

A re-appraisal of *Aralosaurus tuberiferus* (Dinosauria, Hadrosauridae) from the Late Cretaceous of Kazakhstan

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Abstract

Aralosaurus tuberiferus ROZHDESTVENSKY, 1968 (Dinosauria: Hadrosauridae) is based on a fragmentary skull from the Beletinskaya Svita (?Turonian, Late Cretaceous) from the Sakh-Sakh locality of central Kazakhstan. Redescription of the type material reveals that it is a valid taxon, characterised by a hollow nasal crest-like structure located far in front of the orbits and by a well-developed curved crest on the maxilla that borders laterally the caudal part of the premaxillary shelf. Phylogenetic analysis, based on 36 cranial characters, indicates that *A. tuberiferus* is the most basal lambeosaurine hadrosaurid known to date; it is therefore not a gryposaur-like hadrosaurine as previously described. Lambeosaurines originated from Asia and then migrated to North America before or at the beginning of the late Campanian. They remained well diversified in eastern Asia until the late Maastrichtian.

Key-words: *Aralosaurus tuberiferus*, Hadrosauridae, Lambeosaurinae, Late Cretaceous, Kazakhstan, phylogeny, palaeobiogeography.

Résumé

Aralosaurus tuberiferus ROZHDESTVENSKY, 1968 (Dinosauria: Hadrosauridae) est décrit sur base d'un crâne fragmentaire découvert dans la Beletinskaya Svita (?Turonien, Crétacé supérieur) du site de Sakh-Sakh au Kazakhstan central. La redescription du matériel type indique qu'il s'agit bien d'un taxon valide, caractérisé par la présence d'une structure en forme de crête creuse située bien à l'avant des orbites et par une crête courbée très développée sur le maxillaire bordant la portion caudale du rebord prémaxillaire. L'analyse phylogénétique, basée sur 36 caractères crâniens, indique qu'*A. tuberiferus* est le lambeosauriné le plus basal connu à ce jour; ce n'est donc pas un hadrosauriné proche de *Gryposaurus*, comme on le pensait avant. Les lambeosaurinés sont apparus en Asie et ont migré en Amérique du Nord avant ou au début du Campanien supérieur. Ils sont restés bien diversifiés en Asie jusqu'au Maastrichtien supérieur.

Mots-clefs: *Aralosaurus tuberiferus*, Hadrosauridae, Lambeosaurinae, Crétacé supérieur, Kazakhstan, phylogénie, paléobiogéographie.

Introduction

Hadrosauroida, or “duck-billed” dinosaurs, can be defined as those dinosaurs more closely related to Hadro-

sauridae than to *Iguanodon* (WEISHAMPEL & HORNER, 1990; SERENO, 1998). They were the most successful herbivorous dinosaurs in Laurasia during the closing stages of the Cretaceous. During the Campanian and Maastrichtian, they were the primary constituents of many terrestrial vertebrate faunas. In western North America, hundreds of fragmentary to complete hadrosaurid specimens have been collected, including remains of eggs, embryos, hatchlings and juveniles. They were apparently spread world-wide: besides North America, fossils have also been discovered in Central America, South America, Europe, Asia (WEISHAMPEL & HORNER, 1990) 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, characterised by an improved mobility of the upper jaw and by an elaborated dental battery well adapted for feeding on hard vegetables (NORMAN, 1984; WEISHAMPEL, 1984). Besides typical hadrosaurids, the hadrosauroid clade includes a number of less derived forms that evolved in Laurasia from the late Early Cretaceous (YOU *et al.*, 2003) until the Maastrichtian. Hadrosauridae includes members of Hadrosaurinae and Lambeosaurinae subfamilies and their most recent common ancestor (WEISHAMPEL & HORNER, 1990; WEISHAMPEL *et al.*, 1993). With the exception of HORNER (1988, 1990, 1992), all the authors working on hadrosauroid phylogeny accept the monophyly of Hadrosauridae and, within this family, that of the subfamilies Hadrosaurinae and Lambeosaurinae. ‘Flat-headed’ Hadrosaurinae is e.g. characterised by the development of depressed areas around the external nares and by the lateral expansion of their premaxillary beak. Some hadrosaurines, such as *Prosaurolophus*, *Saurolophus*, *Brachylophosaurus* or *Maiasaura* are characterised by the presence of a low, solid cranial crest, whereas others, such as *Edmontosaurus*, *Anatotitan*, or *Gryposaurus*, lack any kind of crest development. Lambeosaurinae is characterised by an important diversity of hollow cranial crests. The nasal cavity is completely modified and extends into this hollow crest, following a very tortuous route. With this hollow crest, it is postulated that lambeosaurines could produce different kinds of trumpeting noises. As different species are char-



Fig. 1 — Geographical location of sites from which hadrosauroid dinosaurs have been recovered in Kazakhstan.

acterised by different shapes of crests, they produced different noises.

Dinosaur discoveries in Central Asia began at the end of the 19th century, when the Russian geologist ROMANOVSKY (1882) described dinosaur tracks on the right bank of Yaknob River, in Tajikistan. In the second decade of the 20th century, more intensive and systematic geological investigations in Eastern Russia and Central Asia lead to the discovery of new dinosaur localities in the Transbaikalian Region, along Amur River, and in Kyzyl Kum Desert of Central Asia (ROZHDESTVENSKY, 1977).

From 1923 to 1926, the Geological Committee of USSR excavated the Kyrk-Kuduk dinosaur locality in the Chuley region of Shymkent / Tashkent area in eastern Kazakhstan (Fig. 1). Most of the fossils were discovered within a conglomerate, possibly Santonian in age (AVERANOV & NESSOV, 1995). RIABININ (1939) described two hadrosaurid taxa from this locality: *Jaxartosaurus aralensis* and *Bactrosaurus prynadai*. *Bactrosaurus prynadai* is based on two dentaries and one maxilla belonging

to juvenile individuals. This taxon is unanimously regarded as a *nomen dubium* (MARYAŃSKA & OSMÓLSKA 1981; WEISHAMPEL & HORNER 1990). *Jaxartosaurus aralensis* was described from the caudal part of one skull, one dentary, one surangular and a few postcranial elements. This taxon can be regarded as a basal Lambeosaurinae (GODEFROIT *et al.*, in press; see also below).

EFREMOV (1932, 1933, 1944) subsequently investigated Central Asian dinosaur localities, from the Aral Sea (Kazakhstan – Uzbekistan) to Issyk-Kul Lake (Kirgizstan), especially from a taphonomic point of view. He concluded that dinosaur-bearing beds were intensively re-deposited during the Paleogene in a vast area north of the Tien-Shan Mountains. As a result of their secondary re-deposition, the bones are found separated and rolled in this area. This theory led to a decreasing interest to Central Asian dinosaur localities, because the probability to find more or less complete skeletons appeared very low.

Subsequent discoveries of more complete dinosaur material in Central Asia partly invalidated EFREMOV's

theory, indicating that the reworking of bone-bearing sediments north of the Tien-Shan was more local than previously thought and occurred during the first half of the Late Cretaceous rather than during the Paleogene (ROZHDESTVENSKY, 1977). In 1957, an expedition of the USSR Academy of Sciences discovered a hadrosaur skull *in situ* in the Beleutinskaya Svita of Sakh-Sakh locality in central Kazakhstan. The age of this formation is not well established: ROZHDESTVENSKY (1974, 1977) advocated for a Turonian age, but without any justification. This specimen, regarded as a hadrosaurine, was described under the name *Aralosaurus tuberiferus* ROZHDESTVENSKY, 1968. In 1961, the nearly complete skeleton of a hadrosaurid was discovered at the Syuk-Syuk wells site, in the same area as the type material of *Jaxartosaurus*, but in a different formation: the Dabrazinskaya Svita (Santonian-Campanian: ROZHDESTVENSKY; lower Santonian: ROZHDESTVENSKY, 1977). This specimen, named *Procheoneosaurus convincens* ROZHDESTVENSKY, 1968, may be attributed to a juvenile lambeosaurine.

