

Archosaurian anatomy and palaeontology. Essays in memory of Alick D. Walker. Edited by D. B. Norman and D. J. Gower

**On Asian ornithopods (Dinosauria: Ornithischia). 4.
Probactrosaurus Rozhdestvensky, 1966**

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The genus *Probactrosaurus* was first established for material discovered by a joint Russian/Chinese expedition to the Chinese autonomous region of Neimongol (Inner Mongolia). Fossils were collected at a site named Maorty (= Maortu). Material attributable to ornithopod dinosaurs was considered sufficiently distinct to permit the definition of two species of the new genus: *Probactrosaurus gobiensis* and *P. alashanicus*. The former species was based on a considerable quantity of skeletal material, much of which is still to be found in the collections of the Palaeontological Institute (PIN), Moscow. The latter was based on far less well-preserved specimens, including a holotype (a posterior skull roof) that can no longer be found in the collections of the PIN and which, along with other materials, was reportedly returned to the Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing. Some remnants of the original material attributed to *P. alashanicus* have been located in the PIN collections. Both taxa, established by A. K. Rozhdestvensky, are re-described using all of the available material collected during the early Sino-Soviet expeditions. *Probactrosaurus alashanicus* is considered to be a junior subjective synonym of *P. gobiensis*. Further comparisons are made with the recently described species *Probactrosaurus mazongshanensis* Lu, 1997. The latter does not appear to be referable to the genus *Probactrosaurus*. *Probactrosaurus* is a gracile ornithopod (ranging between 4 and 6 m in length). The skull is unadorned by any form of cranial crest; however, the premaxillary beak is deflected ventrally and the dentition is similar to that seen in more derived hadrosaurid ornithopods. The postcranial skeleton is notable for its gracility, in particular the elongate forearm and manus, and the retention of a small, conical pollex spine. Systematic analysis suggests that *P. gobiensis* is a derived non-hadrosaurid iguanodontian ornithopod and the basal sister-taxon to the clade Hadrosauridae. The phylogeny of currently known iguanodontians is reviewed. © 2002 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2002, **136**, 113–144.

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INTRODUCTION

Ornithopod dinosaur material (among much else) was collected from Late Mesozoic deposits in China by the joint Sino-Soviet expeditions to Inner Mongolia in 1959/60 (Chow & Rozhdestvensky, 1960; Rozhdestvensky & Chow, 1960; Rozhdestvensky, 1961). Of particular relevance in this instance is that a camp was set up at a site named Maorty¹ (= Maortu) (Chow & Rozhdestvensky, 1960) which is located approximately 480 km due west of the provincial capital of Hohhot (Fig. 1) [Translations of place names in Asia are prone to considerable variability; this has

two sources: the process of transliteration between English, Russian and Chinese – further complicated by the shift to Pin Yin spellings more recently – and the fact that many place names appear to have had only simple phonetic origins. The various spellings are provided here to facilitate reference to the older literature on the subject]. On a more local scale, the site was identified as lying 60 km north of the town Gilantai (= Jartai) on the east side of the Gilantai/Dzhilantay (= Jartai) Salt Lake. The general area of the Maortu locality was described (Chow & Rozhdestvensky, 1960) as comprising two badlands-type areas along the northern edge of a sedimentary basin. The western part of this outcrop is reported to have yielded the most abundant remains, including no less

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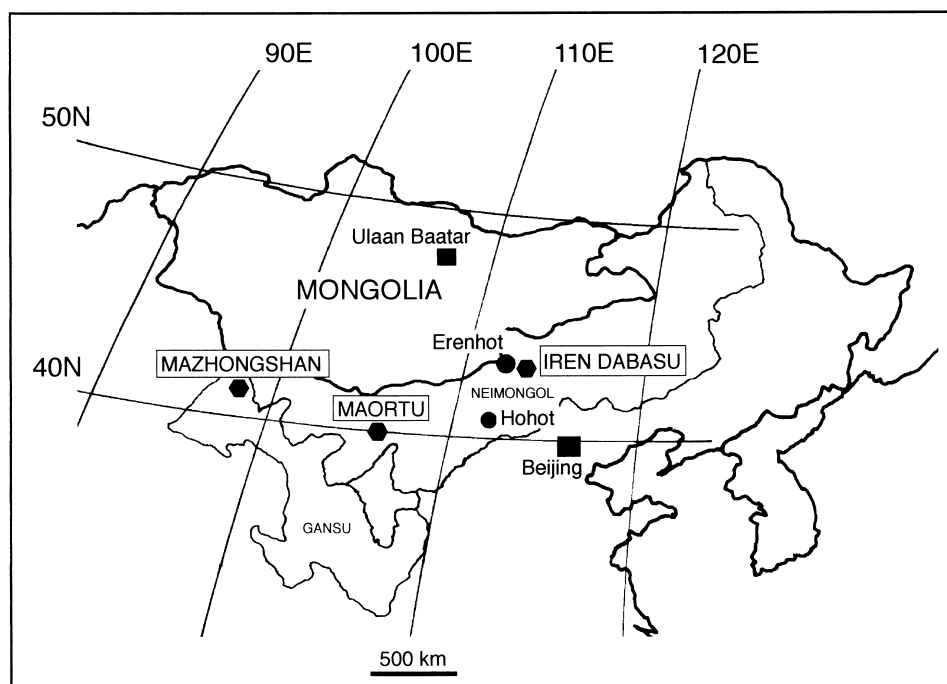


Figure 1. Mongolia and northern China, showing the relative positions of the main dinosaur localities discussed in this article: Iren Dabasu (Neimongol), Maortu (Neimongol) and Mazhongshan (Gansu).

than three partial skeletons of an ornithopod that was claimed to possess anatomical features found in both hadrosaurid and iguanodontid ornithopods.

These preliminary notices were followed by a more detailed report (Rozhdestvensky, 1966) in which the new ornithopod remains were described in some detail and two new names proposed: *Proactrosaurus gobiensis* and *P. alashanicus*. The former species was described on the basis of three partial skeletons and numerous other bones. The partial skull only of the holotype material of *P. gobiensis* (PIN 2232/1) was illustrated. *Proactrosaurus gobiensis* was reported to have been collected from a lower horizon than the latter species ('bottom (first) bone horizon'). It is interesting to note that even this horizon is reported to be divisible into upper and lower 'subhorizons'; these, it is stated, contain parts of individuals which display subtle differences (shape and number of replacement teeth, form of the dorsal part of the skull and proportions of the jaw) and were interpreted by Rozhdestvensky (1966) as indicating the existence of evolutionary intermediates between the taxon which he regarded as more primitive *P. gobiensis*, and the anatomically more derived form which he had named *P. alashanicus*.

Proactrosaurus alashanicus was described as coming from the 'middle (second) bone horizon' of the same area and the material assigned to this species includes a partial skull (the holotype: PIN 2232/46 – which was

also illustrated), and other remains including jaws, vertebrae and limb girdles belonging to several specimens. Rozhdestvensky (1966) distinguished these two species on the basis of differences in the structure of the skull roof: a raised sagittal crest (a difference that he noted might have been caused by deformation of the skull), a high occiput, broader supratemporal fenestrae, an elongate tooth crown, and proportional differences in the form of the girdle and limb bones. He also mentions, elsewhere in the text, differences in the number of replacement teeth (a rudimentary second replacement crown being present in *P. alashanicus* but not in *P. gobiensis*) and subtle differences in the ridge patterns on the enamelled surface of the crowns of the teeth.

The paper was completed by a consideration of the eastern Inner Mongolian hadrosaurid *Bactrosaurus johnsoni* (collected at Iren Dabasu during the AMNH Central Asiatic Expeditions led by Roy Chapman Andrews (Andrews, 1932) and described by Gilmore (1933) which was widely regarded as a basal ('primitive') hadrosaurid. Rozhdestvensky (1966), while accepting its general hadrosaur affinities, specifically rejected Gilmore's claim that *Bactrosaurus* was a primitive lambeosaurine, primarily because it lacked a tubular crest on its skull and because of the breadth of the frontals (which contributed to the dorsal margin of the orbit); he also relegated *Mandschurosaurus mongoliensis* into synonymy with *Bactrosaurus*

(Rozhdestvensky, 1964). Gilmore (1933) had established *M. mongoliensis* on part of the hadrosaurid remains from Iren Dabasu, although in so doing he stressed (1933: 41) the considerable difficulty in establishing the generic affinities of this specimen: '... it seems best to tentatively refer the Mongolian specimen to the genus *Mandschurosaurus* until such time as its true affinities are disclosed.' Rozhdestvensky also mentioned (though he did not illustrate or otherwise identify) some material (a sacrum and humerus) that had been collected from stratigraphically higher beds in the Maortu area. These specimens were claimed to be referable to the genus *Bactrosaurus* and were offered as evidence of the rapid evolutionary transition from an 'advanced iguanodont' to 'primitive hadrosaur' in this part of Asia and that this transition occurred across the Lower Cretaceous–Upper Cretaceous stratigraphic boundary.

Since the time of the original descriptive work by Gilmore, the Iren Dabasu material has received relatively scant attention, but on each occasion authors have suggested major changes to our understanding of the ornithopod taxa found there. Brett-Surman (1979) re-visited the taxonomic issues raised by Rozhdestvensky in relation to the status of *Mandschurosaurus*. He reaffirmed Gilmore's original proposal that two distinct taxa were present at Iren Dabasu, but erected a new generic name *Gilmoreosaurus* to replace the dubious taxon *Mandschurosaurus* (Riabinin, 1930) which had, on Gilmore's admission, been loosely associated with Riabinin's taxon. Weishampel & Horner (1986) reviewed Gilmore's original material and reaffirmed the conclusions of Brett-Surman and Gilmore in recognizing two distinct species of hadrosaur. Weishampel & Horner (1986, 1990) furthermore claimed, contrary to the opinions of Gilmore (1933) and Rozhdestvensky (1966), that *Bactrosaurus johnsoni* showed evidence of 'a hollow supracranial crest' (1986: 38) typical of the lambeosaurine subfamily of hadrosaurids. Evidence for this interpretation was to be found in the shape and orientation of the prefrontal bone. Godefroit *et al.* (1998) collected further material from Iren Dabasu during a joint Sino-Belgian expedition to Inner Mongolia in 1995; this new material was attributed to *Bactrosaurus johnsoni*. Godefroit *et al.* (1998) showed that Gilmore (1933) had been correct in suggesting that *Bactrosaurus* was a noncrested hadrosaurid and that Weishampel & Horner (1986) had misinterpreted the prefrontal bones in the collections of the American Museum of Natural History collections.

In 1997, the results of the Sino-Japanese Silk Road expedition (1992–3) were published (Dong, 1997). These were of particular interest in relation to the Inner Mongolian species of *Probactrosaurus* because a new species was described by Lu (1997) from the adja-

cent province of Gansu at a site in the Gongpoquan Basin of the Mazongshan Area. However it should be noted that this site is 650 km west of the Maortu site that yielded the type species of the genus. Further new ornithopods, that have been suggested as having a bearing on the complex issue of hadrosaurid origins, have been discovered and described in recent years: *Protohadros* (Head, 1998), *Eolambia* (Kirkland, 1998; Head, 2001), *Nanyangosaurus* (Xu *et al.*, 2000), *Jinzhousaurus* (Wang & Xu, 2001) and a new and currently unnamed taxon from Mazongshan (Tang *et al.*, 2001; You Hailu, pers.comm. 2001).

Whatever the final outcome of the ebb and flow of future discussion generated by the new material referred to above, it is clear that the ornithopod fauna collected from Maortu in western Inner Mongolia merits re-investigation because the original osteology was brief and poorly illustrated. The claims made by Rozhdestvensky (1966) concerning the relationship between *Probactrosaurus* and later hadrosaurids (probactrosaurs being regarded as evolutionary intermediaries between iguanodonts and hadrosaurs) can only be examined in the light of a more thorough knowledge of the taxa. Inadequate understanding of the anatomy of *Probactrosaurus* accounts for much of the variation in its systematic placement in recent years (Serenó, 1986, 1997, 1999; Norman, 1990, 1998; Head, 1998, 2001; Kirkland, 1998).

This paper is intended to improve knowledge of the type-species of *Probactrosaurus* and discusses the wider issue of iguanodontian ornithopod systematics and hadrosaur origins. These issues are discussed further in Norman & Weishampel (in press).

STRATIGRAPHIC CORRELATION

Persistent questions remain concerning localities such as Maortu and their stratigraphic correlation both locally and over wider geographical areas (notably across Asia, and between Asia and the European and North American sequences). At present we are forced to rely on, and accept, the circularity implicit in a broad biostratigraphic framework established by A. K. Rozhdestvensky in the 1960s and 1970s. The unsatisfactory nature of the present situation is neatly encapsulated in works such as Currie & Eberth (1993) who have been able to propose, at an extreme end of their range, a Campanian age for the Iren Dabasu deposits in the face of the more widely accepted (?) Cenomanian age (see Godefroit *et al.* [1998] for the most recent account as it relates to ornithopod dinosaur stratigraphy. Okada & Mateer [2000] and Benton *et al.* [2000] also provide evidence of some of the more intractable problems relating to Mesozoic Asian stratigraphic correlation). Most recently a report has been published on the sedimentology, ecology and stratigraphy of the

area where the original material of *Probactrosaurus* was collected (Itterbeek *et al.*, 2001). Charophyte evidence is used to propose a Barremian-Albian age for these deposits. In general terms this estimation correlates with expectations based solely on anatomy and phylogeny. However, for this to be of value palaeobiogeographically, improved stratigraphic resolution is required.

MATERIAL

A catalogue of the material assigned to *Probactrosaurus gobiensis* in the collections of the Palaeontology Institute Nauk (PIN), Moscow is provided below. Specimens are listed in numerical order, with identifications and comments where necessary. Material attributed to *P. alashanicus* in the collections is included in the listing below. However, the latter collection is partial and it was reported verbally that a proportion of the material that was originally collected during the joint expedition was sent to the IVPP (Beijing) at some time between 1966 and 1990.

PROBACTROSAURUS GOBIENSIS

PIN 2232/1 (mounted partial skeleton, quadrupedal pose). Cranial: partial skull roof, premaxilla (r – PIN 2232/1-2), jugal (l – PIN 2232/1-1a), surangular (r – 2232/1-4). Axial: 7 poorly preserved cervical vertebrae, 6 dorsals, 4 sacrals, 22 caudals. Appendicular: scapulae (r & l), coracoid (l), humerus (r & part l), ulna (r & l), radius (r), metacarpals II? III? IV, V? Femur (l), tibia (l), fibula (l & r), metatarsals (left II–IV).

PIN 2232/2-1 – neurocranial fragment; 2-2 – dentary (l – part); 2-5 – coracoid; 2-8 – humerus; 2-9 – metacarpal.

PIN 2232/3-1 – metacarpal

PIN 2232/9-2 – maxilla (partial left)

PIN 2232/10 (mounted partial skeleton, bipedal pose). Cranial: right dentary, partial skull roof, maxilla (PIN 2232/10-2). Axial: 6 cervicals, 18 dorsals, 7 sacrals, 24 caudals. Appendicular: scapula (l & r), coracoid (r), sternal (l), humerus (l & r), radius (l & r), ulna (l & r), manus – all restored in plaster. Ilium (l & r), ischium (l & r), pubis (acetabular fragments) (l & r), femur (l & r), tibia (l & r), fibula (l & r), metatarsals (II–IV, l & r), phalanges (left pes: Iii, IIiii; IVi–iv; right pes: Ii–iii; IIIi–iv; IVi–v); PIN 2232/10-69 – manus phalanx?VII or VIII.

PIN 2232/11-2 – manus phalanx IIIiii; 11-4 – pollex ungual; 11-5 – ungual manus II

PIN 2232/17-1 – skull roof

PIN 2232/18-1 – left dentary (part); 18-5 – metacarpal III; 18-6 – metacarpal; 18-8 – phalanx manus II; 18-9 – large femur (r)

PIN 2232/19-1 – ilium (l) complete

PIN 2232/21-1 – humerus

PIN 2232/23-1 – prementary; 23-2 – two isolated dentary teeth with roots; 23-3 – quadrate; PIN 2232/23-56 – pubis

PIN 2232/24-1 – worn dentary tooth

PIN 2232/27-3 – scapula

PIN 2232/29-2 – ischium (r) complete

PIN 2232/32-1 – tibia (l)

PIN 2232/36-1 – skull roof; 36-2 – dentary; 36-3 – dentary

PIN 2232/37-7 – ilium (? label: *P. alashanicus*)

PIN 2232/39-1 – femur (l)

PIN 2232/3? – left dentary with teeth

Field no. 12017 (PIN 2232/2-) – metacarpals, ilium (left)

Field no. 12068 – metacarpal II.

PROBACTROSAURUS ALASHANICUS

PIN 2232/40-3 – caudal vertebra; 40-5, 40-6 metatarsal block II, III (left)

PIN 2232/41-1 – dentary; 41-2 – scapula; 41-3 – scapula; 41-4 – humerus (incomplete – l)

PIN 2232/42-1 – dentary (r).

SYSTEMATIC PALAEOONTOLOGY

Systematic hierarchy

Ornithischia (Seeley, 1887)

Ornithopoda (Marsh, 1881)

Iguanodontondea

Genus *Probactrosaurus* Rozhdestvensky, 1966

Type species. *P. gobiensis* Rozhdestvensky, 1966

Synonymy. *Probactrosaurus alashanicus* Rozhdestvensky, 1966

Holotype. PIN 2232/1

Referred material. PIN 2232/10 (partial skeleton) and a series of catalogued lots, most of which are disarticulated elements: PIN 2232/2 > 2232/39.

Diagnosis. Ornithopod dinosaur reaching a probable maximum body length of 4–6 m. *Cranial.* Ventrally deflected premaxillary beak margin; small, vertical ectopterygoid sutural facet on jugal; slender jugal; maxillary teeth narrow with prominent primary ridge and no subsidiary ridges; dentary teeth narrow and diamond-shaped with low, distally offset primary ridge and shorter and low subsidiary ridges mesially and distally; tall and interlocking teeth that form a high, posteriorly inclined battery; two replacement crowns beneath the functional tooth in the dental battery, marginal denticles are mammillate. *Postcranial.* Prominent 'acromial' process on anterior edge of scapula; scapular blade straight and little expanded distally; low rounded deltopectoral crest; elongate radius

and ulna; small conical pollex spine; elongate metacarpals II–IV; six fused sacral vertebrae; elongate horizontal anterior process to ilium; deep and distally expanded prepubic blade; stout, curved and ‘booted’ ischium with a large triangular, proximally positioned obturator process; curved distal femoral shaft; distally expanded condyles on femur; partially enclosed anterior intercondylar groove.

Locality. Maortu, 60 km north of Jilantai Lake.

