

Sino-Belgian Cooperation Program

“Cretaceous Dinosaurs and Mammals from Inner Mongolia”¹

1. New *Bactrosaurus* (Dinosauria: Hadrosauroidae) material from Iren Dabasu (Inner Mongolia, P. R. China)

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摘要

1995年中比恐龙考察队在二连浩特(中华人民共和国内蒙古)的二连达布苏组(晚白垩纪),发现一处丰富的骨层,里面至少蕴藏着四具原始鸭嘴龙类恐龙——姜氏巴克龙(*Bactrosaurus johnsoni* GILMORE, 1933)的散骨,研究这批新发现的散骨可以使该物种骨骼很好地得以复原,比如,就可以清晰地显示这是一头平头鸭嘴龙。鸭嘴龙超科构成一个单种系,它有11个共同衍征。姜氏巴克龙是鸭嘴龙类最基本的分类单元,但它缺乏可在该超科的其它已熟知的分类单元中观察到的许多衍征。姜氏巴克龙在鸭嘴龙类种系发生中的基本位置表明二连达布苏组的年代属晚白垩纪早期。

关键词: 姜氏巴克龙、鸭嘴龙类、二连达布苏组、内蒙古、骨学、种系发生

Abstract

In 1995, the Sino-Belgian dinosaur expedition discovered a rich bonebed in the Iren Dabasu Formation (Late Cretaceous) of Erenhot (Inner Mongolia, P.R. China). This bonebed comprised the scattered skeletons of at least 4 specimens belonging to the primitive hadrosaur *Bactrosaurus johnsoni* GILMORE, 1933. The study of the new material allows an accurate osteological reconstruction of this species, e.g. definitely showing that it was a flat-headed hadrosaur. The superfamily Hadrosauroidae is diagnosed as a monophyletic group characterized by 11 synapomorphies. *Bactrosaurus johnsoni* is the most basal taxon of the Hadrosauroidae, as it lacks numerous apomorphies observed in the other well known taxa within this superfamily. The basal position of *Bactrosaurus johnsoni* in hadrosaur phylogeny speaks for an early Late Cretaceous age for the Iren Dabasu Formation.

Key-words: *Bactrosaurus johnsoni*, Hadrosauroidae, Iren Dabasu Formation, Inner Mongolia, osteology, phylogeny.

Résumé

En 1995, l'expédition dinosaurienne sino-belge a découvert un riche "bonebed" dans la Formation d'Iren Dabasu (Crétacé supérieur), près

d'Erenhot (Mongolie intérieure, R.P. Chine). Ce gisement renfermait les squelettes disloqués d'au moins quatre individus de l'hadrosaur primitif *Bactrosaurus johnsoni* GILMORE, 1933. L'étude de ce nouveau matériel permet une bonne reconstitution ostéologique de cette espèce; il a ainsi pu être clairement établi que c'était un animal sans crête. La superfamille des Hadrosauroidae forme un groupe monophylétique caractérisé par 11 synapomorphies. *Bactrosaurus johnsoni* est l'Hadrosauroidae le plus primitif actuellement connu: il ne possède en effet pas de nombreux caractères dérivés observés chez les autres membres suffisamment bien connus de ce taxon. La position basale de *Bactrosaurus johnsoni* dans la phylogénie des hadrosaures plaide en faveur d'un âge Crétacé supérieur plutôt précoce pour la Formation d'Iren Dabasu.

Mots-clefs: *Bactrosaurus johnsoni*, Hadrosauroidae, Formation d'Iren Dabasu, Mongolie intérieure, ostéologie, phylogénie.

Introduction

In March 1995, the Inner Mongolian Museum at Hohhot and the Royal Belgian Institute of Natural Sciences at Brussels signed an agreement for co-operative exploration of dinosaur and early mammal sites in Inner Mongolia (Sino-Belgian Dinosaur Expedition = SBDE). The joint exploration was initially intended to collect more dinosaur material documenting the replacement of Early Cretaceous iguanodontids by hadrosaurids at the? beginning of the Late Cretaceous and the phylogenetic relationships between the two groups. The primitive hadrosaurs *Gilmoreosaurus mongoliensis* and *Bactrosaurus johnsoni* are known from Inner Mongolia since the work of GILMORE (1933). ROZHDESTVENSKY (1966) subsequently described the "iguanodonts" *Probactrosaurus alashanicus* and *P. gobiensis*, also from Inner Mongolia. Moreover, the latter author (1952) established the species *Iguanodon orientalis* (= *I. bernissartensis*, according to NORMAN, 1996) for dinosaur material discovered in a nearby area in southeastern Mongolia. As the taxonomy and phylogenetic relationships of late iguanodontids and early hadrosaurids is unresolved (e.g. BRETT-SURMAN,

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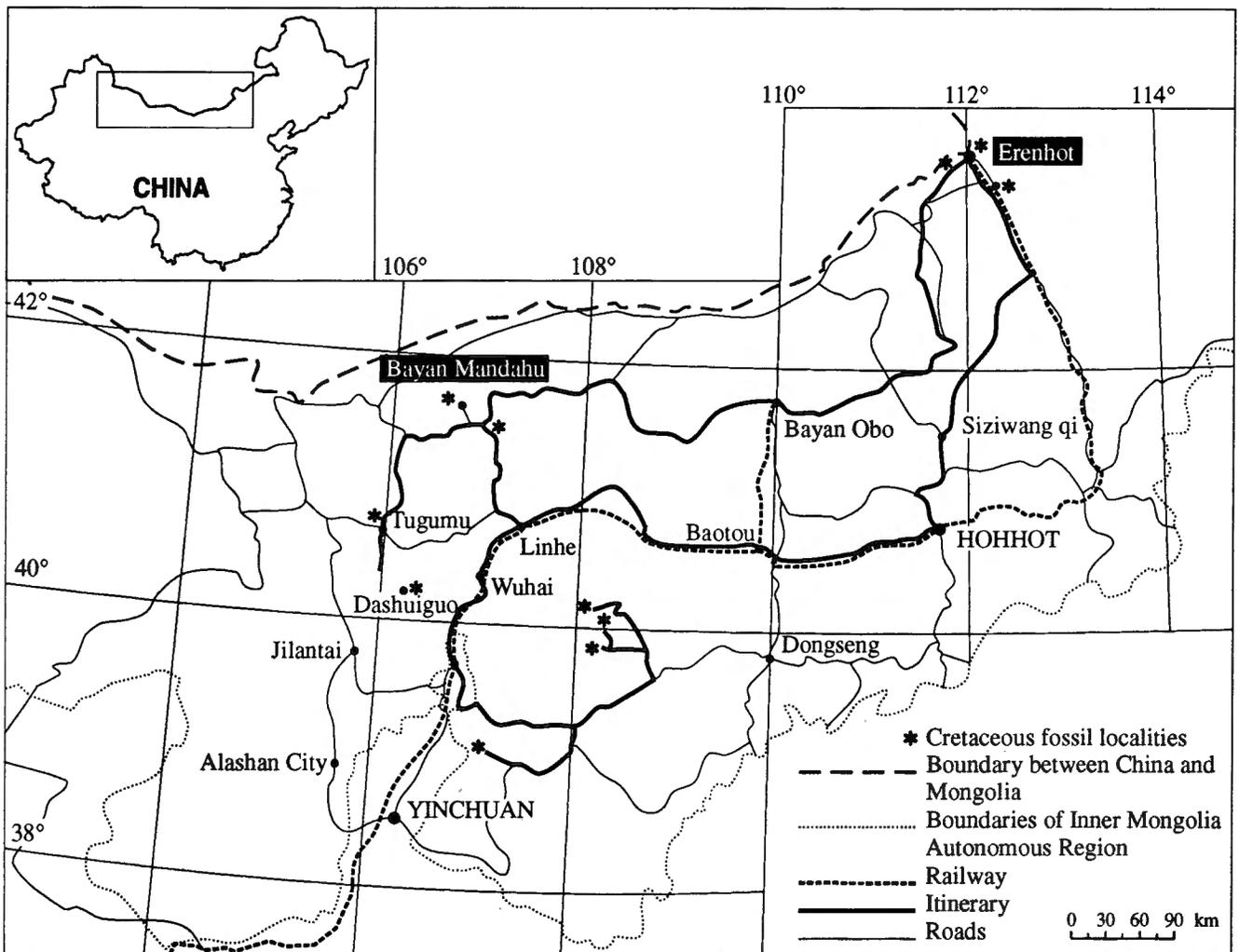


Fig. 1 – Generalized map of the central part of the Inner Mongolia Autonomous Region, showing itinerary of the Sino-Belgian expeditions in 1995 and 1996. Inset map shows the Inner Mongolia Autonomous Region.

1979; WEISHAMPEL & HORNER, 1986; MARYANSKA & OSMOLSKA, 1981a; NORMAN, 1990), description of new material will contribute to the understanding of the problems outlined above.

During September 1995, the SBDE worked near Erenhot and a rich bonebed comprising at least four hadrosaur skeletons was excavated in the Iren Dabasu Formation. In late August and September 1996, the SBDE explored mainly the Bayan Mandahu area (see DONG *et al.*, 1988; DONG, 1993). Several *Protoceratops* skulls, a nearly complete ankylosaur skeleton, a complete turtle, several lizard and mammal skulls and many eggs were discovered. The itinerary followed by the two SBDE expeditions is shown in Figure 1.

New *Bactrosaurus* material from the bonebed discovered in the Iren Dabasu Formation in the Erenhot area is described in the present paper and discussed from a taxonomical and phylogenetical point of view. Our opinion on the age of this material is also presented.

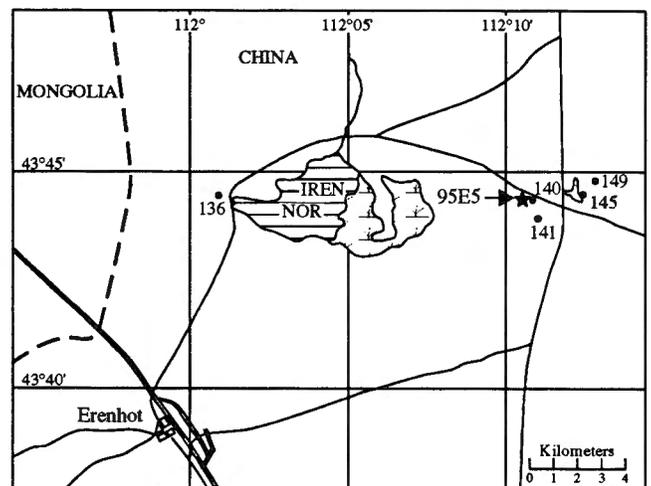


Fig. 2 – Location of fossil locality SBDE 95E5 and American Museum of Natural History localities 141 (type locality of *Bactrosaurus johnsoni*), 149 (type locality of *Gilmoreosaurus mongoliensis*), 136 (type locality of *Alectrosaurus olseni*) and 140 (type locality of *Archaeornithomimus asiaticus*).

Location and general characteristics of the fossil locality

The new *Bactrosaurus* material was collected from a bonebed (Locality SBDE 95E5) about 16km NE of Erenhot and 7 km E of the small salt pan Iren Nor. The coordinates measured in the field (N 43° 44.442; E 112° 10.723) indicate that the locality is very close to the AMNH locality ("Quarry") 140 (Gilmore, 1933, fig. 1) and within a 1 km distance from AMNH 141, the type locality of *Bactrosaurus johnsoni* (Figure 2). The bonebed belonging to the Late Cretaceous Iren Dabasu Formation covered a surface of 7.20 x 4.60 m, was 10 cm thick and was lying at the top of a 40 to 55 cm thick sandy

sequence in which 13 sediment samples were taken (Figure 3). The succession is composed of poorly sorted, fine to very coarse, slightly lithified, brownish grey and buff quartz sand. Samples 3 and 7 are more clay-rich. Quartz grains are mostly medium to fine sized, subrectangular to subrounded (larger grains are generally subrounded), translucent to milky and occasionally reddish due to staining by iron oxides. Argillaceous and slightly calcareous coatings are common. Traces of mica and dark-coloured grains occur. Granulometric curves of samples 1, 2, 6 and 13 (the bonebed) show 2 or 3 peaks (7 µm, 200 µm and 800 µm, respectively).

According to BERKEY & MORRIS (1927), the Iren Dabasu

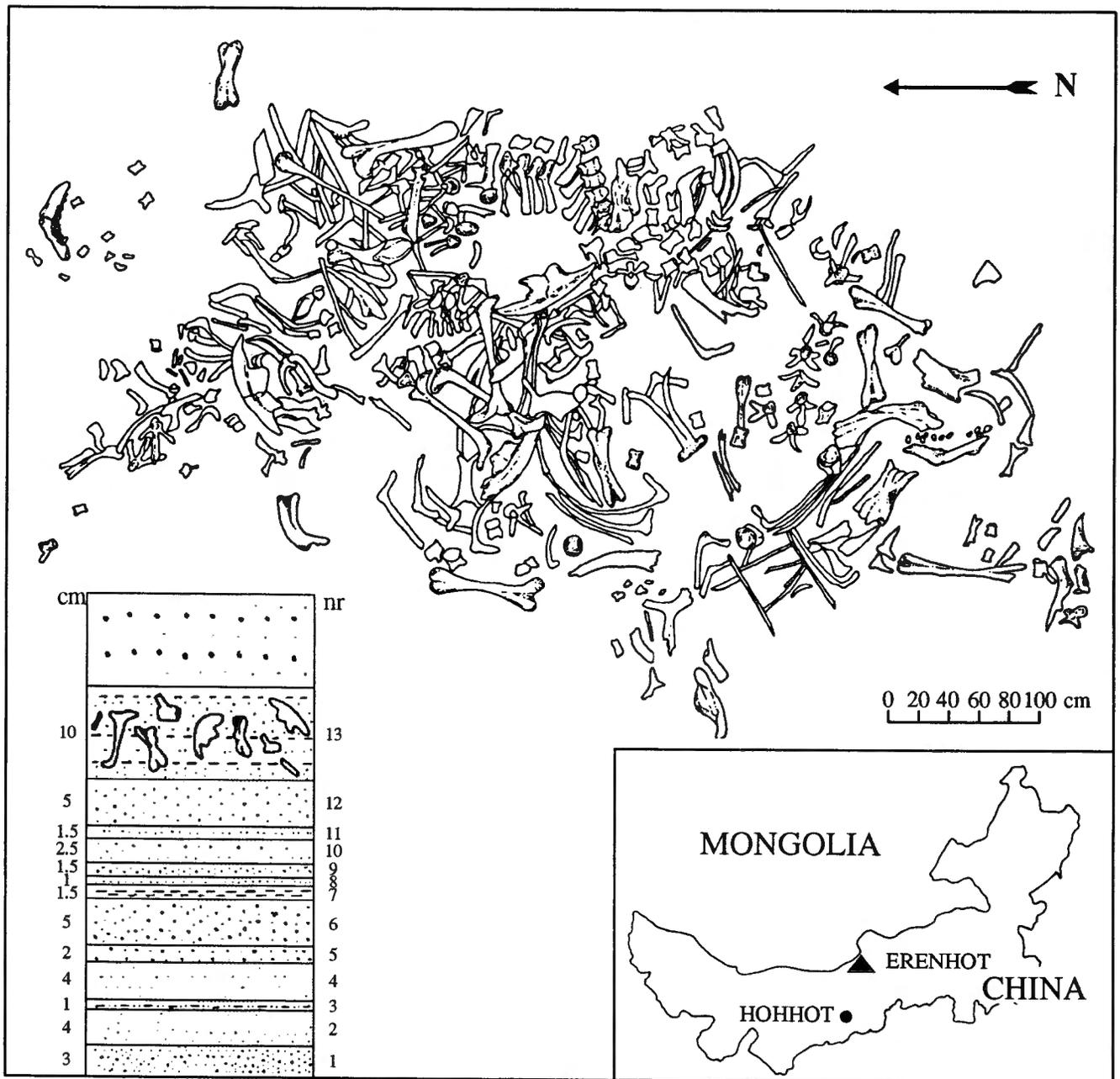


Fig. 3 – Sketch showing bonebed and lithologic succession at Locality SBDE 95E5 near Erenhot. Inset map of the Inner Mongolia Autonomous Region shows location of Erenhot.

Formation was deposited in lacustrine and fluvial environments. CURRIE & EBERTH (1993) interpret the formation as a low-sinuosity braided fluvial system with a main NW direction and with ancillary NE and SW orientated flow systems.

Several hundred skeletal elements were recovered from

the bonebed; almost all belong to *Bactrosaurus johnsoni* and they may represent at least four individuals. A few articulated series, with five to ten vertebrae, of dorsal and caudal vertebrae were collected (Plate 1, Fig. 2). The central southern half of the bonebed is characterized by the accumulation of well preserved pelvic bones and humeri (Plate 1, Fig. 1), with one nearly complete sa-

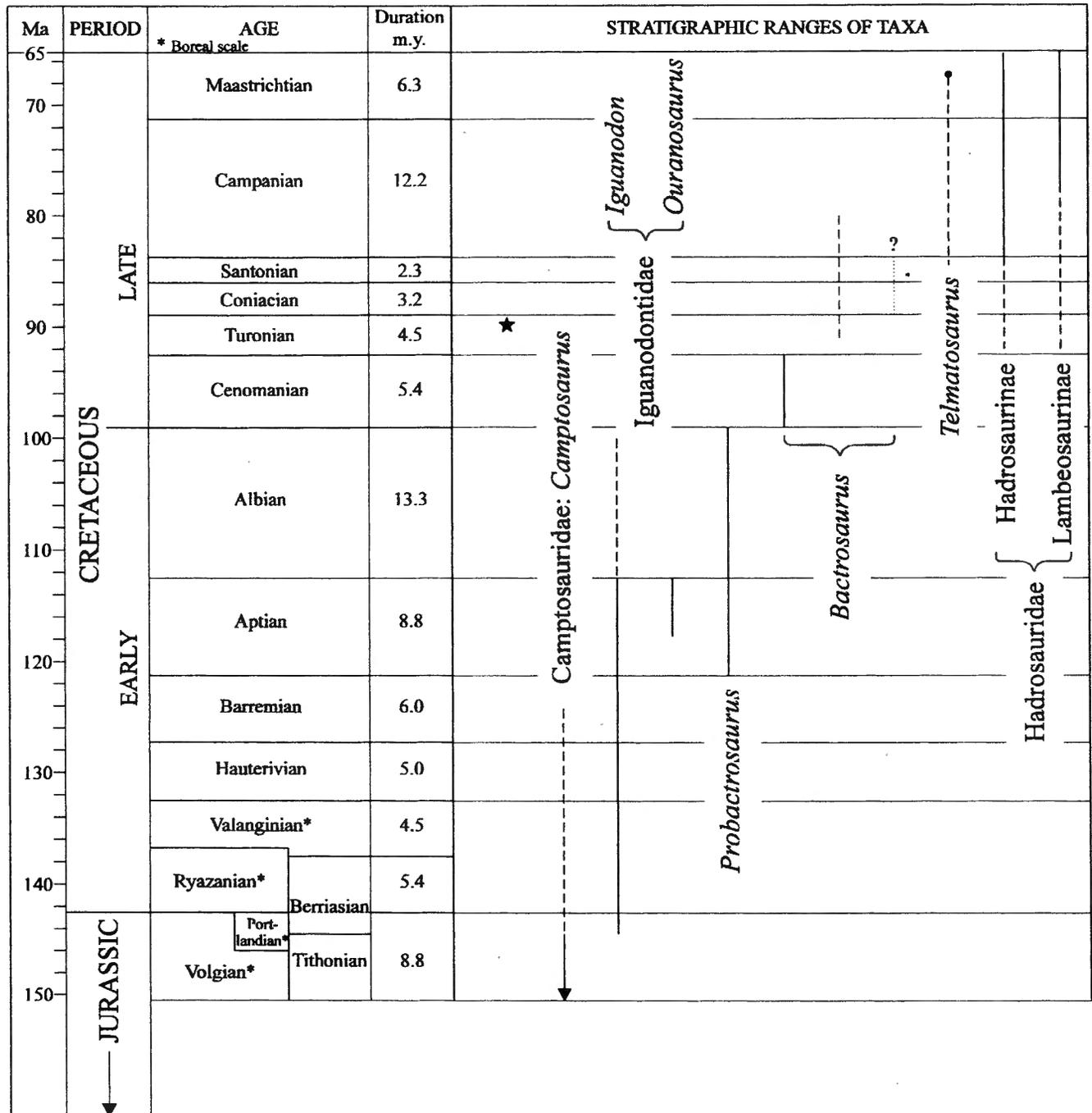


Fig. 4 – Stratigraphical distribution of selected iguanodontians. Hadrosaurinae: dashed line indicates range of *Aralosaurus tuberiferus* from Kazakhstan, according to ROZHDESTVENSKY (1977); Lambeosaurinae: dashed line indicates range of *Jaxartosaurus aralensis* from Kazakhstan, according to ROZHDESTVENSKY (1977); *Bactrosaurus*: full line indicates age of Iren Dabasu Formation favoured in the present paper, dashed line indicates age proposed by JERZYKIEWICZ & RUSSELL (1991), dotted line indicates age proposed by CURRIE & EBERTH (1993); Camptosauridae: dashed line indicates range extension of the family according to *Camptosaurus depressus*; *: stratigraphic level in Kazakhstan corresponding to the transition *Kizylkumemys shuwalovi* - *Lindholmemys martinsoni*. Time scale according to GRADSTEIN & OGG (1996).

crum. Although the orientation of the elements is very variable, a majority of slender and elongated bones (e.g. ribs) show a NE-SW orientated long axis. This observation corresponds well with the NE and SW ancillary flow systems recognized by CURRIE & EBERTH (1993). Pes and manus bones are rare. Considering the monospecific composition of the bonebed (other groups are only represented by one single ornithomimid caudal vertebra) and especially the central location of the pelvic girdle bones with the lighter elements being scattered around, fluvial transportation over a long distance seems unlikely.

Review of the age of the Iren Dabasu formation

The Iren Dabasu Formation is only known from the area around Erenhot. According to GRANGER & BERKEY (1922) and BERKEY & MORRIS (1927, pl. XXIII), the formation rests unconformably on Precambrium rocks and is of Early Cretaceous age because of the primitive aspect of its dinosaur fauna e.g. "undetermined iguanodonts". These were later described by GILMORE (1933) as new hadrosaurid species and since that time the formation has been assigned to the Late Cretaceous. However, its exact stratigraphic position within the Late Cretaceous is matter of discussion and ages ranging from Cenomanian to Campanian have been proposed. The on-going discussion may be summarized as early Late Cretaceous *versus* later Late Cretaceous. A first group of authors favours a Cenomanian (TAQUET, 1975; ROZHDESTVENSKY, 1977), Pre-Turonian (WEISHAMPEL & HORNER, 1986) or Pre-Santonian (BRETT-SURMAN, 1979) age. Their age assignment is based on the primitive character of the hadrosaurid fauna, *Bactrosaurus johnsoni* and *Gilmoresaurus mongoliensis*. A second group proposes a much younger age ranging from Late Turonian to Early Campanian (JERZYKIEWICZ & RUSSELL, 1991), or from Coniacian to Santonian-Campanian (CURRIE & EBERTH, 1993). This age assignment results from the correlation of the Iren Dabasu Formation with the upper part of the Bayn Shire Formation known from different areas in the People's Republic of Mongolia. The type locality of the Bayn Shire Formation is in the eastern Gobi, about 200 km ENE of Erenhot. In the upper part of the Bayn Shire Formation, the turtle *Kizylkumemys shuwalovi* is replaced by *Lindholmemys martinsoni*. In Kazakhstan, this replacement occurs in late Turonian time in proximity to marine strata (NESSOV, 1984). The correlation between the Iren Dabasu Formation and the Bayn Shire Formation is based on similarities in lithofacies and fossil vertebrate assemblages worked out by CURRIE & EBERTH (1993). We are not opposed to a late Turonian, Coniacian-Santonian age for the upper part of the Bayn Shire Formation, however, we question whether the correlation with the Iren Dabasu Formation is well proved. The turtle *Lindholmemys martinsoni* has not been specifically identified in the Iren Dabasu Formation, CURRIE & EBERTH (1993, tab.1) only mention the presence of *Lindholmemys* sp. A striking difference between the Iren Dabasu and Bayn Shire di-

nosaur faunas is that the primitive hadrosaurs *Bactrosaurus johnsoni* and *Gilmoresaurus mongoliensis*, characteristic and common in the Iren Dabasu Formation, have not been reported in the Bayn Shire Formation of Mongolia; there is only mention of one undescribed lambeosaurine from one locality.

BRINKMANN, NESSOV & PENG (1993) pay attention to the similarity in the turtle fauna of the Iren Dabasu Formation and the Bissekety Formation of Uzbekistan, the latter formation being of late Turonian age. However, the occurrence of *Khunnuchelys erinhotensis* BRINKMANN, NESSOV & PENG, 1993 in the Iren Dabasu Formation and of *K. kizylkumensis* BRINKMANN, NESSOV & PENG, 1993 in the Bissekety Formation does not permit a precise age correlation between these two formations

Finally, we stress that the conclusions of the present morphologic and cladistic study of *Bactrosaurus johnsoni* are more compatible with an early Late Cretaceous age for the Iren Dabasu Formation than with a late Turonian – early Campanian age. Indeed, the present cladistic analysis shows that *Bactrosaurus johnsoni* is by far more primitive than any known typical Campanian – Maastriichtian Hadrosauridae. Many skeletal characters appear plesiomorphic, like in the Early Cretaceous Iguanodontidae. The stratigraphic range of the taxa discussed in the cladogram (Figure 38) is shown in Figure 4. A late Turonian – early Campanian age assignment for the Iren Dabasu Formation implies a gap of at least 5 my in the phylogenetic continuity Iguanodontidae – "Probactrosaurs" – "Bactrosaurs" – Hadrosauridae. On the other hand, a Cenomanian age for the Iren Dabasu Formation fills in this gap.

Systematic Palaeontology

Order Ornithischia SEELEY, 1888

Suborder Ornithopoda MARSH, 1881

Infraorder Iguanodontia DOLLO, 1888

Superfamily Hadrosauroidea COPE, 1869 (emend. SERENO, 1986)

Diagnosis: Iguanodontia characterized by more than one replacement tooth in each tooth position; crowns firmly cemented together to form a rigid battery; articular surface of the occipital condyle not steeply inclined downwards; basiptyergoid processes long and slender, projecting more ventrally than the occipital condyle; presence of fontanelles on the skull of younger specimens; absence of surangular foramen; maxillary teeth miniaturized, bearing a single large carina; preacetabular process of ilium very deflected ventrally; antitrochanter of ilium developed; obturator foramen of pubis fully open; transverse widening of the proximal head of the tibia extending distally.

Type genus: *Hadrosaurus* LEIDY, 1858

Included taxa: The superfamily Hadrosauroidae forms a monophyletic group including *Bactrosaurus* GILMORE, 1933, *Telmatosaurus* NOPCSA, 1903 and Hadrosauridae (Hadrosaurinae + Lambeosaurinae). The genera *Mandschurosaurus* RIABININ, 1930, *Gilmoreosaurus* BRETT-SURMAN, 1979, *Taninus* WIMAN, 1929, *Secernosaurus* BRETT-SURMAN, 1979 and *Claosaurus* MARSH, 1890 must be regarded, in the current state of our knowledge, as Hadrosauroidae *incertae sedis*. The phylogenetical position of *Probactrosaurus* ROZHDESTVENSKY, 1966 requires revision (NORMAN, in prep.).

Genus *Bactrosaurus* GILMORE, 1933

Diagnosis: As for the only known species, *Bactrosaurus johnsoni* GILMORE, 1933.

Type species: *Bactrosaurus johnsoni* GILMORE, 1933.

Remark: Following MARYANSKA & OSMOLSKA (1981a) and WEISHAMPEL & HORNER (1990), *Bactrosaurus prynadai* RIABININ, 1939, based on an isolated maxilla and dentaries from the Upper Cretaceous of Kyrkkuduk (Kazakhstan), is regarded as a *nomen dubium*.

Bactrosaurus johnsoni GILMORE, 1933

- 1933 *Bactrosaurus johnsoni*, new genus and species - GILMORE, p. 50, figs. 21-40, pl. 3, fig. 2; pl. 4, pl. 6, figs. 1 & 4; pl. 7, fig. 1.
- 1958 *Bactrosaurus johnsoni* GILMORE-YOUNG, p. 111.
- 1958 ?*Taninus* sp. - YOUNG, p. 111.
- 1966 *Bactrosaurus johnsoni* GILMORE-ROZHDESTVENSKY, p. 103, figs. 3c & 4b.
- 1969 *Bactrosaurus johnsoni* GILMORE 1933 - STEEL, p. 32.
- 1981a *Bactrosaurus johnsoni* GILMORE, 1933 - MARYANSKA & OSMOLSKA, p. 7, fig. 1.
- 1981a ?*Taninus* sp. - MARYANSKA & OSMOLSKA, p. 10.
- 1986 *Bactrosaurus johnsoni* GILMORE, 1933 - WEISHAMPEL & HORNER, p. 39, fig. 2.
- 1986 *Gilmoreosaurus mongoliensis* (GILMORE, 1933) - WEISHAMPEL & HORNER, *partim*, p. 39, fig. 1g.
- 1990 *Bactrosaurus johnsoni* GILMORE, 1933a - WEISHAMPEL & HORNER, p. 557, fig. 26.6a.
- 1990 *Gilmoreosaurus mongoliensis* (GILMORE, 1933a) - WEISHAMPEL & HORNER, *partim*, p. 556.
- 1992 *Bactrosaurus johnsoni* GILMORE, 1933 - SUN *et al.*, 1992, p. 154, fig. 162.

Holotype: AMNH 6553, consisting of dentary, maxillary and other skull fragments; ten dorsal vertebrae, seven sacrales; thirty-six caudals; left scapula, left sternal, both pubes, both ischia, left femur, fibula, complete left foot and part of the right one. These bones have been associated together mainly on the basis of their size.

Paratypes: AMNH 6353, 6365, 6366, 6370, 6372, 6373, 6375, 6379, 6380, 6384, 6385, 6386, 6388, 6389, 6390,

6391, 6392, 6393, 6394, 6395, 6396, 6397, 6398, 6501, 6553, 6574, 6575, 6577, 6578, 6580, 6581, 6582, 6583, 6584, 6585, 6586, 6587.

Locus typicus: Quarry 141 ("JOHNSON'S Quarry"), Erenhot, Inner Mongolia, P.R. China.

Stratum typicum: Iren Dabasu Formation, Upper Cretaceous.

