

***Charonosaurus jiayinensis* n.g., n.sp., a lambeosaurine dinosaur from the Late Maastrichtian of northeastern China**

Pascal Godefroit^{a*}, Shuqin Zan^b, Liyong Jin^b

^a Département de paléontologie, Institut royal des sciences naturelles de Belgique, 29, rue Vautier, 1000 Bruxelles, Belgium

^b Museum of Natural History, Changchun University of Science and Technology, 6 Ximin Zhu street, 130062 Changchun, P.R. China

Received 16 March 2000; accepted 25 April 2000

Communicated by Philippe Taquet

Abstract – Large bonebeds have been excavated in the Late Maastrichtian Yuliangze Formation near Jiayin (Heilongjiang Province, northeastern China). The greatest part of the discovered fossils belong to a new lambeosaurine dinosaur, *Charonosaurus jiayinensis* n.g., n.sp. Phylogenetic analysis, based on 33 cranial, dental and postcranial characters, indicates that this new taxon may be closer to *Parasaurolophus* than any other known Lambeosaurinae. The Late Maastrichtian dinosaur faunas currently known in northeastern Asia are dominated by Lambeosaurinae, although these dinosaurs are not represented any more in synchronous North American and European localities. © 2000 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Maastrichtian / China / vertebrata / dinosaures / Lambeosaurinae

Résumé – *Charonosaurus jiayinensis* n.g., n.sp., un dinosaure lambéosauriné du Maastrichtien supérieur du Nord-Est de la Chine. De grands bonebeds ont été fouillés dans la formation de Yuliangze près de Jiayin (province du Heilongjiang, Chine du Nord-Est). La grande majorité des fossiles découverts appartiennent à un nouveau dinosaure lambéosauriné, *Charonosaurus jiayinensis* n.g., n.sp. Une analyse phylogénétique basée sur 33 caractères crâniens, dentaires et postcrâniens indique que ce nouveau taxon semble plus proche de *Parasaurolophus* que de tout autre lambéosauriné connu. Les faunes du Maastrichtien supérieur connues à ce jour en Asie du Nord-Est sont dominées par des lambéosaurinés, alors que ces dinosaures ne sont plus représentés dans les gisements contemporains d'Amérique du Nord et d'Europe. © 2000 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Maastrichtien / Chine / vertebrata / dinosaures / Lambeosaurinae

Version abrégée

1. Introduction

En 1930, le géologue russe Riabinin décrivit, sous le nom de *Mandschurosaurus amurensis* [20], une série d'ossements découverts le long des rives du fleuve Amour, à proximité du village de Jiayin (Province du Heilongjiang, R.P. Chine ; figure 1) et référencés à la famille des Hadrosauridae. Ce taxon est maintenant considéré

de façon unanime comme un *nomen dubium*. Depuis 1975, plusieurs institutions chinoises ont entrepris de nouvelles fouilles dans la formation de Yuliangze à Jiayin et y ont découvert de nombreux ossements d'hadrosaures. Les fossiles forment de larges *bone-beds* déposés en milieu fluviatile. La grande majorité des ossements appartient à un nouveau genre de Lambeosaurinae, décrit brièvement et discuté dans la présente note.

* Correspondence and reprints: pgodefr@kbinirsnb.be

Des études palynologiques préliminaires (voir également [27, 28]) indiquent que la formation de Yuliangze appartient à la palynozone à *Wodehouseia spinata-Aquilapollenites subtilis*, reconnue dans plusieurs régions du Sud-Est de la Russie [14, 15]. Un âge Maastrichtien supérieur est avancé pour la formation de Yuliangze, parce que *Wodehouseia spinata* est considéré comme un excellent marqueur biostratigraphique pour les formations continentales du Maastrichtien supérieur (« Lancien ») d'Amérique du Nord [9, 11, 17, 22].

2. Paléontologie systématique

Ornithopoda Marsh, 1881

Hadrosauridae Cope, 1869

Lambeosaurinae Parks, 1923

***Charonosaurus jiayinensis* n. gen., n. sp.**

Étymologie. *Charon*, nom du fleuve Styx, dans la mythologie grecque et romaine ; *sauros* (Grec), lézard; *Jiayinensis*, de la localité type Jiayin.

Holotype. CUST J-V1251-57 (Changchun University of Sciences and Technology), un crâne partiel.

Matériel référé. Collections CUST J-III et J-V; GMH Hlj-16, 77, 87, 101, 140, 143, 144, 178, 195, 196, 207, 278, A10, A12 et ‘magnus’ (Geological Museum of Heilongjiang Province, Harbin).

Locus typicus. Rive sud du fleuve Amour (Heilongjiang), 8 km à l'ouest du village de Jiayin (Province du Heilongjiang, R.P. Chine ; 48°53'N, 130°27'E).

Stratum typicum. Formation de Yuliangze (Maastrichtien supérieur, Crétacé supérieur).