Stratigraphic age. Barremian-Albian (Rozhdestvensky, 1966, 1974; Itterbeek *et al.*, 2001)

Comments. This is a very generalized ornithopod in terms of what is currently known of its cranial and postcranial anatomy. The skull does not show any obvious sign of expansion or elaboration of the nasal or dorsal cranial region; the maxillary teeth are narrow, and resemble those seen in nonhadrosaur iguanodontians. The dentary tooth crowns when viewed lingually are, in proportion to the overall dimensions of the lower jaw, smaller and more lanceolate than those typically found in more basal ornithopods and iguanodontians, e.g. *Camptosaurus* (Gilmore, 1909), *Iguanodon* (Norman, 1980, 1986), *Ouranosaurus* (Taquet, 1976), and *Altirhinus* (Norman, 1998). In the postcranial skeleton the forelimb is characterized by a comparatively elongate forearm, retention of a small, conical pollex spine, narrow, elongate and bunched metacarpals II–IV (evidence concerning the structure of the carpus is lacking in the original material, although the pollex spine and structure of the distal radius indicate that carpal bones were present); the remainder of the postcranial skeleton as currently known is similar to that seen in other iguanodontians (cf. *Iguanodon atherfieldensis*; Norman, 1986)

DESCRIPTION

SKULL ANATOMY

For the purposes of description the anatomy of the skull will be divided into sections on the cranium, lower jaw and dentition. The skull is not completely preserved, despite the impression given by Rozhdestvensky (1966: fig. 1; see Fig. 2 here), although a few isolated elements are well preserved. In general the skull (Fig. 3) appears, in overall shape, to approximate to that seen in iguanodontians typified by *Iguanodon* (Norman, 1986), *Eolambia* (Kirkland, 1998) and the least anatomically derived hadrosaurids, such as *Telmatosaurus* (Weishampel *et al.*, 1993) and *Bactrosaurus* (Godefroit *et al.*, 1998).

Cranium

Premaxilla. The isolated right premaxilla (PIN 2232/1-2. Fig. 4) is nearly complete and was figured

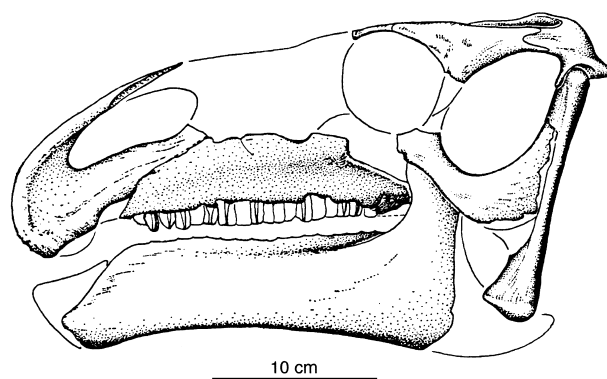


Figure 2. *Probactrosaurus gobiensis* (based on the holotype: PIN 2232/1) as reconstructed by Rozhdestvensky (1966: fig. 1). The most notable error in this reconstruction is the rotation of the quadrate. The ‘left’ quadrate, as illustrated, is the right quadrate viewed in posterior aspect.

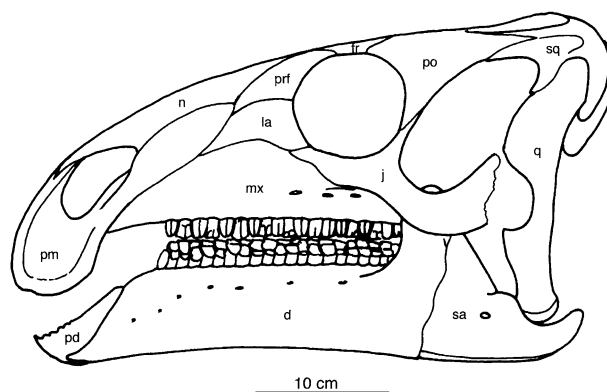


Figure 3. *Probactrosaurus*. Tentative skull reconstruction based on the dissociated materials in the collections (PIN 2232/) of the Palaeontology Institute Nauk, Moscow. The skull table was undoubtedly low and flat, with a low, but narrow sagittal crest. The pose of the premaxilla relative to the bones of the snout (notably the maxilla) is conjectural. The relative proportions of the circumorbital bones are conjectural, and it is not known whether a palpebral was present. The form of the quadratojugal is unknown. Abbreviations: d = dentary; fr = frontal; j = jugal; la = lacrimal; mx = maxilla; n = nasal; pd = premaxilla; pm = premaxilla; po = postorbital; prf = prefrontal; q = quadrate; sa = surangular; sq = squamosal.

(reversed) by Rozhdestvensky in his original restoration of the skull (Fig. 2). It bears some similarity to the isolated premaxilla attributed to *Eolambia* (Kirkland, 1998: fig. 5E–G; Head, 2001: fig. 1A–C). The oral margin projects quite clearly below the level of the maxillary tooth row and its lateral margin is thickened and everted (even though part of this edge has been eroded and reconstructed in plaster). The lateral edge of the

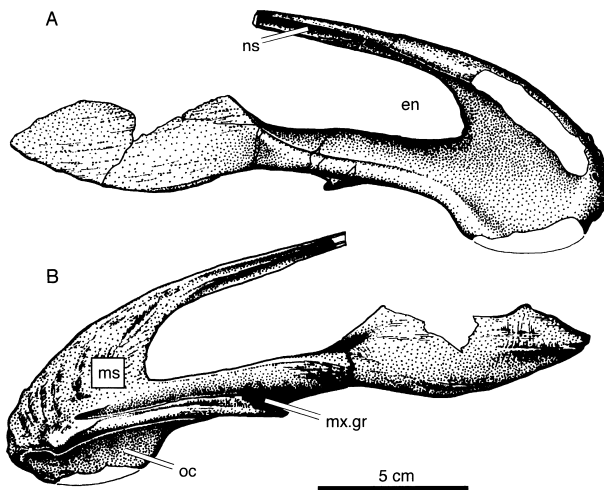


Figure 4. *Probaetrosaurus gobiensis* Rozhdestvensky, 1966. Premaxilla (PIN 2232/1-2) in lateral (A) and medial (B) view. Missing portions of the oral margin and the distal ends of the median and lateral posterior processes. Abbreviations: en = external naris; ms = median suture; mx.gr = groove for the dorsomedial process of the maxilla; ns = nasal spine; oc = dorsal portion of the anterior oral cavity.

oral margin is not reflected dorsally to form a rim bordering the lower edge of the external naris; above this area the external surface forms an oblique sloping depression that leads backward into the main narial chamber. The rostral portion of the oral margin is thickened, rugose and curves dorsally into the base of the internarial nasal spine. The rugose surface around the oral margin undoubtedly supported a keratinous beak (rhamphotheca). Beneath its thickened dorsal edge there is a narrow internarial septum. The mediadorsal (nasal) spine is long and tapering so that it wedged between the anterior ends of the nasal bones; an elongate ventrolateral facet on the mediadorsal spine indicating the attachment area for the nasal (Fig. 4, ns), this facet terminates about midway along the external naris.

The posterolateral portion of the premaxilla is obliquely and transversely expanded in order to floor the rear portion of the external naris, but beyond this the bone becomes laterally compressed and dorsoventrally expanded to form a plate-like sheet running up the side of the snout between the nasal and maxilla. Unfortunately this bone is incomplete, so its sutural relationships and full posterior extent are unclear.

Medially the rostrum of the premaxilla forms an extensive, ridged sutural plate that locked the premaxillae together (ms). The oral region is smoothly arched and in the dorsal midline there is a modest, but prominent secondary palate (oc) that forms a distinct ledge (visible laterally as well as medially). An inclined groove (mx.gr) immediately above this ledge

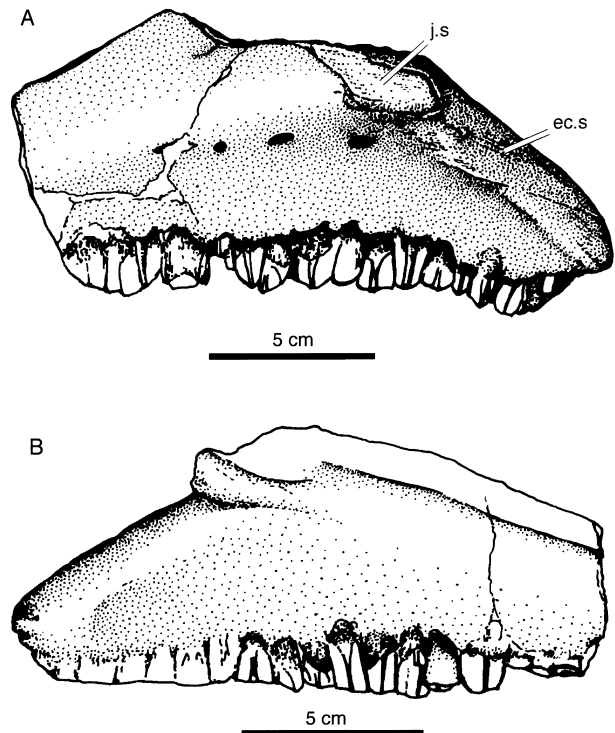


Figure 5. *Probaetrosaurus gobiensis* Rozhdestvensky, 1966. Maxillae with partly preserved dentitions. A, PIN 2232/10-2. Partial left maxilla in lateral view (anterior and mid-dorsal portions missing). B, PIN 2232/9-2. Partial right maxilla in lateral view. Abbreviations: ec.s = sutural surface for the ectopterygoid; j.s = sutural surface for the jugal.

probably corresponds to a recess for the mediadorsal maxillary spine (a very similar feature is seen in the premaxilla of *Eolambia*, *Altirhinus* (Norman, 1998), *Iguanodon* (Norman, 1986) and *Brachylophosaurus* MOR 1071).

Maxilla. (PIN 2232/9-2; 10-2; Fig. 5). Neither of the maxillae (right and left) are complete and both are encrusted with matrix. The reconstruction made by Rozhdestvensky (1966) appears to be based on PIN 2232/10-2. The medial wall of the maxilla is vertical and planar, the lateral wall bulges dorsally forming a mound-like structure that supports the articular surface for the jugal (j.s); the latter is an oblique posterolaterally directed tab, similar in shape to that seen in other iguanodontians (*Iguanodon*, *Altirhinus*, *Eolambia*). The portion of the maxilla posterior to the jugal process has a sloping dorsal profile, the lateral surface of which is obliquely inclined (where it undoubtedly forms the sutural surface for the ectopterygoid – ec.s) and is demarcated by a rounded ridge that forms the upper edge of the buccal (cheek) recess. The lateral surface of the maxilla beneath the jugal process is

recessed and its upper region is marked by a series of prominent neurovascular foramina. The anterior portion of both maxillae tapers, but is abruptly truncated, indicating that the general profile of the maxilla was low and triangular, with the apex offset posteriorly. Both incomplete maxillae show evidence of about 17 vertical tooth positions; on the basis of the estimated proportions of the maxillae a count of 22–23 would seem to be reasonable, and conforms to the figure suggested by Rozhdestvensky (1966: '23 or a few more'). However, it should be stressed that the number of functional and replacement teeth in each alveolus cannot be estimated with any certainty.

Jugal. (PIN 2232/1-1a; Fig. 6). An incomplete left jugal is well-preserved. The anterior ramus and much of the ventral orbital margin are missing, as is the postorbital (dorsal) process. The body of the bone is notably slender (being relatively narrow dorsoventrally).

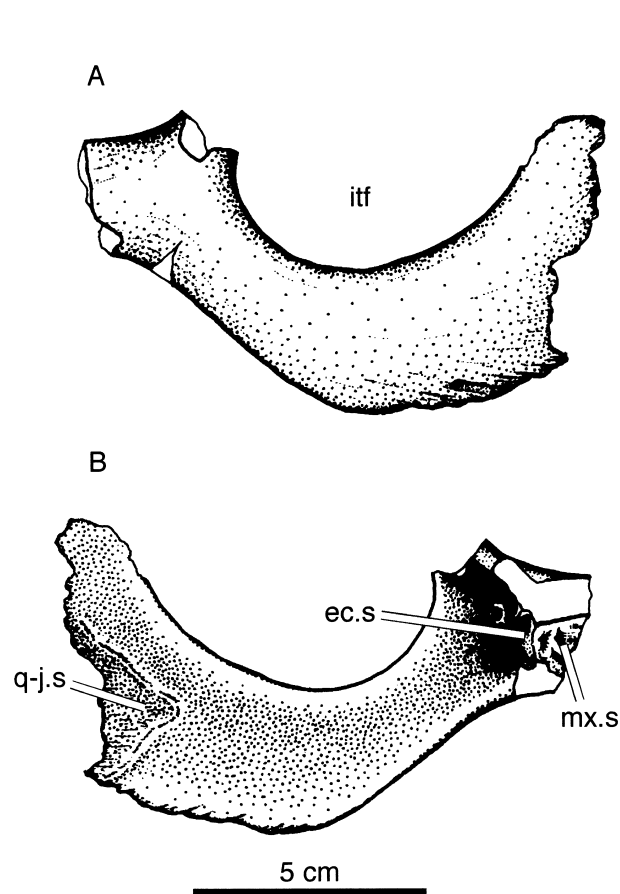


Figure 6. *Probatrosaurus gobiensis* Rozhdestvensky, 1966. Jugal PIN 2232/1-1a (left) in lateral (A) and medial (B) view. Abbreviations: ec.s = suture for the ectopterygoid; itf = lower margin of the infratemporal fenestra; mx.s = sutural surface for the jugal process of the maxilla (Figure 5); q-j.s = suture for the quadratojugal.

Its posterior ramus is deeply embayed dorsally, suggesting a wide and open infratemporal fenestra (itf), whereas the ventral margin is slightly sinuous, with a sweeping and bowed ventral margin with no hint of a prominent downturned tongue adjacent to the coronoid process of the lower jaw (as often seen in iguanodontians). The ventral edge is crenellated. The posterior edge of the jugal is thin and irregular and overlapped the quadratojugal, the medial surface of the jugal shows a depression that indicates the anterior limit of the quadratojugal (q-j.s). Beneath the broken base of the postorbital process the medial surface of the jugal is scarred by a small vertical facet (ec.s) that represents the suture for the ectopterygoid; the area immediately anterior to this facet forms another larger depressed facet for attachment to the maxilla (mx.s). A similar condition of a narrow, vertical, ectopterygoid facet on the jugal has been described in *Protophadros* (Head, 1998).

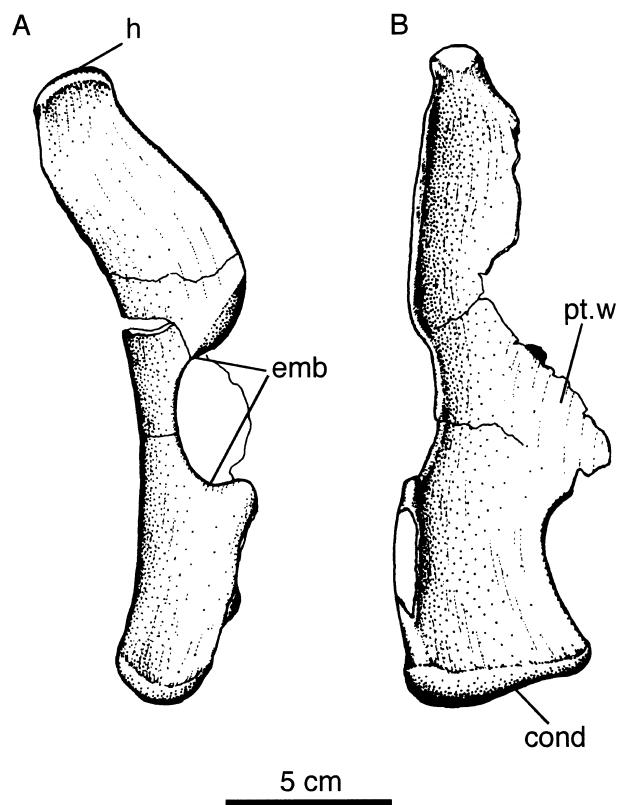


Figure 7. *Probatrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/22-3. Quadrate (right) in lateral (A) and anterior (B) view. Abbreviations: cond = articular condyle for the lower jaw (surangular + articular); emb = embayment in the jugal wing of the quadrate (the facet on the upper edge of this recess may be for the attachment of the quadratojugal); h = dorsal 'head' of the quadrate articulates in a socket on the quadrate; pt.w = pterygoid wing of the quadrate.

Quadrate. (PIN 2232/22-3; Fig. 7). The right quadrate is well-preserved. It comprises a tall, slightly bowed, shaft, terminated dorsally by a relatively small, moderately convex, articular condyle (h) that is supported posteroventrally by a vertical buttress. This head would have fitted snugly into a vaulted recess in the ventral surface of the squamosal. Beneath the anterior margin of the dorsal articular condyle the shaft of the quadrate is deeply and broadly grooved so that it is divided into a narrow and thin lateral sheet of bone connecting with the jugal arch and a medial (pterygoid) wing (pt.w). The margin of the jugal arch sheet is interrupted by a deep embayment for attachment of the quadratojugal and a bevelled edge, presumably for attachment of this bone, is seen on the dorsal edge of the embayment. The embayment is considerably larger than that seen in *Iguanodon* (Norman, 1986) and *Altirhinus* (Norman, 1998) and more reminiscent of that described in *Protohadros* and *Eolambia*; this may reflect the fact that the quadratojugal occluded the (para)quadrate foramen as reported by Head (1998) in *Protohadros* (a condition seen universally in more derived hadrosaurs and, apparently uniquely, in the more basal ornithomimid *Camptosaurus* (Gilmore, 1909)).

The medial (pterygoid) wing of the quadrate is thin and overlapped the wing-like pterygoid, but is damaged so its full extent is unknown.

The ventral end of the quadrate is markedly expanded transversely (Fig. 7B) forming a very broad articular condyle for the glenoid on the lower jaw; as seen in many basal iguanodontians, the lateral portion of the condyle is anteroposteriorly convex, whereas the medial portion is relatively narrow and more ledge-like. Hadrosaurids generally (Weishampel *et al.*, 1993) have a more restricted (less medially expanded) ventral articular condyle, as in *Brachylophosaurus* sp. (MOR 1071).

Skull roof and neurocranium (PIN 2232/36-1; 2232/17-1; 2232/2-1; unregistered; Figs 8, 9). Several partial skulls are preserved in the collections. These provide information on the general configuration of the neurocranium and the surrounding bones of the skull table, but none are particularly well-preserved or prepared. The following general description is possible from this material. The skull table is approximately rectangular in dorsal view (Fig. 8); the supratemporal fenestrae (stf) are large and oval in outline; there appears to have been a modest notch in the posterior midline adjacent to the point at which the squamosals meet the parietal on either side of the sagittal crest.

The *postorbital* (Fig. 8, po) is similar in all essential details to that seen in all basal iguanodontians (*Camptosaurus*, *Iguanodon*, *Ouranosaurus*, etc.) in that it has an approximate 'T' shape in lateral view. The stem of

the 'T' is a curved, tapering element that forms the posterior margin of the orbit and connects to the dorsal process of the jugal through a simple overlapping suture. The dorsal portion of this element is thick and expands medially, producing an angled, heavily sutured surface which abuts the combined frontal-laterosphenoid/parietal along an interdigitate suture (Fig. 8C). Posteriorly the postorbital continues as a triangular, tapering process that overlaps the squamosal; together these form the bar separating supra- and infratemporal fenestrae. The anterior portion of this bar sweeps medially and contacts the parietal in the middle of the anterior rim of the supratemporal fenestra. The supratemporal fenestrae are separated by a narrow and relatively low sagittal crest. The dorsal part of the orbital margin of the postorbital is slightly thickened and rugose; it appears that a short segment of frontal contributes to the orbital margin and thereby separates postorbital and prefrontal.

