

中国东北马斯特里赫特阶的 *Wulagasaurus dongi* (鸭嘴龙亚科)的重新评估与系统发育分析¹⁾

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摘要:通过对黑龙江省乌拉嘎地区晚白垩世渔亮子组地层发现的董氏乌拉嘎龙(*Wulagasaurus dongi*)的原有材料和新材料进行对比研究和重新评估,可以认定以前归入乌拉嘎龙的部分骨骼(包括不完整的脑颅骨、上颌骨和肩胛骨)实际上应该属于赖氏龙类,并相应地修订了其鉴定特征。乌拉嘎龙具有同北美地区发现的短冠龙和慈母龙十分相似的骨学特征:长而楔形的前顶点位于颧骨前支的一半背腹高度处;颧骨后支呈扇形;鸟喙骨的腹突相对较长且纤细;肱骨三角胸嵴较不发育,适度地向前外方扩展;髌骨髁臼上突的腹缘呈不对称的U形,缺乏一条强烈的嵴连接其后部区域与髁臼后突的背缘。系统发育分析结果显示乌拉嘎龙、短冠龙和慈母龙共同构成了鸭嘴龙亚科的一个基干支系。该支系起源于桑托期的亚洲,可能在中坎帕期之前发生分异并通过白令陆桥向北美地区迁徙辐射。

关键词:晚白垩世,鸭嘴龙亚科,乌拉嘎龙,基干类群

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RE-EVALUATION AND PHYLOGENETIC ANALYSIS OF *WULAGASAUROS DONGI*, A HADROSAURINE DINOSAUR FROM THE MAASTRICHTIAN OF NORTHEAST CHINA

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Abstract The diagnosis of the hadrosaurine *Wulagasaurus dongi* is revised in this paper, based on both original and new material recovered from the Upper Cretaceous Yuliangzi Formation at the Wulaga locality in Heilongjiang Province, China. However, we also demonstrate that some specimens previously referred to *W. dongi*, including braincases, maxillae and scapulae, actually belong to typical lambeosaurines. *Wulagasaurus* shares strong morphological similarities with the North American taxa *Brachylophosaurus*

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and *Maiasaura*: a long, wedge-shaped rostral apex positioned at the level of the dorsoventral midpoint of the jugal rostral ramus; a fan-shaped caudal ramus of the jugal with a nearly straight or slightly convex caudal margin; a relatively elongate and slender ventral process of the coracoid; a weakly developed humeral deltopectoral crest that is moderately expanded craniolaterally; and an asymmetrical, strongly convex margin of the iliac supracetabular process, lacking a strong ridge connecting its caudal portion with the dorsal margin of the postacetabular process. Phylogenetic analysis indicates that *Wulagasaurus*, *Brachylophosaurus* and *Maiasaura* form a monophyletic basal clade of hadrosaurines. This basal clade originated in Asia during the Santonian age of the Late Cretaceous. No later than the middle Campanian, the lineage split and then dispersed via the Bering land bridge to North America, where *Brachylophosaurus* and *Maiasaura* diverged from one another.

Key words Late Cretaceous, Hadrosaurinae, *Wulagasaurus*, basal taxon

1 Introduction

The herbivorous Hadrosaurinae is the sister group to Lambeosaurinae, and is an anatomically derived monophyletic clade of ornithomimid dinosaurs characterized by a mediolaterally swollen rostrum, a well-demarcated circumnasal fossa formed by the premaxilla and the nasal, relatively short nasal passages in the ethmoid region, diamond-shaped dentary tooth crowns lacking marginal denticles and the faint ridges that occur on the lingual surface in lambeosaurines, and a bluntly rounded ischial distal end (Horner et al., 2004; Brett-Surman and Wagner, 2007; Prieto-Marquez, 2010). Abundant fossil remains of hadrosaurines, including articulated skeletons, isolated bones, eggs, skin impressions, and even mummified soft tissues, have been collected in the Americas (Lull and Wright, 1942; Brett-Surman, 1979) and East Asia (Hu, 1973; Maryańska and Osmólska, 1981). They preserve considerable information that is helpful in investigating mechanisms of Late Cretaceous dinosaur evolution and discussing intercontinental correlations within the terrestrial Upper Cretaceous.

