New Hadrosaurid Dinosaurs from the Uppermost Cretaceous of Northeastern China

Authors: Godefroit, Pascal, Shulin, Hai, Tingxiang, Yu, and Lauters, Pascaline

Source: Acta Palaeontologica Polonica, 53(1) : 47-74

Published By: Institute of Paleobiology, Polish Academy of Sciences

URL: https://doi.org/10.4202/app.2008.0103

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Acta-Palaeontologica-Polonica on 25 May 2025
Terms of Use: https://complete.bioone.org/terms-of-use

New hadrosaurid dinosaurs from the uppermost Cretaceous of northeastern China

PASCAL GODEFROIT, HAI SHULIN, YU TINGXIANG, and PASCALINE LAUTERS

Godefroit, P., Hai, S., Yu, T., and Lauters, P. 2008. New hadrosaurid dinosaurs from the uppermost Cretaceous of northeastern China. *Acta Palaeontologica Polonica* 53 (1): 47–74.

Several hundred disarticulated dinosaur bones have been recovered from a large quarry at Wulaga (Heilongjiang Province, China), in the Upper Cretaceous (Maastrichtian) Yuliangze Formation. The Wulaga quarry can be regarded as a monodominant bonebed: more than 80% of the bones belong to a new lambeosaurine hadrosaurid, *Sahaliyania elunchunorum* gen. et sp. nov. This taxon is characterised by long and slender paroccipital processes, a prominent lateral depression on the dorsal surface of the frontal, a quadratojugal notch that is displaced ventrally on the quadrate, and a prepubic blade that is asymmetrically expanded, with an important emphasis to the dorsal side. Phylogenetic analysis shows that *Sahaliyania* is a derived lambeosaurine that forms a monophyletic group with the corythosaur and parasauroloph clades. Nevertheless, the exact position of *Sahaliyania* within this clade cannot be resolved on the basis of the available material. Besides *Sahaliyania*, other isolated bones display a typical hadrosaurine morphology and are referred to *Wulagasaurus dongi* gen. et sp. nov., a new taxon characterised by the maxilla pierced by a single foramen below the jugal process, a very slender dentary not pierced by foramina, and by the deltopectoral crest (on the humerus) oriented cranially. Phylogenetic analysis indicates that *Wulagasaurus* is the most basal hadrosaurine known to date. Phylogeographic data suggests that the hadrosaurines, and thus all hadrosaurids, are of Asian origin, which implies a relatively long ghost lineage of approximately 13 million years for basal hadrosaurines in Asia.

Key words: Dinosauria, Hadrosauridae, *Sahaliyania elunchunorum*, *Wulagasaurus dongi*, phylogeny, palaeogeography, Late Cretaceous, China.

Pascal Godefroit [pascal.godefroit@naturalsciences.be] and Pascaline Lauters [plauters@ulb.ac.be], Department of Palaeontology, Institut royal des Sciences naturelles de Belgique, rue Vautier 29, 1000 Bruxelles, Belgium;
Hai Shulin [haishulin@126.com] and Yu Tingxiang, Geological Museum of Heilongjiang, Xiangfang District, Harbin, China.

Introduction

Hadrosauridae were very successful herbivorous dinosaurs during the closing stages of the Cretaceous. During the Campanian and the Maastrichtian, they were the primary constituents of many terrestrial vertebrate faunas. In western North America, hundreds of fragmentary or complete hadrosaurid specimens have been collected, including remains of eggs, embryos, hatchlings, and juveniles. Hadrosaurids reached a nearly world-wide distribution: besides North America, their fossils have also been discovered in Central America, South America, Europe, Asia (Horner et al. 2004), and apparently even in Antarctica (Rich et al. 1999). The main reason for this evolutionary success was probably their very efficient plant-processing masticatory apparatus, with a highly mobile upper jaw and an elaborated dental battery well adapted for feeding on hard vegetation (Weishampel 1984). The palaeogeography of hadrosaurids is complex and there is so far no agreement about their area of origin. Recently Horner et al. (2004) hypothesized a North American origin for the clade. However, this assessment differs from that presented by Milner and Norman (1984) and Godefroit et al. (1998, 2004a, b), who hypothesized an Asian origin, and Brett-Surman (1979), who suggested that their area of origin cannot be determined.

Several new hadrosaurid dinosaurs have recently been described from uppermost Cretaceous deposits along both the Chinese and Russian banks of the Amur River: *Charonosaurus jiayinensis* from the Yuliangze Fm of Jiayin, Heilongjiang Province, China (Godefroit et al. 2000, 2001), *Amurosaurus riabinini* and *Kerberosaurus manakini* from the Udurchukan Formation of Blagoveschensk, Amur Region, Russia (Bolotsky and Kurzanov 1991; Bolotsky and Godefroit 2004; Godefroit et al. 2004b), and *Olorotitan arharensis* from the Udurchukan Formation of Kundur, Amur Region, Russia (Godefroit et al. 2003). A fourth dinosaur locality was recently discovered in 2002, in the Yuliangze Formation of Wulaga, Heilongjiang Province, China (Hai 2004). It has already yielded several hundred isolated dinosaur bones. Two new hadrosaurid taxa from this new locality are described in the present paper. Their phylogenetic analysis brings new insight about the area of origin of the hadrosaurid clade.

Institutional abbreviations.—AEHM, Amur Natural History Museum (Blagoveschensk, Russia); AMNH, American Museum of Natural History (New York, New York, USA); DMNH, Denver Museum of Natural History (Denver, Colorado, USA); FMNH, Field Museum of Natural History (Chicago, Illinois, USA); GMH, Geological Museum of Heilongjiang (Harbin, Heilongjiang Province, P.R. China); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China); MOR, Museum of the Rockies (Bozeman, Montana, USA); PIN, Paleontological Institute of the Russian Academy of Sciences (Moscow, Russia); ROM, Royal Ontario Museum (Toronto, Ontario, Canada); TMP, Tyrrell Museum of Paleontology (Drumheller, Alberta, Canada).

Geographic and geologic settings

The Amur (or Heilongjiang) Region is situated at the border between Far Eastern Russia and the Heilongjiang Province, China. From a geological point of view, this area corresponds to the southern part of the Zeya-Bureya Basin (Fig. 1). This basin formed during Late Jurassic time as a series of N-S trending grabens (Kirillova et al. 1997; Kirillova 2003). The rift infill is composed of Upper Jurassic and Lower Cretaceous volcano-sedimentary deposits; the plate infill is composed of Upper Cretaceous and Tertiary sediments, including Maastrichtian dinosaur-bearing sediments. All the dinosaurs have been found in the Udurchukan Formation of the Tsagayan Group in Russia (Kundur, Blagoveschensk), or in the Yuliangze Formation in China (Jiayin; Sun et al. 2002). Wulaga, situated in the farthest southeastern corner of the Zeya-Bureya Basin near the border with the Lesser Khingan Mountains, is the fourth important dinosaur locality discovered in the Amur-Heilongjiang area. The sediments at Wulaga also belong to the Yuliangze Formation (Hai 2004).

The exposure of the Wulaga dinosaur locality is limited to a short road section a few metres high. Most of the exposed sediments represent a fluvial environment with yellow, coarse-grained channel deposits that have yielded eroded and fragmented bones. Well-preserved bones form a continuous bonebed in a diamictite layer. Such diamictite deposits with dinosaur bonebeds have also been described in neighbouring dinosaur localities: Kundur (Van Itterbeeck et al. 2005) and Blagoveschensk (Lauters et al. in press). They are interpreted as sediment gravity flow deposits that originated from the uplifted areas at the borders of the Zeya-Bureya Basin. At Wulaga, the debris flow deposits have also yielded several skin imprints. The remarkable preservation of vertebrate bones and soft tissues in debris flow deposits has also been observed in Madagascar (Rogers 2005).

The Wulaga dinosaur quarry consists of an accumulation of bones belonging to numerous individuals of different sizes. In this layer, the bones are usually completely mixed together, and articulated elements are rare. More than 80% of the recovered elements are larger than 5 cm (it is not possible to be more precise, because of excavation biases: very small elements can be easily destroyed and some of them have been lost). Therefore, the Wulaga dinosaur-bearing layer can be regarded as a macrofossil bonebed (Mode D; sensu Eberth and Currie 2005).

Fig. 1. **A**. Location of the Amur/Heilongjiang Region in Asia. **B**. A sketch map of the Amur/Heilongjiang Region (modified from Kirillova 2003). The main dinosaur sites are indicated by solid triangles.

The Wulaga bonebed is largely dominated by lambeosaurine bones, which represent about 80% of the diagnostic elements. So far, there is no indication that more than one single lambeosaurine species is represented in this bonebed. Hadrosaurine bones were also unearthed in this locality. Theropods are rare and mainly represented by shed teeth. The Wulaga dinosaur quarry can therefore be regarded as a monodominant bonebed (Mode D2; sensu Eberth and Currie 2005): it consists of the remains of more than one taxon, but it is overwhelmingly dominated (>50%) by skeletal elements from one species. Monodominant bonebeds are common in the geologic record, and the category includes, for example, all the known ceratopsian bonebeds at the Dinosaur Provincial Park in Alberta, Canada (Eberth and Getty 2005). The formation of monodominant bonebeds usually reflects some degree of social interactivity or behavior in the form of herding (Currie and Dodson 1984; Rogers 1990; Eberth and Getty 2005). All the currently known dinosaur localities in the Amur/Heilongjiang region are lambeosaurine monodominant bonebeds. If their origin is biological in nature (Eberth and Getty 2005), the lambeosaurine assemblages of this region may argue against Carrano et al.'s (1999) hypothesis that lambeosaurines were solitary animals, perhaps exhibiting male territoriality.

The age of the dinosaur bearing sediments in the Udurchukan and Yuliangze formations is based on palynological data. Both formations are placed within the *Wodehouseia spinata–Aquilapollenites subtilis* Palynozone (Markevich and Bugdaeva 2001), as defined by Markevich (1994). According to the same authors, this palynozone is early to "middle" Maastrichtian in age. This age estimate is based on comparisons with palynological assemblages in neighbouring basins but lacks any kind of calibration. During the Late Cretaceous, eastern Asia and western North America were part of the same microfloral province, the *Aquilapollenites* Province (Herngreen and Chlonova 1981; Herngreen et al. 1996). Therefore, a comparison of the palynozones of the Western Interior Basin with those of the Russian Far East might be instructive. Such a comparison shows great similarity between the Asian *Wodehouseia spinata–Aquilapollenites subtilis* Palynozone and the North American *Wodehouseia spinata* Palynozone (Nichols 2002). The age of the latter palynozone is late Maastrichtian, based on paleomagnetics, the Ir anomaly and associated phenomena (shocked quartz, spherules) at the K/T boundary (see e.g., Bohor et al. 1984, 1987; Gilmore et al. 1984; Jerzykiewicz and Sweet 1986; Nichols et al. 1986; Lerbekmo et al. 1987, 1999; Sweet et al. 1999). Based on this comparison a late Maastrichtian age for the Asian *Wodehouseia spinata –Aquilapollenites subtilis* Palynozone has been postulated (Godefroit et al. 2004b; Van Itterbeeck et al. 2005).

Nevertheless, this discussion on the exact age of the dinosaur-bearing sediments can only be solved by independent calibrations. Recent absolute age estimates based on fission tracks (Suzuki 2004) and radiometric dating (Li et al. 2004) in selected K/T boundary sections in the Amur/Heilongjiang Region indicate that the K/T boundary is situated lower than previously thought (Sun et al. 2004), and thus argue in favour of a late Maastrichtian age for the dinosaur-bearing sediments in this area.

Systematic palaeontology

One of the most persistent problems with bonebed material that consists of disarticulated and mixed bones belonging to many individual animals is that it is difficult to recognise the number of species that are represented in the locality. Although the fossils described herein were disarticulated, it is clear that they belong to two very different animals; the most abundant is a lambeosaurine, whereas some cranial and postcranial elements undoubtedly belong to a hadrosaurine. Because of the osteological homogeneity of the available material within these two categories, there is so far no data indicating that more than one hadrosaurine and one lambeosaurine would have coexisted at Wulaga at this time.

Dinosauria Owen, 1842

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Hadrosauridae Cope, 1869

Lambeosaurinae Parks, 1923

Genus *Sahaliyania* nov.

Type species: *Sahaliyania elunchunorum* sp. nov., from the Yuliangze Formation (Maastrichtian, Upper Cretaceous) of Wulaga, Heilongjiang province, China.

Derivation of the name: "Sahaliyan" means black in Manchu language and refers to Amur/Heilongjiang River (Sahaliyan Ula).

Diagnosis.—Lambeosaurine dinosaur characterised by the following autapomorphies: paroccipital processes long, very slender, with a slightly convex dorsal border and a slightly concave ventral border; lateral depressions on the dorsal surface of the frontal better developed than in other lambeosaurines, and not associated with a median doming of the bone; quadratojugal notch displaced ventrally; middle of the notch located well below the middle of the height of the quadrate; prepubic blade always more expanded dorsally than ventrally. Also differs from *Charonosaurus*, *Olorotitan*, *Parasaurolophus*, and *Corythosaurus*, by the important ventral deflection of the rostral part of its dentary, which forms an angle of about 30° with the long axis of caudal part of the bone; differs from *Amurosaurus* by the symmetrical alar process on its basisphenoid, its frontals wider than long and by its well-developed maxillary shelf; differs from *Charonosaurus* and *Parasaurolophus* by the short rostral platform of its frontal; differs from *Olorotitan* by the rounded rostral process of its jugal, by the straight ventral margin of its maxilla, and by the longer preacetabular process of its ilium (ratio ilium length/preacetabular length = 2.1); differs from *Tsintaosaurus* by the presence of a rostral platform on its frontal and by the median ramus of its squamosal lower than its paroccipital process.

Sahaliyania elunchunorum sp. nov.

Figs. 2–10.

Derivation of the name: The Elunchun nationality is one of the smallest Chinese minorities. These hunters lived for generations in the Wulaga area.

Holotype: GMH W453, a partial skull.

Type locality: Wulaga (Heilongjiang province, China). Coordinates of the site: N 48°23'40.9'' E 130°08'44.6''.

Type horizon: Yuliangze Formation (*Wodehouseia spinata–Aquilapollenites subtilis* Palynozone, Maastrichtian, Upper Cretaceous).

Material.—Braincase GMH W453; jugals GMH W200-A, W281, W400-5, 424, W unnumbered; maxillae GMH W199; quadrates GMH W31, W271, W342, W367, W394, W404, W476; dentaries GMH W33, W50-1, W105, W140, W153, W201, W227, W228, W290, W298, W324-A, W393, W418, W419-A, W424, W451, 457, W461, W465, W466, W501; scapulae GMH W1, W21, W31, W52, W148, W182, W202, W210, W214, W222, W272, W284, W286, W291, W309, W360, W373, W387, W392, W394, W400-1, W400-6,

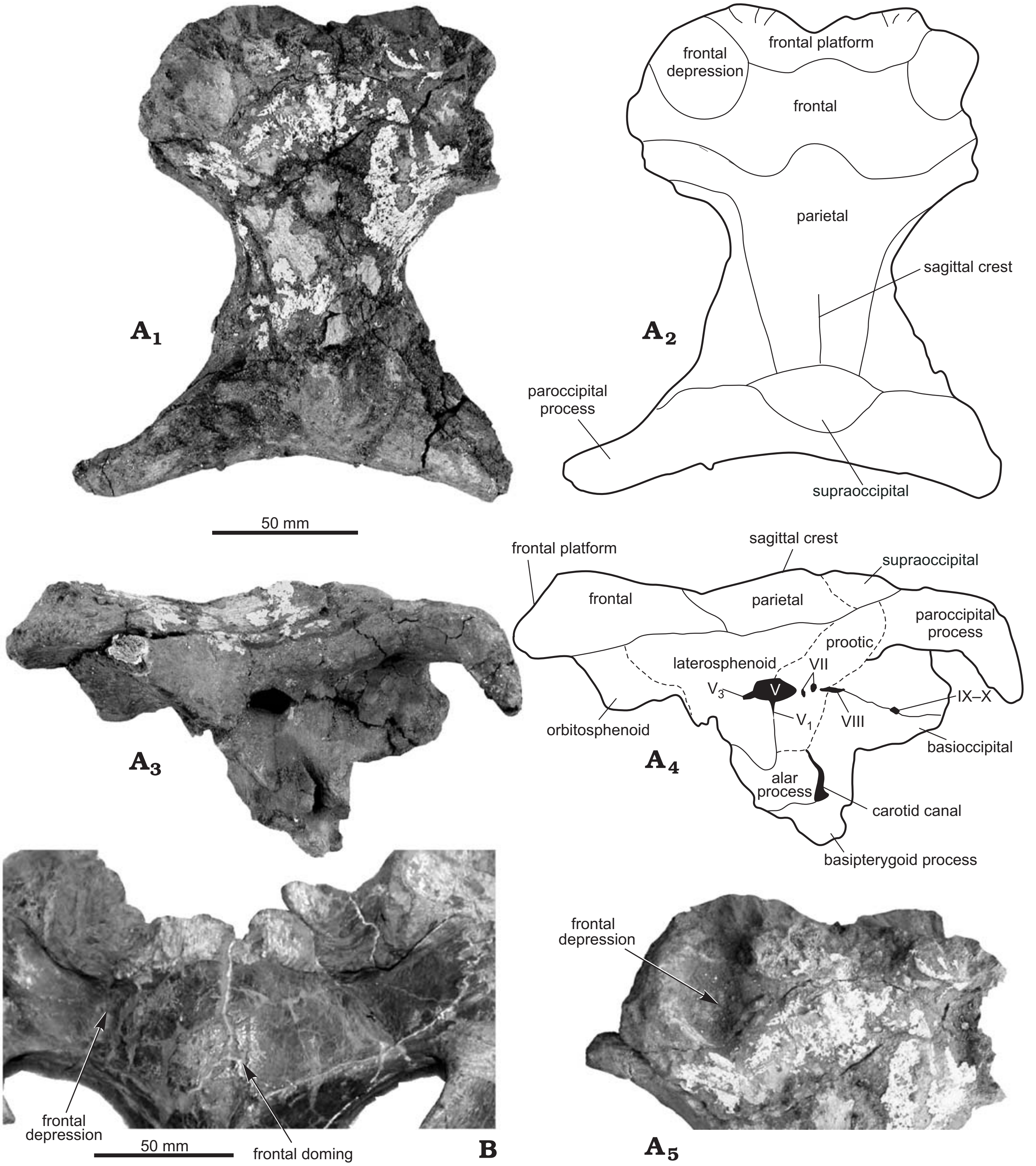

Fig. 2. **A**. The hadrosaurid dinosaur *Sahaliyania elunchunorum* gen. et sp. nov., holotype GMH W453 from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **B**. *Hypacrosaurus altispinus* Brown, 1913, specimen AMNH 5248 from the Upper Cretaceous Horseshoe Canyon Formation of Alberta, Canada. Braincases in dorsal (A_1, A_2) and left lateral (A_3, A_4) views; photographs (A_1, A_3) and explanatory drawings (A_2, A_4), with close-ups of the frontal region in *S. elunchunorum* (A_5) and *H. altispinus* (B). Dotted lines indicate hypothetical sutures.

