of the quadrate cotylus (0); the caudal end of the postorbital caudal ramus extends to a point rostral to the quadrate cotylus and does not overlap the latter (1). ([20], character 133, modified).

Squamosal

87. Length of the precotyloid process of the squamosal (measured as the ratio of its length relative to the width of the quadrate cotylus): precotyloid process distinctly longer than width of the quadrate cotylus (0); precotyloid process shorter than width of quadrate cotylus (1). ([20], character 134, modified).

88. Dorsoventral expansion of the caudolateral surface of the squamosal: unexpanded, shallowly exposed in caudal view (0); greatly expanded dorsomedially, forming a deep, near vertical, well-exposed face in caudal view (in adults) (1). ([20], character 135).
89. Separation of the squamosals at the occipital margin of the skull roof: completely separated by the parietal (0); the squamosal approach the sagittal plane of the skull, separated by a narrow band of parietal (1); extensive intersquamosal joint present at the midline, parietal completely excluded from the sagittal plane of the skull at that particular spot (in adults) (2). ([20], character 136).

90. Rostromedial indenture of the medial ramus of the squamosal: present, medial ramus of the squamosal curves rostromedially, so that the back of the skull appears to be deeply indented rostrally when viewed dorsally (0); absent, medial ramus of the squamosal extends medially, forming a subsquared caudolateral border of the skull roof (1). ([20], character 137).

Frontal

91. Bifurcation of the rostromedial margin of the frontals at the sagittal plane of the skull roof, leaving a V-shaped space in between: present (0); absent (1). ([20], character 138, modified).

92. Nasal articulation surface of the frontal shaped into a rostroventrally-slopping platform: absent (0); present (1). ([20], character 140).

93. Exposure of the frontal along the dorsal margin of the orbit: frontal exposed (0); frontal not exposed (1). ([20], character 143, modified).

94. Frontal upward doming dorsal to the braincase of subadult (and perhaps young adult) specimens: absent (0); present (1). ([20], character 144).

Parietal

95. Maximum length/minimum width proportions of the adult parietal: short, ratio between 1.40 and 2.35 (0); very short, length/width ratio less than 1.40 (1); relatively long, ratio greater than 2.35 (2). ([20], character 147, modified).

96. Orientation of the parietal midline crest: straight and level with the skull roof or slightly down-warped along its length (0); the sagittal crest deepens caudally and is strongly down-warped (1). ([20], character 148).

97. Morphology of the rostromedian process of the parietal that forms a crenulated suture in between the caudomedian margin of the frontals: rectangular, rostrocaudally short and mediolaterally expanded (0); rostrocaudally short and subtriangular to arcuate or absent (1); rostrocaudally elongate and mediolaterally narrow (2). ([20], character 149).

98. Rostral extension of the sagittal crest along the dorsal surface of the parietal: sagittal crest fades away or absent on the rostral third of the parietal (0); sagittal crest extends along the
entire length of the parietal and remains sharp and well defined at the rostral region (1). ([20], character 150, modified).

Basioccipital

99. Length of basioccipital constriction: relatively long and well-developed (0); relatively short and poorly developed (1). ([20], character 153).

Basisphenoid

100. Orientation of the basiptyerygoid processes of the basisphenoid (measured as the angle between the ventral margins of both processes): angle less than 100° (0); angle of 100° or greater (1). ([20], character 154).

101. Development of the alar process of the basisphenoid: moderately developed (0); very well developed, relatively large in size (1). ([20], character 155).

102. Development of the rostral constriction of the basisphenoid, caudal to the basiptyerygoid processes (measured as the ratio between the minimum mediolateral width of the rostral constriction and the maximum width of the basisphenoid across the sphenoccipital tubercles): relatively thick constriction, ratio less than 1.90; very thin constriction, ratio greater than 1.90 (1). ([20], character 158, modified).

Laterosphenoid

103. Extreme reduction of the length of the postorbital process of the laterosphenoid to 25% or less the length of the mediadorsal flange of this element: absent (0); present (1). ([20], character 160).

Supraoccipital

104. Lateroventral corner of the supraoccipital deeply inset into the exoccipital, so that the latter is ‘locked’ between two short flanges that project medially above lateral end of the supraoccipital–exoccipital contact: absent (0); present (1). ([20], character 162).

105. Caudal extension of the exoccipital-supraoccipital shelf above the foramen magnum: very short rostrocaudal length, approximately less than half the diameter of the foramen magnum (0); moderately long, approximately more than half but less than the diameter of the
foramen magnum (1); very long, substantially longer (often twice or more) than the diameter of the foramen magnum (2). ([20], character 163). Character treated as ordered.