Near the Sino-Russian frontier of the Heilongjiang region, several hundred disarticulated bones have been recovered from a large dinosaur quarry at the base of the Wulaga outcrop, which represents the upper member of the lower Maastrichtian Yuliangzi Formation (Hai, 2004). At the Wulaga quarry, a large majority of the bones are tentatively regarded as pertaining to the derived lambeosaurine *Sahaliyana elunchunorum*, but a small quantity of elements are referable to the hadrosaurine *Wulagasaurus dongi* (Godefroit et al., 2008). Therefore, this macrofossil-rich quarry is overwhelmingly dominated by one species, displaying a monodominant condition (mode D2; sensu Eberth and Currie, 2005). These well-preserved hadrosaur bones form a continuous, horizontal bonebed in a grayish green diamictite layer hosted by massive, sandy mudstone with matrix-supported clasts (Hai, 2004; Godefroit et al., 2008). Undoubtedly, the planar sediments with massive diamictites are typical debris flow deposits. The dinosaur-bearing layer can be subdivided into two stratigraphic units, as observed at the Blagoveschensk dinosaur locality (Godefroit et al., 2004; Lauters et al., 2008). Each unit was presumably formed by a single gravity flow event. The upper unit has yielded more bones and larger clasts than the lower one, suggesting that the second gravity flow event was characterized by greater hydraulic sorting and concentration of isolated bones. In addition to the material assigned to *W. dongi* by Godefroit et al. (2008), some further specimens from the Wulaga locality that belong to this species have recently been identified. The purpose of this paper is to extend the original osteological description of *W. dongi* (Godefroit et al., 2008), based on both the newly identified specimens and a re-evaluation of the older ones. This taxon's phylogenetic position in hadrosaur evolution and biogeography are also considered herein.

Institutional abbreviations AMNH, American Museum of Natural History, New York, USA; CMN, Canadian Museum of Nature, Ottawa, Canada; GMH, Geological Museum of Hei-

longjiang Province, Harbin, China; IVPP, Institute of Vertebrate Palaeontology and Palaeoanthropology, Chinese Academy of Sciences, Beijing, China.

2 Systematic paleontology

Dinosauria Owen, 1842

Ornithischia Seeley, 1888

Hadrosauroidea Sereno, 1986

Hadrosauridae Cope, 1869

Hadrosaurinae Cope, 1869

***Wulagasaurus* Godefroit et al., 2008**

***Wulagasaurus dongi* Godefroit et al., 2008**

Holotype GMH W184, right dentary.

Paratypes GMH W166, jugal; GMH W217, dentary; GMH W194, sternal; GMH W320, humerus; GMH W398-A, ischium.

Referred material GMH W394, quadrate; GMH W458, sternal; GMH WH194, GMH W385, coracoids; GMH W286, GMH W392, scapulae; GMH W58, GMH W411, humeri; GMH W359, ilium; GMH W362, ischium; GMH W50-2, GMH W212, fibulae.

Locality and horizon Western hill adjacent to the grain depot of Wulaga Town, Heilongjiang Province; 2nd layer of the Wulaga section within the Yuliangzi Formation, lower Maastrichtian, Upper Cretaceous.

Amended diagnosis Medium-sized hadrosaurine dinosaur characterized by the following autapomorphies: extremely elongated and slender dentary, whose rostrocaudal length is 6.8 times its maximum dorsoventral height; dentary with a markedly dorsally concave diastema; caudal ramus of the jugal extending caudodorsally at a low inclination, forming an angle of about 140° with the jugal long axis. In addition, *W. dongi* differs from basal hadrosauroids in that the humeral deltopectoral crest is moderately expanded craniolaterally, and in that the ventral margin of the supracetabular process is located at approximately the level of the dorsoventral midpoint of the iliac central plate. Also differs from *Brachylophosaurus* and *Maiasaura* in having a relatively short iliac preacetabular process and a faint quadrate buttress.

3 Description and comparisons

The following osteological description combines information from newly identified material of *W. dongi* with observations resulting from a re-examination of the elements originally referred to this species. All the specimens mentioned here are disarticulated, and some are fragmentary.