Arstanosaurus akkurganensis SHILIN & SUSLOV, 1982 was described on the basis of the caudal end of a left maxilla, an associated distal end of a femur and a single isolated tooth, from the Akkurgan locality in central Kazakhstan. Palaeobotanical data suggest a Santonian-Campanian age for the Bostobinskaya Svita, where those fossils were discovered (SHILIN & SUSLOV, 1982). According to NORMAN & KURZANOV (1997), it is not possible to assign the type-material of *Arstanosaurus* to any of the presently known hadrosaurid genera from Kazakhstan, but the most anatomically similar taxon to *Arstanosaurus* would be *Bactrosaurus johnsoni*, from the Iren Dabasu Formation of Erenhot (Inner Mongolia, P.R. China). They therefore suggested a Coniacian-Santonian age for both formations. However, it must be noted that the maxillae of *Arstanosaurus* and *Bactrosaurus* mainly share plesiomorphic characters: dorsal process of maxilla displaced caudally from mid-length of the maxilla, ectopterygoid ridge relatively weak and arched ventrally, and jugal process moderately developed into a small, diagonal projection that locked into a recess on the medial surface of the jugal. Consequently, it is more realistic to refer *Arstanosaurus* as some basal, but indeterminate hadrosauroid.

More recently, NESSOV intensively prospected Mesozoic localities in remote deserts of Central Asia and assembled a considerable collection of fossil vertebrates. He reported the discovery of many isolated hadrosaurid bones at various Late Cretaceous localities in Kazakhstan (NESSOV, 1995, 1997). Unfortunately, all these specimens appear too fragmentary to be diagnostic below familial level.

If their Turonian-Santonian age could be confirmed, the hadrosaurid specimens from Kazakhstan should be the earliest representatives of this family known to date and would fill an important gap in the evolutionary history of hadrosauroid dinosaurs, between late Early Cretaceous – early Late Cretaceous basal, non-hadrosaurid, Hadrosauroidae and Campano-Maastrichtian Hadrosauridae.

In the present paper, the holotype specimen of *Aralosaurus tuberiferus* will be re-examined, because it appears to us that its phylogenetic affinities have not yet been correctly established.

Abbreviations: AEHM: Amur Natural History Museum (Blagoveschensk, Russia); PIN: Palaeontological Institute of the Russian Academy of Sciences (Moscow).

Systematic palaeontology

Dinosauria OWEN, 1842
Ornithischia SEELEY, 1887
Ornithopoda MARSH, 1881
Ankylopollexia SERENO, 1986
Hadrosauriformes SERENO, 1986
Hadrosauroidae COPE, 1869
Hadrosauridae COPE, 1869
Lambeosaurinae PARKS, 1923

Aralosaurus ROZHDESTVENSKY, 1968

Type species. – *Aralosaurus tuberiferus* ROZHDESTVENSKY, 1968

Generic diagnosis. – See specific diagnosis (monospecific genus).

Aralosaurus tuberiferus ROZHDESTVENSKY, 1968

Holotype – PIN 2229, a partial skull comprising much of the skull roof, braincase and left side of the facial region. ROZHDESTVENSKY (1968) also referred postcranial elements to this form, but these bones are apparently lost.

Locus typicus – Sakh-Sakh locality in central Kazakhstan.

Stratum typicum – Beleutinskaya Svita (?Turonian, Late Cretaceous: ROZHDESTVENSKY, 1974, 1977).

Emended diagnosis – Paired nasals rising dorsally far in front of the orbits, forming or participating in a hollow crest-like structure; well-developed curved crest bordering laterally the caudal part of the premaxillary shelf and making the maxilla look trapezoidal in lateral view. Differs also from all other known Lambeosaurinae by the following plesiomorphic characters: frontals participating in the orbital rim and horizontally-oriented prefrontals not participating in the lateral wall of the hollow crest.

Description

Nasal (Fig. 2, A-B; Pl. 1, A-B & D) – Although it is only partly preserved, the nasal is probably the most diagnostic element in the skull of *Aralosaurus*. This bone is not dorsocaudally displaced as in typical Lambeosaurinae,

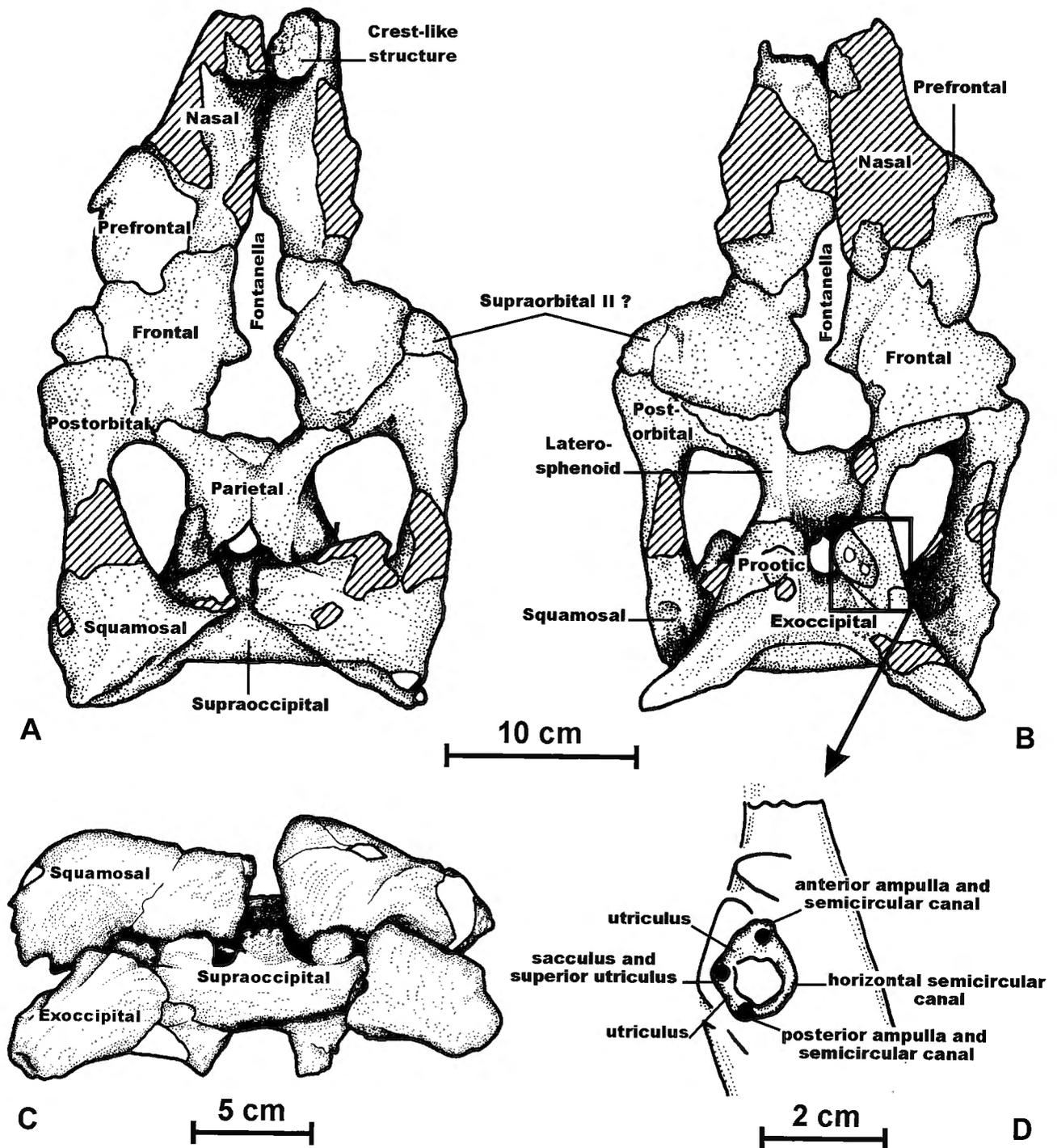


Fig. 2 — Holotype skull of *Aralosaurus tuberiferus* (PIN 2229), from the Beleutinskaya Svita (Late Cretaceous) of Sakh-Sakh locality (Kazakhstan). A: dorsal view; B: ventral view; C: occipital view; D: detail of left otic region.