Exoccipital-opisthotic

106. Orientation of caudal surface of paroccipital processes: faces mediocaudally (0); faces caudally (1). ([20], character 164, modified).

Palate

107. Ectopterygoid-jugal contact: present, the ectopterygoid contacts the medial side of the jugal (0); absent, the jugal lacks an articular facet for the ectopterygoid (1). ([20], character 167).

Regional cranial characters

108. Exposure of the nasal passage: present, nasal passage open and exposed on the lateral side of the rostrum (0); absent, nasal passage nearly or completely enclosed by bone and formation of internal cavities and passages (1). ([20], character 169).

109. Ratio between the length of the narial foramen and the distance between the rostroventral corner of the premaxilla and the rostroventral margin of the prefrontal: very short narial foramen, ratio up to 0.40 (0); moderately long narial foramen, ratio greater than 0.40 but less than 0.60 (1); elongated narial foramen, ratio between 0.60 and 0.65 (2). ([20], character 172).

110. Caudal extent of the nasal passage dorsal and/or caudal to the orbit: absent, nasal passage restricted to the antorbital region of the skull (0); present (1). ([20], character 176, modified).

111. Composition of the caudal margin of the functional external naris: ormed by the nasal dorsally and the premaxilla ventrally (0); formed entirely by the nasal (1); formed entirely by the premaxilla (2). ([20], character 177).

112. Caudodorsal extension of the circumnarial fossa (homologous to the lateral diverticulum inside hollow supracranial crests): the fossa does not reach the caudal margin of the narial foramen and, thus, lacks a caudal margin (0); the fossa extends as far as to surround the caudal margin of the narialforamen, but does not reach the orbit (1); the fossa extends as far...
as the rostrodorsal region of the orbit (2); the fossa extends beyond the orbit, caudodorsal to its caudal margin (3). ([20], character 179).

113. Degree of excavation of the caudal region of the circumnarial fossa: lightly incised (0); deeply incised, but not invaginated in adults (1); deeply incised and invaginated in adults. ([20], character 180, modified). Character treated as ordered.

114. General shape of supracranial crest: absent (0); mediolaterally compressed arcuate protuberance, rostral or, in adults, dorsal to the level to the orbits (1); paddle-like and caudally (as well as slightly dorsally) directed solid blade of bone (2); mediolaterally narrow and paddle-like, extending caudal to the occiput (3); rostrally excavated and rostrally-facing protuberance (4); nasal fold that rises dorsally or caudodorsally to form a laterally excavated promontory (5); hollow supracranial crest (6). Prieto-Márquez (2010, character 184, modified).

115. Palpebral (supraorbital) bone: present (0); absent (1). ([20], character 187, modified).

116. Length/width proportions of the orbit: nearly circular, approximately as wide as it is deep (0); elongated, dorsoventrally deeper than it is wide (1). ([20], character 188).

117. Shape and rostrocaudal width of the dorsal margin of the infratemporal fenestra relative to that of the dorsal margin: subrectangular, with a dorsal infratemporal margin that is approximately as wide as the ventral margin (0); subtriangular, with a dorsal infratemporal margin that is narrower than the ventral margin (1). ([20], character 191).

118. Location of the dorsal margin of the infratemporal fenestra relative to the dorsal margin of the orbit: the dorsal margin of the infratemporal fenestra lies approximately at the same level than the dorsal margin of the orbit and the caudal region of the skull roof is subhorizontal or slightly sloping rostroventrally relative to the frontal plane (0); the dorsal margin of the infratemporal fenestra is substantially more dorsally located than the dorsal margin of the orbit and the caudal region of the skull roof is rostroventrally inclined relative to the frontal plane (1); the dorsal margin of the infratemporal fenestra lies slightly or substantially below the level of the dorsal margin of the orbit and the caudal region of the skull roof is subhorizontal or slightly sloping caudoventrally relative to the frontal plane (2). ([20], character 192).

119. Morphology of the dorsal outline of the supratemporal fenestra: subrectangular, with the long axis directed rostrally (0); oval, with the long axis directed rostrolaterally (1). ([20], character 193, modified).
120. Maximum transverse width of the cranium in dorsal view across the postorbitals relative to the width across the quadrate cotylus of the squamosals: the skull is up to 25% wider across the postorbitals (0); the skull is more than 25% wider across the postorbitals (1). ([20], character 193, modified).

Vertebræ

121. Morphology of the dorsal flange of the axis: dorsally convex flange extending beyond or to the level of the cranialmost region of the postzygapophyses (0); presence of short cranial flange separated from the postzygapophyseal region by a prominent embayment (1). ([20], character 197).

