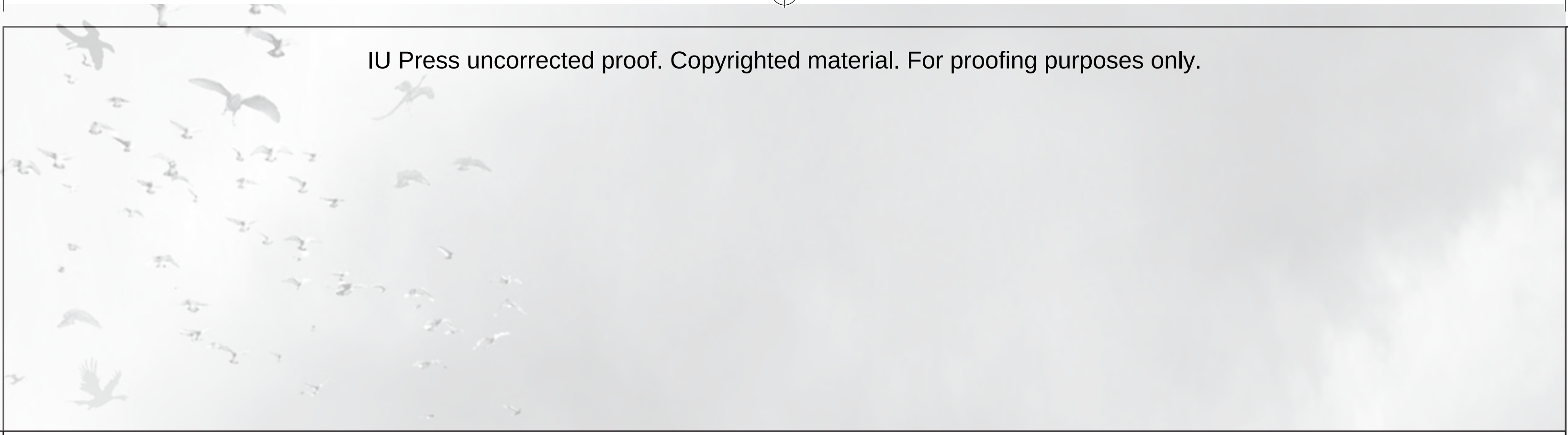


20.1. Geographical locations of sites where hadrosauroid dinosaurs have been recovered in Kazakhstan.

A New Basal Hadrosauroid Dinosaur from the Upper Cretaceous of Kazakhstan

20

**Pascal Godefroit*, François Escuillié,
Yuri L. Bolotsky, and Pascaline Lauters**

AEHM 4/1, a fragmentary specimen from the Bostobinskaya Svita (Santonian–Campanian) of Central Kazakhstan, is described as the holotype of a new genus and species of hadrosauroid dinosaur. *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. is characterized by cranial autapomorphies, as well as a unique combination of characters. The curvature and size of the semicircular canals of the inner ear suggest that *Batyrosaurus rozhdestvenskyi* was an agile biped. A phylogenetic analysis reveals that *Batyrosaurus* is a basal hadrosauroid more derived than *Bolong*, *Equijubus*, *Jinzhousaurus*, and *Altirhinus*, but more primitive than *Probactrosaurus*, *Eolambia*, and *Protohadros*. Basal hadrosauroids were diversified in Asia during the Early Cretaceous and probably migrated into North America after the establishment of the Bering land bridge in the Aptian–Albian. *Batyrosaurus* is the youngest nonhadrosaurid hadrosauroid described so far according to the definition of Hadrosauridae here adopted. A phylogenetic analysis also confirms that hadrosaurids probably had an Asian origin.

Introduction

Hadrosauroidea is a stem-based taxon defined as all Iguanodontoidea closer to *Parasaurolophus* than to *Iguanodon* (Sereno, 1997, amended). Basal hadrosauroids (=nonhadrosaurid Hadrosauroidea) were particularly diversified in Asia during the Early Cretaceous. Some of them (*Jinzhousaurus*, *Bolong*) are represented by fairly complete skeletons, although most basal hadrosauroids are known from partial and disarticulated material. During the closing stages of the Late Cretaceous, Hadrosauroidea were represented by Hadrosauridae, a node-based taxon defined as the most recent common ancestor of *Bactrosaurus* and *Parasaurolphus*, plus all the descendants of this common ancestor (see Norman, 2004, fig. 11.22): they became the most diverse and abundant large vertebrates of Laurasia (Horner et al., 2004). In this chapter, we describe a new basal hadrosauroid from the Santonian–Campanian of Kazakhstan. This is the youngest basal hadrosauroid discovered so far, following the definition of Hadrosauridae here adopted.

The new taxon is based on a fragmentary skeleton, including both cranial and postcranial material, discovered in the Akkurgan locality, east of the Aral Sea in Central Kazakhstan, in the Kzyl-Orda Oblast', 135 km north of the Dzhusala railway station (Fig. 20.1). Shilin (1977) was the first to describe the Akkurgan locality. Shilin and Suslov (1982) allocated the fossiliferous beds in the Akkurgan locality to the Bostobinskaya Svita (=Bostobe Formation; Sues and Averianov, 2009) on the basis of the general similarity of the lithofacies with other outcrops of the formation in this area. Dinosaur fossils were discovered in greenish-gray shales with pink flecks about 2 m below purple shales (Shilin and Suslov, 1982; Norman and Kurzanov, 1997). Abundant plant remains were collected from Akkurgan (Shilin, 1977). This paleoflora is dominated by small and narrow leaves with denticulate margins attributed to the family Ulmaceae (Shilin, 1977). Comparisons with floras elsewhere in Kazakhstan support a Santonian–Campanian age because older Cenomanian to Turonian deposits are dominated by angiosperms belonging to the family Platanaceae, characterized by broader leaves (Shilin, 1978; Shilin and Suslov, 1982).

From this locality, Shilin and Suslov (1982) also described the caudal part of a left maxilla and the associated distal end of a femur that they attributed to a new hadrosaurid dinosaur, *Arstanosaurus akkurganensis*. Norman and Kurzanov (1997) restudied the holotype and one previously unreported maxillary tooth, and they regarded *Arstanasaurus akkurganensis* as a nomen dubium closely related to *Bactrosaurus johnsoni* from the Iren Dabasu Formation of Erenhot (P.R. China) and hadrosauroid material from Baunshin Tsav in Mongolia.

Institutional abbreviations. AEHM, Palaeontological Museum of the Institute of Geology and Nature Management, Far East Branch, Russian Academy of Sciences, Blagoveschensk, Russia; AMNH, American Museum of National History, New York, USA.

Systematic Paleontology

Dinosauria Owen, 1842
Ornithischia Seeley, 1887
Ornithopoda Marsh, 1881
Iguanodontia Dollo, 1888 [Sereno, 1986]
Iguanodontoidea Cope, 1869
Hadrosauroidea Cope, 1869

Batyrosaurus rozhdestvenskyi gen. et sp. nov.
(Figs. 20.2–20.12)

Etymology. The generic name refers to *batyrs*, Kazakh heroic knights; *sauros* (Greek) means "lizard." The specific name refers to the famous Russian paleontologist A. N. Rozhdestvensky for his pioneering works on Middle Asian Iguanodontia.

Holotype. AEHM 4/1, a partial skeleton, including partial skull and mandible, about 60 isolated teeth, paired sternals, a right humerus, a left radius, fragmentary metacarpals, and manual phalanges.

Locality and horizon. Akkurgan locality, east of the Aral Sea in Central Kazakhstan, in the Kzyl-Orda Oblast', 135 km north of the Dzhusala railway station (Fig. 20.1); Bostobinskaya Svita, Santonian–Campanian (Late Cretaceous).

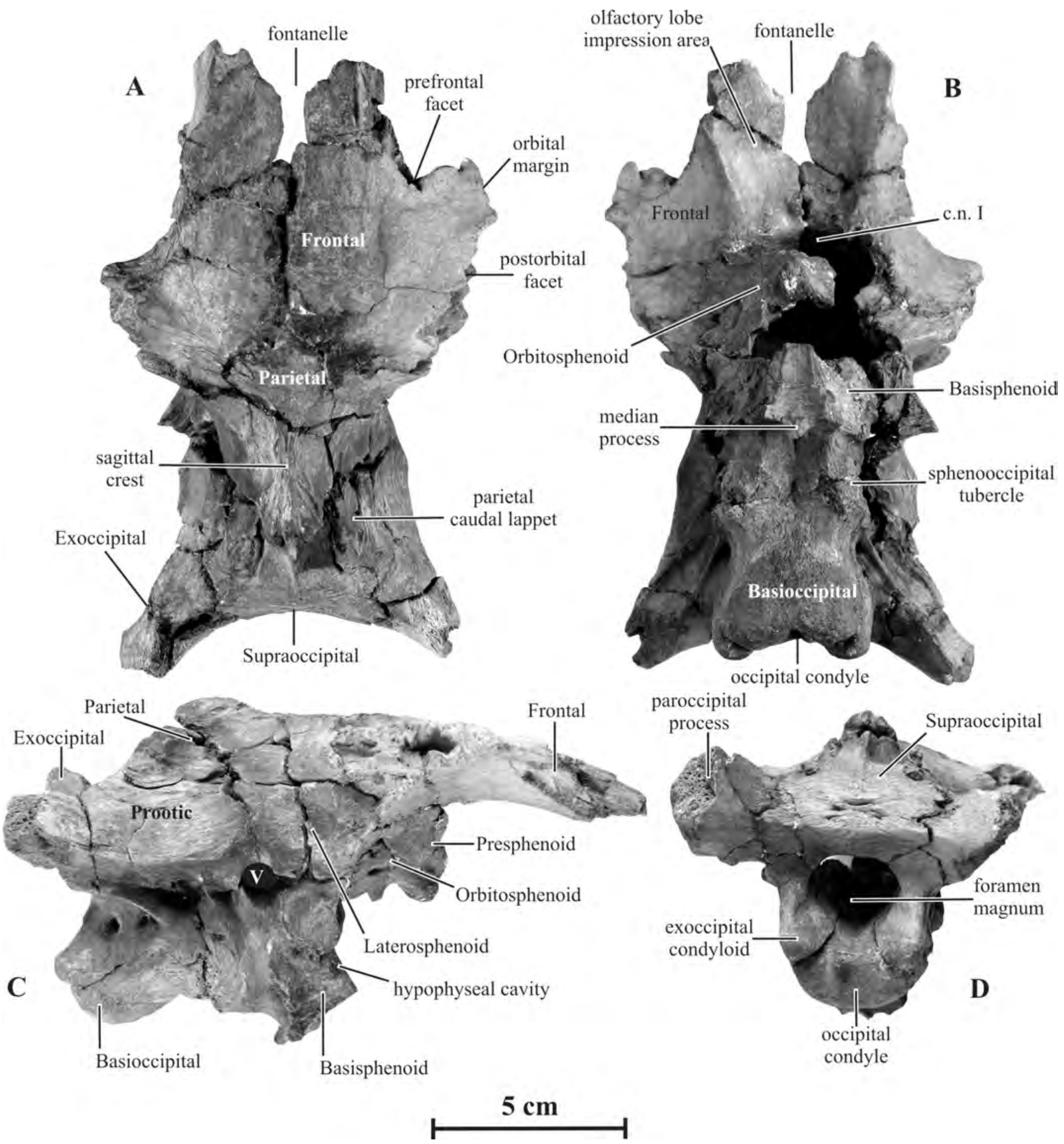
Diagnosis. Nonhadrosaurid hadrosauroid characterized by the following autapomorphies: parietal forming long caudal lappets, which overlie the supraoccipital and are overlain by the squamosals, but remain well separated from the paroccipital wings (character observed in *Bactrosaurus johnsoni*); frontals rostrocaudally elongated, about 1.7 times longer than wide; lateral side of rostral process of jugal bearing a deep horizontal sulcus below the lacrimal facet; glenoid surface of surangular perforated by a foramen.