New topotypes discovered by the SBDE: SBDE 95E5, discovered in Locality 95E5 (43° 44.442' N; 112° 10.723' E; 893.7 m Alt.), is a bonebed composed by several hundreds disarticulated bones belonging to at least four specimens of different sizes: partial braincases, supraoccipital, parietals, frontals, premaxillae, maxillae, nasals, jugals, quadrates, squamosals, lacrimal, prefrontals, post-orbital, supraorbitals, predentaries, dentaries, surangulars, isolated teeth, isolated and connected vertebrae, sacra, ribs, scapulae, coracoids, sternals, humeri, radius, ulna, metacarpals, ilia, ischia, pubes, femur, fibula, astragalus, metatarsals and phalanges.

Emended diagnosis: Non-hadrosaurid Hadrosauroidae characterized by the long and rounded rostral process of its jugal, bearing a very elongated and excavated maxillary facet (1); caudal process of the jugal rather narrow (2); postcotyloid process of squamosal markedly curved backwards (3); club-shaped neural spines of the last dorsal vertebrae, in fully ossified adult specimens (4); distal blade of the scapula very regularly widening towards its end, ratio "length of the scapula / maximal width of the distal blade" < 3.5 (5); prominent and angular deltopectoral crest of the humerus (6); ulnar condyle of the humerus distinctly more developed than radial condyle (7); preacetabular process of the ilium very deflected ventrally (8); ischial shaft very thick and ischial foot greatly expanded (9); femur perfectly straight in lateral view (10); ungual phalanges thick and truncated in adults (11).

The following characters are considered to be plesiomorphic in *Bactrosaurus johnsoni*: maxilla markedly asymmetrical in lateral view (12); about 20 maxillary and dentary tooth positions in adults (13); laterally positioned antorbital fenestra (14); paraquadrate foramen developed (15); massive supraorbitals (16); dentary rostrally downturned (17); dentary teeth bearing one caudal secondary ridge (18); large pubic peduncle (19) and simple ischial peduncle of ilium (20).

Discussion:

Characters (1), (3), (4) and (5) are autapomorphic of *Bactrosaurus johnsoni*. Characters (2), (8), (9), (11), (12), (13), (17) distinguish *Bactrosaurus johnsoni* from the early hadrosauroid *Gilmoreosaurus mongoliensis* (GILMORE, 1933), also discovered in the Iren Dabasu Formation. Characters (6), (7), (10), (13), (14), (15) and (18) distinguish *Bactrosaurus johnsoni* from the basal

hadrosauroid *Telmatosaurus transsylvanicus* (NOPCSA, 1900), from the late Maastrichtian of Romania. The polarity of characters (19) and (20) is unknown in *Telmatosaurus transsylvanicus*, that of character (16) is unknown in both *Gilmoreosaurus mongoliensis* and *Telmatosaurus transsylvanicus*.

GILMORE (1933) described two new hadrosaurid genera from the material discovered, in 1922 and 1923, at Iren Dabasu by the American Museum of Natural History expedition: *Bactrosaurus johnsoni*, from field locality ("Quarry") 141 and *Mandschurosaurus* (*Gilmoreosaurus* BRETT-SURMAN, 1979) *mongoliensis*, from Quarries 145 and 149. The mixing of hadrosaurine and lambeosaurine characters observed in the skeleton of *Bactrosaurus johnsoni* intrigued GILMORE (1933: 51), who regarded this species as an unusual flat-headed Lambeosaurinae. This hypothesis was subsequently retained by STEEL (1969) and BRETT-SURMAN (1979, fig. 1). On the other hand, ROZHDESTVENSKY (1966) removed *Bactrosaurus johnsoni* from the Lambeosaurinae and placed it in the Hadrosaurinae, because of the presence of the frontal bone within the dorsal rim of the orbit in specimen AMNH 6365; he also considered "*Mandschurosaurus*" *mongoliensis* as a synonym of *Bactrosaurus johnsoni*. MARYANSKA & OSMOLSKA (1981a) pointed out that the material used by ROZHDESTVENSKY (1966) to establish the synonymy between *Bactrosaurus johnsoni* and "*Mandschurosaurus*" *mongoliensis* must then exclude the postcranial material and, thus, the holotype of *Bactrosaurus johnsoni*. Following YOUNG (1958), they suggested that more than one species may be present in Quarry 141. They assigned the postcranium AMNH 6553, forming the holotype of *Bactrosaurus johnsoni*, to the family Lambeosaurinae, whereas they tentatively referred the skull roof AMNH 6365 to the Hadrosaurinae? *Tanius* sp. WEISHAMPEL & HORNER (1986) also distinguished two species in Quarry 141, on the base of the cranial elements. The bones with lambeosaurine affinities were referred to *Bactrosaurus johnsoni*, whereas those with hadrosaurine affinities were assigned to *Gilmoreosaurus mongoliensis*. They also tentatively demonstrated that the prefrontals discovered in Quarry 141, all referred to *Bactrosaurus johnsoni*, supported a hollow supracranial crest.

The study of the material discovered by the SBDE expedition in field locality 95E5 reveals that all the specific elements of the skeleton represented by several specimens in the bone-bed, although belonging to at least four individuals of different sizes, are closely similar to each other and consequently do not support the presence of more than one species in this locality. Moreover, comparisons of the specific elements discovered in both Localities 141 and 95E5 prove that they are closely similar and show the same apparent mixing of lambeosaurine and hadrosaurine characters, as originally mentioned by GILMORE (1933) and WEISHAMPEL & HORNER (1986). An identical fortuitous mixing of identical skeletal elements from two different hadrosaurid taxa in two

different bone-beds is considered to be highly improbable. The most logical course is to consider that both bone-beds are monospecific: all the hadrosaurid bones discovered in Localities 141 and 95E5 are referred to *Bactrosaurus johnsoni*; only the material from Quarries 145 and 149 is regarded as belonging to *Gilmoreosaurus mongoliensis*, as originally proposed by GILMORE (1933). The apparent mixing of hadrosaurine and lambeosaurine characters in *Bactrosaurus johnsoni* will be considered in the phylogenetic analysis of this species.

Osteological description of *Bactrosaurus johnsoni*

The osteology of *Bactrosaurus johnsoni* is mainly based on the newly discovered material SBDE 95E5. This material is the property of the Inner Mongolian Museum in Hohhot (P. R. China), but part of the material is temporarily stored at the I.R.Sc.N.B / K.B.I.N. (Brussels, Belgium). Casts of the bones will be made and housed in the latter institution, where they will be registered IRSNB IG28522.

Additional informations primarily concerning the anatomy of the hindlimbs come from the material discovered, in 1922, by the American Museum of Natural History expedition at Quarry 141.

In order to clarify the phylogenetic relationships of *Bactrosaurus johnsoni*, comparisons are proposed with other ornithopods. The data are compiled from personal observations and, mainly, from literature sources: Campanian-Maastrichtian Hadrosauridae from North-America (LULL & WRIGHT, 1942; OSTROM, 1961; BRETT-SURMAN, 1975, 1989; HORNER, 1983, 1988, 1990, 1992; WEISHAMPEL & JENSEN, 1979; WEISHAMPEL & HORNER, 1990), *Saurolophus angustirostris* (MARYANSKA & OSMOLSKA, 1981a, 1984), *Telmatosaurus transsylvanicus* (WEISHAMPEL *et al.*, 1993), *Ouranosaurus nigeriensis* (TAQUET, 1976), *Iguanodon bernissartensis* (NORMAN, 1980), *I. artherfieldensis* (NORMAN, 1986), *Camptosaurus dispar* (GILMORE, 1909) and *Hypsilophodon foxii* (GALTON, 1974).

The standardized anatomical nomenclature for dinosaurs, recommended by WEISHAMPEL *et al.* (1990: 6), is followed in the present paper.

SKULL AND MANDIBLE (Figure 5)

Supraoccipital (Plate 2, Fig. 1):

Description – The supraoccipital is lodged within the mediodorsal area of the occiput. As described by GILMORE (1933: 56), it is a heavy, block-like element which extends rostrally and dorsally as a stout pyramidal median bone between the parietal and the squamosals. Its concave caudoventral border articulates obliquely with the exoccipitals, so that it is completely excluded from the roof of the foramen magnum. The description proposed below is mainly based on the large isolated supraoccipital SBDE 95E5/29. Its dorsal surface bears a very large and

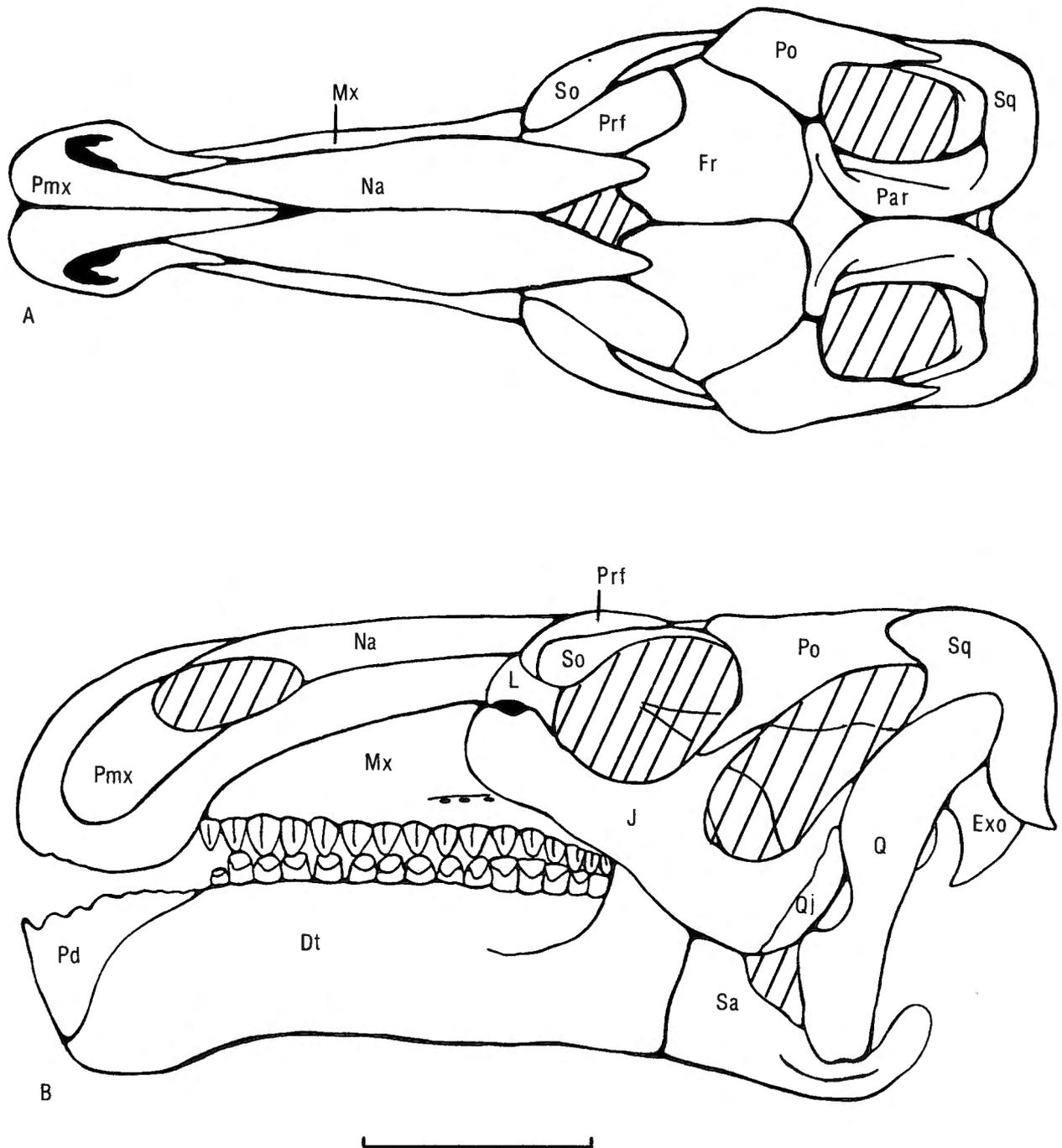


Fig. 5 – Reconstruction of the skull of *Bactrosaurus johnsoni*, from the Iren Dabasu Formation - A: Dorsal view; B: lateral view. Scale bar = 10 cm. Dt: dentary; Exo: exoccipital; Fr: frontal; J: jugal; L: lacrimal; Mx: maxilla; Na: nasal; Par: parietal; Pd: predentary; Pmx: premaxilla; Po: postorbital; Prf: prefrontal; Q: quadrate; Qj: quadrato-jugal; Sa: surangular; So: supraorbital; Sq: squamosal

triangular promontorium; a prominent median crest divides this promontorium into two parts. The *ligamentum nuchae* probably inserted onto the rostradorsal portion of this area. The promontorium is bordered laterally by two large, ovoid and depressed areas for the insertion of the *M. spinalis capitis* and caudoventrally, by a perpendicular, elongated and shallow depression for the insertion of the *M. rectis capitis caudal*. Two prominent knobs lie on the caudolateral corners of the supraoccipital, partially

covering the contact areas for the squamosals. These knobs are not developed on the supraoccipital belonging to smaller individuals (AMNH 6566, for example): it is therefore probably an ontogenetic character.

In ventral view, the rostradorsal portion of the supraoccipital forms a large and very deep depression, which roofed the caudal portion of the myelencephalon. This depression is bordered laterally by two large, elliptical and rough facets, facing rostrally and laterally: they

represent articular facets with the caudolateral parts of the parietal. Caudoventrally to the parietal facets, the articular facets for reception of the medial ramus of the squamosals form two large and semi-elliptical depressed areas along the lateral borders of the supraoccipital; they deeply indent the caudolateral corners of the bone.

Discussion – Primitively in ornithopods, the supraoccipital takes part in the dorsal margin of the foramen magnum: this condition can be observed in *Hypsilophodon foxii* and *Camptosaurus dispar*. The supraoccipital excluded from the foramen magnum is a synapomorphy observed in *Iguanodon bernissartensis*, *Iguanodon atherfieldensis*, *Ouranosaurus nigeriensis*, *Tanius sinensis* (WIMAN, 1929, pl. 5, fig. 5), *Probactrosaurus gobiensis* (NORMAN, 1990), *Bactrosaurus johnsoni*, *Telmatosaurus transsylvanicus* and in Hadrosauridae.

For HORNER (1990), the presence of dorsolateral bosses on the supraoccipital characterizes his clade Lambeosauria, including *Ouranosaurus nigeriensis* and the Lambeosaurinae (his Lambeosauridae). In *Bactrosaurus johnsoni*, it has been shown that the development of these bosses is an ontogenetic character of poor phylogenetic significance, which is probably the case in other ornithopods.

Basioccipital (Figures 6-7; Plate 2, Fig. 2):

Description – As usual in Iguanodontia, the basioccipital contributes to the largest portion of the broad and prominent occipital condyle (**occ**). In caudal view, the condyle has an elliptical outline, with an horizontal great axis. It is incised medially by a deep vertical furrow. In lateral view, the neck separating the occipital condyle from the expanded rostral part of the basioccipital appears relatively long. The articular surface of the condyle is perfectly vertical and perpendicular to the axis of the floor of the neurocranium. The dorsal surface of the basioccipital is grooved in the midline by the floor of the neurocranium (**ncf**): this excavation progressively deepens rostrally. On either side is a pyriform facet for reception of the exoccipital: these facets are distinctly separated from each other along the whole length of the basioccipital, indicating that the latter took part in the ventral rim of the foramen magnum. The rostral part of the basioccipital projects laterally and ventrally to form the caudal part of the sphenoccipital tubercles (**spot**). At the ventral limit of the suture between the basioccipital and the basisphenoid, a small and shallow fossa, formed by both adjacent bones, may mark, following WEISHAMPEL *et al.* (1993), the attachment site of the *M. rectus capitis rostralis* (**mrcr**).

Discussion – WEISHAMPEL *et al.* (1993) postulate that, primitively in Iguanodontia, the exoccipital condyloids nearly or completely exclude the basioccipital from the ventral margin of the foramen magnum: this condition is encountered in *Iguanodon*, *Telmatosaurus transsylvanicus* and Hadrosaurinae, but contrasts with that observed

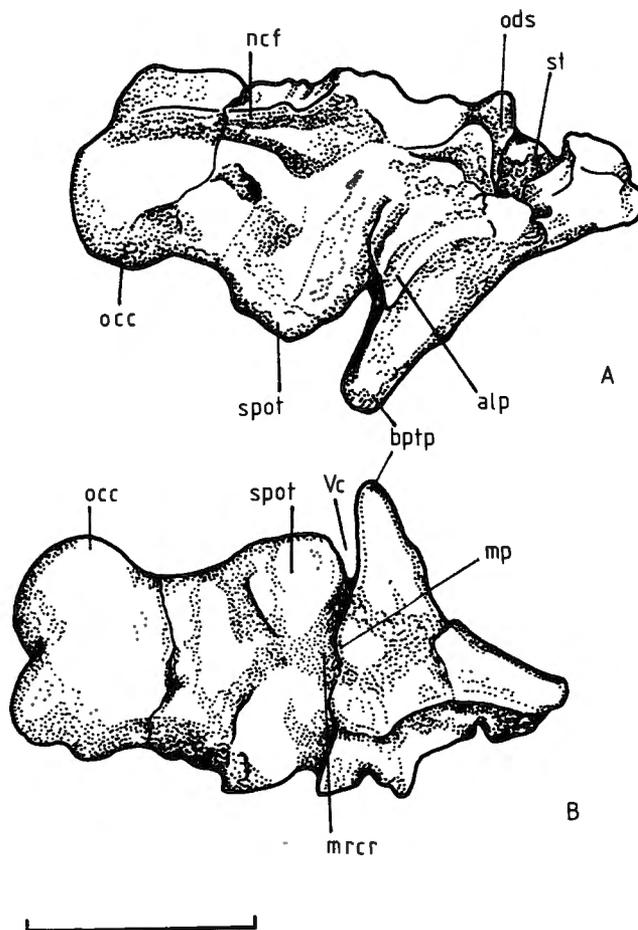


Fig. 6 – Basioccipital - basisphenoid of *Bactrosaurus johnsoni* (SBDE 95E5/1), from the Iren Dabasu Formation - A: dorsolateral view; B: ventral view. Scale bar = 4 cm. alp: alar process; bptp: basipterygoid process; mp: median process; mrcr: insertion of the *M. rectus capitis rostralis*; ods: floor of the neurocranium; occ: occipital condyle; ods: ossified dorsum sellae; spot: sphenoccipital tubercles; st: sella turcica; Vc: Vidian canal.

in *Ouranosaurus* and Lambeosaurinae, in which the exoccipital condyloids are well separated medially, allowing the basioccipital to form the ventral margin of the foramen magnum. Nevertheless, the phylogenetical value of this character is subject to some doubt, as the degree of separation of the exoccipital condyloids seems to show continuous distribution within both iguanodontids and hadrosaurids. It probably depends on the lateral broadening of the occipital condyle observed independently in several lineages. If the basioccipital seems completely excluded from the foramen magnum in *Iguanodon bernissartensis*, it probably participates in a small median portion in *I. atherfieldensis*, *Bactrosaurus johnsoni*, *Telmatosaurus transsylvanicus*, but also in several Hadrosaurinae, such as *Anatotitan copei*. The greatest separation of the exoccipital condyloids, correlated to the broadened occipital condyle, is observed in *Ouranosaurus nigeriensis*, *Tanius sinensis*, as in numerous Lambeosaur-

inae. Moreover, the polarity of this character is subject to discussion. Contrary to WEISHAMPEL *et al.* (1993), HORNER (1990) interpreted the well-separated condyloid condition as primitive in Ornithopoda. This polarity accords with the condition observed in *Camptosaurus dispar* and *Hypsilophodon foxii*.

In *Bactrosaurus johnsoni*, the articular surface of the occipital condyle is perfectly vertical, like in *Telmatosaurus transsylvanicus*, *Taninus sinensis* and in Hadrosauridae. Primitively in Ornithopoda, the condyle is inclined ventrally, as observed in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*.

Basisphenoid and parasphenoid (Figure 6-7; Plate 2, Fig. 2):

Description – The basisphenoid forms the central portion of the floor of the braincase and is closely sutured with the basioccipital. In ventral view, its caudal portion forms the rostral two thirds of the large sphenoccipital tubercles (**spot**). The rostromedian junction point of these tubercles forms a distinct fossa, just in front of the attachment site of the *M. rectus capitis rostralis*. In front of the sphenoccipital tubercles, the basisphenoid forms two symmetrical basiptyergoid processes (**bptp**). They are relatively long and slender and project caudally and more ventrally than laterally: the end of the pterygoid processes is therefore more ventral than the base of the occipital condyle. A prominent median process (**mp**) is set between the pterygoid processes, on the ventral face of the basisphenoid. On the lateral wall of the basisphenoid, the alar process (**alp**) is found directly above the basiptyergoid process, from which it is distinctly detached. The Vidian canal (**Vc**) opens in bottom of the deep groove intercalated between the rostral side of the sphenoccipital tubercle and the caudal side of the basiptyergoid and alar processes: this canal carried the internal carotid foramen and the palatine branch of the facial nerve (cranial nerve VII) through the basisphenoid into the pituitary fossa.

In dorsal view, the floor of the neurocranium forms an enlarged rhomboidal surface at the back of the basisphenoid. Rostrally, the *sella turcica* (**st**), which housed the pituitary gland, forms a large and deep ovoid excavation within the basisphenoid; the bony arch above it represents the ossified *dorsum sellae* (**ods**).

The parasphenoid is completely fused to the rostral part of the basisphenoid. This bone is broken in all the specimens of *Bactrosaurus johnsoni* currently discovered. However, it appears very narrow, forming a pointing spur rostrally to the ventral side of the braincase.

Discussion – In *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*, the pterygoid processes are relatively short and broad and their distal end is nearly on the same horizontal plane as the ventral border of the occipital condyle. In *Bactrosaurus johnsoni*, *Telmato-*

saurus transsylvanicus, Lambeosaurinae and Hadrosaurinae, the pterygoid processes are longer, more slender and project more ventrally than the base of the occipital condyle.

Exoccipital (Figure 7):

Description – The exoccipitals form, in caudal view, the dorsal margin of the foramen magnum and the greatest portion of the occipital plates. AMNH 6370 is the right exoccipital of a juvenile specimen (Locality 141; GILMORE, 1933, fig. 23). Because this specimen is not co-ossified, as in adults, it allows the exact sutures of this bone to be described. In ventral view, the exoccipital condyloids are very developed rostro-caudally and crescentic in outline. They participate in the occipital condyle, where they form the cranio-vertebral joint with the atlas. Above the foramen magnum, the dorsomedial processes of the paired exoccipitals meet each other at the midline, excluding the supraoccipital from the foramen magnum. Between the dorsomedial process and the exoccipital condyloid, a triangular depressed area marks the insertion of the *M. obliquus capitis magnus*. The lateral wall of the exoccipital is pierced by foramina for several cranial nerves. The caudal one enters the foramen magnum just within its external opening and transmitted the hypoglossal nerve (**c.n. XII**). Rostrally, a double foramen can be observed: the caudal branch transmitted the spinal accessory nerve (**c.n. XI**) and the rostral branch, the vagus nerve (**c.n. X**). They are separated from the auditory foramen by a big pillar, which extends from the rostroventral corner of the exoccipital to the ventral border of the paroccipital process. In front of this pillar, a concave surface forms the contact area with the opisthotic.

The paroccipital processes are very large: lateroventrally, they reach the level of the base of the occipital condyle. The dorsal border of the paroccipital processes is concave at the level of the contact facet for the supraoccipital. Laterally to this surface, its dorsal angle inserts into a ventral depression of the squamosal in a synovial joint. The dorsolateral border of the paroccipital process inserts in a groove on the ventral side of the postcotyloid process of the squamosal.

Discussion – The pattern of cranial foramina through the body of the exoccipitals is that observed in Hadrosauridae (OSTROM, 1961; HORNER, 1992) and in *Telmatosaurus transsylvanicus* (WEISHAMPEL *et al.*, 1993). For WEISHAMPEL *et al.* (1993: 366), this condition differs from that observed in *I. atherfieldensis*, *Iguanodon lakotaensis* and possibly *Ouranosaurus nigeriensis*, where the same foramina are found along the suture between the exoccipital and the opisthotic. However, this character must be regarded cautiously: as the exoccipital and the opisthotic are completely fused together in adults, their respective limits are very difficult to discern.

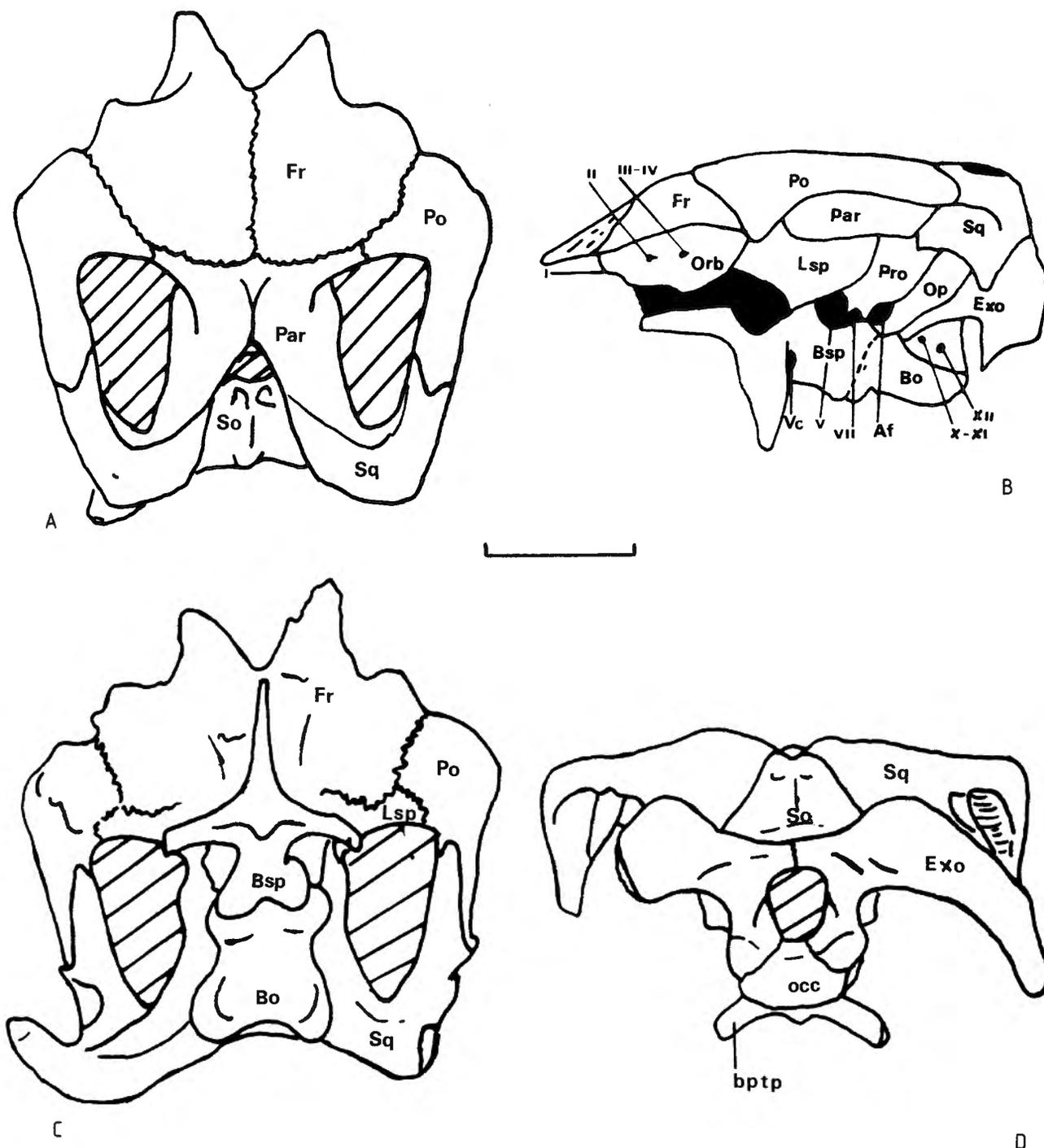


Fig. 7 – Reconstruction of the caudal part of the skull of *Bactrosaurus johnsoni* (after AMNH 6365), from the Iren Dabasu Formation - A: dorsal view; B: lateral view; C: ventral view; D: caudal view. Scale bar = 5 cm. Af: auditory foramen; Bo: basioccipital; bptp: basipterygoid process; Bsp: basisphenoid; Exo: exoccipital; Fr: frontal; Lsp: laterosphenoid; occ: occipital condyle; Op: opisthotic; Orb: orbitosphenoid; Par: parietal; Po: postorbital; Pro: proötic; So: supraoccipital; Sq: squamosal; Vc: Vidian canal; I-XII: foramina for cranial nerves.

Lateral wall of the braincase (Figure 7; Plate 2, Fig. 3b):

Description – The lateral wall of the braincase is formed, from back to front, by the opisthotic, the proötic, the laterosphenoid, the orbitosphenoid and the presphenoid. This part of the skull is mainly described, in the

present paper, from SBDE 95E5/30, but also from AMNH 6365 and 6366 (Quarry 141; GILMORE, 1933, fig. 24).

The opisthotic (Op) is closely fused with the adjacent bones, so that its limits cannot be easily demonstrated. It forms the caudal part of the lateral wall of the braincase. It is limited caudally by the exoccipital, ventrally by the

basioccipital, rostrally by the proötic and dorsally by the parietal and the squamosal. Its lateral side bears a prominent horizontal crest which represents the caudal half of the *crista otosphenoidale*, as it extends into the rostrolateral surface of the paroccipital process. The base of the opisthotic is pierced by the auditory foramen (Af). Dorsally, this foramen communicates with a large excavation of the opisthotic body, which circumscribes the inner ear, while ventrally, the glossopharyngeal nerve (c.n. IX) and the jugular vein exited the braincase.

The **proötic (Pro)** forms the median portion of the lateral wall of the braincase. It is limited caudally by the opisthotic, ventrally by the basisphenoid and dorsally by the parietal; it is covered rostrolaterally by the laterosphenoid. Its lateral surface bears the rostral portion of the *crista otosphenoidale*. This crista is interpreted by WEISHAMPEL (1984) as the origin of the *M. protractor pterygoideus*. The caudoventral corner of the proötic participates in the rostral margin of the auditory foramen and forms the rostral wall of the inner ear. Rostrally, its ventral margin is deeply notched by the caudal margin of the foramen for the trigeminal nerve (c.n. V). The foramen for the facial nerve (c.n. VII) pierces the ventral margin of the proötic between the auditory foramen and the trigeminal foramen.