but keeps its plesiomorphic position, in front of the frontal, as usually observed in basal hadrosauroids and in crestless Hadrosaurinae. The caudal part of the nasal is firmly fixed to the skull roof, being 'sandwiched' between the frontal and the prefrontal. Indeed, the caudal border of the nasal overlaps the rostral border of the frontal, but is widely covered laterally by the medial border of the prefrontal (the dorsal surface of the nasal

is widely depressed at this level). The caudomedial borders of the paired nasals are very thin and emarginated, forming the rostral part of the large fontanella. Rostrally, the nasal suddenly rises upwardly, forming some kind of horn-like or crest-like structure. Unfortunately, this structure is broken off at its base, so it is not possible to infer its shape. Contrary to all other known hadrosaurids except *Lophorhodon atopus*, this nasal structure lies well forward

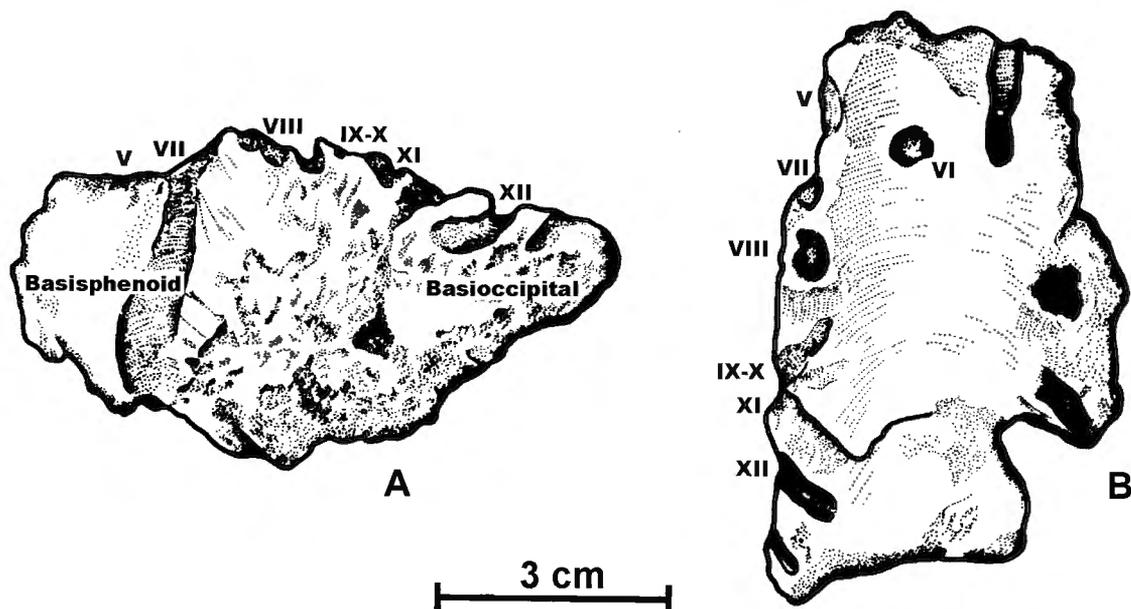


Fig. 3 — Fragmentary basioccipital-basisphenoid of *Aralosaurus tuberiferus* (PIN 2229), from the Beleutinskaya Svita (Late Cretaceous) of Sakh-Sakh locality (Kazakhstan), showing the presumed location of the foramina for cranial nerves V – XII. **A**: left lateral view; **B**: dorsal view.

of the orbits. In rostral view, this structure is clearly hollow in *Aralosaurus*: it is deeply excavated rostrally by a wide groove that directly communicates with the ventral side of the posterior part of the nasal. It is therefore clear that, in *Aralosaurus*, the nasal crest-like structure enclosed a part of the respiratory tract.

Maxilla (Fig. 4; Pl. 1, E-F) – In medial view, the maxilla of *Aralosaurus* looks elevated and asymmetrical, the dorsal process lying behind the middle of the length of the bone. Its medial surface is pierced by a series of interconnected dental foramina. Its lateral surface is pierced by four large foramina. The ectopterygoid shelf is wide and the ectopterygoid ridge, strong and perfectly straight. Behind the dorsal process, the dorsal border of the ectopterygoid shelf forms a strong, medially-inclined palatine process, whose caudal aspect bears a large and roughened articular facet for the palatine. A smaller pterygoid process is developed more caudally on the dorsal border of the pterygoid shelf. The lacrimal forms a deep articular facet on the rostralateral side of the dorsal process. The rostral portion of the maxilla forms a wide shelf, which supported the inner aspect of the maxilla-premaxilla contact. The dorsomedial border of the maxillary shelf is thickened and forms a wide, concave and triangular facet for articulation with the vomer. In front of the dorsal process, the dorsolateral border of the maxilla is developed into a very elevated curved ridge that forms the lateral wall of the premaxillary shelf. The caudal horizontal portion and rostral vertical portions of this ridge form a 90° angle. It must be noted that the great development of this ridge probably limited the potential

for lateral rotation at the maxilla-premaxilla joint implied by the streptostyly mechanism (WEISHAMPEL, 1984). At the base of the curved lateral ridge, a large canal penetrates the premaxillary shelf to open into the very excavated caudomedial surface of the dorsal process. A short, but very deep dorsal sulcus is concealed between, on the one hand, the rostralateral aspect of the dorsal process and, on the other hand, the caudal horizontal part of the curved lateral ridge and the dorsal border of the rostral process of the jugal.

Jugal (Fig. 4; Pl. 1, E-F) – The left jugal of PIN 2229 is still articulated with the maxilla. It is however incompletely preserved. The rostral process is clearly dorsoventrally expanded, as usual in Hadrosauridae, but is nearly completely reconstructed with plaster, so that few valuable characters may be observed on this usually instructive part of the skull. A large lacrimal facet notches the dorsal border of the rostral process. The postorbital process is slender and nearly perpendicular to the great axis of the bone. It is roughly triangular in cross-section although it is very flattened mediolaterally. The neck between the rostral and postorbital processes is relatively long and slender. The caudal process of the jugal is broken off. The ventral flange is rather well developed.

Lacrimal (Fig. 4; Pl. 1, E-F) – Only a very small portion of the lacrimal, in articulation with the dorsal process of the maxilla and with the lacrimal facet of the jugal, is preserved. The ventral floor of the lacrimal canal forms the dorsal side of the preserved fragment. This canal forms a 45° angle with the long axis of the maxilla.

Prefrontal (Figs. 2, A & B; Pl. 1, A & B) – The prefrontal of *Aralosaurus* is also a massive bone. In lateral view, it is flattened and crescentic in outline, forming the rostrorodorsal margin of the orbit. The lateral margin of the prefrontal is roughened, as usually observed in hadrosaurids. According to MARYAŃSKA & OSMÓLSKA, (1979), this roughened lateral area would in fact correspond to supraorbital I, completely fused to the 'true' prefrontal. At the level of the rostrorodorsal corner of the orbit, the dorsal side of the prefrontal is pierced by two foramina, which open into the roof of the orbit. In dorsal view, the prefrontal is very wide. Its medial border is thin and overlaps the nasal. The caudal border of the prefrontal, which articulates with the frontal, is roughened. It forms a stout pyramidal caudomedial process that fits into the deep rostral notch of the frontal.

Frontal (Fig. 2, A & B; Pl. 1, A & B) – The frontal of *Aralosaurus* is massive and particularly wide. Its dorsal surface is essentially flat; however, the bone is slightly more elevated medially, so that it looks slightly concave mediolaterally. The frontal is very thick caudally and forms a persillate and interdigitate contact with the parietal. The caudolateral side of the frontal is also thickened and roughened for interdigitate contact with the postorbital. A small rounded bone, pierced by a foramen, is wedged between the frontal and the postorbital, along the orbital margin. It most probably represents supraorbital II (MARYAŃSKA & OSMÓLSKA, 1979). The rostromedial side of the frontal also contacts the prefrontal in a strong interdigitate suture. Inside the articular facet for the prefrontal, the rostral margin of the frontal is perforated by a deep depression for insertion of the caudomedial process of the prefrontal. This peculiar articulation can also be observed in the basal hadrosauroid *Bactrosaurus johnsoni* (see GODEFROIT *et al.*, 1998, fig. 9). Between the prefrontal and "postorbital II" articular surfaces, the frontal participates for a short distance in the dorsal margin of the

orbit. The frontal and the nasal articulate along a relatively short suture. The rostromedial margin of the frontal is very thin and concave where it formed the caudal margin of a large fontanella.