Osteology

Supraoccipital. The supraoccipital is a stout pyramidal bone that extends upward and forward in the occipital region of the skull (Fig. 20.2D). The inclination of the supraoccipital is sometimes regarded as an important character among Iguanodontoidea (e.g., Sues and Averianov, 2009). It is usually more vertical in basal Iguanodontoidea than in Hadrosauridae. However, this character has not been retained in the present phylogenetic analysis because inclination of the supraoccipital seems progressive in basal Hadrosauroidea. Surprisingly, its intraspecific variability appears high in the lambeosaurine *Amurosaurus riabinini* (P.G., pers. obs.): the apparent inclination might depend on the deformation of the skull as a whole. The supraoccipital–exoccipital contact is marked by a strong horizontal ridge, followed dorsally by a slitlike transverse groove. A tall median crest occupies the dorsal two-thirds of the posterior side of the bone and expands dorsally, forming a knoblike structure in contact with the parietals. This crest is bordered by two elongated and shallowly depressed areas for insertion of M. spinalis capitis. The lateral sides of the supraoccipital are covered by the caudal lappets of the parietals. Under this area, the lateral side of the supraoccipital is irregularly sculptured by grooves and ridges, marking the contact areas with the squamosals. Supraoccipital knobs are not developed on the caudal surface of the bone. Prominent knobs are developed in hadrosaurids (e.g., Ostrom, 1961, Godefroit et al., 2004), and *Levnesovia transoxiana* (see Sues and Averianov, 2009). However, the phylogenetic significance of this character remains doubtful among basal hadrosauroids and hadrosaurids because Godefroit et al. (1998) observed that the development of supraoccipital knobs is apparently an ontogenetic character in *Bactrosaurus johnsoni.* In rostral view, the rostrodorsal part of the supraoccipital is depressed to form the caudal portion of the roof of the myencephalon.

Fused exoccipital–opisthotic. In caudal view, the paired exoccipitals exclude the supraoccipital from the roof of the foramen magnum. The exoccipital condyloids are particularly massive and form the prominent dorsolateral portions of the occipital condyle. In lateral view, the exoccipital condyloids are pierced by three foramina for cranial nerves, caudal to the metotic strut (Fig. 20.3). The caudal foramen for the hypoglossal nerve (XII) is the largest, whereas the foramen for the accessory nerve (XI) is the smallest. Both open medially into the endocranial cavity. The vagus canal (for c.n X., "perilymphatic duct" of authors) is set more dorsally and opens into the metotic ("jugular") foramen. Cranial to the metotic strut, a large auditory recess is divided by an oblique crista interfenestralis into a rostral fenestra ovalis (stapedial recess) and a caudal metotic foramen (Fig. 20.3). The metotic foramen contains separate openings for c.n. IX (dorsal) and the internal jugular vein (ventral).

Prootic. The prootic takes an important part in the formation of the lateral wall of the braincase (Fig. 20.2C). Together with the opisthotic, the medial wall of the prootic is inflated to form the vestibular pyramid



20.2. Braincase of *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype) in dorsal (A), ventral (B), right lateral (C), and caudal (D) views.

that contains the inner ear cavity. A broad and stout caudodorsal branch from the prootic covers the rostromedial part of the fused exoccipital–opisthotic. The dorsal border of this branch also contacts the supraoccipital. The lateral surface of the prootic has a prominent and horizontal crista otosphenoidale that extends into the rostrolateral side of the paroccipital process. The caudoventral portion of the prootic is notched by the rostral margin of the auditory recess, whereas its rostral border is deeply excavated by the caudal margin of the large and round foramen for the Gasserian ganglion of the trigeminal nerve (c.n. V). From this foramen, a vertical groove extends along the lateral surface of the prootic, just behind the basisphenoid process of the laterosphenoid (Fig. 20.3); this ventrally directed groove indicates the passage for ramus mandibularis of the trigeminal nerve (c.n. V_3). Between the notches for the auditory foramen and the trigeminal nerve, the lateral wall of the prootic is pierced by a small rounded foramen for transmission of the facial nerve (c.n. VII). From this foramen, a wide sulcus runs ventrally along the basisphenoid process of the prootic and connects the Vidian canal.

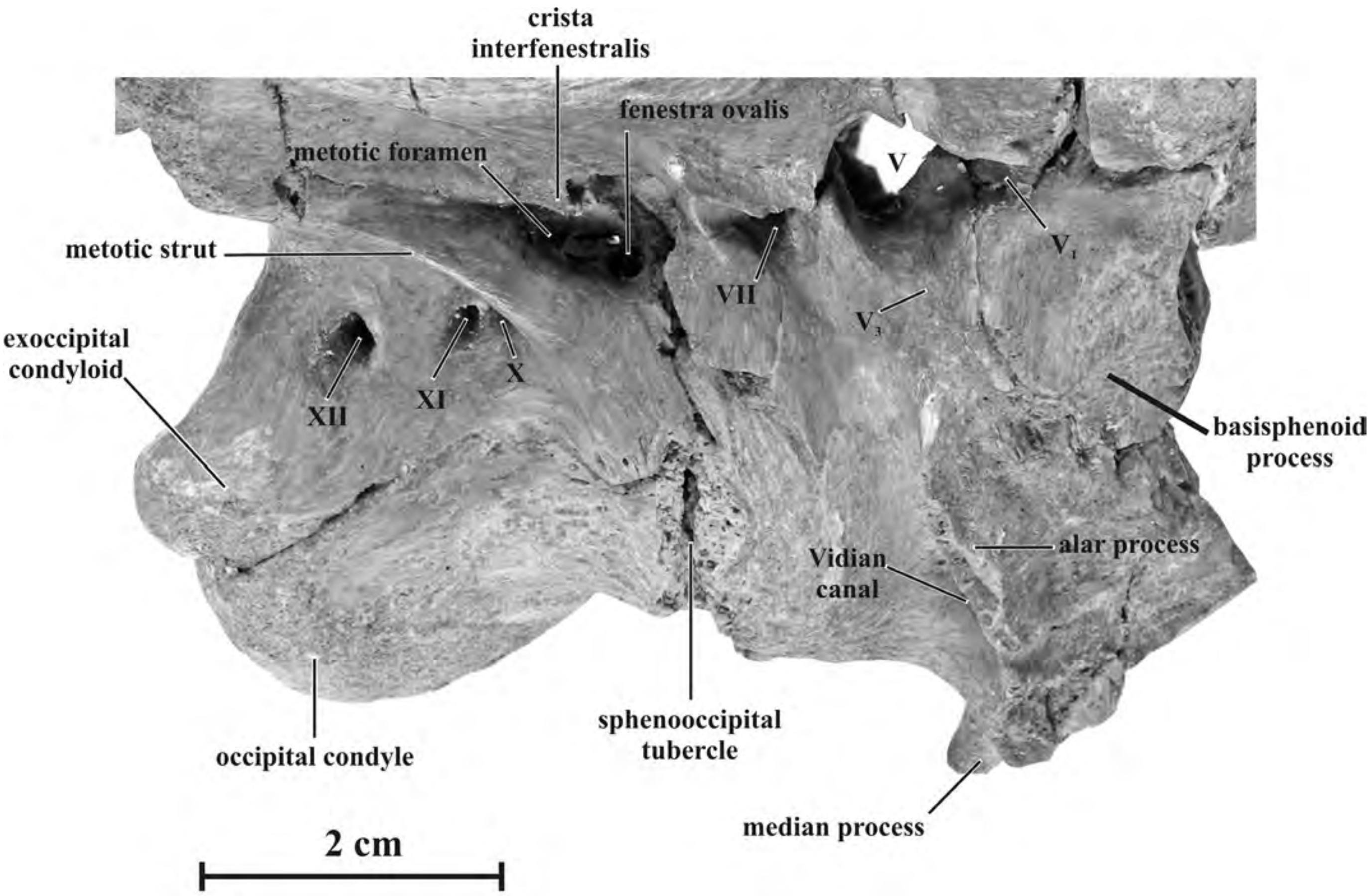
Laterosphenoid. The prootic process of the laterosphenoid forms a wide, triangular and caudally directed wing between the parietal and the prootic (Fig. 20.2C). The basisphenoid process forms a ventrally directed foot that covers the alar process of the basisphenoid and the rostrodorsal part of the ventral flange of the prootic. The angle between the prootic and the basisphenoid processes forms the rostral margin of the foramen for the trigeminal foramen. From this notch, a wide and deep groove extends rostrally along the lateral side of the laterosphenoid, indicating the forward passage of the deep ramus ophthalmicus of the trigeminal nerve (V_1). The rostral border of the basisphenoid process is notched by an elongated foramen for the occulomotor (c.n. III) and abducens (c.n. VI) nerves. The postorbital process is elongated and stout, but its lateral end that articulated with the postorbital is not preserved. The lateral side of the laterosphenoid bears a regularly round crest marking the separation between the orbit and the supratemporal fenestra.

Orbitosphenoid. This rounded bone participates in the rostral part of the lateral wall of the braincase and in the greatest part of the incomplete interorbital septum (Fig. 20.2B,C). Its surface is pierced by foramina for the trochlear (c.n. IV), dorsally, and the optic (c.n. II) nerves.

Presphenoid. The paired presphenoids form the rostral part of the interorbital septum and circumscribe the large median opening for the olfactory nerve (c.n. I; Fig. 20.2B).

Basioccipital. The basioccipital is longer than wide (Fig. 20.2B). The occipital condyle is proportionally wide and low. Its articular surface is perfectly vertical, perpendicular to the braincase, and it is incised by a vertical furrow (Fig. 20.2D). The median part of the dorsal surface of the basioccipital takes a large part in the formation of the foramen magnum. The sphenooccipital tubercles are separated from the occipital condyle by a distinct neck.