The *squamosal* (Fig. 8, sq) forms the upper posterior corner of the skull and the posterolateral half of the supratemporal fenestra; its dorsal margin overhangs the posterior portion of the supratemporal fenestra and the medial process of the squamosal lap against the sides of the sagittal crest. The anterior process runs medial to the postorbital for almost the entire length of the fenestra. The central body of the squamosal anchors the head of the quadrate; it is recessed ventrally to form a pocket for the quadrate head and typically forms anterior and posterior processes that help to stabilize/lock the quadrate head in position (this region is not well preserved in any of the specimens studied). The quadrate lies against, and partially caps, the paroccipital process.

The *frontal* (Fig. 8, fr) is a flat plate sutured to its partner along the midline of the skull roof; its general features are similar to those described for *Altirhinus* (Norman, 1998: fig. 11). There is a small posterior midline notch where the parietal interfingers between the frontals; on either side of this area the frontals curve forward along a coarse, shallowly interdigitate suture with the anterior parietal flange and then the postorbital, terminating along the dorsal orbital margin. There is a short orbital rim, followed by a notch representing the suture for the prefrontal, beyond which the frontal curves medially, and is then again notched as it approaches the midline where it is overlain by the nasal bones. A sagittal section reveals a wedge-like profile, thickest posteriorly. The ventral surface of the frontals reveals the typical 'hour-glass' pattern of ridges and depressions that separate the roof of the common olfactory vestibule from the roof for the anterior chamber of the brain and the adjacent orbital cavities.

The *parietals* (Figs 8, 9p) form a fused, saddle-shaped midline plate with a midline sagittal crest.

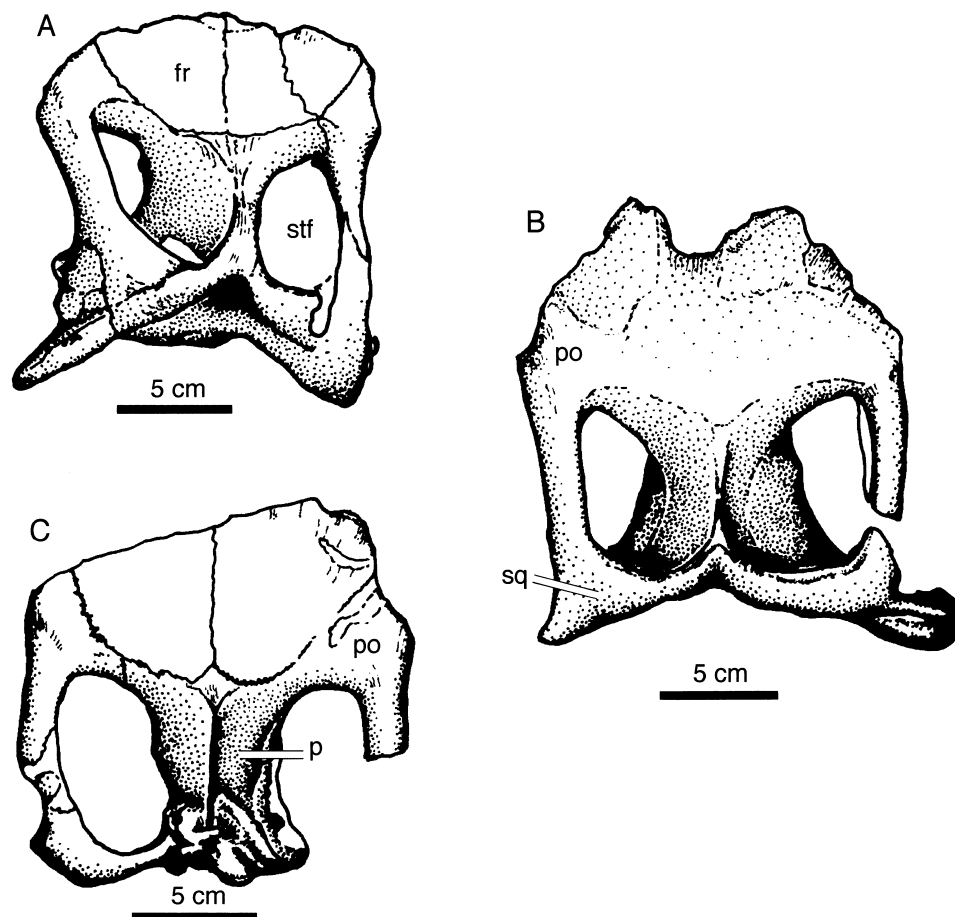


Figure 8. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. Skull table in dorsal view. A, PIN (unregistered). B, PIN 2232/36-1. C, PIN 2232/17-1. Abbreviations: fr = frontal; p = parietal; po = postorbital; sq = squamosal; stf = supratemporal fenestra.

Anteriorly lappets of the parietal splay laterally to contact the frontal-postorbitals, and posteriorly, similar lappets overlie the supraoccipital and contact the dorsal part of the paroccipital wings laterally and are overlain by the medial lappets of the squamosals.

The *neurocranium* (Fig. 9) is capped by the parietals and the supraoccipital more posteriorly, although the latter in this instance has been lost probably because this specimen came from an immature adult in which sutural fusion had not yet occurred. The space occupied by the supraoccipital is represented by a notch in the rear of the braincase between the parietal lappet and the base of the paroccipital process. It was not possible to establish whether the supraoccipital was excluded from the foramen magnum (as might be predicted) in this instance. Beneath the capping bones, the braincase elements strongly resemble those seen in forms such as *Iguanodon* (Norman, 1986: fig. 18). The partly eroded neurocranium (PIN 2232/2-1; Fig. 9) reveals a conventional sidewall to the braincase

comprising an upswept and laterally curved laterosphenoid that appears to terminate in a rounded boss (ls); the ventral edge of this plate is marked by the large groove for the ophthalmic branch of the trigeminal nerve (cn V) and the deep fossa that marks the outer region of the principal foramen for cn V. Posterior to the laterosphenoid the prootic overlaps the opisthotic and together they form a thickened lateral wall of the braincase at the root of the paroccipital process. The latter forms a large, downwardly curved, process which does not bend anteriorly toward its tip. The auditory recess (aud) lies at the junction between prootic and opisthotic. The posterior portion of the sidewall of the braincase is formed by the exoccipital and several large posterior cranial foramina can be seen puncturing the sidewall of the braincase in this region. The posteroventral edge of each exoccipital forms a small dorsal part of the occipital condyle; the remainder of the condyle is formed in the ventral midline by the basioccipital. The latter is much eroded in

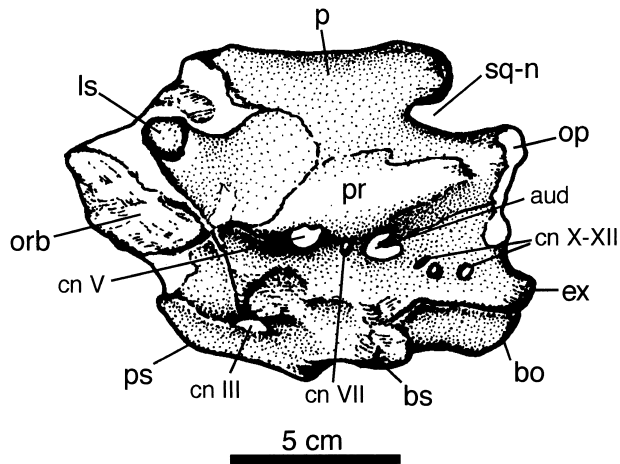


Figure 9. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/2-1. Braincase in left lateral view. Abbreviations: aud = auditory recess (including fenestra vestibuli, exit for cranial nerve [cn] IX and ?jugular); bo = basioccipital; bs = basisphenoid; cn = cranial nerves; cn III = probably includes cn VI and cn VII; ex = exoccipital; ls = laterosphenoid; orb = sphenethmoid/orbitosphenoid plate; op = opisthotic; p = parietal; pr = pro-otic; ps = parasphe-noid; sq-n = notch for attachment of medial portion of squamosal.

this specimen, and along with the basisphenoid and parasphe-noid, forms the floor of the braincase. As with a majority of ornithopods the anterior portion of the braincase adjacent to the orbital cavity is ossified as a sphenethmoid/orbitosphenoid plate (orb).

Lower jaw

Several fragments of the lower jaw are among the collections. None is complete, and only three elements have so far been identified (pre-dentary, dentary and surangular).

A single *pre-dentary* (PIN 2232/23-1. Fig. 10) is well-preserved, lacking only the median ventral process that was (probably) bifid, forming flaps that underlay the anterior tips of the dentaries adjacent to the symphysis. Roughly horseshoe-shaped in plan view (Fig. 10A, B) this median bone resembles that seen in typical large-bodied ornithopods. Posterior rami form a moderately broad occlusal shelf delimited laterally by a low ridge; the latter becomes more prominent as this edge approaches the midline forming a slightly narrower ledge and a more trenchant cutting margin, which is irregular. The bone is punctured by foramina and grooves associated with the attachment and growth of the keratinous sheath. There is a median prominence, separated by distinct gullies on either side (Fig. 10C), which lead, via diagonal vascular grooves on the external surface of the pre-dentary

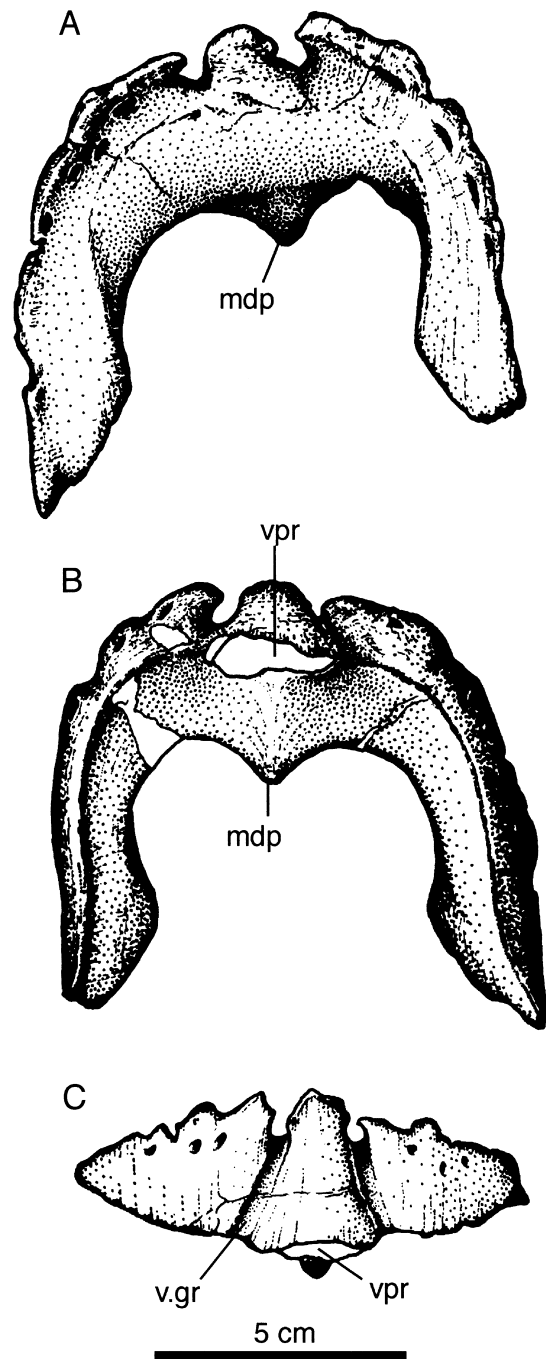


Figure 10. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/23-1. Pre-dentary in anterodorsal (A), posteroventral (B) and anteroventral (C) view. Abbreviations: mdp = median dorsal process; v.gr = vascular groove; vpr = ventral process (broken at base).

(v.gr), toward the notch between the base of the posterior rami and the median root of the ventral flaps. This arrangement of grooves has been observed on a number of occasions on the pre-dentaries of larger ornithopods and connects directly with large neurovascu-

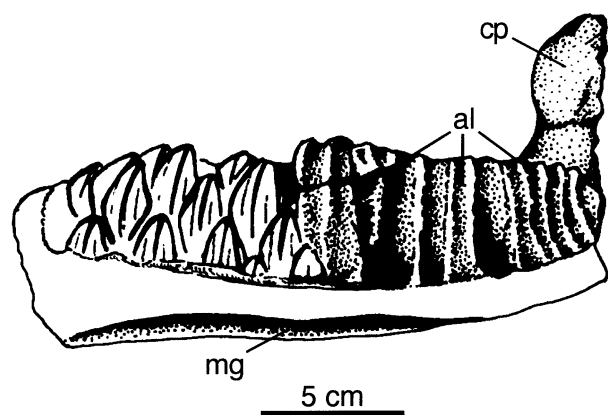


Figure 11. *Probatrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/36-3. Dentary, right (partial). Partially exposed dentition and alveolar trough, anterior and posterior ends missing. Abbreviations: al = alveoli; cp = coronoid process; mg = Meckel's groove.

lar openings found on the anteroventral edge of the dentary. Similar features were noted on the lower jaw of the basal ornithischian *Lesothosaurus* by Sereno (1991), and are probably common to all dinosaurs that possess a predentary. In addition to the (missing) ventral bifid flap that helped to secure the dentaries in position, the ventral surface of the predentary is marked by a shelf for attachment of the edge of the dentary, and the median area immediately above this articular area has the form of a prominent process (Fig. 10, mdp) that clearly helped to clamp the area immediately above the dentary symphysis.

The most complete *dentary* (PIN 2232/10;/2-2;/18-1;/36-2;/36-3. Figs 11, 12) is associated with a partial mounted skeleton. The rear portion is rendered with plaster for display purposes, but the majority of the bone is visible and comparable to several other specimens. There are approximately 23 vertical tooth positions (alveoli) preserved, and a small number of highly eroded replacement crowns are visible in the alveolar trough (Fig. 11). The dentary ramus is straight with a slightly arched ventral margin, and it terminates anteriorly at a scalloped and spout-shaped symphysis and predentary attachment region. The symphysis is ventrally positioned (Fig. 12, sym) quite small and the attachment area for the predentary is represented by the concave, slotted, edentulous region that sweeps upward to merge with the alveolar trough (pd.s). The main body of the dentary accommodates the dentition which fitted into the array of parallel alveolar slots visible in medial view (Fig. 11); there are between 20 and 23 vertical slots preserved on the more complete dentaries in this collection. Beneath the alveolar trough there is a curved groove (Fig. 12, gr) which

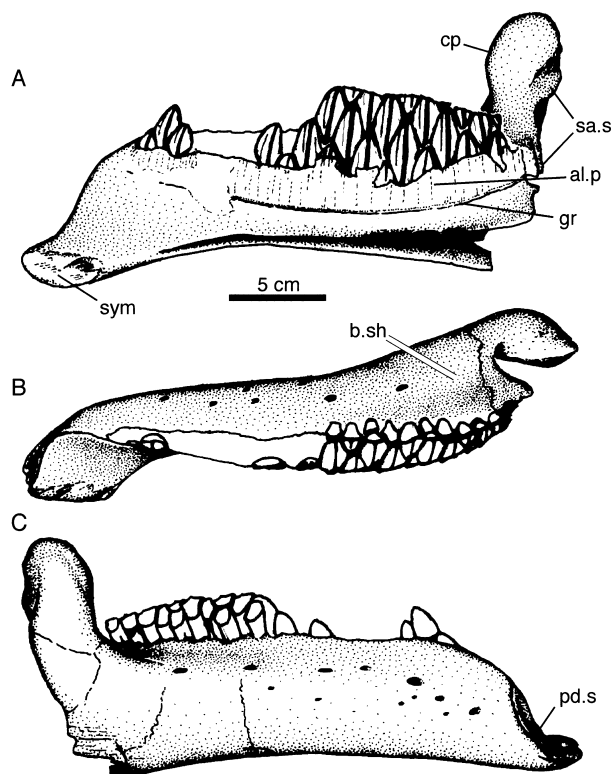


Figure 12. *Probatrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/42-1. Dentary (attributed to '*P. alashanicus*') right, nearly complete, showing part of the dental magazine *in-situ* and showing the presence of two replacement crowns in a single alveolus and an oblique inclination of the occlusal surface. Abbreviations: al.p = alveolar parapet; b.sh = buccal shelf lateral to the dentition; cp = coronoid process; gr = simple groove marking the position of the foramina leading to the dental lamina; pd.s = sutural surface for the predentary; sa.s = surangular; sym = dentary symphysis.

marks the passage for the neurovascular supply to the dental laminae at the base of the alveoli. Above this groove the bone forms a thin, medial, alveolar parapet (al.p). Beneath the groove the body of the dentary is incised horizontally by Meckel's groove (Fig. 11, mg). The lateral surface of the dentary is hemicylindrical and, because the alveoli are located medial to the long axis of the dentary, there is a significant shelf (b.sh) or 'cheek recess'; the posterior end of this recess terminates in a large, elevated coronoid process (cp) that is slightly anteroposteriorly expanded near its apex. The rear edge of the coronoid is slotted for attachment of the surangular (Fig. 12, sa.s).

The *surangular* (PIN 2232/1-4. Fig. 13) is represented by a single, incomplete, specimen. There is a small external foramen, adjacent to the glenoid and its associated lateral lip, a small facet represents the area

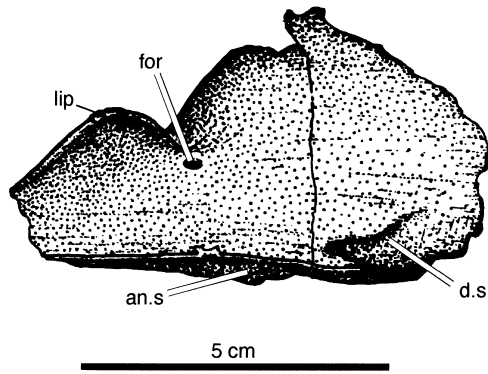


Figure 13. *Proactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/1-4. Surangular (partial right) in lateral view. Abbreviations: an.s = sutural surface for the angular; d.s = sutural surface for a posterior process of the dentary; for = surangular foramen; lip = lateral lip to the quadrate cotylus.

of overlap and attachment between the surangular and dentary (d.s), and there is a groove along the ventral margin that represents the sutural surface for the angular (an.s). It is clear that the angular was visible on the lateral surface of the lower jaw.

No other postdentary bones attributable to this dinosaur were identified among the collections in the PIN.

Dentition

Dentary teeth are quite well preserved in a number of jaws as well as from isolated examples of replacement (PIN 2232/23-2; Figs 14A, B, 15A, 16B) and functional teeth (PIN 2232/24-1; Fig. 15C). The shield-like enamelled surface of the crown in lingual view is elongate and asymmetrically diamond-shaped (Figs 14–16). The asymmetry is marked by the positioning of the primary ridge (slightly distally offset from the median) and the curvature (Fig. 14, sh) of the denticulate margin of the upper half of the crown. As in the case of *Altirhinus* (Norman, 1998) enamel is restricted to the lingual surface of the crown and the marginal denticles. The labial surface of the crown, and likewise the root, is composed of dentine, which is in places smeared with roughened areas of cementum. The ‘body’ of the tooth (root and the labial ‘shell’ that supports the enamelled surface) is bowed vertically (Fig. 14B) and clearly marked by a series of vertical facets (Fig. 14A, B, 1–4); these latter represent the points for attachment of adjacent teeth in the dental battery. This structure and organization is more clearly defined than in the case of the dentary teeth of *Altirhinus* and reflects the fact that the dental battery as a whole was more compact.