Diagnose. Surface dorsale du pariétal régulièrement arrondie, sans crête sagittale ; face latérale du squamosal presque complètement recouverte par la branche caudale du postorbitaire ; processus paroccipitaux et postcotoïdes très bas, atteignant seulement le niveau de la moitié de la hauteur du foramen magnum ; processus alaire du basisphénoïde proéminent et symétrique ; crête tricipitale développée sur l'humérus ; avant-bras allongé et mince, avec un rapport longueur totale/largeur maximale de l'extrémité proximale supérieur à 6,3 pour l'ulna et à 6,6 pour le radius ; processus préacétabulaire de l'ilium plus allongé que chez les autres hadrosauridés connus : rapport longueur de l'ilium/longueur préacétabulaire supérieur à 2,1.

3. Analyse phylogénétique

Afin de clarifier les relations phylogénétiques de *Charonosaurus*, une analyse phylogénétique a été effectuée sur une matrice de 33 caractères et 9 taxa (tableau et appendice, pour la liste des caractères utilisés) au moyen du logiciel Hennig86 [7]. Le cladogramme le plus parcimonieux obtenu est représenté sur la figure 3. *Charonosaurus* partage les synapomorphies suivantes avec les Lambeosaurinae : le pariétal est rac-

courci (rapport longueur/largeur minimale inférieur à 2) et est complètement exclu de la surface occipitale par les squamosaux, le frontal forme une large plate-forme évasée formant le plancher de la crête creuse, le frontal est exclu du bord de l'orbite par le contact latéral entre le postorbitaire et le préfrontal, la face latérale du squamosale est élevée ; le processus rostral du jugal est symétriquement arrondi, la carène médiane des dents sur le dentaire est sinuée, la crête deltopectorale est particulièrement développée en longueur et en largeur et s'étend au-delà de la moitié de la longueur de l'humérus. Au sein des Lambeosaurinae, *Charonosaurus* forme le groupe-frère de *Parasaurolophus*, sur la base des synapomorphies suivantes : la plate-forme du frontal s'étend vers l'arrière, au-dessus de la portion rostrale du pariétal et des fenêtres supratemporales ; l'extrémité distale de la fibula est particulièrement élargie et a la forme d'un club de golf ; le processus ascendant antérieur de l'astragale est équilatéral.

4. Implications paléogéographiques

En Asie du Nord-Est, d'autres gisements rapportés au Maastrichtien supérieur ont également livré des restes de lambéosaurinés : Blagoveschenk et Kundur, dans la région de l'Amour en Russie, et Toyohara-Gun, dans l'île de Sakhaline. Markevitch et Bugdaeva [15] ont montré que ces trois localités fossilifères appartiennent également à la palynozone à *Wodehouseia spinata-Aquilapollenites subtilis* et peuvent dès lors être considérées comme strictement contemporaines de la localité de Jiayin. Il est intéressant de constater que la composition faunique des gisements à dinosaures du Maastrichtien supérieur est radicalement différente en Asie du Nord-Est et en Amérique du Nord. Les ossements de Lambeosaurinae constituent plus de 90 % des fossiles découverts à Jiayin, Blagoveschensk et Kundur, alors que les cératopsiens et les titanosaures semblent totalement absents de ces localités. Au contraire, les gisements du Maastrichtien supérieur d'Amérique du Nord sont dominés, soit par les cératopsiens, soit par les titanosaures, alors que les lambéosaurinés semblent avoir totalement disparu. Les principales théories sur l'extinction des dinosaures à la limite Crétacé-Tertiaire ont jusqu'à présent été échafaudées sur des observations faites sur les grands gisements d'Amérique du Nord. L'étude des gisements asiatiques dominés par des lambéosaurinés suggère que d'autres types de faunes de dinosaures existaient en dehors de l'Amérique du Nord, juste avant la crise Crétacé-Tertiaire. De futurs développements dans l'étude de ces gisements permettront une meilleure compréhension de la véritable biodiversité des dinosaures au cours du Maastrichtien supérieur et permettront de mieux comprendre l'extinction des dinosaures, il y a quelque 65 millions d'années.

1. Introduction

During the summers of 1916 and 1917, the Russian Geological Committee undertook two excavation campaigns along the right side of the Amur River, which forms the western border between Russia and China, in the vicinity of Jiayin (Heilongjiang Province, P.R. China, figure 1). The finds included a series of dinosaur bones, named *Mandschurosaurus amurensis* [19] and referred to the family Hadrosauridae. This species is now unanimously regarded as a nomen dubium, because of the scarcity of the material and of the absence of any diagnostical element. Moreover, as admitted by Riabinin [20] himself, the holotype skeleton is clearly reconstructed from several individuals. This skeleton is so heavily restored that it is currently impossible to distinguish the real bone from plaster restoration. From the same locality, Riabinin [21] also described a very fragmentary ischium, presumed to belong to a hadrosaur, under the name *Sauropodus krystofovici*: this is of course also clearly a nomen dubium. Since 1975, several Chinese institutions have undertaken new excavations near Jiayin and discovered many new hadrosaurian fossils in a limited area. The fossils form large bonebeds extending over several tens of square metres. The disarticulated skeletons of numerous animals are completely mixed together, the apophyses and neural arches of the vertebrae are broken off and the long bones indicate a preferential direction. It is therefore clear that the carcasses of the dinosaurs accumulated in a fluvial environment, with relatively important currents. The fossil assemblage is dominated by lambeosaurine dinosaurs (about 90 % of the discovered bones), along with theropod, ankylosaurian, crocodile and turtle isolated bones. Although both juvenile and adult specimens are represented, the lambeosaurine sample from Jiayin is particularly homogeneous and there is currently no reason to consider that more than one lambeosaurine coexisted in this limited area. The abundance of theropod resorbed teeth indicates either that the lambeosaurines were killed by predators along the river, or that their carcasses were eaten and dismembered by scavengers.

