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A remarkable hollow-crested hadrosaur from Russia: an Asian origin for lambeosaurines

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Abstract

The nearly complete skeleton of a new lambeosaurine dinosaur, *Olorotitan arharensis*, has been discovered in the Maastrichtian Tsagayan Formation at Kundur, Far Eastern Russia. This is the most complete dinosaur skeleton ever discovered in Russia and, with its finely preserved supracranial crest, the most complete lambeosaurine outside North America. This new taxon is remarkable by the unusual shape of its hollow crest and by the important elongation of its neck and of its sacrum. An additional articulation between adjacent neural spines made the proximal third of the tail rigid, but it cannot be excluded that it is a pathological feature. Phylogenetic analysis shows that *Olorotitan* is the sister-taxon of the North American genera *Corythosaurus* and *Hypacrosaurus*. Lambeosaurines originated from Asia and then migrated to North America before or at the beginning of the Late Campanian. **To cite this article: P. Godefroit et al., C. R. Palevol 2 (2003) 143–151.**

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Résumé

Un hadrosaure à crête creuse remarquable de Russie : une origine asiatique pour les lambéosaurinés. Le squelette presque complet d'un nouveau dinosaure lambéosauriné, *Olorotitan arharensis*, a été découvert dans la formation maastrichtienne de Tsagayan à Kundur, au sud-est de la Russie. C'est le squelette de dinosaure le plus complet jamais découvert en Russie et, avec sa crête creuse finement conservée au sommet de son crâne, c'est le lambéosauriné le plus complet en dehors de l'Amérique du Nord. Ce nouveau taxon est remarquable par la forme inhabituelle de sa crête, ainsi que par l'importante elongation de son cou et de son sacrum. Une articulation supplémentaire entre les épines neurales adjacentes rigidifiait la partie proximale de la queue, mais il n'est pas exclu qu'il s'agisse d'un caractère pathologique. L'analyse phylogénétique montre qu'*Olorotitan* est le genre-frère de *Corythosaurus* et d'*Hypacrosaurus* d'Amérique du Nord. Les lambéosaurinés sont originaires d'Asie et ont migré en Amérique du Nord avant ou au début du Campanien supérieur. **Pour citer cet article : P. Godefroit et al., C. R. Palevol 2 (2003) 143–151.**

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Mots clés : Maastrichtien ; région de l'Amour ; Lambeosaurinae ; phylogénie ; paléogéographie ; Russie

Version abrégée

Introduction

Nous décrivons dans cet article le squelette sub-complet d'un nouveau dinosaure lambeosauriné découvert à Kundur, dans la région de l'Amour (Sud-Est de la Russie). C'est le premier squelette sub-complet d'un dinosaure jamais découvert en Russie et le squelette de lambeosauriné le mieux conservé en dehors de l'Ouest de l'Amérique du Nord.

Des études palynologiques préliminaires indiquent que le gisement de Kundur serait d'âge Maastrichtien « moyen » [12] à supérieur [6]. Il appartient en tout cas à la même zone palynologique à *Wodehouseia spinata-Aquilapollenites subtilis* que les gisements de Blagoveschensk et de Jiayin, également situés dans la région de l'Amour, et qui ont également livré de nombreux squelettes désarticulés de lambeosaurinés [2, 6]. À Kundur, les os s'étendent sur plusieurs centaines de mètres carrés. De nombreux os isolés appartenant à des dinosaures lambeosaurinés, hadrosaurinés, théropodes et peut-être nodosauridés, ainsi que des fossiles de crocodiles et de tortues et une dent de mammifère multituberculé, ont été découverts autour du squelette décrit dans cet article.

Paléontologie systématique (Fig. 1)

Dinosauria Owen 1842

Ornithopoda Marsh 1881

Hadrosauridae Cope, 1869

Lambeosaurinae Parks, 1923

Olorotitan arharensis gen. et sp. nov.

Étymologie. '*Olorotitan*' signifie 'cygne géant'; '*arharensis*' se réfère à la région d'Arhara, où l'holotype a été découvert.

Holotype. Amur Natural History Museum (Blagoveschensk, Russie), AEHM 2/845.

Localité et horizon. Kundur, Région de l'Amour, Sud-Est de la Russie. Sommet de la partie inférieure ou partie moyenne de la formation de Tsagayan (palynozone à *Wodehouseia spinata-Aquilapollenites subtilis*), Maastrichtien 'moyen' ou supérieur.