W422, W463, W473; sternals GMH W165, W246, W406-A; humeri GMH W15, W42, W58, W59, W110, W116, W154, W158, W168, W 192-A, W 192-B, W 201, W232, W240, W250, W271, W303, W317, W344, W367, W392, W402, W410, W411, W413-A; ilia GMH WJ1, WJ4, W23, W45, W51, W103, W173, W228, W243-A, W273, W301, W311,

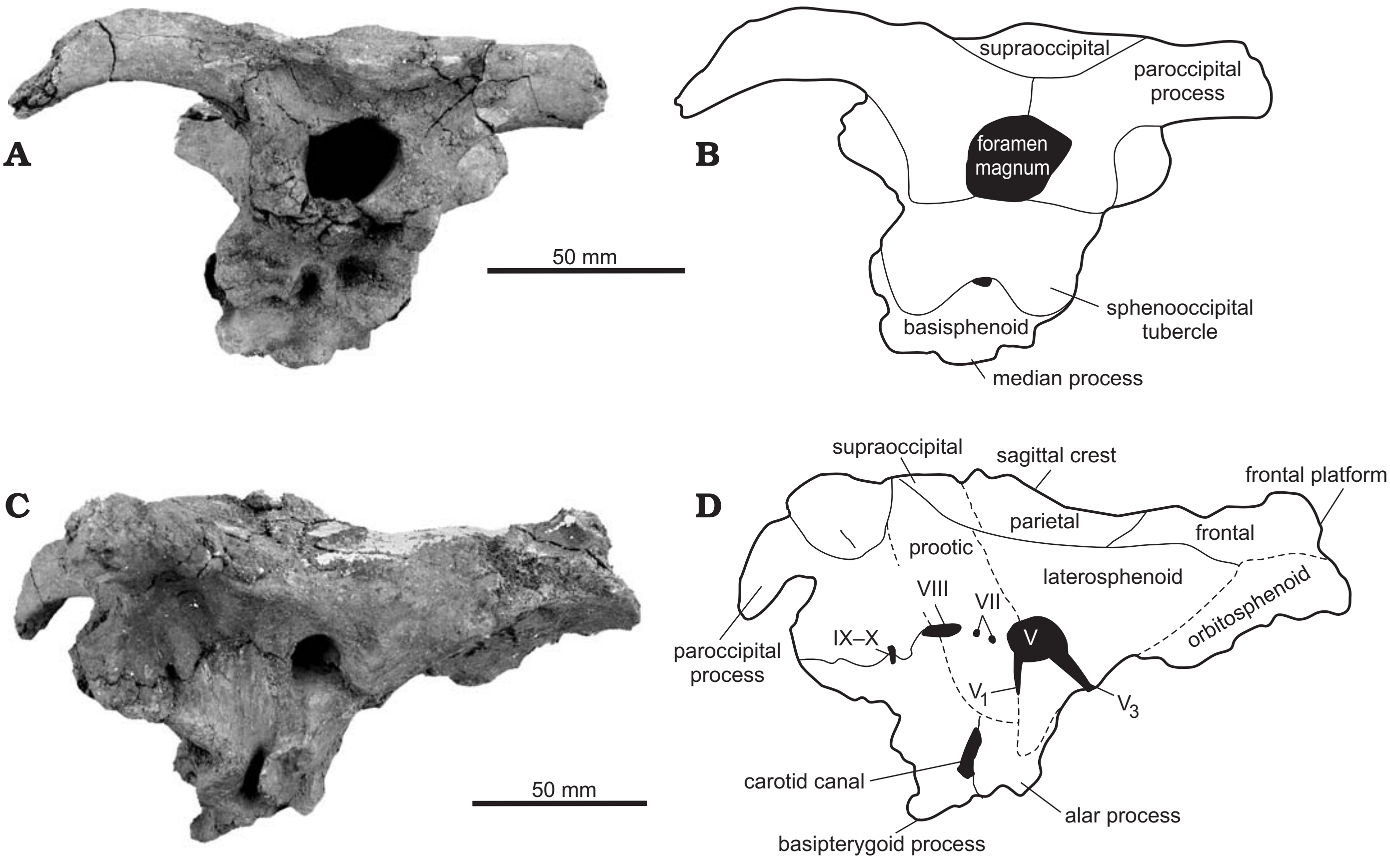

Fig. 3. The hadrosaurid dinosaur *Sahaliyania elunchunorum* gen. et sp. nov. holotype GMH W453 from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. Braincase in caudal (**A**, **B**) and right lateral (**C**, **D**) views. Dotted lines indicate hypothetical sutures. Photographs (A, C) and explanatory drawings (B, D).

W359, W370, W421; ischia GMH W10, W13, W50-6, W51, W136-A, W146, W171, W177, W179, W180, W197, W233-B, W255, W270, W291, W310, W375, W400-13, W404, W415-A, W415-B, W471-D; pubes GMH W10, W13, W51, W136, W146, W171, W177, W179, W180, W197, W233, W270, W291, W 310, W375, W379, W 400-13, W404, W415-A, W 415-B, W471.

Diagnosis.—As for the genus, by monotypy.

Description

Exoccipital-opisthotic complex (Figs. 2, 3).—The basal part of the exoccipital condyloids is eroded, so the morphology of the foramina for cranial nerves IX–XII can not be adequately described. Around the foramen magnum, the dorsal surface of the exoccipital-opisthotic is slightly depressed. The left paroccipital process is complete dorsomedially: it is particularly long, but very slender. Its dorsal border is slightly convex, whereas its ventral border is slightly concave. Although the paroccipital processes are variable in shape, those of *Sahaliyania* are clearly different from those of other known lambeosaurines. In *Charonosaurus*, the paroccipital processes are much shorter and more robust (Godefroit et al. 2001: fig. 5). In *Amurosaurus* (Godefroit et al. 2004b: fig. 7), *Jaxartosaurus* (PIN 1/5009, personal observation), *Tsintaosaurus* (Young 1958: fig. 1), *Corythosaurus* (AMNH 5240, personal observation), *Hypacrosaurus* (ROM 702, personal observation), *Lambeosaurus* (ROM 1218, personal observation), and *Parasaurolophus* (Sullivan and Williamson 1999: fig. 16), the paroccipital processes are also more robust than in *Sahaliyania* and have a more pendant aspect: their mediodorsal border slopes dorsally, whereas their laterodorsal border is strongly inclined ventrally.

Lateral wall of the braincase (Figs. 2, 3).—The different bones that form the lateral wall of the braincase are completely fused together, so their limits cannot always be adequately described. From the rostrolateral side of the paroccipital process, a broad and rounded crista otosphenoidalis runs along the lateral side of the lateral wall of the braincase. Below this crest, the foramen for CN VIII, is small and separated from the postotic foramina by a well-developed and rounded ridge that extends from the ventral border of the paroccipital process to the rostroventral corner of the exoccipital condyloid. However, the trigeminal foramen (for CN V) is very large, as in all hadrosaurids. From this foramen, both the rostrally-directed horizontal sulcus for the ramus ophthalmicus (V_1) and the ventrally-directed vertical sulcus for the ramus mandibularis (V_3) and ramus maxillaris (V_2) of the trigeminal nerve are less clearly marked than in

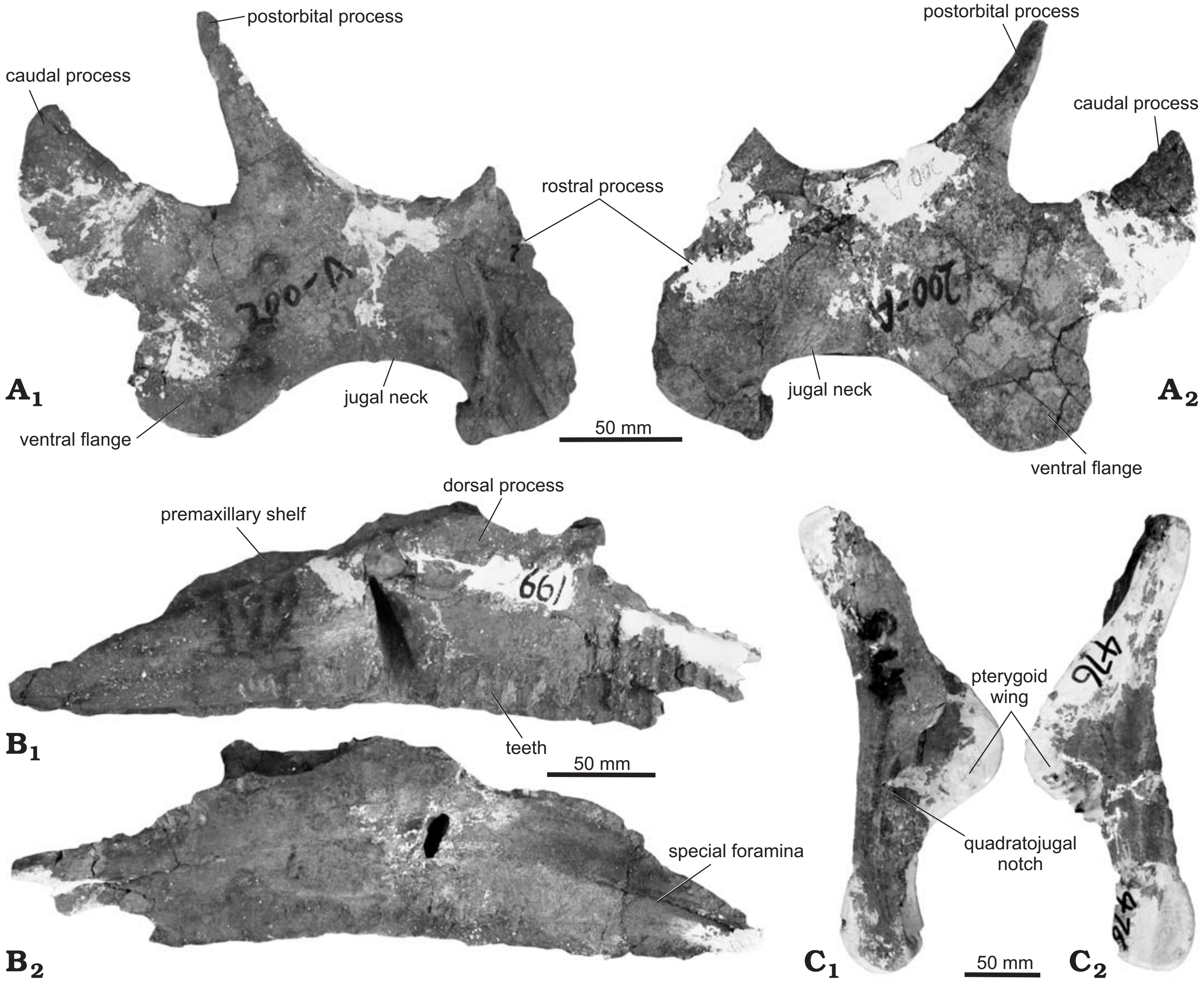

Fig. 4. The hadrosaurid dinosaur *Sahaliyania elunchunorum* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W200-A, left jugal in medial (A_1) and lateral (A_2) views. **B**. GMH W199, left maxilla in lateral (B_1) and medial (B_2) views. **C**. GMH W476, right quadrate in lateral (C_1) and medial (C_2) views.

Amurosaurus. Between the trigeminal foramen and the foramen for CN VIII, the lateral wall of the braincase is pierced by two foramina: the caudodorsal one transmitted the ramus hyomandibularis and the cranioventral one, the ramus palatinus of the facial nerve (CN VII). A small sulcus runs from the latter foramen ventrally along the lateral side of the prootic to the vicinity of the carotid canal; this channel housed the ramus palatinus of the facial nerve. It looks wider, but shallower than in *Amurosaurus*.

Basisphenoid (Figs. 2, 3).—The basisphenoid is eroded in GMH W453, so only a few interesting characters can be observed. In caudal view, a pair of concave processes, separated by a very deep incision, project laterally from the body of the basisphenoid to form the rostral part of the spheno-occipital tubercles. At the junction between the broken basipterygoid processes, a small median process projects caudoventrally. This process is much better developed in *Amurosaurus*. On the other hand, it is absent in *Charonosaurus*. In lateral view, the alar process of the basisphenoid is very developed and nearly symmetrical. This condition is also observed in *Charonosaurus*. In *Amurosaurus*, on the other hand, the alar process is asymmetrical in lateral view. The caudodorsal ramus of the alar process conceals the carotid canal, which carried the internal carotid artery from the lateral surface of the basisphenoid. The internal carotid artery penetrates the basisphenoid through a large canal, visible on the ventral side of GMH W473. The caudal aperture is concealed laterally by the rostroventral ramus of the alar process and the canal opens into the caudoventral part of the hypophyseal cavity.

Supraoccipital (Figs. 2, 3).—The supraoccipital is a pyramidal bone that extends rostrally above the occipital region, between the exoccipital-opisthotic and the parietal. Its external surface is unfortunately too eroded to be adequately described.

Parietal (Fig. 2A).—As usual in lambeosaurines, the parietal of *Sahaliyania* is proportionally short and wide. With a "length/minimal width" ratio = 1.5, it is proportionally much wider than in *Amurosaurus* (1.9 in AEHM 1/232). The rostral portion of its dorsal surface is very slightly convex. Caudally, it forms a low sagittal crest. Even if it is eroded, this crest appears much less developed than in *Amurosaurus*: in this genus, the sagittal crest forms caudally a high triangular process that overhangs the rostrodorsal part of the supraoccipital. The sagittal crest is similarly high in *Jaxartosaurus*, *Tsintaosaurus*, *Corythosaurus*, *Hypacrosaurus*, *Lambeosaurus*, and *Parasaurolophus*. In *Charonosaurus*, on the other hand, the sagittal crest is not developed at all and the dorsal surface of the parietal is, therefore, regularly convex (Godefroit et al. 2001). However, given the eroded state of the dorsal aspect of GMH W479, it seems difficult to draw meaningful conclusions as to the autapomorphic nature of this feature.

Frontal (Fig. 2A).—The complete fusion of the frontals, as observed in this specimen, is unusual in lambeosaurines. It suggests that GMH W453 belongs to an old adult specimen. The dorsal surface of the caudal part of the frontal is perfectly flat in GMH W453. In numerous lambeosaurine specimens, on the other hand, the dorsal surface of the frontal forms a caudomedian doming, as observed in *Hypacrosaurus* (AMNH 5248, Fig. 2B), "*Procheneosaurus convincens*" (PIN 2230), "*Cheneosaurus tolmanensis*" (Lambe 1917), "*Tetragonosaurus erectofrons*" (Parks 1931; Evans et al. 2005), *Jaxartosaurus aralensis* (PIN 5009), and *Amurosaurus riabinini* (AEHM 1/232). Study of the *Amurosaurus* collection suggests that the frontal doming is especially developed in juvenile specimens (Godefroit et al. 2004b). Many large lambeosaurine specimens, like ROM 1940, also completely lack the median dome. Therefore, the absence of a median dome also confirms that GMH W453 does belong to an adult specimen. With a "caudal length/maximal width" ratio (see Godefroit et al. 2004b for a definition of this ratio) estimated at 0.6, the frontal of GMH W453 is much wider than in *Amurosaurus* (1.02 in AEHM 1/232; Godefroit et al. 2004b). As usual in lambeosaurines, the rostral part of the dorsal surface of the frontal is highly modified to form the base of the hollow crest. It forms a broad and strongly grooved platform that slopes forwardly and provides strong attachment of the nasals. In *Sahaliyania*, the rostral platform appears relatively short. Although GMH W453 does belong to an adult specimen, the platform does not extend far caudally. In comparison, it is much better developed in *Charonosaurus* and *Parasaurolophus*: in these genera, the rostral platform extends caudally above the rostral part of the parietal and of the supratemporal fenestrae (Sullivan and Williamson 1999; Godefroit et al. 2001). Although it is short, the frontal platform of *Sahaliyania* is relatively wide, as also observed in adult specimens of *Corythosaurus* (ROM 1940) and *Hypacrosaurus* (Gilmore 1937: fig. 32): in these genera, the rostral platform is either wider than the caudal part of the frontal, or both parts have approximately the same width. However, it is probably an ontogenetic character: in smaller *Corythosaurus* and *Hypacrosaurus* specimens (e.g., AMNH 5248, AMNH 5433), in which the frontals are not fused together and the median doming is well developed, the frontal platform is much narrower than the caudal part of the frontal. In *Amurosaurus*, on the other hand, the rostral platform is always much narrower than the caudal part of the frontal, even in large adult specimens. In this genus, the prefrontal forms the greatest part of the platform that supports the base of the hollow crest (Godefroit et al. 2004b). In *Sahaliyania*, the lateral margin of the frontal forms a thick and interdigitate contact area, rostrally for the prefrontal and caudally for the postorbital. The frontal therefore did not participate in the dorsal margin of the orbit. Between the rostral platform and the lateral contact area for the prefrontal, the dorsal surface of the frontal forms a pair of well-developed cup-shaped depressed areas. Depressions on the dorsal surface of the frontal near the prefrontal and postorbital joints have also been observed in other lambeosaurine taxa, including *Amurosaurus* (AEHM 1/232), *Hypacrosaurus* (AMNH 5248), and *Corythosaurus* (AMNH 5433). In these lambeosaurines, the frontal depressions are, in any case, much smaller than in *Sahaliyania*, and are found associated with the median doming of the frontal, characteristic for juvenile specimens. Frontal depressions have also been described in the hadrosaurine *Brachylophosaurus* (Horner 1988; Prieto-Marquez 2005), but they are less developed than in *Sahaliyania*.

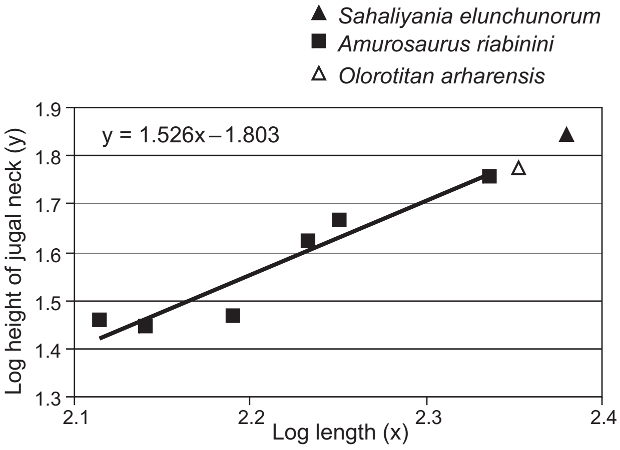

Fig. 5. Relative growth of the height of the jugal neck (y) and of the jugal length (x) in lambeosaurine dinosaurs from the Amur/Heilongjiang region.

Jugal (Fig. 4A).—The jugal of *Sahaliyania* is proportionally short and robust. In lateral view, its rostral process is dorsoventrally expanded. It forms a high lacrimal process and a prominent, hook-like ventral region. The rostral margin of the jugal is convex: it is not perfectly straight, as observed in *Olorotitan*. The best preserved jugal from the Wulaga collection, GMH W200-A, is particularly robust when compared with other lambeosaurine jugals discovered in the Amur Re-

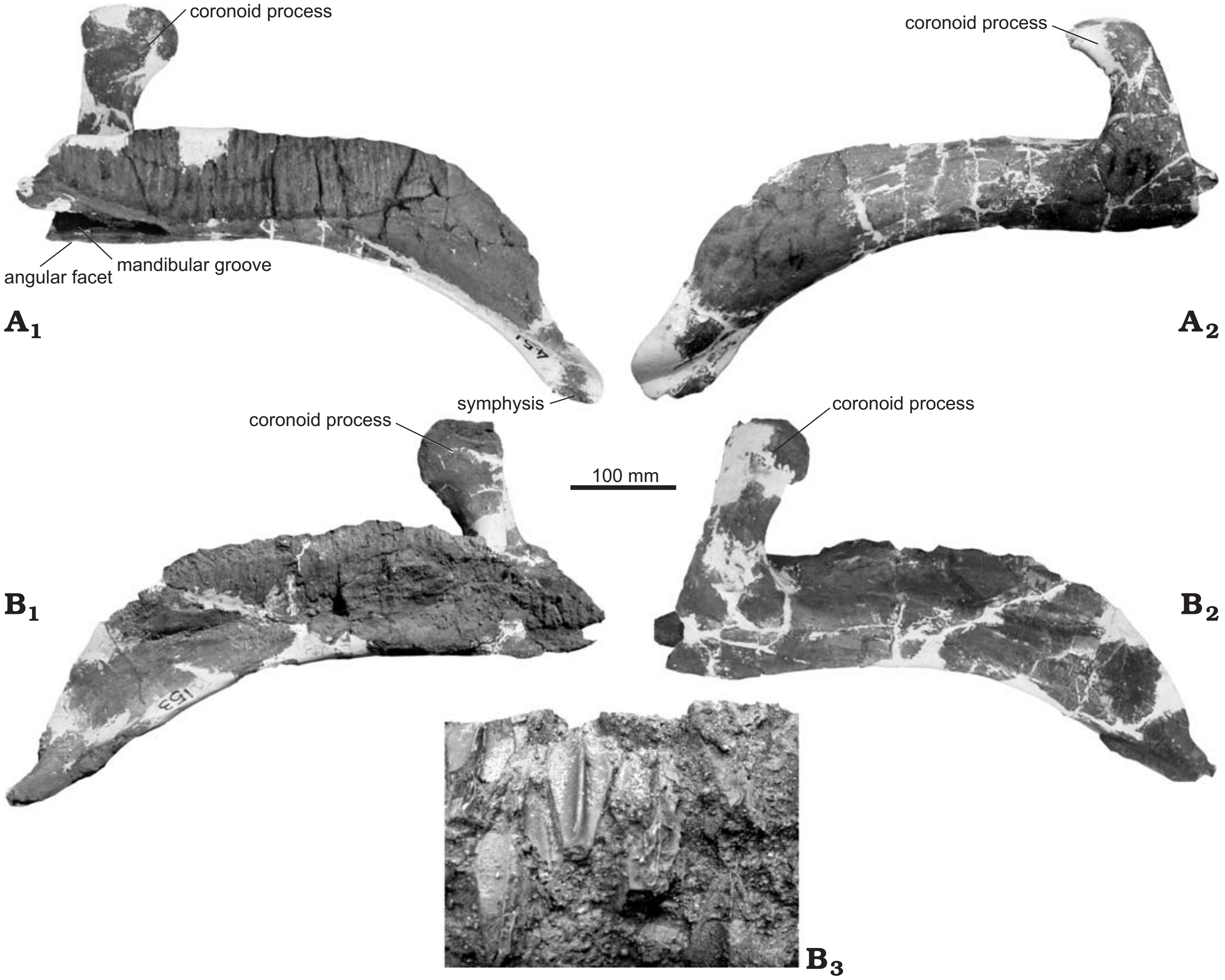

Fig. 6. The hadrosaurid dinosaur *Sahaliyania elunchunorum* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W451, left dentary in medial (A_1) and lateral (A_2) views. **B**. GMH W153, right dentary in medial (B_1) and lateral (B_2) views, and detail of dentary teeth (B_3).

gion (Fig. 4A). However, the relative robustness of the jugal probably reflects the allometric growth of this bone (Fig. 5). Pearson's correlation coefficient between the total length of the jugal (in $\log_{10}$) and the height of the jugal neck (in $\log_{10}$), estimated from the *Amurosaurus* sample, is very high: r = 0.95. The allometry coefficient has been estimated using Teissier's (1948) least squares formula. Indeed, both measurements are herein regarded as interdependent. Positive allometry exists between the length of the jugal and the height of the jugal neck in *Amurosaurus* (k = 1.625). This means that the jugal is proportionally more robust in larger than in smaller specimens. Moreover, two large jugals, respectively belonging to *Olorotitan* (AEHM 2/845) and *Sahaliyania* (GMH W200-A) are located exactly in the extension of the regression line. It indicates that GMH W200-A appears very robust, when compared with *Amurosaurus* specimens, only because it is very large. The apparent robustness of the jugal in *Sahaliyania* specimens at hand is therefore not a diagnostic character, but a consequence of the positive allometry of this character in lambeosaurines. In *Sahaliyania*, the postorbital process of the jugal is robust. Its rostral side is concave for reception of the ventral process of the postorbital. The caudal process is a broad plate that raises caudodorsally. Together with the postorbital process, it circumscribes the ventral margin of the infratemporal fenestra. This fenestra is somewhat narrower in *Sahaliyania* than in *Amurosaurus* or *Charonosaurus*. The ventral border of the caudal process is much expanded and salient, forming a ventral flange that resembles that observed in hadrosaurines.