Jugal The damaged element GMH W166 shows that the jugal is an elongate, triradiate bone that forms the ventral margins of the orbit and the infratemporal fenestra (Godefroit et al., 2008, fig. 14A). In lateral view, the subtriangular rostral ramus has a dorsoventrally expanded base, but tapers to a wedge-shaped rostral apex located at the level of its dorsoventral midpoint. The caudal ramus of the jugal contributes to the caudal margin of the infratemporal fenestra, and is a fan-shaped projection with a slightly convex caudal margin as in *Brachylophosaurus* (Sternberg, 1953; Prieto-Marquez, 2005) and *Maiasaura* (Horner and Makela, 1979). However, unlike in other derived hadrosaurids, the caudal ramus extends caudodorsally at a low inclination, forming an angle of 140° with the long axis of the jugal body.

Quadrate As in other hadrosaurines, but in contrast to lambeosaurines, the quadrate is robust and slightly inclined caudodorsally (Fig. 1A, B). The quadratojugal notch is dorsoventrally wide and rostrocaudally shallow, and shows a symmetrical lateral profile. It is greatly

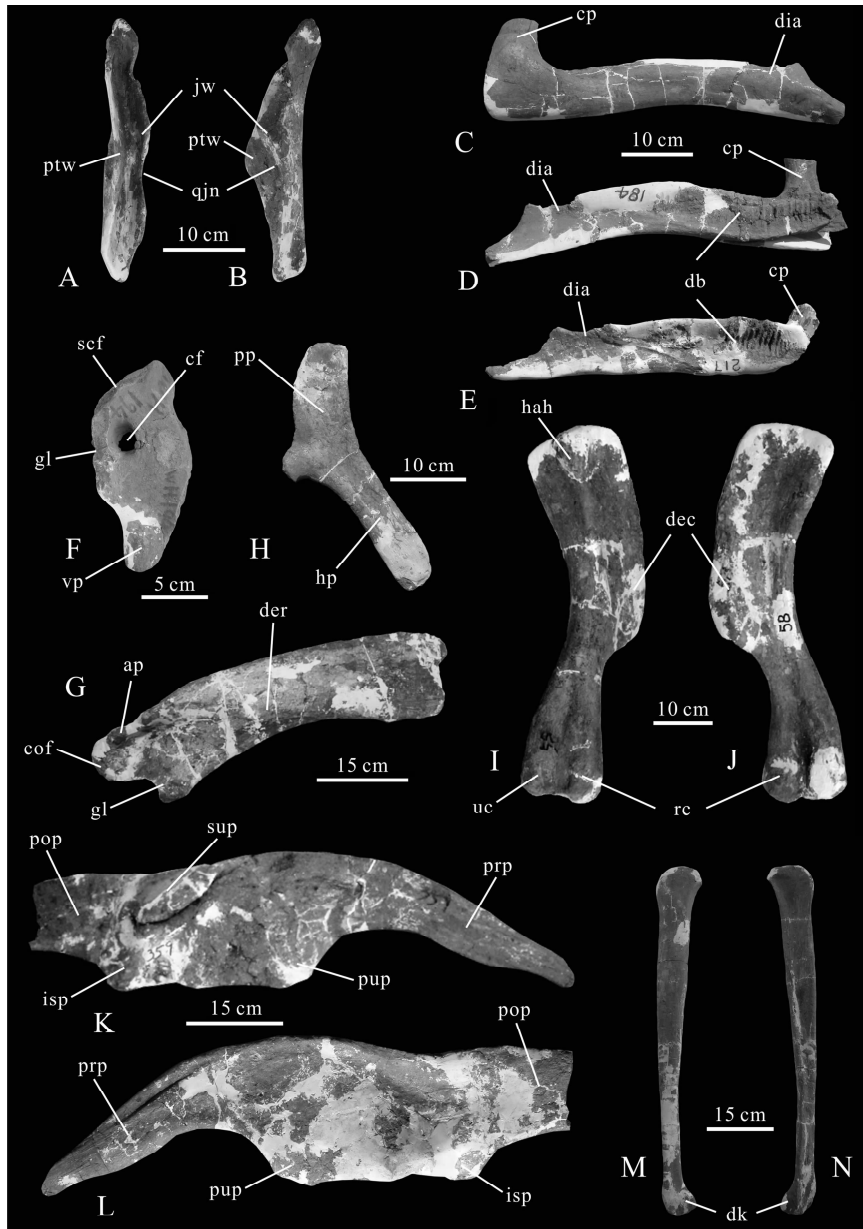


Fig. 1 Specimens of *Wulagasaurus dongi*

A-B. left quadrate (GMH W394) in rostral (A) and lateral (B) views; C-D. right dentary (GMH W184, holotype) in lateral (C) and medial (D) views; E. right dentary (GMH W217) in medial view; F. right coracoid (GMH WH194) in lateral view; G. left scapula (GMH W286) in lateral view; H. left sternal (GMH W458) in cranioventral view; I-J. right humerus (GMH W58) in caudal (I) and cranial (J) views; K-L. right ilium (GMH W359) in lateral (K) and medial (L) views; M-N. right fibula (GMH W50-2) in lateral (M) and medial (N) views

Abbreviations; ap. acromion process 肩峰突; cf. coracoid foramen 喙孔; cof. coracoid facet 乌喙骨关节面; cp. coronoid process 冠状突; db. dental battery 齿排; dec. deltopectoral crest 三角胸嵴; der. deltoid ridge 三角肌嵴; dia. diastema 齿间隙; dk. distal knob 远端结节; gl. glenoid 关节窝; hah. humeral articular head 肱骨关节头; hp. handle-like process 柄状突; isp. ischial peduncle 坐骨柄; jw. jugal wing 颧骨翼; pop. postacetabular process 髌臼后突; pp. proximal plate 近端板; prp. preacetabular process 髌臼前突; ptw. pterygoid wing 翼骨翼; pup. pubic peduncle 耻骨柄; qjn. quadratojugal notch 方颧骨切迹; rc. radial condyle 桡骨髁; scf. scapular facet 肩胛骨关节面; sup. supracetabular process 髌臼上突; uc. ulnar condyle 尺骨髁; vp. ventral process 腹突

