A new basal hadrosauroid dinosaur from the Late Cretaceous of Uzbekistan and the early radiation of duck-billed dinosaurs

Hans-Dieter Sues1,* and Alexander Averianov2

1National Museum of Natural History, Smithsonian Institution, MRC 106, PO Box 37012, Washington, DC 20013-7012, USA
2Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St Petersburg 199034, Russia

Levensovia transoxiana gen. et sp. nov., from the Late Cretaceous (Middle–Late Turonian) of Uzbekistan, is the oldest well-documented taxon referable to Hadrosauroidia sensu Godefroit et al. It differs from a somewhat younger and closely related Bactrosaurus from Inner Mongolia (China) by a tall sagittal crest on the parietals and the absence of club-shaped dorsal neural spines in adult specimens. Levensovia, Bactrosaurus and possibly Gilmoreosaurus represent the earliest radiation of Hadrosauroidia, which took place during the Cenomanian–Turonian and possibly in North America. The second, Santonian-age radiation of Hadrosauroidia included Aralosaurus, Hadrosauridae and lineages leading to Tanius (Campanian) and Telmatosaurus (Maastrichtian). Hadrosauridae appears to be monophyletic, but Hadrosaurinae and Lambeosaurinae originated in North America and Asia, respectively.

Keywords: Dinosauria; Hadrosauroidia; Cretaceous; Asia; radiation; palaeobiogeography

1. INTRODUCTION

The Late Cretaceous (Middle–Late Turonian). Hadrosauridae and lineages leading to Hadrosaurinae and Lambeosaurinae originated in North America and Asia, respectively.

2. SYSTEMATIC PALAEONTOLOGY

Ornithischia Seeley 1887
Ornithopoda Marsh 1881
Iguanodontia Sereno 1986
Hadrosauroidia Cope 1869 (sensu Godefroit et al. 1998)
Gilmoreosaurus arkhangelskii [nomen dubium]: Nessov 1995, p. 49.

(a) Etymology

The new taxon is named for Lev Nessov (1947–1995), using the most accurate English-language spelling of his surname as transliterated from the Cyrillic, and Transoxiana, an ancient name of the lands beyond (trans) the Amu Darya River (Oxus), corresponding to present-day Uzbekistan.

(b) Holotype

USNM 538191, postorbital region of skull roof with nearly complete braincase (figure 1).

(c) Referred materials

ZIN PH 1306/16, subadult skull roof fragment; ZIN PH 1307/16, adult skull roof fragment; USNM 538126, partial braincase and skull roof; CCMGE 565/12457, 566/12457 and ZIN PH 306/16, almost complete adult braincases; USNM 538121, subadult braincase; many isolated cranial and postcranial bones in the collections of: the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); Chernyshev's Central Museum of Geological Exploration, Saint Petersburg (CCMGE); the Zoological Institute, Russian Academy of Sciences, Saint Petersburg (ZIN PH); and the Institute of Zoology, National Academy of Sciences of Uzbekistan, Tashkent (IZANUZ). All referred specimens come from the same locality and horizon (Bissekty Formation at Dzharakuduk). The additional braincases and skull roof fragments are morphologically indistinguishable from the holotype, and the remaining skeletal elements are documented, in most cases, by numerous specimens that show no taxonomically significant variation and thus are referred to a single taxon.

(d) Locality and horizon

Dzharakuduk, Navoi Viloyat (district), central Kyzylkum Desert, Uzbekistan. Bissekty Formation; Late Cretaceous (Middle–Late Turonian).
Diagnosis
A basal hadrosauroid iguanodontian that differs from known non-hadrosaurid iguanodontians in the following features: ectopterygoid–jugal contact absent; predentary gracile and shovel-shaped, with gently rounded anterior margin; surangular foramen absent; and dentary tooth crowns with one primary ridge and faint (if any) secondary ridges. Differs from *Bactrosaurus* (Gilmore 1933) in presence of tall sagittal crest on parietals, absence of lacrimal process on prefrontal, and absence of club-shaped neural spines on dorsal vertebrae in adults. Differs from *Gilmoreosaurus* (Brett-Surman 1979) by shorter contribution of frontal to orbital rim, longer diastema between first dentary tooth and predentary (equivalent to more than one-fifth of tooth row length), and nearly vertical coronoid process of dentary. Differs from more derived Hadrosauridae in absence of well-developed ectopterygoid ridge on maxilla; dentary tooth row and posterior end of dentary terminating at apex of coronoid process; and dentary tooth row bowed lingually in occlusal view.