Maxilla (Fig. 4B).—In lateral view, the maxilla of *Sahaliyania* is asymmetrical, with the dorsal process lying well behind the middle of the bone, as usually observed in lambeosaurines. The rostral part of the maxilla is elongated and slender; it regularly tapers rostrally. It is medially expanded to

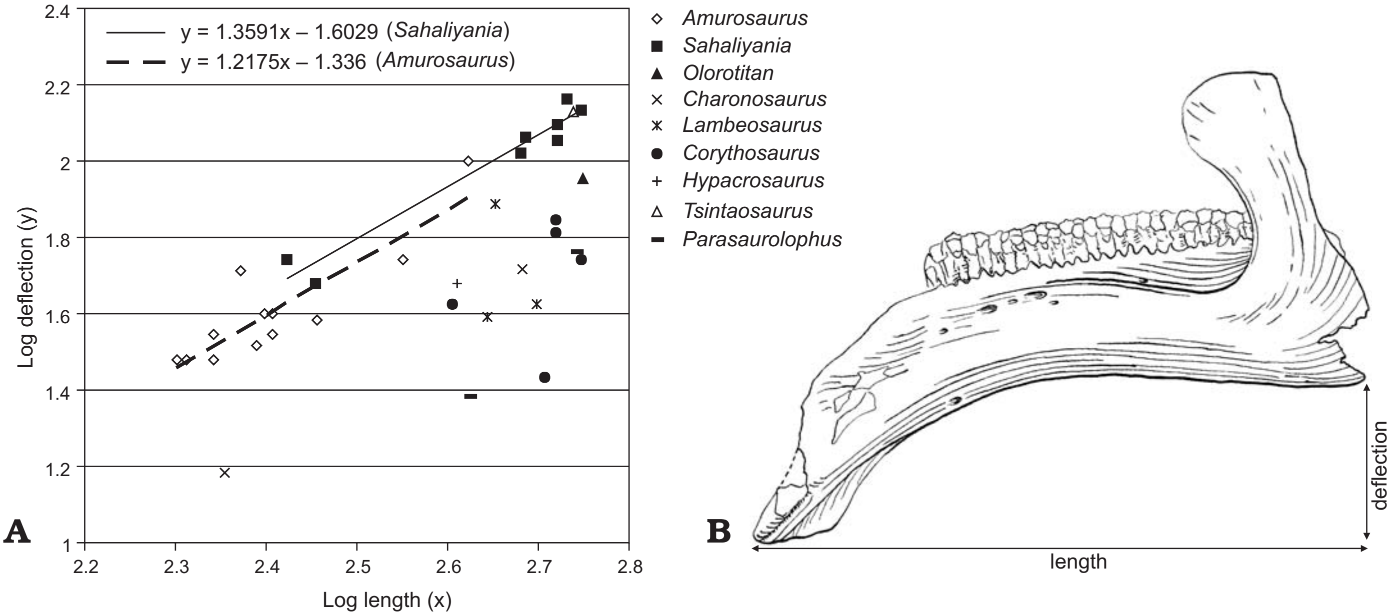

Fig. 7. **A**. Relative growth of the ventral deflection of the rostral part (y) and of the length (x) of the dentary in lambeosaurine dinosaurs. **B**. Explanation of the measurements.

form a wide premaxillary shelf, characteristic for lambeosaurines and better developed than in *Amurosaurus*. The dorsal process and the caudal part of the maxilla are eroded, so only a few interesting characters can be observed on this part of the maxilla. Caudal to the maxillary shelf, a large ovoid neurovascular foramen penetrates the dorsal process to communicate with the excavated caudomedian area of this process. The caudal portion of the maxilla appears short and gracile. The medial surface of the maxilla is perfectly flat and pierced by a series of special foramina interconnected by a gently curving horizontal groove at the middle of the bone.

Several maxillary teeth are preserved on this specimen. However, the dental battery is too incomplete to estimate the minimal number of tooth rows. As usual in hadrosaurids, the maxillary teeth are miniaturised, very narrow, diamond-shaped, perfectly straight and symmetrical. The enamel forms a strong and perfectly straight median ridge on the lateral side of the crown. Their borders are rather coarsely denticulate.

Quadrate (Fig. 4C).—The general morphology of the quadrate of *Sahaliyania* is typical for lambeosaurines. It is proportionally low and robust, and distinctly curved caudally. Although such differences are difficult to quantify, typical hadrosaurine quadrates are usually proportionally more slender and straighter. The proximal head is subtriangular in cross-section and much flattened mediolaterally. The pterygoid wing is robust and rostromedially oriented. A prominent vertical ridge along the caudomedial side of the quadrate shaft marks the contact with the quadrate process of the pterygoid. The jugal wing is regularly rounded and slightly curved inwards. Beneath the jugal wing, the quadratojugal notch, located along the dorsoventral axis of the quadrate, is high and deep. Usually in lambeosaurines, the middle of the quadratojugal notch more or less coincides with the middle of the height of the quadrate. This situation can be observed in *Corythosaurus* (AMNH 5338), *Hypacrosaurus* (MOR 549), *Lambeosaurus* (TMP 66.04.01), *Amurosaurus* (AEHM 1/42), and *Tsintaosaurus* (IVPP K68). In *Sahaliyania*, on the other hand, the quadratojugal notch is distinctly displaced ventrally and the middle of the notch is always set well below the middle of the height of the quadrate. An elongated facet runs along nearly the whole height of the quadratojugal notch, indicating that it was completely covered by the quadratojugal and that the paraquadratic foramen was closed, as usual in hadrosaurids. The distal end of the quadrate forms a large hemispherical lateral condyle that articulated with the surangular component of the mandibular glenoid. A smaller medial condyle, which fitted into the articular component of the mandibular glenoid, is set more dorsally at the base of the pterygoid wing.

Dentary (Fig. 6).—In lateral view, the most striking character that can be observed in the dentary of *Sahaliyania* is the important ventral deflection of its rostral part, which forms an angle of about 30° with the long axis of caudal part of the bone. In large adult specimens, the deflection of the ventral margin of the dentary usually begins somewhat caudal to the middle of the bone. On the other hand, the dorsal margin is deflected in front of the dental battery. Although it is variable, a ventral deflection of the rostral part of the dentary is a usual character in lambeosaurines. In *Sahaliyania* ($r = 0.977$) and *Amurosaurus* ($r = 0.881$), the length of the dentary (in $\log_{10}$) and the height of the ventral deflection (in $\log_{10}$) are strongly correlated (Fig. 7). The allometry coefficient has been estimated in both genera from the slope of the regression line, because the length of the dentary can be regarded, in this case, as an independent variable (Teissier 1948): $k = 1.36$ in *Sahaliyania* and $k = 1.22$ in *Amurosaurus*. Isometry

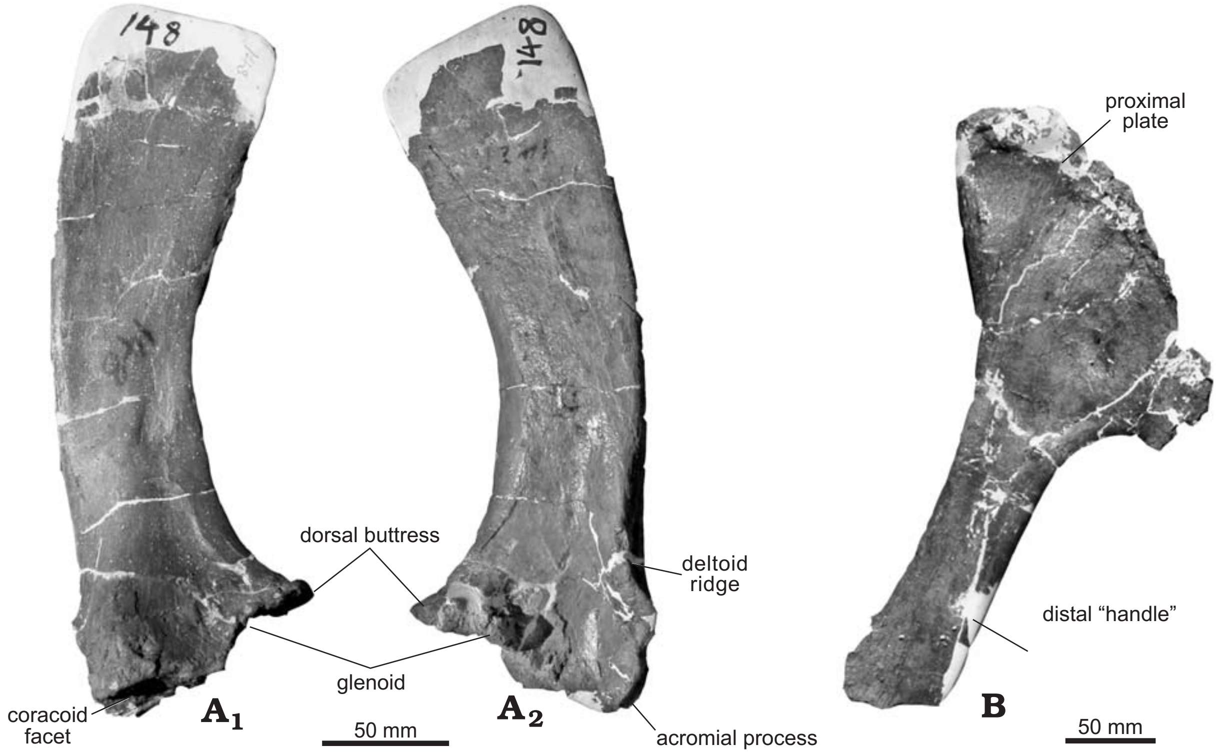

Fig. 8. The hadrosaurid dinosaur *Sahaliyania elunchunorum* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W148, right scapula in medial (A_1) and lateral (A_2) views. **B**. GMH W165, right sternal in ventral view.

(k = 1) can be rejected at p = 0.05. This means that the ventral deflection of the dentary is proportionally more important in larger than in smaller specimens. If the allometry coefficient is higher in *Sahaliyania* than in *Amurosaurus*, this difference is not significant at p = 0.05 (Chassé and Pavé 1975: 287). The allometry coefficient has also been calculated using Teissier's (1948) least squares method (both measurements are regarded, in this case, as interdependent). With this method, the coefficients are much higher: k = 1.57 in *Sahaliyania* and k = 1.41 in *Amurosaurus*. The rostral part of the dentary is more strongly deflected in *Sahaliyania*, *Amurosaurus*, and *Tsintaosaurus* than in other lambeosaurines from Asian and North American lambeosaurines (Fig. 7). However, this observation needs to be confirmed by the statistical study of larger samples. As usual in hadrosaurids, the dental battery of *Sahaliyania* is long and, in larger specimens, the dental battery fits into around 42–44 narrow parallel-sided alveolar grooves, visible in medial view. The edentulous portion is proportionally very short. The rostral articular surface for the predentary is typically scoop-shaped and slightly inclined towards the sagittal axis of the mandible. In dorsal view, the dentary appears less curved externally than that of *Charonosaurus*, for example. The lateral side of the dentary is very convex. It is irregularly pierced by several foramina for vessels and nerves. The coronoid process is high and robust, with a flattened inner side. As is usual in hadrosaurids, it is rostrally inclined and slightly curved inwards; its lateral side bears an extended triangular surface along its dorsal part, marking the insertion of a powerful M. pseudotemporalis. In caudal view, the dentary is deeply excavated by the adductor fossa, which extends rostrally as a deep mandibular groove. Under this groove, the medial side of the dentary bears a very long angular facet. The caudoventral end of the coronoid process bears a large triangular facet for the splenial. A very thin bony plate conceals the dental battery. Its base is pierced by a series of special foramina arranged into a horizontal line. Each foramen strictly corresponds to one tooth row.

The dentary teeth are also diamond-shaped, like the maxillary ones. However, they look proportionally wider than the maxillary teeth, with a "height/width" ratio of about 3 for the teeth located in the middle of the dental battery. They appear proportionally wider than the dentary teeth of *Charonosaurus*. If the median carina is perfectly straight on the caudal and central dentary teeth, it is slightly sinuous on the rostral ones. This character is often observed in lambeosaurines (Godefroit et al. 2001).

Scapula (Fig. 8A).—The Wulaga material includes 25 scapulae of different sizes that closely resemble those of *Olorotitan*. For that reason, they are tentatively referred to *Sahaliyania*. One single specimen from Wulaga is distinctly different from the others, more closely resembling the condition observed in hadrosaurines; this specimen is therefore tentatively referred to the hadrosaurine *Wulagasaurus* gen. nov. (see below). All scapulae are unfortunately very incomplete and roughly restored with plaster. In *Sahaliyania*, the ventral head of the scapula appears more robust and craniocaudally expanded than in *Amurosaurus*. The coracoid suture is large and cup-shaped. It is separated from the acromial process by a concave emargination of the cranioventral border of the scapula. The acromial process extends dorsally into the form of a short rounded deltoid ridge. Both the acromial process and the deltoid ridge appear distinctly less prominent than in other lambeosaurines from the Amur/Heilongjiang region, but this may be an artefact of preservation. The deltoid fossa is wider than in *Amurosaurus*. Caudally to the coracoid facet, a long crescentic depression represents the craniodorsal part of the glenoid. A prominent dorsal buttress that slightly faces laterally supports the scapular portion of the glenoid. Because of the great expansion of the ventral head, the scapular neck appears well contracted. The scapular blade is very thin and long; it is proportionally wider craniodorsally than in *Amurosaurus*. Its cranial and caudal borders are sub-parallel and gently curved caudally. The scapular blade is also smoothly curved inwardly. Its lateral side is slightly convex dorsoventrally, whereas its medial side is slightly concave.

Sternal (Fig. 8B).—As in other hadrosaurids, the sternal of *Sahaliyania* is typically hatchet-shaped. As in lambeosaurines, its proximal plate is enlarged both in length and in width. It is thinner laterally than medially. The proximal plate is distinctly longer than the distal "handle". Although incompletely preserved, the thin lateral border of the proximal plate is distinctly convex. The distal "handle" of the sternal is relatively short, but massive and slightly curved dorsally; its distal end is slightly enlarged. The dorsal side of the "handle" bears many longitudinal striations. Both the proximal and distal borders of the sternal are very roughened, indicating the presence of cartilaginous caps. The ventral side of the sternal is slightly convex mediolaterally, whereas its dorsal side is slightly concave.

Humerus (Fig. 9A).—Twenty-five humeri from the Wulaga collection are typically lambeosaurine in shape, with a long and wide deltopectoral crest that is slightly turned medially, especially in larger specimens. In lambeosaurines, the width of the deltopectoral crest is significantly correlated ($p > 0.05$) to the length of the humerus (Fig. 9B): $r = 0.98$ in *Sahaliyania* and 0.82 in *Amurosaurus*. But the width of the deltopectoral crest apparently develops isometrically when compared to the length of the humerus ($k = 0.96$ in *Sahaliyania* and 0.89 in *Amurosaurus*). The globular proximal articular head forms a rounded buttress on the caudal side of the humerus. The inner tuberosity is less developed on the proximal end of the humerus than the outer tuberosity. On the caudal side of the humerus, a smooth rounded crest descends from the proximal articular head, but it is never as developed as in *Charonosaurus* (see Godefroit et al. 2000); on the cranial side of the humerus, the bicipital gutter is also less well marked than in *Charonosaurus*. Lateral to the humeral head, a large depressed area marks the insertion of a strong M. triceps humeralis posticus, as usually observed in lambeosaurines (Godefroit et al. 2001, 2004b). Medial to the humeral head, a less markedly depressed area indicates the insertion of the M. scapulo-humeralis. The distal portion of the humerus is slightly twisted laterally. The ulnar condyle is slightly more developed than the radial condyle.

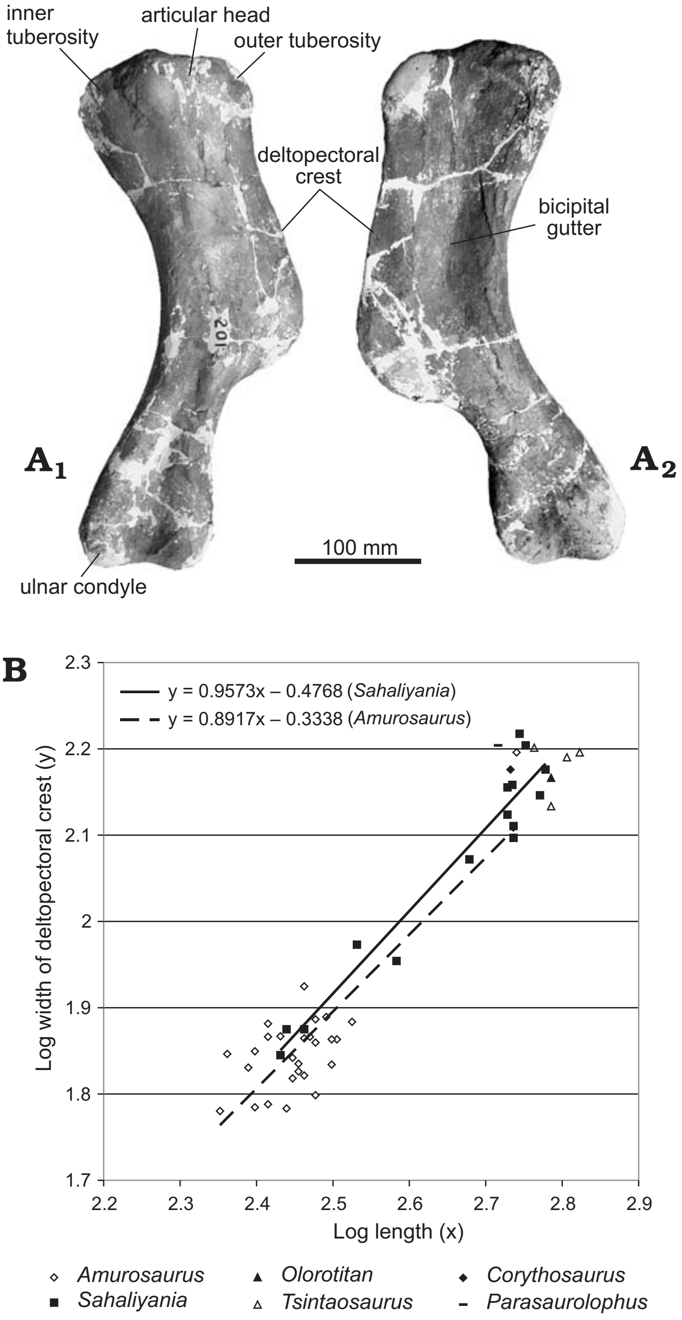

Fig. 9. The hadrosaurid dinosaur *Sahaliyania elunchunorum* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W201, right humerus in caudal (A_1) and cranial (A_2) views. **B**. Relative growth of the width of the deltopectoral crest (y) and of the length of the humerus (x) in lambeosaurine dinosaurs.