Basisphenoid. The basisphenoid is poorly preserved. Two large caudal processes, projecting slightly laterally from the basisphenoid and separated by a wide incision, form the rostral half of the sphenooccipital tubercles. The basipterygoid processes are broken off; between them, a median process projects caudally (Fig. 20.2B). Above the median process, the ventral surface of the basisphenoid is pierced by a small median foramen. Above the basipterygoid process and under the foramen for the trigeminal nerve, the lateral side of the basisphenoid forms the alar process (Fig. 20.3). The caudal part of this process conceals the Vidian canal, which carried the internal carotid artery through the basisphenoid into the hypophyseal cavity. Two other pairs of foramina pierce the caudodorsal wall of the hypophyseal cavity. The ventral openings correspond to the passages for the abducens

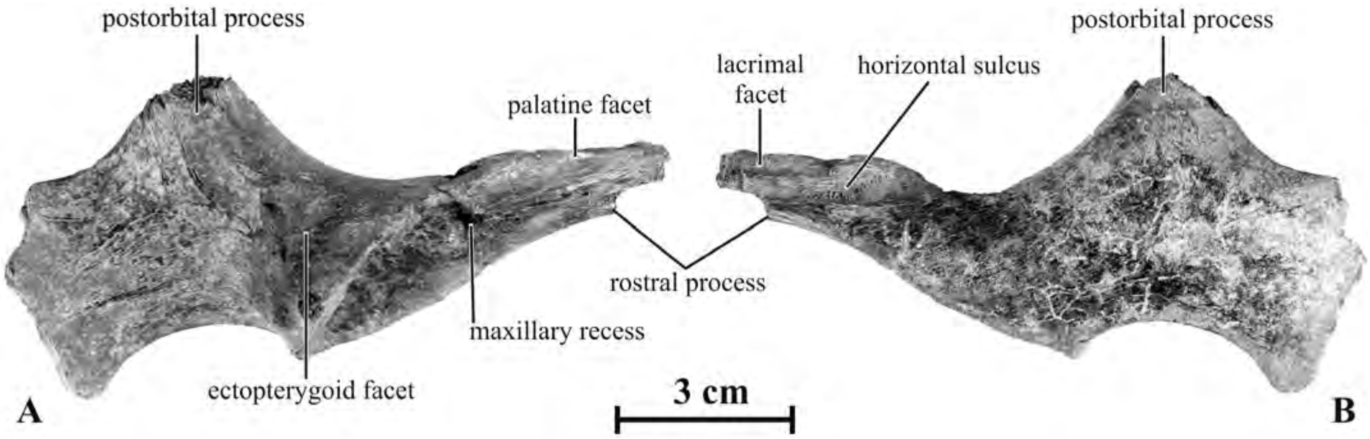


20.3. Close-up of the right ventolateral portion of the braincase of *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype).

nerves (c.n. VI), whereas the dorsal openings are interpreted as passages for ramus caudalis of the internal carotid artery.

Parietal. The fused parietals closely resemble those of *Probactrosaurus gobiensis* and *Bactrosaurus johnsoni*. Rostral lappets of the parietal splay laterally to contact the frontals and the postorbitals (Fig. 20.2A). A wide rhomboid rostromedian process is wedged between the frontals. This process is limited caudolaterally by curved ridges that fuse together at the midlength of the parietal to form the sagittal crest. This crest is much lower than in *Levnesovia transoxiana* (see Sues and Averianov, 2009, fig. 1). Caudal lappets of the parietal cover the lateral sides of the supraoccipital. Irregular ridges on their dorsal surface indicate that they were covered by the squamosals. Similar lappets were also described in *Bactrosaurus johnsoni* (AMNH 6366) and *Probactrosaurus gobiensis* (see Norman, 2002). However, in the latter genus, they contact the paroccipital processes laterally, whereas they remain well separated from the paroccipital process in *Batyrosaurus* and *Bactrosaurus*. In ventral view, the impression for the myencephalon is a narrow and deep depression along the caudal third of the parietal. An ovoid and shallower depression at about the middle of the parietal corresponds to the impression of the cerebellum. The ventral side of the rostromedian process of the parietal has a deep depression corresponding to the location of the caudomedial portion of the cerebrum.

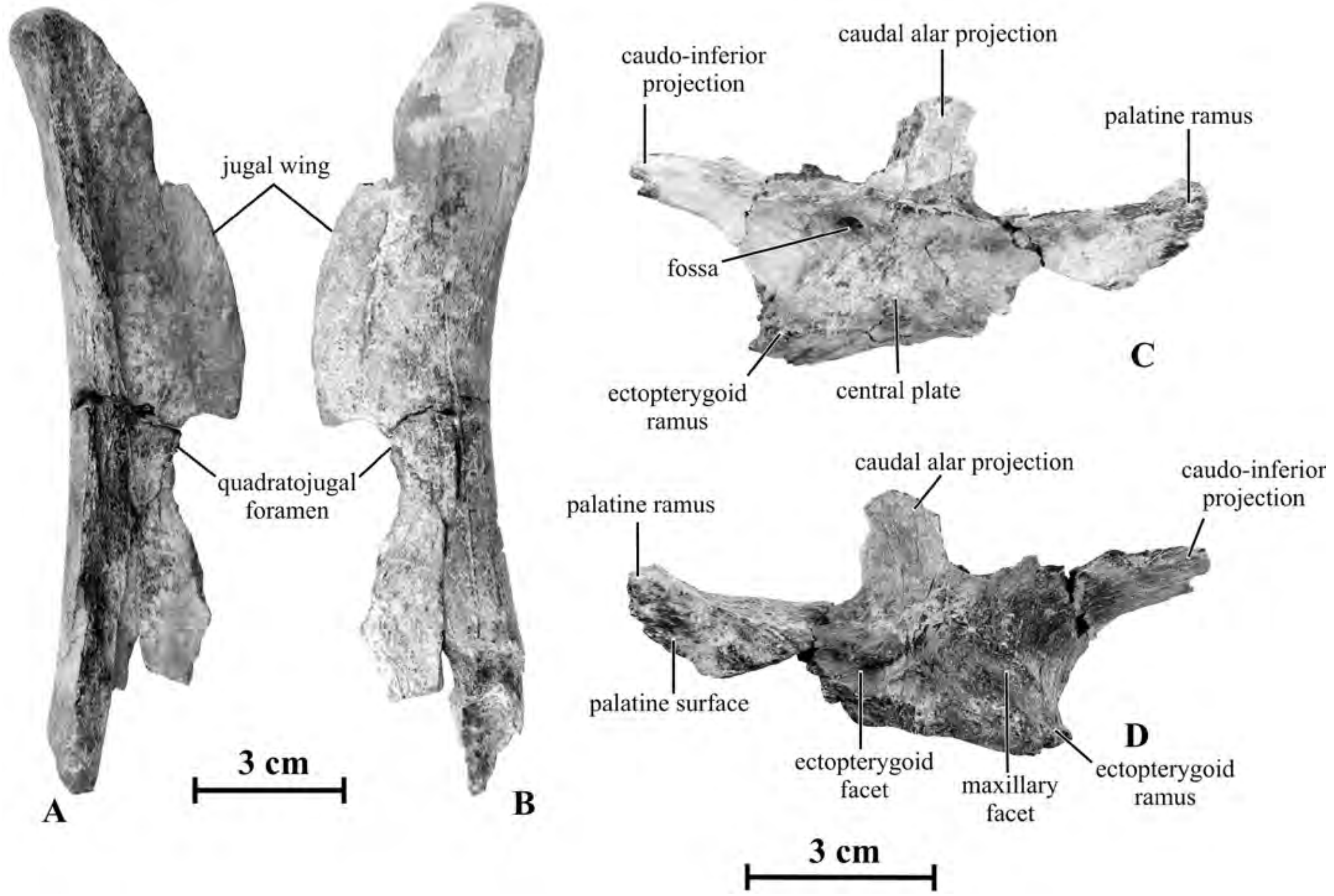
Frontal. The unfused frontals of *Batyrosaurus* appear more elongated rostrocaudally than in other hadrosauroids, being about 1.7 times longer than wide (Fig. 20.2A). Their elongated rostral processes have elongated



20.4. Left jugal of *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype) in medial (A) and lateral (B) views.

nasal facets and are separated from each other by a relatively large fontanelle. The rostrolateral margin of the frontal is notched by a long and thickened articular surface for the prefrontal. The caudomedial corner of the prefrontal notch is excavated by a deep recess for reception of the caudomedial process of the prefrontal, as also observed in other basal hadrosauroids and hadrosaurids, including *Probactrosaurus gobiensis* (P.G., pers. obs.), *Bactrosaurus johnsoni* (see Godefroit et al., 1998), and *Levnesovia transoxiana* (see Sues and Averianov, 2009). The orbital rim is short and thin. The articular surface for the postorbital, on the caudolateral border of the frontal, is particularly long, thick, and persillate. The caudal borders of the paired frontals form a wide midline notch where the rostral process of the parietal interfingers. The dorsal surface of the frontals is slightly domed above the cerebrum area, as also observed in juvenile hadrosauroid specimens, but doming is less pronounced than in juvenile lambeosaurines (Evans et al., 2005). In ventral view, the caudomedial part of the frontal is deeply excavated for the cerebrum. Rostrally, the ventral surface of the nasal process is also excavated by the long impression area of the olfactory lobe (Fig. 20.2B).

Jugal. The left jugal of *Batyrosaurus* is partially preserved and closely resembles that of *Altirhinus kurzanovi* (Fig. 20.4). The rostral process is elongate, asymmetrical, and tapers rostrally. In lateral view, its dorsal margin is nearly straight, whereas its ventral margin is sigmoidal. Its dorsal side has a prominent sulcus for insertion of the lacrimal. Below the lacrimal facet, the lateral side of rostral process has a deep horizontal sulcus that suddenly becomes dorsoventrally higher caudally (Fig. 20.4B). The medioventral surface of the rostral process is deeply excavated to form a long recess into which the jugal process of the maxilla slotted (Fig. 20.4A). Medially, a narrow palatine facet is located between the lacrimal facet and the maxillary recess. Immediately caudal to the maxillary recess, a large triangular depression on the medial side of the jugal represents the articular surface for the ectopterygoid. The base of the ectopterygoid facet is marked by a small knoblike protuberance. Basal Iguanodontoidea (sensu Norman, 2004) retain a large jugal–ectopterygoid joint, as observed in *Iguanodon bernissartensis*, *Mantellisaurus atherfieldensis* (see Norman, 2002), *Ouranosaurus nigeriensis* (see Taquet, 1976, fig. 19), and *Altrihinus kurzanovi* (see Norman, 1998, fig. 9). The ectopterygoid facet is distinctly less developed



20.5. *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype). Left quadrate in medial (A) and lateral (B) views; left pterygoid in medioventral (C) and laterodorsal (D) views.