Diagnose. Crête creuse en forme de casque et processus latéral du prémaxillaire s'étendant postérieurement bien au-delà du niveau de l'occiput ; portion postéro-dorsale du processus dorsal du prémaxillaire, déprimée le long de sa ligne médiane ; processus postorbitaire du jugal très élevé (rapport hauteur du processus postorbitaire/longueur du jugal = 0,9) ; portion antérieure du jugal plus courte que chez les autres lambeosaurinés, avec un bord antérieur parfaitement droit ; maxillaire très asymétrique en vue latérale, avec un bord ventral distinctement tourné vers le bas ; prémaxillaire de forme carrée en vue dorsale ; cou et sacrum très allongés, formés respectivement de 18 vertèbres cervicales et de 15 ou 16 vertèbres sacrées ; articulation supplémentaire entre les épines neurales adjacentes, sur la portion proximale de la queue (il ne peut être exclu qu'il s'agisse d'un caractère pathologique) ; scapula plus allongée que chez les autres hadrosauridés, avec un rapport longueur / hauteur = 6,2.

Analyse phylogénétique (Tableau, Fig. 2)

Une analyse phylogénétique basée sur une matrice de 36 caractères (voir *appendice* et *tableau* pour la liste et la polarité des caractères utilisés) montre qu'*Olorotitan* peut clairement être identifié comme un lambeosauriné sur la base des caractères suivants : crête osseuse creuse au sommet du crâne, préfrontal développé verticalement, narine externe complètement entourée par le prémaxillaire, processus antérieur du jugal tronqué, gouttière du maxillaire large, carène médiane des dents du dentaire sinueuse et crête deltopectorale très développée sur l'humérus. Au sein des lambeosaurinés, *Olorotitan* partage avec le clade des coythosaures (qui inclut *Corythosaurus*, *Hypacrosaurus* et *Lambeosaurus*) l'extension postérieure du processus latéral du prémaxillaire. *Olorotitan* partage avec *Corythosaurus* et *Hypacrosaurus* l'importante participation du nasal dans la formation de la crête supracrânienne.

Implications paléogéographiques

Ce cladogramme montre également que les lambeosaurinés les plus primitifs ont été découverts en Asie.