Ilium (Fig. 10A).—Although they are crushed medio-laterally, the ilia in this sample closely resemble those of lambeosaurines attributed to the *Corythosaurus* lineage by Brett-Surman and Wagner (2007). The preacetabular process

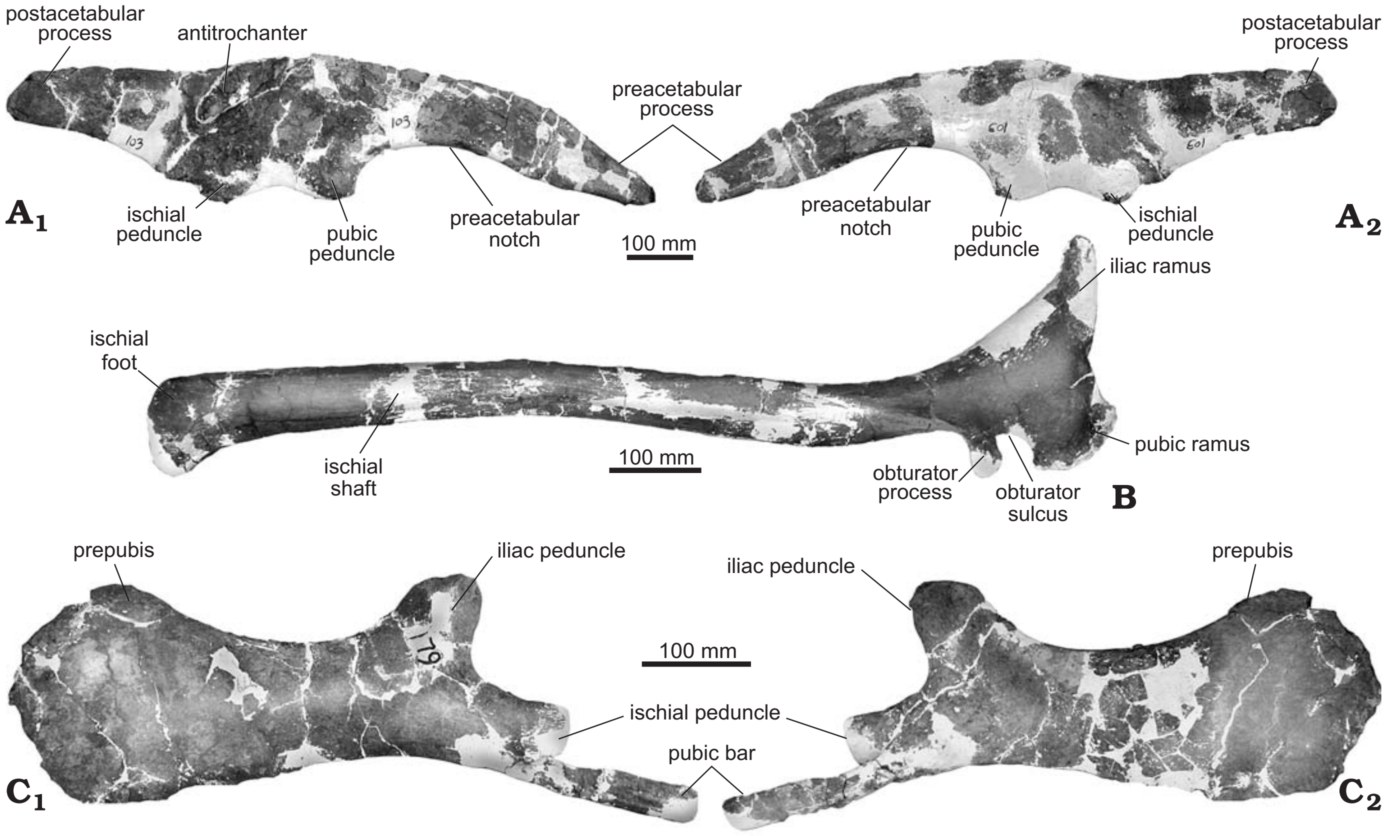

Fig. 10. The hadrosaurid dinosaur *Sahaliyania elunchunorum* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W103, right ilium in lateral (A_1) and medial (A_2) views. **B**. GMH W400-2, right ischium in lateral view. **C**. GMH W179, left pubis in lateral (C_1) and medial (C_2) views.

forms a long and tapering projection from the craniodorsal edge of the iliac blade. It is moderately deflected ventrally and very elongated, closely resembling the condition observed in *Charonosaurus*: in both taxa, the ratio "ilium length/preacetabular length" is around 2.1. The lateral side of the preacetabular process is perfectly flat. Its dorsal edge is very thickened and rounded, whereas its ventral edge is thinner. The caudal half of its medial side bears, at about the dorsal third of its height, a carina. The main blade of the ilium is very high. At the level of the ischial peduncle, its dorsolateral border is folded laterally to form a prominent and roughened antitrochanter. Because it is always crushed in the Wulaga material, the relative development of the antitrochanter, which is an important character in lambeosaurines, cannot be adequately compared with other hadrosaurids discovered in Amur/Heilongjiang region. A strong ridge medially thickens the dorsal part of the main blade of the ilium, in continuity with that on the medial side of the preacetabular process. It fuses caudally with the dorsal border of the ilium, at the level of the ischial peduncle. The preacetabular notch is well developed and rather open, because of the slight ventral deflection of the preacetabular process. The iliac portion of the acetabulum is shallow. The ischial peduncle is craniocaudally elongated. Its articular surface faces caudoventrally and is formed by two sub-rectangular protrusions separated by a well-marked depression. The postacetabular notch is only slightly marked. The postacetabular process is long, high, and sub-rectangular in shape, also resembling the condition described in *Charonosaurus*.

Ischium (Fig. 10B).—The ischia of *Sahaliyania* are typical for lambeosaurines: the ischial shaft is long and very robust, gently sigmoidal in lateral view, and it terminates into a prominent foot-like expansion. Between its dorsal and ventral margins, the medial side of the ischial shaft forms a deep sulcus. The medial side of the ischial foot bears many elongated striations, indicating strong ligamental attachment between paired ischia. The cranial region of the ischium is expanded and it tilts a few degrees laterally. The iliac peduncle is subrectangular and projects craniodorsally; its dorsal articular surface is slightly expanded both mediolaterally and dorsoventrally and is sub-ellipsoidal in cross section. The pubic peduncle is more slender and less differentiated than the iliac peduncle. It is very elongated craniocaudally and very compressed mediolaterally. The articular facet for the pubis is sub-rectangular in cross section. The obturator process is well developed, projecting ventrally lower than the pubic peduncle. Its ventral border is expanded to closely contact the pubic bar. It is prolonged caudally as a strong oblique carina along the medial side of the ischial shaft. The obturator process and the pubic peduncle limit an ovoid and ventrally open obturator gutter.

Table 1. Differences between the four lambeosaurine taxa discovered in Maastrichtian formations of the Amur/Heilongjiang Region.

Characters	*Sahaliyania elunchunorum*	*Amurosaurus riabinini*	*Charonosaurus jiayinensis*	*Olorotitan arharensis*
1. Horizontal groove on exoccipital-opisthotic pilar	–	present	absent	–
2. Median basipterygoid process	small	well developed	absent	–
3. Alar process on basisphenoid	very developed, symmetrical	asymmetrical	very developed, symmetrical	–
4. Paroccipital processes	long, slender, dorsal border slightly convex	long and pending	short	long and pending
5. Sagittal crest	poorly developed	very high caudally	absent	high caudally
6. Participation of prefrontal in the floor of supracranial crest	? small part	about 50%	no	–
7. Proportions of frontals	wider than long	longer than wide	wider than long	–
8. Rostral platform of frontals	short	short	extends above supratemporal fenestra	short
9. Frontal depressions	cup-shaped, even in adults	shallow, only in juveniles	absent in adults	–
10. Caudal ramus of postorbital	–	slender and convex upwards	high and straight	–
11. Dorsal surface of postorbital	–	flat	dorsal promontorium	flat
12. Medial processes of squamosals	–	separated by parietals	meeting in midline of occiput	separated by parietals
13. Rostral process of jugal	rounded	rounded	rounded	straight
14. Height of postorbital process of jugal	–	jugal much longer than high	jugal much longer than high	L/H ratio = 0.9
15. Ventral margin of maxilla	straight	straight	straight	down-turned
16. Lateral profile of maxilla	asymmetrical	asymmetrical	asymmetrical	extremely asymmetrical
17. Maxillary shelf	well developed	poorly developed	well developed	well developed
18. Number of sacral vertebrae	–	–	more than 9	15–16
19. Radius and ulna	–	moderately elongated, sigmoidal	very elongated, straight	–
20. Scapular blade	? 4.5<l/W<5	4.5<l/W<5	4.5<l/W<5/	L/W ratio = 6.2
21. Prepubic blade	important emphasis to the dorsal side	nearly symmetrical	nearly symmetrical	–
21. Ilium length / preacetabular length	>2.1	–	>2.1	<2
22. Distal end of fibula	–	moderately expanded	club-shaped	moderately expanded
23. Cranial ascending process of astragalus	–	skewed laterally	equilateral	skewed laterally

Pubis (Fig. 10C).—The pubes from the sample are intermediate in robustness between those of *Corythosaurus casuarius* and of *Parasaurolophus cyrtocristatus* (Brett-Surman and Wagner 2007). The prepubic neck is relatively short, but massive. The prepublic blade is well expanded. All the specimens discovered at Wulaga are characterized by a very asymmetrical expansion of the prepubic blade, with an important emphasis to the dorsal side. In *Sahaliyania*, the dorsal expansion of the prepubic blade is more important than its ventral expansion (Fig. 11). Even if the prepubic blade is also slightly expanded dorsally in some specimens of *Corythosaurus casuarius* (ROM 1947) and *Lambeosaurus magnicristatus* (TMP 66.04.01; David C. Evans, personal communication 2007), the ventral expansion of the blade remains more important, as usually observed in hadrosaurids. The iliac process of the pubis is prominent and robust; its lateral side bears a strong, vertical and roughened ridge that limits rostrally the acetabular surface of the bone. Its medial side bears a well-marked triangular and striated surface, indicating a close contact with one of the first sacral ribs. The ischial peduncle is long and its articular surface with the ischium is expanded and rounded. The proximal part of the ischial peduncle bears a well-marked ventrolateral boss, also observed in a new hadrosaurine from Kundur (P.G. unpublished data). The postpubic rod is short, robust, mediolaterally compressed and straight. Table 1 summarises the main differences observed in the skeleton of *Sahaliyania* and of the other three lambeosaurines currently described in the Amur/Heilongjiang region: *Charonosaurus jiayinensis*, *Amurosaurus riabinini*, and *Olorotitan arharensis*.

Hadrosaurinae Cope, 1869

Genus *Wulagasaurus* nov.

Type species: *Wulagasaurus dongi* sp. nov., from the Yuliangze Formation (Maastrichtian, Upper Cretaceous) of Wulaga, Heilongjiang province, China.

Derivation of the name: Wulaga is the type locality of this new genus; sauros, the Greek for lizard.

Diagnosis.—Hadrosaurine dinosaur characterised by the following autapomorphies: very slender dentary, with a ratio "length of the dentary battery/maximum height of the dental ramus taken around the middle of the dental battery" >4.5; lateral side of dentary not pierced by foramina; edge of the deltopectoral crest oriented quite cranially; humeral articular head extends distally as a very long and prominent vertical ridge; inner tuberosity much better developed than outer tuberosity on the proximal end of the humerus.

Also differs from all other known hadrosaurines by its short sagittal, less than 2/3 the length of the parietal; differs from *Gryposaurus*, *Kerberosaurus*, *Prosaurolophus*, *Saurolophus*, *Edmontosaurus*, and *Anatotitan* by its short supraoccipital-exoccipital shelf.

Wulagasaurus dongi sp. nov.

Figs. 12–18.

Derivation of the name: In honour of Dong Zhi-Ming, one of the most famous dinosaur specialists, for his fundamental contribution to the knowledge of dinosaurs in China.

Holotype: GMH W184, a right dentary.

Type locality: Wulaga (Heilongjiang province, China). Coordinates of the site: N 48°23'40.9'' E 130°08'44.6''.

Type horizon: Yuliangze Formation (*Wodehouseia spinata–Aquilapollenites subtilis* Palynozone, Maastrichtian, Upper Cretaceous).

Material.—Braincases GMH WJ1, W384, W421; jugal GMH W166; maxillae GMH W233, W400-10; dentary GMH W217; scapulae GMH W267, W411; sternals GMH W194, W401; humeri GMH W320, W515-B; ischium: GMH W398-A.

Diagnosis.—As for the genus, by monotypy.

Description

Exoccipital-opisthotic complex (GMH WJ1, W384, W421; Figs. 12, 13).—The exoccipital condyloids are rostrocaudally long, but mediolaterally compressed. They are pierced by four foramina. The caudal foramen is large and transmitted the hypoglossal nerve (CN XII). More rostrally, the foramen for the accessory nerve (CN XI) is the smallest of the three. The foramen for the vagus (CN X) and the glossopharyngeal (CN IX) nerves is the largest and is set more dorsally than the other two. Below this latter foramen, a fourth one is present in WJ1. It is always small and may represent either a separate passage for the glossopharyngeal nerve, assumed to be the smallest of the cranial nerves, or a rostral root of the hypoglossal nerve. The foramen for CN X is bordered rostrally by a prominent ridge extending from the ventral border of the paroccipital process to the rostroventral corner of the exoccipital condyloid. This pillar is not developed in *Kerberosaurus*. Above this ridge, the rostrodorsal corner of the exoccipital condyloid is deeply excavated by the rostral margin of the auditory foramen. The paroccipital processes are broken off. They contact each other above the foramen magnum. At this level, their dorsal border is perfectly horizontal and forms a prominent caudal ridge below the supraoccipital. Between this ridge and the foramen magnum, the median surface of the exoccipital-opisthotic forms a

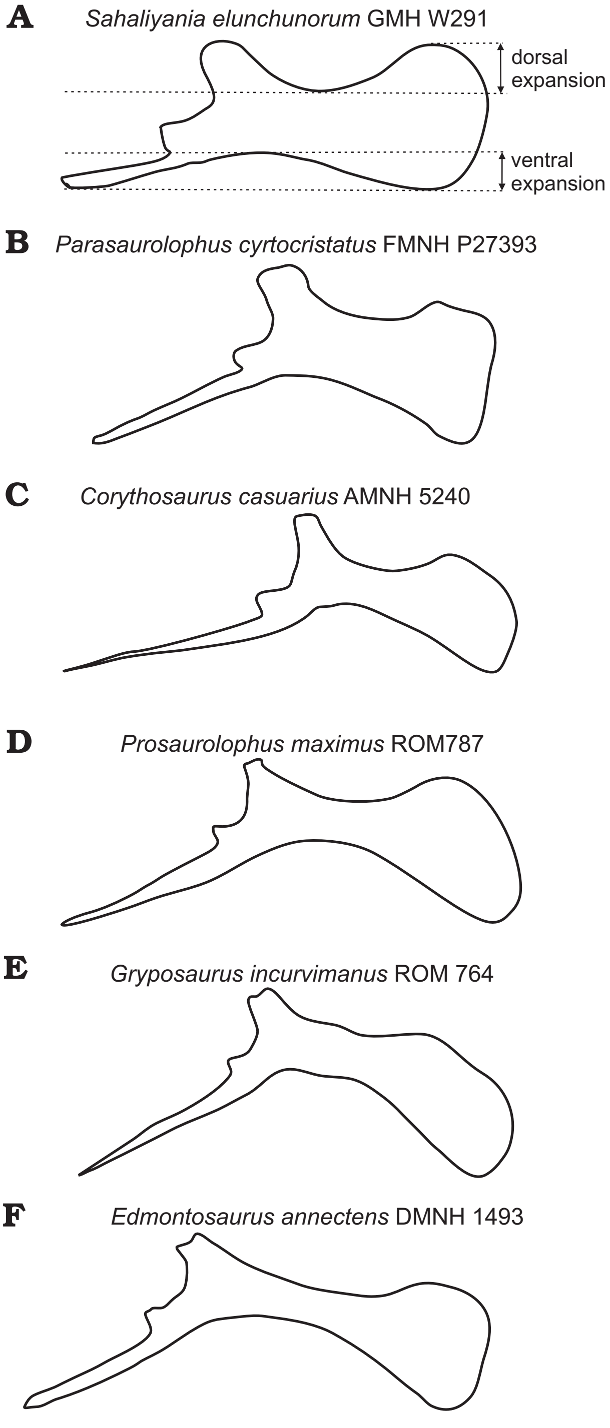

Fig. 11. Pubis shape in various hadrosaurids. A, original data; B–F, after Brett-Surman (1989).

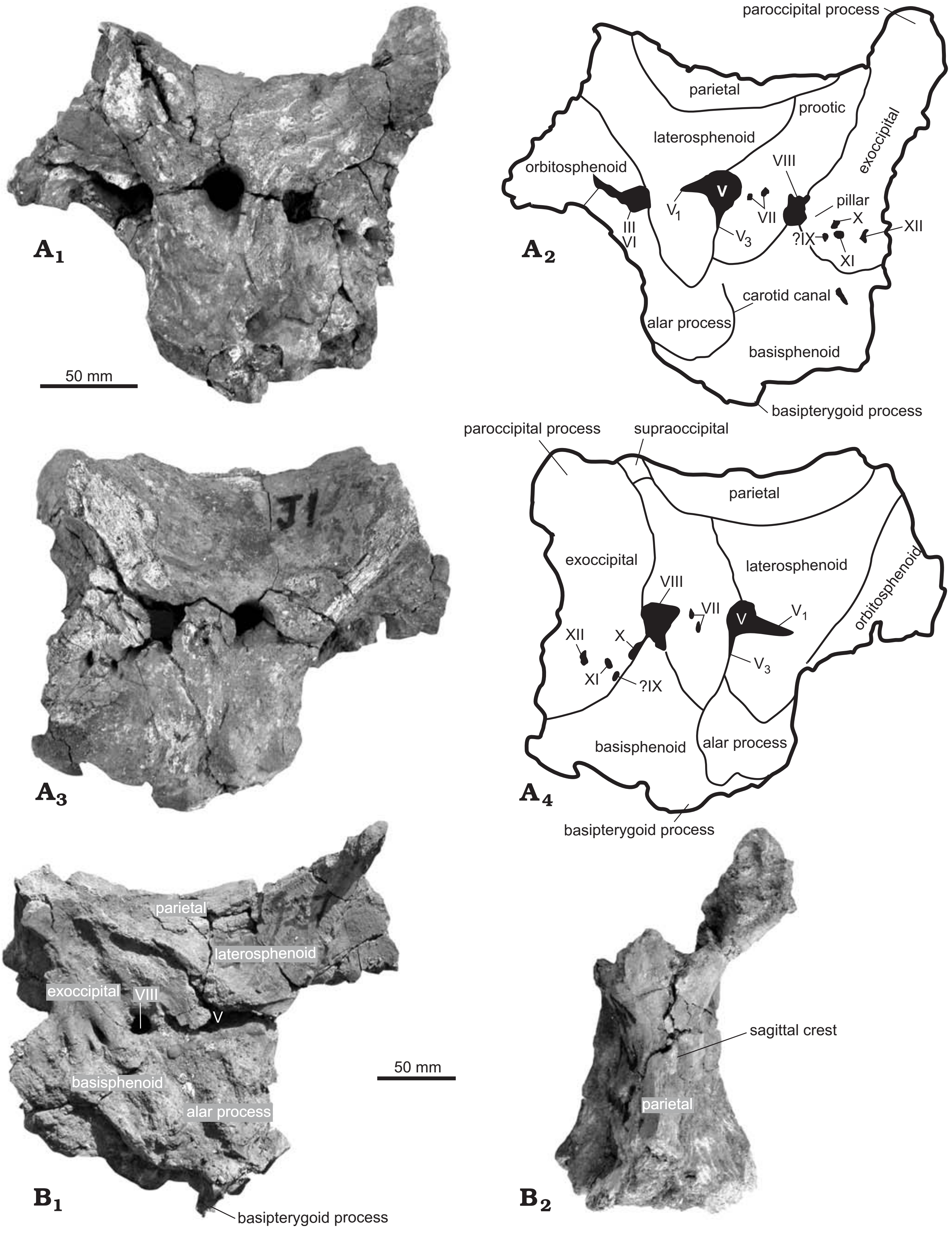

Fig. 12. The hadrosaurid dinosaur *Wulagasaurus dongi* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMHWJ1, braincase in left (A_1, A2) and right lateral (A_3, A_4) views; photographs (A_1, A_3) and explanatory drawings (A_2, A_4). **B**. GMH W421, braincase in right lateral (B_1) and dorsal (B_2) views.

depressed area. However, it does not form an elongated shelf extending caudodorsally above the foramen magnum, as observed in *Kerberosaurus* and in derived North American hadrosaurines. It more closely resembles the condition observed in *Maiasaura* and *Brachylophosaurus* (Horner 1992; Bolotsky and Godefroit 2004; Prieto-Marquez 2005). Lateral to the supraoccipital contact area, the dorsal border of the paroccipital processes steeply slopes dorsally, which contrasts with the more horizontal paroccipital processes of *Sahaliyania*.