The **laterosphenoid (Lsp)** is a large and stout bone which participates in the rostral portion of the lateral wall of the braincase. Caudally, it covers the rostrolateral surface of the proötic, in front of the trigeminal foramen, so that it seems to participate in the rostral margin of this aperture, in lateral view. It is limited ventrally by the basisphenoid, rostrally by the orbitosphenoid and dorsally by the parietal. It extends rostrolaterally from the front of the braincase to abut on a concavity between the medial

and ventral rami of the postorbital. This process extends on the lateral side of the laterosphenoid to form a nearly vertical prominent ridge and separates the orbital cavity from the upper temporal fenestra.

The fused **orbitosphenoid and presphenoid (Orb)** form the rostradorsal wall of the braincase. The orbitosphenoid forms the floor of the olfactive canal, while the presphenoid participates in the interorbital septum, above the parasphenoid. Caudally, they are in close contact with the rostrolateral ramus of the laterosphenoid and abut on the ventral surface of the postorbital. They fuse dorsally with the frontals. They open rostrally in the median plane to form a large olfactive tractus (c.n. I). The paired foramina for the optique nerves (c.n. II) form small gutters on the lateral side of the fused orbitosphenoid-presphenoid. Immediately caudally to these foramina, open those for the nerves III and VI (c.n.n. III-VI).

Discussion – In *Bactrosaurus johnsoni*, the opisthotic does not participate in the paroccipital process. LANGSTON (1960, fig. 152) shows that, on the other hand, the opisthotic clearly participates in the formation of this process, in a young specimen of the Campanian hadrosaurine *Lophorhothon atopus*. However, the systematic value of this character cannot be accurately estimated: in Iguanodontia, the exoccipital and opisthotic are completely fused in adult specimens, so that their limit cannot be precisely observed.

Parietal (Figure 8; Plate 3, Figs. 1 & 3):

Description – The parietals are completely fused at the midline into a single plate. Their lateral face form the median wall of the upper temporal fenestrae. The length

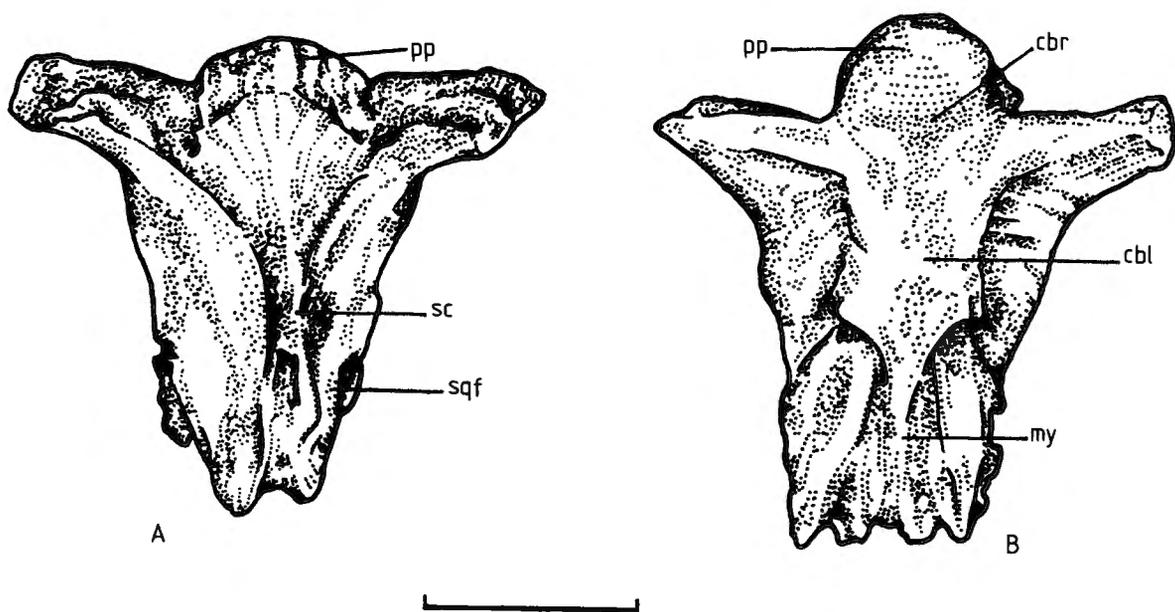


Fig. 8 – Parietal of *Bactrosaurus johnsoni* (SBDE 95E5/2), from the Iren Dabasu Formation- A: dorsal view; B: ventral view. Scale bar = 5 cm. cbl: impression of the cerebellum; cbr: impression of the cerebrum; my: impression of the myelencephalon; pp: parietal process; sc: sagittal crest; sqf: squamosal facet.

of the parietal plate equals its maximal width, taken between its rostralateral corners, and is worth more than twice its minimal width, taken between its caudolateral corners. The sagittal crests (**sc**) are completely fused together along a very short distance on the caudal portion of the bone. Rostrally, they quickly bifurcate and delimit a rhomboidal and flat rostromedian plate, the parietal process (**pp**); the sagittal crests are also slightly divergent quite caudally. The rostral border of the parietals has the shape of a "W" and is persillate, indicating a strong interpenetration with the frontals. The divergent rostralateral corners form a concave articular facet for reception of the caudal ramus of the postorbitals. In lateral view, the caudal border of the parietals is deeply notched by the articular facet for reception of the medial ramus of the squamosals (**sqf**).

In ventral view, the lateral portions of the parietal are bordered, along their whole length, by very developed facets for articulation with the bones forming the lateral wall of the braincase (laterosphenoid, proötic and opisthotic). The median portion bears impressions of some cerebral structures. The first encephalic impression forms a narrow, but deep depression at the level of the caudal third of the parietals: this can be interpreted as the impression of the myelencephalon (**my**). The second impression, ovoid in shape and more shallow than the first, lies at about the middle of the parietal: it is concluded to be the impression of the cerebellum (**cbl**). The ventral side of the parietal plate is deeply excavated by the caudomedial portion of the impression of the cerebrum (**cbr**).

Discussion – In *Bactrosaurus johnsoni*, the ratio "length / minimal width" of the parietal plate > 2 , a primitive condition observed in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *Iguanodon atherfieldensis*, *Tanius sinensis*, *Telmatosaurus transsylvanicus*, or in Hadrosaurinae. Shortening of the parietal is regarded as an independent acquisition of *Ouranosaurus nigeriensis* and Lambeosaurinae.

Frontal (Figure 9; Plate 3, Figs. 2 & 3):

Description – The frontals are the most massive elements of the skull roof. Contrary to the parietals, the paired frontals remain unfused and form a straight interfrontal suture. Each parietal is slightly longer than wide. The caudal border is persillate, for an interdigitate and strong connection with the parietal. The articular facet for reception of the postorbital (**pof**), on the caudolateral border of the frontal, is long, particularly thick, concave and very rough. The articular facet for reception of the prefrontal (**prf**) forms a very large and deep notch on the rostralateral border of the frontal; like the surface for the postfrontal, it is especially thick and rough. Inside the articular facet for the prefrontal, the rostral margin of the frontal is perforated by a deep depression for reception of the caudomedial process of the prefrontal. Between both articular facets, the lateral border of the frontal partici-

pates, along a short distance, in the dorsal margin of the orbit. The articular facet for reception of the nasal (**nf**) forms an elongated, triangular and smoothly concave surface on the dorsal side of the rostromedial corner of the frontal.

In ventral view, the caudomedial corner of the frontal is deeply depressed by the rostralateral portion of the impression area of the cerebrum (**cbr**). In the rostromedial corner of the cerebrum impression, an ovoid, deeply excavated and pitted area of unknown significance can be observed. A similar area was also described on the frontal of Liassic ichthyosaurs (MCGOWAN, 1973, fig. 11). The encephalic impression areas are surrounded by rugosities marking the contact with the laterosphenoid and orbitosphenoid portions of the braincase. Rostromedially, the ventral side of the frontal bears a third encephalic impression. This is ovoid, elongated and shallow and probably represents the impression of the olfactory lobe (**ol**).

As previously described by ROZHDESTVENSKY (1966) and MARYANSKA & OSMOLSKA (1979), a fronto-nasal fontanelle may be well developed in *Bactrosaurus johnsoni*. This structure invades the rostral portion of the interfrontal suture in AMNH6365 and AMNH 6366, for examples. It probably allowed for the gradual development and over-growth of the nasal region.

Discussion – The frontal of *Bactrosaurus johnsoni* is relatively elongated, as in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Tanius sinensis*, *Telmatosaurus transsylvanicus* and in flat-headed Hadrosaurinae. It is rostro-caudally shorter in hadrosaurids with supracranial crests, including Lambeosaurinae, but also *Prosaurolophus*, *Saurolophus*,

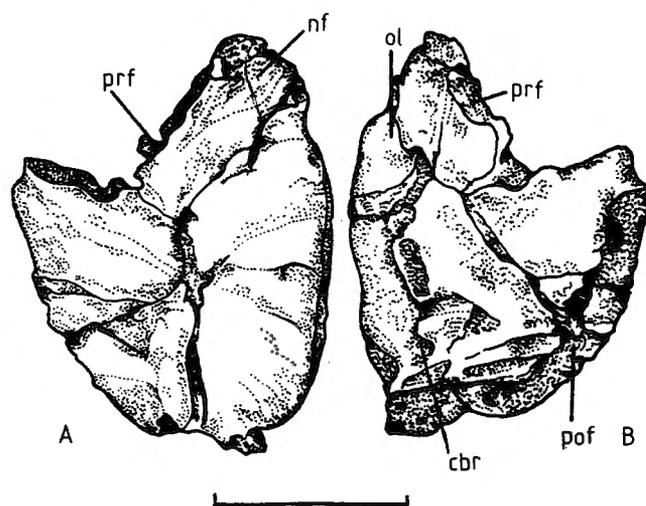


Fig. 9 – Left frontal of *Bactrosaurus johnsoni* (SBDE 95E/3), from the Iren Dabasu Formation - A: dorsal view; B: ventral view. Scale bar = 5 cm. cbr: impression of the cerebrum; nf: nasal facet; ol: impression of the olfactory lobe; pof: postorbital facet; prf: prefrontal facet.

Brachylophosaurus and *Maiasaura* (WEISHAMPEL & HORNER, 1990).

In *Bactrosaurus johnsoni*, the frontal participates in the dorsal orbital rim, as in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Tanius sinensis*, *Telmatosaurus transsylvanicus* and in Hadrosaurinae. It is entirely excluded from the orbit in Lambeosaurinae (WEISHAMPEL & HORNER, 1990).

The fronto-nasal fontanelle can be observed in several flat-headed Hadrosaurinae (see MARYANSKA & OSMOLSKA, 1979, fig. 2). In Lambeosaurinae, fronto-nasal fontanelles have never been identified, but this structure was apparently replaced by premaxillo-nasal fontanelles which apparently played the same role, allowing for the gradual development of the nasal region, but also for the great variability and complication of crest structures (see MARYANSKA & OSMOLSKA, 1979, fig. 3). Fontanelles occurred as long as the nasal region developed, in juvenile specimens, but also during a part of the adult life of the animals. As fontanelles have never been described in more basal ornithopods, including *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*, their presence is tentatively interpreted as a synapomorphy of *Bactrosaurus johnsoni* + more derived hadrosaurs. Nevertheless, because of lack of juvenile specimens, the polarity of this character is questionable in iguanodontids. Fontanelles have never been described in *Telmatosaurus transsylvanicus* neither, but WEISHAMPEL *et al.* (1993: 376) noted that there are no juveniles or subadults in the specimens currently discovered, as indicated by the degree of fusion of the braincase and vertebrae.

Premaxilla (Figure 10; Plate 3, Fig. 4):

Description – The premaxillae of *Bactrosaurus johnsoni* form a short beak, which is not especially expanded laterally, but distinctly deflected ventrally. Their rostral border is gently curved, with a ventral surface strongly, but irregularly denticulate. The denticulations are restricted to the rostral part of the oral margin of the premaxillae. The oral margin and adjacent rostral surface are roughened by pits and striations, suggesting a rhamphothecal covering in life. The rostr dors surface of the premaxilla forms an angle of about 55° with the ventral surface; it is perforated by several foramina. Behind the beak area, the rostromedial wall of the premaxilla is strongly depressed to form the external naris fossa, which is relatively small and forwardly set on the muzzle. A premaxillary foramen perforates the ventral part of the beak, from the interpremaxillary suture to the external border of the external naris. The ascending process of the premaxilla (**apr**) is slightly curved dorsally, narrow and triangular in cross-section; rostrally, it is supported by a thin and incomplete internasal septum. The caudolateral ramus of the premaxilla (**clr**) is tapering and laterally compressed. Its height progressively increases caudally, but the caudalmost portion of the bone is always broken

in the specimens currently discovered. In ventral view, the rostral part of the premaxilla is moderately vaulted and forms a short and thin secondary hard palate separating the rostral parts of the nasal and labial cavities.

Discussion – The premaxillae of *Bactrosaurus johnsoni* extend laterally without other alteration of the margins of the naris fossa. This primitive condition is also retained in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus* and in Lambeosaurinae. In contrast, the lateral borders of the premaxillae fold dorsally to form a prominent reflected lip that marks the ventral wall of the narial fossa in all Hadrosaurinae (WEISHAMPEL & HORNER, 1990; WEISHAMPEL *et al.*, 1993).

The oral margin of the premaxilla is coarsely denticulate in *Bactrosaurus johnsoni*, as in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis* and *Telmatosaurus transsylvanicus*. In Hadrosaurinae and Lambeosaurinae, the oral margin of the premaxilla is rough and slightly serrated. In *Hypsilophodon foxii*, this character is meaningless, as premax-

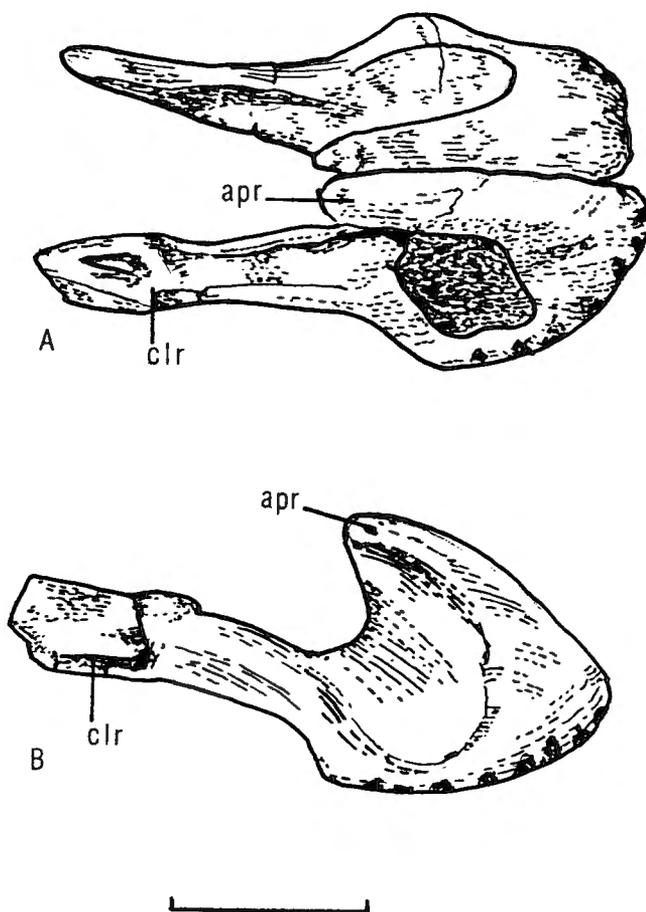


Fig. 10 – Premaxillae of *Bactrosaurus johnsoni* (SBDE 95E5/4-4bis), from the Iren Dabasu Formation - A: dorsal view; B: lateral view of the right premaxilla. Scale bar = 5 cm. apr: ascending process; clr: caudolateral ramus.

illary teeth are preserved.

The external naris of *Bactrosaurus johnsoni* is not particularly enlarged. This primitive condition is retained in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus*, in Lambeosaurinae and in *Maiasaura peeblesorum* (probable reversion in the latter: WEISHAMPEL *et al.*, 1993): the ratio "length of the external naris / basal skull length" < 0.20 . In contrast, the external naris is relatively large (up to 40 percent of the basal skull length) in Hadrosaurinae (HORNER, 1990;

WEISHAMPEL *et al.*, 1993). The small external naris of *Maiasaura peeblesorum* then would constitute a reversal in Hadrosaurinae.

The absence of premaxillary foramen is regarded as a synapomorphy of the Lambeosaurinae (HORNER, 1990; WEISHAMPEL *et al.*, 1993).

Maxilla (Figure 11; Plate 4, Fig. 1):

Description – The maxilla is the most massive bone of the skull. In lateral view, it is triangular in shape, the

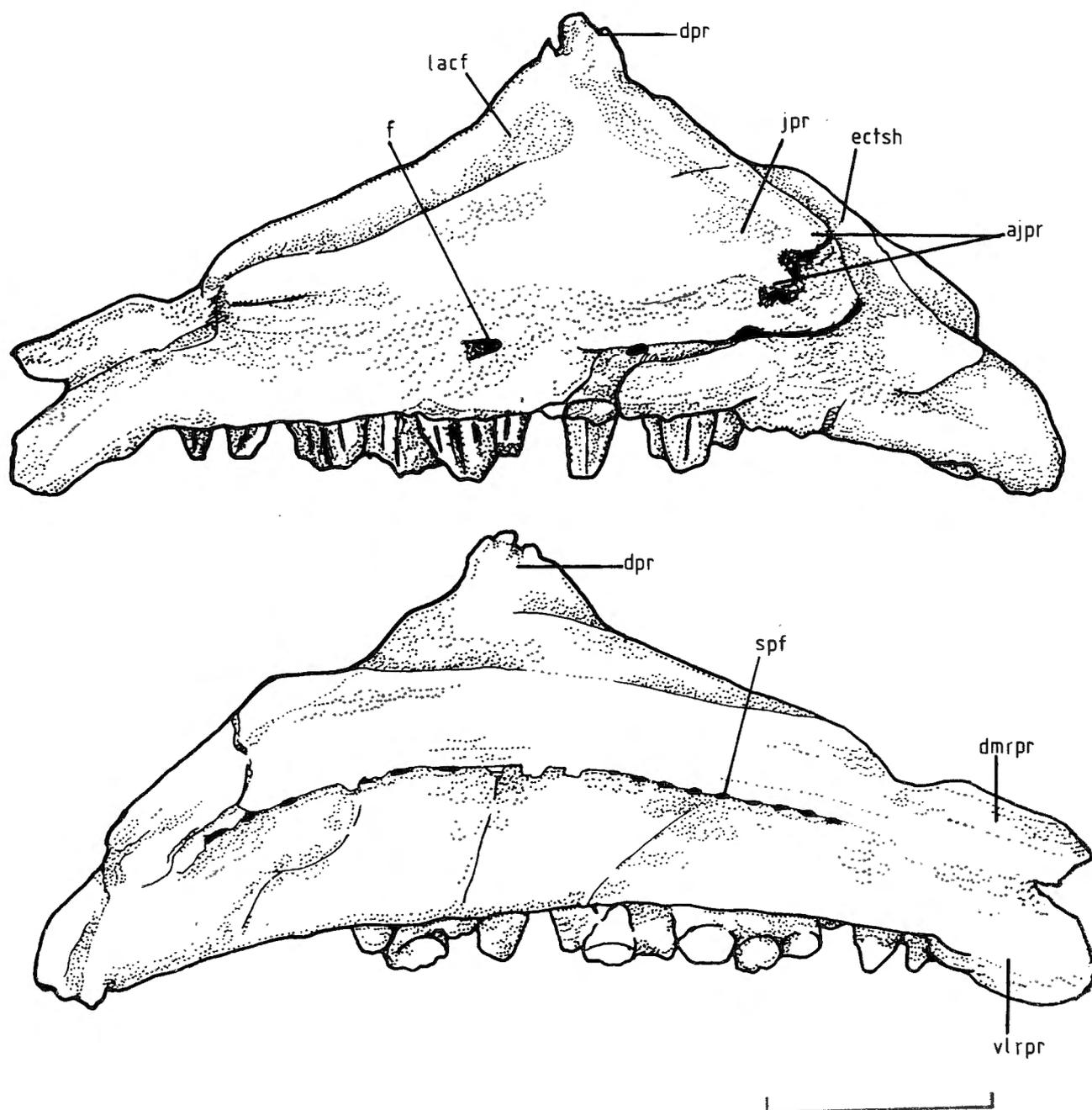


Fig. 11 – Left maxilla of *Bactrosaurus johnsoni* (SBDE 95E5/5), from the Iren Dabasu Formation- A: lateral view; B: medial view. Scale bar = 5 cm. ajpr: apophyses of the jugal process; dmrpr: dorsomedial rostral process; dpr: dorsal process; ectsh: ectopterygoid shelf; f: foramen; jpr: jugal process; lacf: lacrimal facet; spf: special foramina; vlrpr: ventrolateral rostral process.

upper dental row forming the base of the triangle. It is very elongated, about three times as long as high. The high dorsal process (**dpr**) lies somewhat behind the mid-point and forms an angle of 90° between the rostradorsal and the caudodorsal borders of the lateral side. An elongated facet along the rostralateral side of the dorsal process marks the contact with the lacrimal (**lacf**).

As in all advanced ornithopods, the jugal process (**jpr**) forms a prominent elliptical promontorium beneath and caudally to the dorsal process, on the lateral side of the maxilla; this process is inclined towards the apex and slightly rostrally. Its caudal ends bears two apophyses (**ajpr**), separated by a deep notch, to receive the maxillary process of the jugal. The base of the jugal process is pierced by three or four aligned foramina (**f**). They probably represent neurovascular canals that conduct branches of the maxillary nerve and vessels to the labial cavity and cheek region, as in other ornithischians (WEISHAMPEL *et al.*, 1993). Medially to the jugal process, a deep groove penetrates into the body of the maxilla: this groove received the *M. pterygoideus dorsalis* (OSTROM, 1961, fig. 43). A broad ectopterygoid shelf (**ectsh**) continues caudally from this groove. Along the mesiodorsal side of the ectopterygoid shelf, a field of longitudinal ridges probably marks the articular surface for the palatine.

Rostrally, the maxilla is bifid, formed by two processes, a ventrolateral (**vlrpr**) major process and a dorsomedial (**dmrpr**) one. They form together the broad concave contact surface for the reception of the under-surface of the premaxilla. Medially to the dorsal border of the dorsomedial process, and somewhat beneath its level, an horizontal lamina took part, with its symmetrical, in the floor of the external nasal aperture.

The alveolar border of the maxilla is slightly concave. About 30 mm above the alveolar border, the medial maxillary surface is pierced by a series (about 30) of special foramina (**spf**) interconnected by a groove along the whole length of the bone. These can be interpreted as foramina for the entry of nutritive blood vessels and sensory nerves into the dental lamina.

In adult specimens, the alveolar groove contains about 20 tooth positions. Each tooth position contains at least three teeth (functional plus replacement).

Discussion – The maxilla of *Gilmoresaurus mongoliensis*, from the same locality, differs from that of *Bactrosaurus johnsoni* by its dorsal process lying approximately at the mid-point of the bone and by the number of tooth positions significantly higher (29), when compared with specimens of about the same size.

For GILMORE (1933) and WEISHAMPEL & HORNER (1986), the dorsal process of the maxilla lying up behind the midpoint is a lambeosaurine character observed in *Bactrosaurus johnsoni*. Nevertheless, the rostral portion of the maxilla is distinctly longer than the caudal portion in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*. The asymmetry of the maxilla must therefore be regarded as ple-

iomorphic and the symmetrical maxillae, as observed in *Gilmoresaurus mongoliensis* and Hadrosaurinae, as apomorphic. The polarity of this character cannot be confidently established in *Telmatosaurus transsylvanicus*, as the rostral portion of the maxilla is never completely preserved.

The maxilla of *Bactrosaurus johnsoni* is relatively low, compared to that of more derived Hadrosauridae; this is probably related to the development of the maxillary dental battery. A consequence of this elevation of the dorsal process of the maxilla is the migration of the antorbital fenestra to take a position along the upper portion of the premaxillary articular surface; it forms an oval foramen that communicates with the region behind the dorsal process in *Telmatosaurus transsylvanicus* and in Hadrosauridae. This character is not present in *Bactrosaurus johnsoni*, which consequently possessed a laterally positioned antorbital fenestra, as in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*.

The lateral surface of the dorsal process of the maxilla forms the articular surface of the lacrimal. This is regarded as the primitive condition in ornithopods, as it is observed in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus* and Hadrosaurinae. In Lambeosaurinae, on the other hand, the lacrimal fits into a small longitudinal groove below the dorsal edge of the process, giving the impression that the lacrimal is lapped laterally by the maxilla in articulated specimens (WEISHAMPEL & HORNER, 1990).

For HORNER (1990), the presence of two rostral processes characterizes the maxilla of the Hadrosaurinae (his "Hadrosauridae"). The dorsomedial process of the maxilla fits into a groove on the dorsal surface of the lower premaxillary process and participates in the medial floor of the external naris, while the ventrolateral process extends rostrally beneath the premaxilla for support. A similar condition can be observed in species of *Iguanodon*. In lambeosaurines (his Lambeosauridae), on the other hand, there exists only a maxillary shelf (?ventrolateral maxillary process) and a medial flange upon which the premaxilla rests; no maxillary process exists to contact the dorsal portion of the premaxilla. For HORNER (1990), a similar condition can be observed in *Ouranosaurus*, although the rostral portion of the only known maxilla in this genus is broken (TAQUET, 1976, fig. 17, pl. 18, fig. 4). WEISHAMPEL *et al.* (1993) do not believe that a maxillary shelf is developed in *Ouranosaurus* and regard this character as a synapomorphy for the Lambeosaurinae. This hypothesis is followed in the present paper.

For NORMAN (1990), the maxillae of *Iguanodon* and *Ouranosaurus* share two synapomorphies: the jugal process is particularly prominent and projects caudoventrally from the lateral body of the maxilla; the lacrimal process is also prominent and forms the rostral margin of the antorbital fenestra. The presence of a secondary lacrimal

process seems characteristic of *Ouranosaurus nigeriensis* (TAQUET, 1976, fig. 17).

The number of maxillary dental positions is much lower in adult specimens of *Bactrosaurus johnsoni* (about 20) than in any other known hadrosaur: e.g. 29 in *Gilmoreosaurus johnsoni*, 31 in *Telmatosaurus transsylvanicus* and in *Parasaurolophus walkeri*, 35 in *Prosaurolophus maximus*, 38 to 39 in *Lambeosaurus lambei*, 39 in *Corythosaurus casuarius*, 42 in *Maiasaura peeblesorum*, 43 in *Edmontosaurus annectens* and in *Corythosaurus casuarius*, 46 to 47 in *Hypacrosaurus altispinus*, 51 to 53 in *Edmontosaurus regalis*, 52 in *E. saskatchewanensis*, 60 in *Saurolophus osborni*. It seems that this low number of dental positions on the maxilla is a primitive character, as it can also be observed in more basal ornithopods: from 14 to 16 in *Camptosaurus dispar*, 19 in *Iguanodon lakotaensis*, 22 in *Ouranosaurus nigeriensis*, 23 in *Iguanodon atherfieldensis*, but a maximum of 29 dental position can be observed in *I. bernissartensis*. It must be kept in mind that this character is largely size/age dependent.

Nasal (Figure 12; Plate 4, Fig. 3):

Description – The nasal of *Bactrosaurus johnsoni* is long and slender. It is formed by two plates – a lateral and a dorsal one – forming together an angle of about 90°. The dorsal plate is slightly convex dorsally. It roofed the snout caudally to the nostril. The dorsal plates of the paired nasals contact together in a straight suture for much of their length. They diverge rostrally, where they become thin and style-like. At this level, an elongated contact surface marks the rostral recovering of the nasal by the caudal portion of the ascending process of the premaxilla (pmf). The caudal end of the dorsal plate is also divergent

and tapering. It overlapped the rostromedian corner of the frontal. Ventrally, an elongated contact surface runs along the caudal portion of the lateral border of the dorsal plate: it marks the articulation with the prefrontal.

The lateral plate is present along the rostral 3/5 of the bone; it progressively develops from the lateral border of the dorsal plate. Rostrally, the ventral border of the lateral plate is emarginate and formed the caudodorsal margin of the external naris (nar). Its tapering rostral end lays in a bevelled recess along the lateral side of the ascending process of the premaxilla. Caudally to the nasal emargination, the ventral margin of the lateral plate is grooved, so that it locked onto the dorsal margin of the caudolateral ramus of the premaxilla.

Discussion – The description of the nasal of *Bactrosaurus johnsoni* proves that this was a flat-headed animal (*contra* WEISHAMPEL & HORNER, 1986; see below). The nasals are not modified to form any part of a hollow crest, contrary to the Lambeosaurinae. It also shows that the orientation of the prefrontal proposed in the present paper (see below) is correct, as it perfectly articulates with the caudoventral border of the nasal.

The nasal of *Bactrosaurus johnsoni* differs from that of *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and, especially, of *Ouranosaurus nigeriensis*, by its long and slender aspect.

The nasal of *Bactrosaurus johnsoni* participates in the caudodorsal margin of the external naris. This primitive condition is also retained in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus* and Hadrosaurinae. In Lambeosaurinae, on the other hand, the external naris is completely sur-

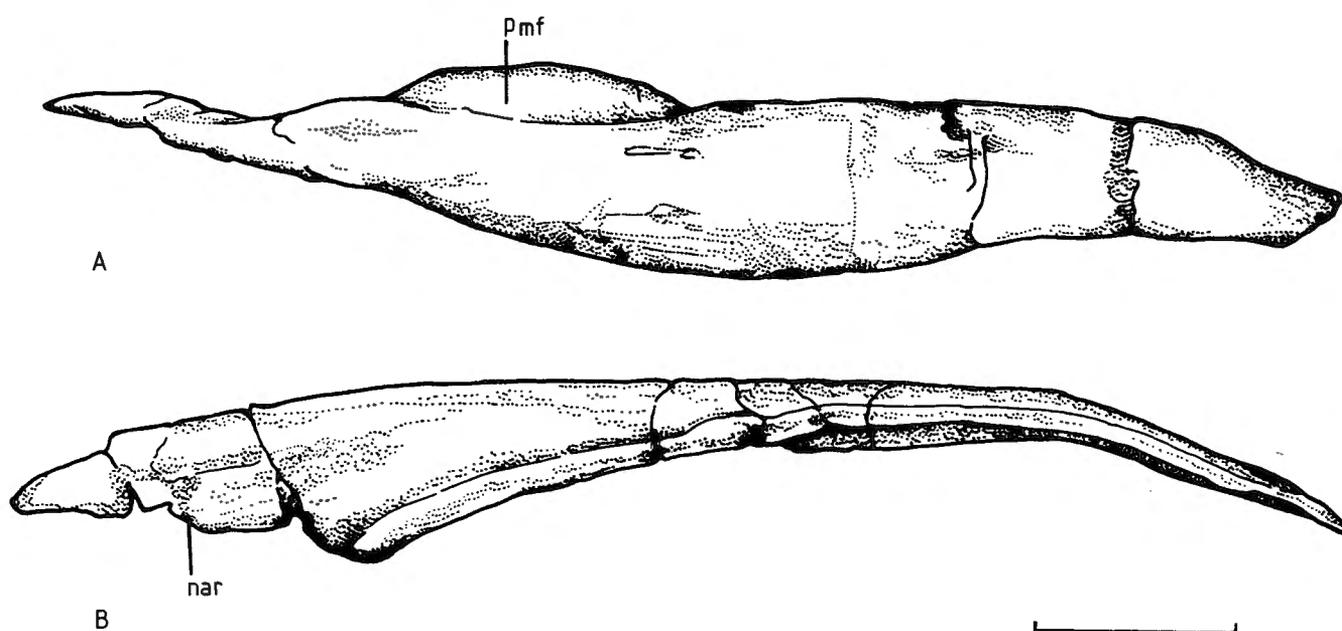


Fig. 12 – Left nasal of *Bactrosaurus johnsoni* (SBDE 95E5/6), from the Iren Dabasu Formation - A: dorsal view; B: lateral view. Scale bar = 5 cm. nar: margin of the external naris; pmf: premaxillary facet.

rounded by the premaxilla (HORNER, 1990; WEISHAMPEL *et al.*, 1993).