Comments
A tall sagittal crest is also present in the non-hadrosaurid hadrosauroid *Tanisius* from the Campanian(?) of Shandong, China (Wiman 1929), and the lambeosaurine hadrosaurid *Amurosaurus* from the Maastrichtian of Far Eastern Russia (Godefroit et al. 2004b). This feature was cited as autapomorphy for *Amurosaurus*, but apparently developed independently in these three taxa. Godefroit et al. (2004b) cited as an additional autapomorphy of *Amurosaurus* the presence of a prominent median process between the basipterygoid processes. Such a process is also present in *Levensosia*. However, the absence of this process in other hadrosaurid taxa may reflect vagaries of preservation rather than a phylogenetically significant feature.

3. Description
(a) Cranium
The premaxillae, nasals and lacrimals are not known. The flat prefrontal lies flush with the surrounding elements and lacks a lacrimal process. Its orbital rim is indented posteriorly, indicating articulation with a free palpebral (see electronic supplementary material 1, figs a and b). A robust postorbital spine-like process fits into a pocket-like recess on the frontal. The frontal is flat and 1.3 to 1.5 times longer than wide (figure 1a,b). Its anterolateral margin is excavated by a deep recess for reception of the prefrontal. The nasal facet is narrow. A small fontanelle was present between the frontals and nasals. The frontal contributes only a short section of the orbital rim between the prefrontal and postorbital. A short
median ramus of the postorbital contacts the frontal and parietal. The frontal and postorbital form a synovial joint with the anterodorsal portion of the laterosphenoid. The postorbital section of the orbital rim is indented, similar to that of the prefrontal. The posterior ramus of the postorbital extends back to the posterior end of the supratemporal fenestra and overlaps the squamosal laterally. The anteroventrally extending, tapering ventral ramus of the postorbital contacts the jugal. The fused parietales are long anteroposteriorly. A short rhomboid anteromedian process of the parietales is wedged between the frontals (figure 1b). The sagittal crest is low anteriorly but tall posteriorly (figure 1d). A prominent sinusoidal groove along the dorsal surface of this crest possibly accommodated an unossified extension of the bony crest. The triangular anterior ramus of squamosal contacts the postorbital. The recess for reception of the proximal head of the quadrate is braced by precoccyloïd and postcoccyloïd processes. The flat postcoccyloïd process extends ventrolaterally, with its distal point deflected anteriorly. Its medial surface contacts the parapophysis. On the ventromedial side there is a wide, saddle-shaped articular area for the dorsal angle of the parapophysis. The medial ramus of the squamosal is a tall vertical plate that curves anteriorly towards the sagittal crest but does not contact it. On its ventral flange there is a concavity over a low projection on the supraoccipital. The maxilla is triangular in side view, with a pointed dorsal apex at about mid-length of the bone (electronic supplementary material 1, fig. c). The only known adult maxilla (USNM 538145) is incomplete anteriorly; it has 23 dental files in the preserved portion, with three teeth per vertical dental file. The anterodorsal margin of the bone is excavated by a prominent premaxillary shelf. The jugal process is short and bump-like; its lateral side is covered by the facet for the jugal process of maxilla (see electronic supplementary material 1, figs f and g). The posterior surface of the supraoccipital is steeply inclined forward, almost