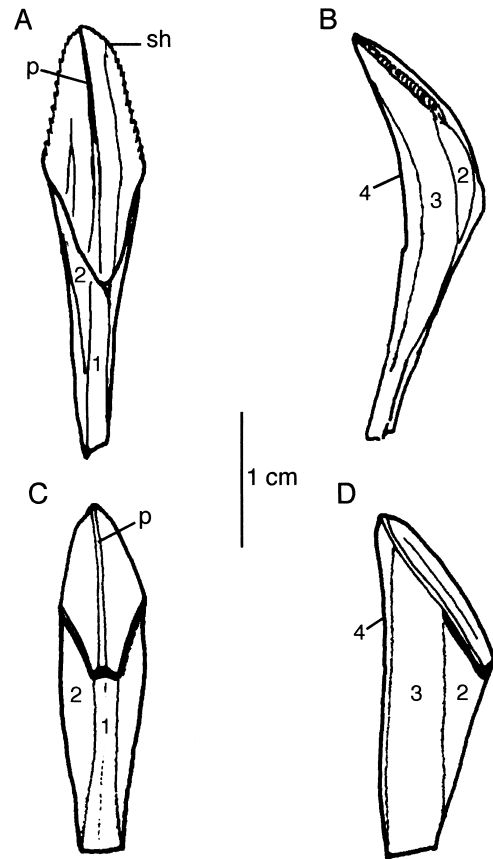


Figure 14. *Proactrosaurus* and lambeosaurine isolated dentary teeth compared. (A) lingual and (B) distal. PIN 2232/23-2 an isolated, complete replacement crown from the left dentition. (C) lingual, and (D) mesial. Drawing of a ‘typical’ lambeosaurine hadrosaurid tooth crown, from the right dentition. Abbreviations: 1–4 = equivalent facets for the articulation of adjacent teeth; p = primary ridge; sh = shoulder region on the mesial edge of the crown. Note the degree of curvature of the root in distal aspect; in this respect proactrosaur teeth more closely resemble those seen in more basal iguanodontians and hadrosaurine hadrosaurids (cf. *Brachylophosaurus* sp. MOR 1071).

The lingual surface of the crown is marked by a number of distinctive features that aid identification. A primary ridge (p), though not significantly elevated, is the most prominent feature running the entire length of the crown and dividing the crown surface into unequal halves. The mesial half is bisected by a narrower and lower (secondary) ridge that is parallel to and nearly coextensive with the primary ridge (Figs 15A, 16B). Topographically, this feature is identical to the secondary ridge identified on the dentary crowns in other iguanodontians (*Iguanodon*, *Ouranosaurus*, *Altirhinus*). The upper part of the mesial margin is strongly curved, producing a shoulder-like

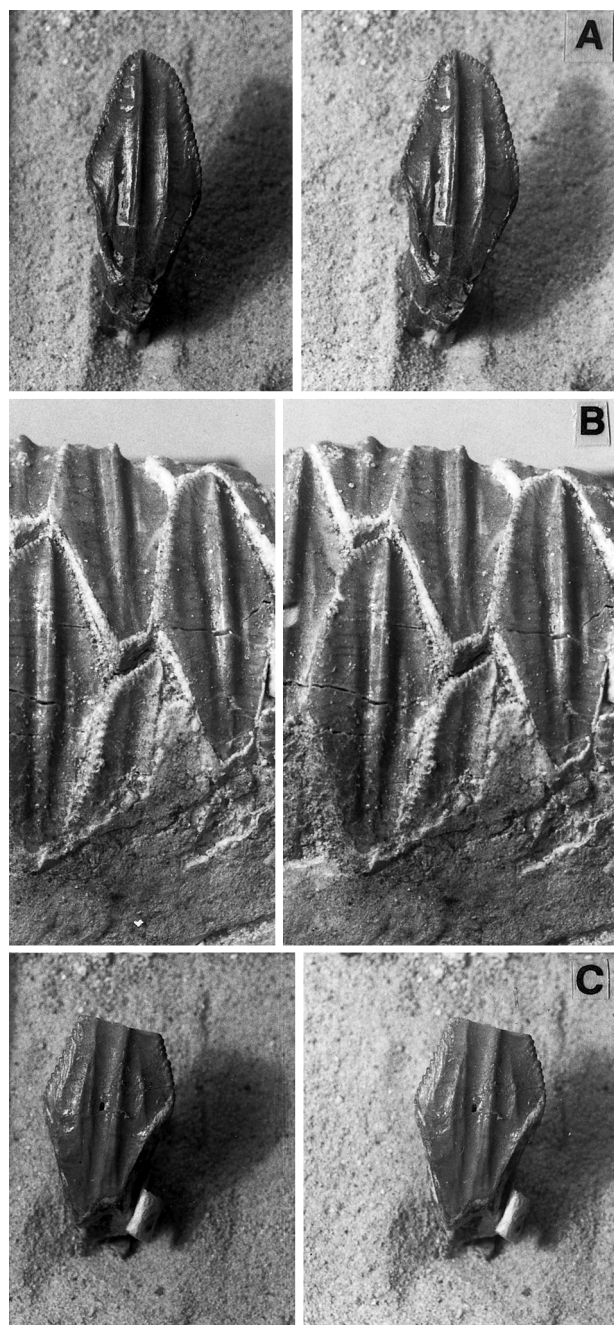


Figure 15. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. Dentary teeth in lingual aspect, as stereoscopic pairs. A, an isolated, unworn dentary crown (PIN 2232/23-2). B, part of a dental magazine of '*P. alashanicus*' (PIN 2232/42-1). C, an isolated and partially worn dentary crown (PIN 2232/24-1). Natural size.

structure (Fig. 14, sh) before merging with the apex of the tooth; the denticulations near the tip of the tooth form more simple tongue-shaped structures without the additional mammillations seen further down the

sides of the crown (Fig. 16C). The mesial edge of the crown is thickened and denticulate. Each of the discrete denticulations seen in lingual view (Fig. 16B) forms a curved and crenulate ledge (Fig. 16C) that wraps (lingual to labial) around the edge of the crown. The lingual surface of the distal half of the crown bears a low, short, but distinct ridge in the widest part of this surface, but it does not extend toward the apex as it does in the case of the primary and secondary ridges. The marginal denticles have the same features as those noted on the mesial edge.

The lower half of the crown shows edges that converge toward the root. The mesial edge is smooth, and has a slightly thickened edge. The distal edge forms more of an everted, oblique ridge as if the original edge of the crown had been literally pinched inward (Fig. 15C); this feature is common to iguanodontian ornithopods (Norman, 1980, 1986, 1998), but in this instance the rolled edge does not appear to bear any evidence of small denticulations. The base of the enamelled surface is obliquely notched; this feature corresponds to the top of a lingually positioned vertical groove on the root (Fig. 14A, 1), which would have been occupied by the replacement crown. The angulation of the notch simply reflects the asymmetry of the apex of the replacement crown (Fig. 15B).

In the general distribution of its topographic features this tooth is surprisingly similar to a typical dentary tooth of *Altirhinus* (Fig. 16A). However, differences exist not only in the structure of the root, but more importantly in the proportions of the crown. A direct comparison reveals that for a similarly sized crown (dorsoventral length) the crown of *Probactrosaurus* is proportionally far narrower. Teeth in *Probactrosaurus* are beginning to exhibit the miniaturization of the individual crowns seen in more derived ornithopods (hadrosaurids; Fig. 14C, D).

Maxillary teeth. Such teeth are not represented by isolated specimens in the collections of the PIN. A little can be gained by examining the maxillary fragments discussed above (Fig. 5). These reveal that the maxillary crowns appear to be narrow and lozenge-like, with thickened and denticulate margins. The labial (enamelled) surface of the crown is characterized by a single, very prominent primary ridge and there is little evidence of subsidiary ridges adjacent to it.

The overall proportions of the maxillary crowns are of considerable interest (phylogenetically), particularly because the maxillary crowns of *Eolambia* show evidence of miniaturization relative to the dentary crowns (pers. obs. 1998) and a similar condition has been reported in *Protohadros* (Head, 1998). Unfortunately it is not possible to report accurately on this matter; it does seem to be the case that the maxillary crowns are not significantly smaller (in overall width)

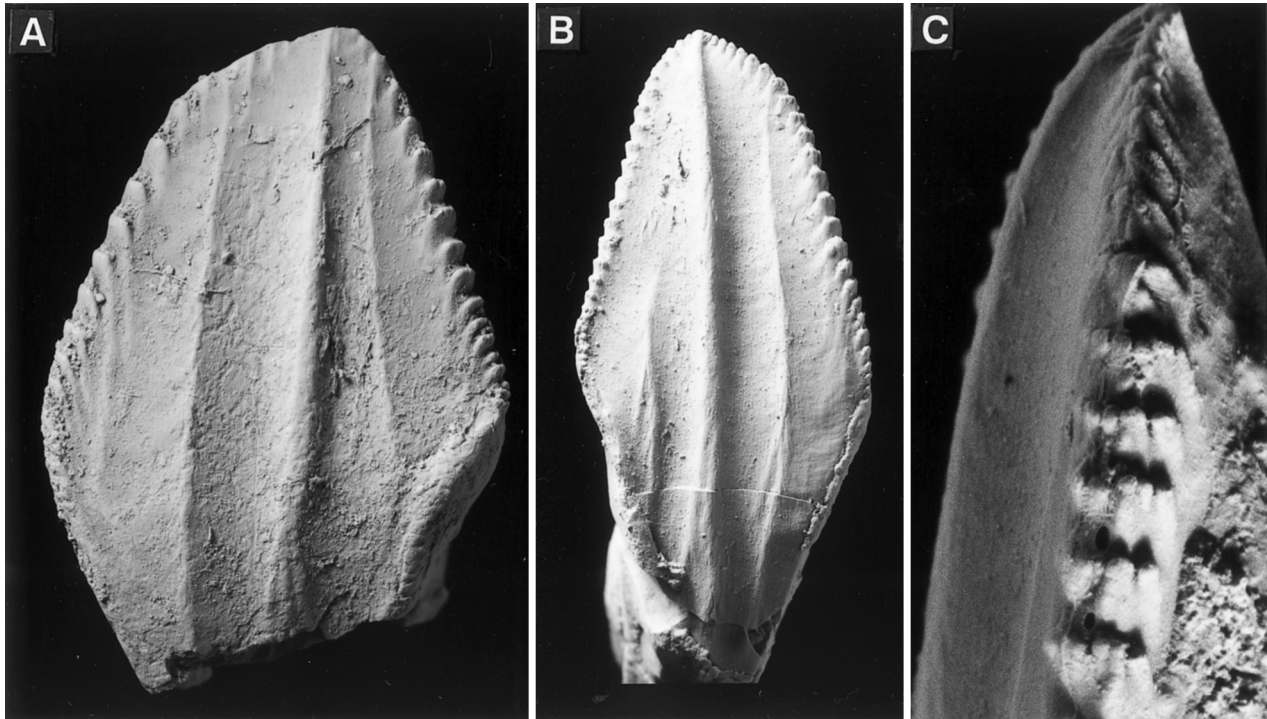


Figure 16. Dentary crowns. A, *Altirhinus kurzanovi*. Isolated replacement dentary crown ; crown hollow, root uncalcified. B, *Probactrosaurus gobiensis* isolated crown (PIN 2232/23-2) in lingual aspect. C, the same crown as in B, but in mesial aspect and under greater magnification, showing details of the structure of the marginal denticles.

than dentary crowns, judged from their appearance in the maxillae, and from the relative size and number of maxillary crowns preserved (or estimated) in observed maxillae.

Tooth replacement. Isolated dentaries show that the dentary teeth emerged from the alveolar trough at a low distal inclination to the vertical. This is seen in the arrangement of grooves in the labial alveolar wall and, when present, the slope of the crowns in the dental battery. The inclination of the crowns matches the asymmetry of the crowns described above. Individual crowns appear to be tightly locked into the battery (Figs 12, 15B) and retain a slight *en echelon* pattern (the mesial edge of the crown overlapping the distal edge of the crowns in the preceding vertical row; Fig. 15B). It would appear that there is evidence (PIN 2232/36-2, 42-1) for the presence of a second replacement crown in the midposterior-section of the dentary dental battery (a feature reported as only present in *P. alashanicus* Rozhdestvensky, 1966). However a second dentary replacement crown has also been reported in *Altirhinus* (a stratigraphically earlier and more basally positioned ornithomimid; Norman, 1998) so the primary systematic value of this feature in the context of the origin of hadrosaurids (emphasized in

Rozhdestvensky's original description) has already been lessened.

POSTCRANIAL ANATOMY

The postcranial anatomy of this species is currently largely unknown, despite the existence of two permanently mounted skeletons in Moscow (PIN 2232/1, quadrupedal pose and PIN 2232/10, bipedal pose). The latter skeleton is slightly better preserved and more complete and forms the basis for much of the description that follows. However, the preservation and preparation of individual bones (particularly the axial skeleton) could be better. Reviews and comparative observations to date have been hampered by having to rely on the relatively brief comparative observations and osteological commentary provided by Rozhdestvensky (1966) in his original descriptive paper. Major parts of this material were dismantled and studied during the course of this work and I am extremely grateful to Dr Sergei Kurzanov for his help in doing this. The material is, unfortunately, far from complete and in need of preparation and conservation; however, much of the salient anatomy is described and illustrated below.

Axial skeleton

Six *cervical vertebrae* are preserved on the mounted (bipedal) skeleton (PIN 2232/10), but they are poorly preserved and largely uninformative. They simply show the generalized features associated with normal ornithopod cervicals (opisthocoelic centra with a large convex anterior condyle, ventral surface with a broad keel, widely separated and arched posterior zygapophyses, parapophysis situated on the side of the centrum, beneath the neurocentral suture).

The *dorsal vertebrae* (Fig. 17) are also poorly preserved and do not show the cervico-dorsal transition with any clarity. Twenty cervico-dorsals are preserved (PIN 2232/10), two of which are associated with the sacro-iliac block (Fig. 18). 'Anterior dorsals' (if correctly identified) are strongly cervicalized, in the sense that the centrum is relatively low, keeled, retains its opisthocoelic character and has a distinctly convex anterior articular surface. Later members in the series develop a taller and more rectangular profile to the centrum, and develop the more typical amphiplatyan articular surfaces; the centra are also laterally compressed, although this may be unduly emphasized by *postmortem* crushing. Dorsally the neural arch forms a taller platform and the anterior zygapophyses are less prominent, and the posterior zygapophyses form short processes at the base of the neural spine. Neural spines were clearly present, but their vertical extent cannot be estimated given the battered nature of the preserved specimens (Fig. 17).

The *sacrum* (Fig. 18) appears, as reconstructed and mounted, to be composed of seven fused vertebrae; however, at least one (Fig. 18, inv.ins) shows evidence of plaster reconstruction and may well not only be an insertion in the series, but may also be inverted. This

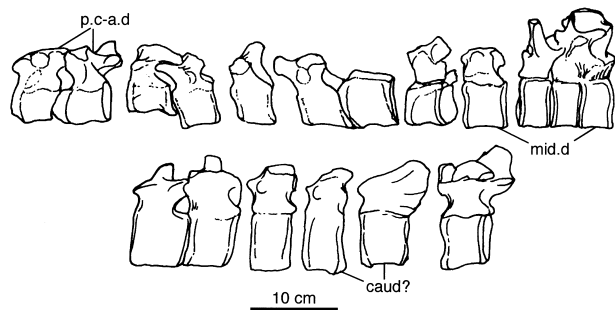


Figure 17. Posterior cervical-dorsal vertebrae from the mounted skeleton of *Probatrosaurus gobiensis*. PIN 2232/10. These specimens are poorly preserved and jumbled, all seem to be missing neural spines and much of the neural platform. Anterior dorsals?posterior cervicals have convexo-concave centra. Abbreviations: caud? = caudal vertebrae; mid.d = mid-dorsal vertebrae; p.c-a.d = posterior cervical/anterior dorsal vertebrae.

latter gives the centrum a 'sulcus', used by Rozhdestvensky as a specific feature. As presently articulated with the ilia in the block, it appears that the posterior sacrals extend considerably beyond the posterior end of the iliac blade; on this basis alone the actual sacral count must be considered to be in some doubt and was in all probability six. Rozhdestvensky (1966) indicated that the sacrum was composed of six fused vertebrae, to which were additionally fused a posterior dorsal and an anterior caudal, creating a 'pseudosacrum' of eight vertebrae. There is no evidence for a ventral sulcus on the last three sacral vertebrae (as claimed by Rozhdestvensky); the sacrum, as preserved, appears to have a modest but distinct ventral keel along most of its preserved length.

The *caudal vertebrae* (Fig. 19) are represented by 24 vertebrae, a few of which are nearly complete. Anterior caudals have a tall and rectangular centrum and a large caudal rib attached across the neurocentral suture at the base of the neural arch. The (presumed) first two caudals seem to lack an obvious haemapophyses (chevron facets) on the posteroventral edge of the articular surface of the centrum; a marked oblique facet is visible on later members in the series (Fig. 19, ph). The 'fourth' centrum in the series (Fig. 19, left) is nearly complete and shows that a relatively tall, slender, obliquely inclined and slightly curved neural spine was present; this offers some insight into the probable existence of prominent sacral and dorsal neural spines. The remainder of the caudals show no

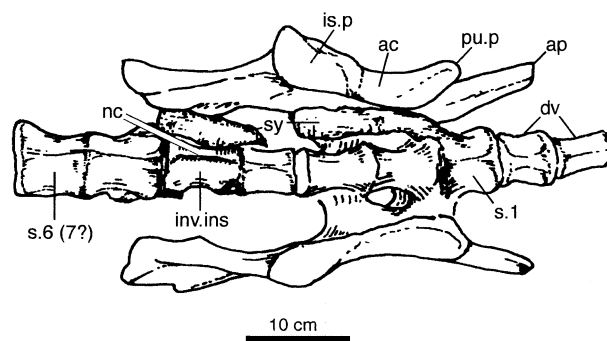


Figure 18. *Probatrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/10. Sacral block in ventral view. This block appears to show a sacrum comprising 7 fused vertebrae. Closer inspection suggests that one of the vertebrae 'inv.ins' is not only inverted (the neural canal, nc, is shown ventrally), but it may well represent an additional (inserted) element judged by the comparative length of the adjacent ilia. Abbreviations: ac = acetabulum; ap = anterior process of the ilium; dv = dorsal vertebrae; inv.ins = an apparently inverted and inserted vertebral centrum; is.p = ischial peduncle; nc = neural canal; pu.p = pubic peduncle; s.1, s.6(7) = numbered sacrals; sy = partial sacricostal yoke.