offset ventrally from the midpoint of the shaft. The faintly developed quadrate buttress is found on the posterior side of the quadrate head. In rostral view, the subelliptical pterygoid wing is separated from the triangular jugal wing by a deep, longitudinal groove.

Dentary Particularly long and slender in lateral view, the dentary consists of a tooth-bearing body and an ascending but incomplete coronoid process (Fig. 1C-E). Teeth are not preserved on the dentary. The length/height ratio of the dentary body is 6.75 in GMH W217, and 6.85 in GMH W184. Regardless of changes throughout ontogeny, the diastema is notably concave dorsally and not strongly inclined ventrally, and separates the articular area for the pre-dentary from the dorsal margin of the dental battery. In dorsal view, the incomplete coronoid process is lateral to the caudal extremity of the tooth row, with a small subdued area in between. There are some slight morphological differences between the two dentaries assigned to *W. dongi* by Godefroit et al. (2008). GMH W217 is slightly smaller than GMH W184, and has a slightly caudally inclined coronoid process, whereas the coronoid process of GMH W184 is nearly vertical. GMH W217 also has a much straighter ventral margin and appears to have fewer tooth positions than GMH W184, in which at least 35 appear to be present. These minor differences are likely attributable to individual variation or ontogeny, even though the size discrepancy between the two dentaries is small.

Coracoid The coracoid comprises a subpentagonal central body bearing a hook-like process ventrally and two articular surfaces caudodorsally (Fig. 1F). The curved ventral process is relatively long and slender, with a height/length ratio of 0.97, unlike the truncated, robust process present in lambeosaurines (Table 1). The entire caudal margin of the ventral process is concave, and the process tapers to a narrow, rounded end. Proximally, the humeral and scapular articular facets form an angle of 110° . The lateral margin of the scapular facet is 15% shorter than that of the glenoid. The coracoid foramen is close to the contact between the humeral and scapular facets.