horizontal, with a tall median crest expanding anteriorly and terminating in a knob-like structure that contacts the parietales. The supraoccipital–exoccipital contact is marked by a strong horizontal ridge, followed anteriorly by a slit-like transverse groove. Distinct knobs at the posterolateral corners of the supraoccipital contact the squamosals. The structure of the braincase is similar to that of other derived ornithopods. The occipital condyle has a vertical articular surface and a strongly convex ventral side. The exoccipitals exclude the basioccipital from the floor of the endocranial cavity. The basal tubera have distinct basioccipital and basisphenoid portions separated by a transverse groove (figure 1a). A deep longitudinal basiophenoidal recess is situated between the tubera. Lateral to the foramen magnum there is a facet on either side, possibly for the proatlas as in *Iguanodon*. Two or three foramina for cranial nerves (c.n.) X–XII perforate the exoccipital posterior to the metotic strut. The vagus canal (for c.n. X, ‘perilymphatic duct’ of authors) opens medially into the metotic (‘jugular’) foramen and the two more posterior canals (c.n. XI and c.n. XII) open medially into the endocranial cavity. On the medial side, a rounded depression housed a diverticulum of the longitudinal venous system above the opening for c.n. XII. Anterior to the metotic strut a large auditory recess is divided by a vertical crista interfenestralis into the stapedial recess (anterior; fenestra ovalis) and metotic foramen (posterior). The metotic foramen contains separate openings for c.n. IX (dorsal) and the internal jugular vein (ventral). Dorsal to the crista interfenestralis, a distinct opisthoptichot suture extends dorsally along the parocipital process (ZIN PH 306/16). The medial wall of the prootic–opisthotic opposite to the fenestra ovalis is inflated into the vestibular pyramid, which contains the inner ear cavity. On the medial surface of the vestibular pyramid there is a foramen for c.n. VIII. On the lateral side of the prootic, anterior to the auditory recess, a deep vertical furrow houses a dorsal opening for cranial nerve VII and a ventral one for the internal carotid artery. More anteriorly, a large, round trigeminal foramen housed the Gasserian ganglion of c.n. V (figure 1c). Separate grooves mark the courses of V1 and V2–3. The orbitosphenoid and presphenoid are fully ossified. In this region of the neurocranium, there is a common opening for left and right c.n. II, a large elliptical foramen for c.n. III and VI, and, dorsally, a much smaller cleft-like opening for c.n. IV. Dorsally, a small foramen possibly represents the passage for the median palatine artery. The presphenoid is a short, plate-like anterior extension of the orbitosphenoid. Its anterior end forms the ventral margin of a large passage for the olfactory bulbs, which opens anteriorly. Three small foramina along the suture between the presphenoid and orbitosphenoid possibly represent exits for the anterior orbital artery, anterior cranial artery and the canal for the venous anastomosis connecting the right and left orbital sinuses. The internal carotid artery enters the pituitary fossa through the common openings with the palatine ramus of c.n. VII below large openings for c.n. VI. The latter exits the endocranial cavity through openings on its ventral floor. The basiophtyroid processes taper ventrolaterally and bear oval articular facets. Between these processes, a long median process extends posteroventrally and
terminates in a slightly thickened end. The basisphenoid continues anteriorly into a prominent median spur formed by the paraphenoid.