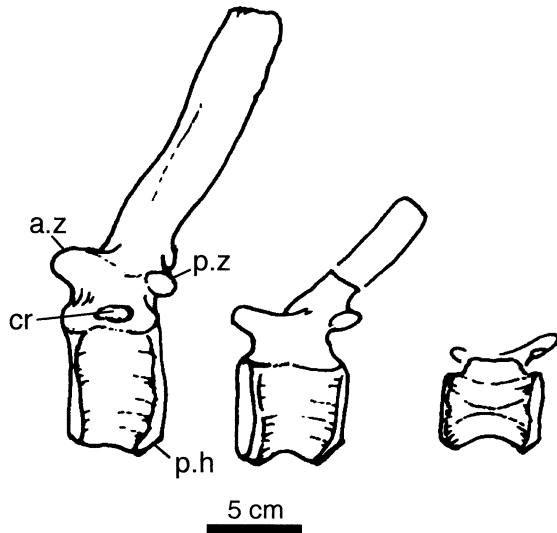


Figure 19. *Probatrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/10. Caudal vertebrae. Examples of proximal, middle and distal caudals. Abbreviations: a.z = anterior zygapophyses; cr = caudal rib; ph = posterior haemapophysis (chevron facet); pz = posterior zygapophysis.

unusual characters: the centra become progressively more squat (Fig. 19, middle), gradually lose the caudal rib and gradually assume a somewhat more elongate quasi-cylindrical form (hexagonal in cross-section; Fig. 19, right). It seems very probable that the tail was composed of 40–50 vertebrae when complete.

Additional elements. No chevrons are preserved among the collections that were examined. Fragments of the ribcage are preserved, but indicate nothing of particular note with respect to this type of ornithomimid dinosaur. Ossified tendons appear not to have been recovered with these specimens and may well have been either missing as a result of taphonomic processes, or may not have been considered worth collecting if they consisted solely of scattered bony rods.

Appendicular skeleton

Pectoral girdle. The *scapula* (Fig. 20A, B) is an essentially strap-like element. The blade is straight in lateral aspect (Fig. 20A), but bowed medially in order to follow the curvature of the ribcage. The distal part of the blade is thin, but only modestly expanded. Proximally the shaft of the blade is thickened and oval in cross-section; it then expands towards the scapular glenoid buttress and coracoid suture. The anterior edge of the scapula curves forward to form a discrete 'acromion' process (acr). Beyond the 'acromion' the edge of the scapula curves posteriorly in a smooth arc,

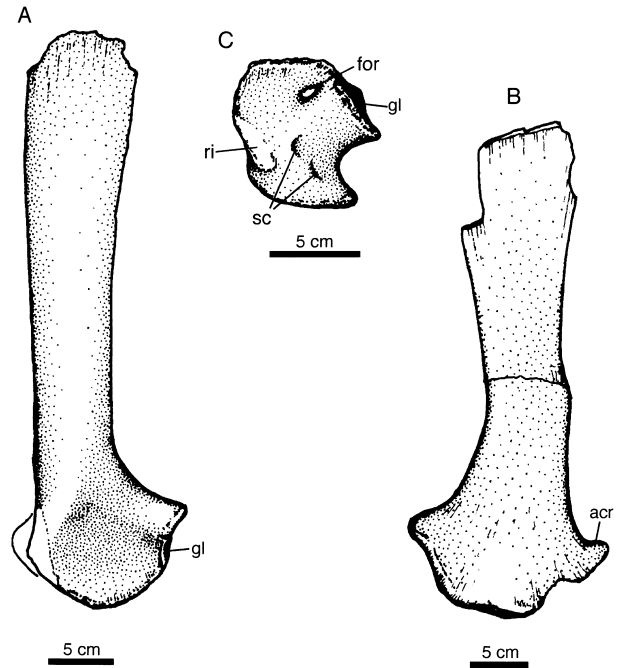


Figure 20. *Probatrosaurus gobiensis* Rozhdestvensky, 1966. A, scapula in lateral view (PIN 2232/1). B, scapula 'alashanicus' in medial view (PIN 2232/41-3). C, coracoid in lateral view (PIN 2232/2-5). Abbreviations: acr = 'acromion' process; for = coracoid foramen; gl = humeral glenoid; ri = coracoid ridge; sc = muscle scars.

which is interrupted slightly by a slight embayment which marks the scapular glenoid (gl). In lateral aspect the proximal end is dished between the acromion and glenoid buttress. The latter is robust and projects posterolaterally from the body of the scapula. This 'style' of scapula is common to *Iguanodon*, *Ouranosaurus*, *Altirhinus* and differs from those seen in typical hadrosaurids in which the scapular blade tends to curve posteriorly and flare distally, whereas the 'acromion' is reflected laterally so that the anterior margin of the proximal end of the scapula appears to be unexpanded anteriorly when the scapula is viewed in lateral aspect.

The *coracoid* (Fig. 20C) has the shape of thickened disk, with two, adjacent, broad notches cut across its posterior edge. The thickened and slightly everted dorsal border is ligamentously bound to the proximal end of the scapula and there is a round and discrete foramen that pierces the coracoid in the angle enclosed by the glenoid lip and the scapular suture (for). The glenoid (Fig. 20C, gl) is a slightly concave, kidney-shaped facet surrounded by an everted lip. Posterior to the glenoid there is an embayment that terminates in a robust sternal process. The remainder of the coracoid has a rugose and medially inclined edge that has an

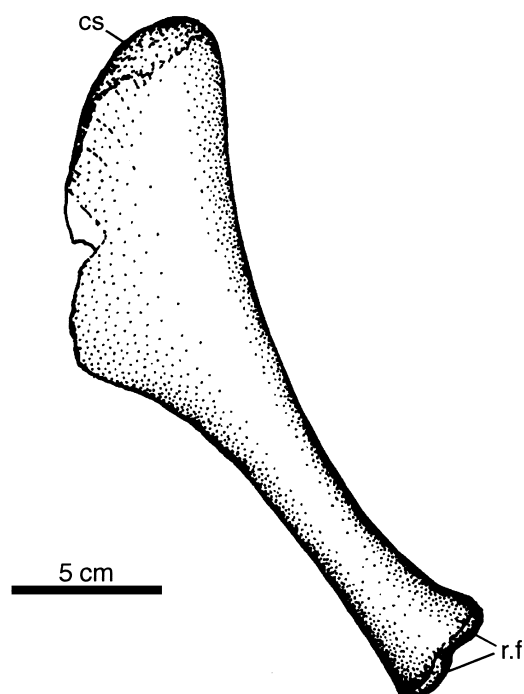


Figure 21. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/10. Sternal bone (left) in external aspect. The anterior end is thickened and capped by cartilage, the medial edge becomes increasingly thin posteriorly. The oblique posterior process has a bifaceted tip for attachment of presumed cartilaginous sternal ribs. Abbreviations: cs = surface for attachment to a coracosternal cartilage; r.f = facets for attachment of sternal ribs.

approximately lunate profile interrupted by an oblique ridge (ri), a feature also noted in the coracoid of *Altirhinus* (Norman, 1998: fig. 26A). The external surface of the coracoid is also marked by at least two deep and distinct muscle scars (sc) on its external surface, just anterior to the embayment below the glenoid.

The *sternal* (Fig. 21) comprises a broader blade-like portion, which is thin medially and thicker laterally (cs); this contracts posteriorly and laterally to produce the 'typical' rod-like sternal extension seen in all ornithopods that are more derived than *Camptosaurus*. The distal end of the 'rod' appears to be bifaceted (r.f) – presumably reflecting the attachment of sternal rib cartilages.

Forelimb. The *humerus* (Fig. 22) is, in overall shape, typical of that seen in many derived dryomorph and some basal hadrosaurid ornithopods (*Telmatosaurus*). Viewed as if held vertically, the proximal end is anteroposteriorly compressed and expanded transversely. The proximal end is thickened and rugose and clearly bore a capping of cartilage in life. The central

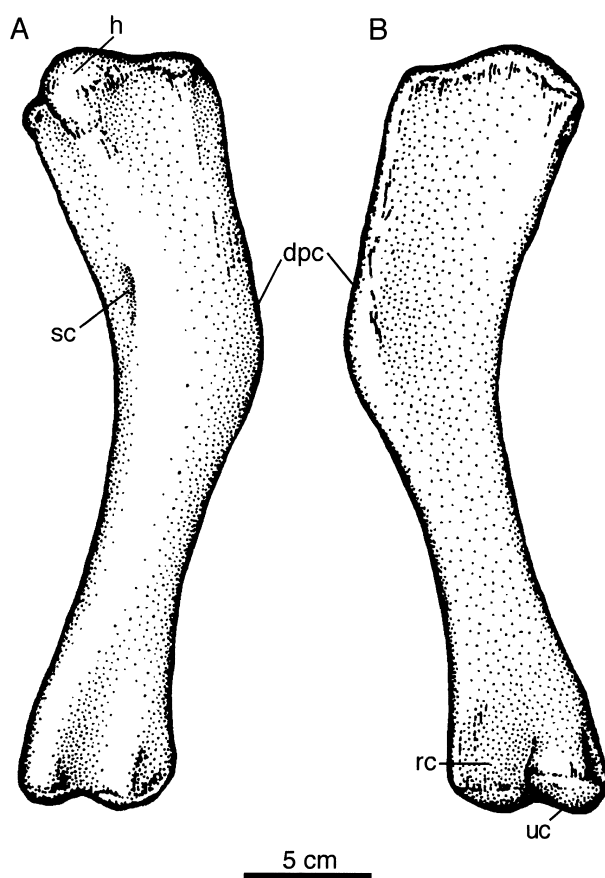


Figure 22. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/2-8. Humerus (right) in (A) posterior and (B) anterior aspect. Abbreviations: dpc = deltopectoral crest; h = articular head; rc = radial condyle; sc = muscle scar; uc = ulnar condyle.

region of the proximal surface is expanded to form a discrete articular condyle or head (h) that is notably expanded posteriorly. On either side of the articular condyle the proximal end of the humerus extends to form distinct shoulders. Distal to the articular zone, the shaft of the humerus is roughly parallel-sided and orientated obliquely laterally so that its medial edge describes a shallow curve. At about midlength it contracts transversely and becomes more rounded in cross-section; simultaneously, its long axis becomes directed medially. Distally it expands transversely as it approaches the distal articular surfaces for the radius and ulna. In anterior aspect the medial ulnar condyle (uc) is more prominently developed, whereas the lateral surface is depressed in order to receive the proximal end of the radial condyle (rc). There is a shallow intercondylar notch between the medial and lateral portions of the distal articular condyles, and on the posterior surface there is a longitudinal groove

associated with the soft tissues attached to the olecranon process of the ulna.

The deltopectoral crest (dpc) has the form of an elongate, thickened edge that extends for approximately half of the total length of the humerus. Distally the dpc merges smoothly with the shaft and does not form a prominent 'angle' on the humeral shaft. Overall, the shaft of the humerus is bowed and slightly sinuous. The degree of curvature appears to change during ontogeny; smaller individuals (PIN 2232/27-3) appear to exhibit more strongly curved humeri. The posterior (extensor) surface of the humerus displays shallow imprints or scars (sc) generated by muscle attachments.

The radius (Fig. 23, rad) is notable for being elongate, somewhat curved and laterally compressed at its distal end. The proximal end forms an essentially rounded shaft, the articular surface of which is expanded to form an almost collar-like structure that surrounds the concave proximal articular surface; this abutted the depressed region on the adjacent lateral humeral condyle (Fig. 22, rc) when the forelimb was flexed. Distally the shaft is roughly circular in cross-section and tapers slightly; its proximal end is scarred by the ligaments that anchored it to the ulna. Further distally the radius expands dorsoventrally and significantly overlaps the mediodorsal surface of the ulna (in the mounted skeletons this articulation is reversed, as shown in Fig. 23). The distal articular surface of the radius is bevelled (c.fac) and separated by a ledge from the main shaft. Although carpal bones are not preserved this conformation is suggestive of the presence of a set of discrete carpals (notably the metacarpal I-radiale block) – this is further supported by the presence (see below) of a spine-like pollex unguis (Figs 25D, 26A), which would be expected to have been articulated against the carpus via a block-like combination of metacarpal I-radiale (Norman, 1980, 1986).

The radius is relatively long, slender and curved when compared to species such as *Iguanodon bernis-*

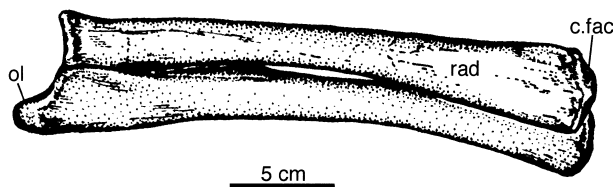


Figure 23. *Probaactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/10. Radius and ulna (right) from the mounted skeleton, misarticulated distally, in lateral view. Abbreviations: c.fac = facets on the distal end of the radius for articulation of the carpal bones; ol = olecranon process; rad = radius.

sartensis and *I. atherfieldensis* and in proportion to the length of the humerus (0.85) this element is more elongated than in the latter two species (0.62–0.78, respectively).

The ulna (Fig. 23) is relatively narrow and elongate. Proximally the shaft of the ulna is expanded to form the principal portion of the elbow joint. There is a modest olecranon process (ol), and immediately distal to this there is a lateral shelf which supported the radial head, and mediodorsal to the shelf there is a low parapet that also constrained the head of the radius medially. Distally the shaft forms a partial dorsal ledge adjacent to the radius, but more distally it becomes compressed and then expands dorsoventrally and forms a slightly convex rounded articular surface for the (presumed) carpal bones.

Ossified elements of the carpus have not been recognized in any of the collections examined to date.

The manus is represented by a number of important elements, which indicate that the manus was elongate (with metacarpals II–IV being relatively slender and mutually appressed; Fig. 26), that a conical (spine-like) pollex (Fig. 25D–G) unguis was present, and that the terminal unguals were flattened and asymmetrical (Fig. 25). There are general similarities to the form of the manus of *I. atherfieldensis* (Fig. 26B) although the manus of *Probaactrosaurus* is more slender and gracile (Fig. 26A). The degree of association of several of the manus bones is, however, open to some doubt, even though they undoubtedly belong with the *Probaactrosaurus* material. This difficulty probably reflects idiosyncrasies associated with the process of accessioning from the original field collection slips.

Metacarpal I has not been identified. *Metacarpal II* (Fig. 24A) was a slender, elongate element (PIN 12068); its shaft is narrow and angular and the lateral surface is flattened where it was ligamentously (l.s) bound to the adjacent metacarpal. The proximal end is strongly convex and probably articulated in a socket formed by the co-ossified metacarpal I-radiale as described in *Iguanodon* (Norman, 1980, 1986). The distal end is modestly expanded to form a simple articular facet for its proximal phalanx. It is likely that this metacarpal was shorter than the larger and more robust metacarpal III and that this effect was accentuated in the articulated manus because the proximal end of metacarpal II was offset with respect to the former. *Metacarpal III* (Fig. 24C) is the largest and most robust element of the manus (PIN 2232/18-5); its proximal end is expanded anteroposteriorly and is broadly convex. In dorsal view the proximal end is somewhat compressed transversely with a medial depression to accommodate the proximal end of metacarpal II. The shaft of the metacarpal is slightly contracted along its length and expands distally to form a broad, almost transversely planar articular surface.

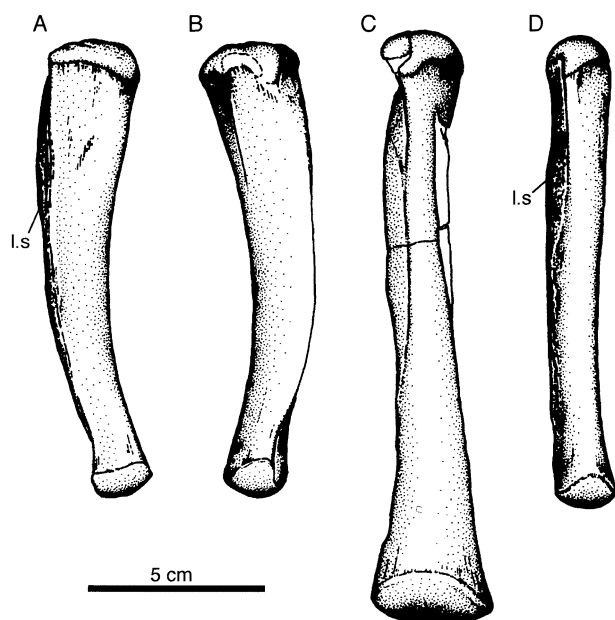


Figure 24. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. Metacarpals. A, PIN 2232/3-1. Metacarpal IV of the right manus in ventral view, and B, MC IV in dorsal view; C, PIN 2232/18-5. Metacarpal III of the left manus in dorsal view. D, PIN 12068. Metacarpal II of the right manus in dorsal view. Abbreviations: l.s. = ligament scars.

Metacarpal IV (Fig. 24A, B) is shorter than metacarpal III; its proximal end is block-like and robust, whereas its distal shaft tapers and curves laterally along its length. The medial surface of the shaft is markedly rugose reflecting the very strong ligamentous connection to the adjacent metacarpal (l.s.). The distal articular surface is relatively small and convex anteroposteriorly, but again nearly planar transversely. *Metacarpal V* was not identified among the collections; it may have been a shorter, dumbbell-shaped bone with a planoconcave proximal surface and a simple convex distal articular condyle.

Phalanges are represented by a few well-preserved elements, and a number of plaster cast specimens that may represent elements that cannot be located at present, or were manufactured to complete the hands on the mounted skeletons. An asymmetrical, slender element (PIN 2232/18-8; Fig. 25A) is typically the shape of the proximal phalanx of digit II; the oblique distal articular surface would enable the 2nd digit to diverge from digit III (corresponding with the situation described in *I. atherfieldensis* Norman, 1986). A large, robust phalanx (PIN 2232/11-2; Fig. 25B) is typical of the proximal phalanx of digit III. Smaller phalanges are less easily placed within the manus, but elongate ones such as PIN 2232/10-69 (Fig. 25C) are similar to those seen in digit V; several of the plaster

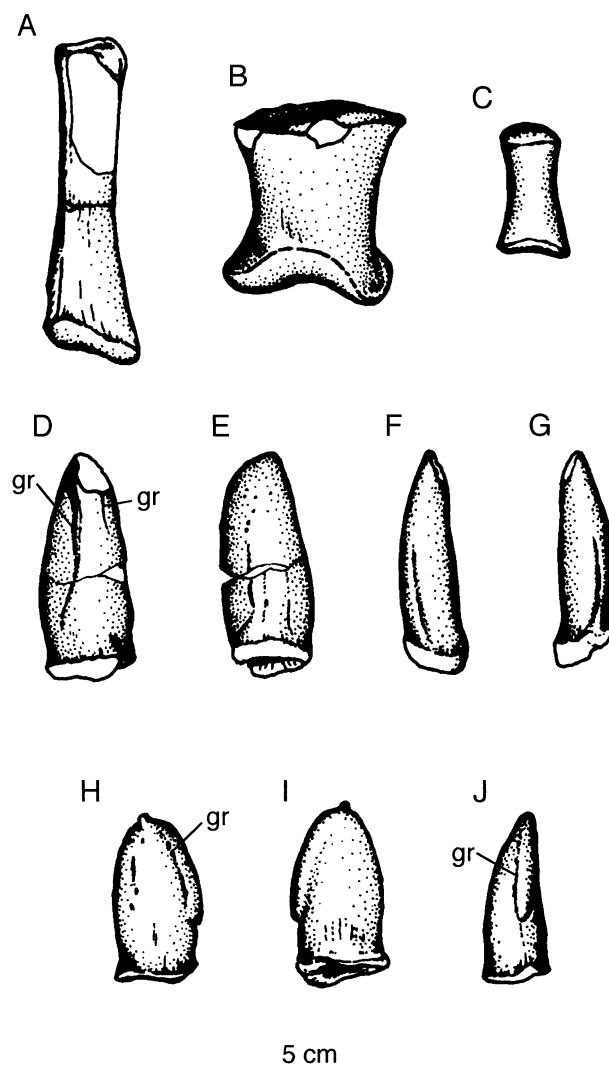


Figure 25. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. A, PIN 2232/18-8. Proximal phalanx, manus II (right). B, PIN 2232/11-2. Proximal phalanx, manus III (right). C, PIN 2232/10-69. Small distal phalanx, manus V. D-G, PIN 2232/11-4. Pollex unguis. H-J, PIN 2232/11-5. Ungual phalanx, manus II. Abbreviations: gr = unguis claw groove.

replicas are of this general form and may well represent digit V elements.