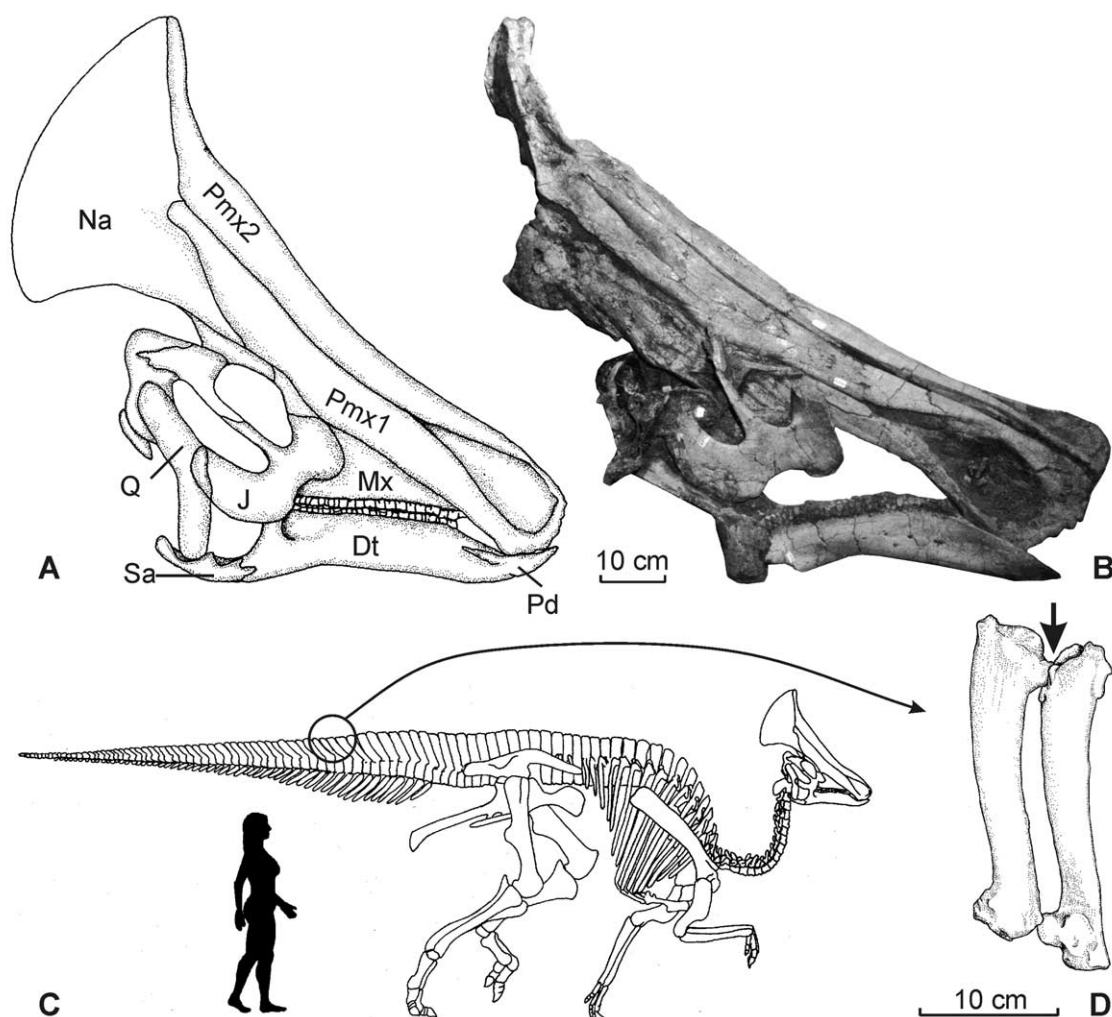


Fig. 1. Skeletal anatomy of *Olorotitan arharensis*. **A.** Reconstruction of the skull in right lateral view (only bones that have been discovered are labeled). **B.** Main part of the skull of the holotype AEHM 2/845 in right lateral view (some deformation results from lateral compression of the skull); the largest part of the nasals, the maxillae, the surangulars, the left dentary and the predentary were found disconnected from this piece and are therefore not represented on this photograph. **C.** Full skeletal reconstruction based on holotype AEHM 2/845. **D.** Detail of caudal neural spines, showing the additional articulation between adjacent neural spines. **Dt**, dentary; **J**, jugal; **Mx**, maxilla; **Na**, nasal; **Pd**, predentary; **Pmx1**, lateral premaxillary process; **Pmx2**, dorsal premaxillary process; **Q**, quadrate; **Sa**, surangular.

Fig. 1. Anatomie squelettique d'*Olorotitan arharensis*. **A.** Reconstitution du crâne en vue latérale droite (seuls les os qui ont été découverts sont nommés). **B.** Crâne de l'holotype AEHM 2/845 en vue latérale droite (la déformation résulte de la compression latérale du crâne); la plus grande partie des nasaux, les maxillaires, les surangulaires, le dentaire gauche et le prédentaire ont été trouvés déconnectés de cette pièce et ne sont dès lors pas représentés sur cette photo. **C.** Reconstitution de l'ensemble du squelette de l'holotype AEHM 2/845. **D.** Détail des arcs neuraux de la queue, montrant l'articulation supplémentaire entre épines neurales adjacentes. **Dt**, dentaire; **J**, jugal; **Mx**, maxillaire; **Na**, nasal; **Pd**, prédentaire; **Pmx1**, processus latéral du prémaxillaire; **Pmx2**, processus dorsal du prémaxillaire; **Q**, carré; **Sa**, surangulaire.

Ce sont, successivement, *Tsintaosaurus spinorhinus* du Campanien de Chine orientale [19], *Jaxartosaurus aralensis* du Santonien du Kazakhstan [15] et *Amurosaurus riabinini* du Maastrichtien de la région de

l'Amour [2]. Dans l'état actuel de nos connaissances, les lambéosaurinés semblent donc avoir une origine asiatique. Ils auraient migré en Amérique du Nord avant ou au début du Campanien supérieur. Une route

terrestre à travers le détroit de Béring s'est probablement ouverte dès l'Aptien-Albien et s'est maintenue jusqu'au Crétacé supérieur, permettant la migration de nombreux groupes de dinosaures, notamment pendant le Campanien et le Maastrichtien [8, 16].