**Mandible**

The predentary is less arcuate than that of *Protohadros* (Head 1998), with a straighter anterior margin and distinct dorsal and ventral median processes (see electronic supplementary material 1, figs h and i), as on the predentary of *Bactrosaurus* (Gilmore 1933, fig. 28). The medial pair of nutrient foramina is large and connected to vascular grooves; the other foramina are smaller and distributed along the entire anterior margin. The largest known dentary (ZIN PH 466/16; see electronic supplementary material 1, figs j and k) has 29 dental files. The anterior end of the dentary is moderately deflected. A short diastema is present between the predentary and first dentary tooth. On the lateral side, a series of vascular foramina along the predentary–dentary contact suggests the presence of a keratinous beak in life. The tooth row bows lingually in dorsal view and terminates only slightly behind the apex of coronoid process. The coronoid process is nearly vertical, with a slight denting process. There is no surangular facet on its medial aspect. The surangular forms the posterior portion of the coronoid process. There is no surangular foramen. The orientation of the angular facet on the surangular indicates that the angular was exposed laterally.

**Teeth**

The teeth of *Levnesovia* closely resemble those of *Bactrosaurus* (Gilmore 1933; Godefroit et al. 1998). The maxillary teeth have lanceolate crowns, which are approximately twice as tall as are wide mediolaterally and bear a prominent medial carina (see electronic supplementary material 1, figs l and m). The dentary teeth have diamond-shaped crowns, which can be three times taller than wide mediolaterally (see electronic supplementary material 1, figs n and o). The medial carina is relatively less prominent and there is at least one secondary longitudinal ridge mesially. It is typically placed closer to the distal margin of the crown. Both maxillary and dentary teeth have marginal denticles supported by short ridges.

**Postcranial skeleton**

The cervical vertebrae of *Levnesovia* are opisthocoelous, with a short centrum and zygapophyses elevated above the level of neural canal (see electronic supplementary material 1, fig. p). No complete sacrum is known, but overlapping partial sacra suggest the presence of seven sacral vertebrae. The coracoid is relatively large, with a small biceps tubercle, short ventral process (‘hook’), and a scapular facet that is longer than the glenoid facet. The humerus bears a low deltopectoral crest, which does not extend beyond the mid-shaft of the bone. Its distal condyles are flattened dorsoventrally and are hoof-like (see electronic supplementary material 1, fig. t).

**Figure 2.** Phylogenetic, temporal and palaeogeographical relationships among derived iguanodontians. The tree is based on the strict consensus tree presented in the electronic supplementary material 4. Taxa shown in red are from Asia, in blue from North America, in yellow from Europe, and in purple from both Asia and North America. Nodes and terminal taxa: 1, Hadrosauridae; 2, Hadrosaurinae; 3, *Telmatosaurus*; 4, Lambeosaurinae; 5, Hadrosaurinae.

4. **PHYLOGENETIC ANALYSIS**

In order to assess the phylogenetic position of *Levnesovia* we performed a phylogenetic analysis of hadrosaurid taxa based on distribution of 138 characters in 34 ornithopod taxa, with *Hypsilophodon* used as the outgroup. The characters were compiled from more than 20 published sources with the addition of a few new characters (see electronic supplementary materials 2 and 3 for the complete list of characters and the character–taxon matrix). The resulting data matrix was analysed using NONA v. 2.0 (Goloboff 1999), run with the WINCLADA v. 1.00.08 interface (Nixon 1999). Multi-state characters were treated as unordered. One thousand repetitions of the parsimony ratchet (island hopper) algorithm recovered four most parsimonious trees, each with a length of 287 steps, a consistency index of 0.54 and a retention index of 0.86. The strict consensus tree is shown in modified form in figure 2 and in full in electronic supplementary material 4.

5. **BASAL RADIATION OF HADROSAUROIDEA**

In this paper, we employ the node-based definition of Hadrosauridae by Godefroit et al. (1998): *Bactrosaurus*, *Telmatosaurus*, Hadrosauridae, their most recent common ancestor and all descendants. Sereno (1997) proposed a node-based definition for Hadrosauriformes (*Iguanodon*,...
Parasaurolophus, their most recent common ancestor and all descendants) and a stem-based definition for Hadrosauridae (all hadrosauriforms closer to Parasaurolophus than to Iguanodon). The problem with Sereno’s definition of Hadrosauridae is that recent analyses, including that in the present paper, have failed to recover a monophyletic Iguanodontidae (or this group is restricted to Iguanodon and Ouranosaurus; Head & Kobayashi 2001; Kobayashi & Azuma 2003). By Sereno’s definition, all iguanodontians more derived than Iguanodon would be hadrosauroids, including recently discovered Probactrosaurus-like taxa from the Mid-Cretaceous of China (You et al. 2003a,b; Godefroit et al. 2005). In our analysis, the monophyly of Hadrosauridae (sensu Godefroit et al. 1998) is supported by seven unambiguous synapomorphies, four of which are not homoplasies (figure 2; see also electronic supplementary material 4). The bootstrap support for this node is 74 per cent.