The nasal of *Bactrosaurus johnsoni* is not marked by a fossa or excavation, which is a plesiomorphy retained in *Hyposilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis* and *Telmatosaurus transsylvanicus*. A marked circumnarial extending onto the nasal unites the Hadrosaurinae clade (HORNER, 1990; WEISHAMPEL *et al.*, 1993). Because of the migration of the nasal cavity in lambeosaurines to a supracranial position, a circumnarial depression is regarded as missing in this taxon.

There is no trace of any solid crest on the nasal of *Bactrosaurus johnsoni*, neither. This is a plesiomorphy also observed in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Telmatosaurus transsylvanicus* and, of course, in Lambeosaurinae, which are characterized by a hollow crest. In *Prosaurolophus maximus* and *Saurolophus osborni*, the nasals and frontals are raised in a narrow, low-lying and solid crest: this character is regarded as a synapomorphy uniting these two genera. *Maiasaura peeblesorum* and *Brachylophosaurus canadensis* share a broad solid crest on their supraorbital region (WEISHAMPEL & HORNER, 1990). This character appeared convergently in *Ouranosaurus nigeriensis*.

Jugal (Figure 13; Plate 4, Fig. 2):

Description – The jugal forms the ventral margin of the orbit and infratemporal fenestra and the ventral half of the postorbital bar. As in virtually all Iguanodontia, it is thin, flat and elongated. The rostral process of the jugal (**rpr**) is very long, but shows little dorsoventral expansion and is rounded. Its medial surface forms a very elongated and excavated maxillary facet (**mxf**), contacting the jugal process of the maxilla; its surface is strongly striated for ligaments that tightly bound the jugal to the maxilla. The caudoventral border of the maxillary contact surface is very elevated and bears a crescentic and very concave maxillary process (**mxpr**), articulating with the two caudal apophyses of the jugal process of the maxilla. A crest, descending from the rostral border of the maxillary process, fitted into the notch separating the apophyses of the jugal process of the maxilla. The facet for articulation with the palatine (**palf**) is bordered ventrally by the salient dorsal border of the maxillary facet and laterally, by a small carina, on the caudodorsal margin of the rostral process. Rostrally to the palatine facet, the dorsal border of the rostral process of the jugal is everted: it probably participated in the ventral margin of the antorbital fenestra.

The ascending process of the jugal (**aspr**), separating the lower portion of the orbit and of the infratemporal fenestra, is thin, triangular in cross-section and inclined caudally. The facet for articulation with the postorbital (**pof**) occupies the apical third of the ascending process; it is very excavated, facing rostrally and laterally.

The caudal process of the jugal (**cpr**) is dorso-ventrally narrow; its rostral and caudal portions form together an

angle of about 110°. The ventral margin of its caudal portion is nearly straight. The lateral side of the caudal process is striated for attachment of the cheek musculature. Medially, it bears a large angular facet for reception of the rostral process of the quadratojugal (**qjf**).

Discussion – The jugal of *Bactrosaurus johnsoni* closely resembles that of *Gilmoreosaurus mongoliensis*, from the same locality: the most striking differences between the two forms are the more elongated rostral process of the former and the more robust caudal process observed in the latter. In *Tanius sinensis*, from the Wanshi series of China, the caudal process of the jugal looks much narrower than in *Bactrosaurus johnsoni*.

The jugal of *Bactrosaurus johnsoni* is rather gracile, like in most advanced ornithomorphs. A striking enlargement of the jugal is apomorphically observed in *Edmontosaurus* and *Anatotitan* (WEISHAMPEL & HORNER, 1990; WEISHAMPEL *et al.*, 1993).

For SERENO (1986), a dorsoventral expansion of the rostral process of the jugal constitutes a synapomorphy for the clade of *Ouranosaurus* + Hadrosauridae. Nevertheless, it must be noted that the dorsoventral expansion observed in *Ouranosaurus nigeriensis*, *Bactrosaurus johnsoni*, *Gilmoreosaurus mongoliensis* and *Tanius si-*

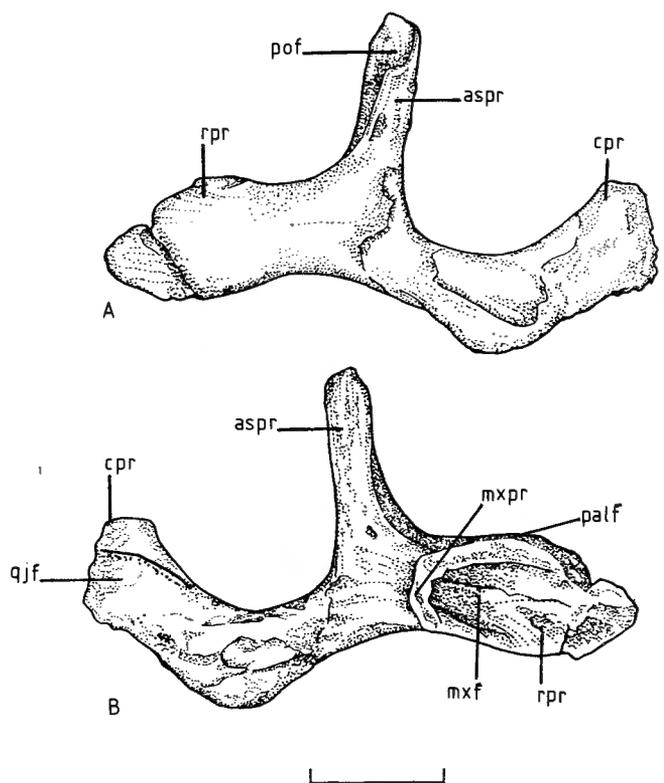


Fig. 13 – Left jugal of *Bactrosaurus johnsoni* (SBDE 95E5/7), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 5 cm. aspr: ascending process; cpr: caudal process; mxf: maxillary facet; mxpr: maxillary process; palf: palatine facet; pof: postorbital facet; qjf: quadratojugal facet; rpr: rostral process.

nensis is less important than in *Telmatosaurus transsylvanicus* and in Hadrosauridae and is rather reminiscent of that of more basal Iguanodontia.

The rostral process of the jugal of Lambeosaurinae is apomorphically truncated and rounded (WEISHAMPEL *et al.*, 1993), although it is elongated and rather angulous in Hadrosaurinae, as well as in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Gilmoresaurus mongoliensis*, *Tanius sinensis* and *Telmatosaurus transsylvanicus*.

In *Bactrosaurus johnsoni*, the ventral margin of the caudal process of the jugal is nearly straight, like in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Gilmoresaurus mongoliensis*, *Tanius sinensis*, *Telmatosaurus transsylvanicus*, Lambeosaurinae and in the majority of the Hadrosaurinae. It is ventrally concave, yielding a scalloped silhouette in lateral view, in *Maia-saura peeblesorum*, *Gryposaurus notabilis* and *Brachy-*

lophosaurus canadensis (WEISHAMPEL *et al.*, 1993). The caudal process of the jugal looks consequently especially shallow in the last three species.

The important elongation of the maxillary facet and the possible participation of the dorsal border of the rostral process in the ventral margin of the antorbital fenestra are regarded as autapomorphic in *Bactrosaurus johnsoni*.

Quadrate (Figure 14; Plate 5, Fig. 1):

Description – The quadrate is a stout pillar-like element forming the suspensorium by which the lower jaw is braced against the braincase. In lateral view, it is very high and relatively narrow rostro-caudally. Its caudal border is regularly concave, so that the body of the quadrate looks curved caudally. The dorsal head, which articulated into the cotyloid cavity of the squamosal, is slightly rounded in lateral view and triangular in dorsal view. A small caudal process is present below the dorsal head on some specimens. The rostral border is sigmoidal.

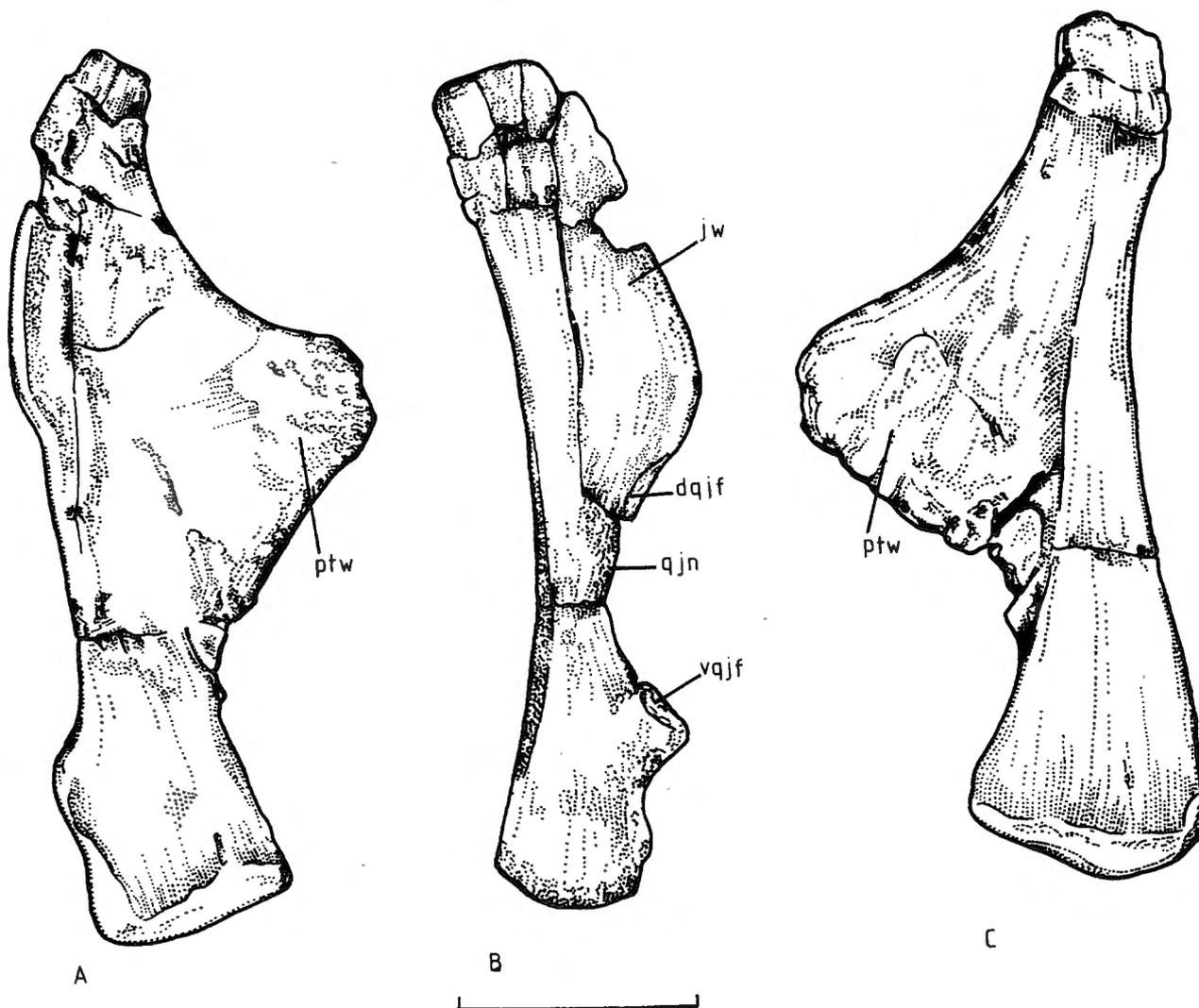


Fig. 14 – Right quadrate of *Bactrosaurus johnsoni* (SBDE 95E5/8), from the Iren Dabasu Formation – A: rostral view; B: lateral view; C: caudal view. Scale bar = 5 cm. dqjf: dorsal quadratojugal facet; jw: jugal wing; ptw: pterygoid wing; qjn: quadratojugal notch; vqjf: ventral quadratojugal facet.

The thin jugal wing (**juw**) forms its convex dorsal half, whereas the quadratojugal notch (**qjn**) forms a long and deep embayment beneath this wing. Two articular facets for the quadratojugal can be observed. The dorsal quadratojugal facet (**dqjf**) is set along the lateral border of the quadratojugal notch, just beneath the jugal wing; the ventral quadratojugal facet (**vqjf**) forms a buttress, facing rostrally and laterally, at the base of the quadratojugal notch.

The large and triangular pterygoid wing (**ptw**) extends medially, forming a right angle with the jugal wing. Relatively thin, its surface is convex rostrally. The area comprised between the pterygoid wings and the lateral wall of the quadrate served as the site of a large fleshy origin of the *M. adductor mandibulae posterior* (OSTROM, 1961, fig. 46). At the base of the pterygoid wing, the caudomedial surface of the quadrate displays a small medial ridge, against which a stout caudal shaft of the pterygoid abuted, apparently reënforcing quadrate immobility (OSTROM, 1961).

The ventral condyle of the quadrate is well rounded and distinctly bicondylar, being transversely broad and medially inclined.

Discussion – The quadrate of *Gilmoreosaurus mongoliensis* differs from that of *Bactrosaurus johnsoni* in being less curved in lateral view, but also in its ovate dorsal head.

The presence of well marked quadratojugal facets at the base and at the top of a large and deep quadratojugal notch indicates that a paraquadrate foramen was developed in *Bactrosaurus johnsoni*, as in *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis* and, probably, in *Gilmoreosaurus mongoliensis*. Such a foramen is not developed in Hadrosauridae and probably in *Telmatosaurus transsylvanicus* (WEISHAMPEL *et al.*, 1993). The situation is not clear in *Camptosaurus dispar*. In *Hypsilophodon foxii*, the paraquadrate foramen lies entirely within the body of the quadratojugal.

The transversely broad and bicondylar ventral head of the quadrate, as observed in *Bactrosaurus johnsoni*, *Gilmoreosaurus mongoliensis* and *Telmatosaurus transsylvanicus* is regarded as a plesiomorphy retained in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*. In contrast, all Hadrosaurinae and Lambeosaurinae share a relatively narrow and sub-hemispherical mandibular condyle (WEISHAMPEL & HORNER, 1990; WEISHAMPEL *et al.*, 1993).

Squamosal (Figure 15; Plate 5, Fig. 2):

Description – The squamosal forms the caudodorsal corner of the skull. It participates in the caudal part of the supratemporal fenestra and connects the braincase medially to the suspensorium ventrally and the postorbital region rostrally. No squamosal is completely preserved in the material currently referred to *Bactrosaurus johnsoni*, but the study of specimens discovered in Lo-

cality 95E5 permits a good reconstruction of this bone. The medial ramus (**mr**) tapers and curves rostrally to contact the lateral side of the parietal. From AMNH 6365 and 6366, it appears that the medial rami of the paired squamosals are well separated from each other. The rostral ramus (**rr**) of the squamosal is short, broad and slightly curved outwards; it articulates with the caudal ramus of the postorbital. The lateroventral part of the squamosal bears two processes: the precotyloid process and the postcotyloid process (**pocp**). They limit a concave area, the cotyloid cavity, which received the dorsal head of the quadrate. The precotyloid process is very incompletely preserved on the material currently referred to *Bactrosaurus johnsoni*. The postcotyloid process is prominent and triangular in cross-section. It extends downwards and slightly outwards; in lateral view, it is markedly curved caudally. Its rostromedial side is grooved by the contact surface for the paroccipital process of the exoccipital (**parf**). At the angle between the postcotyloid process and the medial ramus, the ventral side of the squamosal bears a deep elliptical articular cupule, forming a synovial joint with the dorsal angle of the paroccipital process (**parcup**).

Discussion – Because of the rostral slope of the medial rami of the paired squamosals, the back of the skull looks deeply indented when viewed from above. Such an indentation seems to be plesiomorphic in ornithomorphs, as it can also be observed in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus* and *Tanius sinensis*. The caudal border of the skull is more or less straight in Hadrosaurinae and Lambeosaurinae.

The medial rami of the paired squamosals are well separated at the midline by the parietal in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*,

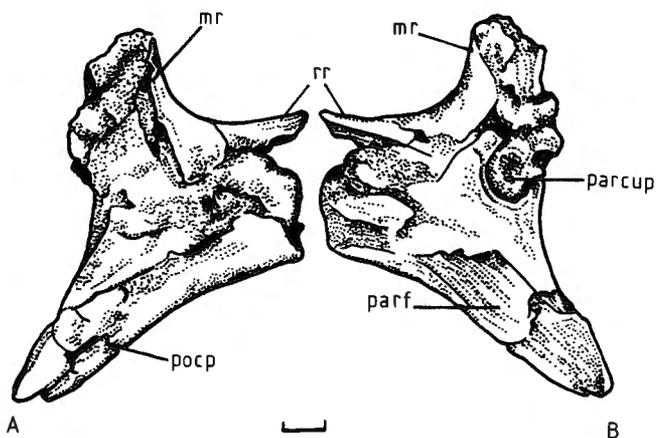


Fig. 15 – Right squamosal of *Bactrosaurus johnsoni* (SBDE 95E5/9), from the Iren Dabasu Formation – A: dorso-lateral view; B: ventromedial view. Scale bar = 1 cm. mr: medial ramus; parcup: paroccipital cupule; parf: paroccipital facet; pocp: postcotyloid process; rr: rostral ramus

Ouranosaurus nigeriensis, *Bactrosaurus johnsoni*, *Tanius sinensis* and *Telmatosaurus transsylvanicus*. In Hadrosaurinae, these rami tend to meet at the midline, or are only separated by a thin median flange of the parietals. In Lambeosaurinae, the squamosals contact one another along the midline in an elevated occipital crest (WEISHAMPEL & HORNER, 1990).

The postcotyloid process markedly curved backwards constitutes an autapomorphy of *Bactrosaurus johnsoni*, as, to our knowledge, it has not been reported in any other known ornithomimid.

Lacrimal (Figure 16):

Description – Only one incomplete lacrimal (SBDE 95E5/10) can be identified in the material currently referred to *Bactrosaurus johnsoni*; the ventral plate of this bone is missing. The lateral side of the bone is slightly concave both dorso-ventrally and rostro-caudally. Its caudodorsal corner forms a large, triangular and rugose facet which contacted the supraorbital (sof). The caudal surface of the lacrimal, which participated in the rostral margin of the orbit (rmo), is very broadened and very concave. It is perforated by a large caudal foramen for the

lacrimal canal (cflc). In front of the orbital margin, the medioventral border of the lacrimal is deeply excavated by a circular maxillary depression (mxd), which capped the dorsal end of the dorsal process of the maxilla. In front of the maxillary depression, the rostral foramen of the lacrimal canal (rflc) opens into the nasal cavity. Both depressions are separated from each other by the maxillary apophysis of the lacrimal (mxap). The caudal part of the dorsal border of the lacrimal forms a broad and concave surface for reception of the prefrontal (prf). Rostrolaterally to the latter, lies the concave contact surface for the caudolateral ramus of the premaxilla (pmf).

Discussion – Although incomplete, the lacrimal of *Bactrosaurus johnsoni* seems particularly thick, when compared with that *Gilmoreosaurus mongoliensis* (AMNH 6551), *Iguanodon atherfieldensis* and *Ouranosaurus nigeriensis*. As the lacrimal is extensively overlapped by the neighbouring bones, this bone is usually described briefly in most hadrosaurids and precise comparisons with these forms are consequently impossible in the current state of our knowledge.

Prefrontal (Figure 17; Plate 5, Fig. 3):

Description – In lateral view, the prefrontal is crescentic in outline and formed by two portions. The caudal ramus (cr), which forms the rostradorsal portion of the orbital margin, is smoothly rounded and relatively flat dorso-ventrally. Its caudal and medial margins, which contacted the rostralateral notch of the frontal, are thick and very roughened; a caudomedial process (cmp) lodged into the deep depression inside the articular surface for the prefrontal of the frontal. In dorsal view, an elongated contact facet for the nasal (nf) runs along the medial border of the caudal portion of the prefrontal. The rostral plate (rpl) of the prefrontal is higher and much thinner mediolaterally. It is excavated internally where it enclosed the nasal cavity. A foramen (f) perforates its lateral wall. A triangular lacrimal process (lpr) extends ventromedially to the rostral plate. The dorsal side of the lacrimal was set between the lateral side of this lacrimal process and the ventral border of the rostral plate.

Discussion – The interpretation of the prefrontal bone of *Bactrosaurus johnsoni* proposed above is completely different from that proposed by WEISHAMPEL & HORNER (1986). Indeed, these authors describe prefrontals which, by their vertical nature, may support the lateral wall of a hollow supracranial crest. This interpretation is consistent with the inclusion of *Bactrosaurus johnsoni* within the subfamily Lambeosaurinae, as argued by these authors. A careful reexamination of the material preserved in the AMNH and a detailed comparison with the material recently discovered in Iren Dabasu indicate that the orientation of the prefrontals proposed by WEISHAMPEL & HORNER (1986, fig. 3) is not correct. AMNH 8587 is not a right, but a left prefrontal: the “vertical lateral wall”

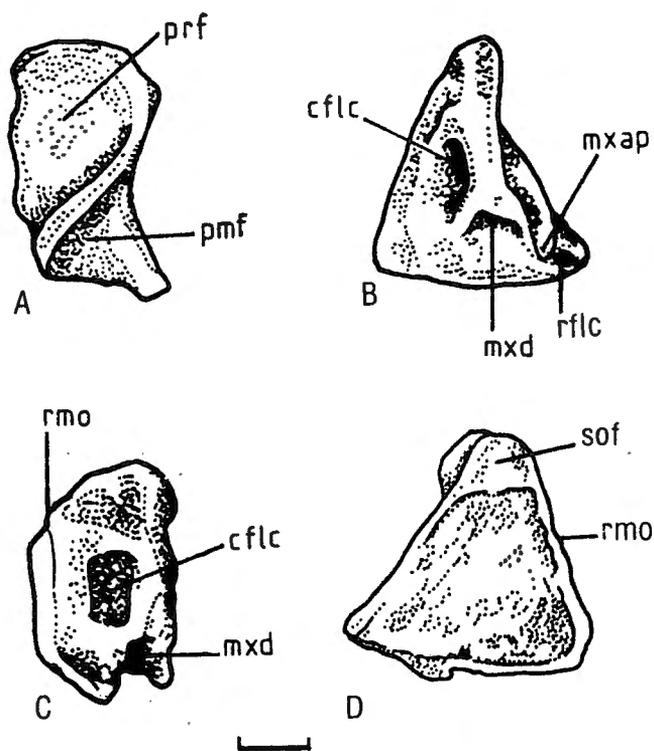


Fig. 16 – Left lacrimal of *Bactrosaurus johnsoni* (SBDE 95E5/10), from the Iren Dabasu Formation - A: rostral view; B: medial view; C: caudal view; D: lateral view. Scale = 1 cm. cflc: caudal foramen for the lacrimal canal; mxap: maxillary apophysis; mxd: maxillary depression; pmf: premaxillary facet; prf: prefrontal facet; rflc: rostral foramen for the lacrimal canal; rmo: rostral margin of the orbit; sof: supraorbital facet.

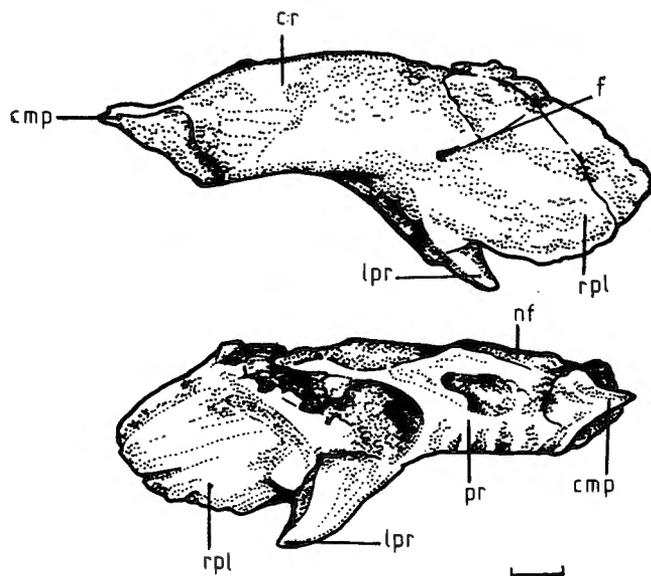


Fig. 17 – Right prefrontal of *Bactrosaurus johnsoni* (SBDE 95E5/11), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 1 cm. cmp: caudomedial process; cr: caudal ramus; f: foramen; lpr: lacrimal process; rpl: rostral plate.

corresponds in fact to the rostral plate of the prefrontal. The new orientation of the prefrontals proposed in the present paper permits good articular relationships of the prefrontals with the kinds of frontals and nasals discovered in both localities 141 and 95E5.

Consequently, the prefrontals of *Bactrosaurus johnsoni* resemble, because of their flat caudal ramus, those found in Hadrosaurinae, but also in more basal ornithopods. Comparisons with the isolated prefrontal of *Iguanodon atherfieldensis* (see NORMAN, 1986, fig. 13) is particularly instructive. It can be concluded that there is no trace of hollow supracranial crest in the hadrosauroid material currently discovered in Iren Dabasu.

Postorbital (Figure 7; Plate 5, Fig. 4):

Description – The postorbital is a triradiate bone, formed by a medial, a caudal and a ventral ramus, oriented at about 90° from each other.

The medial ramus contacts the frontal and the rostrolateral corner of the parietal. It forms the rostrolateral corner of the upper temporal fenestra and the caudodorsal corner of the orbit. It is excavated ventrally to receive the lateral process of the laterosphenoid. The postorbital and the laterosphenoid are not fused together, but form a synovial joint (TAQUET, 1976; WEISHAMPEL, 1984).

The caudal ramus is elongated and limits laterally the upper temporal fenestra. It articulates caudally with the squamosal on a long and oblique suture.

The ventral ramus is incompletely preserved on the material currently referred to *Bactrosaurus johnsoni*. It is thin, triangular in cross-section and inclined forwards. Together with the ascending process of the jugal, it

formed the postorbital bar, separating the orbital cavity from the lower temporal fenestra.

Discussion – The postorbital of *Bactrosaurus johnsoni* closely resembles that of *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, Lambeosaurinae and generalized Hadrosaurinae. In species of *Edmontosaurus*, *Anatotitan copei* and possibly *Shangtungosaurus giganteus*, the body of the postorbital is deeply excavated on its orbital surface: the postorbital consequently flares from the side of the orbit and greatly restricts the upper part of the infratemporal fenestra (OSTROM, 1961; WEISHAMPEL & HORNER, 1990).

Supraorbital (Plate 5, Fig. 5):

Description – The supraorbitals are large spin-like elements, formed by a rostral plate and a caudal ramus. They contacted the prefrontal and / or the lacrimal. The rostral plate is rhomboidal in outline; its external surface is very convex dorso-ventrally, while its medial articular surface is deeply concave and roughened. The caudal ramus is triangular in cross-section and flattened dorso-ventrally; it curves outwards and slightly upwards.

Discussion – The presence of supraorbitals is a primitive character in ornithopods observed, for examples, in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis* and *Bactrosaurus johnsoni*. This bone is not reported in *Telmatosaurus transsylvanicus*, but the referred cranial material is incomplete in this species. MARYANSKA & OSMOLSKA (1981) and HORNER (1983) showed that in Lambeosaurinae and Hadrosaurinae, the absence of supraorbital bones can be explained by their fusion with the prefrontals: in these taxa, the “prefrontal” is therefore a coalescence of the true prefrontals with the supraorbitals. Additional supraorbitals fuse with the orbital margin of the frontals and sometimes with the postorbitals.

Predentary (Plate 6, Fig. 2):

Description – The predentary of *Bactrosaurus johnsoni* has the shape of an horseshoe, as usual in Iguanodontia. It is short and regularly curved, except in juveniles specimens, in which the rostral rim is straighter. In ventral view, the median part of the predentary is depressed, for reception of the rostral end of the dentaries. In the symmetry plan, the ventral part of the predentary bears two apophyses, a large plate-like rostroventral one and a smaller caudodorsal one, both inclined caudally: the predentary was more firmly anchored against the dentary symphysis by means of this bilobed median plate. The rostradorsal border of the predentary is strongly and regularly denticulate; beneath the denticulations are accompanying foramina. The denticulations progressively lessen caudolaterally.

Discussion – The predentary of *Bactrosaurus johnsoni* is closely similar to that assigned to *Gilmoreosaurus mongoliensis* (AMNH 6369, see GILMORE, 1933, fig. 14). A strongly denticulate oral margin can be observed in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigerensis*, *Bactrosaurus johnsoni* and *Gilmoreosaurus mongoliensis* (the predentary is not preserved in *Telmatosaurus transylvanicus*, but the oral margin of its premaxilla is strongly denticulate). This structure is interpreted as the scar of attachment of a cornified rhamphotheca (OSTROM, 1961). In Hadrosaurinae and Lambeosaurinae, the denticulations tend to become obliterated in adult specimens, but this reduction is less constant than that of the premaxilla oral

denticulations. *Maiasaura peeblesorum*, e.g., keeps a strongly denticulate predentary oral margin (HORNER, 1983, fig. 3a).