Ungual phalanges are preserved in two instances. PIN 2232/11-4 (Fig. 25D-G) represents a small, but typical, pollex unguis. The phalanx has a deep concave articular facet (which may have housed a remnant of the disc-shaped proximal phalanx identified in *I. bernissartensis*; Norman, 1980). The main body of the phalanx has the form of a dorsoventrally compressed cone. There is a well-preserved claw groove (gr) visible on the mediadorsal surface, and the much

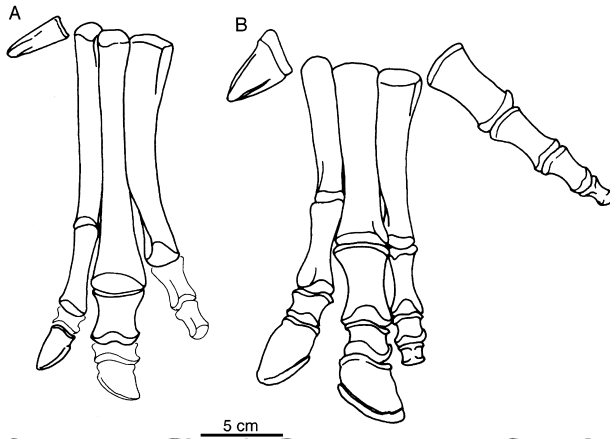


Figure 26. Restoration of the manus of (A) *Probaectrosaurus gobiensis* compared to the manus of (B) *Iguanodon atherfieldensis* (BMNH R.5764). No attempt has been made to restore digit V of the manus. Note, in particular, the more slender proportions of the metacarpals of *P. gobiensis* and the proportionally smaller pollex unguis.

reduced remnant of a similar groove near the apex mediolaterally. The tapering sides of the pollex are puckered and rugose in places, reflecting the attachment of the keratinous spine. The distal end of the claw is fractured.

Another, probably associated unguis (PIN 2232/11-5; Fig. 25H–J) has the tapering and asymmetric form of a typical unguis phalanx of digit II of the manus (see Norman, 1986, 1998; Fig. 26B). The specimen is dorsoventrally compressed and has a shallow and obliquely concave articular surface. The dorsal surface of the unguis is marked by a well-developed lateral shelf, which supports the adjacent claw groove (a feature not seen along the medial edge). All these features appear to suggest that this digit formed an arrangement that would have allowed the manus digits II–IV to be hyperextended for use in weight support while feeding on low browse, or occasionally when moving slowly in quadrupedal mode (Norman, 1980). The shorter and more blunt version of unguis phalanx typical of digit III was not seen in the collections.

Pelvic girdle. The *ilium* (Fig. 27) is well-preserved in several examples. The anterior (dorsal) process (PIN 2232/19-1; Fig. 27A, C) is long, laterally compressed and twists along its length so that the distal portion faces dorsolaterally rather than laterally; the process tapers slightly and ends in a rounded tip, the entire process is very little decurved along its length. The medial surface of the anterior process develops a medial shelf toward the main body which provides an area for abutment of the dorsal part of the sacral ribs (srs); facets are developed for sacral rib attachment on

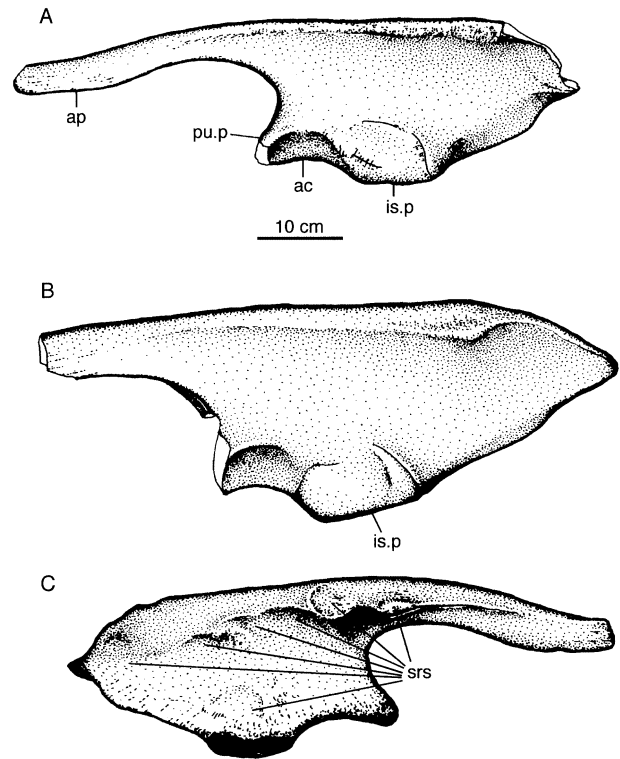


Figure 27. *Probaectrosaurus*. Ilium. A & C, PIN 2232/19-1. Left ilium lacking only a small part of the acetabular margin and posterior blade. B, PIN 12017. Left ilium, labelled '*P. alashanicus*', rather less complete, missing the distal end of the anterior process and the pubic peduncle. Abbreviations: ac = acetabulum; ap = anterior process; is.p = ischial peduncle; pu.p = pubic peduncle; srs = sutural contact areas for the sacral ribs/sacricostal yoke.

the medial surface of the ilium (Fig. 27C). The dorsal edge is horizontal and slightly thickened forming a typically everted lip in the region of the blade immediately above the ischial peduncle. The posterior part appears to taper to form a triangular outline. The lateral face is slightly concave and the ventral edge is embayed where it forms the acetabulum. The pubic peduncle (pu.p) is robust, triangular in cross-section and diverges from the anterior process and between them there is a broad embayment. The acetabular margin is shallow, and not marked by a strong supra-acetabular crest – this structure appears to be formed almost entirely by the margin of the pubic peduncle in ornithopods. The ischial peduncle (is.p) is a very large boss-like structure; its lateral surface is faceted and has the appearance of an approximate topographic equivalent of the avian antitrochanter (which in birds forms an articular pad for the dorsal part of the greater femoral trochanter).

The *pubis* (Fig. 28) is incompletely preserved in all examples examined. The best example appears to be a

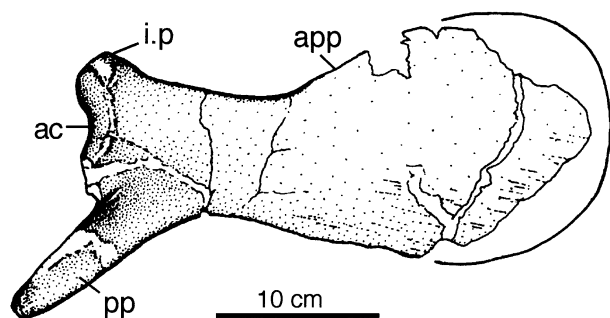


Figure 28. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/23-56. Pubis, right, incompletely preserved. Abbreviations: ac = acetabulum; app = anterior pubic process; i.p = iliac peduncle; posterior pubic ramus.

right pubis (PIN 2232/23-56). The anterior pubic process (app) has the form of a deep, laterally compressed blade; its distal end is expanded dorsally and ventrally. The acetabular region displays a prominent iliac peduncle (i.p), which is attached to the pubic peduncle of the ilium via a large, intervening pad of cartilage. The acetabular margin is well defined dorsally, but rapidly dwindles ventrally; the posterior margin is broken away, but would have formed a backwardly directed lip that contacted the ischium. The posterior pubic ramus (pp) is moderately robust, and though incomplete would have formed a modest tapering process lying parallel the ischial shaft.

The *ischium* (Fig. 29) is a robust, J-shaped bone (PIN 2232/29-2). The iliac peduncle (I.p) is a broad, flat-faced pad with a lip-like everted margin. Anterior to this there is a deep embayment for the acetabulum and beyond this a narrow, angular pubic peduncle (p.p), indicating a simple butt-joint with the acetabular margin of the pubis, and beneath this a flat-edged contact with the base of the posterior pubic process. A large, triangular obturator process (obt) is present on the medial side of the proximal portion of the ischial shaft. Beyond the obturator process the shaft tapers to an essentially rounded cross-section (although the base of the obturator process extends as a curved ridge that merges with the posteromedial edge of the shaft). The distal shaft curves gently anteriorly before expanding to form a large ischial 'boot' that is laterally compressed and projects anteriorly.

Hindlimb. The *femur* (Figs 30, 31) is typical of any reasonably large non-hadrosaurid iguanodontian. The proximal end bears a medially off-set articular head which is convex dorsally and supported beneath by flat sides. Lateral to the condylar surface the proximal surface is uniformly covered by a cartilaginous cap and this area of bone forms a distinct saddle-shaped

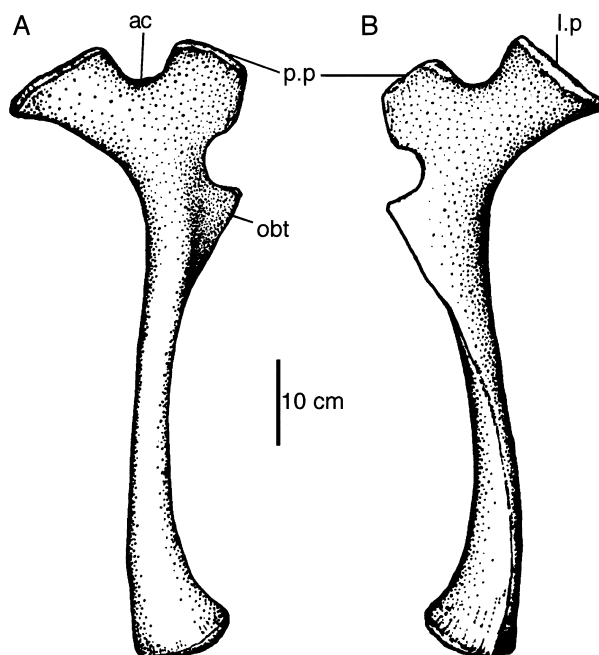


Figure 29. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/29-2. Ischium, right in lateral (A) and medial (B) view. Abbreviations: ac = acetabulum; I.p = iliac peduncle of the ischium; obt = obturator process; p.p = pubic peduncle of the ischium.

region (Fig. 31A) that expands laterally to form the greater trochanter (g.tr). With the femoral head this entire region forms a trochlear surface. The greater trochanter is expanded anteroposteriorly and forms a raised lateral edge. A separate, flattened and rather blade-like anterior trochanter (a.tr) is present beyond the anterolateral corner of the greater trochanter and separated from it by a narrow cleft. The base of the anterior trochanter is a prominent eminence that develops as a broad ridge from the anterolateral edge of the femoral shaft. The shaft of the femur is angular in cross-section. The ridge that supports the anterior trochanter marks the edge of a longitudinal shallow trough that extends from the centre of the 'saddle' on the proximal surface downwards and progressively medially as it approaches the distal articular condyles. This feature accentuates the axial twisting that is a notable feature of dinosaurian femora. The middle of the shaft bears a prominent, blade-like fourth trochanter that projects from the posteromedial edge. An isolated femur (PIN 2232/18-9; Fig. 31) is very large (750 mm long) and well-preserved and reveals that the femur has a deep tip to the fourth trochanter, a condition that very strongly resembles that seen occasionally in well-preserved examples associated with the genera such as *Camptosaurus* (Gilmore, 1909), *Iguanodon* (Norman, 1986) and *Ouranosaurus*

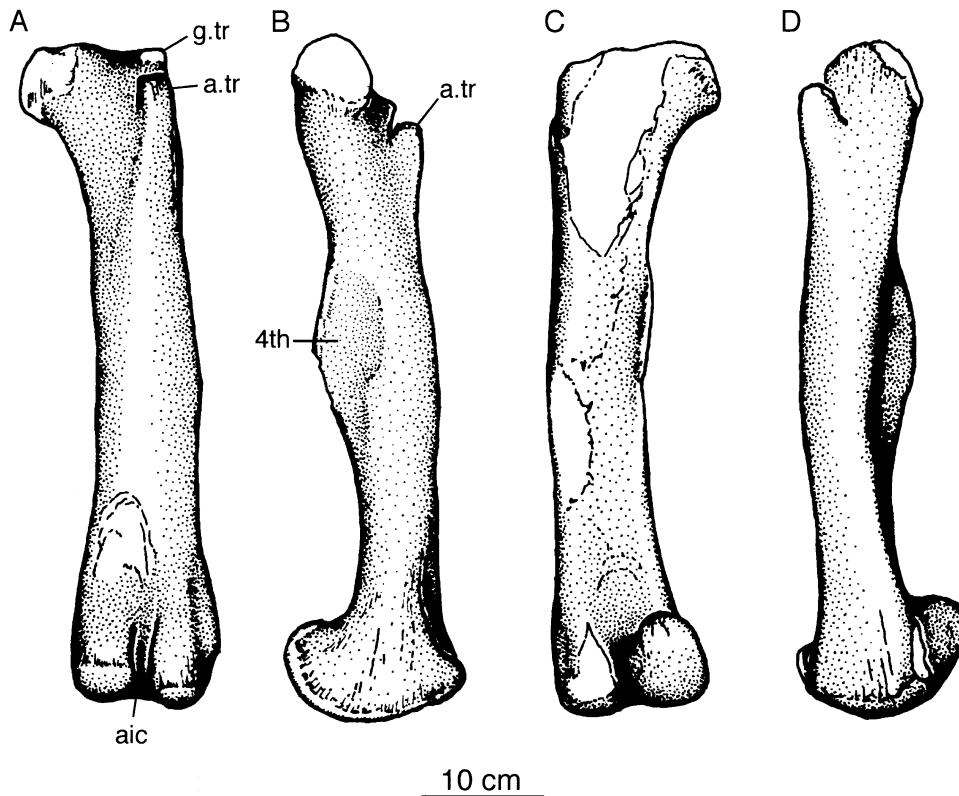


Figure 30. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/39-1. Femur, left, in dorsal (A), medial (B), ventral (C) and lateral (D) views. Abbreviations: 4th = fourth trochanter; aic = anterior intercondylar groove; a.tr = anterior trochanter; g.tr = greater trochanter.

(Taquet, 1976). The distal portion of the femoral shaft is bowed both laterally and anteriorly, and the distal condyles are prominent and expanded. Anteriorly the intercondylar groove (aic) is a well-developed open trough that is partially enclosed by lips formed from the expansion of the lateral and medial condyles. Both condyles are expanded and strongly convex anteroposteriorly. The medial condyles is larger and more robust, with a very bulbous posterior extension; the lateral condyle has a narrower, more blade-like posterior extension (broken off in Fig. 30C, D), and these two features flank a broader, open posterior intercondylar trough.

The *tibia* (Fig. 32) has a very conventional form. The shaft is expanded at both ends. Proximally there is a very prominent almost wing-like cnemial crest (cc) that projects laterally to enclose an embayment for the head of the fibula. The cnemial crest accentuates the axial twisting seen in the tibia. Directly behind the cnemial crest there are two posteriorly projecting condylar lips separated by a narrow median cleft. Distally the tibia is expanded transversely and its distal end is prominently stepped. The broader medial por-

tion has a raised step for the attachment of the astragalus (ast), and there is a large facet for the attachment of the ascending portion of the astragalus (as.s). Laterally there is a narrow, distally off-set prominence that bears an anterolaterally scarred surface for the attachment of the distal end of the fibula (fib.s). The distal, 'articular' surface represents the attachment area for the body of the calcaneum and lateral portion of the astragalus. In contrast to the femur the tibial shaft is bowed posteriorly along its length.

The *fibula* (Fig. 32B) is expanded proximally and lies against the recess on the lateral surface of the upper end of the tibia. Distally the fibula is a narrow shaft that expands into a small, boot-like structure that fits on a ligament scarred facet on the anterolateral edge of the distal end of the tibia. The boot-like structure fits against a recess on the anterior half of the calcaneum.

The *tarsals* are very poorly represented among the collections. PIN 2232/10 exhibits a partial attached right astragalus (Fig. 32B, ast). Distal tarsals are unknown.

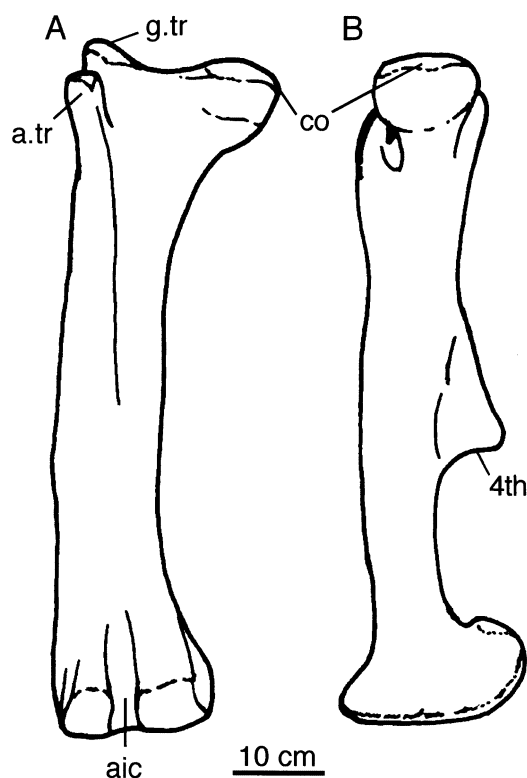


Figure 31. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/18-9. Femur, well-preserved (right) outline drawing to show salient anatomical features. Abbreviations: as for Figure 30; co = condylar head of the femur.