Preliminary study of the abundant mega- and palynoflora of the Yuliangze Formation [27–29] indicates that it belongs to the *Wodehouseia spinata*–*Aquilapollenites subtilis* palynozone, recognized in several regions of south-eastern Russia [14, 15]. The abundance of *Wodehouseia spinata* speaks for a Late Maastrichtian age for the Yuliangze Formation, as this species is regarded as a good biostratigraphic indicator for typical Late Maastrichtian ('Lancian') formations in North America, such as the Scollart Formation in Alberta [22], the Lance Formation in Wyoming [11], the Hell Creek Formation in Montana and the Dakotas [9], the Laramie, Arapahoe and the lower part of the Denver Formations in Colorado [17].

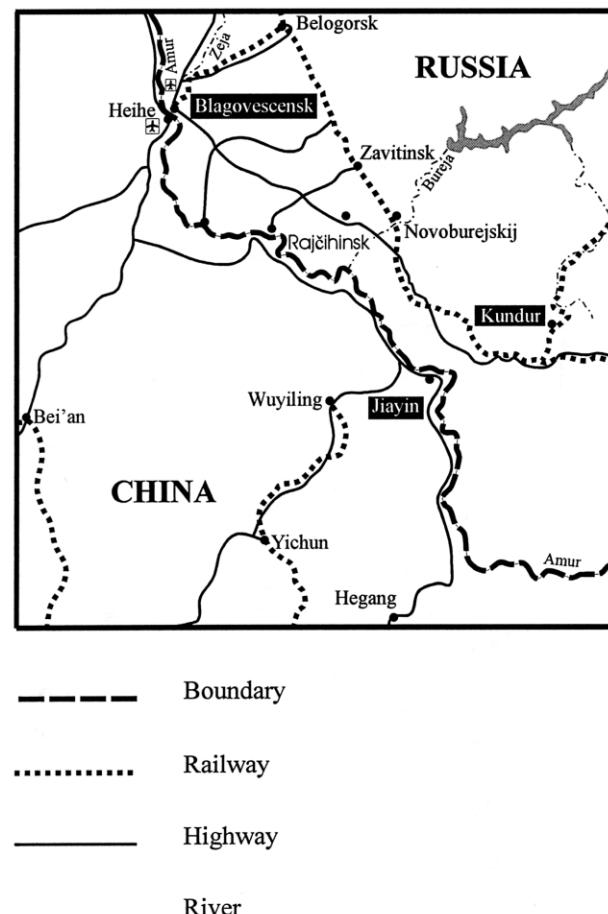


Figure 1. Geographic location of Late Maastrichtian dinosaur localities in the Heilongjiang Province (P.R. China) and the Amur area (Russia). Scale: 1:5 267 000.

Figure 1. Localisation géographique des gisements à dinosaures du Maastrichtien supérieur dans la province du Heilongjiang (R.P. Chine) et la région de l'Amour (Russie). Échelle: 1/5 267 000.

2. Systematic palaeontology

Ornithopoda Marsh, 1881

Hadrosauridae Cope, 1869

Lambeosaurinae Parks, 1923

***Charonosaurus*, n. gen.**

Etymology. *Charon*, boatswain of Styx River in Greek and Roman mythology; *sauros* (Greek), lizard.

Type species. *Charonosaurus jiayinensis*, n. sp.

***Charonosaurus jiayinensis*, n. sp.**

Etymology. *Jiayinensis*, from the type locality Jiayin.

Holotype. CUST J-V1251-57 (Changchun University of Sciences and Technology), a partial skull.

Referred material. Collections CUST J-III and J-V; GMH Hlj-16, 77, 87, 101, 140, 143, 144, 178, 195, 196, 207, 278, A10, A12 and 'magnus' (Geological Museum of Heilongjiang Province, Harbin).