Dentary (Figure 18; Plate 6, Fig. 1):

Description – The dentary is the largest bone of the mandible. Its lateral surface is roughly rectangular, with parallel ventral and dorsal margins, and prominently convex dorso-ventrally along its entire length. It is pierced by several foramina (f) for vessels and nerves. The dental alveolae regularly emarginate its dorsal margin. Rostrally, the dentary projects slightly ventrally and medially to form a scoop-shaped articulation surface for

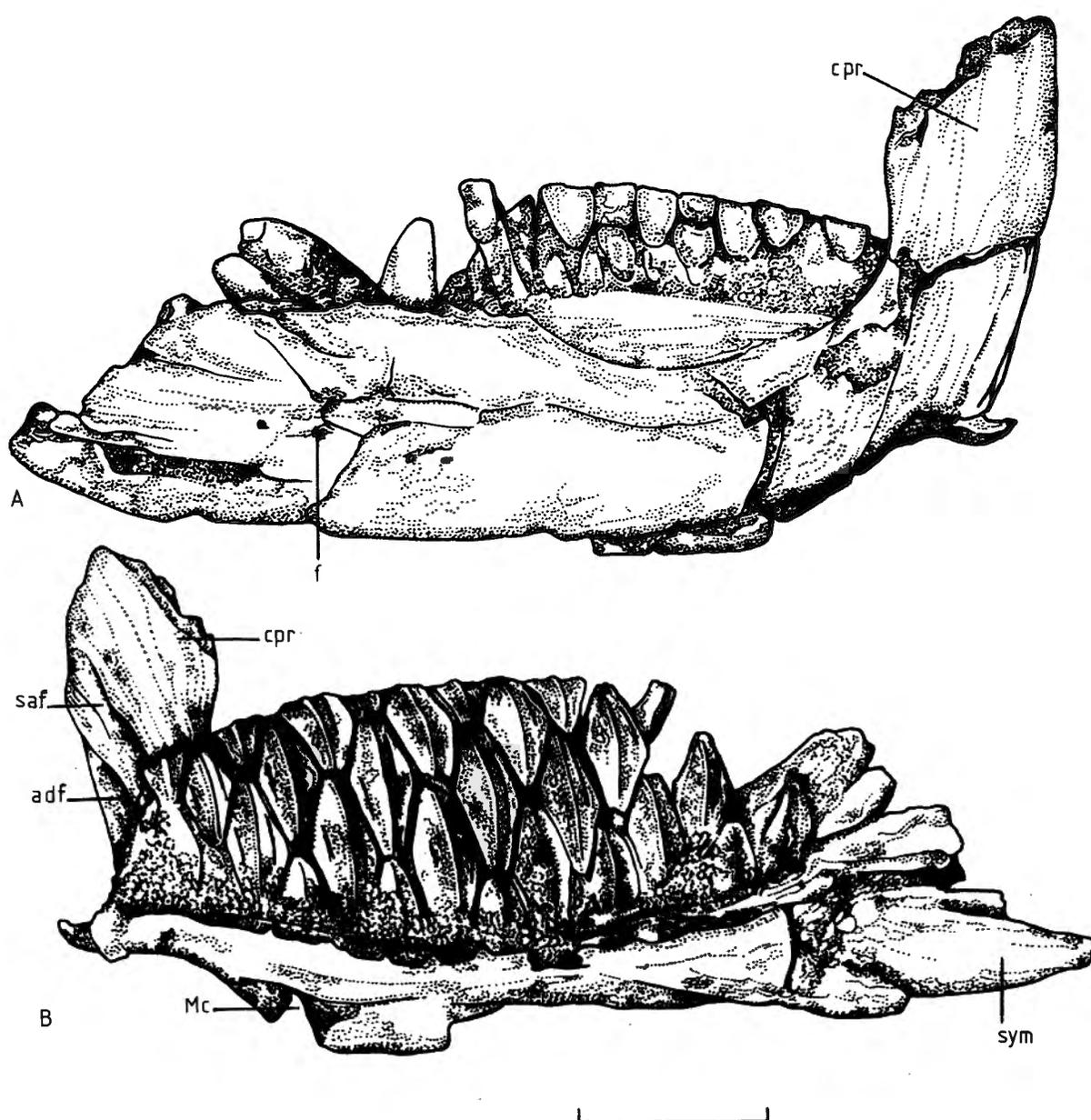


Fig. 18 – Left dentary of *Bactrosaurus johnsoni* (SBDE 95E5/12), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 5 cm. adf: adductor fossa; cpr: coronoid process; f: foramen; Mc: Meckel canal; saf: surangular facet; sym: mandibular symphysis.

the prementary. The mandibular symphysis (**sym**) seems linear and short and seems slightly inclined to the long axis of the mandible.

The coronoid process (**cpr**) is very high, slender and nearly vertical. Its lateral surface is very convex both rostro-caudally and dorso-ventrally, whereas its medial side is concave: the process consequently looks curved inwards. In caudal view, its double caudal border circumscribes a large and very deep triangular fossa, representing the rostral portion of the adductor fossa (**adf**). The medial side of the coronoid process bears, parallel to its caudal border, an elongated depressed facet for reception of the surangular (**saf**). Most of the adductor musculature (e.g. *Mm. adductor mandibulae externus*, *pseuptygoideus*) originated from the dorsal and caudal surfaces of the coronoid process (see OSTROM, 1961 for a detailed study of the jaw musculature in hadrosaurs).

The mandibular battery was medially concealed by a thin bony plate, broken in the specimens currently discovered in Iren Dabasu. A row of special foramina perforates the base of the alveolar chambers. About 20 alternating dental rows extend from the back of the articulation for the prementary to the back of the coronoid process. Therefore, there is no trace of diastema at the rostral end of the dentary. Each row is composed by one functional tooth and at least two replacement teeth.

The Meckel canal (**Mc**) is set along the ventral border of the dentary, from the caudal end of the symphysis to the coronoid process; it forms rostrally a furrow which progressively broadens and deepens caudally.

Discussion – The dentary of *Gilmoresaurus mongoliensis* mainly differs from that of *Bactrosaurus johnsoni* because of its perfectly straight long axis, of its inclined mandibular symphysis and of its rostral end turning less strongly medially. For WEISHAMPEL & HORNER (1986), the ventral projection of the rostral end of the dentary, as observed in *Bactrosaurus johnsoni*, is a characteristic of the Lambeosaurinae; in the Hadrosaurinae, on the other hand, the body of the dentary remains right along its full length. Nevertheless, it must be noted that the condition observed in Lambeosaurinae is probably plesiomorphic in Hadrosauridae, as it also occurs in more basal ornithomorphs, such as *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* or, to a lesser degree, *Ouranosaurus nigeriensis*. It must also be noted that several Hadrosaurinae, such as *Gryposaurus notabilis* or *Brachylophosaurus canadensis* show a relatively important ventral projection of the rostral end of the dentaries.

Ancestrally in Ornithischia, the dentary dentition begins immediately behind the caudal limits of the lateral processes of the prementary (WEISHAMPEL *et al.*, 1993). This condition is retained in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Bactrosaurus johnsoni*, *Gilmoresaurus mongoliensis* and *Telmatosaurus transsylvanicus*. In contrast, *Ouranosaurus nigeriensis* and Hadrosauridae possess a diastema between the prementary and the most mesial

dentary tooth position. For NORMAN (1990: 157), this feature may be an important biomechanical indicator rather than a phylogenetically important character.

Ancestrally in reptiles, the coronoid process is inclined caudally or nearly straight. This condition is retained in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Bactrosaurus johnsoni* and *Telmatosaurus transsylvanicus*. In Hadrosauridae, on the other hand, the coronoid process is inclined rostrally, towards the orbit, rather than towards the infratemporal fenestra (OSTROM, 1961: 74).

The presence of at least three dentary teeth per tooth position, as observed in *Bactrosaurus johnsoni*, has long been identified as a synapomorphy for Hadrosauridae (LULL & WRIGHT, 1942; OSTROM, 1961). Ancestrally for Ornithischia, the dentary dentition is formed by a single functional tooth and a single replacement one: this condition is observed in basal Iguanodontia.

The number of dentary tooth rows in *Bactrosaurus johnsoni* is similar to that observed in *Iguanodon bernissartensis* (25), *I. atherfieldensis* (22) or *Ouranosaurus nigeriensis* (23). The number of tooth positions is distinctly higher in more derived hadrosaurs: 29 in *Parasaurolophus walkeri*, 30 in *Telmatosaurus transsylvanicus*, 37 in *Corythosaurus casuarius*, 34 to 40 in *Prosaurolophus maximus*, 40 to 41 in *Lambeosaurus lambei*, 44 in *Edmontosaurus annectens* and *Edmontosaurus saskatchewanensis*, 48 to 49 in *Edmontosaurus regalis* and 50 in *Saurolophus osborni*, for examples.

Surangular (Figure 19; Plate 7, Fig. 1):

Description – The surangular is the second largest mandibular element. It forms the caudal part of the coronoid process, the lateral aspect of the mandibular glenoid and a portion of the retroarticular process. Its rostral portion is not preserved in the material currently discovered; its caudal portion is gently curved inwards. In dorsal view, the glenoid (**gl**) is a large, shallow and cup-shaped depression. Its lateral margin forms a prominent convex lip, overhanging the lateral wall of the bone. In front of the glenoid, a large depression of the medial wall of the surangular represents the caudal portion of the adductor fossa (**adf**). Beneath the glenoid, the medial side of the surangular forms an elongated groove for the insertion of the *M. pterygoideus dorsalis* (**mpdif**); this facet extends caudally towards the inner side of the retroarticular facet. The articulation facet for the angular (**angf**) forms a long and broad gutter extending along the caudal portion of the ventral side of the surangular, between the medial and the lateral walls of the bone.

The retroarticular process of the surangular (**rapr**) is lobate and upturned above the glenoid. It is triangular in cross-section, with a very thin ventral edge. The *M. pterygoideus ventralis* was inserted on its lateral aspect.

Discussion – In *Bactrosaurus johnsoni*, the lateral wall of the surangular is not pierced by a surangular foramen.

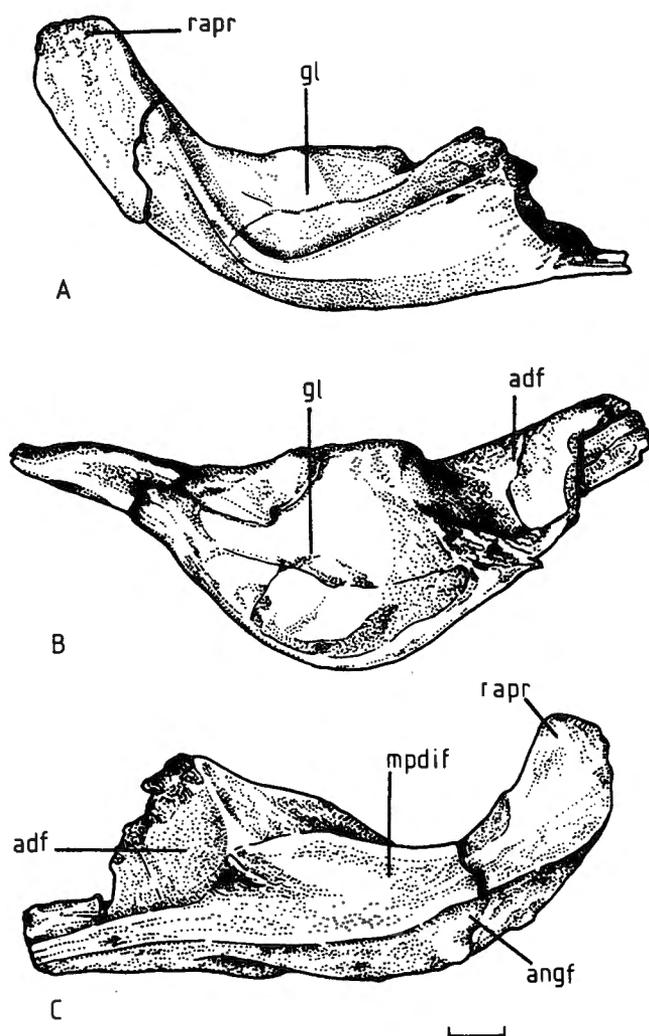


Fig. 19 – Right surangular of *Bactrosaurus johnsoni* (SBDE 95E5/13), from the Iren Dabasu Formation - A: lateral view; B: dorsal view; C: medial view. Scale bar = 1 cm. adf: adductor fossa; angf: angular facet; gl: glenoid; mpdif: insertion facet for the *M. pterygoideus dorsalis*; rapr: retroarticular process.

This foramen is primitively present in the body of the surangular near the mandibular glenoid in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*. In contrast, *Telmatosaurus transsylvanicus*, Hadrosaurinae and Lambeosaurinae also lack this foramen.

Teeth (Plate 7, Fig. 2):

Description – Both maxillary and dentary dentitions are organized into dental batteries, consisting of one functional tooth and two or three replacement teeth, firmly cemented together.

The maxillary teeth are lanceolate and much higher than broad. The crowns bear enamel only on their labial side. The lingual side is very convex and strongly truncated by continuous wearing. The labial side bears a prominent median carina. The marginal denticles are

small and relatively numerous, depending on the size of the animal and on the degree of wearing.

The leaf-shaped dentary teeth are distinctly larger, proportionally wider and more compressed medio-laterally than the maxillary teeth. Some dentary teeth are slightly recurved distally. The enamel is present only on the lingual side of their crown. The labial side is always strongly truncated because of intensive wearing. The lingual side bears a median carina: it is less prominent than that on the maxillary teeth and slightly displaced distally. A second longitudinal ridge can be observed on all the dentary teeth, mesially to the median carina. The distalmost dentary teeth bear a third caudal longitudinal ridge. The marginal denticles are also small and numerous. The mesial denticles are supported by a short ridge on the enamelled lingual side of the crown; distal denticles are not supported by ridges. The angle between the crown and the root is not important, more than 145° .

Discussion – The general proportions of the teeth greatly depend on the size of the animal in *Bactrosaurus johnsoni*, as probably in other ornithomimids, so that comparisons must be made very cautiously.

The maxillary teeth of *Bactrosaurus johnsoni* are typically hadrosaurian: the labial side bears a single median ridge and the marginal denticulations are small. They seem miniaturized when compared to the dentary teeth. In contrast, maxillary teeth appear broader in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*; moreover, the labial enamel bears secondary ridges and the denticulations are more prominent.

In contrast, the dentary teeth of *Bactrosaurus johnsoni* look more typically iguanodontian: they are distinctly broader and bear secondary ridges. Moreover, the crown is slightly recurved distally. All these characters can also be observed in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*. The dentary teeth of *Telmatosaurus transsylvanicus* are also relatively broad and recurved distally. The mesial denticles are supported by short ridges, as in *Bactrosaurus johnsoni*. A very slight, mesially-placed secondary ridge can be observed on some teeth. They differ from the dentary teeth of *Bactrosaurus johnsoni* by the complete absence of distal secondary ridge. In all Hadrosaurinae and Lambeosaurinae, the dentary teeth are miniaturized and the lingual enamel bears a single median carina.

For HORNER (1990) and WEISHAMPPEL *et al.* (1993), the angle between the crown and root of dentary teeth is primitively relatively high (less than 130°) in *Camptosaurus dispar*, *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus* and Lambeosaurinae, like in *Bactrosaurus johnsoni*. In Hadrosaurinae and species of *Iguanodon*, on the other hand, this angle is less than 130° . For HORNER (1990), this character is an argument to unite these taxa within a single monophyletic group, the Ha-

drosauria. For WEISHAMPEL *et al.* (1993), this character would have evolved convergently in *Iguanodon* and Hadrosaurinae, which is a more parsimonious hypothesis. However, precise measurements are needed to confirm the distribution of this character.

AXIAL SKELETON

Vertebrae:

In the specimens recently discovered in Locality 95E5 by the SBDE, the neural arches of the dorsal vertebrae are usually not fused to the centra, indicating that the specimens gathered in this bone-bed are not fully ossified adults, but younger individuals.

Atlas (Plate 7, Fig. 3) – SBDE 95E/37 is the only intercentrum nr.1 referable to *Bactrosaurus johnsoni*. In cranial view, it is crescentic in shape and particularly enlarged transversely. Craniodorsally, it forms a shallow concave depression which articulated with the occipital condyle. Behind this surface, a smaller, but better marked depression received the ventral side of the odontoid process. The caudal surface, which articulated with the axis complex, is smoothly concave. The caudolateral corners are truncated by the articular facets for the atlantal ribs.

Axis (Figure 20; Plate 7, Fig. 4) – SBDE 95E5/14 is composed by the odontoid process (centrum nr.1), the centrum nr.2 and the neural arch; the intercentrum nr.2, not fused to the other elements, is lost. The odontoid process (**odpr**) is massive, progressively thickening caudally. Its craniodorsal side, which formed the floor of the neural canal, is slightly concave transversely; its ventral

side is, on the other hand, very convex transversely. The centrum nr.2 (**C2**) is relatively short and very opistho-coelous. Its cranioventral surface forms a concave and crescentic contact area for the intercentrum nr.2. It is expanded laterally at both ends and contracted about the middle. Its ventral surface is keeled. The parapophysis (**p**) is borne by the cranial edge of the lateral side of the centrum. The neural arch forms a huge neural spine (**ns**), extremely expanded cranio-caudally. Cranially, the neural spine is tapering; its height progressively grows caudally. Behind the level of the neural canal, the neural spine is subdivided into two divergent laminae. The prezygapophyses (**przyg**) are set under the cranial end of the neural spine, at the level of the roof of the neural canal; their elliptical articular surfaces face upwards, laterally and slightly cranially. The postzygapophyses (**pozyg**) are set under the caudal end of the neural spine; they face downwards, laterally and slightly cranially. Behind the prezygapophysis, the transverse process extends obliquely backwards to form a rather prominent diapophysis (**d**).

Cervical vertebrae (Figure 21; Plate 8, Figs. 1, 2 & 4) –

The centra of the cervical vertebrae are strongly opistho-coelous: they form a large hemispherical cranial articular surface and a deeply concave, cup-shaped caudal articular surface. In the cranialmost cervical vertebrae, the centrum is proportionally short, wide and low; it progressively becomes proportionally longer and higher towards the back of the neck, looking more like the heart-shaped dorsal centra. All the cervical centra are wider caudally than cranially and are slightly contracted in the middle. Ventrally, the centra are keeled; above the keel, the lateral walls are slightly concave and may be pierced by a small nutritive foramen. On the cranialmost vertebrae, the parapophysis (**p**) is set on the cranial end of an horizontal ridge, in the middle of the lateral side of the centrum; towards the back of the neck, the parapophyses progressively migrate at the base of the transverse processes of the neural arch.

The neural arch forms a wide and regularly arched neural canal. On the cranialmost cervical vertebrae, a pair of prezygapophyseal processes (**przpr**) diverge forwards, upwards and outwards. Their dorsal end supports the rounded and flat prezygapophyses, which look upwards and inwards. The transverse process (**trpr**) forms a small tubercle at the base of each prezygapophyseal process. The importance of the transverse processes quickly increases along the cervical series: they become longer, stouter and more curved downwards and backwards, as they progressively integrate the prezygapophyseal processes. The diapophyses (**d**) are set at the end of the transverse processes; they progressively become larger and higher along the cervical series. The postzygapophyseal processes (**pozpr**) are long and curved and they diverge backwards and outwards; their ventral side bears the large and elliptical postzygapophyses, which look downwards and outwards. Along the cervical series, the bases of the postzygapophyseal processes tend to fuse

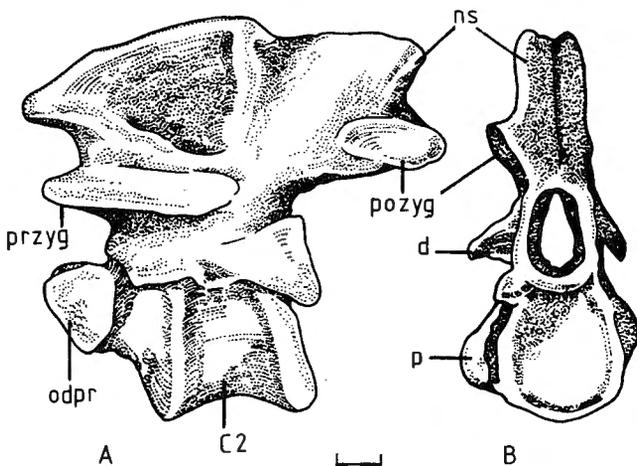


Fig. 20 – Axis of *Bactrosaurus johnsoni* (SBDE 95E5/14), from the Iren Dabas Formation - A: lateral view; B: caudal view. Scale bar = 1 cm. C2: second centrum; d: diapophysis; ns: neural spine; odpr: odontoid process; p: parapophysis; pozyg: postzygapophysis; przyg: prezygapophysis.

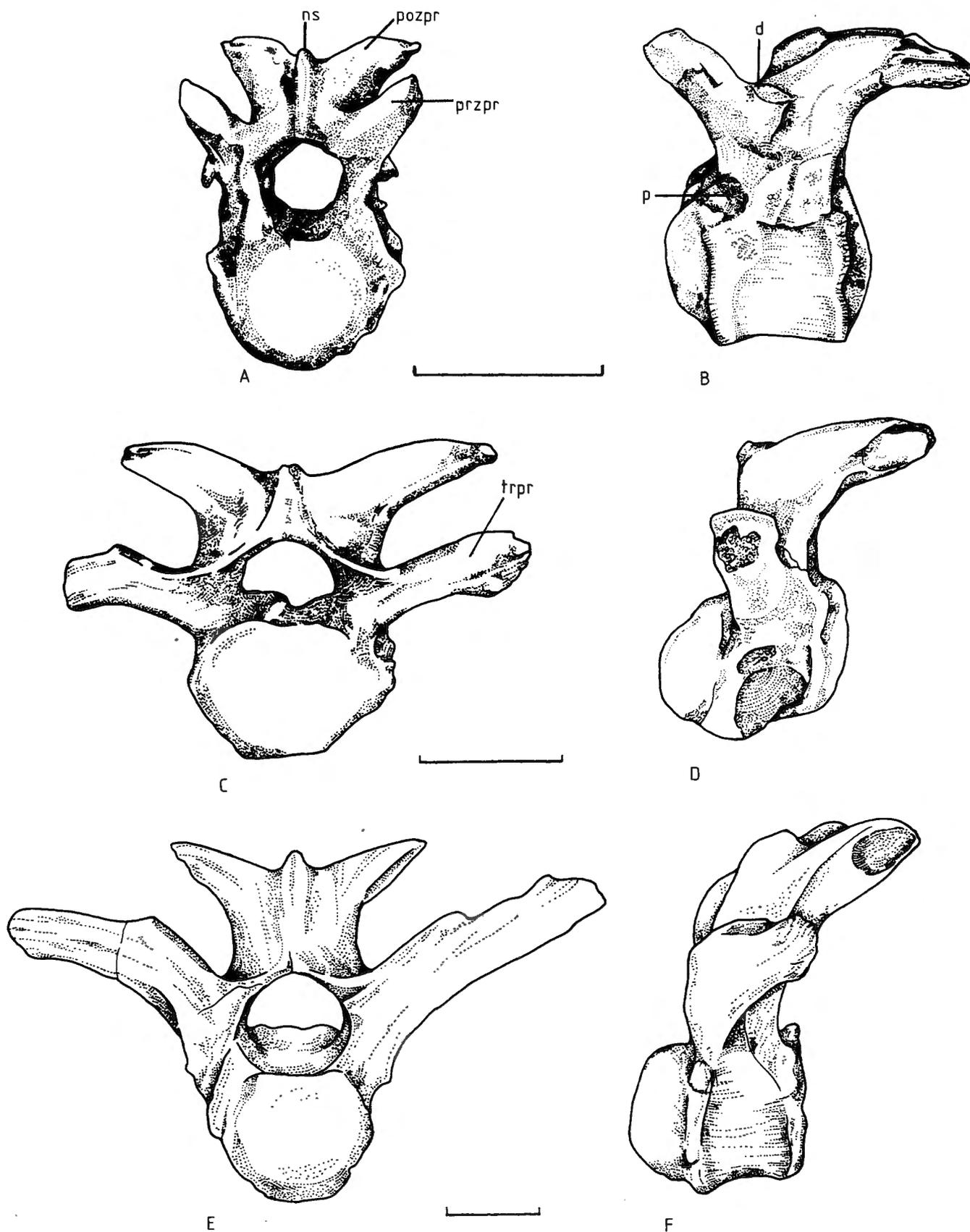


Fig. 21 – Cervical vertebrae of *Bactrosaurus johnsoni* (SBDE 95E5/15-17)), from the Iren Dabasu Formation - A-B: ?3rd cervical vertebra; C-D: cranial cervical vertebra; E-F: caudal cervical vertebra. A, C, E: cranial views; B, D, F: lateral views. Scale bars = 5 cm. d: diapophysis; ns: neural spine; p: parapophysis; pozpr: postzygapophyseal process; przpr: prezygapophyseal process; trpr: transverse process.

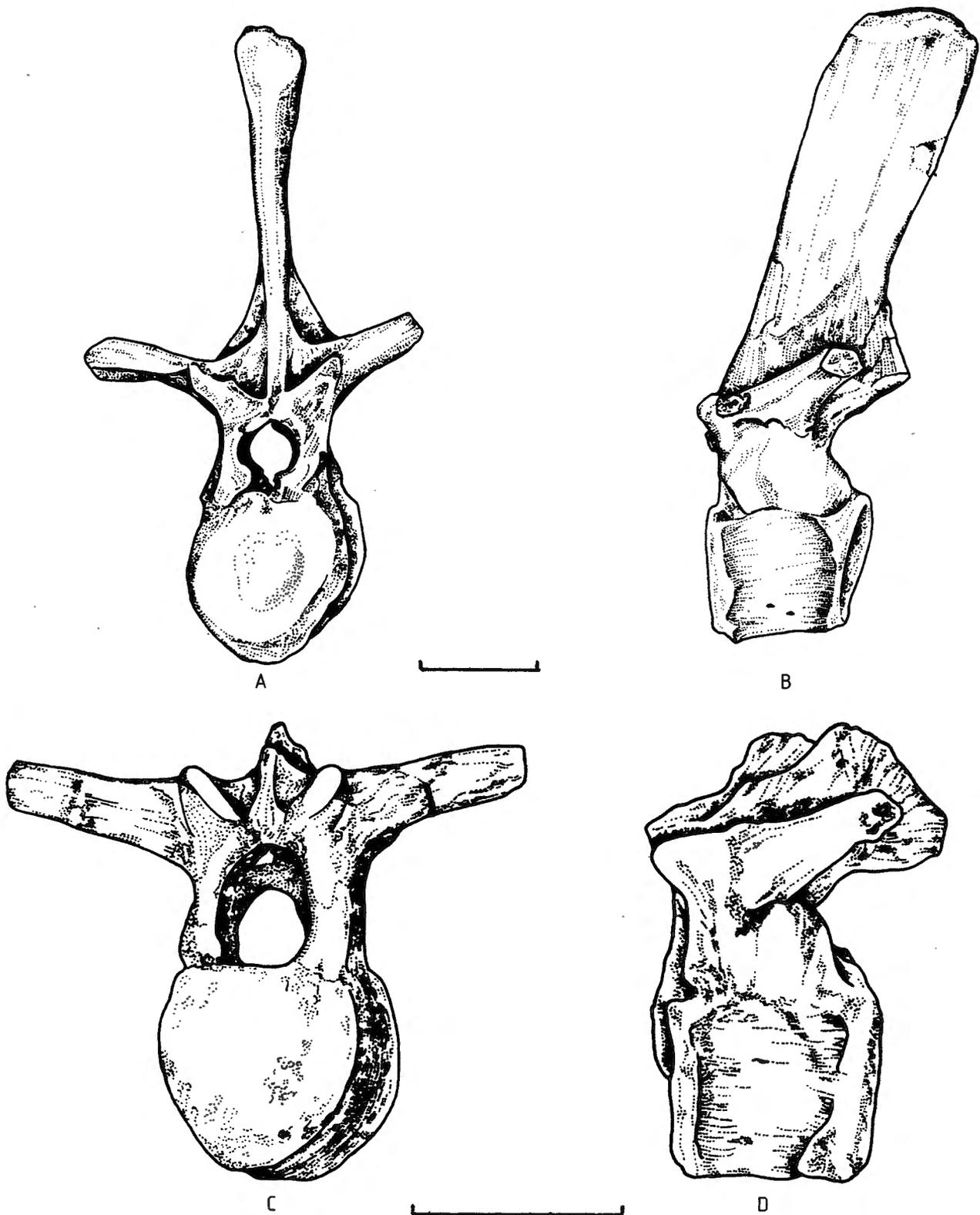


Fig. 22 – Dorsal vertebrae of *Bactrosaurus johnsoni* (SBDE 95E5/18-19), from the Iren Dabasu Formation- A-B: cranial dorsal vertebra; C-D: more caudal dorsal vertebra. A,C: cranial views; B-D: lateral views. Scale bars = 5 cm.

together, so that they become higher and less divergent. The neural spine (ns) forms a small tubercle between the postzygapophyseal processes. It progressively develops into a rather prominent hook-shaped blade.

Dorsal vertebrae (Figure 22; Plate 8, Fig. 3) – The centra of the dorsal vertebrae are amphiplatyan. They progressively become proportionally longer, higher and more narrow through the dorsal series. In cranial and

caudal views, the articular surfaces are typically heart-shaped: the ventral surface forms a well marked median keel, joining the cranial and caudal articular surfaces. The lateral faces of the centra are strongly contracted in the middle and are pierced by several nutritive foramina, irregularly distributed. The dorsal surface of each centrum is occupied by two large, elliptical and very rugose articular facets for the neural arch; between these facets, the median surface of the dorsal side is concave, forming the floor of the medular duct.

The neural arch is more important than on the cervical vertebrae. The ventral surface of the peduncles is very elongated cranio-caudally, convex and very rugous. Cranially, the prezygapophyses are more developed and elliptical in shape, with a cranio-caudal great axis; their articular surface looks upwards, inwards and slightly forwards. The diapophyses are very long and strong; their ventral side bears a strong carina, joining the caudoventral corner of the peduncle. On the cranial dorsal vertebrae, they are strongly inclined caudally and slightly dorsally; they are more horizontal at the back of the dorsal series. Between the prezygapophyses and the diapophyses, the parapophyses form kidney-shaped processes on the lateral sides of the neural arch. The importance of the parapophyses progressively decreases along the dorsal series: they progressively migrate along the cranial border of the diapophyses to completely fuse with them on the caudalmost dorsal vertebrae. The postzygapophyses are large and elliptical, separated from each other by a deep indentation at the base of the neural spine; they look downwards, outwards and slightly backwards.

The height of the neural spines progressively increases caudally. In fully-ossified adult specimens (for example, AMNH 6553, Quarry 141; see GILMORE, 1933, fig. 29), the vertebrae of the caudal half of the series are characterized by high massive club-shaped spines. Moderately wide at the base, there is a steady increase in transverse diameter from bottom to top. The top of the neural spine is very rugose, indicating that it was covered by cartilage in life. The relative height of the spine is therefore an ontogenetic character, the bony part of the neural spine being proportionally shorter in younger specimens, since they were terminated by cartilage in life. The neural spine of the cranialmost dorsal vertebrae have a strong backwards inclination; those of the mid-dorsal region stand erect, while they slope slightly forwards at the back of the series.