In ventral view, the caudomedial portion of the frontal is very deeply excavated by the rostral part of the cerebrum. Around this area, strong rugosities mark the contact area with the laterosphenoid and orbitosphenoid portions of the braincase. Rostromedially, the ventral side of the frontals bears elongate but shallow encephalic impressions for the olfactory lobes.

Postorbital (Figs. 2, A & B; Pl. 1, A & B) – The postorbital of *Aralosaurus* is particularly robust. Its caudal process is a stout and perfectly straight rod, whose lateral side is regularly convex, whereas its flattened medial side covers the rostral process of the squamosal along nearly its whole length. The caudal process progressively becomes mediolaterally thinner caudally. The dorsal process of the postorbital is very thick. Its roughened medial border forms a strong interdigitate suture with the frontal and its caudomedial corner contacts the parietal along a short distance. The rostral border of the dorsal process is not completely fused with the small element interpreted as supraorbital II. The jugal process is broken off; it is triangular in cross-section and particularly robust. At the junction between the three processes, the internal side of the postorbital forms a pocket-like depression that received the postorbital process of the laterosphenoid.

Parietal (Fig. 2, A; Pl. 1, A) – Although it is incompletely preserved, the parietal of *Aralosaurus* is short. The width of its proximal end is greater than its maximal length and the ratio "maximal length / minimal width" < 2. The contact area with the frontal is broken, but it seems that the parietal formed a small rostromedian process that inserted between the paired frontals. The rostromedial ends of the parietal contact the postorbital. Although its

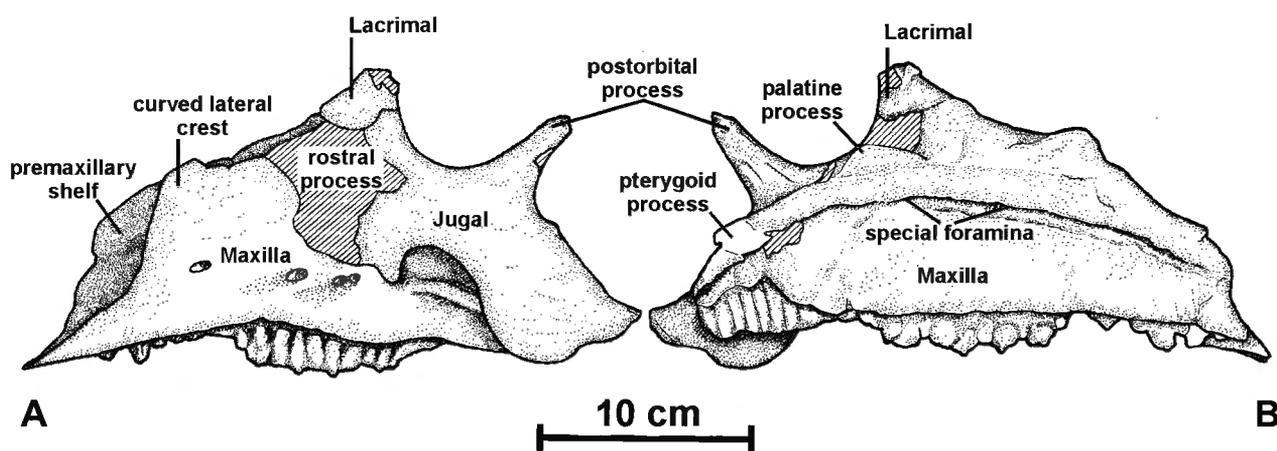


Fig. 4 — Left maxillary complex of *Aralosaurus tuberiferus* (PIN 2229), from the Beletinskaya Svita (Late Cretaceous) of Sakh-Sakh locality (Kazakhstan). A: lateral view; B: medial view.

dorsal surface is also destroyed, it appears that the parietal of *Aralosaurus* bore a strong sagittal crest. Caudally, the parietal forms a pair of ventral projections that cover the dorsolateral parts of the supraoccipital. Ventrally, the parietal forms a long, straight suture with the laterosphenoid. Its caudoventral borders probably contacted the prootic. The impression zone of the cerebellum forms a well-marked ovoid depression in the centre of the ventral side of the parietal. The rostral portion of the bone is very deeply excavated by the caudal portion of the impression zone of the cerebrum.

Squamosal (Figs. 2, A-C; Pl. 1, A-C) – The most important characters of the squamosal in *Aralosaurus* are its elevated lateral wall and median ramus, and its steeply-sloping dorsal border. Consequently, the back of the skull looks raised in lateral view. In occipital view, the medial ramus of the squamosal is higher than the paroccipital process. The medial articular surface of the medial ramus is very thick and rough, which means that it probably intimately contacted the caudal process of the parietal and that squamosals were separated from each other by the parietal along their entire height. The ventromedial corner of the medial ramus forms a cup-shaped articular surface for synovial articulation with the prominent knobs of the supraoccipital. The rostral process of the squamosal is long and rostrally tapering. Its medial side is regularly convex, whereas its flattened lateral side is covered by the caudal ramus of the postorbital along its whole length. The lateral side of the squamosal bears a well-developed elliptical facet, against which the caudal end of the postorbital applied. Both the pre- and post-cotyloid processes are broken off. The angle between the postcotyloid process and the medial ramus is deeply excavated for reception of the dorsal angle of the paroccipital process. The cotylus is wide and deeply excavated for reception of the proximal head of the quadrate. The inner side of the squamosal, which forms the caudolateral margin of the supratemporal fenestra, is gently inclined inward and upward.

Quadrate – The quadrate of *Aralosaurus* is proportionally high, slender, and gently curved backward. Its proximal head is rounded, sub-triangular in cross-section, and flattened mediolaterally. The jugal wing is narrow and slightly curved inwardly. The quadratojugal notch is high and deep. A long facet runs along nearly its entire height, indicating that the notch was completely closed by the quadratojugal. The pterygoid wing is oriented craniomedially at an angle of about 60° with the jugal wing. A prominent ridge, at the junction between the pterygoid wing and the quadrate shaft, marks the contact area with the ventral process of the pterygoid. The distal part of the quadrate is broken off.

Laterosphenoid (Fig. 2, B; Pl. 1, B) – As usual in hadrosauroids, the laterosphenoid is a very robust element. The prootic process is incompletely preserved, so that the precise relationships between the laterosphenoid,

the prootic and the parietal cannot be accurately delimited. However, it can be asserted that the laterosphenoid forms a long and straight suture with the parietal. The ventrally-directed basisphenoid process is also broken off. The angle between the prootic and the basisphenoid processes forms the rostral margin of c.n. V. The post-orbital process is long and stout. Its rostral end fits into the socket on the ventral side of the postorbital. From the tip of the postorbital process toward the basisphenoid process, the lateral side of the laterosphenoid bears a rounded crest that marks the separation between the orbit and supratemporal fenestra. The rostradorsal border of the postorbital process is very broadened for intimate contact with the ventral surface of the frontal.

Prootic (Fig. 2, B & D; Pl. 1, B) – The prootic of *Aralosaurus* is a massive element that takes an important part in the formation of the braincase. A stout caudodorsal ramus covers the rostradorsal part of the exoccipital-opisthotic. The lateral surface of the prootic bears a very prominent *crista orbitosphenoidale*. The rostral portion of the bone is notched by the caudal margin of the large foramen for the trigeminal nerve (c.n. V). Because the ventral part of the prootic is broken, it is possible to observe, in ventral view, traces of the endolymphatic system, so that it is possible to reconstruct the route of the semicircular canals. Three foramina open within three depressed areas, set to form a triangle. The rostral depression possibly marks the impression area for the anterior *ampulla* and the rostral foramen, the opening of the anterior semicircular canal. The caudal depressed area would correspond to the posterior *ampulla*, and the caudal foramen, to the opening of the posterior semicircular canal. The medial depression would correspond to the impression area for the *sacculus*, and the medial foramen, to the opening of *superior utriculus*. The rostral and caudal depressed areas are connected by a well-marked groove that would correspond to the impression area of the horizontal semicircular canal. Both the rostral and caudal depressions are connected to the medial depressed area by less well-marked grooves that would represent the impressions for the *utriculus*.