122. Development of the postzygapophyseal proceses of cranial and middle cervical vertebrae: relatively low and relatively short, less than three times the rostrocaudal breadth of the neural arch (0); relatively high and relatively long, three times or more longer than the breadth of the neural arch (1). ([20], character 198).

123. Height of the neural spine relative to that of the centrum of the tallest posterior dorsal or sacral vertebrae (in adults): relatively high neural spine, ratio greater than 2.10 (0); relatively low neural spine, ratio up to 2.10 (1). ([20], character 200, modified).

124. Slightly elongated neural spines in the cranial dorsal vertebrae, forming a 'wither-like' region above the pectoral girdle: absent (0); present (1). ([20], character 201).

125. Minimum count of co-ossified vertebrae in the sacral region (including single dorsal and caudal contributions: seven or fewer (0); eight or more (1). ([20], character 202).

Sternal

126. Length of the 'handle-like' caudolateral process of the sterna relative to that of the craniomedial plate (excluding the caudoventral process): caudolateral process slightly shorter or as long as the craniomedial plate (0); caudolateral process longer than the craniomedial plate (1). ([20], character 204).
Coracoid

127. Ratio between the length of the lateral margin of the facet for the scapular articulation and the length of the lateral margin of the glenoid: slightly longer scapular facet, ratio greater than 1 and up to 1.30 (0); glenoid longer than the scapular facet, with a ratio up to 1 (1). ([20], character 206, modified).

128. Angle between the lateral margins of the facet for scapular articulation and the glenoid: angle greater than 115° (0); angle up to 115° (1). ([20], character 207).

129. Morphology of the craniomedical margin of the coracoid: convex or straight, associated to a moderate development and slightly projected biceps tubercle (0); oncave, associated to a relatively large and lateroventrally projected biceps tubercle (1). ([20], character 208).

130. Development of the 'hook-like' ventral process of the coracoid, measured as the ratio between the dorsoventral depth and the breadth of the process: relatively short, ratio less than 0.65 (0); relatively long, ratio more than 0.65 (1). ([20], character 209, modified).

131. Curvature of the ventral hook-like process of the coracoid (0); recurved, so that the process is caudoventrally directed (1). ([20], character 210).

Scapula

132. Lateral profile of the dorsal margin of the scapula: craniocaudally straight from the cranial margin of the coracoid facet to the distal end of the blade (0); curved, dorsally convex, curvature originating at the level of the dorsal margin of the pseudacromion process, and most pronounced over the dorsoventral constriction (1). ([20], character 211).

133. Scapular length, ratio between the craniocaudal length of the scapula (from the cranial end of the acromion process to the distal margin of the blade) and the dorsoventral depth of the cranial end (from the cranial end of the acromion process to the ventral apex of the glenoidal facet): relatively short scapula, ratio up to 4 (0); relatively long scapula, ratio greater than 4 (1). ([20], character 212).

134. Dorsoventral expansion of the distal region of the scapular blade (measured as a ratio between the depth of the distal end of the blade and the depth of the proximal region): ratio less than 1 (0); ratio of 1 or greater (1). ([20], character 213).
135. Proximal constriction (scapular 'neck'), ratio between the dorsoventral width of the proximal constriction and the dorsoventral depth of the cranial end of the scapula: narrow 'neck', ratio up to 0.60 (0); relatively broad 'neck', ratio greater than 0.60 (1). ([20], character 214).

136. Morphology and orientation of the pseudoacromial process of the scapula: recurved, so that the cranial region is dorsally or craniodorsally directed (0); horizontal, occasionally with minor and subtle dorsal or ventral curvatures, so that the cranial region is cranially or mostly cranially directed (1). ([20], character 215).

137. Cranial extension of the craniodorsal region of the scapula (bearing the coracoid facet), measured as a ratio between the distance from the coracoid joint and the cranial end of the pseudoacromial process and the height between this and the ventral apex of the glenoidal facet: short craniodorsal region, ratio less than 0.45 (0); long craniodorsal region, ratio of 0.45 or greater (1). ([20], character 217).

138. Development of the deltoid ridge: dorsoventrally narrow convexity limited to the proximal region of the scapula, near the pseudoacromial process from which it develops, with a poorly demarcated ventral margin (0); dorsoventrally deep and craniocaudally long, with a well demarcated ventral margin (1). ([20], character 218).

**Humerus**

139. Length of the deltopectoral crest of the humerus (measured as the ratio between the proximodistal length of the crest and the proximodistal length of the humerus): proximodistally short crest, ratio less than 0.48 (0); ratio between 0.48 and 0.55 (1); very long crest, ratio greater than 0.55 (2). ([20], character 219).