Sacral vertebrae (Figure 23; Plate 9, Fig. 1) – In AMNH 6553 (Quarry 141; GILMORE, 1933, figs. 31-32), the synsacrum is nearly complete. The SBDE discovered, in Locality 95E5, two sacra: SBDE 95E5/39 is formed by seven coössified centra and sacral ribs; SBDE 95E5/40, less complete, is formed by four coössified centra with incomplete sacral ribs. In *Bactrosaurus johnsoni*, the synsacrum is formed by seven vertebrae. The centra are proportionally short, low and wide. Their diameter progressively grows caudally. The articular surfaces are

elliptical and flat, except the caudal surface of the last centrum, which is very concave. Between the articular surfaces, the centra are strongly contracted. The ventral side of the first centrum is always slightly keeled. In succeeding centra, the ventral surface develops a broad and shallow haemal sulcus in SBDE 95E5/39. The last sacral centrum develops a flat ventral surface. In AMNH 6553 and SBDE 95E5/40, on the other hand, the ventral surface of the sacral centra tends to be slightly keeled, without haemal sulcus. Small nutritive foramina are irregularly distributed on the ventral side of the centra. As the sacral ribs are borne at the junction between two sacral centra, the parapophyses of adjacent vertebrae form a continuous, large, prominent and kidney-shaped articular surface.

The zygapophyses of adjacent vertebrae are fused together. The diapophyses form stout processes, slightly oblique caudally. Their lateral ends are thick and rounded. They are connected to the corresponding parapophysis by a prominent and rounded ridge.

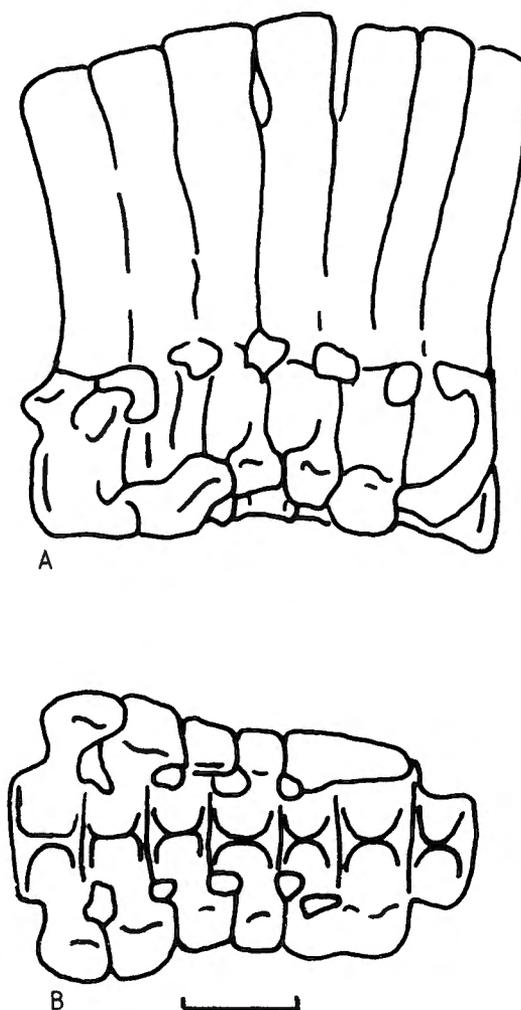


Fig. 23 – Reconstruction of the sacrum of *Bactrosaurus johnsoni* (after AMNH 6553), from the Iren Dabasu Formation - A: lateral view; B: ventral view. Scale bar = 10 cm.

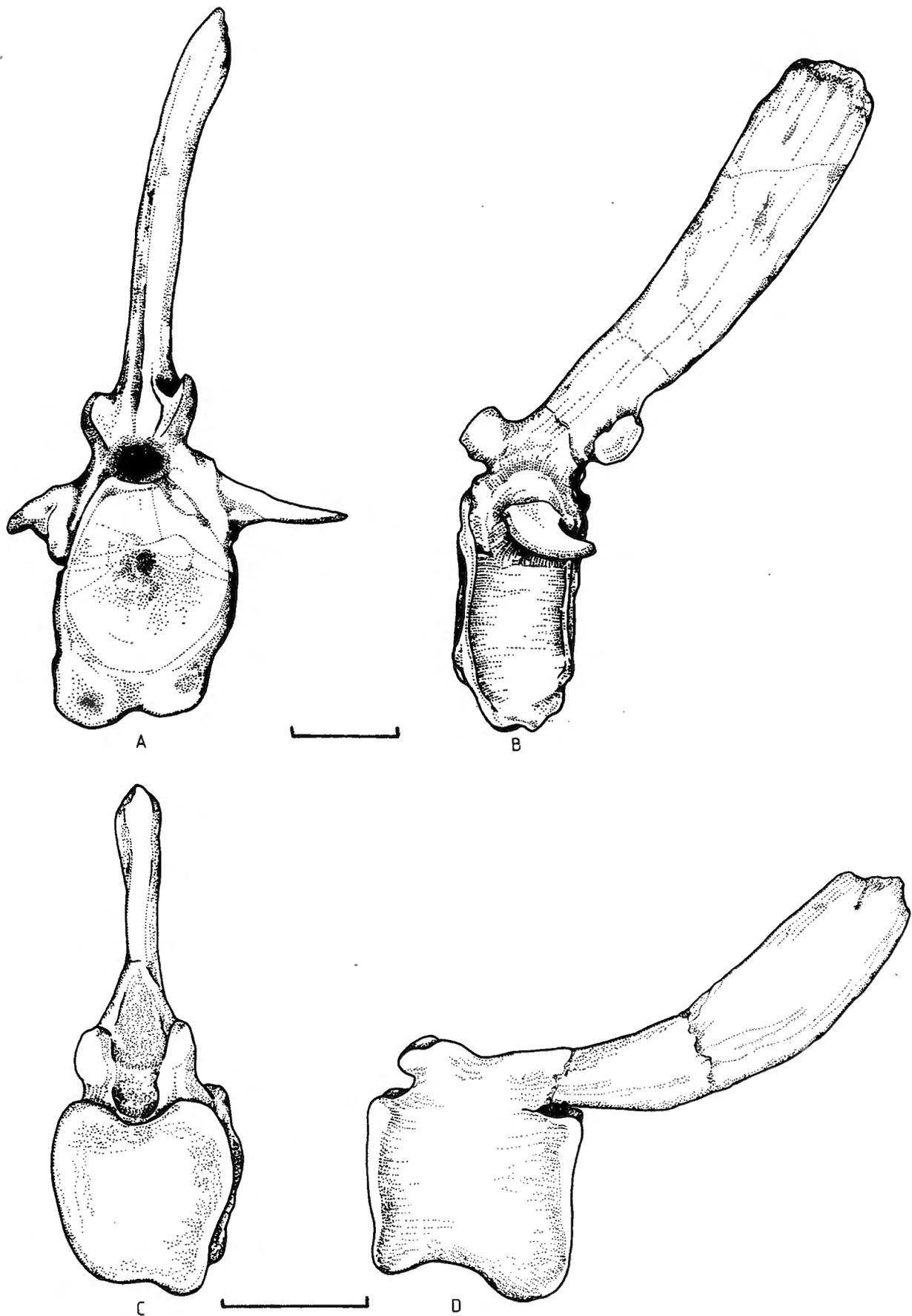


Fig. 24 – Caudal vertebrae of *Bactrosaurus johnsoni* (SBDE 95E5/20-21), from the Iren Dabasu Formation - A-B: proximal caudal vertebra; C-D: distal caudal vertebra. A,C: cranial views; B-D: lateral views. Scale bars = 5 cm.

The neural spines are high and form, in AMNH 6553, a nearly continuous plate. Their basal portion is fused, but their upper third remains distinct, except sacrals two and three, which are joined at the top. GILMORE (1933: 65) noted that coössification of the sacral neural spines is certainly an ontogenetical character. The tops of sacral spines two, three, four and five are transversely expanded, but lack the club-like thickening observed in the last dorsals.

Caudal vertebrae (Figure 24; Plate 8, Figs. 5 & 6) –

The caudal centra are amphiplatyan. In proximal caudal vertebrae, the centra are short, narrow and very high; the articular surfaces are sub-rectangular. The articular facets for the caudal ribs are very rough and concave and they truncate the laterodorsal corners of each centrum, extending on the lateroventral corners of the neural arch. The lateral sides of the centra are slightly concave cranio-caudally and flat to slightly convex dorso-ventrally. The ventral side is very concave, both cranio-caudally and dorso-ventrally. Four large and concave haemapophyses are present on the ventral margins of the articular surfaces; the distal are usually somewhat larger than the proximal ones, with slightly more prominently everted edges. The centra progressively diminish in size towards the end of the tail. The centra become proportionally longer than high and the articular surfaces become hexagonal. The lateral articular facets for the caudal ribs disappear on the distalmost vertebrae and the haemapophyses become progressively less prominent.

In the proximal caudal vertebrae, the lateral sides of the neural arch form concave and rough facets for articulation with the caudal ribs, in continuity with those on the centrum. The prezygapophyses form cranial rami, with elliptical articular facets looking upwards, inwards and slightly forwards. At the base of the caudal edge of the neural spine, the postzygapophyses form flat and elliptical facets looking downwards, outwards and slightly backwards. The size of the zygapophyses and of the neural duct progressively decreases towards the end of the tail.

The neural spine is high on the proximal caudal vertebrae. It is inclined and curved backwards. It usually bears, on its lateral sides, strong longitudinal ridges, marking the insertion of strong tendons, which rigidified the tail. The top of the neural spine is rough, as it was covered by cartilage in life. The caudal edge is very thin, whereas the cranial border tends to form a concave gutter. Towards the end of the tail, the neural spines progressively become lower and more strongly inclined backwards.

Discussion – In *Bactrosaurus johnsoni*, the odontoid process is coalescent with the axis, as in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *Ouranosaurus nigeriensis* and *Telmatosaurus transsylvanicus*. On the other hand, the odontoid appears to be a free element in Hadrosauridae (LULL & WRIGHT, 1942; WEISHAMPEL & HORNER, 1990).

The neural spines of the dorsal, sacral and cranial caudal vertebrae of *Bactrosaurus johnsoni* are relatively high. It is generally admitted that the neural spines are usually taller in Lambeosaurinae than in Hadrosaurinae. Unfortunately, this character cannot be adequately quantified, as the height of the neural spines greatly varies within the vertebral series; moreover, younger specimens have lower neural spines, as it is not fully ossified apically. The height of the neural spine is exaggerated in *Ouranosaurus nigeriensis*. For HORNER (1990), it is one of the characters permitting to ally *Ouranosaurus* with the Lambeosauridae in a clade Lambeosauria. It is more generally admitted that this character appeared independently in several ornithopod lineages (TAQUET, 1976; NORMAN, 1990).

The generic name “*Bactrosaurus*” refers to the apically wide and club-shaped neural spines of the last dorsal vertebrae. GILMORE (1933: 63) noted that “this feature...-distinguishes them from all the other known members of the Hadrosauridae”. Indeed, this character seems to be an autapomorphy of *Bactrosaurus johnsoni*, as it has not been reported in any known ornithopod. It must nevertheless be noted that this seems to be an ontogenetical character, as it is not observed in dorsal vertebrae belonging to younger individuals, in which the top of the neural spines is not fully ossified. The first caudal vertebrae of *Barsboldia sicinskii*, from the Nemegt formation of Mongolian Peoples’s Republic, are characterized by similar club-shaped neural spines (MARYANSKA & OSMOLSKA, 1981b).

Primitively in ornithopods, the ventral side of the sacrum is flat to slightly keeled: this condition is observed in *Hypsilophodon foxii*, *Ouranosaurus nigeriensis* (contra HORNER, 1990), *Telmatosaurus transsylvanicus* and Lambeosaurinae. A slight longitudinal depression is sometimes developed on the last sacral vertebrae of *Camptosaurus dispar*. It has been shown that this character is also variable in *Bactrosaurus johnsoni*. In *Iguanodon bernissartensis*, the first sacral centra are keeled, whereas a broad and shallow haemal sulcus is progressively developed on the last ones (NORMAN, 1980). This sulcus is less marked in *Iguanodon atherfieldensis* (NORMAN, 1986). In all Hadrosaurinae, the sacrum bears a median ventral groove that extends axially along at least the last four of five centra (WEISHAMPEL & HORNER, 1990, contra WEISHAMPEL *et al.*, 1993). It can be concluded that the presence of an haemal sulcus on the sacrum is usually regarded as a good character permitting to distinguish the Hadrosaurinae from the Lambeosaurinae. In less derived ornithopods, on the other hand, it seems too variable, even at the intraspecific level, to be useful phylogenetically.

Ribs:

Cervical ribs – The proximal end of the cervical ribs is formed by two divergent rib heads (tuberculum and capitulum), borne by a distinct neck. Distally, they merge to form a short and curved rib shaft, which is convex ex-

ternally and concave internally. The following changes can be observed through the cervical series: the capitulum neck becomes much longer than the tuberculum neck, the two rib heads tend to lie in the same transverse plane along the shaft of the rib, rather than being divergent and the rib shaft becomes progressively longer.

Dorsal ribs (Plate 9, Fig. 2) – The morphology of the dorsal ribs is not characteristic. The capitulum is rather small and is supported by a long and gently curved neck. The tuberculum is elliptical in shape and form a shoulder area on the rib. The shaft is long and relatively slender; it curves outwards and inwards, tapering to a compressed distal tip. Its cranial surface is convex, whereas its caudal surface is flat. Its inner border is thinner than its outer border. A prominent ridge curves downwards from the craniodorsal edge of the tuberculum across the cranial surface of the shaft.

Sacral ribs – The sacral ribs are borne at the junction between the coössified sacral centra. The base of each rib is firmly fused to the parapophyse and diapophyse. Their distal ends are very expanded and fuse together to form the iliac bar. In SBDE 95E5/39, this bar is formed by the first five sacral ribs; the sixth pair remains free. The two iliac bars are closest to the centra at the level of the junction between the second and third centra; they progressively diverge caudally. Their lateral surface is concave and looks downwards, perfectly following the shape of the medial surface of the ilium. Four pairs of large foramina remain free between the lateral side of the centra, the sacral ribs and the iliac bars. In AMNH6553,

the sixth pair of sacral ribs participate in the iliac bar. This is probably an ontogenetical character.

Haemal arches – The articular heads of the chevron bones are expanded cranio-caudally and are divided by a transverse ridge into an cranial and a caudal facet which articulate against the haemapophyses of adjacent bones. Beneath the triangular neural canal, the haemal arches coalesce to form a long and narrow neural spine, transversely compressed and curved backwards.

SCAPULAR GIRDLE AND FORE LIMB

Scapula (Figure 25, Plate 10, Fig. 1):

Description – The scapula is long, robust and slightly curved inwards. Its dorsal margin is nearly straight, whereas its ventral margin is markedly concave. The distal blade is very expanded dorso-ventrally; the width of the scapula very regularly lessens along the two thirds of its length, to grow again towards its proximal end. The proximal end of the scapula is very massive, but less expanded dorso-ventrally than its distal blade. The coracoid suture (**cors**) is broad and very rugose. Along this suture, the internal surface of the scapula bears a shallow groove, forming a portion of an internal passage prolonging the coracoid foramen. Above the coracoid suture, the lateral side of the scapula bears a prominent and rugose acromial process (**acpr**). A buttressing deltoid ridge (**delr**) extends ventrodistally from the base of the acromial process to merge progressively with the scapular blade. Ventrally to the deltoid ridge, the lateral side of the

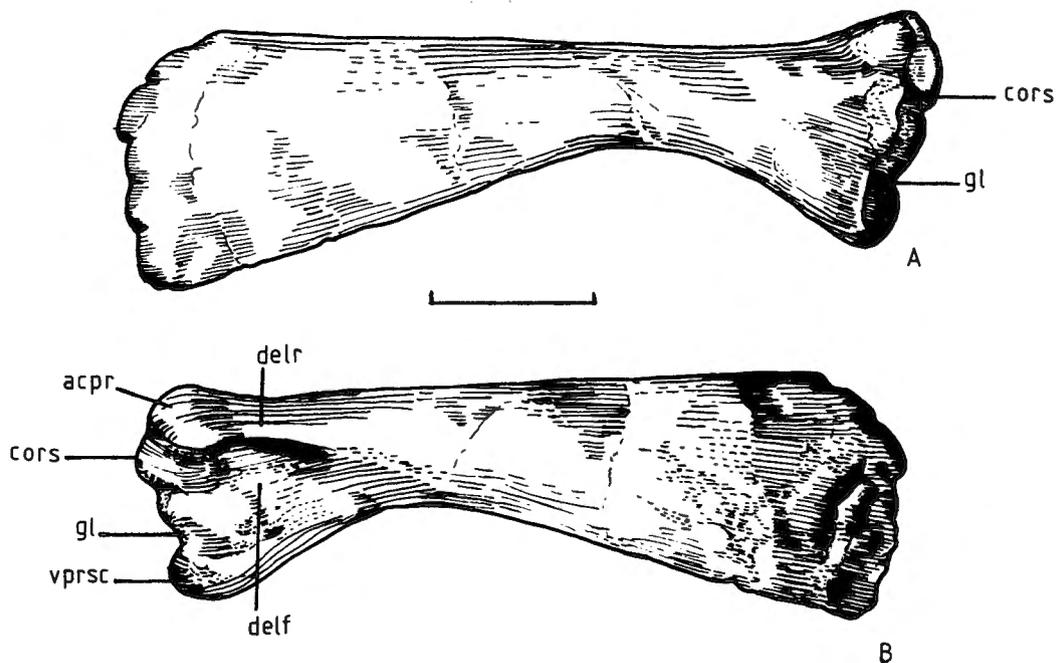


Fig. 25 – Left scapula of *Bactrosaurus johnsoni* (AMNH 6553), from the Iren Dabasu Formation - A: medial view; B: lateral view. Scale bar = 10 cm. acpr: acromial process; cors: coracoid suture; delf: deltoid fossa; delr: deltoid ridge; gl: glenoid; vprsc: ventral protuberance of the scapula.

proximal end is filled out by the deltoid fossa (**delf**). Under the coracoid suture, the dorsal part of the glenoid (**gl**) forms a large crescentic depression. On the lateral side of the scapula, the glenoid is overhung by a prominent ventral protuberance (**vprsc**).

Discussion – The scapula of *Bactrosaurus johnsoni* is characterized by the important dorso-ventral expansion of its distal blade: the ratio “length of the scapula / maximal width of the distal blade” < 3.5 , which is a value lower than in any known Hadrosauridae (see BRETT-SURMAN, 1989, table 5), but also lower than in *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Gilmoreosaurus mongoliensis* and *Telmatosaurus transylvanicus*. The distal expansion of the scapular blade is particularly regular in *Bactrosaurus johnsoni*.

Lambeosaurinae are reputed to possess scapulae with expanded distal blade, while Hadrosaurinae have scapulae with near-parallel sides (WEISHAMPEL & HORNER, 1990; HORNER, 1990). However, the situation seems more complicated in hadrosaurids than usually described. BRETT-SURMAN (1975, 1989) shows that the scapula of the hadrosaurine *Anatotitan copei* more closely resembles the lambeosaurine variety and that, on the other hand, the scapula of lambeosaurine *Lambeosaurus lambei* more closely resembles the hadrosaurine variety. He also shows that the scapula displays a considerable variety of shapes within the lineages and even within the genera. For all these reasons, the shape of the scapula is not regarded, in the present paper, as a good character to establish the phylogenetic relationships of the derived ornithopods (*contra* HORNER, 1990; WEISHAMPEL *et al.*, 1993).

Coracoid (Figure 26; Plate 10, Fig. 3):

Description – The coracoid is short, stocky and a little more elongated cranio-caudally than dorso-ventrally. It is very thick caudally and it progressively becomes thinner cranially. Its outer surface is convex cranio-caudally, while its inner surface is concave. Its caudal border is formed by two distinct surfaces, forming together an angle of about 120° and separated from each other by a narrow gutter. The caudoventral surface is large and concave: it participated in the lower half of the glenoid cavity (**gl**). The caudodorsal surface is convex, very irregular and oriented dorsally and slightly medially: it contacted the proximal end of the scapula (**scf**). The coracoid foramen (**corf**), piercing the coracoid close to its caudal border, is large and elliptical: it is completely closed and it does not communicate with the caudal gutter between the contact surface for the scapula and the glenoid surface. The ventral border of the coracoid is very concave. The cranioventral corner forms a rather prominent hook, pointed ventrally. The cranial and dorsal borders are regularly convex and roughened.

Discussion – The coracoid of *Bactrosaurus johnsoni* closely resembles that of *Iguanodon atherfieldensis*, *Ou-*

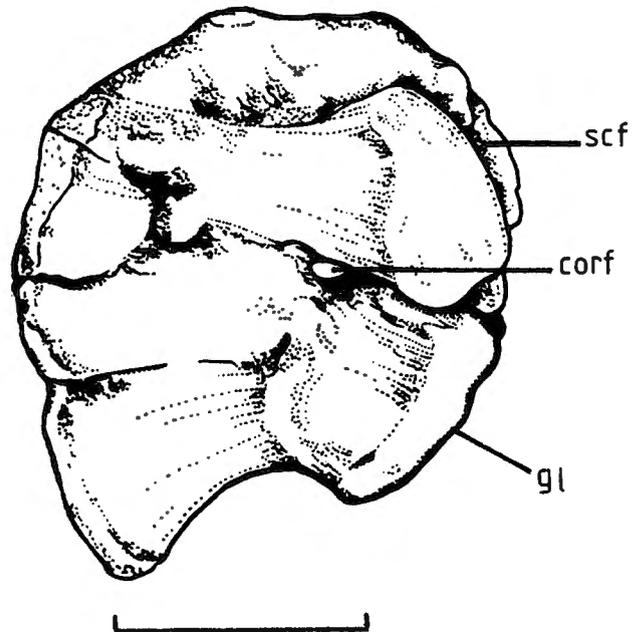


Fig. 26 – Right coracoid of *Bactrosaurus johnsoni* (SBDE 95E5/22), from the Iren Dabasu Formation - medial view. Scale bar = 5 cm. corf: coracoid foramen; gl: glenoid; scf: scapular facet.

anosaurus nigeriensis, *Gilmoreosaurus mongoliensis* and *Telmatosaurus transylvanicus*. The coracoid foramen is always open in *Iguanodon bernissartensis*. In *Camptosaurus dispar*, the coracoid is rectangular in shape, the scapular surface is twice as large as the glenoid and the

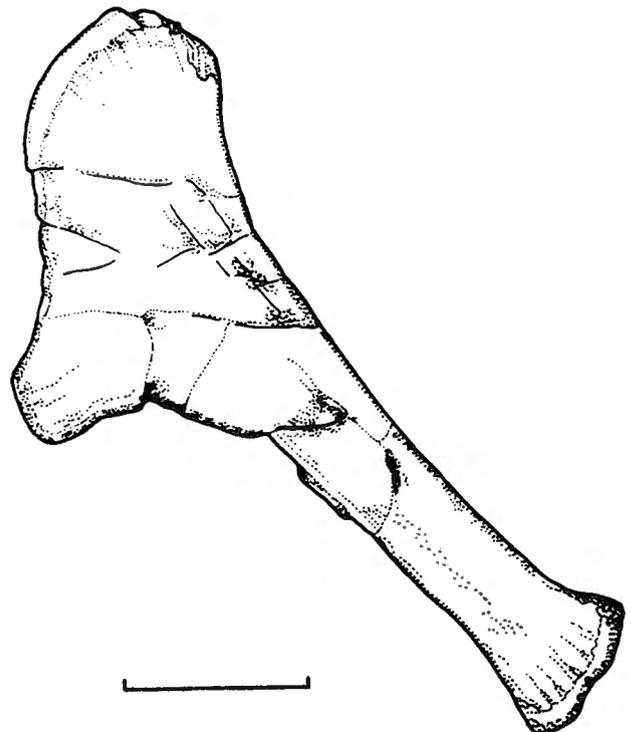


Fig. 27 – Left sternal of *Bactrosaurus johnsoni* (SBDE 95E5/23), from the Iren Dabasu Formation - cranial view. Scale bar = 5 cm.

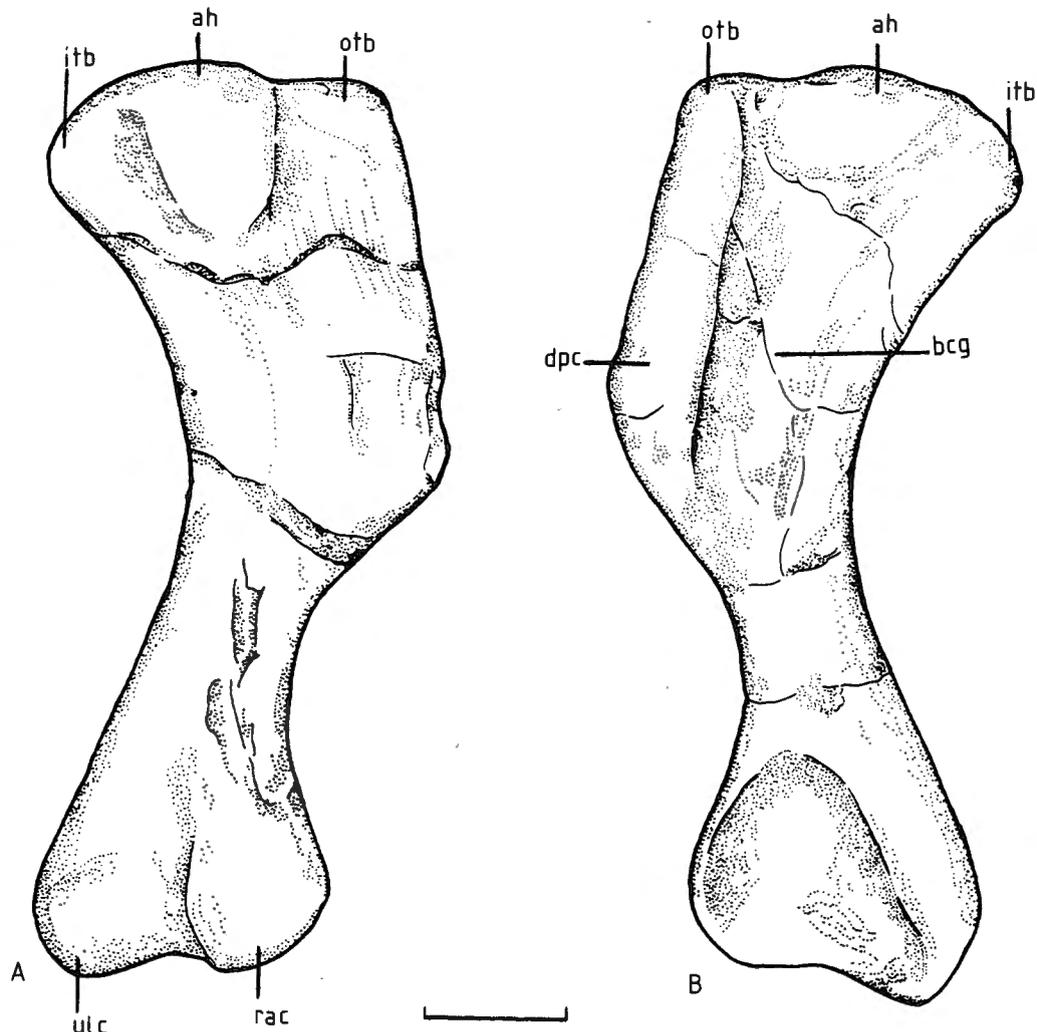


Fig. 28 – Right humerus of *Bactrosaurus johnsoni* (SBDE 95E5/24), from the Iren Dabasu Formation - A: caudal view; B: cranial view. Scale bar = 5 cm. ah: articular head; bcg: bicipital gutter; dpc: deltopectoral crest; itb: inner tuberosity; otb: outer tuberosity; rac: radial condyle; ulc: ulnar condyle.

coracoid hook is rudimentary. In Hadrosauridae, the coracoid hook is longer and pointed cranioventrally, rather than ventrally (BRETT-SURMAN, 1975).

Sternal (Figure 27; Plate 10, Fig. 2):

Description – The sternals are long, thin and relatively slender. They are roughly hatchet-shaped in ventral view. The proximal blade is enlarged and nearly flat. Its medial edge, which contacted the paired sternal, is concave and particularly thin; farther cranially, this edge curves outwards and becomes thicker and rugose: it was probably capped by cartilage. The caudal ramus of the sternal is particularly long, flattened dorso-ventrally and perfectly straight. It diverges caudolaterally and forms a blunt and slightly everted end: for NORMAN (1980), this blunt end formed the focal point for attachment of some cartilaginous sternal ribs.

Discussion – In *Hypsilophodon foxii* and *Camptosaurus* (DODSON & MADSEN, 1981; ERICKSON, 1988), the sternals form simple plates. In *Iguanodon bernissartensis*, *Igua-*

nodon atherfieldensis, *Ouranosaurus nigeriensis*, *Bactrosaurus johnsoni* and in Hadrosauridae, they form rod-shaped caudolaterally directed processes. The sternals of *Bactrosaurus johnsoni* look proportionally longer, more slender and thinner than those of *Iguanodon bernissartensis*, *I. artherfieldensis* and *Ouranosaurus nigeriensis*. The sternals are usually ignored in the literature about hadrosaurian osteology; BRETT-SURMAN (1975) did not observe any significant variation in the few specimens he examined, but he noticed that no conclusion can be reached, due to lack of material. However, the sternals of *Bactrosaurus johnsoni* closely resemble those figured in *Anatosaurus annectens* (LULL & WRIGHT, 1940, fig. 21). The shape of the median border and the development of a blunt distal end seem variable in *Iguanodon bernissartensis*. These characters are therefore regarded as too variable to be phylogenetically useful.

Humerus (Figure 28; Plate 10, Fig. 4):

Description – The humerus is relatively robust and cranio-caudally flattened. Its proximal head is broad medio-

laterally and flattened cranio-caudally, producing a shallow concave cranial surface and a convex caudal surface. In the middle of the proximal end, the articular head of the humerus (**ah**) is supported by a buttress on its caudal surface and is flanked by one inner (**itb**) and one outer (**otb**) tuberosities. Both are set more cranially than the articular head; the outer tuberosity is separated from the articular head by a shallow groove, while the inner tuberosity is connected to the articular head by a continuous and convex border. From the inner tuberosity, the shaft of the humerus curves concavely outwards and downwards to the distal ulnar condyle. From the outer tuberosity, the shaft develops a prominent and angular deltopectoral crest (**dpc**), extending along the proximal half of the humerus. The border of this crest is well rounded, rugose and turned cranially; its caudal border bears an important scar marking the insertion of the powerful *M. pectoralis*, while its cranial side bears well marked insertion areas for the *M. deltoideus clavicularis* and the *M. brachialis*. The bicipital gutter (**bcg**) is very developed on the cranial side of the humerus, between the deltopectoral crest and the medial border. Beneath the middle of the shaft, the lateral border of the humerus contracts and the shaft tapers slightly before expanding into the distal radial condyle.