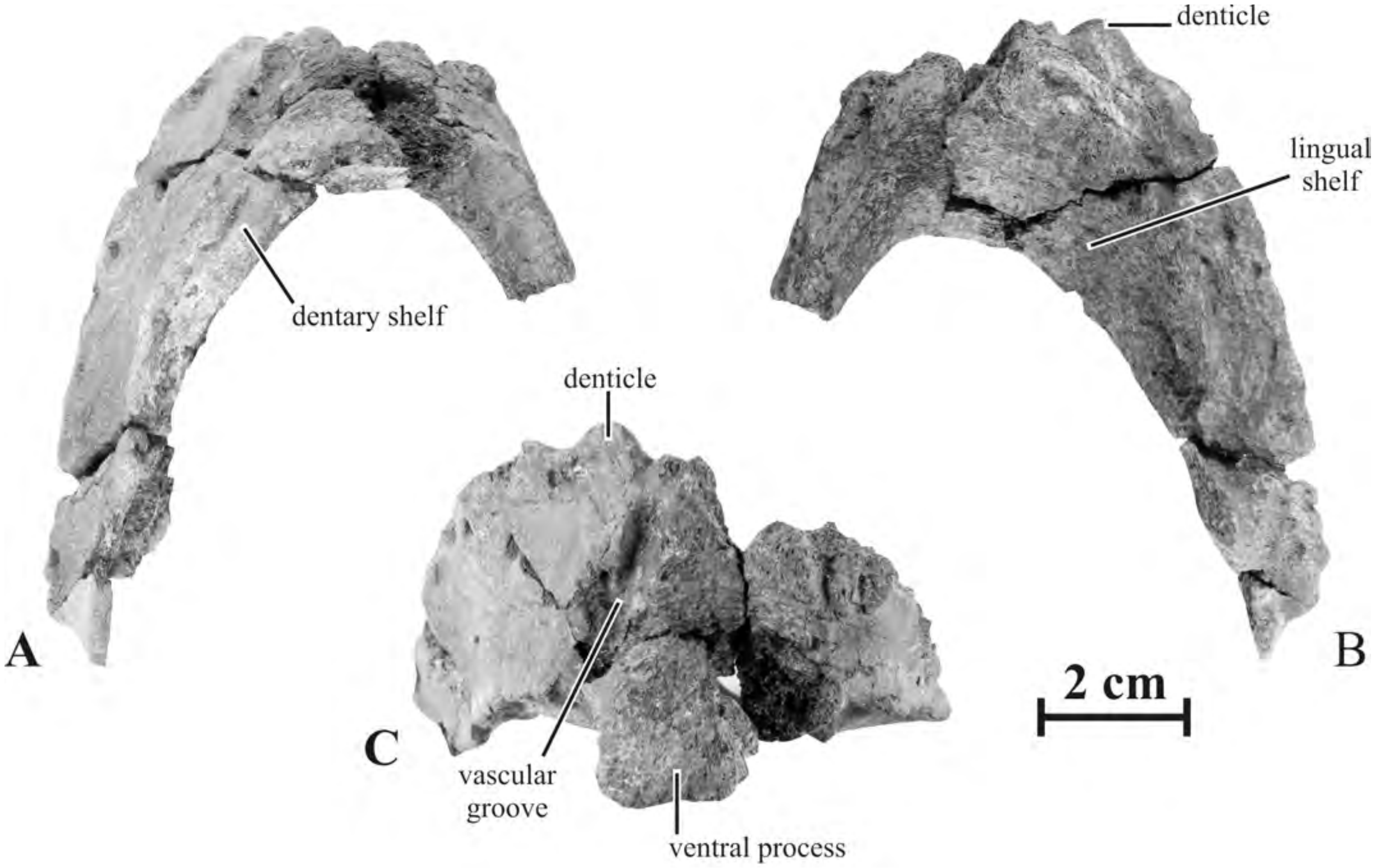
and slitlike in *Protohadros byrdi* (see Head, 1998, fig. 5) and *Probactrosaurus gobiensis* (see Norman, 2002, fig. 6). It is absent in *Bactrosaurus johnsoni* (see Godefroit et al., 1998, fig. 13), *Levnesovia transoxiana* (see Sues and Averianov, 2009), and Euhadrosauria. Both the postorbital and the caudal processes of the jugal are broken off. Under the postorbital process, the ventral margin of the jugal is moderately concave, as also observed in *Altirhinus kurzanovi* (see Norman, 1998, fig. 9), whereas it is distinctly straighter in *Protohadros byrdi* (see Head, 1998, fig. 5) and *Probactrosaurus gobiensis* (see Norman, 2002, fig. 6).

Quadrate. The dorsal portion of the left quadrate is preserved in the holotype. As is usual in basal hadrosauroids, it is slightly curved caudally (Fig. 20.5A,B). Its dorsal articular surface is triangular in cross section and only moderately developed. It is supported caudoventrally by a vertical buttress, also described in *Altirhinus kurzanovi* (see Norman, 1998) and *Probactrosaurus gobiensis* (see Norman, 2002). The pterygoid wing is completely destroyed. The jugal wing is smoothly convex, being interrupted by a fairly deep embayment for the quadratojugal foramen. Two distinct bevelled articular facets, respectively above and at the base of the quadratojugal notch, articulated with the quadratojugal. This situation can also be observed in *Altirhinus kurzanovi*, *Probactrosaurus gobiensis*, *Jeyawati rugoculus*, *Bactrosaurus johnsoni*, and *Gilmoreosaurus mongoliensis*, suggesting that the quadratojugal notch was not completely occluded by the quadratojugal in these taxa. In *Levnesovia transoxiana* (see Sues and

Averianov, 2009), probably *Telmatosaurus transsylvanicus* and Euhadrosauria, the quadratojugal facet is continuous along the whole height of the emargination.

Pterygoid. A partial left pterygoid is preserved in the holotype material (Fig. 20.5C,D). The palatine ramus forms an essentially horizontal, although slightly inclined dorsally, flattened plate. Its dorsolateral side forms an extensive contact surface for the palatine (Fig. 20.5D). At the base of the palatine ramus the pterygoid forms a thickened central plate. Caudal to the palatine suture, the lateral side of the central plate has a cup-shaped depression that accommodated a projection from the ectopterygoid. Immediately caudal to the ectopterygoid articulation, there is a shallow sulcus that articulated with the maxilla. The ectopterygoid ramus is short but robust and projects caudolaterally from the central plate. Its lateral side has a scarred attachment area for the ectopterygoid and the maxilla. The caudal alar projection is incompletely preserved; it extends dorsomedially from the central plate. The caudoinferior projection extends caudodorsally. Its medial side has a prominent buttressing flange, which widens as it merges with the central plate to form the area of the basal articulation. A deep elliptical fossa perforates the ventral side of the central plate just in front of the caudoinferior projection (Fig. 20.5C).

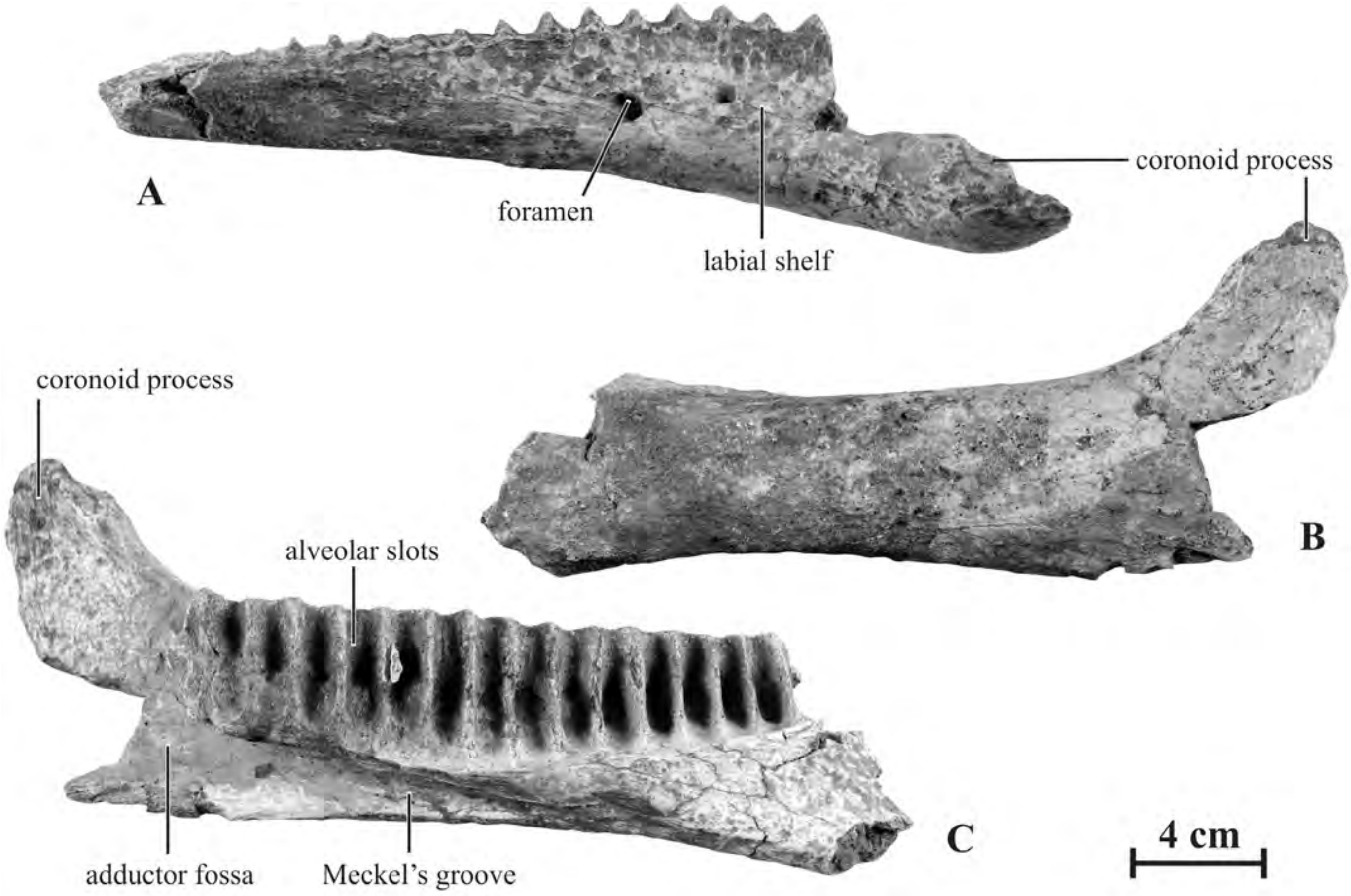
Predentary. This horseshoe-shaped median bone is similar in general structure to that of *Altirhinus kurzanovi* (see Norman, 1998, fig. 15). Its dorsal border has a graduated series of conical denticles, which are replaced further laterally by a rounded ridge (Fig. 20.6B). The edge of the predentary limits a moderately developed lingual shelf, broader caudally than rostrally. Under the denticles, the bone is punctured by foramina and grooves, probably associated with the attachment of a keratinous beak. The ventral surface of the predentary forms a shelf that fitted on the rostral edge of the dentary (Fig. 20.6A). A well-developed ventral process helped to secure the dentaries in position (Fig. 20.6C). The rostral surface of the predentary has two diagonal vascular grooves that connect the dorsolateral corner of the ventral process to the base of the median denticle. These grooves are also well developed in *Iguanodon bernissartensis*, *Mantellisaurus atherfieldensis* (P.G., pers. obs.), *Ouranosaurus nigeriensis* (see Taquet, 1976, fig. 28), *Jinzhousaurus yangi* (see Barrett et al., 2009, fig. 1), *Altirhinus kurzanovi* (see Norman, 1998, fig. 15), *Probactrosaurus gobiensis* (see Norman, 2002, fig. 10), *Protohadros byrdi* (see Head, 1998, fig. 10d), *Bactrosaurus johnsoni* (see Godefroit et al., 1998), *Levnesovia transoxiana* (see Sues and Averianov, 2009), and *Tethyshadros insularis* (see Dalla Vecchia, 2009). The development of these diagonal grooves is variable among Euhadrosauria, but they are usually less marked than in more basal Iguanodontoidea. As in *Altirhinus kurzanovi* (see Norman, 1998), there is no evidence of a median process immediately above the dentary symphysis. However, this part of the predentary is not perfectly preserved in *Batyrosaurus*, and the notion that it is an artefact of preservation cannot be excluded. This median process is, on the other hand, well developed in *Probactrosaurus gobiensis* (see Norman, 2002), *Bactrosaurus johnsoni* (see Godefroit et al., 1998), *Protohadros byrdi* (see Head, 1998), and *Levnesovia transoxiana* (see Sues and Averianov, 2009).



20.6. Predentary of *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype) in ventral (A), dorsal (B), and rostral (C) views.