140. Lateroventral expansion of the deltopectoral crest of the humerus (measured as the ratio between the width of the humerus across the distal fourth of the deltopectoral crest and the width of the distal shaft at the point of maximum curvature): poorly expanded deltopectoral crest, ratio less than 1.65 (0); ratio between 1.65 and 1.90 (1); very expanded deltopectoral crest, ratio greater than 1.90 (2). ([20], character 220).

141. Degree of angulation of the ventral margin of the deltopectoral crest: well-rounded (0); extending abruptly from the humeral shaft to give a distinct angular profile (1). ([20], character 221).

142. Overall proportions of the humerus (measured as the ratio between the total length and the width of the lateral surface of the proximal end of the humerus: ratio between 4.25 and 4.90
(0); relatively short and stocky humerus, ratio less than 4.25 (1); relatively long and thin humerus, ratio greater than 4.90 (2). ([20], character 222, modified).

**Ulna**

143. Length of the ulna relative to its dorsoventral thickness (measured at mid-shaft): ratio length/width less than 10 (0); ratio length/width equal or larger than 10 (1). ([20], character 223).

**Manus**

144. Manual digit I: presence of metacarpal I and one ungual phalanx (0); entire digit I absent (1). ([20], character 226).

**Ilium**

145. Angle of ventral deflection of the preacetabular process: angle greater than 150º (0); angle of 150º or less (1). ([20], character 232).

146. Dorsoventral depth of the proximal region of the preacetabular process (measured as a ratio between this and the dorsoventral distance between the pubic peduncle and the dorsal margin of the ilium): shallow, less than half the depth of the cranial central blade, ratio less than 0.50 (0); approximately as deep as the cranial central blade depth, ratio between 0.50 and 0.55 (1); deeper than half the depth of the cranial central blade, ratio greater than 0.55 (2). ([20], character 233).

147. Dorsoventral depth of the central blade (expressed as a ratio between this and the distance between the pubic peduncle and the caudodorsal prominence of the ischial peduncle): ratio of 0.80 or greater (0); ratio less than 0.80 (1). ([20], character 234).

148. Position of the ventralmost margin of the supraacetabular process relative to the caudoventral margin of the lateral ridge of caudal protuberance of the ischial peduncle: apex located caudodorsally (0); apex located craniodorsally (1). ([20], character 235).

149. Development of the lateroventral projection of the supraacetabular process: forms a longitudinal and continuous 'swelling' or reflected border along the dorsal margin of the central blade and the proximal region of the postacetabular process, with a depth up to 25%
the depth of the ilium (0); projected lateroventrally at least 25% (but less than half) the depth of the ilium (1); projects lateroventrally between half and three quarters of the dorsoventral depth of the ilium (2); projects lateroventrally to overlap totally or at least half of the lateral ridge of the caudal prominence of the ischial peduncle (3). ([20], character 236).

150. Symmetry of the lateral profile of the supraacetabular process: asymmetrical, with a caudally skewed lateral profile (0); symmetrical or with a slightly caudally skewed profile (1). ([20], character 238).

151. Morphology of the lateroventral margin of the supraacetabular process: craniocaudally sinuous (0); widely arched (1); U-or V-shaped (2); subrectangular, with a shallow notch that divides the ventral margin in two poorly demarcated lobes (3). ([20], character 239).

152. Morphology of the ischial peduncle: relatively large and dorsoventrally deep (longer than wide), subconical, with a proximal region that is only slightly craniocaudally wider than the distal end of the process (0); relatively shorter (wider or as wide as long) and triangular, with a proximal region that is much craniocaudally wider than the distal end (1). ([20], character 241).

153. Morphology of the ischial peduncle: formed by a single and large, oval ventral protrusion (0); composed of a large and oval ventral protrusion and by a smaller, caudodorsally located prominence emerging from the caudodorsal ridge (1); formed by two protrusions of similar size, the caudalmost one located slightly caudodorsally (2). ([20], character 242).

154. Ratio between the craniocaudal length of the postacetabular process and the craniocaudal length of the central blade of the ilium: short postacetabular process, ratio up to 0.80 (0); postacetabular process nearly as long as the central plate, ratio greater than 0.80 but less than 1.1 (1); postacetabular process substantially longer than the central plate, ratio of 1.1 or greater (2). ([20], character 243).