Lateral wall of the braincase (GMH WJ1, W384, W421; Fig. 12).—Although this area is not finely preserved in the *Wulagasaurus* specimens at hand, several interesting characters can be observed. The crista otosphenoidalis is much less developed than in *Sahaliyania*. Although such a character is extremely difficult to quantify, it appears that this crest is usually better developed in lambeosaurines than in hadrosaurines. The foramen for CN VIII is rounded and nearly as large as the opening for the trigeminal nerve. A ventrally-directed sulcus for transmission of the ramus maxillaris (V$_2$) and ramus mandibularis (V$_3$) of the trigeminal nerve runs vertically from the latter opening. This sulcus is not developed in *Kerberosaurus*, but a deep pocket-like depression excavates the basisphenoid process of the prootic. The rostrally-directed horizontal sulcus for the ramus ophthalmicus (V$_1$) is better developed in *Kerberosaurus* than in *Wulagasaurus*.

Basioccipital–basisphenoid complex (GMH WJ1, W384, W421; Figs. 12, 13).—This part of the skull is also incompletely preserved in *Wulagasaurus*. The basioccipital is relatively elongated and narrow. The sphenoccipital tubercles are not very prominent. Between the basipterygoid processes, there is also a well-developed median process, as observed in *Sahaliyania*. This process is apparently not developed in *Kerberosaurus*. The alar process of the basisphenoid, which conceals the carotid canal, is well developed and bilobate, as previously observed in the lambeosaurine *Charonosaurus* (Godefroit et al. 2000).

Supraoccipital (GMH WJ1; Fig. 13).—The straight basis of this pyramidal bone is inserted between the dorsomedial borders of the paired paroccipital processes. The dorsal surface of the supraoccipital is strongly sculptured, as usually described in hadrosaurids. Deeply depressed areas for insertion of the M. spinalis capitis and M. rectis capitis posterior circumscribe a prominent median promontorium laterally and ventrally. Lateral to these depressed areas, the caudolateral corners of the supraoccipital form a pair of prominent knobs, which insert in the notched caudoventral corners of the squamosals.

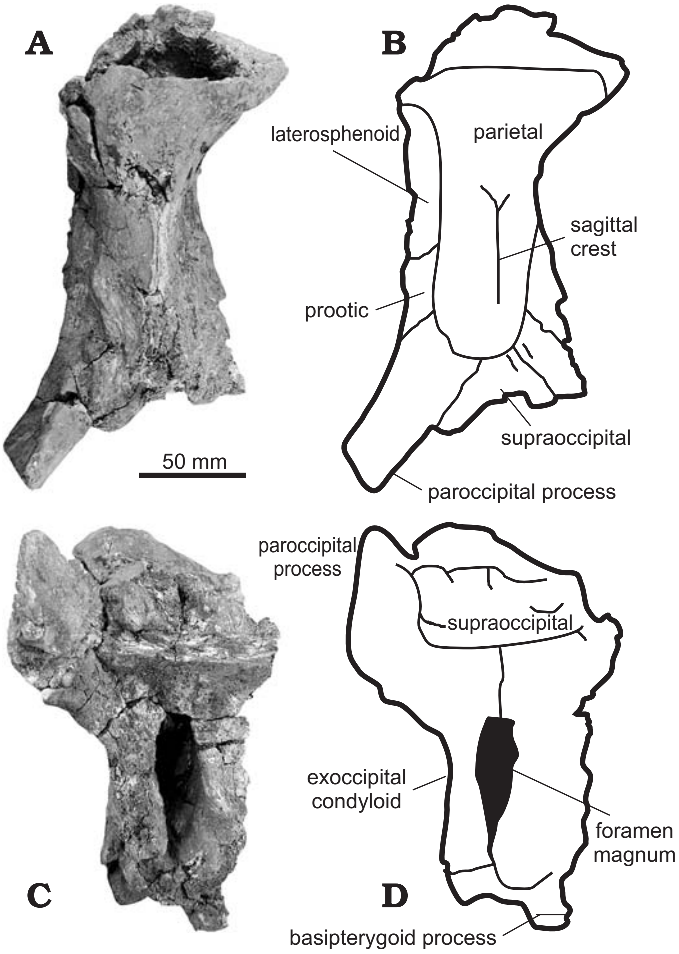

Fig. 13. The hadrosaurid dinosaur *Wulagasaurus dongi* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. GMH WJ1, braincase in dorsal (**A**, **B**) and caudal (**C**, **D**) views. Photographs (A, C) and explanatory drawings (B, D).

Parietal (GMH WJ1, W384, W421; Figs. 12, 13).—The parietal of *Wulagasaurus* contrasts with that of *Sahaliyania* in being proportionally long and very narrow: the ratio "length/minimal width" is >2.5. The sagittal crest is well developed on the caudal part of the parietal; on the other hand, the rostral half of the bone is devoid of a crest and its dorsal surface is regularly convex. This is the situation usually observed in lambeosaurines and in more basal forms, like *Iguanodon*, *Probactrosaurus*, and *Bactrosaurus* as well. In these forms, the parietal crest measures less than two-thirds the length of the parietal and less than half the length of the supratemporal fenestra. In typical hadrosaurines, on the other hand, the sagittal crest is longer, extending nearly along the whole length of the bone, and more than half the length of the supratemporal fenestra, as observed in *Maiasaura* (Albert Prieto-Marquez personal communication 2007), *Brachylophosaurus* (Prieto-Marquez 2005: fig. 8, A), *Gryposaurus* (Parks 1920: pl. 3: 2), *Prosaurolophus* (Horner 1992), *Kerberosaurus* (Bolotsky and Godefroit 2004), *Saurolophus angustirostris* (personal observation), *Edmontosaurus* (Lambe 1920: fig. 4), and *Anatotitan* (personal observation). In *Wulagasaurus*, the rostral portion of the parietal is apparently not depressed around the contact area with the frontals, as it is described in *Kerberosaurus* (Bolotsky and Godefroit 2004). The caudolateral part of the parietal is notched to receive the large lateral knobs of the supraoccipital.

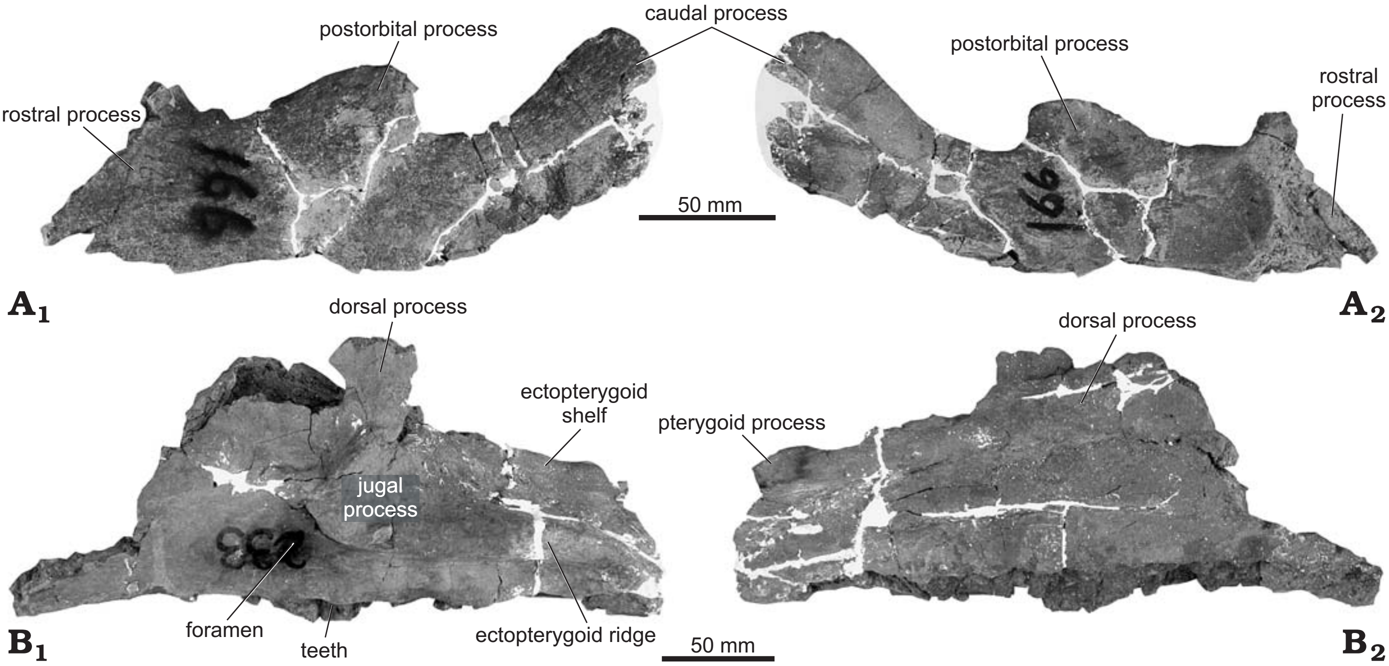

Fig. 14. The hadrosaurid dinosaur *Wulagasaurus dongi* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W166, left jugal in lateral (A_1) and medial (A_2) views. **B**. GMH W233, left maxilla in lateral (B_1) and medial (B_2) views.

Jugal (GMH W166; Fig. 14A).—Although it is incomplete, this partial jugal is clearly different from the specimens referred to *Sahaliyania*: it looks proportionally more elongated and more slender, with a more steeply inclined caudal process. It more closely resembles the jugals of non-edmontosaur hadrosaurines. For that reason, it is tentatively regarded as belonging to *Wulagasaurus*.

Maxilla (GMH W233, W400-10; Fig. 14B).—Maxillae referred to *Wulagasaurus* are incompletely preserved in the Wulaga material: the specimens lack their rostral portion and the dorsal process is broken off. However, they display a typically hadrosaurine morphology: the base of the dorsal process is rostrocaudally elongated and the distal portion of the bone is very long and robust, contrasting with the more gracile condition observed in GMH W199 and in lambeosaurines. It may therefore be hypothesized that the complete maxilla of *Wulagasaurus* was roughly symmetrical when viewed laterally, as usually observed in hadrosaurines. Caudoventral to the dorsal process, the lateral side of the maxilla forms a short and low jugal process, which is very concave and slightly faces dorsally. This condition contrasts with the wide and prominent jugal process observed in *Kerberosaurus* and in a new hadrosaurine from Kundur. It more closely resembles the condition observed in *Edmontosaurus* (see Lambe 1920: fig. 12). However, this character cannot be adequately quantified and is therefore not really useful from a phylogenetic point of view. Ventral to the jugal process, the lateral side of the maxilla is pierced by a single foramen. Three to five foramina usually perforate the lateral surface of the maxilla in hadrosaurids, below and in front of the jugal process. It is also the case in the basal hadrosauroids *Altirhinus* (Norman 1998), *Probactrosaurus* (Norman 2002: fig. 5), and *Bactrosaurus* (Godefroit et al. 1998). As is usual in hadrosaurids, the ectopterygoid ridge is very prominent and set very low on the lateral side of the maxilla. It is nearly horizontal; only the distal part is deflected ventrally. The ectopterygoid shelf is long, very wide and dorsoventrally concave. The caudal part of the dorsal border of the maxilla bears a large hook-like pterygoid process.

Maxillary teeth are typical for hadrosaurids and do not significantly differ from those described above in *Sahaliyania*.

Dentary (GMH W184, W217; Fig. 15).—These dentaries are proportionally much more elongated and slender than those of other hadrosaurids described to date. In GMH W184, the ratio “length of the dentary battery/maximum height of the dental ramus taken around the middle of the dental battery” is around 4.6. In *Anatotitan copei*, from the late Maastrichtian of western North America, the dentary also appears very elongated, but in this case it is the result of the extreme elongation of the diastema: the ratio “length of the dentary battery/maximum height of the dental ramus taken around the middle of the dental battery” = 3.16 in AMNH 5730. The slenderness of the dentary in *Wulagasaurus* is apparently not the result of allometric growth in hadrosaurids. Indeed, Lauters (2005) showed that there is a significant negative allometry between the height and the length of the dentary in *Amurosaurus*: it means that the dentaries of larger specimens look more slender than those of juveniles. On the other hand, GMH W184 (525 mm) and GMH W217 (>535 mm) are more slender than the dentaries of larger advanced hadrosaurines. In medial view, the dental magazine is long, but unfortunately too eroded to estimate the number of alveolar

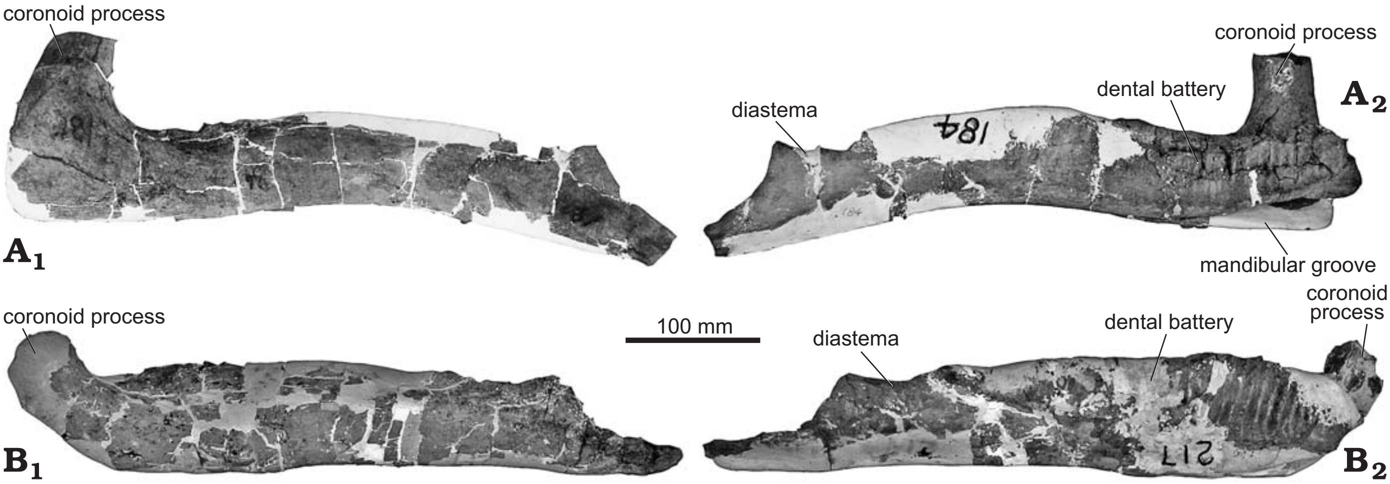

Fig. 15. The hadrosaurid dinosaur *Wulagasaurus dongi* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. Holotype GMH W184, right dentary in lateral (A_1) and medial (A_2) views. **B**. GMH W217, right dentary in lateral (B_1) and medial (B_2) views.

grooves. The height of the dental magazine regularly decreases rostrally. It means that tooth replacement was probably more limited in the rostral part of the dental battery that in the caudal part. In front of the dental magazine, the diastema forms an elongated notch on the dorsal border of the dentary. In *Wulagasaurus*, the diastema is about 4 times shorter than the dental magazine. In front of the diastema, the dorsal border of the dentary slopes ventrally to form the concave articular surface for the predentary. The ventral border of the dentary is not strongly deflected ventrally, like in *Sahaliyania*, but it is smoothly concave in lateral view, as it is usually observed in hadrosaurines. As observed above, the degree of ventral deflection of the rostral part of the dentary is variable in hadrosaurids and difficult to estimate. Moreover, its polarity is also problematic. Pending more detailed studies on the variation of this character in North American hadrosaurids, we do not include this character in the phylogenetic analysis presented below. The lateral side of the dental ramus is smoothly convex dorsoventrally. There is no trace of vascular foramina, as those usually observed in other hadrosaurids. The coronoid process is broken off, but it is inclined rostrally, as in other hadrosaurids. The adductor fossa is very deep and both the mandibular groove and the angular facet are particularly elongated, extending further than the caudal third of the length of the dentary.

Scapula (GMH W267, W411; Fig. 16B, C).—These specimens significantly differ from the other scapulae discovered at Wulaga and more closely resemble hadrosaurine scapulae, with a long and narrow scapular blade (Brett-Surman and Wagner 2007). Although it is heavily damaged and roughly restored with plaster, the proximal head appears less expanded dorsoventrally than in *Sahaliyania*. The acromial process is more laterally oriented and the deltoid ridge is more prominent. The deltoid fossa is narrower, but deeper. The long scapular blade is thicker, but appears less expanded craniocaudally.

Sternal (GMH W194, W401; Fig. 16A).—Although they are not completely preserved, these sternals are different from those described under *Sahaliyania*, rather displaying a typical hadrosaurine morphology (Brett-Surman and Wagner 2007): the proximal plate is distinctly less expanded, both in length and in width, than in *Sahaliyania*. Consequently, the distal “handle” is longer than the proximal plate. The “handle” is very robust. Its ventral side is convex, whereas its dorsal side is flat. Its distal end is slightly expanded and bears longitudinal striations on both sides.