Dentary. The left dentary is rather well preserved, although the right one is fragmentary. The dentary ramus is long, robust, and straight, with a ventral margin slightly arched at the level of the symphysis (Fig. 20.7B). The dentary teeth fitted into the array of narrow and parallel alveolar slots on the lingual side of the dentary ramus; 16 vertical slots are preserved in the left specimen, and the total number of slots was probably less than 20 (Fig. 20.7C). The alveolar slots are much deeper and straighter than in *Penelopognathus weishampeli* (see Godefroit et al., 2005, fig. 3) and *Altirhinus kurzanovi* (see Norman, 1998, fig. 16); in the latter taxa, the alveolar slots remain irregular and shaped by the dentary crowns. The dental battery did not extend beyond the level of the coronoid process. The lateral side of the dentary ramus is convex, and the labial shelf is well developed between the dental battery and the coronoid process (Fig. 20.7A). Two large foramina perforate the labial shelf. The coronoid process is high, and the right specimen is slightly rostrocaudally expanded near its apex; it is slightly inclined caudally. The rear edge of the coronoid is slotted for attachment of the surangular. In caudal view, the dentary is excavated by the large adductor fossa, which extends rostrally as a deep Meckel's groove (Fig. 20.7C).

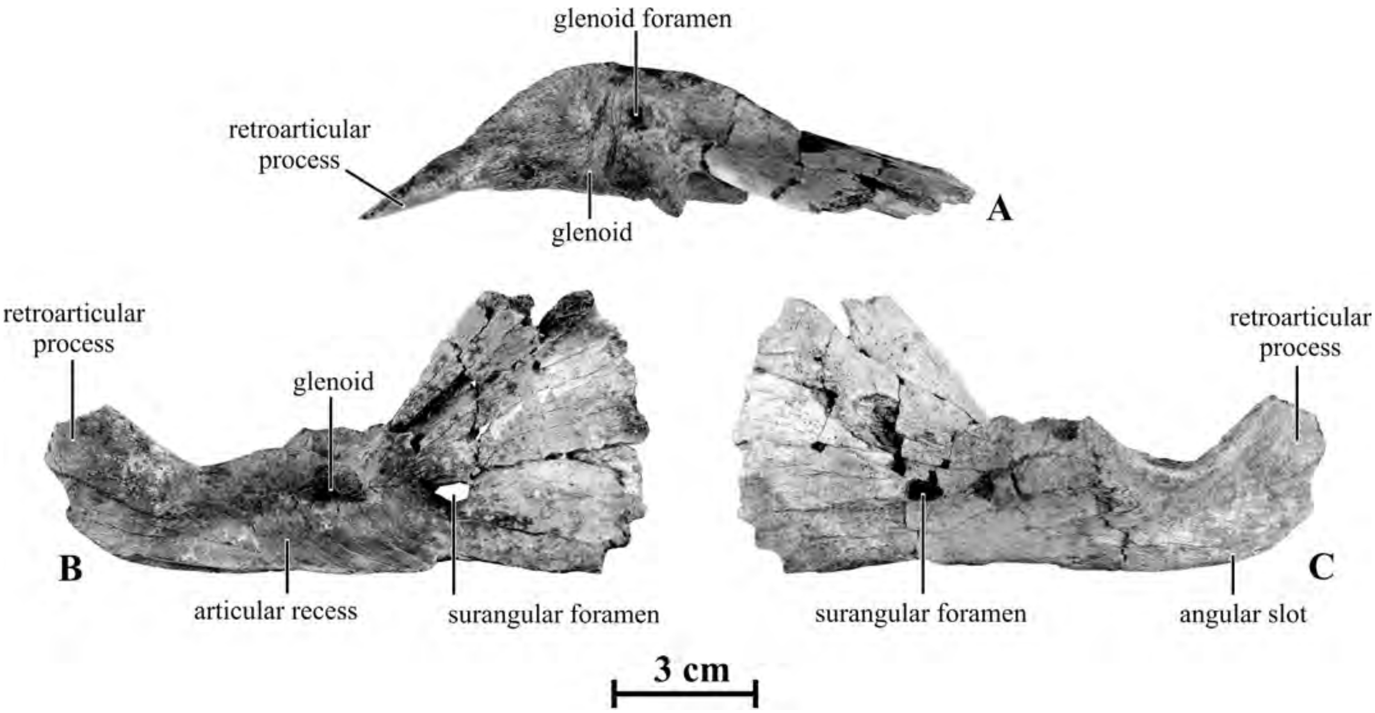
Surangular. The retroarticular process of the surangular is lobate and upturned above the glenoid (Fig. 20.8B,C). It is mediolaterally compressed, with a thin ventral edge. In dorsal view, the glenoid is a long, shallow, and cup-shaped depression (Fig. 20.8A). A smooth transverse ridge bisects it. Rostral to this ridge, a small elliptical foramen perforates the glenoid. This foramen has not yet been described in other iguanodontoids. The lateral margin of the glenoid forms a prominent upturned lip, overhanging the



20.7. Left dentary of *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype) in dorsal (A), lateral (B), and medial (C) views.

lateral wall of the bone. Rostroventral of the lateral lip a rounded surangular foramen is present, as also seen in basal Iguanodontoidea, including *Bolong yixianensis* (see Chapter 19 in this book), *Jinzhousaurus yangi* (see Barrett et al., 2009), *Altirhinus kurzanovi* (see Norman, 1998, fig. 17), *Probactrosaurus gobiensis* (see Norman, 2002, fig. 13), and *Protohadros byrdi* (see Head, 1998, fig. 12). This foramen is absent in *Bactrosaurus johnsoni* (see Godefroit et al., 1998, fig. 19), *Levnesovia transoxiana* (see Sues and Averianov, 2009), *Telmatosaurus transsylvanicus* (see Weishampel et al., 1993), *Tethyshadros insularis* (see Dalla Vecchia, 2009), and Euhadrosauria. The medial lip of the glenoid is less elevated than the lateral lip, and its rostral end forms a prominent horizontal process. Beneath the medial lip, a deep recess marks the area for attachment of the articular. The attachment surface for the angular forms an elongated and deep slot on the ventral side of the surangular. This facet is slightly inclined laterally, indicating that the angular was well visible on the lateral aspect of the mandible. Rostrally, the surangular forms a curved and thin wall that formed the lateral wall of the adductor fossa beneath and behind the coronoid process.

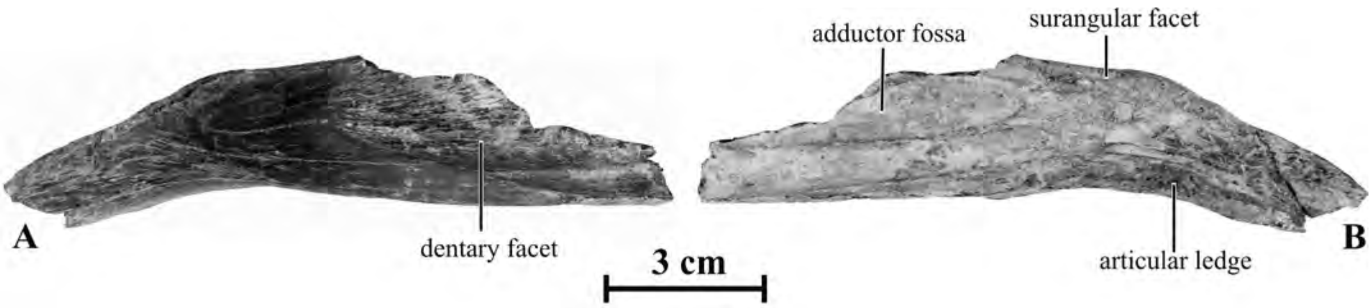
Angular. The right angular is well preserved and closely resembles that of *Altirhinus kurzanovi.* The left one is more fragmentary. This bone is long and sinuous. Rostrally, its lateral side bears an extended, depressed, and scarred surface that was overlapped by the dentary (Fig. 20.9A). The medial side of its dorsal edge bears an elongated bevelled surface that fitted against the ventral slot of the surangular (Fig. 20.9B). A thin horizontal ridge bisects the rostral half of the medial side of the angular; according to



20.8. Left surangular of *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype) in dorsal (A), medial (B), and lateral (C) views.

Norman (1998), this ridge would be associated with the muscle attachment to the floor of the adductor fossa. At the rear of the medial side, beneath the contact surface for the surangular, a roughened ledge probably represents the attachment for the articular. The ventral surface of the angular is essentially flat.

Dentary teeth. The enamel is restricted to the lingual side of the crown and to the marginal denticles. The root and the labial side of the crown are composed of dentine, smeared with rough areas of cementum. In mesial and distal views, the tooth is arched lingually (Fig. 20.10B). A vertical lingual facet and two pairs of mesial and distal facets run along the root and of the base of the crown. These facets represent the contact areas with adjacent teeth within the dental battery. The organization of these facets closely resembles the condition observed in *Probactrosaurus gobiensis* (see Norman, 2002, fig. 14) and in more advanced hadrosauroids. The facets are less clearly defined in *Penelopognathus weishampeli* (see Godefroit et al., 2005) and especially *Altirhinus kurzanovi* (see Norman, 2002), reflecting the fact that the dental battery as a whole was less compact in these taxa. The labial side is always strongly truncated because of intensive wearing. The enameled lingual side of the crown is asymmetrically diamond shaped (Fig. 20.10A). Although the proportions of the crown are variable within the dental battery, the height/width ratio of the crown is less than 2. A prominent primary ridge runs the entire height of the crown, dividing the crown surface into two unequal halves. A less prominent secondary ridge, parallel to the primary ridge, bisects the larger mesial half of the crown and always reaches the upper part of the mesial margin. This secondary ridge is situated halfway between the mesial edge of the crown and the primary ridge. A third ridge is faintly developed close to the mesial edge of the crown. A tiny tertiary ridge is developed on some teeth, close to the distal edge. The distal half of the crown also bears a vertical tertiary ridge. On the upper part