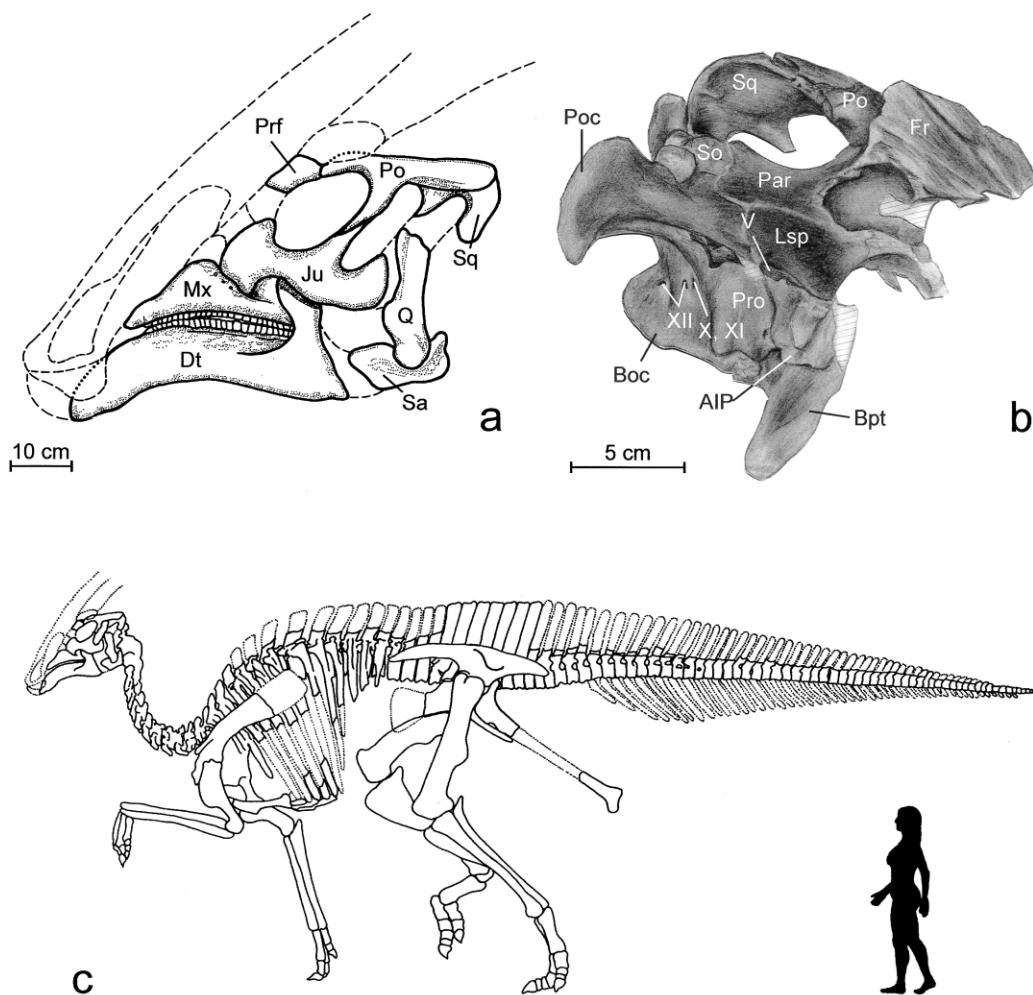


Figure 2. *Charonosaurus jiayinensis*, from the Late Maastrichtian of China. **a:** reconstruction of the skull in left lateral view. **b:** holotype CUST J-V1251-57 (back of the skull) in right lateral view. **c:** reconstruction of the whole skeleton. Abbreviations: AIP, alar process; Boc, basioccipital; Bpt, basipterygoid process; Dt, dentary; Fr, frontal; Ju, jugal; Lsp, laterosphenoid; Mx, maxilla; Par, parietal; Po, postorbital; Poc, paroccipital process; Prf, prefrontal; Pro, prootic; Q, quadrate; Sa, surangular; So, supraoccipital; Sq, squamosal. V, X–XII: foramina for cranial nerves.

Figure 2. *Charonosaurus jiayinensis*, du Maastrichtien supérieur de Chine. **a:** reconstitution du crâne en vue latérale gauche. **b:** holotype CUST J-V1251-57 (arrière du crâne) en vue latérale droite. **c:** reconstitution du squelette complet. Abréviations : AIP, processus alaire ; Boc, basioccipital ; Bpt, processus basiptérygoïde ; Dt, dentaire ; Fr, frontal ; Ju, jugal ; Lsp, latérosphénioïde ; Mx, maxillaire ; Par, pariétal ; Po, postorbitaire ; Poc, processus paroccipital ; Prf, préfrontal ; Pro, proötique ; Q, carré ; Sa, surangulaire ; So, supraoccipital ; Sq, squamosal. V, X–XII : foramen pour les nerfs crâniens.

Locus typicus. Southern banks of Amur (Heilongjiang) River, 8 km west to Jiayin village (Heilongjiang Province, P.R. China; 48° 53' N, 130° 27' E).

Stratum typicum. Yuliangze Formation (Late Maastrichtian, Late Cretaceous).

Diagnosis. Dorsal surface of parietal regularly rounded, without sagittal crest; lateral side of squamosal nearly completely covered by caudal ramus of postorbital; paroccipital and postcotyloid processes very low, extending only at mid-height of foramen magnum; alar process of basisphenoid prominent and symmetrical; tricipital crest developed on the humerus; forearm elongated and slender, with a ratio 'total length/maximal

width of the proximal head' > 6.3 for the ulna and > 6.6 for the radius; preacetabular process of ilium more elongated than in other known hadrosaurids: ilium length / preacetabular length > 2.1.