Table 1 Measurements of the hook-like process of the coracoid in hadrosaurid taxa

Taxon and specimen number	Maximum dorsoventral height (mm)	Maximum craniocaudal length (mm)	Height/length ratio
<i>Brachylophosaurus canadensis</i> (CMN 8893)	82.8	83.0	0.99
<i>Gryposaurus latidens</i> (AMNH 5465)	95.0	115.3	0.82
<i>Wulagasaurus dongi</i> (GMH WH194)	76.5	79.0	0.97
<i>Hypacrosaurus altispinus</i> (CMN 8501)	80.8	112.2	0.72
<i>Tsintaosaurus spinorhinus</i> (IVPP V 725)	68.5	108.5	0.63

Scapula The scapula, located beneath the anterior dorsal vertebrae in lateral view, is a strap-shaped element that extends and curves caudodorsally from its articulation with the coracoid and the humerus (Fig. 1G). It is moderately arched to follow the contour of the rib cage, in clear contrast to the straight dorsal margin of the scapula in *Gilmoresaurus* and *Bactrosaurus* (Gilmore, 1933; Brett-Surman, 1979). The acromion process is an unbent, cranially directed protrusion along the proximodorsal margin of the scapula, projecting slightly laterally. The lateral surface of the scapula bears a prominent and robust deltoid ridge, as in other hadrosaurines. The lunate glenoid lies caudoventral to the coracoid facet, and the length of its long axis is 20% greater than the depth of the latter.

Sternal This element is a hatchet-shaped bone that consists of a proximal plate and a distal handle-like process (Fig. 1H). Its cranioventral surface is gently convex whereas its caudodorsal surface is slightly concave, particularly on the proximal plate. The proximal plate is

dorsoventrally compressed and subrectangular in shape. The caudoventral part of the proximal plate forms a broad, bluntly rounded, medial directed prominence. As in other hadrosaurines, the distal handle-like process is longer than the proximal plate (Brett-Surman and Wagner, 2007).

Humerus The humerus closely resembles those of other hadrosaurines in being long and transversely slender (Fig. 1I, J). Proximally, the humeral head forms a well developed, globular protuberance between the internal and external tuberosities. Distal to the humeral head are a shallow bicipital sulcus craniomedially and a subcylindrical buttress caudolaterally, which extend longitudinally along the proximal shaft of this element. The deltopectoral crest ends distally at a well-defined distolateral corner near the midpoint of the shaft, forming a marginal angle of nearly 120° . This crest projects cranio-laterally, and its lateral labium becomes thicker as it passes distally. The distalmost part of the crest is 150% as wide as the humeral neck. At the distal end of the humerus, the ulnar condyle is larger than the radial one. In caudal view, they are separated by a deep intercondylar groove for reception of the olecranon of the ulna. It is notable that the humerus GMH W320, which was referred to *W. dongi* by Godefroit et al. (2008), is difficult to confidently diagnose as belonging to this taxon. This specimen appears distorted as a result of post-depositional processes, and is largely reconstructed in plaster. It probably belongs to *W. dongi* based on its general proportions, but this is difficult to confirm. A second humerus (GMH W515-B) assigned to *W. dongi* by Godefroit et al. (2008), but not illustrated or described in detail, could not be located for the present study.

Ilium The ilium is a cranio-caudally elongated and mediolaterally compressed bone, forming the dorsal half of the acetabular margin ventrally (Fig. 1K, L). In lateral view, the dorsal margin is sigmoid in outline, with a shallow embayment over the pronounced supracetabular process. The supracetabular process abruptly evaginates ventrolaterally from the dorsal border of the central body, reaching approximately the level of the dorsoventral midpoint of the central body. Its ventral margin is asymmetrical and strongly convex, and is not connected by a well-demarcated ridge to the proximodorsal margin of the postacetabular process. This condition can be also observed in *Brachylophosaurus* and *Maiasaura*. Anterior to the central body, the preacetabular process extends and curves cranioventrally to form a long, mediolaterally narrow pendant, with an angle of 148° between its long axis and the horizontal. The ventral edge of the preacetabular process is embayed, leaving a space between the proximal end of the process and the triangular pubic peduncle. Below the antitrochanter, the ischial peduncle consists of two small, rounded knobs. The postacetabular process is poorly preserved, and its tip is eroded.