Les lambeosaurinés étaient les dinosaures dominants dans la région de l'Amour au cours du Maastrichtien « moyen » à supérieur. Dans l'état actuel de nos connaissances, ils étaient représentés par trois genres : *Olorotitan* à Kundur, *Amurosaurus* à Blagoveschensk [2] et *Charonosaurus* à Jiayin [6]. En Amérique du Nord, les derniers lambeosaurinés sont, semble-t-il, d'âge Maastrichtien inférieur [18] ; les faunes maastrichtiennes supérieures y sont dominées, soit par des cératopsiens, soit par des titanosauridés, groupes qui ne sont apparemment pas représentés dans la région de l'Amour. Le développement de faunes dinosauriennes différentes après le Maastrichtien inférieur reflète vraisemblablement une sorte d'isolement géographique entre l'Asie orientale et l'Amérique du Nord occidentale à cette période, ou des différences climatiques ou paléoécologiques, qui doivent encore être élucidées.

1. Introduction

Hadrosaurs were very successful dinosaurs during the closing stages of the Cretaceous. Of this group, lambeosaurines are the most spectacular because of the radical modification of their nasal cavity and the concomitant elaboration of strange hollow crests above their skull. Here we report the discovery of the skeleton of a new lambeosaurine dinosaur from the Maastrichtian of Kundur, in the Amur region (Far Eastern Russia). This is the first sub-complete dinosaur skeleton from Russia and the most complete lambeosaurine skeleton outside western North America, with a particularly finely preserved supracranial crest.

Preliminary palynological investigations show that Kundur locality may be synchronous to Blagoveschensk and Jiayin localities [6, 12]. These latter two sites are also located in Amur Region (although Jiayin is located along the Chinese banks of Amur River) and have also yielded many lambeosaurine disarticulated skeletons [2, 6]. The three dinosaur sites from the Amur region apparently belong to the same *Wodehouseia spinata-Aquilapollenites subtilis* palynozone and would therefore be 'Middle' [12] or Late [6] Maas-

trichtian in age. The skeleton described herein was excavated during 1999 to 2001 field campaigns. At Kundur, bones extend over at least several hundreds square metres. Disarticulated bones belonging to lambeosaurine, hadrosaurine, theropod and maybe nodosaurid dinosaurs, and to turtles and crocodiles as well, accompanied the skeleton described herein. Screen washing also yielded one multituberculate mammal tooth to date.

2. Systematic palaeontology

Dinosauria Owen 1842

Ornithopoda Marsh 1881

Hadrosauridae Cope, 1869

Lambeosaurinae Parks, 1923

Olorotitan arharensis gen. et sp. nov.

Etymology. '*Olorotitan*' means 'gigantic swan'; '*arharensis*' refers to Arhara County where the holotype was discovered.

Holotype. Amur Natural History Museum (Blagoveschensk, Russia), AEHM 2/845.

Locality and horizon. Kundur, Amur Region, Far Eastern Russia. Top of basal part or middle part of Tsagayan Formation (*Wodehouseia spinata* - *Aquilapollenites subtilis* palynozone), 'Middle' or Late Maastrichtian, Late Cretaceous.

Diagnosis. Helmet-like hollow crest and lateral premaxillary process developed caudally far beyond the level of the occiput; caudodorsal part of the dorsal premaxillary process depressed along the midline; postorbital process of the jugal very high (ratio 'height of postorbital process/length of jugal' = 0.9); rostral portion of the jugal shorter than in other lambeosaurines, with a perfectly straight rostral margin; very asymmetrical maxilla in lateral view, with ventral margin distinctly down turned; prementary square in dorsal view; neck and sacrum very elongated, with respectively 18 cervical and 15 or 16 sacral vertebrae; additional articulation between adjacent neural spines on the proximal third of the tail (it cannot be excluded that this is a pathological feature); scapula more elongated than in other hadrosaurids, with L/W ratio = 6.2.

Abridged description (Fig. 1). *Olorotitan arharensis* was a rather large lambeosaurine, comparable in size with *Parasaurolophus cyrtocristatus* [3]. Its skull appears long and massive, mainly because of the important development of the hollow supracranial crest.