Derived iguanodontians that are paraphyletic relative to Hadrosauridae are known from the Early Cretaceous of both Asia (Alitirhinus, Equijubus, Fukuisaurus, Jinzhousaurus, Lanzhousaurus, Nanyangosaurus, Penelopognathus, Probactrosaurus, Shuangmiaosaurus) and North America (Cedroestes, Eolambia, Planicoxa). Some of these taxa are based only on incomplete material and are in need of further study. The most derived of these iguanodontians is Protohadros from the Cenomanian of Texas (Head 1998). This may suggest a North American origin for Hadrosauridae (Head 1998; Head & Kobayashi 2001).

Our analysis indicates two distinct radiations of non-hadrosaurid hadrosauroids (figure 2). The first radiation occurred during the Cenomanian–Turonian (possible starting in the Late Albian) and is currently poorly documented. Maxillary teeth with a single pronounced median carina from the Cenomanian of France and western Russia (electronic supplementary material 5) belong either to the earliest hadrosauroids or to derived non-hadrosaurid iguanodontians like Protohadros. Isolated dentary teeth with diamond-shaped crowns that lack secondary ridges have been reported from the Cenomanian of England (‘Trachodon cantabricensis’) and Uzbekistan (‘Gilmoreosaurus atavus’), possibly representing the oldest known records of Hadrosauridae (figure 3a).

Levensoria from the Bisskey Formation (Middle–Late Turonian) of Uzbekistan is the oldest well-known taxon referable to Hadrosauridae. It is closely related to Bactrosaurus from the Iren Dabasu Formation of Inner Mongolia, China (Gilmore 1933; Weishampel & Horner 1986; Godefroit et al. 1998), but differs from the latter especially in the presence of a tall sagittal crest on the parietals and the absence of club-shaped dorsal neural spines in adults. Gilmoreosaurus from the Iren Dabasu Formation is probably also a hadrosaurid but is poorly known and thus was not included in our analysis. The age of the Iren Dabasu Formation is still poorly constrained. Initially, it was considered Early Cretaceous or Cenomanian (see review in Van Itterbeeck et al. 2005). More recently, a Campanian age for this formation has been commonly cited based on an incorrect reference to Currie & Eberth (1993). Actually, these authors concluded that the Iren Dabasu Formation at Iren Nor is ‘best considered early Senonian in age’ (Currie & Eberth 1993, p. 140), which is Coniacian. Nessov (1995, 1997) and...
The second radiation of non-hadrosaurid hadrosauroids occurred during the Santonian. Hadrosauroids more derived than *Bactrosaurus* and *Levnesovia* share a well-developed ectopterygoid ridge on the maxilla and a dentary tooth row that is straight in occlusal view and terminates behind the apex of the coronoid process. *Tanius* from the Campanian (?) of China may also belong to this radiation, but no jaws are known for this taxon (Wiman 1929; figure 2). *Tełmatosaurus* from the Maastrichtian of Romania (Weishampel et al. 1993; figure 2) is a late survivor of this Santonian radiation. The next clade of Hadrosauroidea, comprising Hadrosaurinae, Lambeosaurinae and *Aralosaurus* from the Santonian-Campanian of Kazakhstan (Rozhdestvensky 1968), is supported by seven unambiguous apomorphies (electronic supplementary material 3) and has a bootstrap support of 70 per cent. *Aralosaurus*, previously considered the most basal lambeosaurine (Godefroit et al. 2004a), actually lacks a hollow supracranial crest, although it is probably close to the ancestry of Lambeosaurinae.

The oldest records referable to Hadrosaurinae are remains from the Santonian Eutaw Formation of Mississippi, USA (Kaye & Russell 1973) and the Late Santonian or Early Campanian *Lophorhothon* from the Moreeiville Chalk of Alabama, USA (Langston 1960; figure 3c). The oldest records of Lambeosaurinae are found in Santonian to Early Campanian strata in Kazakhstan: *Yaxartosaurus* and *Procheneosaurus convincens* (based on a juvenile skeleton; Rozhdestvensky 1968; Norman & Kurzanov 1997; figure 3c). This palaeobiogeographical pattern of the earliest Hadrosaurinae and Lambeosaurinae suggests that the former group originated in North America and the latter in Asia. During the Campanian and Maastrichtian, Hadrosauridae reached their widest geographical distribution, entering South America and Antarctica, and both subfamilies were present in Asia and North America.

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