Humerus (GMH W320, W515-B; Fig. 17A).—The deltopectoral crest of these humeri is distinctly less developed than in the other specimens of similar size found in Wulaga locality. It more closely resembles the condition encountered in hadrosaurines. For that reason, those humeri are tentatively associated with the *Wulagasaurus* material. The most striking character of these specimens is the orientation of their deltopectoral crest. Usually in hadrosaurids, the edge of the deltopectoral crest is oriented laterally, or slightly craniolaterally. In GMH W320 and W515-B, on the other hand, the edge of the deltopectoral crest is oriented quite cranially, at an angle of 90° to its usual orientation. Although these humeri are not completely preserved, it is unlikely that the unusual orientation of their deltopectoral crest is an artefact of preservation. Indeed, post-mortem deformation at this level would have completely destroyed the thin deltopectoral crest. But there is no breakage between the base of the deltopectoral crest and the shaft of the humerus either in GMH W320 or in GMH W515-B. Therefore, we consider that this orientation of the deltopectoral crest was present in the living animal. Of course, this configuration of the deltopectoral crest influences the whole morphology of the bone. The bicipital gutter is much deeper and, on the proximal side of the bone, the humeral head is more prominent than in other hadrosaurids. The articular head extends distally as a very long and prominent vertical ridge, much better developed

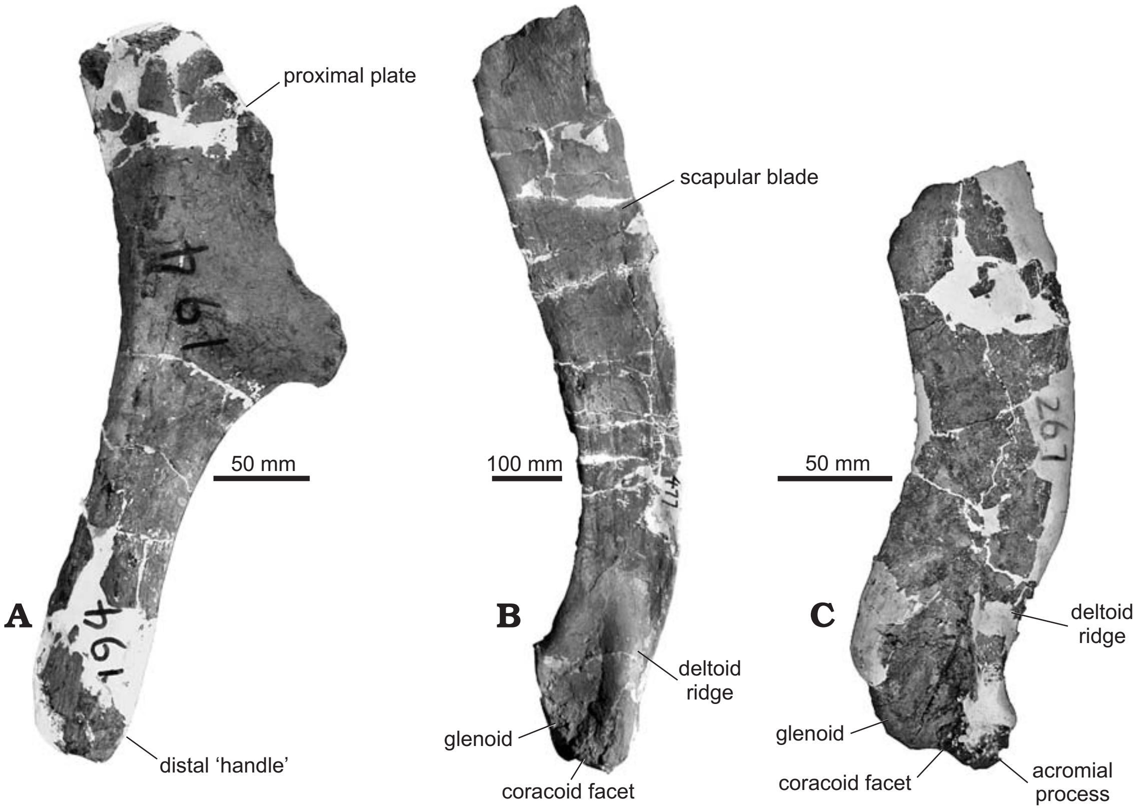

Fig. 16. The hadrosaurid dinosaur *Wulagasaurus dongi* gen. et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W194, right sternal in ventral view. **B**. GMH W411, right scapula in lateral view. **C**. GMH W267, right scapula in lateral view.

than in other hadrosaurids. Because of the concomitant cranial orientation of the deltopectoral crest and the important development of the caudal crest, the craniocaudal maximum diameter of the humerus is much more important than the mediolateral diameter, which is an uncommon character among hadrosaurids. Also contrasting with the normal hadrosaurid condition, the inner tuberosity is much better developed than the outer tuberosity on the proximal end of the humerus. The distal end of the humerus is slightly turned laterally, as usually described in hadrosaurids. It is unfortunately too crushed to be adequately described.

Ischium (GMH W398-A; Fig. 17B).—Although it is very incomplete, this specimen significantly differs from the other ischia discovered at the Wulaga locality and described above under *Sahaliyania*. The ischial shaft is very slender, straight and rod-like. The minimum circumference of the shaft is 128 mm, for a total length greater than 1100 mm. This is very low, when compared to lambeosaurine specimens of similar size (compare with GMH W400-2: length = 1098 mm, minimum circumference of the shaft = 161 mm). This is the condition usually observed in hadrosaurines. For this reason, GMH W398-A is tentatively referred to *Wulagasaurus*.

Hadrosauridae indet.

The Wulaga locality has also yielded many other hadrosaurid isolated bones that do not display any diagnostic character. For that reason, it cannot be decided whether these bones belong to *Sahaliyania*, *Wulagasaurus*, or any other hadrosaurid. These bones are listed in Appendix 1. Pending the discovery of associated specimens, these bones are not described in the present paper and are referred to as Hadrosauridae indet.

Phylogenetic analysis

Fifty-six cranial, dental and post-cranial characters, as compiled from Weishampel et al. (1993), Godefroit et al. (1998, 2001, 2004a, b), Bolotsky and Godefroit (2004), Horner et al. (2004), and Prieto-Marquez (2005), have been used to determine the systematic position of *Sahaliyania elunchunorum* and *Wulagasaurus dongi* (see Appendices 2 and 3). The non-hadrosaurid hadrosauroid *Bactrosaurus johnsoni* Gilmore, 1933, revised by Godefroit et al. (1998), has been chosen as outgroup, because its anatomy is now particularly well documented and familiar to the authors of the present paper. In this analysis, the hadrosaurids are treated at the generic level, although several North American genera are widely considered to contain more than one species (Horner et al. 2004). But most of these genera are currently under revision by other authors (e.g., Albert Prieto-Marquez and David Evans) and it is not the purpose of the present paper to interfere with these studies. As a general rule, the type species has been chosen as representative for multispecific genera. How-

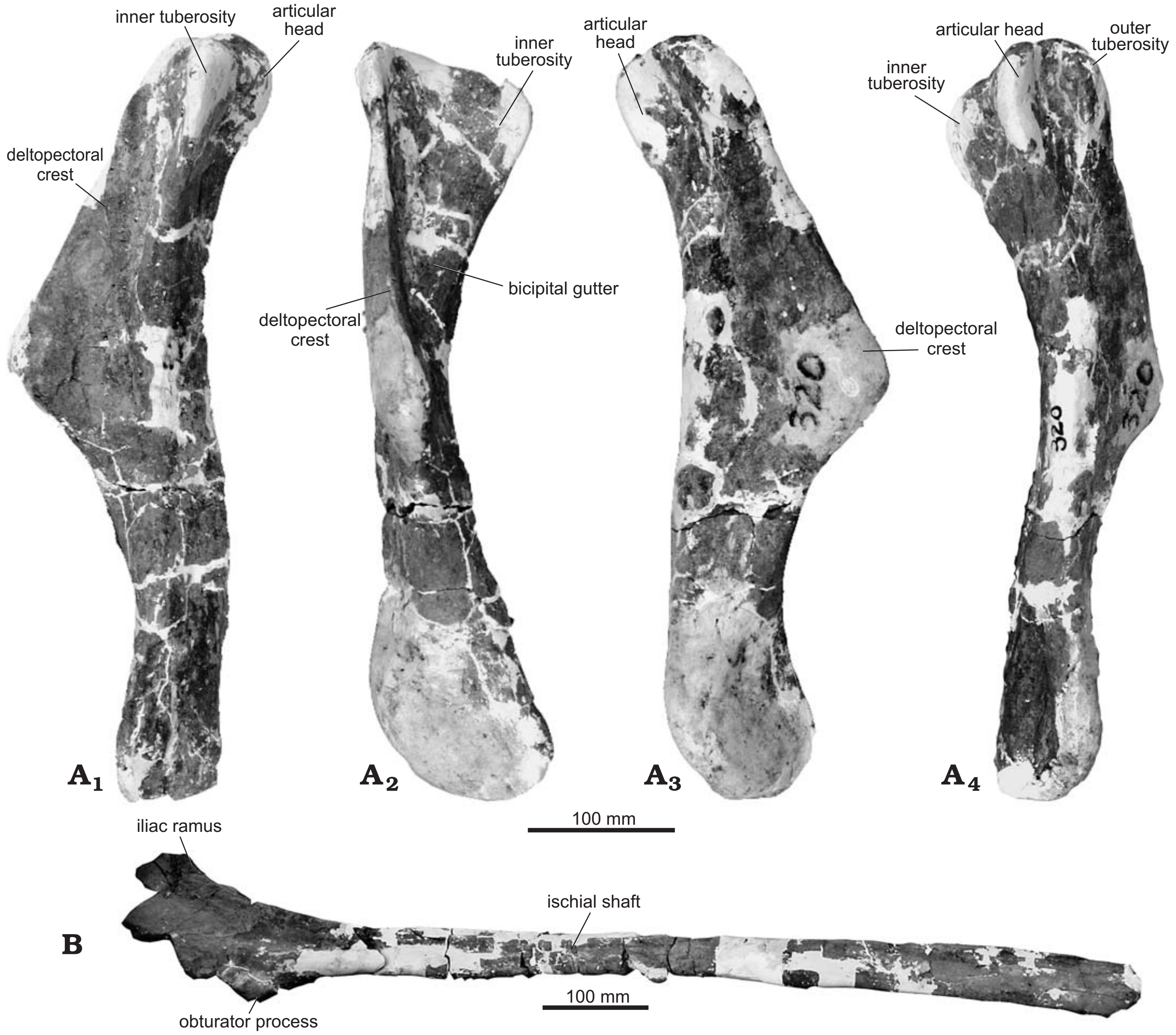

Fig. 17. The hadrosaurid dinosaur *Wulagasaurus dongi* gen et sp. nov. from the Upper Cretaceous Yuliangze Formation at the Wulaga quarry, China. **A**. GMH W320, right humerus in medial (A_1), cranial (A_2), lateral (A_3), and caudal (A_4) views. **B**. GMH W398-A, ?left ischium in ?lateral view.

ever, the polarity of the characters in *Saurolophus* is based on *S. angustirostris* Rozhdestvensky, 1952 specimens housed in the PIN, which the senior author could examine in detail. It probably explains some differences observed with the character matrix published by Prieto-Marquez (2005), who studied *Saurolophus osborni* material in the AMNH (Albert Prieto-Marquez, personal communication 2007).We left out from this analysis taxa that clearly require a systematic revision, or are known from too fragmentary material, such as *Hadrosaurus foulkii* Leidy, 1858, *Kritosaurus navajovius* Brown, 1910 (= *Anasazisaurus horneri* Hunt and Lucas, 1993 + *Naashibitosaurus ostromi* Hunt and Lucas, 1993), *Lophorhothon atopus* Langston, 1960, *Claosaurus agilis* (Marsh, 1872), and *Secernosaurus koerneri* Brett-Surman, 1979. Although the lambeosaurine *Nipponosaurus sachalinensis* was recently revised by Suzuki et al. (2004), we did not take this taxon into consideration in the present phylogenetic analysis. Indeed, after direct examination of the type specimen, we believe that this taxon is best regarded as a *nomen dubium*. The characters regarded as diagnostic by Suzuki et al. (2004) can be observed in other hadrosaurids: robust (?) coronoid process of the surangular, slight development of the axis, and strong (?) deflection of the lateral margin of the first phalanx on digit IV. Moreover, characters regarded as synapomorphic with *Hypacrosaurus altispinus* are either widely distributed within lambeosaurines (development of an ischial foot, in any case much smaller than in *H. altispinus*), or cannot be properly evaluated due to damage (shape of the ventral flange of the jugal). In any case, we believe that the juvenile status of *Nipponosaurus*, together with the fact that it lacks most of the phylogenetically important portions of the skull hinders attempts to determine its systematic position within lambeosaurines (see also Evans and Reisz 2007).

The 56 characters were equally weighted and analysed with PAUP*4.0b10 (Swofford, 2002), both with ACCTRAN and DELTRAN transformations. Seven most parsimonious trees of 80 steps resulted from a branch-and-bound search, with a consistency index of 0.92 and a retention index of 0.97. The strict consensus tree of the seven most parsimonious trees is presented in Fig. 18 and a complete list of apomorphies is found in Appendix 4. The topology of the consensus tree is similar to those previously published by Weishampel and Horner (1990), Weishampel et al. (1993), Bolotsky and Godefroit (2004), Godefroit et al. (2004a, b), and, particularly, by Evans and Reisz (2007). To assess the stability of tree morphologies, a bootstrap analysis (1000 replicates using the Branch-and-Bound algorithm) was performed using this option in PAUP. The bootstrap values, indicated in Appendix 4, are not very high, indicating that the phylogenetic hypothesis presented here is not strongly supported and is liable to changes as new taxa and characters are added and other re-evaluated, as this is usually the case in palaeontological studies in which many taxa are very partially known. However, the bootstrap values presented here are, in average, slightly higher than those obtained by Evans and Reisz (2007) in their phylogenetic analysis of Lambeosaurinae, the only previous analysis of hadrosaurids in which bootstrap values have been reported.

Sahaliyania may be regarded as a derived lambeosaurine (Fig. 18): it forms a monophyletic group with the corythosaur and parasauroloph clades (sensu Chapman and Brett-Surman 1990). This group is characterised by the following unambiguous (no differences in positioning of a character in ACCTRAN and DELTRAN optimisations) characters: a shortened frontal, with a "posterior length/maximal width" <0.6 (character 7[1]), and 42–45 tooth positions in dentary tooth row (character 41 [2]). However, the position of *Sahaliyania* within this group cannot be resolved. A more precise evaluation of the phylogenetic position of *Sahaliyania* will require the discovery of more complete specimens, with preserved supracranial crest structures.

Although the material referred to *Wulagasaurus* is more fragmentary than that of *Sahaliyania*, its phylogenetic position can be more easily determined. *Wulagasaurus* is undoubtedly a hadrosaurine, because it is characterised by the following unambiguous synapomorphies: maxilla with a long and robust caudal portion (character 32) and tapering distal end of the ischium (character 53[2]). But *Wulagasaurus* appears to be the most basal hadrosaurine known to date. Its sagittal crest is relatively short as in *Bactrosaurus johnsoni*, other basal hadrosauroids, and lambeosaurines. In all other considered hadrosaurines, on the other hand, the parietal crest is much longer, more than two-thirds the length of the parietal (character 3). As previously discussed by Prieto-Marquez (2005), *Maiasaura* and *Brachylophosaurus* form a robust clade (bootstrap value = 88), characterised by the following synapomorphies: solid supracranial crest, present but not excavated by the posterior circumnarial fossa (character 20[1]), short squamosal prequadratic process only slightly longer than anteroposterior width of quadrate cotylus (character 24), rostral process of jugal isosceles-triangle-shaped (character 30[2]), jugal flange strongly projected ventrally into a semicircular boss (character 31[2]), anterior mediolateral width of predentary greater than twice anteroposterior length of lateral process (character 40[2]), and plantar keel on unguals (character 56). The remaining hadrosaurines form a monophyletic group characterised by a premaxilla with a lip reflected along entire rim (character 10[2–3]), an extended supraoccipital/exoccipital shelf (character 26), and by a rostral process of jugal asymmetrically strongly upturned (character 30[3]).

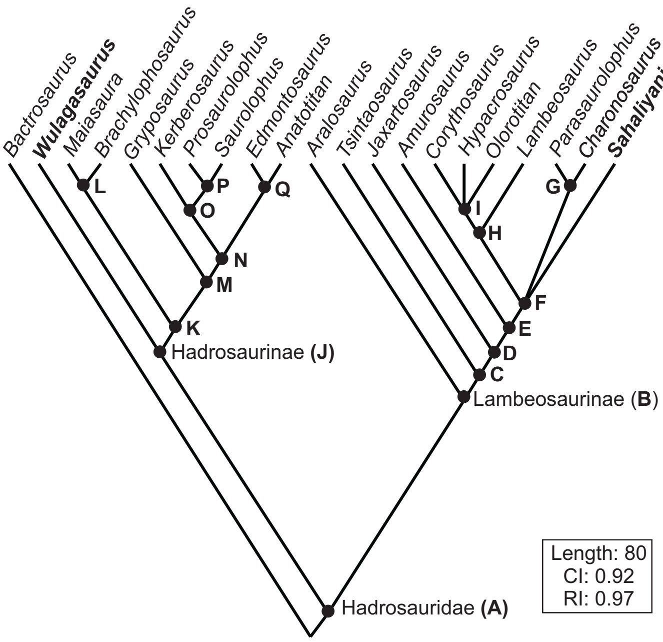

Fig. 18. Phylogenetic relationships of *Sahaliyania elunchunorum* and *Wulagasaurus dongi* within the Hadrosauridae. Letters correspond to the nodes defined in Appendix 4.

Ghost lineage analysis

The basal phylogenetic position of *Wulagasaurus* among hadrosaurines is discordant with its late stratigraphic distribution. Such discordance can be assessed through the use of ghost lineage durations (GLDs). Norell (1992) defined ghost lineages as missing sections of a clade implied by phylogeny. Because sister taxa have the same time of origin, it is therefore possible to establish the minimal age for the origin of

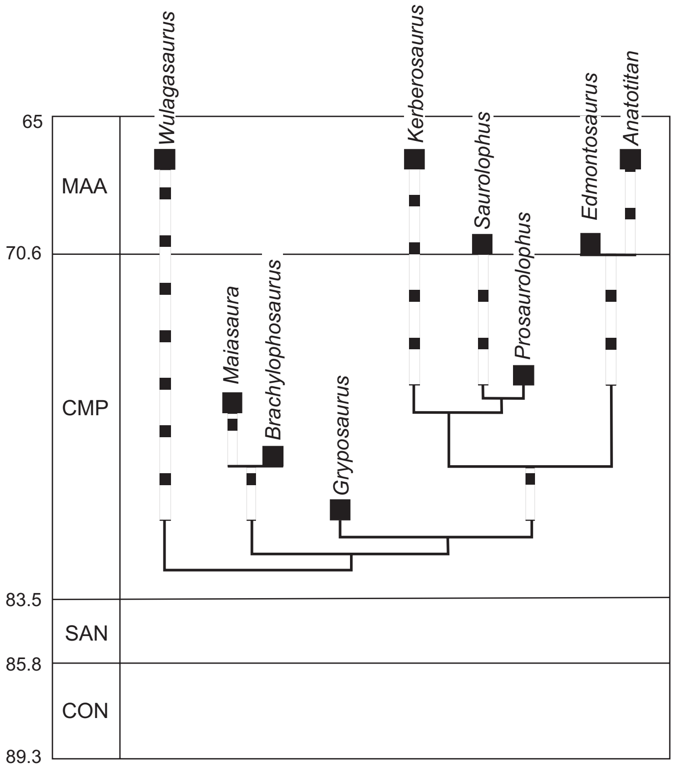

Fig. 19. Stratigraphically-calibrated relationships of hadrosaurine dinosaurs. Solid symbols indicate the first stratigraphical occurrence of the taxa, whereas hatched symbols indicate ghost lineages. Dates are millions of years before present. CMP: Campanian; CON: Coniacian; MAA: Maastrichtian; SAN: Santonian.

clades: the origin of a clade cannot occur later than the first occurrence of its sister taxon. Ghost lineage duration can be calibrated using a geochronological scale: for sister taxa, it is the difference between the first occurrence of the younger taxon and the first occurrence of the older one. GLDs can consequently be regarded as an estimation of the completeness of the fossil record from a phylogenetic perspective (Weishampel 1996).

As discussed above, *Wulagasaurus* is probably late Maastrichtian in age. The oldest relatively well-dated representative for the sister-group of *Wulagasaurus* is probably *Gryposaurus latidens*, from Lithofacies 3 of the Two Medecine Formation in Montana (oldest occurrence around 80 million years; Horner et al. 2001). This means that the *Wulagasaurus* lineage must have diverged from the lineage leading to more advanced hadrosaurines at least by the early Campanian (Fig. 19) yielding a GLD of approximately 13 million years for the *Wulgasaurus* lineage. Such a high GLD value means that a number of taxa have yet to be discovered if the phylogenetic continuity, as implied by the obtained topologies, is to be maintained.

GLDs for lambeosaurines have been estimated and discussed in other papers (Godefroit et al. 2004a, b). Because the phylogenetic position of *Sahaliyania* cannot be precisely assessed, it is not possible to contribute substantial information in this regard.