This crest has an unusual shape, being markedly different from all North-American lambeosaurines: it extends caudally further than in the helmet-crested forms. A bony plate found between the dorsocaudal part of the skull and the neck is identified as well-developed paired nasal bones. If this interpretation is correct, the nasals participated in more than half of the surface of the supracranial crest and this crest was distinctly more developed ventrally in *Olorotitan* than in species of *Parasaurolophus*, as reconstructed in Fig. 1A. The rostral part of the muzzle is rounded and very roughened. The large external naris is lacrimiform and, as usual in lambeosaurines, is completely surrounded by the premaxilla. The lateral premaxillary process is particularly large and extends caudally beyond the level of the occiput. The dorsal premaxillary process is responsible for the concave profile of the skull in lateral view. It extends far beyond the level of the occiput. The caudal part of the premaxilla progressively tapers distally; its dorsal surface is distinctly depressed along the midline, while its concave ventral surface was covered in life by the nasal. The nasal is badly preserved, its largest part being crushed and displaced; it formed an important part of the hollow crest, ventrocaudally to the premaxilla. The quadrate is robust and curved, with a wide pterygoid wing. A very high postorbital process characterizes the jugal of *Olorotitan arharensis*: the ratio ‘height of postorbital process / length of jugal’ = 0.9; in front of this process, the rostral part of the jugal is proportionally shorter than in other hadrosaurids. The rostral process of the jugal is also very expanded dorso-ventrally, with a perfectly straight rostral border. The maxilla closely resembles that of *Tsintaosaurus spinorhinus* [19] in being very markedly asymmetrical in lateral view and in having a distinctly down turned ventral alveolar border; the rostral maxillary shelf is very developed. With its square outline, the prementary also resembles that of *Tsintaosaurus spinorhinus* [19]. The dentary is relatively low and not markedly down turned; the dental battery is composed of about 32 rows. The diastema is rather long, about two thirds the length of the dental battery. Dentary teeth are proportionally less high than in *Charonosaurus jiyinensis* [6].

The neck, including the proatlas, is completely preserved. It is remarkably elongated, formed by 18 cervical vertebrae, although a maximum of 15 cervical vertebrae was previously reported in hadrosaurid dino-

saur [11, 18]. The neural spines of the dorsal vertebrae are not as elevated as in *Hypacrosaurus altispinus*, but are similar in proportions with those of *Corythosaurus casuarius*. The sacrum consists of 15 or 16 vertebrae, including dorsosacral and caudosacral contributions, whereas the sacrum of adult hadrosaurids usually consists of 10 to 12 vertebrae [11, 18]. The neural spines of the sacrals are the tallest of the series, but are distinctly lower than in *Barboldia sicinskii* [13]. The tail is composed of more than 70 vertebrae in articulation. The neural spines and haemal arches on the caudal vertebrae are not as elongated as in *Hypacrosaurus altispinus* [18]. On the proximal third of the tail, the tips of adjacent neural spines form an additional articulation that made this part of the vertebral column particularly rigid: the proximal border of the distal spine forms a knob-like process that inserts into a cup-shaped depression on the distal border of the preceding spine. This feature seems too regular to be regarded as pathological; however, this latter hypothesis cannot be rejected pending the discovery of other *Olorotitan* specimens.

The fused sternals are of lambeosaurine morphology, with a relatively long proximal ‘paddle’. The scapula is more elongated than in other hadrosaurids [3]: although the thin borders of this bone are slightly damaged, the *L/W* ratio may be confidently estimated at 6.2. The coracoid is stout, with a relatively small coracoid hook and a very prominent knob for insertion of a powerful *M. biceps*. The humerus is very robust, with a very developed deltopectoral crest, as usually observed in lambeosaurines [6].

The ilium resembles that of *Corythosaurus casuarius* and *Lambeosaurus lambei*, with a very deflected preacetabular process, a rather robust postacetabular process and a massive antitrochanter. The ischium is robust and its distal end is footed, as usual in lambeosaurines; however, the general robustness of the bone and the development of the distal foot are less than in *Hypacrosaurus altispinus* and *Parasaurolophus cyrtocristatus*. Both the femur and the tibia are equal in size. The lesser trochanter of the femur is particularly prominent, but the fourth trochanter of the femur and the cnemial crest of the tibia are moderately developed. The astragalus and calcaneum are fused to the tibia and fibula. The astragalus is laterally skewed, as observed in all hadrosaurids except *Parasaurolophus* and *Charonosaurus* [3, 6].