Ischium Although the ischium is incomplete, enough of its lateral profile is preserved to confirm that the distal shaft of this bone has a bluntly rounded terminus (Godefroit et al., 2008, fig. 14A). In GMH W362, the acetabular margin of the pubic peduncle is more dorsally positioned than the upper edge of the ischial shaft. In addition, the caudodorsal corner of the iliac peduncle does not project caudodorsally. These features approach the general condition that occurs in other hadrosaurines (Parks, 1920; Lull and Wright, 1942).

Fibula The fibula is an elongated and mediolaterally compressed element, whose distal third is twisted so that the cranial surface faces slightly medially (Fig. 1M, N). It is cranio-caudally expanded at the proximal end, and gradually becomes narrower towards the mid-shaft. Medially, the proximal two-thirds of the fibular shaft is occupied by a distally tapering triangular surface that is shallowly concave and marked by fine longitudinally oriented striations. The distal end of the fibula expands modestly in the cranial direction to form a subtriangular condyle, unlike the club-shaped condyle seen in *Gryposaurus*, *Saurolophus* and most lambeosaurines.

Elements questionably referred to *W. dongi* Originally, Godefroit et al. (2008) regarded three fragmentary braincases (GMH WJ1, GMH W384, GMH W421), two partial maxillae (GMH W233, GMH W400-10) and two damaged scapulae (GMH W267, GMH W477)

as also pertaining to the hadrosaurine *W. dongi*. However, it should be noted that these preliminary identifications are questionable. Re-examination of the specimens shows that their morphological features are inconsistent with those of the hadrosaurines, but similar to the general traits shared by the helmet-crested lambeosaurines. For example, the braincase possesses numerous derived lambeosaurine synapomorphies, such as a strongly dorsally concave sagittal crest that becomes very narrow and sharp along the posterior two-thirds of the parietal, a relatively short supraoccipital-exoccipital shelf above the foramen magnum, and a basiptyergoid process that is caudally offset relative to the round trigeminal foramen (GMH WJ1 and GMH W421). Likewise, the maxilla of GMH W233 appears to bear a symmetrical, diamond-shaped jugal articular surface, whose lower half faces dorsolaterally and whose ventral apex lies at the rostral end of the ectopterygoid ridge. Although the dorsal ramus and rostradorsal shelf of the maxilla are not intact, the preserved morphology is sufficient to indicate lambeosaurine affinities. In addition, the acromion process of the scapula GMH W267 is slightly recurved and oriented craniodorsally. This feature is also closer to the condition present in derived lambeosaurines. Consequently, all of these specimens actually represent derived lambeosaurine elements. Rather than belonging to *W. dongi*, they are probably referable to *Sahaliyana elunchunorum*, the derived lambeosaurine that occurs in the same sedimentary layer. Finally, the sternal GMH W401 was regarded by Godefroit et al. (2008) as pertaining to *W. dongi*. However, this element is damaged and, given its small size, probably comes from a juvenile. We regard its taxonomic affinities as uncertain.

4 Phylogenetic analysis

Godefroit et al. (2008) found *Wulagasaurus dongi* to be the most basal hadrosaurine. In order to test this hypothesis using the new morphological information revealed in this study, we created a data matrix consisting of 224 cranial characters and 110 postcranial characters for phylogenetic analysis. These characters were taken or modified from recently published character lists for phylogenetic analyses of iguanodontoids, such as Weishampel et al. (1993), Godefroit et al. (1998, 2001, 2008), Horner et al. (2004), Evans and Reisz (2007), Gates and Sampson (2007), Prieto-Marquez (2005) and Prieto-Marquez and Wagner (2009), with 42 new characters added. Four basal iguanodontoid taxa, including *Iguanodon bernissartensis*, *Mantellosaurus atherfieldensis*, *Jinzhouosaurus yangi* and *Ouranosaurus nigeriensis*, were used as outgroups.