155. Brevis shelf at the base of the postacetabular process: present (0); absent (1). ([20], character 244, modified).

156. Geometry of the lateral profile of the postacetabular process: the ventral margin converges caudodorsally to meet the horizontal dorsal margin, forming a tapering caudal end and producing a triangular lateral profile of the process (0); dorsal and ventral margins parallel or slightly convergent, forming a distinct (rectangular or subcircular) caudal margin (1). ([20], character 247).
157. Orientation of the dorsal margin of the postacetabular process relative to the acetabular margin: horizontal dorsal margin, parallel or nearly parallel to the acetabular margin (0); caudodorsally oriented dorsal margin, rising dorsally relative to acetabular margin (1). ([20], character 248).

Pubis

158. Orientation of the dorsoventral expansion of the prepubic process: the dorsal region of the expansion is more expanded than the ventral region, so that distally the process is dorsally directed (0); the ventral region is more expanded than the dorsal region, so that the distal expansion is ventrally directed (1). ([20], character 252).

159. Geometry of the dorsoventral expansion of the prepubic process (in lateral or medial views): circular to oval expansion, extensive and convex ventral margin (0); subsquared distal dorsal margin, expansion dorsoventrally taller than craniocaudally long, very pronounced proximal dorsal concavity and nearly straight distal ventral margin (1); ellipsoidal, expansion craniocaudally longer than dorsoventrally tall, well-pronounced concavities of the dorsal and ventral proximal margins (2); oval expansion, dorsoventrally taller than craniocaudally long, well-pronounced concave profiles of dorsal and ventral proximal margins (3); rectangular, craniocaudally longer than dorsoventrally tall, nearly straight profiles of the dorsal and ventral proximal margins (4). Prieto-Márquez (2010, character 249). ([20], character 253).

160. Craniocaudal length of the proximal constriction of the prepubic process of the pubis relative to length of the dorsoventral expansion: constriction slightly shorter than the dorsoventral expansion, which begins at the proximal region of the process (0); constriction and distal expansion have approximately the same length (1); constriction longer than the dorsoventral expansion, which is restricted to the distal region of the process (2). ([20], character 255, modified).

161. Relative position of maximum concavity of the dorsal and ventral margins of the prepubic process: maximum ventral concavity achieved adjacent to the proximal region of the postpubic process, maximum dorsal concavity located further distally (0); maximum ventral concavity located ventral to or slightly caudal to the maximum dorsal concavity (1). ([20], character 256).

162. Total length of the pubis, as the ratio between the craniocaudal distance from the acetabular margin to the distal margin of the prepubic process and the distance from the dorsal margin
of the iliac peduncle and the ventral margin of the proximal postpubic shaft: short, ratio less than 3; long, ratio greater than 3. ([20], character 262, modified).

Ischium

163. Development of a caudal curvature of the distal margin of the iliac peduncle: absent or faintly developed (0); presence of a well-developed curvature in the caudodorsal corner, so that the peduncle appears 'thumb-like' in lateral and medial profiles (1). ([20], character 263, modified).

164. Elongation of the iliac peduncle of the ischium (ratio between the proximodistal length and the craniocaudal width of the distal margin): relatively short peduncle, ratio less than 2 (0); relatively long peduncle, ratio greater than 2 (1). ([20], character 264, modified).

165. Relative orientation of the acetabular and caudodorsal margins of the iliac peduncle of the ischium: margins are either parallel or slightly convergent relative to each other (correlated with a greater expansion of the craniodorsal corner of the peduncle) (0); margins become slightly to greatly divergent near the proximal region of the peduncle (1). ([20], character 266).

166. Orientation of the craniocaudal axis of the pubic peduncle (perpendicular to its articular margin) relative to the ischial shaft: ventrally inclined, angle up to 130° (0); slightly inclined ventrally or parallel, angle greater than 130° (1). ([20], character 267, modified).

167. Length/width proportions of the pubic peduncle: approximately as long or slightly longer proximodistally as the distal articular surface is dorsoventrally wide (0); proximodistally shorter than the dorsoventral width of the distal articular surface (1). ([20], character 268, modified).

168. Relative position of the dorsal acetabular margin of the pubic peduncle: ventral to or at the same level as the dorsal margin of the ischial shaft (0); peduncular margin set dorsal to the dorsal margin of the ischial shaft (1). ([20], character 269).

169. Dorsoventral thickness of the mid-shaft of the ischium (measured as a ratio between this and the length of the entire shaft): relatively thick shaft, more than 5% the length of the ischial shaft (0); very thin shaft, up to 5% the length of the ischial shaft (1). ([20], character 270, modified).
170. Morphology of the distal region of the ischial shaft: ventrally expanded, forming a large 'foot' or 'boot-like' process (0); slightly expanded into a blunt end (1). ([20], character 271, modified).