Exoccipital – opisthotic (Fig. 2, B & C; Pl. 1, B & C) – The fused exoccipital – opisthotic are partially preserved in PIN 2229. The base of the lateral wall and the posterior wall of the braincase are broken. The paroccipital processes are strongly developed, but their distal end is also broken off. Lateral to the insertion area for the supraoccipital, each paroccipital process forms a dorsal angle that forms a synovial joint with the ventral depression of the squamosal. Medial to the paroccipital processes, the dorsal parts of both exoccipitals meet each other to form the roof of the foramen magnum. This area is only slightly depressed and the supraoccipital is therefore separated from the roof of the foramen magnum for only a short distance. The exoccipital condyloids are broken off. However, a small canal at the rostral end of the ventral side of the preserved fragment marks the passage way for

cranial nerves IX-X. The rostradorsal corner of the exoccipital condyloids is deeply notched by the caudal margin of the auditory foramen.

Basioccipital and basisphenoid (Fig. 3) – A fragment of the fused basioccipital and basisphenoid of PIN 2229 is preserved. The traces for the different cranial nerves can be identified on the dorsal side of this fragment. However, this bone is too eroded to provide any valuable information.

Supraoccipital (Fig. 2, A & C; Pl. 1, A & C) – As usual in hadrosaurids, the supraoccipital is a stout pyramidal bone that extends dorsally and rostrally in the occipital region of the skull. Its straight base is firmly inserted between the dorsomedial borders of the paired paroccipital processes. Its dorsal surface bears a stout rectangular promontorium ornamented with a strong median crest. Two very depressed areas, covered by the caudoventral projections of the parietal, border this promontorium. The caudolateral corners of the supraoccipital form very prominent bosses, which articulate with the medioventral corner of the median ramus of the squamosal. In ventral view, the rostradorsal part of the supraoccipital is very depressed to form the caudal portion of the roof of the myelencephalon.

Phylogenetic affinities of *Aralosaurus tuberiferus*

ROZHDESTVENSKY (1968) reconstructed the skull of *Aralosaurus tuberiferus* with a nasal bone arched anterior to

the orbits (Fig. 5) and classified this taxon within the flat-headed Hadrosaurinae subfamily, mainly because of similarities in the morphology of the skull roof. Many subsequent authors followed this classification and reconstruction (see e.g. WEISHAMPEL & HORNER, 1990, fig. 26.2; FASTOVSKY & WEISHAMPEL, 1995; NORMAN & SUES, 2000, fig. 24.6). All pointed out the resemblance of the skull of *Aralosaurus*, in lateral view, with that of *Gryposaurus*, a flat-headed hadrosaurine from the late Campanian of western North America: both taxa apparently share a preorbital nasal arch. Unfortunately, the fragmentary bones described by ROZHDESTVENSKY as forming respectively the middle part of the nasal and the posterior part of the premaxilla are currently missing. These fragments would have been very useful to reconstruct the morphology of the circumnarial region in *Aralosaurus* and to check the assumption of the presence of a nasal arch in this taxon. In any case, one important difference can be observed in the posterior part of the nasals between *Gryposaurus* and *Aralosaurus*. In *Gryposaurus*, the transverse width of the posterior part of the paired nasals is distinctly narrower: this character can be regarded as a synapomorphy for advanced hadrosaurines (HORNER, 1992; Appendix 1). In *Aralosaurus*, on the other hand, the posterior part of the nasals remains transversely wide, as observed in basal Hadrosaurioidea.

In fact, the skull of *Aralosaurus* does not display any hadrosaurine synapomorphy. The dorsal process of the maxilla lies behind the middle of the bone, as primitively observed in Hadrosaurioidea (GODEFROIT *et al.*, 1998). In

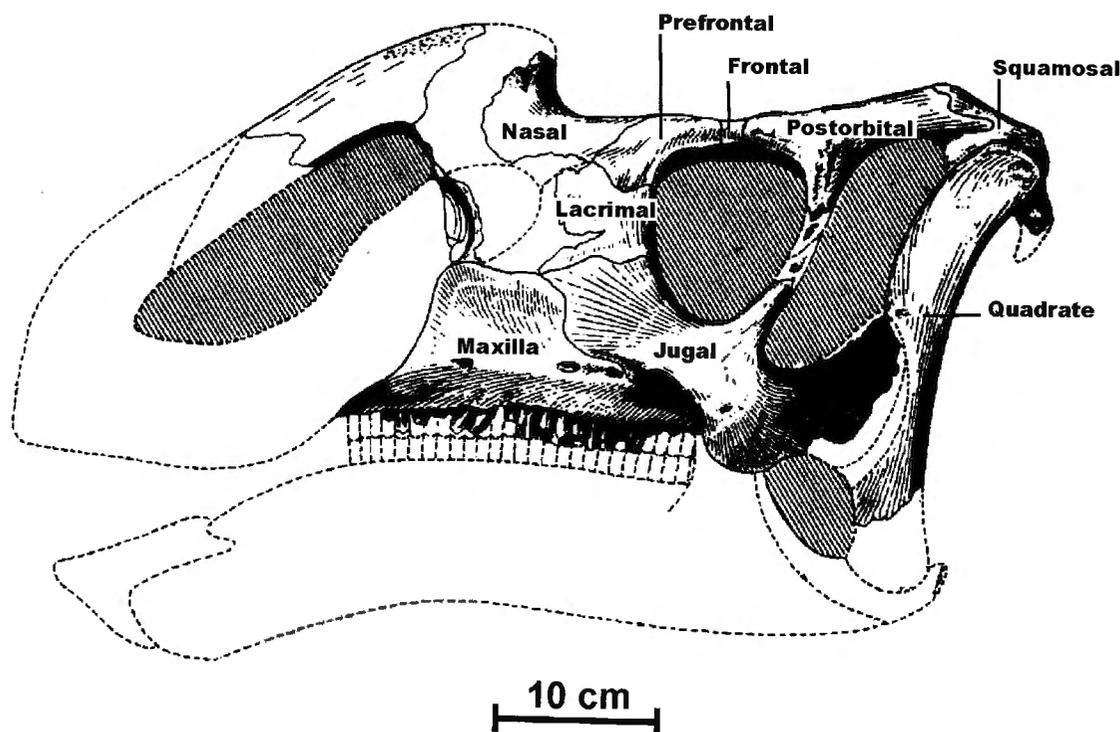


Fig. 5 — Reconstruction of the skull of *Aralosaurus tuberiferus* in left lateral view, after ROZHDESTVENSKY (1968).

hadrosaurines, on the other end, the maxilla looks more or less symmetrical in medial view, its dorsal process lying close to the middle of the bone. *Gryposaurus* and other advanced hadrosaurines are also characterised by an important development of the supraoccipital /exoccipital shelf roofing the occipital aspect of the skull above the foramen magnum (HORNER, 1992). Such a shelf is only poorly developed in *Aralosaurus*, and also in *Maiasaura*, *Brachylophosaurus*, Lambeosaurinae and basal Hadrosauroidae.

HORNER (1992) suggested that *Aralosaurus* could be a Lambeosaurinae rather than a Hadrosaurinae. He based his assumption on the morphology of the anterior part of the maxilla. In *Aralosaurus*, this part of the maxilla forms an extended shelf that supported the ventral part of the premaxilla. This character is a synapomorphy for lambeosaurines (HORNER, 1990; WEISHAMPEL *et al.*, 1993). In hadrosaurines and basal Hadrosauroidae, on the other hand, this shelf is not developed and the anterior part of the maxilla is bifid. HORNER (1992) believed that the development of squamosal bosses on the supraoccipital of *Aralosaurus* is also a lambeosaurine synapomorphy, but GODEFROIT *et al.* (1998) showed that this is clearly an ontogenetic character.

