

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

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Levnesovia transoxiana gen. et sp. nov., from the Late Cretaceous (Middle–Late Turonian) of Uzbekistan, is the oldest well-documented taxon referable to Hadrosauroidea *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. *Levnesovia*, *Bactrosaurus* and possibly *Gilmoresaurus* represent the earliest radiation of Hadrosauroidea, which took place during the Cenomanian–Turonian and possibly in North America. The second, Santonian-age radiation of Hadrosauroidea 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; Hadrosauroidea; Cretaceous; Asia; radiation; palaeobiogeography

1. INTRODUCTION

The Late Cretaceous duck-billed dinosaurs (Hadrosauridae) were one of the most diverse and geographically most widely distributed clades of herbivorous dinosaurs. Their evolutionary success has been related to a series of complex transformations of the masticatory apparatus in derived ornithopods, resulting in more sophisticated oral food processing (Norman & Weishampel 1985). The early stages of the evolution of Hadrosauroidea and Hadrosauridae are still poorly known, and previous hypotheses about the historical biogeography of these groups (Brett-Surman 1979; Milner & Norman 1984; Head 1998; Head & Kobayashi 2001) were hampered by lack of clear phylogenetic definitions and inadequate stratigraphic and phylogenetic resolution for critical taxa. Here we describe the oldest well-known hadrosauroid, provide a new phylogenetic analysis of derived iguanodontian ornithopods based on the distribution of 138 characters and discuss the basal radiation of Hadrosauroidea.

2. SYSTEMATIC PALAEOLOGY

Ornithischia Seeley 1887

Ornithopoda Marsh 1881

Iguanodontia Sereno 1986

Hadrosauroidea Cope 1869 (*sensu* Godefroit *et al.* 1998)

Levnesovia transoxiana gen. et sp. nov.

Cionodon(?) *kysylkumense* [nomen dubium]: Riabinin 1931, p. 116.

Gilmoresaurus arkhangel'skiyi [nomen dubium]: Nessov 1995, p. 49.

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(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).