Femur

171. Degree of curvature of the distal half of the femoral shaft: slightly curved caudomedially (0); absence of curvature, straight distal shaft (1). ([20], character 275).

172. Lateral profile of the caudoventral margin of the fourth trochanter: triangular and ending in a caudally, and slightly ventrally, directed point (0); smooth and arcuate (1). ([20], character 276).

Pes

173. Length/width proportions of metatarsal III (measured as the ratio between its proximodistal length and its mediolateral breadth at mid-shaft): elongated, ratio of 4.50 or greater (0); relatively short, ratio less than 4.50 (1). ([20], character 282, modified).

174. Length/width proportions of the disc-shaped pedal phalanges III2-III3: up to three times (or less) wider than they are proximodistally long (0); more than three times wider than they are proximodistally long (1). ([20], character 284).

175. Morphology of the pedal unguals: proximodistally elongated and arrow-shaped, with a bluntly truncated tip and prominent claw grooves (0); mediolaterally broad and proximodistally shortened, rounded shield or hoof-like shaped, with reduced or absent claw grooves (1). ([20], character 285).

176. Ridge on the plantar surface of pedal unguals: absent (0); present (1). ([20], character 286).

File S3: character-taxon matrix

Probactrosaurus gobiensis

248
Bactrosaurus johnsoni
0000000200000010000000000000010100?1001000000000000000000001000000000000000000000000
000000000000000000000000000000000000000000010000110000000000
110000110010

Parasaurolophus walkeri
111??????111?11110101011111111011110000/1?///101211?0112213010221211001121000
121111111101????10111//12//6111210?1011010111111000221101201312120111112110101110001
1????

Olorotitan arharensis
11111102111?11112110100101111111110?11110000/1?///1012112?1122130100112?11001101
001110111111101110010?11/12//611?21001011011111111100022111?1201112121(01)11?????1?11
00011????

Maiasaura peeblesorum
1112110211?21112111111001111111111111?2131101000011100010211111201201111010100110
0110102110020111110111100120411001100111111111111011011011201203121111121100
11110110011

Brachylophosaurus canadensis
111211021112112121210001111111111111?2131101000011100010211111201201111010100110
010101011100201111101110101030211001100011111111111111101101011120120312111112110
0011110110011

Acritavus gaglarsoni
1112110?111????????2110011011111??????3110100000????00102111?112012011101?010001??
00021100000011111?1110?01?????????????????????????????????????????????????????????????1?11?

Gryposaurus notabilis
1211101211?00010310201001101111111111111111112110100100?0220202111011211211021001?1000
01110011000020011?000121103011011010001101111110011111121111121122?111411100
11111111111

Gryposaurus monumentensis
12121012111010103102010021011111111111111112110100100102202021110112112111211001000
Gryposaurus latidens

Kritosaurus navajovius

Prosaurolophus maximus

Saurolophus osborni

Saurolophus angustirostris

Edmontosaurus annectens

Edmontosaurus regalis

Hadrosaurus foulkii
Lophorhoton atopus

Wulagasaurus dongi

Kerberosaurus manakini

Kundurosaurus nagornyi

File S4: Tree description of the larger cladogram (Fig. 20)

Character transformations were evaluated under unambiguous, fast and slow optimisation options in Winclada (Nixon, 2002); unambiguous synapomorphies are those that diagnose a node under both fast and slow optimisations. Node numbers refer to Fig. 20. The synapomorphies supporting each clade are indicated by a pair of numbers. The number to the left of the dash is the character number corresponding in the list in Appendix 2, whereas the number between brackets represents the character state. Numbers in bold are unambiguous and unequivocal (CI = 1) synapomorphies.

Node A (Hadrosauridae): Unambiguous: 1 (1), 4 (1), 5 (1), 65 (2), 77 (1), 90 (1), 106 (1), 114 (5), 143 (1), 148 (1), 149 (2), 153 (2), 156 (1); Fast: 3 (1), 10 (1), 11 (1), 13 (1), 17 (1), 18 (1), 19 (1), 20 (1), 22 (1), 25 (1), 26 (1), 28 (1), 29 (1), 30 (1), 31 (1), 32 (1), 34 (1), 36 (1), 40 (1), 41 (1), 51 (1), 56 (1), 58 (2), 59 (1), 60 (1), 61 (1), 63 (1), 64 (1), 68 (2), 73 (1), 75 (1), 97 (1), 99 (1), 100(1), 104 (1), 111 (1), 112 (1), 115(1), 116 (1), 117 (1), 122 (1), 125 (1), 128 (1), 129 (1), 130 (1), 131 (1), 132 (1), 133 (1), 135 (1), 150(1), 151 (2), 154 (1), 155 (1), 158 (1), 160(1), 161 (1), 170 (1).