Biogeography

It has been shown (e.g., see Godefroit et al. 2004a, b) that lambeosaurine hadrosaurids probably have an Asian origin. Indeed, the most basal and/or the oldest lambeosaurines have been discovered in Asia: *Aralosaurus tuberiferus*, from the Beleutinskaya Svita (?Turonian) of Kazakhstan, *Tsintaosaurus spinorhinus*, from the Wangshi Formation (Campanian, according to Buffetaut 1995), *Jaxartosaurus aralensis*, from the Syuksyuk Formation of Kazakhstan (Santonian, according to Averianov and Nessov 1995), and *Amurosaurus riabinini*, from the Maastrichtian Udurchukan Formation of Amur Region in Russia. In western North America, the oldest well-dated lambeosaurines have been discovered in upper Campanian formations (Horner et al. 2004); all belong to the advanced parasauroloph or corythosaur clades. The most parsimonious hypothesis is therefore that ancestors of the parasauroloph and corythosaur clades migrated from eastern Asia towards western North America before or at the beginning of the late Campanian. Other dinosaur taxa followed this migratory route during the Cretaceous: basal Neoceratopsia (Chinnery and Weishampel 1998), Ankylosauridae (Maryańska 1977), Tyrannosauroidea (Xu et al. 2006), and Troodontidae (Russell and Dong 1993). A land route between Asian and Cordilleran America across the Beringian isthmus probably opened during the Aptian–Albian and persisted during the Late Cretaceous (Jerzykiewicz and Russell 1991; Russell 1993).

Until very recently, a North American origin for the hadrosaurines seemed likely because the most basal and oldest (Santonian) forms of this clade were found in this area (Horner et al. 2004). With Asian basal lambeosaurines and North American basal hadrosaurines, the birthplace of the monophyletic Hadrosauridae remained very conjectural. It was all the more problematic that basal non-hadrosaurid Hadrosauroidea have been discovered in Asia (*Altirhinus*, *Probactrosaurus*, *Bactrosaurus*, *Gilmoreosaurus*), in North America (*Eolambia*, *Protohadros*) and even in Europe (*Telmatosaurus*). The discovery of *Wulagasaurus* is therefore very important from a palaeogeographical perspective. Indeed, this Asian hadrosaurine is regarded, in the present analysis, as the most basal hadrosaurine. Therefore, it suggests that hadrosaurines, like lambeosaurines, would have an Asian origin. It means that the common ancestor for hadrosaurines and lambeosaurines probably lived in Asia as well. While a lineage of basal hadrosaurines, leading to *Wulagasaurus*, stayed in Asia, the common ancestor for more advanced hadrosaurines migrated to western North America, probably by Santonian time. During the Campanian and early Maastrichtian, several independant hadrosaurid lineages returned into Asia from western North America.

The study of the Wulaga dinosaur material confirms that both the lambeosaurines and the hadrosaurines were diversified in eastern Asia during the late Maastrichtian. Lambeosaurines were the dominant herbivorous dinosaurs in this area, whereas ceratopsians were apparently not represented. In western North America, on the other hand, ceratopsians are usually the most abundant dinosaurs in late Maastrichtian faunas, whereas lambeosaurines are absent or represented by rare and doubtful isolated bones (Boyd and Ott 2002).

If latest Cretaceous hadrosaurids are well diversified in eastern Asia, the geographical distribution of each taxon appears very limited. So far, four dinosaur localities have been really excavated in the Amur/Heilongjiang Region. As previously discussed, these localities belong to the same palynozone and can therefore be regarded as roughly synchronous. *Charonosaurus* is limited to the Jiayin locality, *Sahaliyania* and *Wulagasaurus* to Wulaga, *Amurosaurus* and *Kerberosaurus* to Blagoveschensk, *Olorotitan* and a new hadrosaurine to the Kundur locality. It may be hypothesized that such distribution reflects strict habitat preferences in taxa as they relate to diversified and contrasted palaeoenvironments in eastern Asia at the end of the Cretaceous (Markevich and Bugdaeva 2001). Similar restricted biogeographic ranges have been observed in North American hadrosaurids as well (Lehman 1987, 1997, 2001; Horner et al. 2004). However, it is also possible that the apparent patchy palaeogeographical distribution of latest Cretaceous hadrosaurids in eastern Asia reflects the fragmentary state of our knowledge. Indeed, systematic studies of dinosaur localities in the Amur/Heilongjiang region began recently and several promising localities are still to be excavated.

Acknowledgements

The authors would like to thank Dong Zhi-Ming (IVPP) and Sun Ge (Jilin University, Changchun, China), who established the connections between the Chinese and Belgian members of the team and supported this study. Yuri L. Bolotsky (AEHM), Vladimir R. Alifanov and Evgenii N. Kurochkin (both PIN), Eugene S. Gaffney, Mark A. Norell, and Carl Mehling (all AMNH), John R. Horner (Museum of the Rockies, Bozeman, USA), Philip J. Currie (Royal Tyrrell Museum of Paleontology, Drumheller, Canada), and Kevin Seymour (ROM) provided access to the collections under their care. Jimmy Van Itterbeeck (Katholieke Universiteit Leuven, Belgium), Yuri L. Bolotsky (AEHM), David B. Weishampel (Johns Hopkins University, Baltimore, USA), Albert Prieto-Márquez (Florida State University, Tallahassee, USA), David Evans (ROM), and Rosine Orban (Université Libre de Bruxelles, Belgium) gave helpful comments and advice on various aspects of the manuscript. This study was partly realised through the execution of S&T bilateral cooperation agreements on behalf of the Belgian State, Federal Scientific Policy. P.L. researches are granted by the "Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture" (FRIA).

References

Averianov, A. and Nessov, L. 1995. A new Cretaceous mammal from the Campanian of Kazakhstan. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1995: 65–74.

Bohor, B.F., Foord, E.E., Modreski, P.J., and Triplehorn, D.M. 1984. Mineralogic evidence for an impact event at the Cretaceous–Tertiary boundary. *Science* 224: 867–869.

Bohor, B.F., Triplehorn, D.M., Nichols, D.J., and Millard, H.T.J. 1987. Dinosaurs, spherules, and the "magic" layer: a new K-T boundary clay site in Wyoming. *Geology* 15: 896–899.

Bolotsky, Y.L. [Bolockij, Û.L.] and Kurzanov, S.K. 1991. The hadrosaurs of the Amur Region [in Russian]. *In*: *Glubinnoe Tihookeanskogo Obranleniâ*, 94–103. Amur KNII, Blagoveŝensk.

Bolotsky, Y.L. and Godefroit, P. 2004. A new hadrosaurine dinosaur from the Late Cretaceous of Far Eastern Russia. *Journal of Vertebrate Palaeontology* 24: 354–368.

Boyd, C. and Ott, C.J. 2002. Probable lambeosaurine (Ornithischia, Hadrosauridae) specimen from the Late Cretaceous Hell Creek Formation of Montana. *Journal of Vertebrate Paleontology* 22 (Supplement to No. 3): 38A.

Brett-Surman, M.K. 1979. Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. *Nature* 277: 560–562.

Brett-Surman, M.K. 1989. *A revision of the Hadrosauridae (Reptilia: Ornithischia) and Their Evolution During the Campanian and Maastrichtian*. 272 pp. Unpublished Ph.D. thesis, George Washington University, Washington D.C.

Brett-Surman, M.K. and Wagner, J.R. 2007. Discussion of character analysis of the appendicular analysis in Campanian and Maastrichtian North American hadrosaurids—variation and ontogeny. *In*: K. Carpenter (ed.), *Horns and Beaks. Ceratopsian and Ornithopod Dinosaurs*, 135–169. Indiana University Press, Bloomington.

Brown, B. 1910. The Cretaceous Ojo Alamo Beds of New Mexico with description of the new dinosaur genus *Kritosaurus*. *Bulletin of the American Museum of Natural History* 28: 267–274.

Brown, B. 1913. A new trachodont dinosaur, *Hypacrosaurus*, from the Edmonton Cretaceous of Alberta. *Bulletin of the American Museum of Natural History* 31: 131–136.

Buffetaut, E. 1995. An ankylosaurid dinosaur from the Upper Cretaceous of Shandong (China). *Geological Magazine* 132: 683–692.

Carrano, M.T., Janis, C.M., and Sepkoski, J.J. 1999. Hadrosaurs as ungulate parallels: lost lifestyles and deficient data. *Acta Palaeontologica Polonica* 44: 237–261.

Chapman, R.E. and Brett-Surman, M.K. 1990. Morphometric observations on hadrosaurid ornithopods. *In*: K. Carpenter, K.F. Hirsch, and J.R. Horner (eds.), *Dinosaur Eggs and Babies*, 163–177. Cambridge University Press, Cambridge.

Chassé, J.L. and Pavé, A. 1975. *Probabilités statistiques et biologie*. 326 pp. Editions Cedic, Paris.

Chinnery, B.J. and Weishampel, D.B. 1998. *Montanoceratops cerorhynchus* (Dinosauria: Ceratopsia) and relationships among basal neoceratopsians. *Journal of Vertebrate Paleontology* 18: 569–585.

Cope, E.D. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North-America. *Transactions of the American Philosophical Society* 14: 1–252.

Currie, P.J. and Dodson, P. 1984. Mass death of a herd of ceratopsian dinosaurs. *In*: W.-E. Reif and F. Westphal (eds.), *Third Symposium of Mesozoic Terrestrial Ecosystems*, 52–60. Attempto Verlag, Tübingen.

Eberth, D.A. and Currie, P.J. 2005. Vertebrate taphonomy and taphonomic modes. *In*: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park, a Spectacular Ancient Ecosystem Revealed*, 453–477. Indiana University Press, Bloomington.

Eberth, D.A. and Getty, M.A. 2005. Ceratopsian bonebeds: occurrence, origins, and significance. *In*: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park, a Spectacular Ancient Ecosystem Revealed*, 501–536. Indiana University Press, Bloomington.

Evans, D.C., Forster, C.A., and Reisz, R.R. 2005. The type specimen of *Tetragonosaurus erectofrons* (Ornithischia: Hadrosauridae) and the identification of juvenile lambeosaurines. *In*: P.J. Currie and E.B. Koppelhus (eds.), *Dinosaur Provincial Park, a Spectacular Ancient Ecosystem Revealed*, 349–366. Indiana University Press, Bloomington.

Evans, D.C. and Reisz, R.R. 2007. Anatomy and relationships of *Lambeosaurus magnicristatus*, a crested hadrosaurid dinosaur (Ornithischia) from the Dinosaur Park Formation, Alberta. *Journal of Vertebrate Paleontology* 27: 373–393.

Gilmore, C.W. 1933. On the dinosaurian fauna of the Iren Dabasu Formation. *Bulletin of the American Museum of Natural History* 67: 23–78.

Gilmore, C.W. 1937. On the detailed skull structure of a crested hadrosaurian dinosaur. *Proceedings of the United States National Museum* 84: 481–491.

Gilmore, J.S., Knight, J.D., Orth, C.J., Pillmore, C.L., and Tschudy, R.H. 1984. Trace elements patterns at a non-marine Cretaceous–Tertiary boundary. *Nature* 307: 224–28.

Godefroit, P., Dong, Z.-M., Bultynck, P., Li, H., and Feng, L. 1998. New *Bactrosaurus* (Dinosauria: Hadrosauroidea) material from Iren Dabasu (Inner Mongolia, P.R. China). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 68 (Supplement): 3–70.

Godefroit, P., Zan, S., and Jin, L. 2000. *Charonosaurus jiayinensis* n.g., n.sp., a lambeosaurine dinosaur from the Late Maastrichtian of northeastern China. *Comptes rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes* 330: 875–882.

Godefroit, P., Zan, S., and Jin, L. 2001. The Maastrichtian (Late Cretaceous) lambeosaurine dinosaur *Charonosaurus jiayinensis* from north-eastern China. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 71: 119–168.

Godefroit, P., Bolotsky, Y., and Alifanov, V. 2003. A remarkable hollow-crested hadrosaur from Russia: an Asian origin for lambeosaurines. *Comptes Rendus Palevol* 2: 143–151.

Godefroit, P., Alifanov, V., and Bolotsky, Y. 2004a. A re-appraisal of *Aralosaurus tuberiferus* (Dinosauria, Hadrosauridae) from the Late Cretaceous of Kazakhstan. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 74 (Supplement): 139–154.

Godefroit, P., Bolotsky, Y.L., and Van Itterbeeck, J. 2004b. The lambeosaurine dinosaur *Amurosaurus riabinini*, from the Maastrichtian of Far Eastern Russia. *Acta Palaeontologica Polonica* 49: 585–618.

Hai, S.L. 2004. The dinosaur mass graves found in the Wulaga Region, Heilongjiang Province. *In*: Dong W. (ed.). *Proceedings of the Ninth Annual Symposium of the Chinese Society of Vertebrate Paleontology*, 9–16. China Ocean Press, Beijing.

Herngreen, G.F.W. and Chlonova, A.F. 1981. Cretaceous microfloral provinces. *Pollen et Spores* 23: 441–555.

Herngreen, G.F.W., Kedves, M., Rovnina, L.V., and Smirnova, S.B. 1996. Cretaceous palynofloral provinces: a review. *In*: J. Jansonius and D.C. McGregor (eds.), *Palynology: Principles and Applications*, 1157–1188. American Association of Stratigraphic Palynologists Foundation, College Station.

Horner, J.R. 1988. A new hadrosaur (Reptilia, Ornithischia) from the Upper Cretaceous Judith River Formation of Montana. *Journal of Vertebrate Paleontology* 8: 314–321.

Horner, J.R. 1992. Cranial morphology of *Prosaurolophus* (Ornithischia: Hadrosauridae) with description of two new hadrosaurid species and an evaluation of hadrosaurid phylogenetical relationships. *Museum of the Rockies Occasional Paper* 2: 1–119.

Horner, J.R., Schmitt, J.G., Jackson, F., and Hanna, R. 2001. Bones and rocks of the Upper Cretaceous Two Medecine-Judith River clastic wedge complex, Montana. *In*: C.L. Hill (ed.), Society of Vertebrate Paleontology 61th Annual Meeting: Mesozoic and Cenozoic Paleontology in the Western Plains and Rocky Mountains. *Museum of the Rockies Occasional Paper* 3: 1–14.

Horner, J.R., Weishampel, D.B., and Forster, C.A. 2004. Hadrosauridae. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria, second edition*, 438–463. University of California Press, Berkeley.

Hunt, A.P. and Lucas, S.G. 1993. Cretaceous vertebrates of New Mexico. *Bulletin of the New Mexico Museum of Natural History and Science* 2: 77–91.

Jerzykiewicz, T. and Russell, D.A. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research* 12: 345–377.

Jerzykiewicz, T. and Sweet, A.R. 1986. The Cretaceous–Tertiary boundary in the central Alberta Foothills. I: Stratigraphy. *Canadian Journal of Earth Sciences* 23: 1356–1374.

Kirillova, G.L. 2003. Cretaceous tectonics and geological environments in East Russia. *Journal of Asian Earth Sciences* 21: 967–977.

Kirillova, G.L., Markevich, V.S., and Bugdaeva, E.V. 1997. Correlation of geologic events in the Cretaceous basins of Southeast Russia. *Geology of Pacific Ocean* 13: 507–526.

Lambe, L.M. 1917. On *Cheneosaurus tolmanensis*, a new genus and species of trachodont dinosaur from the Edmonton Cretaceous of Alberta. *Ottawa Naturalist* 30: 117–123.

Lambe, L.M. 1920. The hadrosaur *Edmontosaurus* from the Upper Cretaceous of Alberta. *Memoirs of the Canada Department of Mines and Geological Survey* 120: 1–79.

Langston, W. Jr. 1960. The vertebrate fauna of the Selma Formation of Alabama. Part VI. The dinosaurs. *Fieldiana, Geological Memoirs* 3: 313–361.

Lauters, P. 2005. *Etude de population et taphonomie du gisement à hadrosauridés (Dinosauria: Ornithopoda) de Blagoveschensk, Russie*. 80 pp. Unpublished Master thesis, Université Libre de Bruxelles, Brussels.

Lauters, P., Bolotsky, Y.L., Van Itterbeeck, J., and Godefroit, P. (in press). Taphonomy and age profile of a latest Cretaceous dinosaur bonebed in Far Eastern Russia. *Palaios*.

Lehman, T.M. 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 60: 189–217.

Lehman, T.M. 1997. Late Campanian dinosaur biogeography in the Western Interior of North America. *In*: D.L. Wolberg, E. Stump, and G.D. Rosenberg (eds.), *Dinofest International*, 223–240. Academy of Natural Sciences, Philadelphia.

Lehman, T.M. 2001. Late Cretaceous Dinosaur Provinciality. *In*: D.H Tanke and K. Carpenter (eds.), *Mesozoic Vertebrate Life*, 310–328. Indiana University Press, Bloomington.

Lerbekmo, J.F., Sweet, A.R., and Davidson, R.A. 1999. Geochemistry of Cretaceous–Tertiary (K-T) boundary interval: south-central Saskatchewan and Montana. *Canadian Journal of Earth Sciences* 36: 717–724.

Lerberkmo, J.F., Sweet, A.R., and Louis, R.M.S. 1987. The relationship between the iridium anomaly and palynological floral events at three Cretaceous–Tertiary boundary localities in western Canada. *Geological Society of America Bulletin* 99: 325–330.

Leidy, J. 1858. *Hadrosaurus foulkii*, a new saurian from the Cretaceous of New Jersey. *Proceedings of the Academy of Natural Sciences of Philadelphia* 10: 215–218.

Li, X., Li, W., Chen, P., Wan, X., Li, G., Song, B., Jiang, J., Liu, J., Yin, D., and Yan, W. 2004. Shrimp U-Pb zircon dating of the uppermost Cretaceous Furao Formation near the Heilong River: An age closest to the K/T boundary. *Chinese Science Bulletin* 49: 860–862.

Markevich, V.S. 1994. Palynological zonation of the continental Cretaceous and early Tertiary of eastern Russia. *Cretaceous Research* 15: 165–177.

Markevich, V.S. [Markevič, V.S.] and Bugdaeva, E.V. 2001. Chapter 5: Correlation of the Upper Cretaceous and Palaeogene plant-bearing deposits of the Russian Far East [in Russian]. *In*: E.V. Bugdaeva (ed.), *Flora i dinozavry na granice mela i paleogena Zejsko-Bureinskogo Bassejna*, 79–96. Dal'nauka, Vladivostok.

Marsh, O.C. 1872. Notice on a new species of *Hadrosaurus*. *American Journal of Science, series 3* 3: 301.

Marsh, O.C. 1881. Classification of the Dinosauria. *American Journal of Science, series 3* 23: 81–86.

Maryańska, T. 1977. Ankylosauridae (Dinosauria) from Mongolia. *Palaeontologica Polonica* 30: 85–151.

Milner, A.R. and Norman, D.B. 1984. The biogeography of advanced ornithopod dinosaurs (Archosauria: Ornithischia)—a cladistic-vicariance model. *In*: W.-E. Reif and F. Westphal (eds.), *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers*, 145–150. Attempto Verlag, Tübingen.

Nichols, D.J. 2002. Palynology and biostratigraphy of the Hell Creek Formation in North Dakota: a microfossil record of plants at the end of Cretaceous time. *In:* J.H. Hartman, K.R. Johnson, and D.J. Nichols (eds.), *The Hell Creek Formation and the Cretaceous–Tertiary boundary in the northern Great Plains: an integrated continental record of the end of the Cretaceous. Geological Society of America, Special Paper* 361: 393–456.

Nichols, D.J., Jarzen, D.M., Orth, C.J., and Oliver, P.Q. 1986. Palynological and iridium anomalies at the Cretaceous–Tertiary boundary, South-Central Saskatchewan. *Science* 231: 714–717.

Norell, M.A. 1992. Taxic origin and temporal diversity: the effect of phylogeny. *In*: M. Novacek and Q. Wheelers (eds.), *Extinction and Phylogeny*, 89–118. Columbia University Press, New York.

Norman, D.B. 1998. On Asian ornithopods (Dinosauria: Ornithischia). 3. A new species of iguanodontid dinosaur. *Zoological Journal of the Linnean Society of London* 122: 291–348.

Norman, D.B. 2002. On Asian ornithopods (Dinosauria: Ornithischia). 4. Redescription of *Probactrosaurus gobiensis* Rozhdestvensky, 1966. *Zoological Journal of the Linnean Society of London* 136: 113–144.

Owen, R. 1842. Report on British fossil reptiles. Part II. *In*: *Report of the Eleventh Meeting of the British Association for the Advancement of Science, Held at Plymouth, July 1841*, 66–204. London.

Parks, W.A. 1920. The osteology of the trachodont dinosaur *Kritosaurus incurvimanus*. *University of Toronto Studies, Geological Series* 11: 1–74.

Parks, W.A. 1923. *Corythosaurus intermedius*, a new species of trachodont dinosaur. *University of Toronto Studies, Geological Series* 15: 5–57.

Parks, W.A. 1931. A new genus and two new species of trachodont dinosaurs from the Belly River Formation of Alberta. *University of Toronto Studies, Geological Series* 31: 1–11.