Abridged description (figure 2)

Charonosaurus jiayinensis was a large ornithopod: the femora reach a length of 135 cm and are therefore longer than in any other known hadrosaur except *Shantungosaurus giganteus* Young, 1958 [30]. The supratemporal fenestrae are proportionally short and wide. The dorsal surface of the frontal is highly modified to support the base of a hollow crest: it forms a very broad and excavated platform, strongly inclined forwards and

ornamented by long and deep longitudinal grooves. The caudolateral part of the frontal projects dorsally and overhangs the rostral portion of the parietal and of the supratemporal fenestra. The rostroradial surface of the postorbital forms also a thickened promontorium that participated in the base of the supracranial crest. The caudal ramus of the postorbital is long and broad, nearly completely covering the lateral side of the squamosal. The parietal is relatively short and does not extend caudally towards the occipital surface of the skull; its dorsal surface is smoothly convex and does not bring any trace of a sagittal crest. The lateral side of the squamosal is particularly elevated above the cotyloid cavity. The postcotyloid process of the squamosal and the paroccipital process of the exoccipital are, on the other hand, shortened ventrally, extending only at mid-height of the foramen magnum. The rostral process of the jugal is dorso-ventrally expanded and symmetrically rounded in lateral view. As in all Hadrosauridae, the ectopterygoid ridge is strongly developed on the lateral side of the maxilla; unlike Hadrosaurinae, the dorsal process lies behind the mid-point of the maxilla. The quadrate closely resembles that of North-American Hadrosauridae: a continuous elongated articular facet extends along the dorsal part of the quadratojugal notch, indicating that the paraquadrate foramen was absent, and its ventral head is dominated by a large hemispheric lateral condyle that articulated with the angular component of the mandibular glenoid [24]. As in Hadrosauridae, the basioccipital neck supporting the occipital condyle is shortened and the articular surface of the latter is perfectly vertical. The basipterygoid processes extend well below the level of the occipital condyle; above each basipterygoid process, the lateral side of the basisphenoid forms a large, symmetrical and well-detached alar process, formed by one rostral and one caudal wing. The supraoccipital bears a pair of prominent craniodorsal knobs, lodging into caudolateral depressions of the parietal. The robust dentary is strongly deflected rostrally, forming an angle of about 30° with the long axis of the bone. The dental battery of the dentary is formed by about 40 tooth rows in adult specimens; because the teeth are very high, each row is formed by only 2 or 3 teeth, with one to two functional ones. The diastema is very short in juveniles and more extended in larger individuals. Dentary teeth are very high, the largest dental crowns reaching 50 mm in height, with a height/length ratio > 4; they bear a single sinuous vertical ridge. The sacrum is composed of 9 co-ossified vertebrae. Transformations of the forelimb and pectoral girdle are essentially linked to the elongation of the forearm and to the concomitant development of a strong bicipital and tricipital musculature. The proximal head of the scapula bears, on its caudolateral side, a prominent buttress marking the insertion area of a powerful *M. triceps scapulare laterale externum* [18]. The coracoid is typically hadrosaurian in shape, with a prominent hook-like process pointing cranio-ventrally

[3]; even in juvenile specimens, its lateral side bears a very prominent knob for insertion of a very strong *M. biceps*. The humerus develops a prominent deltopectoral crest extending down below the mid-point of the bone and a wide bicipital gutter on its cranial side; a caudal tricipital crest is developed in all specimens, but is particularly prominent in older individuals. Both the ulna and radius are very elongated and slender, with a 'total length / maximal width of the proximal head' ratio > 6.3 for the ulna and > 6.6 for the radius. The preacetabular process of the ilium is longer than in other hadrosaurs (see [3]), with a 'ilium length / preacetabular length' ratio > 2.1, but it is not very deflected ventrally; the antitrochanter is particularly prominent. The distal end of the ischium forms an expanded footed knob. The prepubic blade is relatively short and high and abruptly expands cranially. The distal head of the fibula is greatly expanded and club-shaped. The cranial ascending process of the astragalus forms an equilateral triangle in cranial view.

3. Phylogenetic analysis

In order to clarify the phylogenetic relationships of *Charonosaurus*, a cladistic analysis was performed on a 33-character dataset (see appendix, for the list of characters), using Hennig 86 software [7]. The resulting character-taxon matrix is shown in the table. Characters that cannot be directly observed on the available *Charonosaurus* material have been left out. We also excluded the controversial 'lambeosaurine' *Tsintasaurus* Young, 1958 [30] and *Eolambia* Kirkland, 1998 [10] from this analysis, as it appears to us that these taxa require revision. A single most parsimonious cladogram was obtained (figure 3). The following lambeosaurine synapomorphies can be observed in *Charonosaurus*: shortened parietal ('length/minimal width' ratio < 2) completely excluded from the occipital surface by the squamosals, frontal forming a broad excavated platform as a floor for the hollow crest, frontal excluded from the orbital rim by postorbital-prefrontal joint, vertical caudal portion of the prefrontal, elevated lateral side of the squamosal, rounded and symmetrical rostral process of the jugal, sinuous median carina of the dentary teeth, and very developed deltopectoral crest (both in length and in width) of the humerus extending down below the mid-point of the bone. Within Lambeosaurinae, *Charonosaurus* and *Parasaurolophus* are closely united on the basis of the frontal platform extending backwards above the rostral part of the parietal and supratemporal fenestra, the very enlarged club-shaped distal end of the fibula, and the equilateral cranial ascending process of the astragalus.