Three metatarsals (II–IV) are known in *Probactrosaurus*. There are no indications of a rudimentary metatarsal I, but the collection techniques may not have guaranteed its recovery. An articulated right pes (Fig. 33) is mounted with PIN 2232/10 (bipedal skeleton) and is described here. The three metatarsals are closely appressed and moderately elongate. Metatarsal II is the narrowest of the three and has a noticeably laterally compressed proximal articular surface. The shaft of metatarsal II is attached obliquely to the posteromedial side of the shaft of metatarsal III and this arrangement creates the divergence of digit II from III. Metatarsal III is dominant by virtue of its size and length; it has a large triangular proximal surface that is slightly convex and contributes to the simple uniaxial ankle hinge. Distally the shaft is triangular in section and expanded distally where it forms a large mildly trochlear articular facet for the base of digit III. Metatarsal IV has a D-shaped outline in proximal view with the ‘flat’ surface (in fact slightly indented) attached to the lateral surface of metatarsal III. The shaft of the metatarsal is more robust than that of metatarsal II, and the distal portion of its shaft

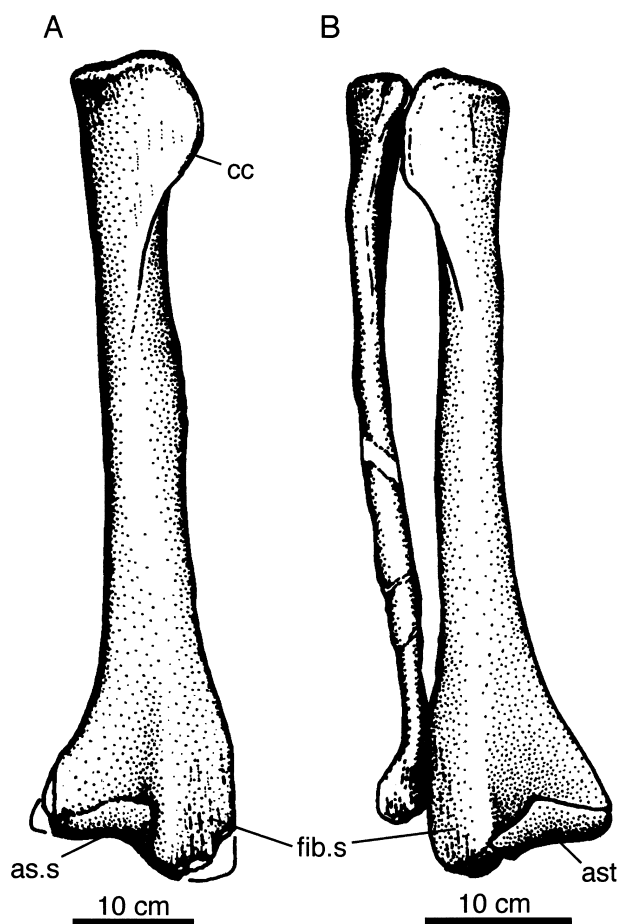


Figure 32. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. A, PIN 2232/32-1. Tibia in anterior (dorsal) view. B, PIN 2232/10 (mounted skeleton) showing the articulated tibia, fibula and astragalus in anterior view. Abbreviations: as.s = sutural surface for the astragalus; ast = astragalus; cc = cnemial crest; fib.s = sutural surface for attachment of the fibula.

diverges from metatarsal III, rather than being closely appressed along its length as is the case with metatarsal II. This general configuration is common to the majority of ornithopod feet.

The digits of the pes have a perfectly conventional form. The formula is 3 : 4 : 5. The proximal phalanges are large, more block-like elements, with succeeding phalanges being smaller in all dimensions, but more noticeably axially shortened, apart from the unguis. These latter appear to be elongate, blunt-ended and somewhat distinctive in shape with less obvious claw grooves and yet not having the shortened and distinctly more genuinely hoof-shaped unguis seen in the majority of hadrosaurids. The unguis of digit II is twisted medially and the mirror image of that of digit IV. Digit III is roughly symmetrical.

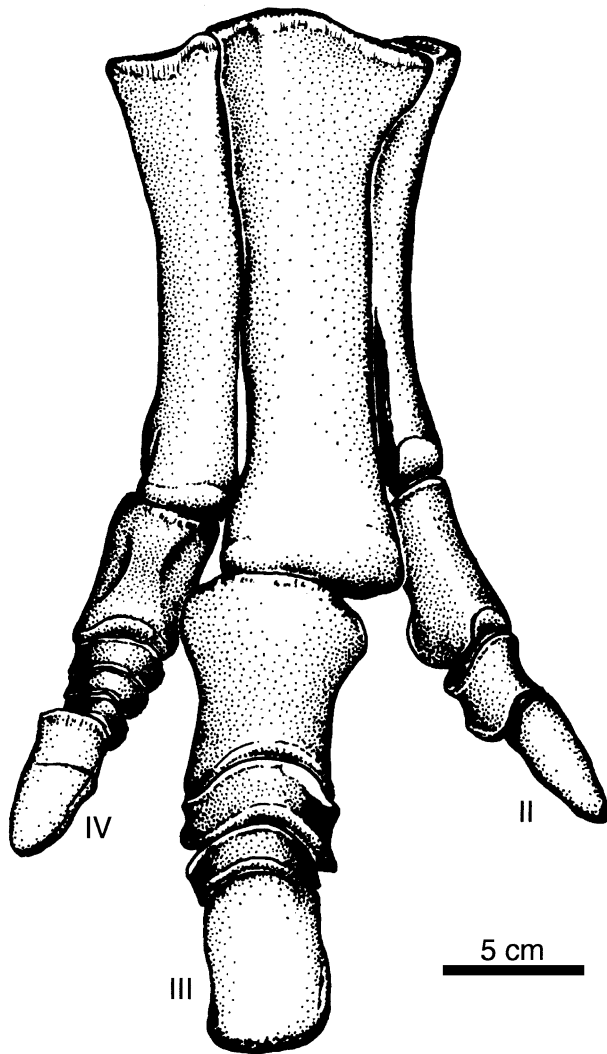


Figure 33. *Probactrosaurus gobiensis* Rozhdestvensky, 1966. PIN 2232/10. Pes, right, in articulation, based on the skeletal mount.

DISCUSSION

GENERAL AND COMPARATIVE COMMENTS

The anatomy of *Probactrosaurus* has been of considerable interest since it was first described by Rozhdestvensky (1966) as an ornithopod that was intermediate, both temporally and in its anatomy, between the then known typically Jurassic/Lower Cretaceous *Iguanodon*-like ornithopods and the more derived Upper Cretaceous hadrosaurids.

Anatomically the skull of *Probactrosaurus* (Fig. 3) is not modified by a cranial crest and appears to conform in most respects to that seen in typical basal iguanodontians. The premaxillary margin of the beak is not markedly expanded laterally but, as is the case in a number of more derived iguanodontians, shows a

marked ventral deflection; the prementary also has as a consequence a low and extremely oblique setting on the tip of the dentary. The circumorbital region is not well known, and the presence or absence of a palpebral cannot be established. The temporal region shows large ovoid fenestrae, and the jugal has a slender, almost strap-like, shape. The jugal also retains sutural contact with the ectopterygoid. The lower jaw is robust and marked by a large, vertical and laterally offset coronoid process; the surangular possesses a foramen adjacent to the jaw joint, and the angular suture suggests that the angular had a lateral exposure. The dentition is of considerable interest, although the maxillary teeth are as yet poorly known. The dentary teeth are, in comparison with those of *Altirhinus kurzanovi* (Fig. 16), undergoing a transformation in crown shape: becoming smaller, more lanceolate, more nearly symmetrical. The dentition is also more hadrosaurid like (Figs 11–16), with the crowns being closely packed, the roots showing well-defined vertical facets for adjacent replacement teeth, and the occlusal surface becoming high and tilted backward as well as broader (buccolingually) by the addition of another tooth crown; the alveoli also form parallel-sided slots, rather than being moulded into the ‘ghosts’ of tooth crowns. However, unlike hadrosaurids more generally, the edges of the crowns bear mammillate denticles (Fig. 16C).

Postcranially the skeleton exhibits fewer derived features (although significant sections of the axial skeleton remain to be described). The shoulder girdle and humerus are very similar to those described in non-hadrosaurid iguanodontians, while more distally the forelimb is notable for the elongation of the forearm, retention of a small, conical, pollex unguis, and the marked slenderness of metacarpals II–IV (Fig. 26). The sacrum appears to comprise only six sacrales nearly all of which are ventrally keeled. The pelvis and hindlimb are generally typical of large mediportal ornithopods, although the femur appears to lack the specializations seen in hadrosaurids.

TAXONOMY OF *PROBACTROSAURUS*

Rozhdestvensky (1966) established two species of the genus *Probactrosaurus*: *P. gobiensis* and *P. alashanicus*. It is unfortunate that the fate of much of the material referred to *P. alashanicus*, including the holotype (PIN 2232/46) is unclear at present. It has been reported (S. Kurzanov, pers. comm.) that some of this material was shipped to China in the decades following the initial discovery and description. At present the latter’s whereabouts are not known with certainty by the author. In the light of this few comments can be made except to say that the validity of the separation of these two species must be considered to be an open question.

Rozhdestvensky listed a number of characteristics (anatomical and geological) by which these two species could be diagnosed, and separated osteologically. These are listed below. In addition he noted that several specimens exhibited an intermediate set of characters

Probactrosaurus gobiensis

Skull slightly wider across the orbits than across the occiput. Fronto-parietal crest. Occiput low. Supratemporal fenestra elongate ellipsoid. Broad and straight intertemporal arch. Long narrow dentary. Diphyodont dentition (generally?). Posterior auxiliary ridge does not rise above half crown height. Height : width ratio of crowns 2.1–2.3. Proximal end of scapula moderately dilated (2.5 times the width of central shaft). Postacetabular blade of ilium not massive. Prepubic blade dilated 2 times minimum width of blade. Iliac head of ischium triangular. Fourth trochanter on proximal half of femoral shaft. Inner condyle wider than outer condyle. Proximal end of tibia slightly dilated. Deep incision between anterior condyles. Metatarsals moderately dilated.

Probactrosaurus alashanicus

Skull not broader across orbits than occiput (but admitted that this might originate from distortion). Fronto-parietal crest. Occiput slightly higher. Supratemporal fenestra ellipsoid but not elongate. Intertemporal arch narrow and curved. Posterior supplementary ridge reaches margin of crown. Height : width ratio of crowns 2.3. Rudimentary 3rd tooth in jaw. Proximal scapula dilated 3 times central shaft. Ilium dorsal edge dilated. Massive postacetabular blade. Stronger dilation of the prepubic blade. Iliac process of ischium trapezoidal. Medial shift of 4th trochanter. Inner condyle not as broad as in *P. gobiensis*. Incision between condyles not so deep. Metatarsal proportions differ.

Evaluation

Differences in the structure of the skull table (overall width, height, shape of supratemporal fenestrae, presence or absence of a sagittal crest) all appear to be subject (as admitted by Rozhdestvensky) to distortion and are subjective. No significant differences in dental morphology could be detected in the specimens observed in the PIN. The scapular dimensions vary depending upon the preservational condition of the element – typical ‘gobiensis’ scapulae (Fig. 20A) have broken acromion processes, whereas typical ‘alashanicus’ scapulae (Fig. 20B) are more complete. The ilia attributed to both species are very similar in general proportions (Fig. 27A, B) and the hindlimb elements are indistinguishable.

The significance of the stratigraphic separation (*P. gobiensis* form a Lower (first) bone horizon, *P. alashanicus* from a Middle (second) bone horizon) is difficult to assess; this is made more so by Rozhdestvensky’s description of an intermediate horizon that is reported to have contained bones of an ‘intermediate’ status.

Valid species: *Probactrosaurus gobiensis*
Rozhdestvensky, 1966.

Junior subjective synonym: *P. alashanicus*
Rozhdestvensky, 1966

Probactrosaurus mazongshanensis Lu, 1997

This species was described on the basis of fragmentary skull and some postcranial material. On the basis of the structure of the teeth and femur it is clear that this belongs to a nonhadrosaurid iguanodontian. The dentary crowns, which were illustrated in detail are not closely similar to those of *P. gobiensis* and bear a closer resemblance to those pertaining to the genus *Altirhinus*.

Evaluation

While clearly a nonhadrosaurid iguanodontian, the material attributed to this species is not referable to the genus *Probactrosaurus*.

PHYLOGENETIC RELATIONSHIPS OF DERIVED
ORNITHOPODS AND THE POSITION OF
PROBACTROSAURUS

Systematic analyses undertaken since the mid-1980s that have attempted to include *Probactrosaurus* have been hampered by lack of reliable and detailed anatomical information (Serenó, 1986, 1997, 1999; Norman, 1990, 1998; Head, 1998, 2001; Kirkland, 1998). More recently expeditions have brought to light new taxa that will open further questions relating to the systematic position of *Probactrosaurus* and its immediate relatives (Lu, 1997; Xu *et al.*, 2000; Tang *et al.*, 2001; H-L. You, personal communication, 2001).

Serenó was the first to provide a cladistically based position for *Probactrosaurus*. ‘Contrary to previous suggestions of close affinity with the hadrosaurs (Rozhdestvensky, 1966), *Probactrosaurus* appears to be more distantly related to hadrosaurs than either *Iguanodon* or *Ouranosaurus*. However, additional articulated skeletal remains of *Probactrosaurus* are necessary to establish its phylogenetic position with greater confidence’ (Serenó, 1986; 249). Since then, Norman (1990, 1998), Head (1998, 2001), Kirkland (1998) and Norman & Weishampel (in press) have advocated positions closer to that of Rozhdestvensky.

In the light of the redescription provided above, a systematic analysis of *Probactrosaurus* and related ornithopods was undertaken. Eighteen taxa were selected for preliminary analysis and scored against 67 anatomical characters (Appendix 1), character-states are listed in (Appendix 2). These data were prepared using MacClade 4 (Maddison & Maddison, 2000) and analysed using PAUP* 4.0b10 (Swofford, 1998). In this analysis the outgroups are *Dryosaurus* and *Camptosaurus*, all characters were run 'unordered', there was no weighting of characters and the data were analysed using the Branch-and-Bound option within PAUP to retrieve the most parsimonious trees. Following the initial analytic trial the data were further analysed by: (i) selectively removing and restoring taxa that appeared to be responsible for node collapse in the strict-consensus trees; and (ii) using the reweighting option in PAUP* to assess the overall character performance with respect to tree topology.

Results

The full data set produced six equally parsimonious trees (length 116 steps [max 350, min 86] CI 0.74, RI 0.89, RC 0.66). The generalised topology of these trees is represented by the strict consensus of all six trees (Fig. 34A) and is dominantly serially pectinate. Ambiguity surrounds the positions of *Lurdusaurus arenatus* Taquet & Russell, 1999 and the 'Mazongshan ornithopod' (You Hailu pers. comm. 2001), as well as *Eolambia caroljonesa* Kirkland, 1998 and *Altirhinus kurzanovi* Norman 1998).

The data were then reanalysed after the characters had been reweighted by maximum value of rescaled consistency indices. This analysis produced three equally most parsimonious trees, the strict consensus of which is presented as Fig. 34B. (Statistics: tree length 76.64 steps, CI 0.89, RI 0.96, RC 0.86) representing a core set of relationships between the taxa and resolving *Altirhinus* and *Eolambia*. It can be noted at this point that *Probactrosaurus* maintains a consistent position as the basal sister-taxon to the Hadrosauridae: (*Telmatosaurus* (*Bactrosaurus* (*Lambeosaurinae* (*Hadrosaurinae*)))).

A further analysis of the data was carried out. Character reweighting was returned to parity and the poorly known taxon from Mazongshan was deleted. This reanalysis produced two equally most parsimonious trees, which differed only in the implied relationship between *Eolambia* and *Altirhinus* (as serially derived or as sister-taxa). Statistics: tree length 114 steps [max 341, min 86], CI 0.75, RI 0.89, RC 0.67. Repeating the character reweighting option generated a single most-parsimonious tree (Fig. 35). Statistics: tree length 76.8 [max 272.9, min 69.9], CI 0.91, RI 0.97, RC 0.88.

Phylogenetic inferences

The overall topology of the trees derived from this analysis provide the basis for the following brief conclusions (see also Norman & Weishampel, in press).

1. *Dryosaurus* (Galton, 1981, 1983; Janensch, 1955) and *Camptosaurus* (Gilmore, 1909), temporally and anatomically, represent the least derived of the ornithopods considered in this analysis.
2. *Iguanodontidae*, advocated by Norman (1984, 1986, 1990, 1998) is not supported by the data in this set of analyses. This confirms the conclusion of Sereno (1986) and Head (1998, 2001).
3. *Iguanodontoidea*. Serially more derived than *Camptosaurus* is a major clade that should be recognised as *Iguanodontoidea* (incorrectly termed 'Iguanodontia' in Norman, 1998 and renamed as 'Hadrosauriformes' by Sereno, 1997, 1998, 1999). This clade can be defined as *Iguanodon* and all iguanodontians more closely related to *Edmontosaurus* than to *Camptosaurus*. These are recognised by the acquisition of some of the following characters: a strongly offset premaxilla relative to the maxilla border, a well-developed 'diastema', a complex peg-in-socket articulation between jugal and maxilla, an elevated finger-like coronoid process, mammillate marginal denticles, reduction in mesiodistal width of the maxillary crowns relative to the dentary crowns, lengthening and bunching of metacarpals II-IV and the development of flattened hoof-shaped ungual phalanges II & III of the manus, deepening of the prepubic blade, shortening of the postpubic blade, partial enclosure of the anterior intercondylar groove of the femur, triangular (rather than pendant) fourth trochanter, and blunt pedal ungual phalanges.
4. *Stem lineage taxa* (*Iguanodon*, *Ouranosaurus*, *Altirhinus*, *Eolambia*, *Protohadros*) appear to acquire the following characters at least partly in piecemeal fashion: loss of the lateral opening of the antorbital fenestra (linked to the broadening of the dorsal maxillary process), lateral displacement of the coronoid process and development of a medial shelf between the coronoid and the dentition, restriction of dental enamel to one side of the crown, increase in the number of replacement crowns in the dentary, deeper and greater expansion of the prepubic blade. This result (Figs 34, 35) refutes the clade named *Hadrosaurioidea* based on the topology created by the analysis of Sereno (1986) comprising *Ouranosaurus* as the basal sister-taxon to the Hadrosauridae. This result supports the views of Norman (1986, 1990, 1998), Head (1998, 2001) and Kirkland (1998).
5. *Probactrosaurus* + *Hadrosauridae*. This node is currently marked by closer packing and cementing