Prieto-Marquez, A. 2005. New information on the cranium of *Brachylophosaurus canadensis* (Dinosauria, Hadrosauridae), with a revision of its phylogenetic position. *Journal of Vertebrate Paleontology* 25: 144–156.

Rich, T.H., Vickers-Rich, P., Fernandez, M., and Santillana, S. 1999. A probable hadrosaur from Seymour Island, Antarctic Peninsula. *In*: Y. Tomida, T.H. Rich, and P. Vickers-Rich (eds.), *Proceedings of the second Gondwanan dinosaur symposium. National Science Museum Monographs* 15: 219–222.

Rogers, R.R. 1990. Taphonomy of three dinosaur bone beds in the Upper Cretaceous Two Medecine Formation of northwestern Montana: evidence for drough-related mortality. *Palaios* 5: 394–413.

Rogers, R.R. 2005. Fine-grained debris flows and extraordinary vertebrate burials in the Late Cretaceous of Madagascar. *Geology* 33: 297–300.

Rozhdestvensky, A.K. [Roždestvenskij, A.K.] 1952. Discovery of an iguanodont in Mongolia. [in Russian]. *Doklady AN SSSR* 84: 1243–1246.

Russell, D.A. 1993. The role of Central Asia in dinosaurian biogeography. *Canadian Journal of Earth Sciences* 30: 2002–2012.

Russell, D.A and Dong, Z.-M. 1993. A nearly complete skeleton of a new troodontid dinosaur from the Early Cretaceous of the Ordos Basin, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* 30: 2163–2173.

Seeley, H.G. 1887. On the classification of the fossil animals commonly called Dinosauria. *Proceedings of the Royal Society of London* 43: 165–171.

Sullivan, R.M. and Williamson, T.E. 1999. A new skull of *Parasaurolophus* (Dinosauria: Hadrosauridae) from the Kirkland Formation of New Mexico and a revision of the genus. *New Mexico Museum of Natural History and Science* 15: 1–52.

Sun, G., Akhmetiev, M.A., Dong, Z.M., Ashraf, A.R., Sun, Y.W., Bugdaeva, E.V., Dilcher, D.L., Golovneva, L., Harding, I., Johnson, K., Kezina, T.V., Kodrul, T.M., Lu, J.S., Markevich, V.S., Nishida, H., Okada, H., Park, S.O., Sun, C.L., Xiong, X.Z., Xing, Y.L., and Zhou, Z.L. 2002. In search of the Cretaceous–Tertiary boundary in the Heilongjiang River Area of China. *Journal of Geoscientific Research in Northeast Asia* 5: 105–113.

Sun, G., Akhmetiev, M.A., Ashraf, A.R., Sun, Y.W., Dong, Z.M., Bugdaeva, E.V., Markevich, V.S., Kezina, T.V., Kodrul, T.M., Johnson, K., Nichols, D.J., Nishida, H., Okada, H., Sun, C.L., Suzuki, S., Dilcher, D.L., Lu, J.S., Luo, K.L., Bolotsky, Y.L., Hicks, J.F., Yang, H.X., Harding, I., and Quan, C. 2004. Recent advance on the research of Cretaceous–Tertiary boundary in Jiayin of Heilongjiang, China. *In*: G. Sun, Y.W. Sun, M.A. Akhmetiev, and A.R. Ashraf (eds.), *Proceedings of the 3rd Symposium on Cretaceous Biota and K/T Boundary in Heilongjiang River Area*, 1–6. Changchun, China.

Suzuki, S. 2004. Fission-track zircon age of a tuff sample from the Tsagayan Formation, the Amur River Area, the Russian Far East. *In*: G. Sun, Y.W. Sun, M.A. Akhmetiev, and A.R. Ashraf (eds.), *Proceedings of the 3rd Symposium on Cretaceous Biota and K/T Boundary in Heilongjiang River Area*, 75–76. Changchun, China.

Suzuki, D., Weishampel, D.B., and Minoura, N. 2004. *Nipponosaurus sachalinensis* (Dinosauria: Ornithopoda): anatomy and systematic position within Hadrosauridae. *Journal of Vertebrate Paleontology* 24: 145–164.

Sweet, A.R., Braman, D.R., and Lerbekmo, J.F. 1999. Sequential palynological changes across the composite Cretaceous–Tertiary boundary claystone and contiguous strata, western Canada and Montana, U.S.A. *Canadian Journal of Earth Sciences* 36: 743–768.

Swofford, D.L. 2002. *Phylogenetic Analysis Using Parsimony (and Other Methods). Version 4.0b10*. 40 pp. Sinauer Associates, Sunderand, Massaschusetts.

Teissier, G. 1948. La relation d'allométrie. *Biometrics* 4: 14–48.

Van Itterbeeck, J., Bolotsky, Y.L., Bultynck, P., and Godefroit, P. 2005. Stratigraphy, sedimentology and palaeoecology of the dinosaur-bearing Kundur section (Zeya-Bureya Basin, Far Eastern Russia). *Geological Magazine* 142: 735–750.

Weishampel, D.B. 1984. Evolution of jaw mechanisms in ornithopod dinosaurs. *Advances in Anatomy, Embryology and Cell Biology* 87: 1–110.

Weishampel, D.B. 1996. Fossils, phylogeny and discovery: a cladistic study of the history of tree topologies and ghost lineage durations. *Journal of Vertebrate Paleontology* 16: 191–197.

Weishampel, D.B. and Horner, J.R. 1990. Hadrosauridae. *In*: D.B. Weishampel, P. Dodson, and H. Osmólska (eds.), *The Dinosauria*, 534–561. University of California Press, Berkeley.

Weishampel, D.B., Norman, D.B., and Grigorescu, D. 1993. *Telmatosaurus transsylvanicus* from the Late Cretaceous of Romania: the most basal hadrosaurid dinosaur. *Palaeontology* 36: 361–385.

Xu, X., Clark, J.M., Forster, C.A., Norell, M.A., Erickson, G.M., Eberth, D.A., Jia, C., and Zhao, Q. 2006. A basal tyrannosauroid from the Late Jurassic of China. *Nature* 439: 715–717.

Young, C.C. 1958. The dinosaurian remains of Laiyang, Shantung. *Palaeontologia Sinica, series C* 16: 1–138.

Appendix 1

Indeterminate hadrosaurid material from Wulaga.

Cervical vertebrae: GMH W137, W143, W159-A, W204, W234, W244, W340, W400-1, W400-8, W406-C, W407.

Dorsal vertebrae: GMH W35, W130, W154, W224, W225, W226, W247, W326, W427

Sacra: W163, W344, W400-5.

Caudal vertebrae: GMH W8, W172, W231, W281, W288, W342-A, W342-B, W358, W399, W400-9, W471-A.

Ulnae: GMH W36, W111, W126, W127, W151, W167, W208, W216, W253, W283, W352-B, W 400-6.

Radii: GMH W16, W17, W18, W124, W235, W241-A, W241-B, W310, W343, W378, W388, W398, W400-4.

Tibiae: GMH W5, W9, W11, W30, W50-3, W104, W115, W123, W128, W129, W139, W143, W144, W153-A, W165, W167, W168, W169, W185, W194, W211, W239, W242, W251, W253, W294, W296, W298, W299, W302-A, W304, W316, W328, W355, W356, W390, W391, W393, W409, W400-10A, W413, W415, W426, W427, W430, W447, W460, W464, W468, W477, WJ1, WJ3, WJ9, WJ10, WJ13, WJ15, WJ15-A, WJ6.

Fibulae: GMHW12, W17, W29, W32, W38, W41, W50-2, W51, W108, W181, W190, W203, W205, W212, W229, W236, W240, W250, W251, W254, W265, W267, W280, W281, W285, W292, W295, W302, W305, W319, W325, W374, W392, W400-11, W400-12, W405, W408, W411, W456, WJ6, WJ7, WJ12.

Femora: GMH W40, W44, W47, W50, W50-4, W100, W114, W122, W125, W142, W143, W155, W161, W164, W167, W168, W169, W195, W22, W239, W261, W270-A, W275, W287, W291, W292, W293, W300, W308, W312, W314, W315, W316, W368, W400, W412, W415, W416, W420, W424, W464, WJ18.

Metatarsals II: GMH W28, W53, W147, W213, W274.

Metatarsals III: GMH W34, W51, W107, W150, W198, W277, W394, W397, W400-6, W400-14.

Metatarsals IV: GMH W55, W93, W228-A.

Appendix 2

Characters and character states used for the phylogenetic analysis of *Sahaliyania elunchunorum* and *Wulagasaurus dongi*. Compiled from Weishampel et al. (1993), Godefroit et al. (1998, 2001, 2004a, b), Bolotsky and Godefroit (2004), Horner et al. (2004), Prieto-Marquez (2005), and Evans and Reisz (2007).

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. Parietal sagittal crest relatively short, less than 2/3 the length of the parietal (0), or relatively long, more than 2/3 the length of the parietal (1). *Contra* Horner et al., 2004.
4. Midline ridge of parietal straight to slightly downwarped along length (0), or strongly downwarped to below the level of the postorbital-squamosal bar (1).
5. Frontal participating in the orbital rim (0), or excluded by postorbital-prefrontal joint (1).
6. Hollow supracranial crest absent (0), or developed (1).
7. Frontal relatively long, with a "caudal length/maximal width" ratio >0.75 (0), very shortened frontal, with a "caudal length/maximal width" <0.6 (1), or secondary elongation resulting of the backward extension of the frontal platform (2). Character treated as ordered.
8. Deeply excavated frontal platform absent (0), occupying the rostral part of the frontal in adult (1), or extending above the rostral portion of the supratemporal fenestra (2). Character treated as ordered.
9. Premaxillae narrow, expanded laterally less than two times width at post-oral constriction, margin oriented nearly vertically (0), or expanded transversely to more than two times postoral constriction, margin flared laterally into a more horizontal orientation (1).
10. Premaxillary reflected rim absent (0), deflected at anterolateral corner and posteriorly reflected (1), reflected along entire rim and narrow (2), reflected along entire rim, but thickened at anteroventral corner (3). Character treated as ordered.
11. Premaxillary foramen present (0), or absent (1).
12. Premaxillary, auxiliary narial fossa absent (0), or present (1).
13. Posterior premaxillary process short, not meeting the lateral premaxillary process posterior to external naris (0), or posterior premaxillary process long, meeting the lateral premaxillary process behind the external naris to exclude the nasal, nasal passage enclosed ventrally by folded, divided premaxillae (1).
14. Lateral premaxillary process stopping at the level of the lacrimal (0), or extending further backward above the skull roof (1). Character treated as unordered.
15. External naris/basal skull length ratio <0.2 (0), or >0.3 (1).
16. Posteriormost apex of external naris formed entirely by nasal (0), formed by nasal (dorsally) and premaxilla (ventrally) (1), or formed entirely by premaxilla (2). Character treated as unordered.
17. Circumnarial depression absent (0), light depression incised into nasal and premaxilla (1), or marked by a well-developed ridge and sometimes invagined (2). Character treated as ordered.
18. Nasal restricted to area rostral to braincase, *cavum nasi* small (0), or nasal retracted caudally to lie over braincase in adults resulting in convoluted, complex narial passage, *cavum nasi* enlarged (1).

19. Nasal does not participate in a hollow crest (0), participates in a small part of the hollow crest and is excluded from the caudodorsal border of the crest (1), participates in half of the crest or more and forms the caudodorsal aspect of the crest (2), or forms the entire crest (3, autapomorphic for *Tsintaosaurus*). Character treated as unordered.
20. Solid supracranial crest absent (0), present but not excavated by the caudal circumnarial fossa (1), present and excavated laterally by the circumnarial fossa (2). Character treated as unordered.
21. Supraorbital free (0), or fused to the prefrontal (1).
22. Caudal portion of the prefrontal oriented horizontally (0), or participating in the lateroventral border of the hollow crest (1).
23. Median ramus of squamosal lower than paroccipital process (0), or higher than paroccipital process (1).
24. Squamosal prequadratic process strikingly longer than rostrocaudal width of quadrate cotylus (0), or short, only slightly longer than rostrocaudal width of quadrate cotylus (1).
25. Posterior surface of supraoccipital nearly vertical (0), or steeply inclined forwardly at an angle of about 45° (1).
26. Supraoccipital/exoccipital shelf limited (0), or very extended (1) above the foramen magnum.
27. Postorbital pouch absent (0), or well-developed (1).
28. Dorsal surface of postorbital flat (0), or thickened to form a dorsal promontorium (1).
29. Rostral process of the jugal tapering in lateral view to fit between maxilla and lacrimal (0), or dorso-ventrally expanded (1).
30. Rostral process of the jugal angular and slightly asymmetrical in lateral view (0), rounded and symmetrically very expanded (1), isosceles-triangle-shaped (2), or asymmetrically strongly upturned (3). Character treated as unordered.
31. Jugal flange slightly developed, dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange approximately equal to minimum dorsoventral depth of rostral segment of jugal between rostral and postorbital process (0), dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange less than twice minimum dorsoventral depth of rostral segment of jugal between rostral and postorbital process (1), or strongly projected ventrally into semicircular boss, dorsoventral depth of jugal from ventral border of infratemporal fenestra to ventral edge of flange twice or nearly twice minimum dorsoventral depth of rostral segment of jugal between rostral and postorbital process (2). Character treated as ordered.
32. Apex of maxilla caudal to centre (short caudal portion of maxilla) (0), or at or rostral to center (long and robust caudal portion of maxilla) (1).
33. Maxillary foramen on rostrolateral maxilla (0), or on dorsal maxilla along maxilla-premaxilla suture (1).
34. Ectopterygoid ridge faintly developed and inclined caudally (0), or strongly developed and nearly horizontal (1).
35. Rostromedial process developed on the maxilla (0), or wide sloping maxillary shelf (1).
36. Paraquadratic foramen present (0), or absent (1).
37. Distal head of quadrate transversely expanded (0), or dominated by a large hemispheric lateral condyle (1).
38. Diastema between first dentary tooth and predentary short, no more than width of 4 or 5 teeth (0), moderate, equal to approximately 1/5 to 1/4 of tooth row (1), long, more than 1/3 of tooth row, but less than 1/2 (2), or extremely long, more than 2 of tooh row (3). Character treated as ordered.
39. Coronoid process sub-vertical (0), or inclined rostrally (1).
40. Rostral mediolateral width of predentary less than or equal to rostrocaudal length of lateral process (0), rostral mediolateral width greater than or equal to rostrocaudal length of lateral process (1), or rostral mediolateral width greater twice rostrocaudal length of lateral process (2). Character treated as ordered.
41. Number of tooth positions in dentary tooth row (adult specimens): 30 or less (0), 34–40 (1), 42–45 (2), 47 or more (3). Character treated as ordered.
42. Dentary crowns broad with a dominant ridge and secondary ridges (0), or miniaturised with or without faint secondary ridges (1).
43. Median carina of dentary teeth straight, (0) or sinuous (1).
44. A maximum of 7 (0), or a minimum of 8 (1) sacral vertebrae.
45. Posterior dorsal and sacral neural spines relatively short, less than 3 times centrum height (0), or elongate, more than three times centrum height (1).
46. Coracoid hook small and pointed ventrally (0), or prominent and pointed cranioventrally (1).
47. Biceps tubercle on coracoid small (0), or large and laterally projecting (1).
48. Proximal plate of sternal shorter than distal “handle” (0), or proximal plate longer than distal “handle” (1).
49. Deltopectoral crest of the humerus moderately (0), or strongly developed, extending down below midshaft (1).
50. Antitrochanter of ilium absent or poorly developed (0), or prominent (1).
51. Ischial peduncle of ilium as a single large knob (0), or formed by two small protrusions separated by a shallow depression (1).
52. Postacetabular process of ilium tapers caudally to nearly a point, wide brevis shelf (0), or postacetabular process sub-rectangular, no brevis shelf (1).
53. Distal end of ischium forming a moderately expanded knob (0), hypertrophied and footed (1), or tapering distally (2). Character treated as unordered.
54. Distal head of fibula moderately expanded into the shape of a ball (0), or greatly expanded and club-shaped (1).
55. Cranial ascending process of astragalus laterally skewed (0), or equilateral in shape (1).
56. Plantar keels on unguals absent (0), or present (1).

Appendix 3

Character matrix used for the phylogenetic analysis of *Sahaliyania elunchunorum* and *Wulagasaurus dongi*.

	1–5	**6–10**	**11–15**	**16–20**	**21–25**	**26–30**	**31–35**	**36–40**	**41–45**	**46–50**	**51–55**	**56**
Bactrosaurus	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	0
Aralosaurus	?1?00	100??	?????	??0?0	101?1	0001?	?0111	11???	?????	?????	?????	?
Tsintaosaurus	01001	10010	??0??	??030	11001	00011	10111	11111	11111	11111	11100	0
Jaxartosaurus	01001	101??	?????	????0	11001	0001?	?????	?????	?????	?????	?????	?
Amurosaurus	01011	101??	?????	????0	11101	00011	10111	1111?	111??	11111	11100	0
Corythosaurus	01011	11110	10110	20120	11101	00011	10111	11111	21111	11111	11100	0
Hypacrosaurus	01011	11110	10110	20120	11101	00011	10111	11111	21111	11111	11100	0
Olorotitan	01011	11110	10110	20120	11??1	0??11	10111	1111?	21111	11111	11100	0
Lambeosaurus	01011	11110	10110	20110	11101	00011	10111	11111	21111	11111	11100	0
Parasaurolophus	11011	12210	10100	20110	11101	00111	10111	11111	21111	11111	11111	0
Charonosaurus	11011	112??	?????	????0	11101	00111	10111	1111?	?1111	11111	11111	0
Sahaliyania	?10?1	111??	?????	????0	11??1	0??11	101?1	1111?	211??	??111	111??	?
Wulagasaurus	?00??	?????	?????	?????	????1	0????	?1?1?	??11?	?????	??00?	??2??	?
Maiasaura	00100	00011	01000	01001	10011	00012	21110	11112	21010	11001	11200	1
Brachylophosaurus	00100	00011	01001	01001	10011	00012	21110	11212	21010	11001	11200	1
Gryposaurus	00100	00012	01001	01000	10001	10013	11110	11111	21010	11001	11200	0
Kerberosaurus	001?1	000??	?????	?2??0	10001	1?013	11110	11???	2?0??	11???	?????	0
Saurolophus	00101	00012	01001	12002	10001	10013	11110	11211	31?10	11001	11200	?
Prosaurolophus	00101	00012	01001	12002	10001	10013	11110	11211	21010	11001	11200	0
Anatotitan	00100	00013	01001	12000	10001	11013	11110	11311	31010	11001	11200	0
Edmontosaurus	00100	00013	01001	12000	10001	11013	11110	11311	31010	11001	11200	0

Appendix 4

List of apomorphies for all ingroup taxa. Letters indicate nodes designated in Fig. 18. For multistate characters, the number between brackets refers to the character state (see Appendix 3). Characters are followed by an "a", when supported only by ACCTRAN or accelerated optimisation, and by a "d" when supported only by DELTRAN, or delayed optimisation; bs, bootstrap value.

A (Hadrosauridae): 9, 21, 25, 29, 31(1), 33, 34, 36, 37, 38(1), 39, 40(1), 41(1), 42, 44, 46, 47, 50, 51, 52.

B (Lambeosaurinae; bs = 93): 2, 6, 11a, 16(2)a, 19(1)a, 30(1)a, 35, 43a, 45a, 48a, 49a, 53(1)a.

C (bs = 79): 5, 22, 30(1)d, 43d, 45d, 48d, 49d, 53(1)d.

D (bs = 54): 8(1), 13a, 18a.

E (bs = 59): 4, 23.

F (bs = 70): 7(1), 41(2), 11d, 13d, 16(2)d, 18d, 19(1)d.

G (parasauroloph clade: Chapman and Brett-Surman 1990; bs = 95): 1, 28, 54, 55.

H (corythosaur clade: Chapman and Brett-Surman 1990; bs = 82): 14.

I (bs = 63): 19(2).

J (Hadrosaurinae; bs = 76): 10(1)a, 12a, 15a, 17(1)a, 30(2)a, 32, 41(2)a, 53(2).

K (bs = 75): 3, 10d, 12d, 17(1)d, 41(2)d.

L (bs = 88): 20(1), 24, 30(2), 31(2), 40(2), 56.

M (bs = 72): 10(2), 15d, 26, 30(3), 38(2)a.

N (bs = 78): 16(1), 17(2), 38(2).

O (bs = 54): 5.

P (bs = 58): 20(2).

Q (bs = 95): 10(3), 27, 38(3), 41(3).