The skull of *Aralosaurus* displays other lambeosaurine synapomorphies. The parietal is very shortened and proportionally wide with a "maximal length / minimal width" ratio < 2. In hadrosaurines and basal Hadrosauroidae, on the other hand, the parietal is proportionally longer and narrower (WEISHAMPEL *et al.*, 1993; GODEFROIT *et al.*, 2001). The lateral side of the squamosal is higher than the paroccipital process in *Aralosaurus*, as in North American lambeosaurines, so that the caudal portion of the skull looks raised in lateral view (GODEFROIT *et al.*, 2001, in press). In hadrosaurines and basal Hadrosauroidae, on the other hand, the squamosal is proportionally lower above the cotylus. However, the most persuasive argument for a lambeosaurine affinity of *Aralosaurus* is the morphology of the nasal, which forms a crest-like structure in front of the orbits. Nasal bosses or crests are of course observed in several hadrosaurine taxa, such as *Maiasaura*, *Brachylophosaurus*, *Prosaurolophus* and *Saurolophus*, but the crest is solid in these genera. In *Aralosaurus*, on the other hand, the nasal boss is clearly hollow and encloses part of the respiratory tract. Extension of the nasal cavity inside a hollow crest is usually regarded as the principal landmark of the lambeosaurine subfamily.

Aralosaurus displays several cranial features that indicate that this taxon occupies a very basal position within the lambeosaurine phylogeny. Although it is modified to form a crest-like structure, the nasals keep their primitive position, in front of the orbits, and their original contacts with the frontals and prefrontals. In more advanced lambeosaurines, on the other hand, the nasals migrate to a caudodorsal position, because of the important development of the premaxillae and lose contacts with the frontals and, in some cases, with the prefrontals. In *Aralosaurus*, the dorsal surface of the frontals remains

flat. In more advanced lambeosaurines, on the other hand, the attachment area of the hollow crest forms a very distinctive recess on the rostradorsal surface of the frontals (GODEFROIT *et al.*, 2001). The rostral part of the prefrontal also remains unmodified in *Aralosaurus*, being horizontal as in basal Hadrosauroidae and hadrosaurines. In more derived lambeosaurines, on the other hand, the prefrontal becomes more elevated and also participates in the formation of the base of the hollow crest (WEISHAMPEL *et al.*, 1993; GODEFROIT *et al.*, 2001).

The presence of a well-developed frontal-nasal fontanelle also confirms the primitive condition of the skull of *Aralosaurus*. LANGSTON (1960) was the first to describe such a structure in the hadrosaurines *Lophorhothon atopus* and *Edmontosaurus annectens*. He considered the frontal-nasal fontanelle as a juvenile character of the hadrosaurid skull and further commented that hadrosaurine frontals are usually very thin above the respiratory tract. ROZHDESTVENSKY (1966, 1968) observed this fontanelle in the skulls of *Bactrosaurus johnsoni* and *Aralosaurus tuberiferus*, but disagreed with the opinion that this structure is a juvenile character, suggesting for this opening a function connected with olfaction or respiration. GODEFROIT *et al.* (2004) also observed that, in the skull of a rather young specimen of the basal lambeosaurine *Amurosaurus riabinini* (AEHM 1/232), the rostral border of the frontal forms a median hemispherical notch that may probably be derived from the frontal-nasal fontanelle. In the present paper, we follow MARYAŃSKA & OSMÓLSKA's (1979) opinion that the frontal-nasal fontanelle is an ontogenetic character present in juvenile and young adult specimens. We regard it as plesiomorphic within Hadrosauridae. Indeed, it is present in basal Hadrosauroidae (*Bactrosaurus*), Hadrosaurinae (*Lophorhothon*, *Edmontosaurus*) and basal Lambeosaurinae (*Aralosaurus*, *Amurosaurus*). It seems absent in more derived Lambeosaurinae, even in very young specimens, in which it is replaced by a premaxilla-nasal fontanelle, playing essentially the same role as the frontal-nasal fontanelle (MARYAŃSKA & OSMÓLSKA, 1979).

A cladistic analysis of hadrosaurid dinosaurs was performed, using PAUP*4.0b10 program (SWOFFORD, 2000), in order to determine exactly and to visualise the phylogenetic position of *Aralosaurus* within this family. This cladogramme is based on 36 cranial characters. The non-hadrosaurid hadrosauroid *Bactrosaurus johnsoni*, recently 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. The characters used in the present analysis are described and discussed in Appendix 1, the data matrix is presented in Appendix 2, and a complete list of apomorphies is found in Appendix 3. The presence of a fontanelle has not been taken into account, because it is an ontogenetic character that cannot be observed in taxa only represented, in the current state of our knowledge, by adult specimens. The heuristic search option found one single most parsimonious tree, with a length of 45 steps, a consistency index (CI) of 0.93 and a retention

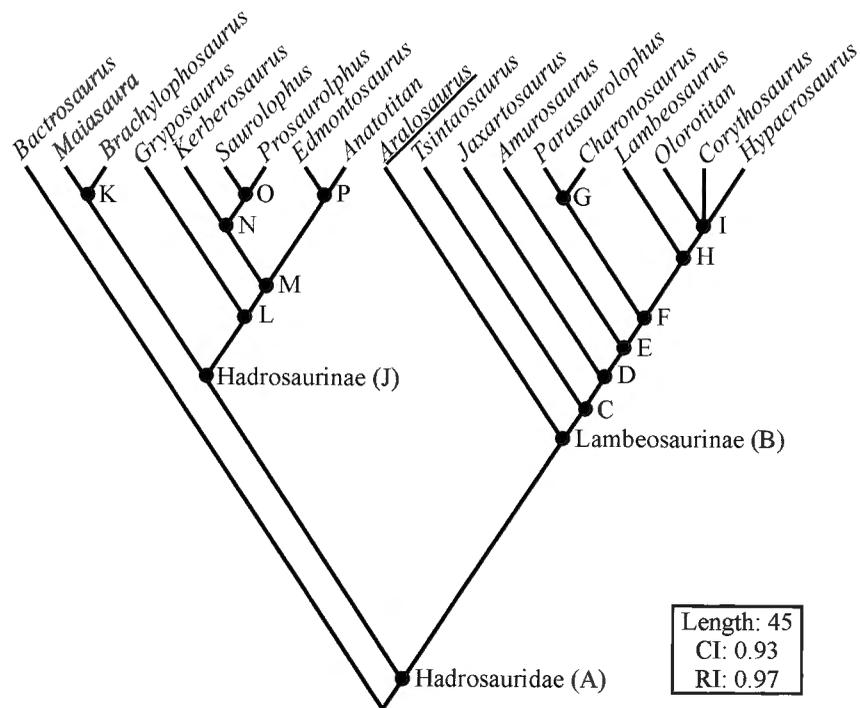


Fig. 6 — Cladogramme of Hadrosauridae, showing the phylogenetic relationships of *Aralosaurus tuberiferus*. Letters correspond to nodes defined in Appendix 3.

index (RI) of 0.97 (Fig. 6). This cladogramme clearly demonstrates that *Aralosaurus* is a basal lambeosaurine, not a hadrosaurine, as previously asserted. With most derived lambeosaurines, it shares the following unambiguous cranial synapomorphies: the ratio “length / minimal width” of the parietal < 2 (character 2), a hollow supra-cranial crest is developed (character 4), and the maxillary shelf is well developed (character 34). The elevated lateral side of the squamosal (character 23) is convergently acquired in *Aralosaurus* and in Node E (*Amurosaurus* + (parasaurolophini clade + corythosaurini clade)). With the exception of *Aralosaurus*, all other lambeosaurines share the following unambiguous synapomorphies: the frontal is excluded from the orbital rim (character 3, convergently acquired in some hadrosaurines) and the prefrontal participates in the lateroventral border of the hollow crest (character 22).