The matrix of 334 characters and 53 taxa was analyzed in PAUP version 4.0b10 (Swofford, 2002), using a heuristic search under ACCTRAN optimization, with random setting and 1000 replicates (see Supplementary Information at <http://www.ivpp.cas.cn/cbw/gjzdwxb/xbwzml/>). All characters were equally weighted and unordered. This comprehensive phylogenetic analysis yielded 144 most parsimonious trees, with a tree length of 933 steps, a consistency index of 0.517 and a retention index of 0.861. Fig. 2 shows the strict consensus tree derived from the 144 most parsimonious trees. Specifically, our cladistic analysis agrees with that of Godefroit et al. (2008) in placing *Wulagasaurus* in a relatively basal position within the Hadrosaurinae. However, the results of our analysis indicate that *Wulagasaurus* and the *Brachylophosaurus-Maiasaura* clade are sister taxa, together forming a clade at the base of the Hadrosaurinae that is weakly supported by bootstrap (62%) and Bremer decay (2) values.

Wulagasaurus possesses some striking traits which are similar to those seen in *Brachylophosaurus* and *Maiasaura*, including a long and wedge-shaped rostral apex situated at the level of the dorsoventral midpoint of the jugal rostral process, a fan-shaped jugal caudal process bearing a slightly convex caudal margin, a sharply ascending slope along the dorsolateral margin of the symphyseal region of the dentary, a ratio of less than 1.62 between the maximum width of the humerus at the deltopectoral crest and at the neck, and a supracetabular process of the ilium with an asymmetrical, strongly convex margin and a poorly defined caudal portion.