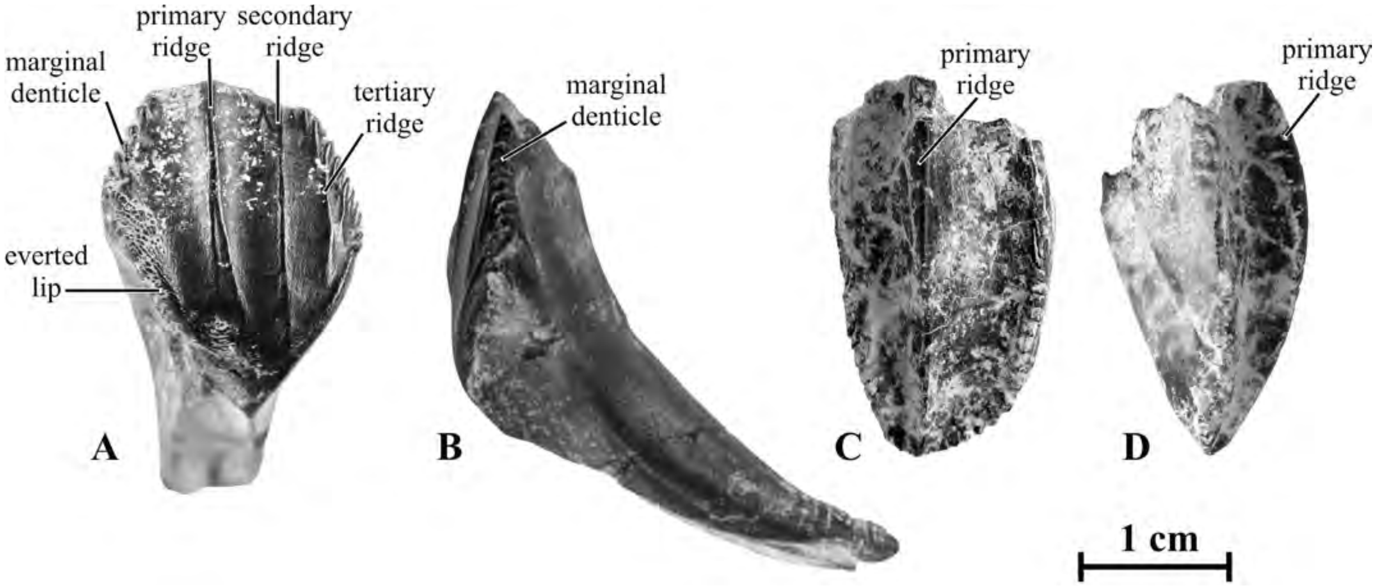


20.9. Right angular of *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype) in lateral (A) and medial (B) views.

of the edge of the crown, the denticulations form simple tongue-shaped structures. The structure of the marginal denticulations becomes more elaborated further down the sides of the crown. The edge becomes thickened, and each of the denticulations forms a curved and crenulated ledge, with additional denticulations, which wrap around the edge of the crown. On the mesial half of the crown, a variable number of subsidiary ridges are extensions of the bases of the marginal denticles. Marginal denticles are not developed on the edges along the lower part of the crown. At this level, the mesial edge is only slightly thickened. The distal edge forms an everted, oblique lip, as if the edge of the crown had been pinched inward. Small denticulations are developed on its surface, as also observed in *Iguanodon bernissartensis*, *Altirhinus kurzanovi*, and *Penelopognathus weishampeli*, but the surface of the ledge is apparently smooth in *Probactrosaurus gobiensis*. The distal everted edge is not developed in *Bactrosaurus johnsoni*, *Eolambia caroljonesa*, *Protohadros byrdi*, *Telmatosaurus transsylvanicus*, *Tethyshadros insularis*, and Euhadrosauria.

Maxillary teeth. About 30 maxillary teeth were discovered in association with the holotype material. Although no maxilla was discovered, it is highly probable that all belong to this specimen. The maxillary teeth are proportionally narrower and more lozenge shaped in labial view than the dentary teeth, and their structure is much simpler. The mesiolingual and distolingual side of the crows are channeled to accommodate the edges of adjacent replacement crowns. A prominent, keellike primary ridge (Fig. 20.10D) extends along the enameled labial side of the crown, limiting a larger mesial surface and a narrower distal surface (Fig. 20.10C). In *Probactrosaurus gobiensis*, *Bactrosaurus johnsoni*, *Levnesovia transoxiana*, *Protohadros byrdi*, *Telmatosaurus transsylvanicus*, *Tethyshadros insularis*, and Euhadrosauria, the maxillary crowns are symmetrical. The primary ridge is similarly keellike in *Altirhinus kurzanovi* (see Norman, 1998), *Levnesovia transoxiana* (see Sues and Averianov, 2009), and *Tethyshadros insularis* (see Dalla Vecchia, 2009). Contrary to *Altirhinus kurzanovi* (Norman, 1998), there is no subsidiary ridge. Denticulations are restricted to the apical half of the crown. Close to the apex, they have a simpler, tongue-shaped structure; they progressively form a curved and crenulated ledge.

Sternal. The sternals of *Batyrosaurus* are typically hatchet shaped (Fig. 20.11A). The proximal plate is about the same size as the distal "handle" and appears proportionally wider than in *Probactrosaurus gobiensis* (see Norman, 2002, fig. 21). It is thinner laterally than medially. Although it is incompletely preserved, the thin medial border of the proximal plate is distinctly convex. The distal handle of the sternal is massive and slightly



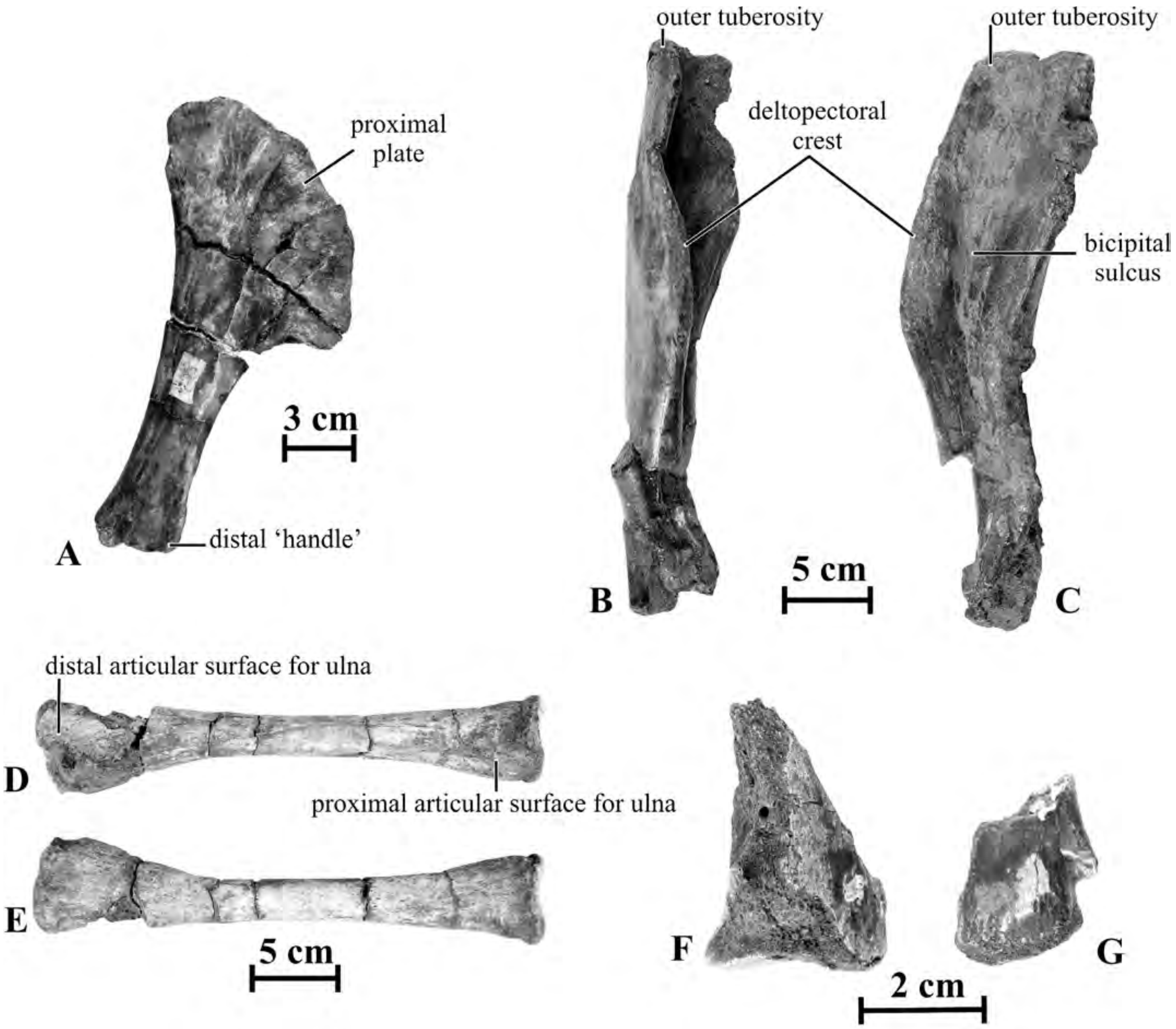
20.10. *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype). Left dentary tooth in lingual (A) and mesial (B) views; right maxillary tooth in labial (C) and distal (D) views.

curved dorsally; its distal end is slightly enlarged. The dorsal side of the handle has many longitudinal striations. Both the proximal and distal borders of the sternal are roughened, indicating the presence of cartilaginous caps in life.

Humerus. The right humerus is partially preserved in *Batyrosaurus.* The deltopectoral crest is proportionally longer than in *Probactrosaurus gobiensis* (see Norman, 2002, fig. 22), extending well below the middle of the bone, and its lateral edge is turned toward the cranial side of the bone (Fig. 20.11C). Nevertheless, the deltopectoral crest is not as wide as in lambeosaurines. The articular head is globular and separated from the outer tuberosity by a shallow sulcus. The medial side of the humerus is regularly concave. The cranial side of the humerus has a regularly concave and deep bicipital sulcus. Its regularly convex caudal side displays a well-marked scar generated by muscle attachments along its medial edge, as also described in *Probactrosaurus gobiensis* (see Norman, 2002, fig. 22). The distal portion of the humerus is heavily damaged and cannot be adequately described.

Radius. The left radius appears distinctly less robust than in *Altirhinus kurzanovi* (see Norman, 1998, fig. 28). In medial view, it is nearly perfectly straight (Fig. 20.11E). The proximal end of the radius is well expanded, but more compressed mediolaterally than in hadrosaurids; its caudolateral side forms an elongated and flattened surface where it articulated with the ulna (Fig. 20.11D). The distal end is expanded craniocaudally, and an elongated articulation facet on its lateral side faces cranially, suggesting that it fitted obliquely against the distal end of the ulna, as previously described in *Mantellisaurus atherfieldensis* (see Norman, 1986, fig. 49) and *Altirhinus kurzanovi* (see Norman, 1998, fig. 28).

Phalanges. Several fragmentary metacarpals and hand phalanges are preserved in the holotype specimen, but they are too poorly preserved to be adequately described. One eroded ungual phalanx (Fig. 20.11F) is tentatively identified as a pollex spike because it closely resembles that of *Probactrosaurus gobiensis* (see Norman, 1998, fig. 25d–g). Its base is rounded in cross section, but distally, it becomes compressed in the dorsopalmar



20.11. *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype). A, Right sternal in ventral view. Right humerus in lateral (B) and cranial (C) views. Left radius in lateral (D) and medial (E) views. F, Ungual phalanx of digit I in medial or lateral view. G, Partial ungual phalanx of digit II in dorsal view.

plane. Its proximal articular surface is concave. A well-developed ridge extends along the preserved portion of its lateral side. A second ungual is much more compressed in the dorsopalmar plane and has the tapering and asymmetric shape of an ungual phalanx of digit II (Fig. 20.11G). A well-developed mesial or lateral shelf supports a dorsal groove.