This cladogramme also provides information elements on the evolution of the hollow crest in lambeosaurine dinosaurs. The evolutionary sequence observed in basal lambeosaurines reveals a progressive backward migration of the crest, correlated with the integration of a greater number of bones in its formation. In *Aralosaurus*, the base of the hollow crest is set far from the rostral margin of the orbits; neither the prefrontals nor the frontals participate in its formation and both bones consequently keep their plesiomorphic morphology (nothing is known about the premaxillae). In *Tsintaosaurus*, the hollow crest is set vertically above the rostral margin of the orbits; the prefrontals are distinctly modified to participate in the

proximolateral aspect of the crest (character 22) and the rostral border of the frontal is slightly upturned where it buttresses the base of the crest. The premaxilla apparently does not participate in the formation of the crest (YOUNG, 1958; BUFFETAUT & TONG-BUFFETAUT, 1993). In all more advanced lambeosaurines, from *Jaxartosaurus* onward, the hollow crest migrated above the skull roof and the dorsal surface of the frontal is highly modified in a deeply excavated platform that supports the base of the crest (character 7 (1)). The parasaurolophini and corythosaurini clades (BRETT-SURMAN, in CHAPMAN & BRETT-SURMAN, 1990) share a shortening of the frontal region (character 6 (1)). In these lambeosaurines, the nasals lose contact with the external naris (character 10) and migrate in a dorsocaudal position (character 17) because of the preponderant participation of the premaxilla in the formation of the crest. The polarity for these characters remains unknown in *Jaxartosaurus* and *Amurosaurus*. The backward extension of the supra-cranial crest is even more pronounced in the parasaurolophini clade, in which the frontal platform overhangs the supratemporal fenestra (character 7 (2)).

Discussion

NORELL (1992) defined ghost lineages as missing sections of a clade implied by phylogeny. As sister taxa have the same time of origin, it is therefore possible to establish the minimal age for the origin of clades: the origin of a

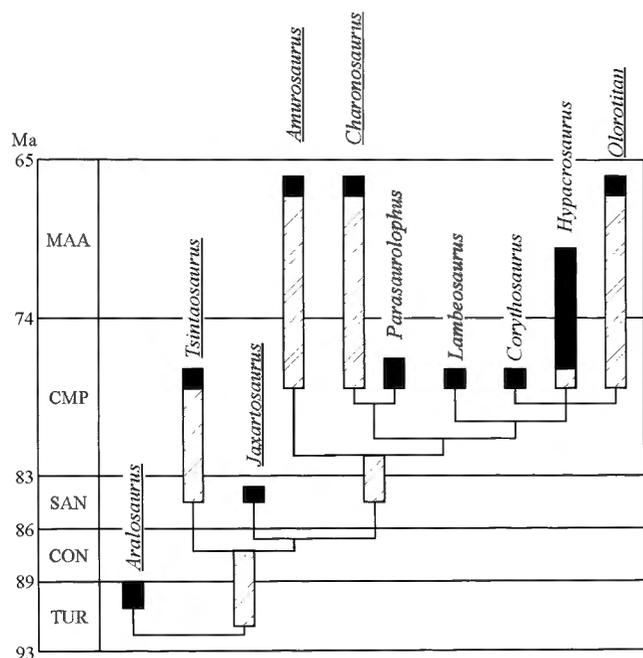


Fig. 7 — Stratigraphically-calibrated cladogram of phylogenetic relationships of Lambeosaurinae. Solid symbols indicate stratigraphical occurrence of a taxon, whereas hatched symbols indicate ghost lineages. Asian taxa are underlined. Abbreviations: CMP, Campanian; CON, Coniacian; MAA, Maastrichtian; SAN, Santonian; TUR, Turonian. Dates are millions of years before present.

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.

Fig. 7 represents the ghost lineages identified for lambeosaurine phylogeny. It indicates that the ghost lineage durations are relatively long for Asian taxa and therefore suggests that many hadrosaurid taxa must be missing in this part of the world during the Late Cretaceous interval (WEISHAMPEL, 1996). Figs. 6 and 7 also suggest that lambeosaurine dinosaurs have an Asian origin. Indeed, the most basal lambeosaurines are successively *Aralosaurus tuberiferus*, from the Beletinskaya Svita (?Turonian) of Kazakhstan, *Tsintaosaurus spinorhinus*, from the Wangshi Formation (Campanian, according to BUFFETAUT, 1995) of eastern China, *Jaxartosaurus aralensis*, from the Syuksyuk Formation of Kazakhstan (Santonian, according to AVERIANOV & NESSOV, 1995), and *Amurosaurus riabinini*, from the late Maastrichtian Udurchukan Formation of Amur Region in Russia (GODEFROIT *et al.*, 2004). In western North America, the oldest well-dated and well-identified lambeosaurines have been discovered in Upper Campanian formations (WEISHAMPEL & HORNER, 1990); all belong to the advanced parasaurolophini or corythosaurini clades. It means that lambeosaur-

ines migrated towards western North America before or at the beginning of the late Campanian, like many other dinosaur taxa: basal Neoceratopsia (CHINNERY and WEISHAMPEL, 1998), Ceratopsidae (NESSOV & KAZNYSHKINA, 1989), Ankylosauridae (MARYAŃSKA, 1977), Tyrannosauridae (MADER & BRADLEY, 1989; BUFFETAUT *et al.*, 1996), and Troodontidae (RUSSELL & DONG, 1993). During most of the Late Cretaceous, an interior seaway divided North America into a western Cordilleran region and an eastern shield region. 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 & RUSSELL, 1989; RUSSELL, 1993).

Lambeosaurines apparently survived in Asia until the end of the Cretaceous. By late Maastrichtian times, they even became the dominant herbivorous dinosaurs in the Amur Region, being represented by *Amurosaurus riabinini* BOLOTSKY & KURZANOV, 1991, *Charonosaurus jiayinensis* GODEFROIT, ZAN & LI, 2000 and *Olorotitan arharensis* GODEFROIT, BOLOTSKY & ALIFANOV, 2003. In North America, on the other hand, Lambeosaurinae apparently disappeared during late Maastrichtian time, or are represented only by very scarce and doubtful material (BOYD & OTT, 2002).

Hadrosaurines are less well represented in Asia than lambeosaurines. The oldest Asian representatives of the former subfamily would be *Shantungosaurus giganteus* HU, 1973, and maybe *Tanius sinensis* WIMAN, 1929, both from the Campanian Wangshi Series of eastern China. *Gilmoreosaurus mongoliensis* (GILMORE, 1933), from the Iren Dabasu Formation of Inner Mongolia, is herein regarded as a non-hadrosaurid Hadrosauridae. Other valid hadrosaurine taxa discovered in Asia include *Saurolophus angustirostris* ROZHDESTVENSKY, 1952, from the early Maastrichtian Nemegt Formation of Mongolia, and *Kerberosaurus manakini*, BOLOTSKY & GODEFROIT, 2004, from the ?late Maastrichtian Udurchukan Formation of the Amur Region. Hadrosaurines are apparently represented in North America from the Santonian onward (WEISHAMPEL & HORNER, 1990) and the most basal forms of this subfamily known to date were found in this area (see BOLOTSKY & GODEFROIT, 2004 for a more extended discussion on hadrosaurine palaeogeography). Thus, a North American origin for the hadrosaurine subfamily seems more likely in the current state of our knowledge.

Consequently, the birthplace of the monophyletic Hadrosauridae still remains conjectural: the oldest and/or more primitive lambeosaurines are Asian, although the oldest and/or more primitive hadrosaurines are North American. It is all the more uncertain since basal non-hadrosaurid Hadrosauridae have been discovered in Asia (*Equijibus*, *Proactrosaurus*, *Bactrosaurus*, *Gilmoreosaurus*), in North America (*Eolambia*, *Protohadros*) and even in Europe (*Telmatosaurus*). The study of pre-Campanian hadrosaurids, whose fossils are unfortunately too often fragmentary and badly dated, and the quest for new fossils must therefore be intensified in order to clarify this problem.

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Appendix 1

Characters and character states for determining the phylogenetic position of *Aralosaurus tuberiferus*. Most of those characters were previously discussed by GODEFROIT *et al.* (1998, 2001) and are therefore not described in detail in the present paper.