4. Palaeobiogeographical implications

In northeastern Asia, other Late Maastrichtian localities have yielded lambeosaurine fossils: Blagoveschensk

Table. Character-taxon matrix used in the phylogenetic analysis of *Charonosaurus*, with *Iguanodon* regarded as outgroup.

Tableau. Matrice des caractères et des taxa utilisés lors de l'analyse phylogénétique de *Charonosaurus jiayinensis*, avec *Iguanodon* comme groupe extérieur.

<i>Iguanodon</i>	00000	00000	00000	00000	00000	00000	000
<i>Bactrosaurus</i>	11000	00000	10000	00011	11000	00100	100
<i>Telmatosaurus</i>	11000	00010	11011	00011	1100?	0????	1??
<i>Hadrosaurinae</i>	11000	00010	11111	11111	12011	01111	100
<i>Charonosaurus</i>	11112	11111	11011	11111	12101	11112	111
<i>Parasaurolophus</i>	11112	11111	11011	11111	12101	11112	111
<i>Corythosaurus</i>	11111	11111	11011	11111	12101	11112	100
<i>Hypacrosaurus</i>	11111	11111	11011	11111	12101	11112	100
<i>Lambeosaurus</i>	11111	11111	11011	11111	12101	11112	100

and Kundur, in the Russian Amur region (see figure 1), and Toyohara-Gun in Sakhalin Island. Markevitch and Bugdaeva [15] show that these three fossil localities also belong to the same *Wodehouseia spinata-Aquilapollenites subtilis* palynozone and are consequently strictly synchronous to the Jiayin locality. As at Jiayin, the large bonebeds discovered at Blagoveschensk and Kundur are near-monospecific, a single lambeosaurine constituting more than 90 % of the fauna, along with isolated theropod, ankylosaurian, crocodile and turtle bones. The lambeosaurine *Amurosaurus riabinini* Bolotsky and Kurzanov, 1991 [2] was described from a partial skull from Blagoveschensk. Many differences can be observed with the skull of *Charonosaurus jiayinensis*, including a shorter frontal platform suggesting a different kind of supracranial crest, a well-developed sagittal crest, longer paroccipital processes, a longer parietal, and particularly well-separated squamosals. Meanwhile, numerous new specimens have been discovered at Blagoveschensk. The study of this material, as that found at Kundur, is in preparation by Bolotsky and Godefroit. A single partial skeleton of a juvenile speci-

men, named *Nipponosaurus sachalinensis* Nagao, 1936 [16], was found at Toyohara-Gun; this taxon is currently regarded as a Lambeosaurinae incertae sedis [25]. However, its metacarpal elements differ from those of *Charonosaurus jiayinensis* in being well expanded at both ends, with a slightly curved shaft [3].

The composition of Late Maastrichtian dinosaur faunas appears radically different in northeastern Asia and North America. Lambeosaurinae constitute more than 90 % of the fossils discovered at Jiayin, Blagoveschensk and Kundur, while ceratopsian and titanosaurid dinosaurs are apparently absent from currently known Late Maastrichtian localities in Asia. In western North America, on the other hand, Late Maastrichtian dinosaur assemblages are dominated either by ceratopsians or titanosaurs [12]. The presence of Lambeosaurinae in Late Maastrichtian localities from western North America is not substantiated. Sullivan and Williamson [23] demonstrate that, with the possible exception of one fragmentary specimen (see [26]) whose age remains equivocal, all the currently known *Parasaurolophus* specimens come from strata dated between 76 and 73 Ma. The youngest North American Lambeosaurinae would consequently be *Hypacrosaurus altispinus*, from the Horseshoe Canyon Formation in Alberta [6]. *Pararhabdodon isonensis*, the only European lambeosaurine from northern Spain and southern France, is probably Late Campanian–Early Maastrichtian in age (Pereda Suberbiola, pers. com.).

Late Maastrichtian dinosaur localities that document the crucial K/T extinction are mainly concentrated in western North America [1, 5]. The age of potential Late Maastrichtian dinosaur localities in Romania [8], southern France [13] and India [4] still needs to be corroborated. The study of lambeosaurine-dominated Late Maastrichtian localities in northeastern Asia suggests that different kinds of dinosaur communities existed outside North America just before the K/T crisis. Future developments in the study of these localities would lead to a better understanding of the real dinosaur biodiversity during the Late Maastrichtian and would clarify the extinction pattern of non-avian dinosaurs, some 65 Ma ago.

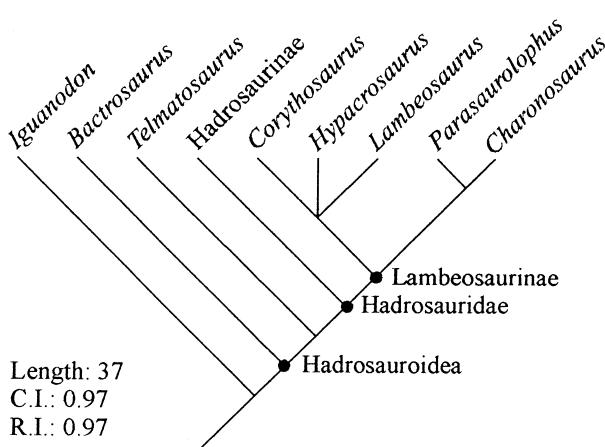
**Figure 3.** Cladogram showing the phylogenetic relationships of *Charonosaurus jiayinensis*.