Paleoneurology

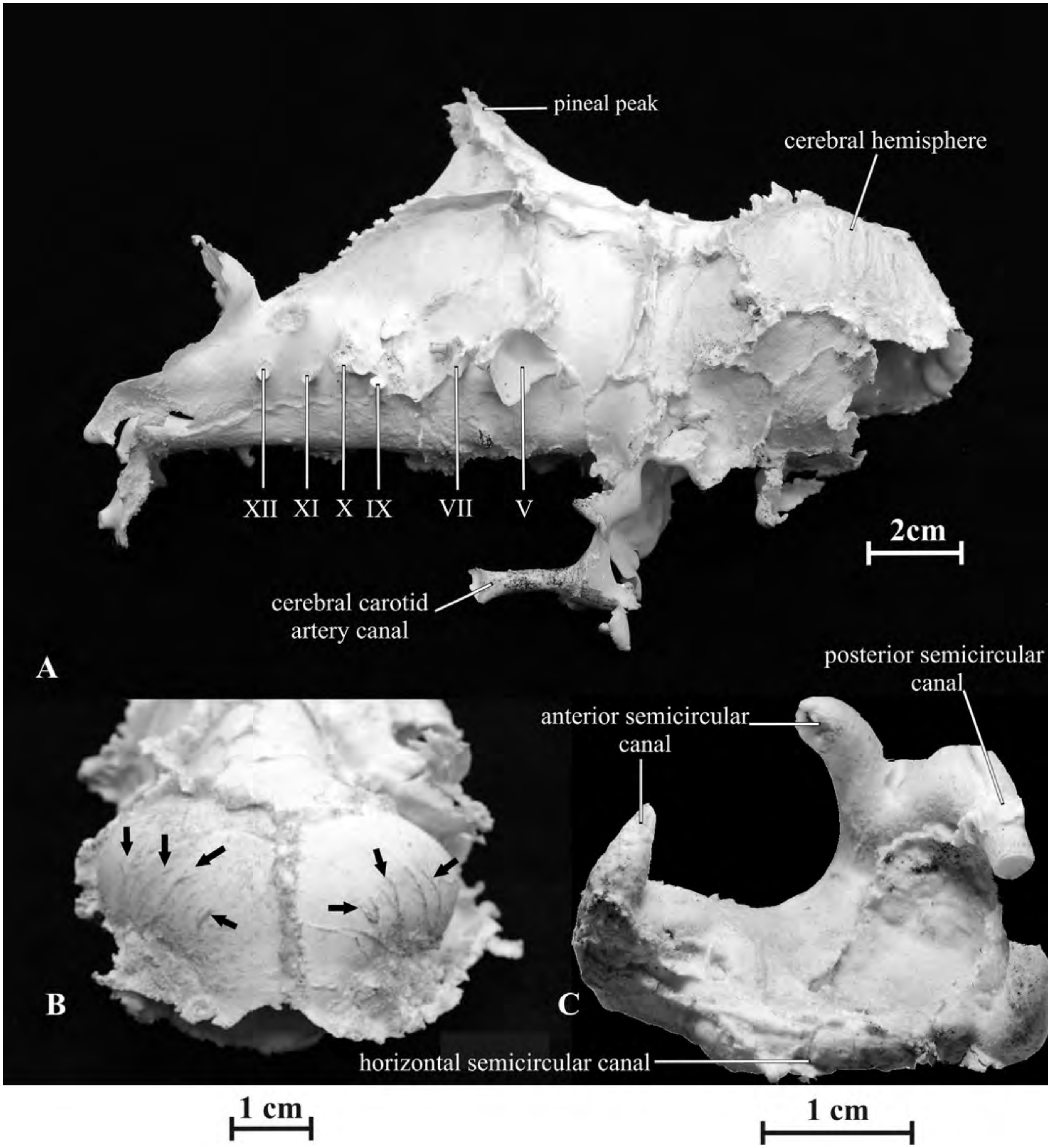
A silicone endocast of *Batyrosaurus rozhdestvenskyi* (AEHM 4/1) was made. The braincase was prepared by covering the smallest foramina and fractures with modeling clay. A thin layer of Vaseline was then sprayed onto the endocranial cavity. Silicone was then mixed with a catalyst and poured into the endocranial cavity to create a first endocranial silicone layer of the cast. This first layer was dried for at least 24 hours. Silicone was then again poured at intervals to create other layers. This technique allows the strengthening of the endocranial cast and prevents its tearing. When the last layer of silicone was completely dry, the endocranial cast was pulled out, and the braincase was then cleaned.

It has often been hypothesized that the brain of sauropsids does not fill the endocranial cavity, and the reasonable assumption is that the endocast is essentially a cast of dura mater (Osborn, 1912; Jerison, 1973; Hopson, 1979). Precisely how much of the endocranial cavity was occupied by the brain was a matter of great debate in paleoneurology (Jerison, 1973; Hopson, 1979; Hurlburt, 1996; Larsson, 2001). Recently, Evans (2005) and Evans et al. (2009) demonstrated for hadrosaurids and pachycephalosaurids that the portion of the endocast corresponding to the telencephalon faithfully represents the contours of the underlying brain. Indeed, valleculae can be observed on endocasts of these dinosaurs (Evans, 2005; P.L., pers. obs.). In *Batyrosaurus rozhdestvenskyi*, valleculae can also distinctly be observed on the anterior part of the telencephalon area (Fig. 20.12B), indicating that at least this part of the brain was in close contact with the bones and reflects the shape of the brain. It is the first time that valleculae are reported in non-hadrosaurid Iguanodontia. The presence of these valleculae indicates that the shape and dimensions of the endocast accurately reflects the general organization of the brain.

As is usual in ornithopods, the general organization of the brain in *Batyrosaurus rozhdestvenskyi* more closely resembles that observed in crocodilian than in birds or pterosaurs (Witmer et al., 2003). When the lateral semicircular canal is horizontal, the great axis of the brain has an inclination of approximately 30 degrees. The brain endocast measures 105 mm from the rostral margin of the cerebrum to the caudal hypoglossal branch, and measures 45.8 mm in maximal width, across the cerebrum. The endocast is relatively narrow, except the rostral part, which is round and enlarged. The telencephalon is round and pear shaped in dorsal view. The cerebral hemispheres are broad and slightly flattened dorsoventrally. The brain is marked by two constrictions: the first one is located just behind the telencephalon. The second and more marked constriction is located behind the large triangular peak above the midbrain region. This constriction housed the inner ear and semicircular canals. The width of the brain remains nearly constant through the medulla. The midbrain and hindbrain are undifferentiated.

A large triangular peak (Fig. 20.12A) projects dorsally above the midbrain region and extends rostrally and caudally over the cerebral and hindbrain regions, respectively. Similar peaks are observed on a wide variety of dinosaur brains, including *Allosaurus* and *Tyrannosaurus* (Hopson, 1979), *Majungasaurus* (Sampson and Witmer, 2007), and to a lesser extent in *Hypacrosaurus*, *Corythosaurus*, and *Lambeosaurus* (Evans et al., 2009). This feature can also be observed in *Iguanodon* and *Mantellisaurus* (see Chapter 16 in this book). It is possible that the dural space housed a well-developed pineal apparatus (epiphysis). Pineal glands are present in extant birds (Breazile and Hartwig, 1989), and evidence for pineal-like tissue in alligators was presented by Sedlmayr et al. (2004).

The ventral part of the telencephalon cannot be described because of the incompleteness of the braincase. As it is always the case in basal iguanodontoid (Andrews, 1897) and hadrosaurid endocasts (Lull and Wright, 1942; Evans et al., 2009), the optic lobes and the cerebellum cannot be



20.12. *Batyrosaurus rozhdestvenskyi* gen. et sp. nov. (AEHM 4/1, holotype). A, Endocranial cast in right lateral view. B, Telencephalon in rostral view; black arrows indicate the valleculae. C, Endosseous labyrinth of the left inner ear in lateral view.

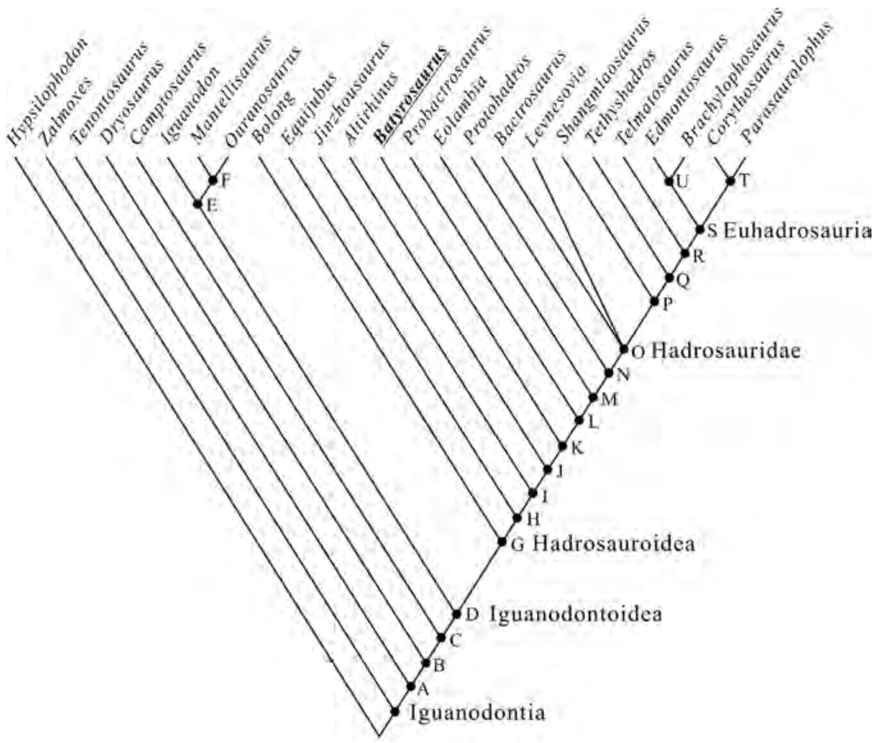
adequately described. This can be partly explained by the impossibility of casting the rostroventral part of the endocranial cavity.

The caudal part of the pituitary fossa and the paired internal carotid arteries coming ventrodorsally through the fossa can be observed on the endocast.

The left inner ear is well preserved and was molded (Fig. 20.12C). The three semicircular canals form regular loops. The anterior semicircular canal is longer than the posterior semicircular canal, and the horizontal is the shortest of the three. As noted by Sipla et al. (2004), large, well-curved semicircular canals, as observed in *Batyrosaurus*, are consistent with agile locomotion. Moreover, an enlarged anterior semicircular canal reflects adaptation to bipedal locomotion, as is the case in theropods and in bipedal basal ceratopsians (*Psittacosaurus*; Zhou et al., 2007). Therefore, the curvature and relative size of the semicircular canals suggest that *Batyrosaurus rozhdestvenskyi* was an agile biped. However, this hypothesis needs to be supported by other inferences that can be drawn from the postcranial skeleton and from trackways—data that are not available so far.

Phylogenetic Relationships of *Batyrosaurus*

A phylogenetic analysis was conducted in order to assess the relationships of *Batyrosaurus rozhdestvenskyi* within Iguanodontia. This analysis was already described in detail in Chapter 19 in this book. The character list is presented in Appendix 19.2, the data matrix in Appendix 19.3, and the description of the strict consensus tree in Appendix 19.4 of Chapter 19. Three most parsimonious trees of 183 steps, with a consistency index (CI) of 0.73, a retention index (RI) of 0.90, and a rescaled consistency index (RCI) of 0.66 resulted from a heuristic search performed by PAUP 4.0 beta 10 (Swofford, 2000). The strict consensus tree (Fig. 20.13) shows that *Batyrosaurus rozhdestvenskyi* occupies a more advanced position within Hadrosauroidea than the Early Cretaceous taxa *Bolong yixianensis* and *Jinzhousaurus yangi* from the Yixian Formation of Liaoning province (China; Wang and Xu, 2001; Wu and Godefroit, in this book), *Equijubus normani* from the Xinminbao Group of Gansu province (China; You et al., 2003b), and *Altirhinus kurzanovi* from the Hühteeg Svita of Mongolia (Norman, 1998). With *Probactrosaurus gobiensis* and more advanced Hadrosauroidea, it forms a clade (k, according to Fig. 20.13), characterized by the following unambiguous (i.e., characters that do not change placement under both ACCTRAN and DELTRAN optimizations) synapomorphies: dentary teeth are set in narrow, parallel-sided grooves (character 53), maxillary teeth lack secondary ridges (character 65 [1 to 2]), and the dentary teeth have a faintly developed tertiary ridge that does not reach the apex of the crown (character 70). The bootstrap value for clade k is not particularly high (75%). Although it is not included in the present phylogenetic analysis, *Penelopognathus weishampeli*, from the Bayan Gobi Formation of Inner Mongolia (China; Godefroit et al., 2005), appears more primitive than *Batyrosaurus rozhdestvenskyi* because the alveolar grooves are less clearly developed on the medial side of the dentary and because the dentary teeth have a well-developed tertiary ridge that reaches the apex of the crown. Although *Batyrosaurus rozhdestvenskyi* closely resembles *Probactrosaurus gobiensis* from the Early Cretaceous Dashuiguo Formation of Inner Mongolia (China; Norman, 2002), the phylogenetic analysis suggests that the latter taxon is more derived because it shares the following unambiguous synapomorphies with more advanced Hadrosauroidea: the jugal–ectopterygoid articulation is more reduced, forming small vertical ectopterygoid facet on the medial side of the jugal (character 34); the primary ridge is closer to the midline on the maxillary crowns (character 66); and the distal shelf at the base of the dentary crowns is well developed but smooth (character 71). The bootstrap support for this node is high (97%).