Node B: Unambiguous: 8 (1); Fast: 175 (0); Slow: 170 (1).
Node C (Saurolophidae): Unambiguous: 2 (1), 9 (1), 67 (1), 70 (1), 84 (1), 141 (1), 157 (1), 167 (1);
Fast: 6 (1), 89 (1), 112 (2), 139 (1), 140 (2); Slow: 3 (1), 10 (1), 11 (1), 13 (1), 14 (1), 18 (1), 20 (1),
22 (1), 25 (1), 26 (1), 28 (1), 29 (1), 30 (1), 31 (1), 32 (1), 34 (1), 36 (1), 40 (1), 58 (2), 59 (1), 60 (1),
63 (1), 64 (1), 73 (1), 97 (1), 99 (1), 100 (1), 104 (1), 115 (1), 116 (1), 122 (1), 15 (1), 129 (1), 130 (1),
131 (1), 132 (1), 133 (1), 135 (1), 144 (1), 151 (2), 155 (1), 158 (1), 161 (1).

Node D (Lambeosaurinae): Unambiguous: 16 (1), 47 (1), 49 (1), 55 (1), 57 (1), 66 (2), 74 (1), 75 (2), 78 (1), 81 (1), 82 (1), 88 (1), 92 (1), 93 (1), 94 (1), 95 (1), 96 (1), 108 (1), 110 (1), 111 (2), 114 (6), 118 (2), 119 (1), 124 (1), 139 (2), 142 (1), 163 (1); Fast: 12 (1), 17 (2), 56 (0), 61 (2), 68 (3), 71 (0), 76 (1), 138 (0), 149 (1), 160 (2), 170 (0); Slow: 41 (1), 68 (3), 140 (2), 150 (1).

Node E (Saurolophinae): Unambiguous: 105 (1), 136 (1); Fast: 4 (2), 37 (1), 39 (2), 41 (3), 43 (1), 45 (1), 72 (1), 79 (1), 85 (1), 126 (1), 159 (2), 168 (1), 169 (1); Slow: 61 (1), 75 (1), 138 (1), 139 (1), 170 (1).

Node F: Unambiguous: 20 (2), 98 (1); Fast: 140 (0); Slow: 17 (1), 37 (1), 39 (2), 41 (3), 43 (1), 45 (1), 51 (1), 56 (1), 68 (2), 85 (1), 111 (1), 112 (2), 126 (1), 128 (1), 160 (1), 168 (1), 175 (1).

Node G (Brachylophosaurini): Unambiguous: 91 (1), 101 (1), 102 (1), 120 (1); Fast: 12(2), 16 (2),
21 (1), 50 (1), 62 (1), 89 (2), 114 (2), 121 (1), 150 (0), 151 (3), 169 (0), 176 (1); Slow: 4 (2), 6 (1), 71 (1), 72 (1), 89 (2), 117 (1).

Node H: Unambiguous: 27 (1), 81 (1), 87 (1), 95 (2); Fast: 79 (0); Slow: 12 (2), 16 (2), 19 (1), 50 (1),
62 (1), 121 (1), 151 (3), 154 (1), 159 (1), 176 (1).

Node I: Unambiguous: 53 (1), 66 (1), 69 (1), 72 (2), 105 (2); Fast: 6 (0), 7 (1), 9 (2), 86 (1), 117 (0),
118 (1), 123 (1), 137 (1), 140 (1), 147 (1) 154 (2), 159 (4), 162 (1), 173 (1), 174 (1); Slow: 79 (1).

Node J: Unambiguous: 2 (2), 14 (0), 17 (3), 95 (2); Fast: 71 (0), 112 (1); Slow: 4 (2); 89 (1); 126 (1),
137 (1), 140 (1), 147 (1), 150 (1), 154 (2), 159 (4), 162 (1).

Node K (Gryposaurus): Unambiguous: 41 (2), 52 (0), 56 (2), 114 (1), 133 (0), 134 (0), 142 (2), 146 (1); Fast: 9 (1), 19 (0), 48 (1), 53 (2), 54 (1), 75 (0), 97 (0), 109 (3); Slow: 7 (1), 112 (1).

Node L: Unambiguous: 39 (1); Fast: 54 (2); Slow: 48 (1), 53 (2), 54 (2), 75 (0), 86 (1), 97 (0), 109 (3),
118 (1).

Node M: Unambiguous: 1 (2), 23 (1), 24 (1), 50 (2), 51 (2), 68 (1), 76 (1), 83 (1), 113 (1), 117 (1),
164 (1); Fast: 86 (0), 118 (0); Slow: 9 (2), 19 (1), 74 (1).