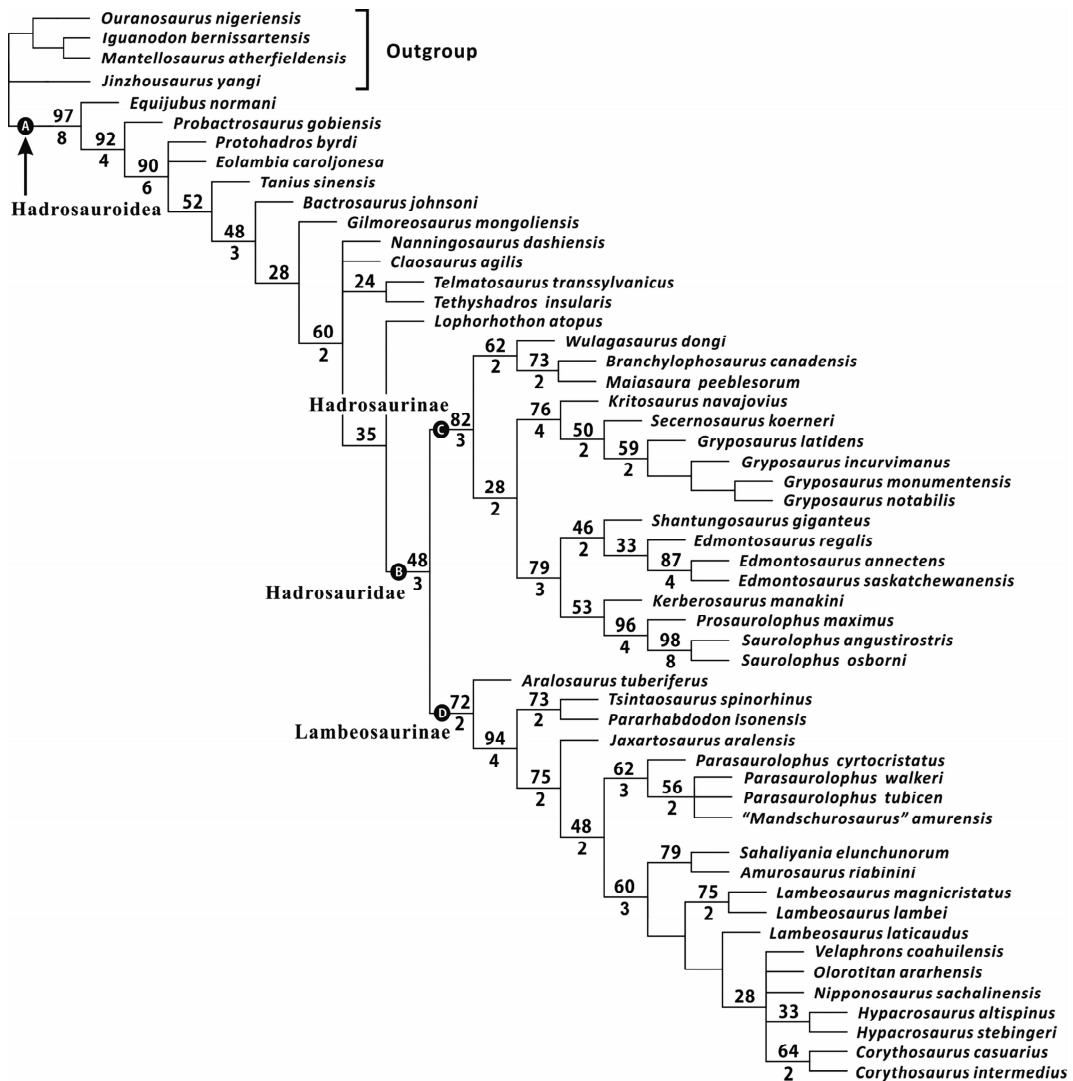


Fig. 2 Strict consensus cladogram of iguanodontoids showing the systematic position of *Wulagasaurus dongi*. The phylogenetic analysis resulted in 144 most parsimonious trees of 933 steps, each with a consistency index of 0.517 and a retention index of 0.861; values above nodes represent bootstrap proportions (%); values beneath nodes represent Bremer support; bootstrap values lower than 20 and Bremer decay values less than 2 are not shown

5 Biogeographic implications

In combination with the stratigraphic ages of various hadrosaurine taxa, the results of the phylogenetic analysis have suggested that the clade formed by *Wulagasaurus*, *Brachylophosaurus* and *Maiasaura* is likely to have originated in Asia during the late Santonian. No later than the middle Campanian, the lineage may have split and later dispersed to North America via the Bering land bridge, where *Brachylophosaurus* and *Maiasaura* diverged. Similarly, the existence of *Kerberosaurus* and *Shantungosaurus* indicates that some other major clades of hadrosaurines also appeared in Asia and subsequently migrated to North America, where they diversified rapidly.

This pattern supports the possibility that hadrosaurines originated in Asia. Thus, the lineage splitting of early hadrosaurids possibly took place in Asia, based on current assumptions regarding the Asian origins of hadrosaurines and lambeosaurines (Milner and Norman, 1984; Godefroit et al., 2004; 2008). Dispersals of hadrosaurines and lambeosaurines from Asia to western North America may have been very frequent and prevalent from the late Santonian to the Maastrichtian, following the shortest route across the Bering land bridge (Zharkov et al., 1998; Blakey, 2001). By contrast, dispersal of derived hadrosaurids from Asia to Europe in the same period was impeded by a marine transgression affecting much of Europe and Western Asia (Dalla Vecchia, 2006).

6 Conclusion

Osteological re-evaluation of previously collected material assigned with varying degrees of certainty to *Wulagasaurus dongi* prompted us to conclude that this material is adulterated with some specimens that should actually be referred to lambeosaurines. *Wulagasaurus* displays several salient features which are often observed in hadrosaurines, such as a hatchet-shaped sternal with a distal handle-like process that is longer than the proximal plate, a long and caudoventrally tapering ventral process of the coracoid, a prominent deltoid ridge on the scapula, a moderately craniolaterally expanded deltopectoral crest on the humerus, and a slightly elevated pubic peduncle of the ischium.

A comprehensive phylogenetic analysis focusing on the hadrosauroid ingroup indicates that *Wulagasaurus* is the sister taxon to the *Brachylophosaurus-Maiasaura* clade, forming a monophyletic group at the base of Hadrosaurinae. A number of morphological resemblances among the three taxa lend credibility to this result. It is likely that this basal hadrosaurine clade originated in Asia and subsequently dispersed to North America, following a biogeographical pattern also seen in some other hadrosaurine groups. This topology has provided valuable evidence supporting the hypothesis that the ancestral area of hadrosaurines was located in Asia.

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