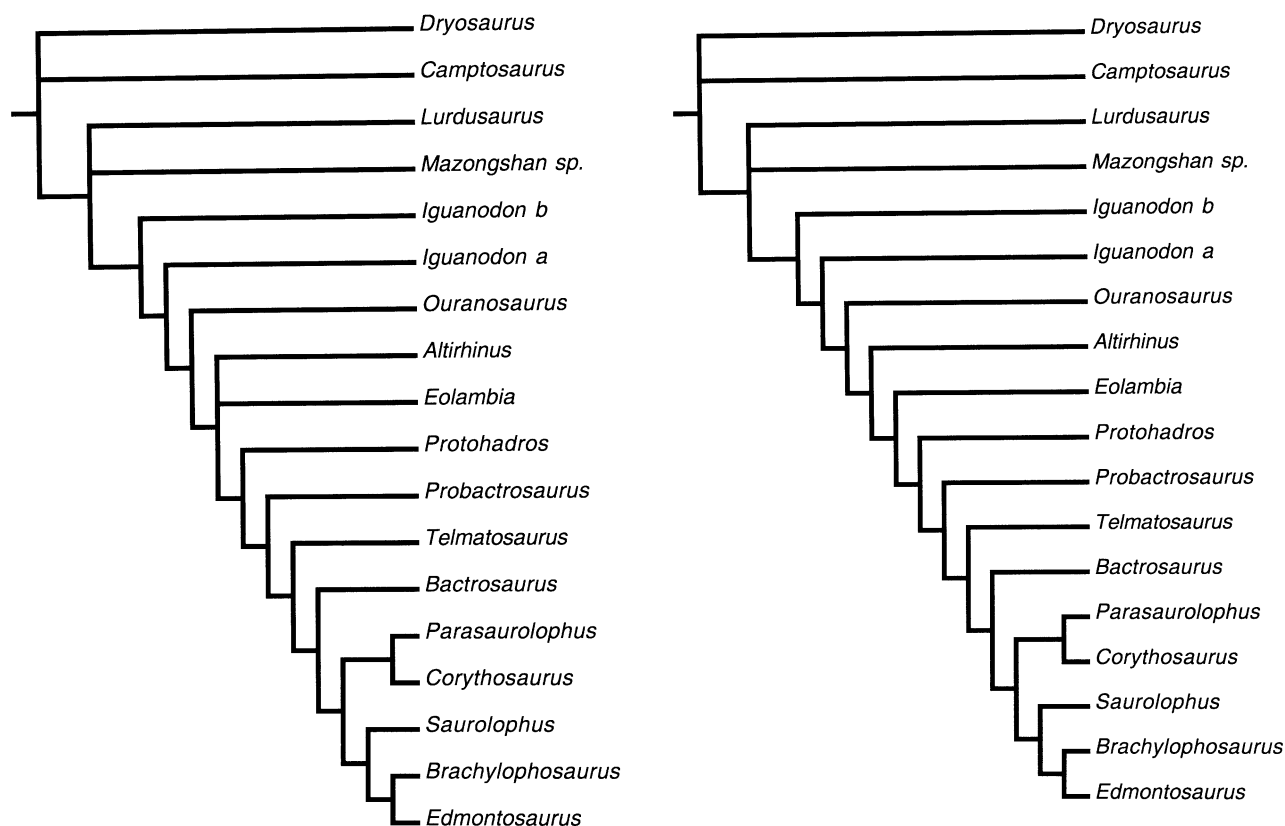


Figure 34. A. Strict consensus tree based on six equally most parsimonious trees produced by running the data matrix in Appendix 1. Tree length 116 steps. Consistency index: 0.741. Retention index: 0.886. Rescaled consistency index 0.657. B. Strict consensus tree generated from three equally most parsimonious trees after the data has been analysed following character reweighting by using the maximum values of the rescaled consistency indices. CI: 0.982. RI: 0.959. RC: 0.856.

of the roots of the teeth in the lower jaw, development of parallel alveolar slots, a broadening of the occlusal surface of the dentary magazine, the development of longer and more slender foearn bones, and longer and slender metacarpals and an anterior expansion of the distal femoral condyles. Recent discoveries of *Jinzhousaurus yangi* Wang & Xu, 2001 and *Nanyangosaurus zhugeii* Xu *et al.*, 2000 indicate a close, so far unresolved relationship among *Probactrosaurus* and Hadrosauridae (Norman & Weishampel, in press). Any attempt to re-define the Hadrosauoidea in relation to these taxa would be premature at present and risks further confusion following the generation of a considerable number of clade names in recent years.

6. *Hadrosauridae* (*sensu* Weishampel *et al.*, 1993) includes *Telmatosaurus* (Weishampel *et al.*, 1993) and all more derived (euhadrosaurian) ornithopods. This clade is recognised by deepening of the jugal anterior process and the loss of the jugal-ectopterygoid suture, closure of the auadrate (paraquadratic)

foramen, expansion of the dorsal edge of the coronoid process, loss of the surangular foramen, migration of the angular to the medial side of the lower jaw, lateral deflection of the 'acromion' process of the scapula, closure of the anterior intercondylar groove of the femur.

7. *Bactrosaurus*. Occupies a position outside the Euhadrosauria consistent with the observations of Head (2001).
8. *Euhadrosauria* (*sensu* Weishampel *et al.*, 1993) includes the lambeosaurines and hadrosaurines (Weishampel & Horner, 1990) and is a very strongly supported clade.

SUMMARY AND CONCLUSIONS

Probactrosaurus is an ornithopod dinosaur known from several partial skeletons collected from the (probable) early Late Cretaceous (Barremian-Albian) of Maortu, Neimongol, China. When first described

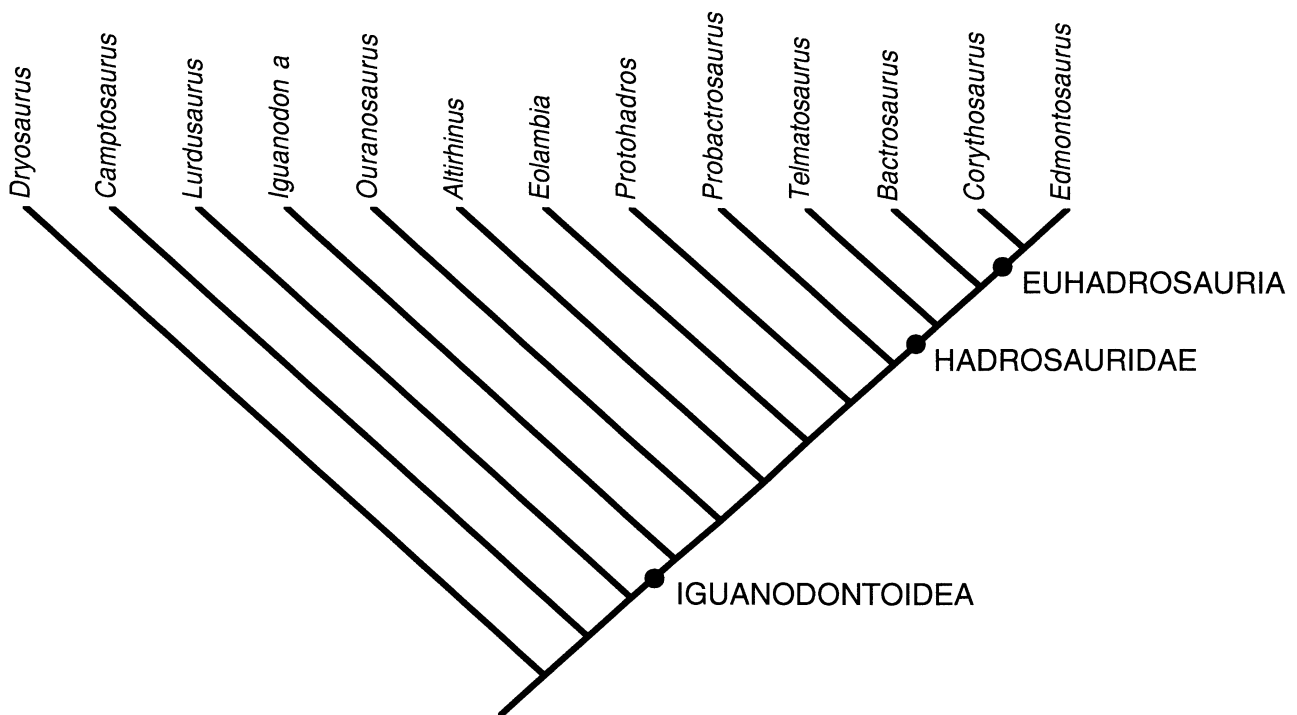


Figure 35. Summary tree following removal of ‘Mazongshan sp’ and three hadrosaurid species (*Parasaurolophus*, *Brachylophosaurus* and *Saurolophus*). This generated two equally most parsimonious trees. The data were then rerun again using the reweighting option, which generate the topology shown here. See the Results and Phylogenetic Inferences sections.

(Rozhdestvensky, 1966) this genus was proposed as an anatomical and evolutionary intermediate between the Early Cretaceous Eurasian genus *Iguanodon* and the Late Cretaceous Asiamerican hadrosaurids. Subsequent systematic analysis (Sereno, 1986) challenged this original view and generated in turn further dissenting opinions (Norman, 1990, 1998; Head, 1998, 2001; Kirkland, 1998).

All of the material attributed to *Probactrosaurus*, and identifiable within the collections of the PIN, Moscow, has been re-studied. On the basis of the material examined there is no clear support for two species of the genus *Probactrosaurus*. As a consequence *P. alashanicus* is relegated to junior subjective synonymy within the species. *P. gobiensis* Rozhdestvensky, 1966. Material assigned to the new species *P. mazongshanensis* is not referable to the genus *Probactrosaurus*.

Probactrosaurus gobiensis is a derived iguanodontian ornithopod. It possesses a crestless skull, notable for the ventral deflection of the premaxillary beak margin and the development of smaller, more symmetrical dentary teeth, and of a dental battery that is strongly reminiscent of that seen in more derived hadrosaurid ornithopods. The postcranial skeleton is very

similar to that seen in gracile iguanodontians such as *Iguanodon atherfieldensis* (Norman, 1986) and the manus retains a small, conical pollex. Additionally the forearm and metacarpals of the manus are gracile and elongate as seen commonly among more derived hadrosaurids.

When subjected to systematic analysis *Probactrosaurus* appears consistently as the basal sister-taxon to the clade Hadrosauridae, belatedly confirming the views originally promulgated by A.K. Rozhdestvensky. *Ouranosaurus* appears consistently as a basal iguanodontian, whereas three newly described taxa (*Eolambia*, *Protohadros* and *Altirhinus*) occupy a position distal to *Probactrosaurus*, further resolution of their relationships is hampered in part by the incomplete nature of their remains. Several new, partial remains of closely related iguanodontians have been recovered and described in recent years, ranging from potentially more basal forms such as *Lurdusaurus* and the new specimen from Mazongshan, as well as apparently derived forms such as *Jinzhousaurus* and *Nanyangosaurus*, all of which will add considerably to our understanding of the evolution of iguanodontians and their bearing on the evolution of the hadrosaurs.

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APPENDIX 1

TAXON CHARACTER-STATE MATRIX

	1	1111111112	2222222223	3333333334	4444444445	5555555556	66666666
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567
<i>Dryosaurus</i>	000000000	010000?000	0000000000	0000000000	0000000000	0000000000	0000010
<i>Camptosaurus</i>	000000000	000000?001	0000000000	0000000000	1000000010	0100000000	0000000
<i>Iguanodon a</i>	0100000000	0100110000	0100100000	1001010000	1000100011	0110000110	0011011
<i>Iguanodon b</i>	0100000000	0100110000	0001000000	1001010000	1000100011	0111000110	0011011
<i>Ouranosaurus</i>	0110000000	0001110000	0101000000	1001010000	20?0100011	0110000210	00110?1
<i>Lurdusaurus</i>	???????00?	?????????0	0?????00??	???????????	??00100010	0110000110	00000??
<i>Protohadros</i>	?100000001	1??1?10?01	0111110001	111101?011	???????????	???????????	?????????
<i>Altirhinus</i>	0100000001	1000100000	0111110001	1101010001	??001000?1	0111000111	?01???1
<i>Eolambia</i>	010?00000?	???1110?0?	?101110?01	110101?0?1	100??1?01?	0111000??0	0??10??
<i>Mazongshan sp.</i>	0100000000	?1?0?0?0?0	00001?000?	1100010001	???????????	???????????	?????????
<i>Probactrosaurus</i>	010000?00?	?????10000?	0000110001	12110?0011	1000101012	0110000210	00111?1
<i>Telmatosaurus</i>	0100000001	?1?1?0?001	0000211011	12110100?1	??10?0????	???????????	?0121??
<i>Bactrosaurus</i>	010000000?	0?0111100?	0000211101	1211010011	1021100??1	??0000021?	01221?2
<i>Edmontosaurus</i>	1110000001	1011211001	1100211111	2211121012	1121111122	1211111211	1122122
<i>Brachylophosaurus</i>	1100000001	1011211101	1100211111	2211121012	1121111122	1211111211	1122122
<i>Saurolophus</i>	1101001001	1111211101	1100211111	2211121?12	1121111122	1211111211	0122122
<i>Parasaurolophus</i>	0101012101	1112211211	1111211111	2211121112	2121111122	1211111210	0122122
<i>Corythosaurus</i>	0101112111	1112211211	1111211111	2211121112	2121111122	1211111210	0122122

APPENDIX 2

CHARACTER-STATE LISTING

Using a variety of anatomical characters that feature drawn from character lists published in Sereno (1986), Weishampel *et al.* (1993), Head (1998) and others.

- Dorsal aspect of the premaxilla narrower than width across orbital region of skull roof (0), lateral expansion of premaxillae equals or exceeds width across orbital region of skull roof (1).
- Premaxillary margin. Slightly ventrally offset from occlusal plane of the dentition (0), very strongly ventrally deflected (1).
- Lateral margin of the premaxilla reflected dorsally: absent (0), present (1).
- Premaxilla overlaps prefrontal (0), extends posteriorly, beyond posterior margin of prefrontal (1).
- Frenestrae present in the posterior extensions of the premaxillae. Absent (0), present (1).
- Boundary of the external naris defined by the premaxilla and nasal (0), premaxilla only (1).
- Posterior narial depression. Absent (0), present (1), secondarily covered by premaxilla (2).
- Nasal cavity position. Anteromedial to orbits (0), diverticulae above orbits (1).
- Helmet-shaped hollow crest. Absent (0), present (1).
- Position of external antorbital fenestra. Between lacrimal and maxilla (0), on anterior dorsal margin of maxilla (1).
- Dorsal process of the maxilla. Narrow, finger-shaped process (0), expanded, laterally flattened plate-like structure (1).
- Lacrimal-nasal contact. Present (0), absent (1).
- Palpebral bone. Present (0), absent or fused to orbital margin (1).
- Anterior portion of the jugal. Tapering (0), expanded dorsoventrally (1), expanded and bluntly truncated (2).
- Jugal–Maxilla suture. Scarf joint (0), ‘finger-in-recess’ joint (1), butt-jointed (2).
- Ventral edge of the jugal. Smooth, shallow curve (0), strongly angular (1).
- Jugal-ectopterygoid articulation. Present (0), absent (1).
- Frontal shape. Flat rectangular (0), short, broad, covered by large scarf joint for nasals (1), large scarf joint includes premaxillae (2).
- Frontal in orbital margin: present (0), excluded (1).
- Quadrangle (paraquadrangle) foramen. Present (0), absent (1).
- Quadrangle articular condyle. Transversely broad (0), narrow and hemispherical (1).
- Gap or ‘diastema’ between prementary and 1st dentary tooth. Short (0), pronounced (1).
- Dentary ramus. Straight (0), anterior end strongly deflected ventrally (1).
- Dentary ramus. Parallel sided (0), deepens rostrally (1).

25. Coronoid process shape. Elevated, but oblique (0), long, finger-shaped, perpendicular (1), markedly anteroposteriorly expanded apex (2).
26. Coronoid process position. Laterally offset and dentition curves into its base (0), laterally offset and a horizontal shelf separates dentition from coronoid process (1).
27. Surangular foramen. Present (0), absent (1).
28. Angular position. Visible on lateral surface of the lower jaw (0), not visible laterally (1).
29. Dentary crown shape in lingual aspect. Broad, shield-like lingual surface with more than one vertical ridge (0), narrow, diamond-shaped, single median ridge (1).
30. Dentary enamel. Thin veneer labially, thick lingually (0), exclusively lingually (1).
31. Marginal denticles. Simple, tongue-shaped (0), curved, mammillated ledge (1), absent or reduced to small papillae (2).
32. Tooth root emplacement. Not cemented (0), partially cemented (1), rugose, angular-sided roots (2).
33. Alveolar trough grooves. Shaped by dentary crowns (0), narrow parallel-sided grooves (1).
34. Relative width of maxillary and dentary crowns. Maxillary crowns approximately equal in width with dentary crowns (0), narrower (1).
35. Dentary tooth size: broad and shield-like (0), small, narrow and lanceolate (1).
36. Mamillary crown shape. Shield-shaped (0), elongate lozenge (1), sub-diamond-shaped (2).
37. Ridge pattern on maxillary crowns. Very prominent primary ridge (0), reduced primary ridge (1).
38. Angulation of crown face relative to root on dentary teeth. Smooth (0), abrupt (1).
39. Occlusal surface of dentary tooth row. Single tooth depth (0), multiple tooth depth (1).
40. Replacement crowns in dentary. One (0), two (1), three or more (2).
41. Mid-dorsal neural spines. Short and rectangular height and length very similar (0), height more than twice length (1), height more than 4 times length (2).
42. Sacral count. Seven or fewer (0), eight or more (1).
43. Scapular blade. Straight (0), curved (1), curved and flared (2).
44. Scapular 'acromion'. Prominent on anterior margin of scapula (0), reflected laterally (1).
45. Sternal shape. Reniform (approximately kidney-shaped) (0), hatchet-shaped (1).
46. Humerus shape. Gently sigmoid with low, rounded deltopectoral crest (0), short, angular with prominent dpc (1).
47. Radius proportions. Less than 80% of the length of the humerus (0), greater than 80% of humeral length (1).
48. Carpal structure. Fully ossified (0), reduced (1).
49. Metacarpal 1 shape. Normal elongate bone (0), short, block-like set against carpals (1), absent (2).
50. Metacarpals II–IV arrangement. Dumbbell-shaped and spreading (0), closely appressed (1), elongate (2).
51. Manus digit 1. Present (0), absent (1).
52. Manus ungual digit 1. Claw-like (0), conical (1), absent (2).
53. Manus unguals II & III. Claw-like (0), flattened, twisted and hoof-like (1).
54. Anterior process of ilium. Long, laterally compressed (0), strongly downturned (1).
55. Dorsal edge of ilium above ischial peduncle. Horizontal, no significant notch above ischial peduncle (0), strongly notched (1).
56. Dorsal flange on ilium. Thickened dorsal edge above ischial peduncle (0), prominent everted, with a pendant flange (1).
57. Posterior blade of ilium. Triangular, tapering posteriorly (0), rectangular (1).
58. Anterior pubic blade. Blade-like, unexpanded distally (0), blade with constricted proximal portion followed by a distal expansion (1), short constriction and deeply expanded (2).
59. Posterior pubic ramus. Terminates adjacent to distal end of ischium (0), shorter than ischium, no pubic symphysis (1).
60. Ischial shaft. Curved (0), straight (1).
61. Ischial tip. Anteroposterior expansion (0), narrow (1).
62. Femoral shaft. Distal half of shaft curved posteriorly (0), straight (1).
63. Femur, 4th trochanter. Pendant (0), large, triangular (1), curved, laterally compressed eminence (2).
64. Femur, anterior intercondylar groove. Open, U-shaped trough (0), partially enclosed by expansion of anterior condyles (1), fully enclosed canal (2).
65. Femur, distal condyle shape. Moderately expanded anteroposteriorly (0), strongly expanded (1).
66. Metatarsal 1. Well developed and articulates with proximal phalanx (0), slender, splint-like (1), absent (2).
67. Pedal ungual phalanges. Dorsoventrally flattened, but elongate and pointed (0), elongate, but bluntly truncated tip with prominent claw grooves retained (1), broad, short with rounded shield (hoof)-like shape and reduced or absent claw groove (2).