Figure 3. Cladogramme montrant les relations phylogénétiques de *Charonosaurus jiayinensis*.

Acknowledgements. The authors thank Xing Yuling (Geological Museum of Heilongjiang), Sun Chang Qing (Heilongjiang Provincial Museum) and Y. Bolotsky (Amur KNII, Blagoveschensk) for access to material in their care. Li Hong, Yang Huijuan and Dong Zhi-Ming kindly facilitated P.G.'s journey in Heilongjiang Province. Ann Wauters, Chen Chang-Jung and H. De Potter realized the drawings for this paper. This work was supported by the Belgian Prime Minister's Office of Scientific, Technical and Cultural Affairs and by a FNRS travel grant to P.G.

Appendix. List of characters treated in the phylogenetic analysis.

Appendice. Liste des caractères traités lors de l'analyse phylogénétique.

1: occipital condyle inclined caudoventrally (0), or vertical (1); **2:** basipterygoid processes short (0), or extending well below the level of the ventral border of the occipital condyle (1); **3:** ratio 'length /minimal width' of the parietal > 2 (0), or < 2 (1); **4:** parietal exposed on the occipital surface (0), or completely hidden by the squamosals (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 participating in the orbital rim (0), or excluded by postorbital-prefrontal joint (1); **7:** caudal portion of the prefrontal oriented horizontally (0), or vertically (1); **8:** lateral side of the squamosal low (0), or elevated (1); **9:** rostral process of the jugal tapers in lateral view (0), or dorso-ventrally expanded (1); **10:** rostral process of the jugal essentially angular (0), or rounded and symmetrical in lateral view (1); **11:** jugal-ectopterygoid joint present (0), or absent (1); **12:** antorbital fenestra surrounded by the jugal and/or the lacrimal (0), or completely surrounded by the maxilla (1); **13:** maxilla asymmetrical (0), or symmetrical (1) in lateral view; **14:** ectopterygoid ridge faintly (0), or strongly (1) developed on the lateral side of the maxilla; **15:** paraquadratic foramen present (0), or absent (1); **16:** distal head of the quadrate transversely expanded (0), or dominated by a large hemispheric lateral condyle (1); **17:** mandibular diastema absent (0), or well developed (1); **18:** coronoid process sub-vertical (0), or inclined rostrally (1); **19:** surangular foramen present (0), or absent (1); **20:** two (0), or three or more (1) dentary teeth in each alveolus; **21:** maxillary crowns broad with subsidiary ridges (0), or miniaturized with a single ridge (1); **22:** dentary crowns broad with two subequal ridges (0), broad with a dominant ridge and secondary ridges (1), or miniaturized without secondary ridges (2) {character treated as ordered}; **23:** median carina of dentary teeth straight, (0) or sinuous (1); **24:** angle between root and crown of dentary teeth more (0), or less (1) than 130°; **25:** coracoid hook small and pointed ventrally (0), or prominent and pointed cranio-ventrally (1); **26:** deltopectoral crest of humerus moderately (0), or strongly (1) developed, extending down below the mid-point of the bone (Godefroit et al., in prep.); **27:** a maximum of 7 (0), or a minimum of 9 (1) sacral vertebrae; **28:** antitrochanter of ilium absent or poorly developed (0), or prominent (1); **29:** ischial peduncle of ilium as a single large knob (0), or formed by two small protrusions separated by a shallow depression (1); **30:** distal end of ilium forming a moderately expanded knob (0), tapering distally (1), or hypertrophied and footed (2) {character treated as unordered}; **31:** transverse widening of tibia restricted to the proximal head (0), or extending along the diaphysis (1); **32:** distal head of fibula moderately expanded into the shape of a ball (0), or greatly expanded and club-shaped (1); **33:** cranial ascending process of astragalus laterally skewed (0), or equilateral in shape (1).