Table

Character-taxon data matrix used in the phylogenetic analysis of *Olorotitan*, with *Bactrosaurus* as outgroup.

Matrice de caractères et des taxa utilisés lors de l'analyse phylogénétique d'*Olorotitan*, avec *Bactrosaurus* comme groupe extérieur.

<i>Bactrosaurus</i>	00000	00000	00000	00000	00000	00000	000000
Hadrosaurinae	00100	00000	01001	01101	11110	10110	111100
<i>Tsintaosaurus</i>	01110	0??10	2?101	01011	11111	11011	111000
<i>Jaxartosaurus</i>	01111	0????	?110?	?????	?????	?????	??????
<i>Amurosaurus</i>	01111	0????	?1111	11011	1111?	11011	?11000
<i>Parasaurolophus</i>	11112	21010	01111	11011	11110	11011	111011
<i>Charonosaurus</i>	11112	1????	?1111	11011	1111?	11011	111011
<i>Lambeosaurus</i>	01111	11111	01111	11011	11110	11011	111000
<i>Corythosaurus</i>	01111	11111	11111	11011	11110	11011	111000
<i>Hypacrosaurus</i>	01111	11111	11111	11011	11110	11011	111000
<i>Olorotitan</i>	??1?	?111?	1??1	11011	11111	11011	111000

Two other lambeosaurine dinosaurs have previously been described in Maastrichtian deposits from the Amur region: *Amurosaurus* [2] and *Charonosaurus* [6]. In both genera, the rostral process of the jugal is more rounded, the postorbital process of the jugal is proportionally lower, the maxilla is less asymmetrical and less distinctly down turned, and the scapular blade is shorter than in *Olorotitan*. In *Amurosaurus*, the rostral maxillary shelf is less developed than in *Olorotitan*. *Charonosaurus* also differs from *Olorotitan* by its distinctly higher dentary teeth, its shorter sacrum (9 vertebrae; unknown in *Amurosaurus*), its longer praetabular process on the ilium, its club-shaped distal end of the fibula and its astragalus equilateral in cranial view [6].

3. Phylogenetic analysis

In order to clarify the systematic position of *Olorotitan arharensis*, a cladistic analysis was performed on a 36-character dataset, using Paup 4.0 software [17]. The resulting character-taxon matrix (see the appendix, for the list of the characters used in the analysis) is shown in the Table. Analysis of the data matrix results in a single 40-step tree with a Consistency Index of 0.975 and a Retention Index of 0.98 (Fig. 2). The basal Hadrosauroida *Bactrosaurus johnsoni* [5] and Hadrosaurinae were used as successive outgroups. *Olorotitan arharensis* is clearly a lambeosaurine dinosaur on the basis of several synapomorphies: a hollow supracranial crest, a vertically developed prefrontal, external nares completely surrounded by the premaxillae, a truncated rostral process of the jugal, a wide maxillary shelf, sinuous median

carinae on dentary teeth and a strongly developed deltopectoral crest on humerus. Within lambeosaurines, *Olorotitan* shares with the corythosaur clade (including *Corythosaurus*, *Hypacrosaurus* and *Lambeosaurus*) the caudal extension of the lateral premaxillary process. With *Corythosaurus* and *Hypacrosaurus*, *Olorotitan* shares the important participation of the nasal in the supracranial crest.

4. Palaeobiogeographical implications

This cladogram also clearly demonstrates that the most basal lambeosaurine dinosaurs come from Asian localities. These are successively *Tsintaosaurus spinorhinus*, from the Wangshi Series of Shandong Province in eastern China [19] (Campanian [4]), *Jaxartosaurus aralensis*, from the Syuksyuk Formation of Kazakhstan [15] (Santonian [1]), and *Amurosaurus riabinini*, from the Maastrichtian Tsagayan Formation of Amur Region [2]. *Eolambia caroljonesa*, from the Albian-Cenomanian of eastern Utah, was first described as the most basal lambeosaurine [9], but is now rather regarded as a non-hadrosaurid Hadrosauroida [6, 7]. In the current state of our knowledge, it may therefore be asserted that lambeosaurines originated in Asia. In western North America, the oldest well-dated and well-identified lambeosaurines have been discovered in Upper-Campanian formations [18]. It means that lambeosaurines migrated towards western North America before or at the beginning of the Late Campanian. A land route between Asia and western North America across the Beringian isthmus probably opened during the Aptian-Albian and persisted during the Late Cretaceous. Besides lambeosaurines, other