20.13. Strict consensus tree of Iguanodontia, showing the phylogenetic relationships of *Batyrosaurus rozhdestvenskyi*. Letters correspond to nodes defined in Appendix 19.4.

In our analysis, the monophyly of Hadrosauridae is supported by the following unambiguous synapomorphies: the jugal–ectopterygoid articulation is absent (character 34 [1 to 2]), the surangular foramen is absent (character 57), and the marginal denticles are reduced on both the maxillary and dentary teeth (character 62 [1 to 2]). The relative position of *Bactrosaurus johnsoni* and *Levnesovia transoxiana* at the base of Hadrosauridae cannot be resolved in our analysis. Euhadrosauria (sensu Horner et al., 2004 = Hadrosaurinae + Lambeosaurinae) is a robust clade (bootstrap value = 100%) characterized by 11 unambiguous synapomorphies.

Paleogeography of Hadrosauroidea

Several authors (e.g., You et al., 2003b; Godefroit et al., 2005; Prieto-Márquez, 2008) have already pointed out that Asia occupied a central place in the radiation of Hadrosauroidea during the Lower Cretaceous. The phylogenetic analysis presented here confirms this hypothesis: the Asian taxa *Bolong yixianensis*, *Equijubus normani*, *Jinzhousaurus yangi*, *Altirhinus kurzanovi*, *Batyrosaurus rozhdestvenskyi*, and *Probactrosaurus gobiensis* represent successive steps in the evolution of nonhadrosaurid Hadrosauroidea. With the exception of *Batyrosaurus rozhdestvenskyi*, all come from Lower Cretaceous deposits. *"Probactrosaurus" mazongshanensis* Lü, 1997, *Nanyangosaurus zhugeii* Xu, Zhao, Lü, Huang, Li, and Dong, 2000, *Penelopognathus weishampeli* Godefroit et al., 2005, and *Jintasaurus meniscus* You and Li, 2009, have not been included in the phylogenetic analysis but are also potential basal Hadrosauroidea from the Lower Cretaceous of Asia. With its Santonian–Campanian age, *Batyrosaurus rozhdestvenskyi* is the youngest nonhadrosaurid Hadrosauroidea. In our analysis, the North American taxa *Eolambia caroljonesa* and *Protohadros byrdi* are the most derived nonhadrosaurid Hadrosauroidea and are successive sister taxa for hadrosaurids. *Eolambia caroljonesa* was discovered in the lower

Cenomanian (Garrison et al., 2007; Gradstein et al., 2008) Mussentuchit Member of the Cedar Mountain Formation in Utah, which includes other taxa with Asian affinities, such as tyrannosauroids, ceratopsians, and pachycephalosaurs. These records are the earliest known representatives of these groups in western North America (Cifelli et al., 1997; McDonald et al., 2010b). These occurrences can be attributed to an immigration of Asian taxa, including Hadrosauroidea, into western North America after the establishment of the Bering land bridge in the Aptian–Albian (Russell, 1993). Older members of the Cedar Mountain Formation have yielded remains of Iguanodontia incertae sedis, including *"Iguanodon" ottingeri* Galton and Jensen, 1979, *Planocoxa venenica* DiCroce and Carpenter, 2001, *Cedrorestes crichtoni* Gilpin, DiCroce, and Carpenter, 2007, *Iguanocolossus fortis* McDonald et al., 2010 (a), and *Hippodraco scutodens* McDonald et al., 2010 (a). *Protohadros byrdi*, from the Cenomanian Woodbine Formation of Texas, is a bit younger than *Eolambia caroljonesa*. McDonald et al. (2010b) recently described *Jeyawati rugoculus*, a new hadrosauroid dinosaur from the Moreno Hill Formation (middle Turonian) of New Mexico. This new hadrosauroid was described after the completion of the present phylogenetic analysis, and for that reason, it could not be included in the cladogram here (Fig. 12.13). However, the phylogenetic analysis presented by McDonald et al. (2010b) shows that *Jeyawati* is a basal hadrosauroid more derived that *Probactrosaurus*, *Eolambia*, and *Protohadros*, but more basal than *Shuangmiaosaurus*, *Bactrosaurus*, and *Telmatosaurus*. It confirms that basal hadrosauroids became diversified in North America at the beginning of the Late Cretaceous.

The results of the phylogenetic analysis here performed suggest an Asian origin for hadrosaurids and confirms an important evolutionary radiation for this clade around the Turonian (Sues and Averianov, 2009; McDonald et al., 2010b). Indeed, the most basal hadrosaurids are *Bactrosaurus johnsoni* Gilmore, 1933, from the Iren Dabasu Formation of Inner Mongolia, China (Turonian–Coniacian, according to Averianov, 2002, but early Maastrichtian, according to Van Itterbeeck et al., 2005), *Levnesovia transoxiana* Sues and Averianov, 2009, from the Bissekty Formation (middle–late Turonian) of Uzbekistan, and *Shuangmiaosaurus gilmorei* You, Ji, Li, and Li, 2003a, from the Sumjawan Formation (Cenomanian–Turonian) of western Liaoning province, China. According to Prieto-Márquez and Norell (2010), *Gilmoreosaurus mongoliensis* (Gilmore, 1933), from the Iren Dabasu Formation of Inner Mongolia, is also a hadrosaurids as defined here. According to McDonald et al. (2010b), the sister taxon of hadrosaurids, as defined here, would be *Jeyawati rugoculus*, also from the Turonian from New Mexico. *Telmatosaurus transsylvanicus* (Nopcsa, 1900), from the early Maastrichtian Sănpetru and Densus-Ciula Formations of the Haţeg Basin in Romania, and *Tethyshadros insularis* Dalla Vecchia, 2009, from the late Campanian–early Maastrichtian Liburnian Formation of northeastern Italy, are more advanced basal hadrosaurids. According to Dalla Vecchia (2009), hadrosaurids most probably reached the eastern part of the European Archipelago by dispersal through insular hopping along the southwestern margin of Asia during the late Campanian.

Prieto-Márquez (2010a) recently published a new global phylogeny of hadrosauroids (also after the analysis here presented was completed). He found that the nearest outgroups for Euhadrosauria (his Hadrosauridae) are *Claosaurus agilis* Marsh, 1872, from the Coniacian of Kansas, and *Lophorhothon atopus* Langston, 1960, from the Santonian of Alabama. He also considers *Hadrosaurus foulkii* Leidy, 1858, from the Campanian of New Jersey, as the most basal Euhadrosauria. Thus, Prieto-Márquez (2010b) hypothesized that Euhadrosauria originated in eastern North America at least as early as the Coniacian. However, eastern North American hadrosaurids are fragmentary and remain poorly understood, and we personally consider that this interesting hypothesis still requires support by the discovery and analysis of more complete material.

Godefroit et al. (2008) described *Wulagasaurus dongi* (also known from fragmentary material) from the Maastrichtian of northeastern China, as the most basal hadrosaurine described so far. This hypothesis implies a long ghost lineage of basal hadrosaurines in Asia. However, this hypothesis was not retained by Prieto-Márquez (2010b), who considered that *Wulagasaurus* is nested within "kritosaurs," and that hadrosaurines (his Saurolophinae) originated in North America.

If the origin of hadrosaurines remains conjectural, lambeosaurine hadrosaurids clearly have an Asian origin, according to recent phylogenies (e.g., Godefroit et al., 2003, 2004; Evans and Reisz, 2007; Evans, 2010). The oldest lambeosaurines were discovered in Kazakhstan, including *Jaxartosaurus aralensis* Riabinin, 1939, from the Syusyuk Formation (Santonian; Averianov and Nessov, 1995) of the Alimtau range (=Kyrk-Kuduk) in the Chuley Region of southeastern Kazakhstan, and the juvenile skeleton named *Procheneosaurus convincens* from the Dabrazinskaya Svita (Santonian; Rozhdestvensky, 1974) at the Syuk-Syuk Wells site, in the same area. According to Godefroit et al. (2004), Evans and Reisz (2007), Evans (2010), and Prieto-Márquez (2010a), *Aralosaurus tuberiferus* Rozhdestvensky, 1968, from the Beleutinskaya Svita (Turonian–Santonian, Rozhdestvensky, 1968), or the Bostobinskaya Svita (according to Nessov, 1995 and Sues and Averianov, 2009) of the Sakh-Sakh locality is the most basal lambeosaurine; conversely, Sues and Averianov (2009) regard this taxon as the sister taxon for Euhadrosauria (their Hadrosauridae).

Around the Santonian, the iguanodontoid fauna was thus diversified in Kazakhstan, including basal lambeosaurines (*Jaxartosaurus*, "*Procheneosaurus*" *convincens*, ?*Aralosaurus*) and relict nonhadrosaurid Hadrosauroidea (*Batyrosaurus*). The possibility exists that *Batyrosaurus rozhdestvenskyi* and *Arstanasaurus akkurganensis*, which are from the same locality, belong in fact to the same taxon because the holotypes do not possess diagnostic overlapping elements. In fact, the holotype maxilla of *Arstanosaurus akkurganensis* displays a series of plesiomorphic characters (dorsal process caudally placed, ectopterygoid ridge relatively weak and curved ventrally, jugal process moderately developed into a diagonal projection) that are not incompatible with the assessed phylogenetic position of *Batyrosaurus rozhdestvenskyi*. However, the isolated tooth associated with the holotype of *A. akkurganensis* (see Norman and Kurzanov, 1997, fig. 3) is different from the maxillary teeth associated with the holotype of *B. rozhdestvenskyi:* the crown is more lanceolate and the primary ridge is much less prominent and is closer to the midline. These observations support a separate taxonomic status.

Because Turonian–Santonian dinosaur faunas are still poorly known worldwide, further investigations in Upper Cretaceous dinosaur localities of Kazakhstan will be important for a better understanding of the biogeographical history of advanced Iguanodontoidea and of the early radiation of hadrosaurids. During the Campanian and Maastrichtian, Euhadrosauria reached their widest geographical distribution: they entered South America and Antarctica, both Lambeosaurinae and Hadrosaurinae were particularly diversified in Asia and North America, and at least Lambeosaurinae were represented in Europe.

Acknowledgments

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