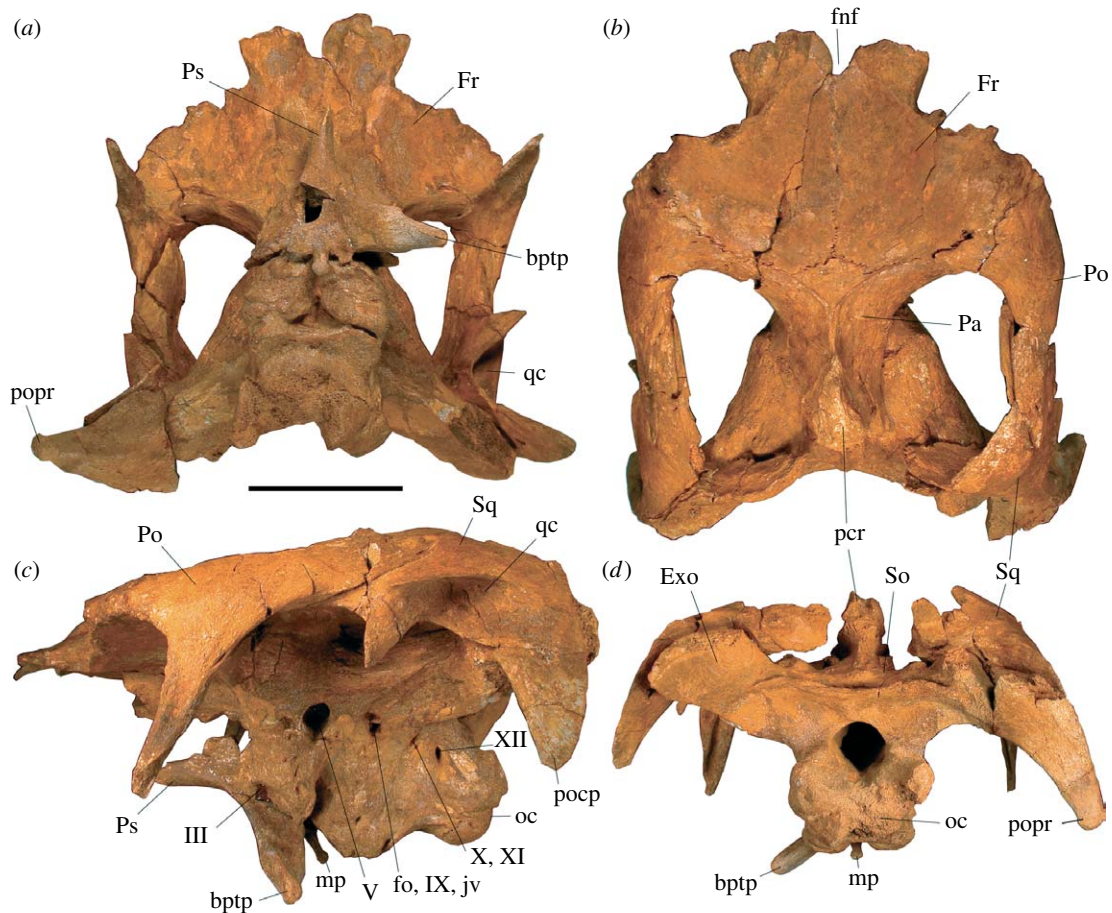


Figure 1. *Levnosovia transoxiana* gen. et sp. nov., partial skull USNM 538191 (holotype) in (a) ventral, (b) dorsal, (c) left lateral and (d) posterior views. Dzharakuduk, central Kyzylkum Desert, Uzbekistan; Bissekty Formation, Upper Cretaceous (Turonian). Abbreviations: bptp, basiptyergoid process; Exo, exoccipital; fnf, fronto-nasal fontanelle; fo, fenestra ovalis; Fr, frontal; jv, foramen jugular vein; mp, median process; oc, occipital condyle; Pa, parietal; pcr, parietal crest; Po, postorbital; pccp, postcotyloid process; popr, paroccipital process; Ps, parasphenoid; qc, quadrate cotyle; So, supraoccipital; Sq, squamosal. Roman numerals denote cranial nerves. Scale bar, 10 cm.

(e) *Diagnosis*

A basal hadrosauroid iguanodontian that differs from known non-hadrosauroid 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 *Gilmoresaurus* (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 Hadrosauroidea in absence of well-developed continuous ectopterygoid ridge on maxilla; dentary tooth row and posterior end of dentary terminating at apex of coronoid process; and dentary tooth row bowed linguallly in occlusal view.

(f) *Comments*

A tall sagittal crest is also present in the non-hadrosaurid hadrosauroid *Tanius* 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 basiptyergoid processes. Such a process is also present in *Levnosovia*. However, the absence of this process in other hadrosauroid 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 posteromedial 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 parietals are long anteroposteriorly. A short rhomboid anteromedian process of the parietals is wedged between the frontals (figure 1*b*). The sagittal crest is low anteriorly but tall posteriorly (figure 1*d*). 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 precotyloid and postcotyloid processes. The flat postcotyloid process extends ventrolaterally, with its distal point deflected anteriorly. Its medial surface contacts the paroccipital process. On the ventromedial side there is a wide, saddle-shaped articular area for the dorsal angle of the paroccipital process. 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. On lateral surface three to five large foramina form a horizontal row. Medially, a deep, cleft-like depression for insertion of *m. pterygoideus dorsalis* (Ostrom 1961) separates the jugal process from the alveolar region of the maxilla. This depression opens anteriorly into the alveolar canal, extending anterior and lateral to the dental battery. Posterior to the depression, a rugose shelf contacted the ectopterygoid. The alveolar margin of the maxilla is slightly concave. The anterior process of the jugal is shallow dorsoventrally and apparently had a thin triangular anterior projection that contacted the premaxilla and separated the maxilla and lacrimal externally, as indicated by its contact facet on the maxilla. Its dorsal side has a prominent groove for insertion of the lacrimal. Medially, a narrow palatine facet is situated between the lacrimal facet and deep recess for the jugal process of maxilla (see electronic supplementary material 1, fig. d). The slender dorsal (post-orbital) process extends approximately perpendicular to the long axis of the bone. The posterior process of the jugal is taller dorsoventrally and shorter anteroposteriorly than the anterior process, contacting the quadratojugal with its truncated posterior side. The quadratojugal notch of the quadrate is wide and poorly defined (see electronic supplementary material 1, fig. e). The quadratojugal facet around the notch suggests closure of the 'paraquadrate' foramen. The mandibular condyle of the quadrate is triangular in distal view, with an anteroposteriorly expanded lateral condyle (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 parietals. 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 ornithomorphs. 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 1*a*). A deep longitudinal basisphenoidal 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 stapedia 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 opisthotic–prootic suture extends dorsally along the paroccipital 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 1*c*). Separate grooves mark the courses of V_1 and V_{2-3} . 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 basiptyergoid 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 parasphenoid.