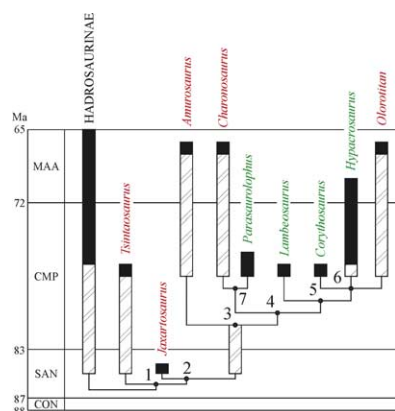


Fig. 2. Stratigraphically calibrated cladogram of phylogenetic relationships of Lambeosaurinae, including *Olorotitan*. Solid symbols indicate stratigraphical occurrence of a taxon, while hatched symbols indicate ghost lineages [14]. Asian taxa are in red, whereas North American taxa are in green. Unambiguous synapomorphies supporting the nodes are: (1) (Lambeosaurinae): hollow supraccranial crest, vertically developed prefrontal, external nares completely surrounded by premaxillae, truncated rostral process of jugal, wide maxillary shelf, sinuous median carinae on dentary teeth, strongly developed deltopectoral crest on humerus; (2) deeply excavated rostral platform occupying the rostral part of frontals in adults; (3): high lateral side of squamosal; (4): frontal wider than long; (5) (corythosaur clade): caudal extension of lateral premaxillary process, enlarged *cavum nasi proprium*; (6): nasal forming half of crest; (7) (parasauroloph clade): parietal completely excluded from occiput, frontal platform extending above the rostral portion of supratemporal fenestra, distal head of fibula greatly expanded and club-shaped, cranial ascending process of astragalus equilateral in shape. **CMP**, Campanian; **CON**, Coniacian; **MAA**, Maastrichtian; **SAN**, Santonian. Dates are millions of years before present.

Fig. 2. Cladogramme des lambeosaurinés, calibré par l'échelle stratigraphique. Les blocs en noir indiquent la présence stratigraphique d'un taxon donné, alors que les blocs hachurés indiquent les lignées fantômes [14]. Les taxa asiatiques sont en vert, les taxa nord-américains sont en rouge. Les synapomorphies supportant les différents nœuds sont : (1) (Lambeosaurinae) : crête supraccranienne creuse, préfrontal orienté verticalement, narine externe complètement entourée par le prémaxillaire, processus antérieur du jugal tronqué, gouttière maxillaire élargie, carène médiane sinueuse sur les dents du dentaire, crête deltopectorale très développée sur l'humerus ; (2) : plate-forme frontale profondément creusée occupant la portion antérieure du frontal ; (3) : côté latéral du squamosal élevé ; (4) : frontal plus large que long ; (5) (clade de corythosaures) : extension postérieure du processus latéral du prémaxillaire, *cavum nasi proprium* élargi ; (6) : nasal formant la moitié de la crête ; (7) (clade des parasaurolophes) : pariétal complètement exclu de l'occiput, plate-forme du frontal s'étendant au-dessus de la partie antérieure de la fenêtre supratemporale ; extrémité distale de la fibula très élargie en forme de club de golf, processus ascendant antérieur de l'astragale de forme équilatérale. **CMP**, Campanien ; **CON**, Coniacien ; **MAA**, Maastrichtien ; **SAN**, Santonien. Les dates sont en millions d'années.

dinosaur groups are known to have originated in Asia and then have migrated to western North America through this route by Campanian-Maastrichtian time: basal Neoceratopsia, maybe Ceratopsidae, Ankylosauridae, Tyrannosauridae, and Troodontidae [8, 16]. Fig. 2 shows that, within lambeosaurines, representatives of corythosaur clade and parasauroloph clade have been discovered both in North America and in eastern Asia (Amur Region). In North America, they are Late Campanian or Early Maastrichtian in age, while they are 'Middle' to Late Maastrichtian in age in Amur Region. This indicates that faunal exchanges were particularly important between both regions by Late Campanian or Maastrichtian times.