References

- [1] Archibald J.D., Extinction, Cretaceous, in: Currie P.J., Padian K. (Eds.), Encyclopedia of Dinosaurs, 1997, pp. 221–230.
- [2] Bolotsky Y.L., Kurzanov S.K., The hadrosaurs of the Amur Region, in: Geology of the Pacific Ocean Border, 1991, pp. 94–103.
- [3] Brett-Surman M.C., A revision of the Hadrosauridae (Reptilia: Ornithischia) and their evolution during the Campanian and Maastrichtian, unpublished thesis, G. Washington University, Washington DC (1989).
- [4] Chatterjee S., Rudra D.J., K-T events in India: impact, rifting, volcanism and dinosaur extinction, Mem. Queensland Mus. 39 (1996) 489–532.
- [5] Dodson P., Tatarinov L.P., Dinosaur extinction, in: Weishampel D.B., Dodson P., Osmolska H. (Eds.), The Dinosauria, 1990, pp. 55–62.
- [6] Eberth D.A., Edmonton Group, in: Currie P.J., Padian K. (Eds.), Encyclopedia of Dinosaurs, 1997, pp. 199–203.
- [7] Farris J.S., Hennig 86 reference, version 1.5, Copyright J.S. Farris (1988).
- [8] Grigorescu D.A., Stratigraphic, taphonomic and palaeoecologic approach to a 'forgotten land': the dinosaur-bearing deposits from the Hateg Basin (Transylvania-Romania), Acta Palaeontol. Polonica 28 (1983) 103–121.
- [9] Hotton C.L., Palynology of the Cretaceous–Tertiary boundary in central Montana, USA, and its implications for extraterrestrial impact, unpublished thesis, University of California, Davis, 1988.
- [10] Kirkland J.J., A new hadrosaurid from the Upper Cedar Mountain Formation (Albian-Cenomanian: Cretaceous) of eastern Utah: the oldest known hadrosaurid (Lambeosaurine?), New Mexico Mus. Nat. Hist. Sci. 14 (1998) 283–302.
- [11] Leffingwell H.A., Palynology of the Lance (Late Cretaceous) and Fort Union (Paleocene) formations of the type Lance area, Wyoming, Geol. Soc. Am. Spec. Paper 127 (1970) 1–64.
- [12] Lehman T.M., Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America, Palaeogeogr. Palaeoclimatol. Palaeoecol. 60 (1987) 189–217.
- [13] Le Lœuff J., Buffetaut E., Martin M., The last stages of dinosaur faunal history in Europe: a succession of Maastrichtian dinosaur assemblages from the Corbières (southern France), Geol. Mag. 131 (1994) 625–630.
- [14] Markevitch V.S., Palynological zonation of the continental Cretaceous and Early Tertiary of eastern Russia, Cretaceous Res. 15 (1994) 165–177.
- [15] Markevitch V.S., Bugdaeva Y.V., Flora and correlation of layers with dinosaur fossil remains in Russia's Far East, Tikhookeanskaya Geol. 16 (1997) 114–124, (in Russian with English summary).
- [16] Nagao T., *Nipponosaurus sachalinensis*, a new genus and species of trachodont dinosaur from Japanese Sachalin, J. Fac. Sci. Hokkaido Imp. Univ. Series 4 (3) (1936) 185–220.
- [17] Newman K.R., Biostratigraphic correlation of Cretaceous–Tertiary boundary rocks, Colorado to San Juan Basin, New Mexico, Geol. Soc. Am. Spec. Paper 209 (1987) 151–164.
- [18] Norman D.B., On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda), Bull. Ins. Roy. Sci. Nat. Belg. Sci. Terre 56 (1986) 281–372.
- [19] Riabinin A.N., A mounted skeleton of the gigantic reptile *Trachodon amurensis* nov. sp., Izvest. Geol. Komissiya 44 (1925) 1–12, (in Russian with English summary).
- [20] Riabinin A.N., *Manschurosaurus amurensis* nov. gen. nov. sp., a hadrosaurian dinosaur from the Upper Cretaceous of Amur River, Mém. Soc. paléontol. Russie 2 (1930) 1–36, (in Russian with English summary).

- [21] Riabinin A.N., On the age and fauna of the dinosaur beds on the Amur River, Mém. Soc. Russe Minéral. (2) 59 (1930) 41–51, (in Russian with English summary).
- [22] Srivastava S.K., Pollen biostratigraphy and paleoecology of the Edmonton Formation (Maestrichtian), Alberta, Canada, Palaeogeogr. Palaeoclimatol. Palaeoecol. 7 (1970) 221–276.
- [23] Sullivan R.M., Williamson T.E., A new skull of *Parasaurolophus* (Dinosauria: Hadrosauridae) from the Kirkland Formation of New Mexico and a revision of the genus, New Mexico Mus. Nat. Hist. Sci. 15 (1999) 1–52.
- [24] Weishampel D.B., Evolution of jaw mechanism in ornithopod dinosaurs, Adv. Anat. Embryol. Cell. Biol. 87 (1984) 1–110.
- [25] Weishampel D.B., Horner J.R., Hadrosauridae, in: Weishampel D.B., Dodson P., Osmolska H. (Eds.), The Dinosauria, 1990, pp. 534–561.
- [26] Weishampel D.B., Jensen J.A., *Parasaurolophus* (Reptilia: Hadrosauridae) from Utah, J. Paleontol. 53 (1979) 1422–1427.
- [27] Xing Y.L., Yu T.X., Dong H.M., The dinosaur fossil locality in Jiayin County of Heilongjiang Province and its research history, Heilongjiang Geol. 5 (1994) 17–26, (in Chinese with English summary).
- [28] Yang D.S., Observations on the palaeogeography and environment of the Late Cretaceous titanosaur–hadrosaur fauna at Jiayin in Heilongjiang Province, Nat. Res. Heilongjiang Prov. (1987) 11–18, (in Chinese).
- [29] Yang D.S., Wei Z.Y., Li W.R., Preliminary note on some hadrosaurs from the Cretaceous of Jiayin, Heilongjiang, Nat. Res. Heilongjiang Prov. (1986) 1–10, (in Chinese).
- [30] Young C.C., The dinosaurian remains of Laiyang, Shantung, Palaeontol. Sinica, Series C 16 (1958) 1–138, (in Chinese and English).