1. Parietal participating in the occipital aspect of the skull (0), or completely excluded from the occiput (1).
2. Ratio 'length / minimal width' of the parietal > 2 (0), or < 2 (1).
3. Frontal participating in the orbital rim (0), or excluded by postorbital-prefrontal joint (1).
4. Hollow supracranial crest absent (0), or developed (1).
5. No solid supracranial crest (0), broad solid supracranial crest (1), or narrow solid supracranial crest (2). Character treated as unordered.
6. Frontal longer than wide (0), wider than long (1), or secondary elongation resulting of the backwards extension of the frontal platform (2). Character treated as ordered.
7. 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.
8. Premaxillary foramen present (0), or absent (1).
9. Lateral premaxillary process stopping at the level of the lacrimal (0), or extending further backwards (1).
10. External naris surrounded by both the nasal and the premaxilla (0), or completely surrounded by the premaxilla (1).
11. Premaxillary beak relatively narrow (0), or laterally expanded (1).
12. Reflected premaxillary lip absent (0), or developed (1).
13. External naris relatively small (0), or enlarged (1).
14. Circumnarial depression absent (0), or extending onto the nasal (1).
15. Caudal border of circumnarial depression smoothly marked (0), or marked by a well-developed ridge.
16. Caudal end of circumnarial depression located rostral (0), or above or posterior to the rostral end of the orbit (1).
17. Nasal located rostral to the frontal (0), or migrated in a dorsocaudal position (1).
18. Caudal part of the nasals relatively wide (0), or very narrow anterior and posterior to orbits (1).
19. *Cavum nasi proprium* relatively small (0), or enlarged (1).
20. Nasal forming a small part of the hollow crest (0), half of the crest (1), or the entire crest (2).
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. Lateral side of the squamosal low (0), or elevated (1).
24. Supraoccipital / exoccipital shelf limited (0), or very extended (1) above the foramen magnum.
25. Postorbital pouch absent (0), or well-developed (1).
26. Dorsal surface of postorbital flat (0), or thickened to form a dorsal promontorium (1).
27. Rostral process of the jugal tapering in lateral view (0), or dorso-ventrally expanded (1).
28. 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.
29. Jugal relatively slender (0), or very massive (1).
30. Ventral projecting boss on jugal absent (0), or strongly developed (1).
31. Maxilla markedly asymmetrical (0), or nearly symmetrical in lateral view (1).
32. Antorbital fenestra surrounded by the jugal and/or the lacrimal (0), or completely surrounded by the maxilla (1).
33. Ectopterygoid ridge faintly (0), or strongly (1) developed on the lateral side of the maxilla.
34. Rostromedial process developed on the maxilla (0), or wide maxillary shelf (1).
35. Paraquadrate foramen present (0), or absent (1).
36. Distal head of quadrate transversely expanded (0), or dominated by a large hemispheric lateral condyle (1).

Appendix 2

Character – taxon matrix for phylogenetic analysis of *Aralosaurus tuberiferus*.

<i>Bactrosaurus</i>	00000	00000	00000	00000	00000	00000	000000
<i>Aralosaurus</i>	?1010	00???	?????	000??	10100	01?00	01111?
<i>Tsintaosaurus</i>	01110	00???	?????	000?2	11000	01100	011111
<i>Jaxartosaurus</i>	01110	01???	?????	?????	11000	0????	???????
<i>Amurosaurus</i>	01110	01???	?????	?????	11100	01100	011111
<i>Parasaurolophus</i>	11110	22101	00000	01000	11100	11100	011111
<i>Charonosaurus</i>	11110	12?0?	?????	?10??	111?0	11100	011111
<i>Lambeosaurus</i>	01110	11111	00000	01010	11100	01100	011111
<i>Olorotitan</i>	???10	?1111	00000	010?1	11?0?	?1100	011111
<i>Corythosaurus</i>	01110	11111	00000	01011	11100	01100	011111
<i>Hypacrosaurus</i>	01110	11111	00000	01011	11100	01100	011111
<i>Maiasaura</i>	00001	00000	10010	00000	10000	01201	111011
<i>Brachylophosaurus</i>	00001	00000	10110	00000	10000	01201	111011
<i>Gryposaurus</i>	00?00	00000	11110	00100	10010	01000	111011
<i>Kerberosaurus</i>	00100	00??0	??111	00100	1001?	?1300	111011
<i>Saurolophus</i>	00102	00000	11111	10100	10010	01300	111011
<i>Prosaurolophus</i>	00102	00000	11111	10100	10010	01300	111011
<i>Edmontosaurus</i>	00000	00000	11111	00100	10011	01310	111011
<i>Anatotitan</i>	00000	00000	11111	00100	10011	01310	111011

Appendix 3

List of apomorphies for all ingroup taxa. Letters indicate nodes designated in Fig. 19. For multistate characters, the number between brackets refers to the character state (see Appendix 1). Character are followed by an 'a', when supported only by ACCTRAN or fast optimisation, and by a 'd', when supported only by DELTRAN, or slow optimisation.

A (Hadrosauridae): 21, 27, 32, 33, 35, 36.

B (Lambeosaurinae): 2, 4, 8a, 10a, 28(1)a, 34.

C: 3, 22, 28(1)d.

D: 7(1), 17a.

E: 23.

F: 6(1), 8d, 10d, 17d.

G (parasaurolophini clade; after CHAPMAN & BRETT-SURMAN, 1991): 1, 7(2), 26.

H (corythosaurini clade): 9, 19.

I: 20.

J: 11, 13a, 14, 31.

K (brachylophosaurini clade): 5(1), 28(2), 30(1).

L: 12, 13d, 18, 24.

M: 15, 28(3).

N: 3.

O (saurolophini clade): 5(2), 16.

P (edmontosaurini clade): 25, 29.

Explanation of Plate 1

Holotype skull of *Aralosaurus tuberiferus* (PIN 2229), from the Beleutinskaya Svita (Late Cretaceous) of Sakh-Sakh locality (Kazakhstan). **A**: skull roof in dorsal view; **B**: skull roof in ventral view; **C**: occipital aspect of the skull; **D**: rostral view of the hollow crest-like structure formed by the paired nasal; **E**: left maxillary complex in lateral view; **F**: left maxillary complex in medial view.

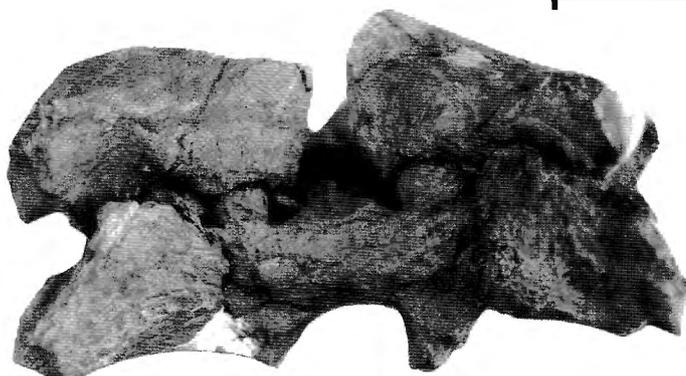


10 cm



A

B



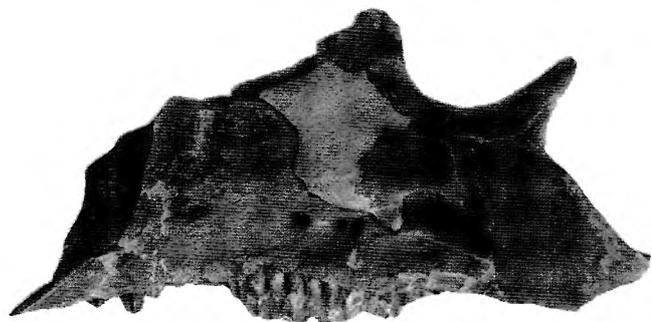
5 cm



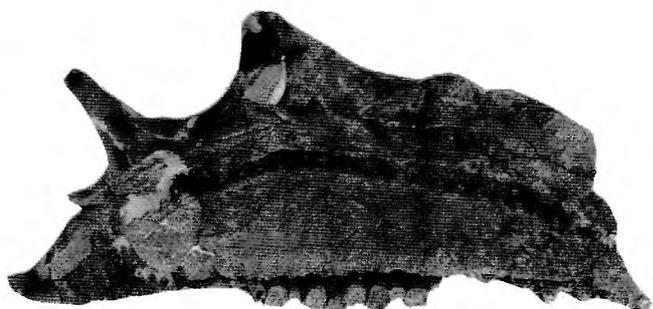
2 cm

C

D



10 cm



E

F