Lambeosaurine are the dominant herbivorous dinosaurs in Late Cretaceous localities of the Amur region, being represented, in the current state of our knowledge, by three genera: *Olorotitan* from the Kundur locality, *Amurosaurus* from the Blagoveschensk locality [2], and *Charonosaurus* from the Jiayin locality along the Chinese banks of the Amur River [6]. Palynological data indicate that these three localities are synchronous and should be 'Middle' [12] or Late [6] Maastrichtian in age. In North America, the latest well-identified representatives of the lambeosaurine subfamily are Early Maastrichtian in age [18] and Late-Maastrichtian dinosaur faunas are dominated either by ceratopsian or titanosaurid dinosaurs [10], groups that are not represented in Maastrichtian localities of the Amur region. The development of very different kinds of dinosaur communities after the Early Maastrichtian may reflect geographical isolation between eastern Asia and western North America during this period, or differences in climatic or palaeoecological conditions that still need to be investigated.

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Appendix. List and polarity of the characters treated in the phylogenetic analysis of *Olorotitan*.

1. Parietal participating in the occipital aspect of the skull (0), or completely excluded from the occiput (1). 2. Ratio 'length/minimal width' of the parietal > 2 (0), or < 2 (1). 3. Frontal participating in the orbital rim (0), or excluded by postorbital-prefrontal joint (1). 4. Hollow supracranial crest absent (0), or developed (1). 5. Deeply excavated frontal platform absent (0), occupying the rostral part of the frontal in adults (1), or extending above the rostral portion of the supratemporal fenestra (2); character treated as ordered. 6. Frontal longer than wide (0), wider than long (1), or secondary elongation resulting of the backwards extension of the frontal platform (2); character treated as unordered. 7. Premaxillary foramen present (0), or absent (1). 8. Lateral premaxillary process stopping at the level of the lacrimal (0), or extending further backwards (1). 9. Nasal participating in the border of the external naris (0), or external naris completely surrounded by premaxilla (1). 10. *Cavum nasi proprium* relatively small (0), or enlarged (1). 11. Nasal forming a small part of the hollow crest (0), half of the crest (1), or the entire crest (2); character treated as unordered. 12. Supraorbital free (0), or fused to prefrontal (1). 13. Caudal portion of prefrontal perfectly horizontal (0), or participating in the lateroventral border of the hollow crest (1). 14. Lateral side of the squamosal low (0), or elevated (1). 15. Rostral process of the jugal tapering in lateral view (0), or dorso-ventrally expanded (1). 16. Rostral process of the jugal angular (0), or truncated in lateral view (1). 17. Antorbital fenestra surrounded by the jugal and/or the lacrimal (0), or completely surrounded by the maxilla (1). 18. Maxilla markedly asymmetrical (0), or nearly symmetrical in lateral view (1). 19. Rostromedial process developed on the maxilla (0), or maxillary shelf developed (1). 20. Ectopterygoid ridge faintly (0), or strongly (1) developed on the lateral side of the maxilla. 21. Paraquadratic foramen present (0), or absent (1). 22. Distal head of quadrate transversely expanded (0), or dominated by a large hemispheric lateral condyle (1). 23. Mandibular diastema absent (0), or well devel-

oped in adult specimens (1). 24. Coronoid process sub-vertical (0), or inclined rostrally (1). 25. Predentary rounded in dorsal view (0), or angular (1). 26. Dentary crowns broad with a dominant ridge and secondary ridges (0), or miniaturized without secondary ridges (1). 27. Median carina of dentary teeth straight, (0), or sinuous (1). 28. Angle between root and crown of dentary teeth more (0), or less (1) than 130°. 29. Coracoid hook small and pointed ventrally (0), or prominent and pointed cranio-ventrally (1). 30. Deltopectoral crest of humerus moderately (0), or strongly (1) developed, extending down below the mid-point of the bone. 31. A maximum of 7 (0), or a minimum of 8 (1) sacral vertebrae. 32. Antitrochanter of ilium absent or poorly developed (0), or prominent (1). 33. Ischial peduncle of ilium as a single large knob (0), or formed by two small protrusions separated by a shallow depression (1). 34. Distal end of ilium forming an expanded foot (0), or tapering distally (1). 35. Distal head of fibula moderately expanded into the shape of a ball (0), or greatly expanded and club-shaped (1). 36. Cranial ascending process of astragalus laterally skewed (0), or equilateral in shape (1).

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