The distal end is slightly twisted externally. It is formed by a radial and an ulnar condyles. The radial condyle (**rac**) is distinctly less developed than the ulnar condyle (**ulc**), which extends more distally. Both are separated by a shallow intercondylar groove more developed caudally than cranially; it received the olecranon process of the ulna.

Discussion – The humerus of *Bactrosaurus johnsoni* closely resembles that of *Gilmoresaurus mongoliensis* and that of Hadrosaurinae (particularly that of *Kritosaurus incurvimanus*). This bone is moderately elongated and the deltopectoral crest is well developed, angular and extends not below the midpoint of the element; the ulnar condyle is distinctly more developed than the radial condyle. In *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus* and, particularly, *Camptosaurus dispar*, the humerus is more gracile and the deltopectoral crest is less developed and less angular; the radial and ulnar condyles appear less asymmetrical. On the other hand, the humerus of Lambeosaurinae usually appears much more robust and the deltopectoral crest is distinctly wider; it can extend below the midpoint of the element. Nevertheless, BRETT-SURMAN (1989) shows that the length/width ratio is an insufficient feature to delineate subfamilies and must therefore be abandoned as a taxonomic criterion, as an important overlapping can be observed between Hadrosaurinae and Lambeosaurinae.

Ulna (Figure 29; Plate 11, Fig. 1):

Description – The ulna of *Bactrosaurus johnsoni* is long and straight. Proximally, the olecranon process (**olpr**) is

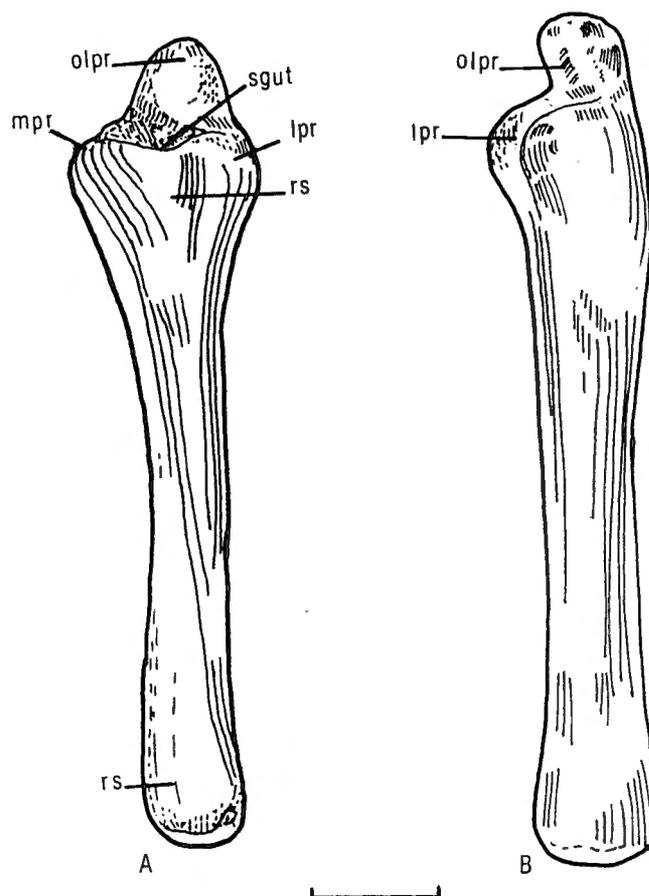


Fig. 29 – Left ulna of *Bactrosaurus johnsoni* (SBDE 95E5/42), from the Iren Dabasu Formation - A: cranial view; B: lateral view. Scale bar = 5 cm. lpr: lateral process; mpr: median process; olpr: olecranon process; rs: radial surface; sgut: sigmoidal gutter.

stout, prominent and rounded; its caudal surface is very convex, whereas its cranial surface is flattened. This process is separated from the body of the ulna by a concave sigmoidal gutter (**sgut**), which articulated with the humerus; this gutter is very roughened, indicating that it was covered by cartilage in life. The proximal part of the ulnar body is very enlarged medio-laterally. Its caudal surface is very rounded transversely. Cranially, it forms a large and transversely concave articular surface for reception of the proximal head of the radius (**rs**). It is bordered medially by a very prominent process (**mpr**), which progressively lessens distally. The lateral proximal process (**lpr**) is distinctly less developed. Between both processes, the proximal border of the ulnar body bears a prominent knob, marking the insertion of a very strong tendon, common for the *M. biceps (coraco-antebrachialis)* and the *M. brachialis (humero-antebrachialis)*. The width of the ulna progressively lessens distally and the section of the bone becomes elliptical, with a great axis oriented obliquely. The distal head is slightly enlarged again and is triangular in cross-section. Its craniomedial side bears a triangular facet, elongated proximo-distally, for reception of the distal end of the radius. The distal articular surface is slightly concave.

Discussion – In *Hypsilophodon foxii* and *Camptosaurus dispar*, the articulation for the humerus forms an enlarged bump and the olecranon process is not present; the medial and lateral processes are slightly developed and the distal end is well expanded. On the other hand, the olecranon process forms a large and robust hook in *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Bactrosaurus johnsoni*, *Telmatosaurus transsylvanicus* and in Hadrosauridae; the medial and lateral processes are more prominent, but the distal end is less expanded.

The ulna of *Bactrosaurus johnsoni* is relatively thick and robust, like that of *Iguanodon atherfieldensis* and *Parasaurolophus cyrtocristatus*. In *Ouranosaurus nigeriensis*, *Telmatosaurus transsylvanicus* and in most Hadrosauridae, the ulna appears proportionally more gracile. On the other hand, the ulna of *Iguanodon bernissartensis* appears proportionally short and very robust.

Radius (Plate 11, Fig. 2):

Description – The radius is distinctly shorter than the ulna. It is slender, mainly cylindrical and slightly curved cranially. Both ends are slightly expanded. The proximal end is semi-circular in cross-section; its caudal flat surface lodged into the cranioproximal concavity of the ulna. The distal end of the radius is mainly expanded cranio-caudally and triangular in cross-section. Its caudolateral side forms a slightly concave triangular facet which applicated against the distal end of the ulna. The distal articular surface is convex.

Discussion – The radius of *Bactrosaurus johnsoni*, like its ulna, is relatively robust and closely resembles that of *Iguanodon atherfieldensis* and *Parasaurolophus cyrtocristatus*. The radius of *Ouranosaurus nigeriensis* and of most derived Hadrosauridae appears more gracile, whereas that of *Iguanodon bernissartensis* is more robust.

Hand:

Description – Very few bones from the hand are currently known in *Bactrosaurus johnsoni*. Metacarpal III is long, slender and somewhat transversely compressed. Its proximal head is convex and subrectangular in cross-section. The medial and lateral sides of the shaft are flattened, indicating a close contact with metacarpals II and IV. The distal head is slightly enlarged palmo-dorsally; it forms a well developed articular surface with a very shallow intercondylar groove.

Metacarpal IV is also relatively long and slender. Its proximal end is broad, roughly triangular and convex. The shaft is contracted distally and diverged from metacarpal III. Both its palmar and medial sides are concave. Its medial side bears a well marked apophysis, below its middle part, which appears to have reinforced the attachment between digits III and IV. The dorsal side is nearly flat and the lateral side is rounded. The distal end is

semicircular in cross-section, transversely compressed and slightly expanded palmo-dorsally into a narrow and convex condyle.

The first phalanx of digit III is a very massive element. Its proximal end is very expanded both transversely and palmo-dorsally; it forms a slightly concave proximal articular surface. Distally, the sides of this phalanx are contracted and the ventral side becomes rugose, marking the insertion of the flexor tendon. The expanded distal end forms a well-developed articular surface, strongly convex palmo-dorsally; the important dorsal extension of this surface indicates that hyper-extension of digit III was possible.

SBDE 95E5/67 is tentatively interpreted as the first phalanx of digit II or IV. It is a dumbbell-shaped element, compressed palmo-dorsally. Its dorsal side is convex, whereas its palmar side is slightly concave and roughened, marking the insertion of the flexor ligament. Both its articular surfaces are slightly concave.

Discussion – The few elements of the hand discovered in Locality 95E5 are very similar to the corresponding elements in *Iguanodon atherfieldensis*. The morphology of the first phalanx of digit III is very interesting from a biomechanical point of view. The continuation of the distal articular surface onto the dorsal side of its shaft allow the phalanges to be hyper-extended. This function is compatible with the production of a stable digitigrade foot. It was therefore possible that *Bactrosaurus johnsoni* could use its forelimbs for weight-support and locomotion, at least occasionally.

PELVIC GIRDLE AND HIND LIMB

Ilium (Figure 30; Plate 12, Fig. 1):

Description – The ilium forms an elongated and transversely compressed lamina, about 3.8 times as long as high. It is formed by a preacetabular process (**pracp**), a main blade (**mbl**) and a postacetabular process (**poacp**). When viewed from above, the dorsal rim of the ilium is sigmoidal:

The preacetabular process is a long and tapering projection from the craniodorsal edge of the iliac blade, forming about half of the length of the ilium. Its is strongly deflected ventrally and curved outwards. Its dorsal edge is very rounded, whereas its ventral edge is sharp. It also becomes twisted along its length, so that the medial surface progressively faces obliquely dorsomedially towards its cranial end. Its medial side is perfectly flat. Its lateral side bears a strong carina, which extends forwards in a shallow curve and progressively diminishes in size before disappearing near the cranial end. This carina produces a broad ventral shelf on the preacetabular process, which represents the insertion surface of the *M. ilio-tibialis 2* (**mit2**).

The main blade of the ilium is relatively high. Its dorsal border is rounded, sigmoidal and thicker at its cranial and caudal ends. The cranial half of the lateral side is slightly

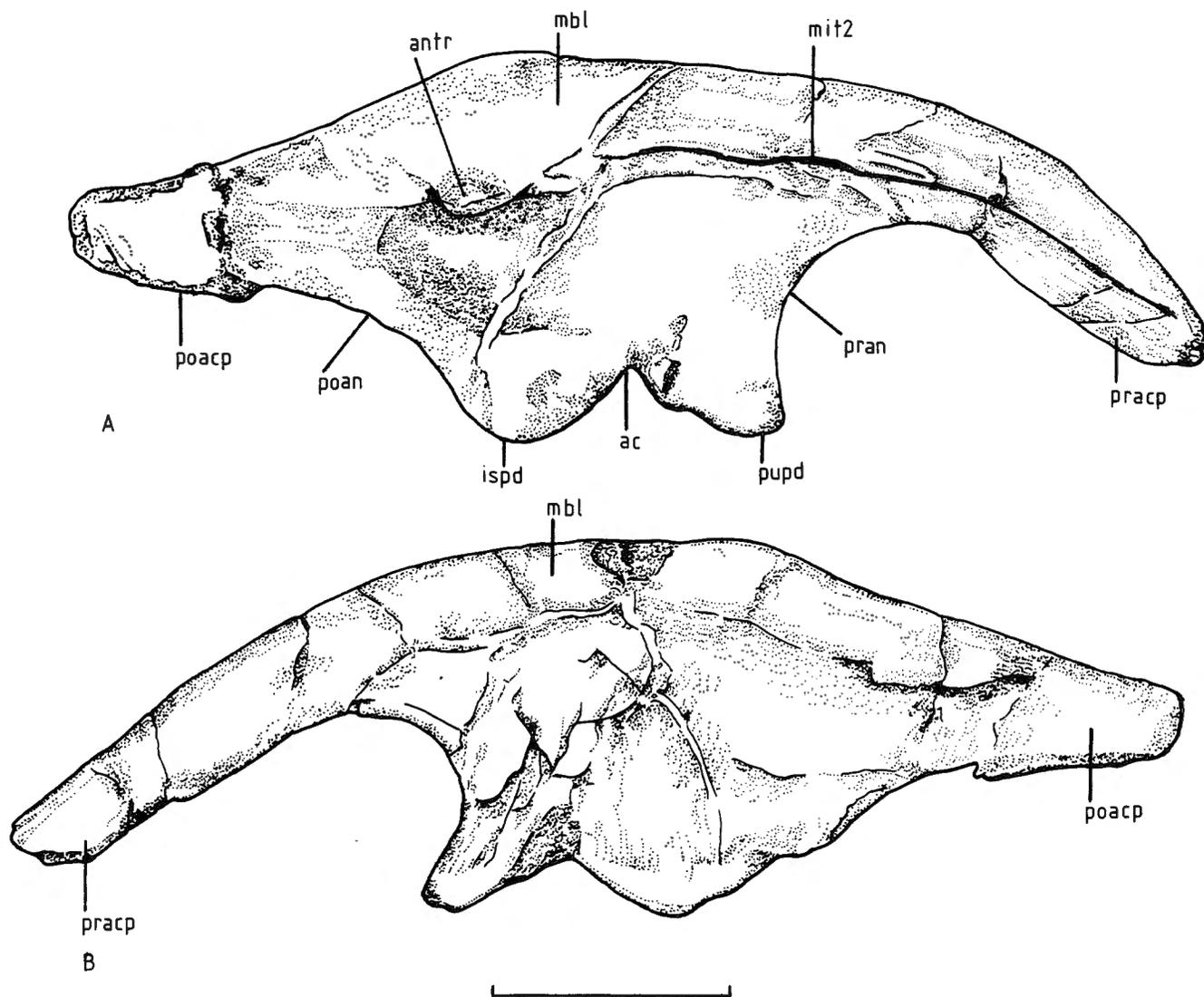


Fig. 30 – Right ilium of *Bactrosaurus johnsoni* (SBDE 95E5/25), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 10 cm. ac: acetabulum; antr: antitrochanter; ispd: ischial peduncle; mbl: main blade; mit2: insertion area of the *M. ilio-tibialis* 2; poacp: postacetabular process; poan: postacetabular notch; pracp: preacetabular process; pran: preacetabular notch; pupd: pubic peduncle.

convex cranio-caudally, while its caudal half is slightly concave. The lateral side is separated from the dorsal side by a very developed carina, in continuity with the lateral carina of the preacetabular process. The height of this carina progressively diminishes caudally. At the level of the postacetabular notch, the dorsolateral border of the ilium is folded to form a rather well-developed antitrochanter (**antr**). The ventral side of the main blade of the ilium forms two notches and one cavity, separated by two peduncles, as described by TAQUET (1976) in *Ouranosaurus nigeriensis*. The preacetabular notch (**pran**) is well marked and not very open, because of the important ventral deflection of the preacetabular process. The pubic peduncle (**pupd**) is a relatively long and massive process extending rostroventrally. The iliac portion of the acetabulum (**ac**) is relatively deep and asymmetrical. The ischial peduncle (**ispd**) is elongated cranio-caudally and massive, but not very prominent. The

postacetabular notch (**poan**) is less marked than the preacetabular one.

The postacetabular process is short, massive and triangular in lateral view. Its dorsal border is very thickened laterally and oblique inwards.

Discussion – BRETT-SURMAN (1975) compares the morphology of the ilium in several hadrosaur genera and in *Camptosaurus*. He recognizes five types of ilia among hadrosaurs. The ilium of *Bactrosaurus* may be considered as an ideal structural intermediate between that of iguanodontids and that of hadrosaurids, as it presents a mosaic of advanced, primitive and intermediate characters:

- The preacetabular process is very deflected ventrally, as in *Iguanodon bernissartensis* and in Hadrosauridae. In *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon artherfieldensis* and *Ouranosaurus nigeriensis*, this process appears more horizontal.

- The postacetabular process looks proportionally more elongated and reduced in height than in *Camptosaurus dispar* and *Ouranosaurus nigeriensis*; nevertheless, it is less elongated than in most hadrosaurids.
- The antitrochanter is present, but not very developed in *Bactrosaurus johnsoni*. It is absent in *Camptosaurus dispar*, sketched in *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*, well developed in Hadrosaurinae and usually very developed in Lambeosaurinae.
- The pubic peduncle of *Bactrosaurus johnsoni* is long, massive and extends cranioventrally, as in *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *Iguanodon atherfieldensis* and *Ouranosaurus nigeriensis*. In Hadrosauridae, this peduncle is reduced in size, proportionally less massive and it does not extend as far cranioventrally (BRETT-SURMAN, 1975).
- The ischial peduncle of *Bactrosaurus johnsoni* bears a single large rugose knob, as that of *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis*

and *Ouranosaurus nigeriensis*. In Hadrosauridae, it consists of two small protrusions separated by a shallow depression (BRETT-SURMAN, 1975).

The ilium of *Gilmoreosaurus mongoliensis* closely resembles that of *Bactrosaurus johnsoni*. Nevertheless, the preacetabular process seems significantly more deflected ventrally in the latter.

Ischium (Figure 31; Plate 12, Fig. 2):

Description – The ischium is long, shaft-like and relatively robust. Its cranial end is expanded dorso-ventrally, flattened laterally and triradiate: it forms an iliac ramus, a pubic ramus and an “obturator process”. The iliac ramus (**ilr**) is the largest. Its dorsal end, which contacted the ischial peduncle of the ilium, is very rugose and thickened medially. The pubic ramus (**pur**) is elongated cranio-caudally, compressed laterally and hatchet-shaped. Its rugose cranial surface contacted the ischial peduncle of the pubis, while its narrow ventral border contacted the

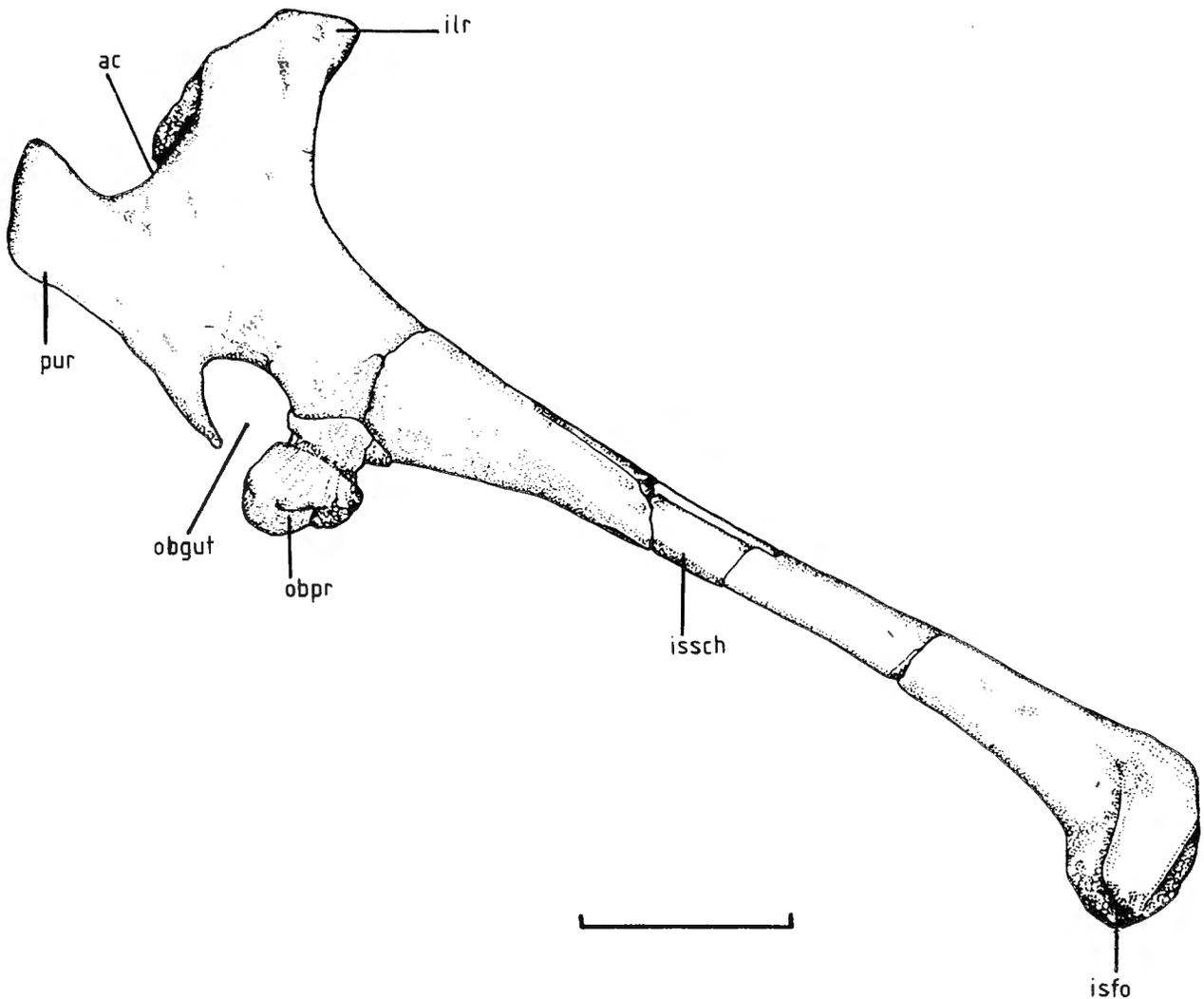


Fig. 31 – Right ischium of *Bactrosaurus johnsoni* (SBDE 95E5/26), from the Iren Dabasu Formation - medial view. Scale bar = 10 cm. ac: acetabulum; ilr: iliac ramus; isfo: ischial foot; issch: ischial shaft; obgut: obturator gutter; obpr: obturator process; pur: pubic ramus.

pubic bar. Its concave dorsal border forms, in continuity with the ventral border of the iliac ramus, the caudal margin of the acetabulum (**ac**). The caudoventral corner of the pubic ramus is very salient and partially closes the obturator gutter. The "obturator process" (**obpr**) is very developed, higher than the pubic ramus. It is set in a very cranial position. Its ventral border is expanded and closely contacted the pubic bar. The caudal border of the obturator process is prolonged caudally as a carina on the medial side of the ischial shaft. The obturator gutter (**obgut**) is ovoid in shape, with an cranio-caudal great axis, and open ventrally.

The ischial shaft (**issch**) is long, very thick, elliptical in cross-section and slightly compressed laterally. It is distinctly curved outwards and very slightly ventrally. Its distal end is expanded ventrally into a very prominent ischial foot (**isfo**). The caudal third of the ischial shaft is very flat and bears medially numerous rugose striations, indicating its attachment to the paired ischium.

Discussion – As previously noted by TAQUET (1976: 139), the ischium of *Bactrosaurus johnsoni* closely resembles that of *Ouranosaurus nigeriensis*. In both genera, the ischial shaft is nearly straight: it is distinctly curved ventrally in *Iguanodon bernissartensis* and *I. atherfieldensis* and moderately curved in *Camptosaurus dispar*. It is perfectly straight in Hadrosauridae.

The stout ischial shaft and the very prominent ischial foot are also features shared by *Bactrosaurus johnsoni* and *Ouranosaurus nigeriensis*. The footed knob is always present in Lambeosaurinae, although its development

varies from one genus to another. It is also present in more basal iguanodonts *Camptosaurus dispar*, *Iguanodon bernissartensis* and *Iguanodon atherfieldensis* (contra HORNER, 1990). In Hadrosauridae, on the other hand, the ischial shaft progressively narrows caudally, without expanded ischial foot (WEISHAMPEL & HORNER, 1990).

The obturator gutter is large and deep in *Bactrosaurus johnsoni*, as in *Camptosaurus dispar*, *Iguanodon bernissartensis*, *Iguanodon atherfieldensis* and *Ouranosaurus nigeriensis*. It tends to be less markedly excavated in Hadrosauridae (BRETT-SURMAN, 1975). In these latter, the obturator gutter tends to close in older individuals (BRETT-SURMAN, 1975; WEISHAMPEL & HORNER, 1990), but this character is too inconstant to be phylogenetically useful.

Pubis (Figure 32; Plate 12, Fig. 3):

Description – The pubis is composed of 3 portions: the prepubis, the middle part and the pubic bar. The prepubis (**prpu**) is proportionally much elongated cranio-caudally than previously described by GILMORE (1933, fig. 37) and BRETT-SURMAN (1975: 28), on incomplete material. This plate is very compressed laterally; the ventral border is thinner than the dorsal border. Both the ventral and dorsal borders are symmetrically convex. A well marked and relatively long neck, with ventral and dorsal borders symmetrically concave, separates the prepubis from the middle part of the pubis.

The middle part of the pubis is thickened. The dorsal process (**dpr**), which contacted the pubic peduncle of the

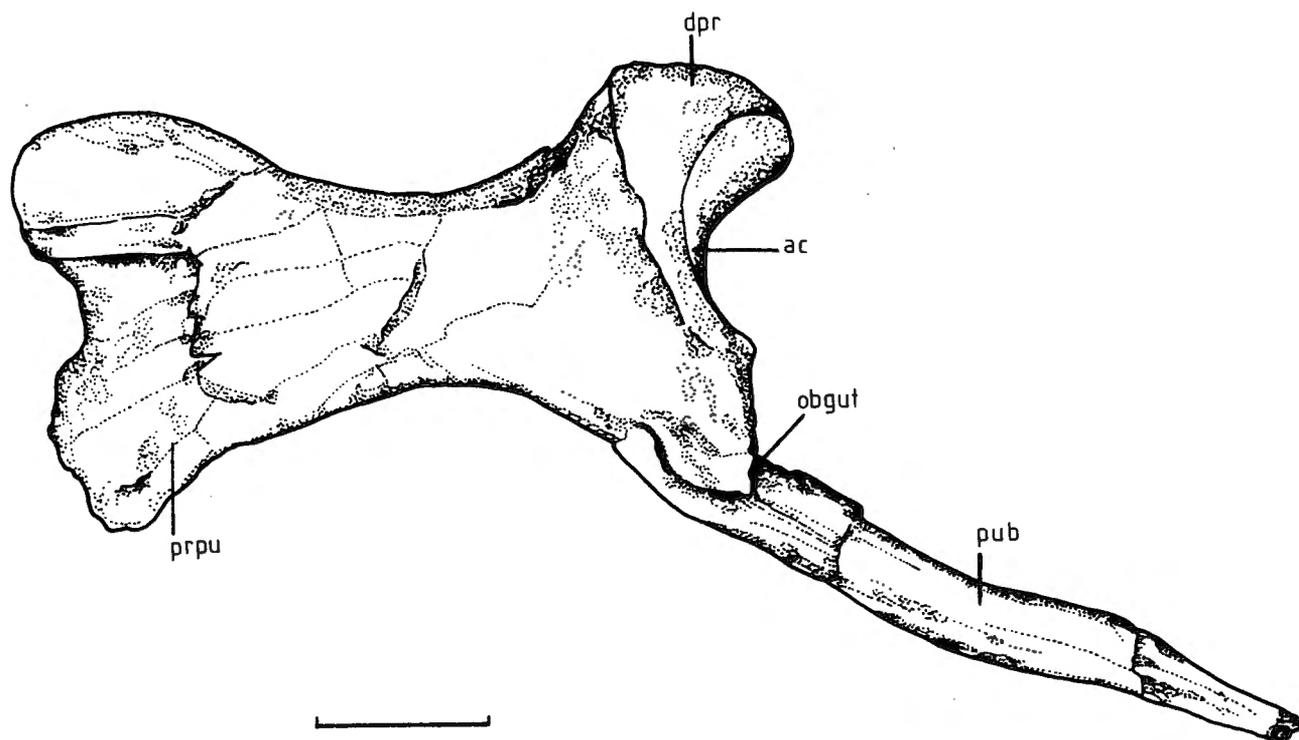


Fig. 32 – Left pubis of *Bactrosaurus johnsoni* (SBDE 95E5/27), from the Iren Dabasu Formation - lateral view. Scale bar = 5 cm. ac: acetabulum; dpr: dorsal process; obgut: obturator gutter; prpu: prepubis; pub: pubic bar.

ilium, is rather stout; its medial side bears a prominent, rough and oblique ridge, descending to the level of the ventral part of the acetabulum. The caudal border of the middle part of the pubis is regularly concave, forming the cranial margin of the acetabulum (**ac**). The ischial peduncle, which contacted the pubic ramus of the ischium, forms the caudoventral corner of the middle part of the pubis.

The pubic bar (**pub**) is straight, relatively thin and not very long. Cranially, it is triangular in cross-section, but it progressively tapers and flattens dorso-ventrally towards the caudal end. It inserts on the caudomedial side of the middle part of the pubis. An obturator gutter (**obgut**), largely open caudally, is circumscribed between the cranio-lateral side of the pubic bar and the medial side of the ischial peduncle.

Discussion – In *Bactrosaurus johnsoni*, the relative length and robustness of the pubic bar are similar to those observed in *Iguanodon bernissartensis*, *I. atherfieldensis*

and *Ouranosaurus nigerensis*. Primitively in ornithopods, this process is longer than the prepubis and as long as the ischial shaft, as observed in *Hypsilophodon foxii* and *Camptosaurus dispar*. In Hadrosauridae, on the other hand, it is proportionally shorter and more slender than in *Bactrosaurus johnsoni* (see LULL & WRIGHT, 1942; BRETT-SURMAN, 1975; WEISHAMPEL & HORNER, 1990).