(b) Mandible

The prementary 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 prementary 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 prementary and first dentary tooth. On the lateral side, a series of vascular foramina along the prementary–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 distinct coronoid 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.

(c) 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 mesiodistally 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 mesiodistally (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.

(d) 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 compressed mediolaterally. A lateral swelling is present in place of the lateral process (antitrochanter) of the ilium. The pubis has a short iliac peduncle; its anterior (prepubic) process has a long neck (see electronic supplementary material 1, fig. r). A small process enclosing the obturator gutter posteriorly is variably present. The distal condyles of the femur are expanded anteriorly, with their anterior ends enclosing an extensor tunnel in the largest known specimens (electronic

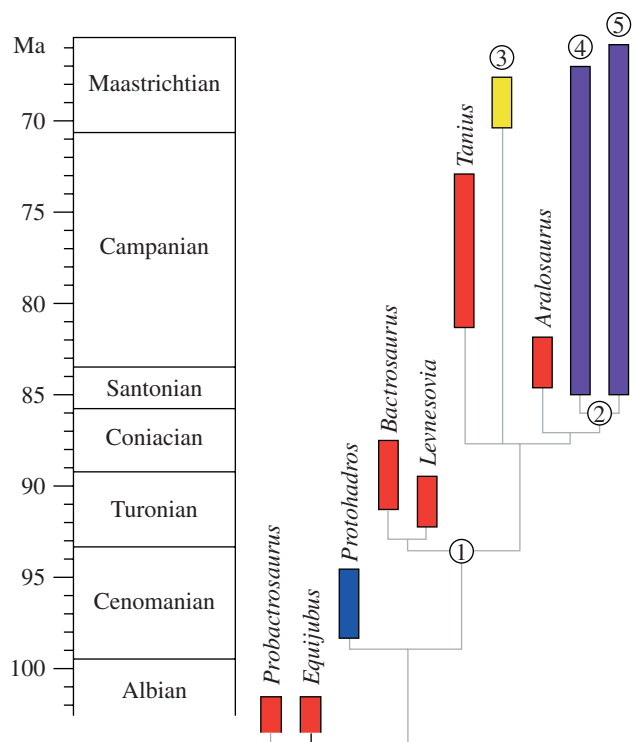


Figure 2. Phylogenetic, temporal and palaeogeographical relationships among derived iguanodontians. The tree is based on the strict consensus tree presented in the electronic supplementary material 4. Taxa shown in red are from Asia, in blue from North America, in yellow from Europe, and in purple from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

supplementary material 1, fig. s). The pedal ungual phalanges are flattened dorsoventrally and are hoof-like (see electronic supplementary material 1, fig. t).

4. PHYLOGENETIC ANALYSIS

In order to assess the phylogenetic position of *Levnesovia* we performed a phylogenetic analysis of hadrosauroid taxa based on distribution of 138 characters in 34 ornithomimid 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 Hadrosauroidea 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 Hadrosauroidae (all hadrosauriforms closer to *Parasaurolophus* than to *Iguanodon*). The problem with Sereno's definition of Hadrosauroidae 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 Hadrosauroidae (*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 (*Altirhinus*, *Equijubus*, *Fukuisaurus*, *Jinzhousaurus*, *Lanzhousaurus*, *Nanyangosaurus*, *Penelopognathus*, *Probactrosaurus*, *Shuangmiaosaurus*) and North America (*Cedrorestes*, *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 Hadrosauroidae (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 (figure 3a; electronic supplementary material 5) belong either to the earliest hadrosauroids or to derived non-hadrosauroid iguanodontians like *Protohadros*. Isolated dentary teeth with diamond-shaped crowns that lack secondary ridges have been reported from the Cenomanian of England (*Trachodon cantabrigiensis*) and Uzbekistan (*Gilmoresaurus atavus*), possibly representing the oldest known records of Hadrosauroidae (figure 3a).