Node N (Saurolophini): Unambiguous: 41 (1), 73 (0), 80 (1), 81 (1), 93 (1), 109 (2), 113 (2); Fast:
112 (2), 121 (1), 179 (3), 169 (0); Slow: 7 (1), 174 (1).
Node O (Saurolophus): Unambiguous: 39 (1), 53 (0), 79 (0), 82 (1), 83 (2), 89 (2), 112 (3), 114 (3), 124 (1), 140 (2), 142 (1), 143 (0), 162 (0); Fast: 139 (2), 168 (0); Slow: 121 (1); 149 (3); 173 (1)

Node P (Edmontosaurini): Unambiguous: 114 (0), 154 (1), 160 (2); Fast: 7 (0), 12 (1), 16 (1), 20 (3), 44 (1), 46 (1), 62 (1), 85 (0), 97 (2), 120 (1), 159 (2), 174 (0); Slow: 112 (1), 169 (1).

Node Q: Fast: 53 (2), 82 (1), 134 (0), 142 (1), 145 (0).

Node R (Edmontosaurus): Unambiguous: 73 (2), 84 (2), 103 (1), 113 (2); 137 (0), 139 (2), 159 (3); Slow: 12 (1), 16 (1), 20 (3), 44 (1), 46 (1), 62 (1), 85 (0), 97 (2), 120 (1).

Appendix 5: Tree description of the reduced cladogram (Fig. 21)

Character transformations were evaluated under unambiguous optimisation option in Winclada (Nixon, 2002); unambiguous synapomorphies are those that diagnose a node under both fast and slow optimisations. Node numbers refer to Fig. 21. The synapomorphies supporting each clade are indicated by a pair of numbers. The number to the left of the dash is the character number corresponding in the list in Appendix 2, whereas the number between brackets represents the character state. Numbers in bold are unambiguous and unequivocal (CI = 1) synapomorphies.

Node C (Saurolophidae): 2 (1), 3 (1), 4 (1), 5 (1), 9 (1), 13 (1), 17 (3), 18 (1), 22 (1), 25 (1), 26 (1), 28 (1), 29 (1), 30 (1), 31 (1), 32 (1), 36 (1), 40 (1), 59 (1), 64 (1), 67 (1); 70 (1), 89 (1), 90 (1), 106 (1), 116 (1), 125 (1), 129 (1), 130 (1), 131 (1), 132 (1), 133 (1), 135 (1), 141 (1), 148 (1), 155 (1), 156 (1), 157 (1), 158 (1), 161 (1), 167 (1).

Node D (Lambeosaurinae): 16 (1), 47 (1), 49 (1), 55 (1), 66 (2), 78 (1), 82 (1), 88 (1), 92 (1), 93 (1), 94 (1), 96 (1), 108 (1), 110 (1), 114 (6), 118 (2), 119 (1), 124 (1), 140 (2), 142 (1), 163 (1).

Node E (Saurolophinae): 4 (2), 37 (1), 39 (2), 43 (1), 45 (1), 56 (1), 85 (1), 98 (1), 105 (1), 126 (1), 136 (1); 149 (2), 168 (1), 170 (1).

Node G (Brachylophosaurini): 12 (2), 16 (2), 17 (1), 27 (1), 50 (1), 62 (1), 71 (1), 87 (1), 91 (1), 101 (1), 102 (1), 120 (1), 121 (1), 151 (3), 176 (1).

Node J: 2 (2), 66 (1), 69 (1), 79 (1), 105 (2), 123 (1), 137 (1), 147 (1), 162 (1), 169 (1).
Node K (Gryposaurus): 41 (2), 52 (0), 54 (1), 56 (2), 114 (1), 117 (0), 133 (0), 134 (0), 142 (2), 146 (1), 154 (2).

Node L: 39 (1), 54 (2).

Node M: 1 (2), 9 (2), 23 (1), 24 (1), 50 (2), 51 (2), 68 (1), 76 (1), 83 (1), 113 (2), 164 (1).

Node N (Saurolophini): 73 (0), 80 (1), 93 (1), 109 (2), 154 (2), 169 (0).

Node O (Saurolophus): 39 (1), 79 (0), 82 (1), 83 (2), 89 (2), 124 (1), 140 (2), 142 (1), 143 (0), 162 (0).

Node R (Edmontosaurus): 12 (1), 16 (1), 20 (3), 44 (1), 46 (1), 62 (1), 73 (2), 84 (2), 85 (0), 97 (2), 103 (1), 120 (1), 137 (0), 139 (2), 159 (3).