Levnesovia from the Bissekty Formation (Middle–Late Turonian) of Uzbekistan is the oldest well-known taxon referable to Hadrosauroidae. 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. *Gilmoresaurus* from the Iren Dabasu Formation is probably also a hadrosauroid 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 Itterbeek *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

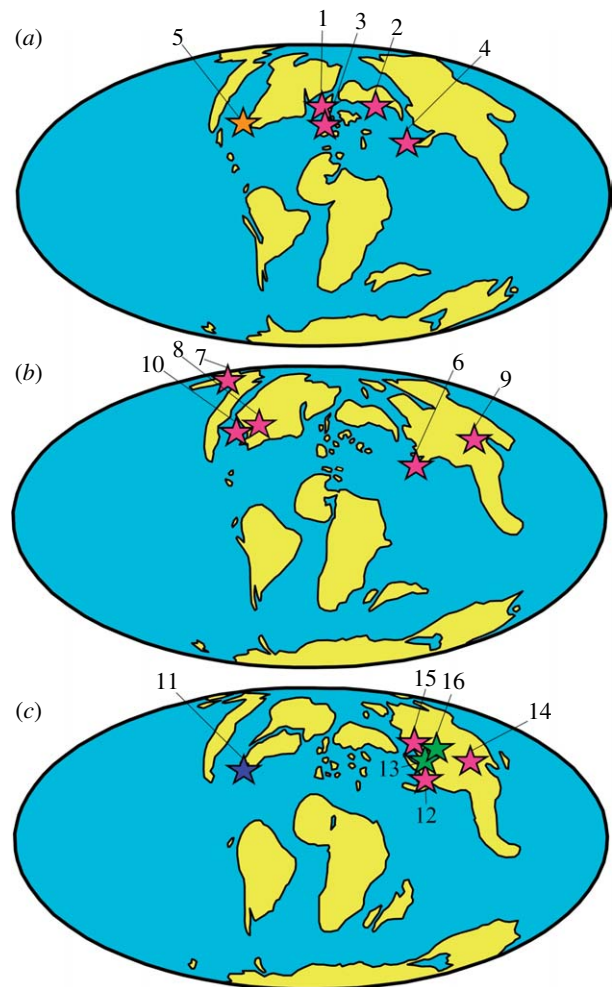


Figure 3. Palaeogeographical distribution of derived iguanodontians during the (a) Late Albian–Cenomanian, represented by the Cenomanian, 95 Ma; (b) Turonian–Coniacian, represented by the Turonian, 90 Ma; and (c) Santonian, 85 Ma. *Protohadros* is shown in orange, non-hadrosaurid hadrosauroids in pink, hadrosaurines in blue and lambeosaurines in green. For the list of occurrences see electronic supplementary material 5. Palaeogeographical maps modified from Smith *et al.* (1994).

Averianov (2002) discussed the evidence for correlating the vertebrate assemblages of the Iren Dabasu, upper Bain Shire, and Bissekty formations, and suggested a Turonian–Coniacian age for the Iren Dabasu. Van Itterbeek *et al.* (2005) suggested a Maastrichtian age for the Iren Dabasu Formation based on similarities in charophytes and ostracodes to the Nemegt Formation on Mongolia. However, we consider this conclusion problematic because many of the microfossil taxa considered have a much greater stratigraphic range than Maastrichtian. On the contrary, the Turonian age of the Bissekty Formation is well constrained by its intercalation with fossiliferous marine strata. The only other Turonian-age records of Hadrosauroidae are a skeleton from the Matanuska Formation of Alaska and fragmentary remains from the Moreno Hill Formation in New Mexico (Pasch & May 1997; McDonald *et al.* 2006; figure 3b). The next oldest hadrosauroid is *Claosaurus* from the Niobrara Chalk Formation of Kansas, which is Late Coniacian to Early Santonian in age (Carpenter *et al.* 1995; figure 3b). None of these records is currently diagnostic at a lower taxonomic level.

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). *Telmatosaurus* 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 *Lophorhynchon* from the Mooreville 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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