In more generalized ornithopods, as observed in *Camptosaurus dispar* and *Hypsilophodon foxii*, the prepubic blade is very slender and the prepubic blade and neck are not differentiated. In derived advanced ornithopods, the prepubic blade is more expanded dorso-ventrally and well separated from the neck. However, the shape of the prepubic blade varies greatly in iguanodontids and hadrosaurids and may be useful in generic identification (HORNER, 1979; WEISHAMPEL & HORNER, 1990), but probably not in the establishment of phylogenetic relationships. The prepubis of *Bactrosaurus johnsoni* is of intermediate shape, as in *Iguanodon atherfieldensis*, *Ouranosaurus nigerensis* or *Prosaurolophus maximus*; it is

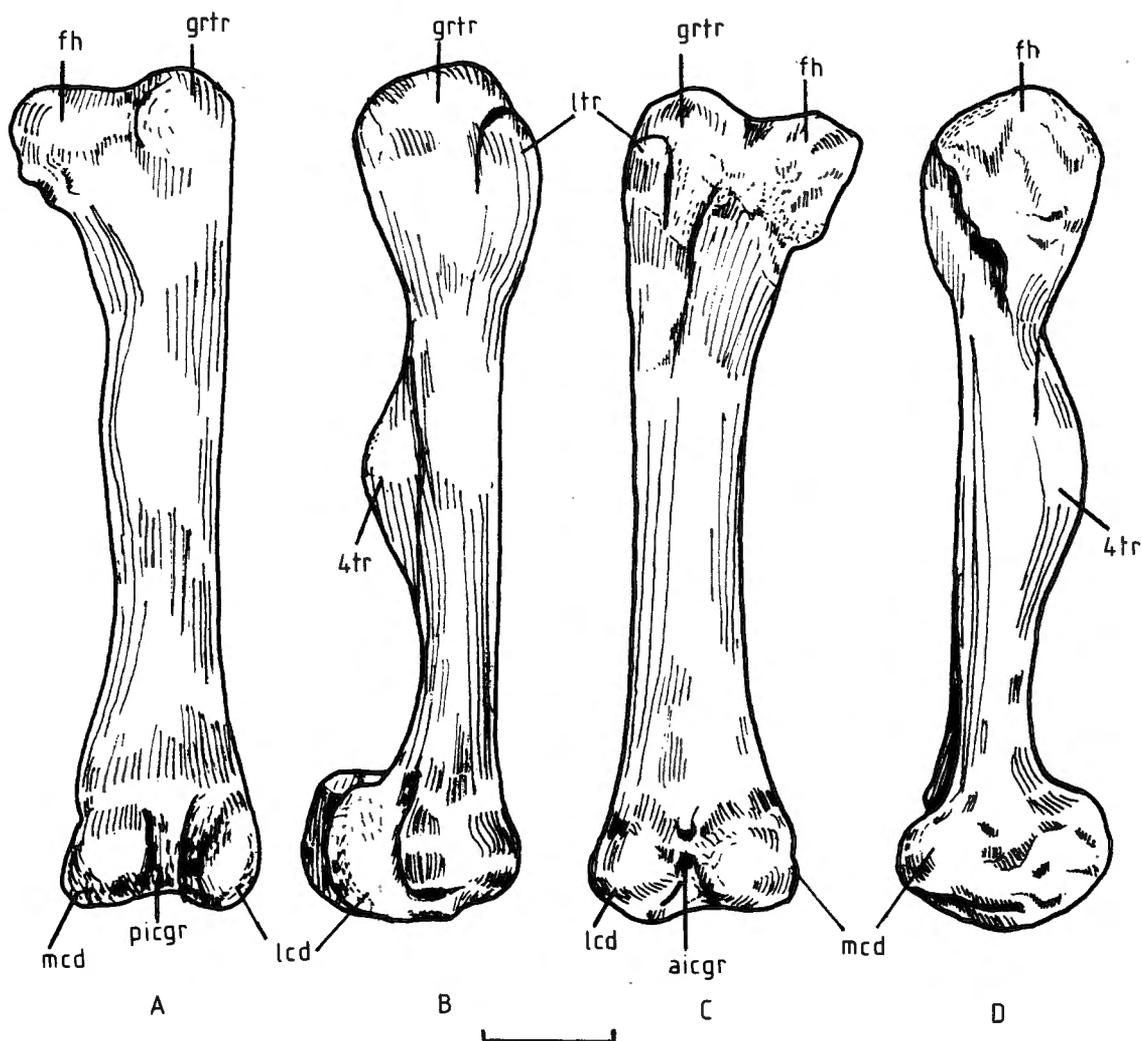


Fig. 33 – Right femur of *Bactrosaurus johnsoni* (AMNH 6577), from the Iren Dabasu Formation - A: caudal view; B: lateral view; C: cranial view; D: medial view. Scale bar = 5 cm. aicgr: anterior (cranial) intercondylar groove; fh: femoral head; grtr: greater trochanter; lcd: lateral condyle; ltr: lesser trochanter; mcd: medial condyle; picgr: posterior (caudal) intercondylar groove; 4tr: fourth trochanter.

not as slender as in *Iguanodon bernissartensis*, *Gilmoreosaurus nigeriensis* or *Edmontosaurus edmontoni*, for examples, but not as robust as in *Parasaurolophus cyrtocristatus*. BRETT-SURMAN (1975) relies the shape of the prepubic blades, in advanced Hadrosauridae, to the general robustness of the animal: the most gracile forms have the most elongated pubis; whereas the most robust forms also have the shortest pubis; this conclusion is probably invalid in the case of iguanodontids.

The obturator foramen is closed in *Camptosaurus dispar*, partially open caudally in *Iguanodon bernissartensis*, *Iguanodon atherfieldensis* and *Ouranosaurus nigeriensis*. It is fully open caudally, forming a gutter, in *Bactrosaurus johnsoni*, *Gilmoreosaurus mongoliensis* and in Hadrosauridae. In *Hypsilophodon foxii*, it can be closed or open.

Femur (Figure 33; Plate 13, Fig. 1):

Description – Two right femora (AMNH 6577) belonging to juvenile individuals were discovered by the AMNH expedition in Quarry 141. These bones are particularly finely preserved and the description proposed below is mainly based on these specimens, but also on the type material (AMNH 6553) and on SBDE 95E5/88.

The femur is long and robust. Its proximal end is broad and saddle-shaped. The femoral head (**fh**) is globular, large and set at an angle to the shaft on a stout and short neck. The greater trochanter (**grtr**), set externally to the femoral head, is moderately developed. Its apex lies at the same level as that of the femoral head. On the cranio-proximal angle of the femur, the lesser trochanter (**ltr**) is well developed, particularly in juvenile individuals. A scar on its lateral surface marks the insertion of the *M. iliofemoralis*. The greater and lesser trochanters are separated by a shallow and narrow gutter, which extends on the medial surface of the proximal part of the femoral shaft.

The femoral diaphysis is straight, relatively slender in juveniles, but very robust in adult specimens. It is nearly circular in cross-section. The fourth trochanter (**4tr**) lies along its caudomedial side. This thin piece of bone is particularly prominent and triangular in lateral view. It therefore provided a large attachment area for powerful protractor and retractor muscles. Unfortunately, the surface of the femoral shaft is not sufficiently well preserved to allow a detailed description of the different muscular attachment areas.

The articular surfaces of the distal condyles are greatly expanded cranio-caudally. The medial condyle (**med**) is the larger. The lateral surface of the lateral condyle (**lcd**) bears a deep longitudinal groove, which received the distal tendon of the *M. ilio-fibularis*. Both distal condyles extend caudally for a considerable distance and their distal articular surfaces are gently convex cranio-caudally. Cranially, the distal condyles meet each other to form an intercondylar “tunnel” (**aicgr**), that surrounded the insertion tendon of the *M. ilio-tibialis* on its way to the cnemial crest of the tibia. They are separated caudally by

a deep caudal intercondylar groove (**picgr**). Both grooves are set in the same plane.

Discussion – BRETT-SURMAN (1975: 33) notices that the femur of *Bactrosaurus johnsoni* and *Gilmoreosaurus mongoliensis* are typically hadrosaurian in design and that he cannot find any diagnostic character permitting to designate any “type” of femora in hadrosaurs. The femur of *Iguanodon bernissartensis*, *Iguanodon atherfieldensis* and *Ouranosaurus nigeriensis* is also very similar. ROMER (1927: 258) shows that the evolution of the femur is very discrete in the morphological series *Camptosaurus* - *Iguanodon* - ‘*Anatosaurus*’ (*Trachodon*): the femur becomes a little more massive, the lesser trochanter tends to fuse with the diaphysis and the fourth trochanter loses its pending aspect. TAQUET (1976: 143) places the femur of *Ouranosaurus nigeriensis* like that of *Iguanodon*, between that of *Camptosaurus* and that of ‘*Anatosaurus*’.

The femoral diaphysis of *Camptosaurus dispar* seems distinctly curved, when viewed laterally, as in *Hypsilophodon foxii*. It is nearly straight in *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Bactrosaurus johnsoni* and in Hadrosauridae. It is slightly bowed laterally in *Telmatosaurus transsylvanicus*.

The cranial intercondylar groove is always closed in *Bactrosaurus johnsoni*, like in *Gilmoreosaurus mongoliensis* and *Telmatosaurus transsylvanicus*. This character is frequent in Hadrosauridae. For WEISHAMPPEL & HORNBERGER (1990: 552), the presence of this channel may be species dependent, but it is not age dependent. The intercondylar groove is always open in *Camptosaurus dispar*, *Iguanodon bernissartensis* and *I. atherfieldensis*; it is also open in *Ouranosaurus nigeriensis*, except in one isolated femur (TAQUET, 1976: 143).

Tibia (Figure 34; Plate 13, Fig. 2):

Description – The tibia of *Bactrosaurus johnsoni* has never been described nor figured previously. The description proposed below is mainly based on a tibia belonging to a juvenile and associated with the type material (AMNH 6553; Quarry 141). The tibia is perfectly straight. Its proximal head is considerably widened transversely: this widening is progressive, extending on the proximal part of the diaphysis. The cnemial crest (**cncr**) is very developed on the cranio-proximal corner of the tibia; in cranial view, this crest is not perfectly straight, but it is curved externally. Its ventral edge appears, therefore, oblique. The medial side of the proximal head is very convex. Its caudal corner is enlarged by the presence of a large internal condyle (**icd**). A lateral condyle (**lcd**) is set on the lateral side of the proximal head. Both are of approximately equal size and are separated from each other by a deep and narrow groove.

The diaphysis is long, straight and ovoid in cross-section. Proximally, the great axis is oriented cranio-caudally. It progressively orients transversely towards its distal end. Its lateral side bears a prominent ridge that

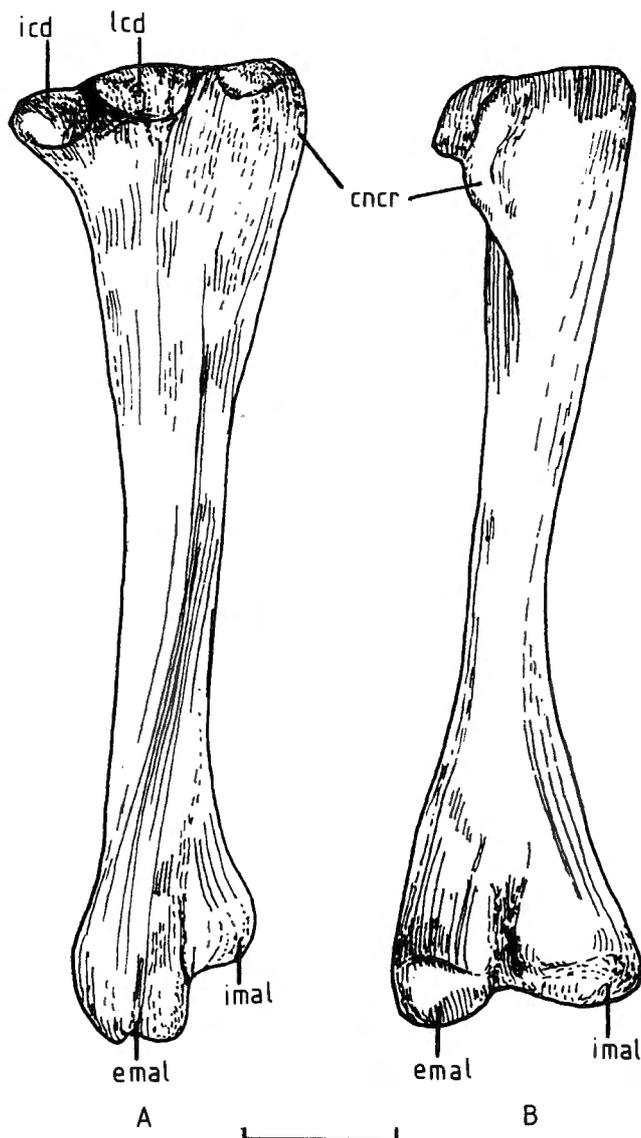


Fig. 34 – Right tibia of *Bactrosaurus johnsoni* (AMNH 6577), from the Iren Dabasu Formation - A: lateral view; B: cranial view. Scale bar = 5 cm. cncr: cnemial crest; emal: external malleolus; icd: internal condyle; imal: internal malleolus; lcd: lateral condyle.

extends on the lateral corner of the external malleolus.

The distal head of the tibia is nearly as wide as its proximal head. Its great axis is oblique, forming an angle of about 120° with the great axis of the proximal head. Its cranial side is flat: its external border contacted the distal part of the fibula. The external malleolus (**emal**) is very salient distally. On the other hand, the internal malleolus (**imal**) is very salient craniomedially. The articular surface of the internal malleolus is turned towards the craniolateral side of the tibia: it fitted into the dorsal articular facet of the astragalus. Its medial side bears a small longitudinal adductor crest. The articular surface of the external malleolus is turned towards the caudomedial side of the tibia. Its medial portion contacted the astragalus, whereas the external portion contacted the calcaneum.

Discussion – In *Hypsilophodon foxii*, *Camptosaurus dispar*, *Iguanodon bernissartensis*, *I. atherfieldensis* and *Ouranosaurus nigeriensis*, the transverse widening of the proximal head of the tibia is quite proximal (TAQUET, 1976); it is more progressive, extending on the proximal portion of the diaphysis in *Bactrosaurus johnsoni*, *Gilmoreosaurus mongoliensis*, *Telmatosaurus transsylvanicus* and in Hadrosauridae.

The external condyle is nearly as voluminous as the internal condyle in *Ouranosaurus nigeriensis* and *Bactrosaurus johnsoni*. It is, on the other hand, much smaller in *Camptosaurus dispar*, *Iguanodon bernissartensis* and *I. atherfieldensis* (TAQUET, 1976); this character seems variable in Hadrosauridae.

Fibula (Plate 13, Fig. 3):

Description – The fibula is a slender and nearly straight bone. Its proximal head is dorso-ventrally expanded, crescentic in proximal view and rough; it is usually more expanded caudally than cranially. Its lateral side is convex, whereas its medial side is concave. This proximal head fitted into a concavity of the arcuate cnemial crest of the tibia. Below the proximal head, the shaft tapers towards the distal end. Its lateral side is regularly convex cranio-caudally, while its medial surface is slightly concave. The distal head is expanded and twisted, so that it applicated against the craniolateral side of the distal portion of the tibia.

Discussion – No diagnostical or phylogenetically interesting character can be distinguished on the fibula of *Bactrosaurus johnsoni*, which closely resembles that of other Iguanodontia.

Tarsus (Figure 35; Plate 14, Figs. 1 & 2):

Description – **The astragalus** is very large, extending towards the medial border of the tibia. In dorsal view, the articular surface for the internal malleolus of the tibia (**ast**) occupies the medial two-thirds of its proximal side; this surface is regularly concave cranio-caudally. The lateral third of the proximal side of the astragalus forms a depression concave cranio-caudally and very oblique outwards. The external malleolus of the tibia and the calcaneum articulated against this surface. In caudal view, the dorsal border of the astragalus forms a very prominent ascending process (**papr**), which accommodated against the caudal side of the tibia. The craniomedial corner of the astragalus forms also an ascending process (**aapr**), less extended than the caudal one, but very high. The cranial side of the astragalus bears a large and deep depression below the cranial ascending process.

The calcaneum is stout and trapezoidal in outline, when viewed from above. It is distinctly longer cranio-caudally than wide. Its proximal side forms two articular facets. These facets are concave cranio-caudally and separated from each other by an oblique transverse ridge.

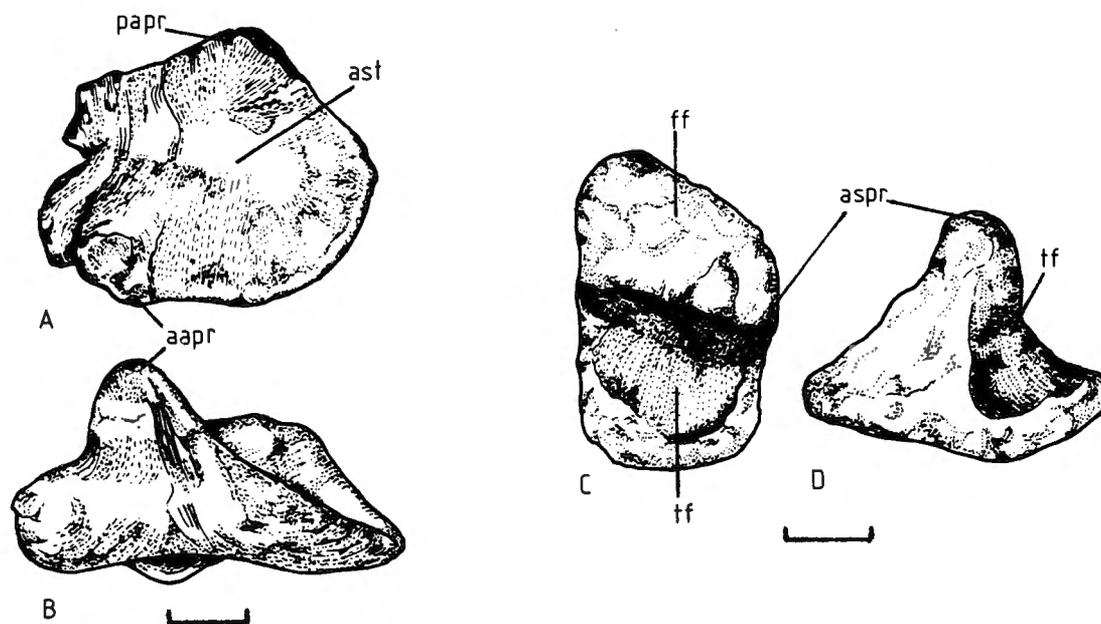


Fig. 35 – Right tarsus of *Bactrosaurus johnsoni* (AMNH 6577), from the Iren Dabasu Formation - A: astragalus, dorsal view; B: astragalus, cranial view; C: calcaneum, dorsal view; D: calcaneum, medial view. Scale bars = 3 cm. aapr: anterior (cranial) ascending process; aspr: ascending process, ast: articular surface for the tibia; ff: fibular facet; papr: posterior (caudal) ascending process; tf: tibial facet.

They are limited laterally by a longitudinal crest, while they are open medially: they look consequently inclined inwards. The cranial facet (ff) is triangular in shape: it received the distal articular surface of the fibula. The caudal articular facet (tf) is larger and deeper than the cranial one; it articulated with the external malleolus of the tibia. The transverse ridge becomes progressively higher outwards; meeting the external longitudinal ridge, it forms a prominent ascending process (aspr). The medial surface of the calcaneum, which articulated with the astragalus, is very rough.

The fourth distal tarsal is a small and thin bony disk, which fitted between the distal surface of the calcaneum and the metatarsal IV. Its proximal surface is slightly concave, while its distal surface is convex. Its lateral border is thicker than its medial border and rough.

Discussion – The astragalus and calcaneum of *Bactrosaurus johnsoni* closely resemble those of *Iguanodon atherfieldensis*, *Ouranosaurus nigeriensis* and Hadrosauridae. In *Camptosaurus dispar*, the astragalus looks more rectangular in cranial view and the ascending processes of the astragalus are less prominent (BRETT-SURMAN, 1975).

Metatarsals and phalanges (Figure 36; Plate 14, Figs. 3-5):

Description – Two complete left feet and one partial right foot are included in the type material of *Bactrosaurus johnsoni* (AMNH 6553, Quarry 141; GILMORE, 1933, fig. 39). They all belong to adult specimens. The description below is mainly based on these fossils.

Metatarsal II is the shortest of the series. Its proximal end is very compressed laterally and planto-dorsally expanded. Its proximal articular surface is narrow and slightly convex cranio-caudally. Its shaft is, on the other hand, compressed cranio-caudally. Its medial surface, in contact with metatarsal III, is nearly flat. Beneath the middle of the shaft, the craniolateral border of metatarsal II forms a prominent lip-like projection which appears to have reinforced the attachment between metatarsal II and III. Beneath this lip, the shaft diverges from metatarsal III. The distal articular surface faces obliquely inwards; caudally, it bears a slight intercondylar groove, to guide the phalangeal flexor tendon.

Metatarsal III is the largest and stoutest metapodial. Its proximal articular surface is roughly triangular and more developed cranio-caudally than transversely; its medial side is very concave cranio-caudally for reception of metatarsal II. The shaft is very contracted both cranio-caudally and transversely. Distally, the shaft expands to form a large, saddle-shaped and very rough articular surface. The intercondylar groove is very developed and divides the distal articular surface into two subequal parts.

Metatarsal IV is larger than metatarsal II, but distinctly smaller than metatarsal III. Its proximal head is slightly expanded cranio-caudally and transversely; its medial side is very concave, where it fits against metatarsal III, while its lateral side is very convex. The proximal articular surface is cup-shaped, for reception of tarsal IV. Beneath the proximal head, the medial side of the shaft forms a triangular depressed area, which extends about half-way down the shaft. Beneath this surface, a large triangular knob fitted against the lateral

surface of metatarsal III. Distally, the shaft of metatarsal IV slopes laterally away from metatarsal III. The distal articular surface is very convex cranio-caudally; both its medial and lateral sides are very concave. Its caudal side bears a slight intercondylar groove, similar to that observed in metatarsal II.

GILMORE (1933: 72) estimated that the digital formula of *Bactrosaurus johnsoni* is 0, 3, 4, 5, 0. The proximal phalanges are very massive, block-like bones. Their proximal articular surface is concave, rough and very broadened, whereas their distal articular surface is less broadened, convex and saddle-shaped. Their plantar surface bears a large, triangular and rough surface for insertion of powerful flexor tendons.

The intermediate phalanges are shortened proximodistally, but broadened transversely. They get progressively smaller and proportionally shorter distally. Their proximal articular surface is deeply concave, while their distal surface is very convex and saddle-shaped. Both the



Fig. 36 – Left metatarsus of *Bactrosaurus johnsoni* (AMNH 6553), from the Iren Dabasu Formation – dorsal view. Scale bar = 5 cm.

plantar and dorsal sides of these phalanges are depressed and very rough, for insertion of powerful tendons.

The ungual phalanges are large and hoof-like. They are very arched and flattened planto-dorsally towards their tip. Well marked claw-grooves run along either side, converging towards the tip of the ungual. The unguals of digits II and IV are asymmetrical, being twisted away from digit III. In adult specimens, the distal margin of the unguals is squarely truncated and very rough. This feature of the unguals give them an unfinished appearance.

Discussion – The phalangeal count of the pes is the same in *Bactrosaurus johnsoni* (0, 3, 4, 5, 0), as in *Iguanodon bernissartensis*, *I. atherfieldensis*, *Ouranosaurus nigeriensis*, *Gilmoreosaurus mongoliensis* and in Hadrosauridae. In *Iguanodon bernissartensis* and *I. atherfieldensis*, digit I is represented by a spinlike metatarsal alone. Within Hadrosauridae, *Claosaurus agilis* apparently also possessed metatarsal I (LULL & WRIGHT, 1942). The presence or absence of this tiny bone is not conclusive, as it can easily be lost during fossilisation. Metatarsal I remains well developed and the phalangeal count is 2, 3, 4, 5, 0 in *Hypsilophodon foxii* and *Camptosaurus dispar*.

The ungual phalanges are hoofed in *Bactrosaurus johnsoni*, as in *Iguanodon bernissartensis*, *I. atherfieldensis* and Hadrosauridae. In *Hypsilophodon foxii* and *Camptosaurus dispar*, on the other hand, the unguals remain clawed. In the type specimen of *Gilmoreosaurus mongoliensis* (AMNH 6551, Quarry 149; GILMORE, 1933, fig. 20), the unguals are of typical *Camptosaurus* form.

NATURAL POSTURE OF *BACTROSAURUS JOHNSONI*

Bactrosaurus johnsoni is known from specimens discovered in bonebeds. Incomplete and disarticulated skeletons belonging to several individuals of different sizes were mixed together after subaerial maceration and transportation along a relatively short distance (see above). Therefore, in the current state of our knowledge, the reconstruction proposed in Figure 37 is composite, because it is based on elements belonging to several individuals. The exact proportions of the different skeletal parts remain consequently conjectural, waiting for the discovery of complete specimens.

GILMORE (1933, fig. 40), who first proposed a reconstruction of *Bactrosaurus johnsoni*, presents this animal in a bipedal and bending walking gait. On the other hand, PAUL (*in* BRETT-SURMAN, 1989, pl. 12) represents it in a quadrupedal running gait. The posture and gait of derived ornithomorphs has been debated by numerous authors, including DOLLO (1883, 1905), LULL & WRIGHT (1942), GALTON (1970), NORMAN (1980, 1986), ALEXANDER (1985), BULTYNCK (1993) and CHRISTIAN & PREUSCHOTT (1996). GALTON (1970) asserted that hadrosaurs were bipedal and that the straight part of the vertebral column was probably held more or less horizontal while running.

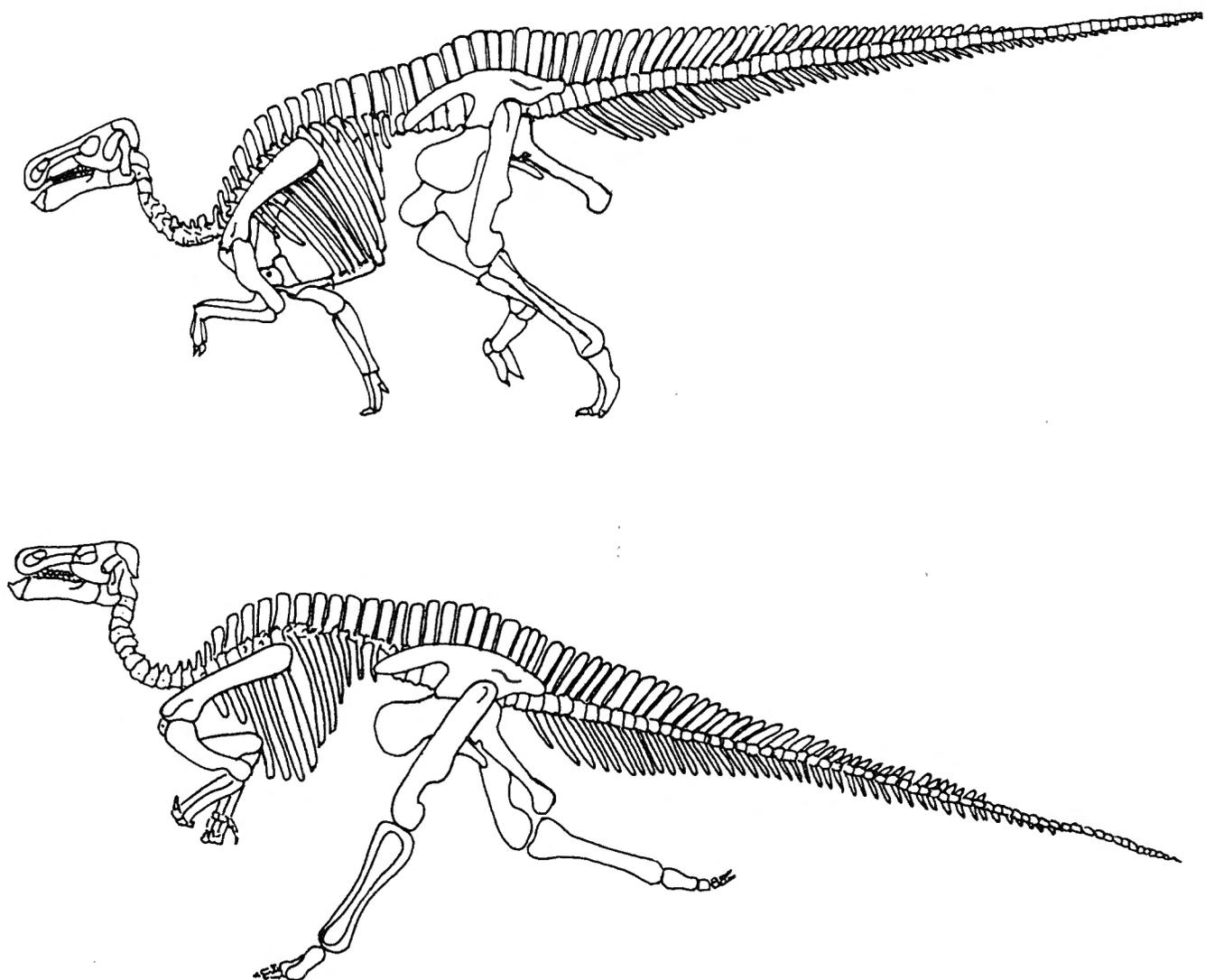


Fig. 37 – Full skeletal restoration of *Bactrosaurus johnsoni*, from the Iren Dabasu Formation, in quadrupedal pose (after G. PAUL in BRETT-SURMAN, 1989, pl. 12, modified) and in bipedal pose.

Bipedality can be demonstrated by, among others, the non-graviportal structure of the forelimbs: the radius, ulna and metacarpals of hadrosaurs are elongated when compared to the humerus, indicating that the forelimbs were mainly used as prehensile organs. Undoubted quadrupedal dinosaurs and graviportal mammals are, on the other hand, characterized by their robust forelimbs, with relatively short ulna and radius and cuboid metacarpals. NORMAN's (1980) index of forelimb proportions is derived by multiplying together the ratios of the lengths "radius / humerus" and "metacarpal III / humerus". The resultant value is a numerical indication of the degree of elongation of the distal segment of the limb. This function seems to be discriminant between typical quadrupeds (value greater than 0.3) and bipeds (value lesser than 0.15).

In *Bactrosaurus johnsoni*, the index of forelimb proportions may be cautiously estimated from the material discovered in Locality 95E5. This material includes four

complete humeri, one radius and one metacarpal III. It may be postulated that the radius belongs to the same individual as one of the humeri; in that case, the ratio of the lengths "radius / humerus" would range from 0.72 to 0.8. If the same reasoning is followed for the metacarpal III, the ratio of the lengths "metacarpal III / humerus" would range from 0.27 to 0.33. The resultant index of forelimb proportions would consequently range from 0.27 to 0.33. This value is similar to that calculated in *Kritosaurus incurvimanus* (0.31; GALTON, 190, tab.1); it is significantly higher than that calculated in *Iguanodon bernissartensis* (0.16; NORMAN, 1980, tab.1), *I. atherfieldensis* (0.21, *Ibidem*) and *Ouranosaurus nigeriensis* (0.17; TAQUET, 1976: 158). From the proportions of its forelimb, *Bactrosaurus johnsoni* appears to be a conventionally bipedal ornithomimid. Nevertheless, the ulna and the radius look relatively robust, the scapular blade is enlarged for insertion of a strong deltoid musculature and digit III could be hyper-extended: these elements

Table 1 – Character - taxon data matrix. For the signification of the numbers, see text.

Character	<i>Hypsil.</i>	<i>Camptos.</i>	<i>Iguanod.</i>	<i>Ouranos.</i>	<i>Bactros.</i>	<i>Telmatos.</i>	<i>Hadros.</i>	<i>Lambeos.</i>
1	0	0	1	1	1	1	1	1
2	0	0	1	1	1	1	1	1
3	0	0	1	1	1	1	1	1
4	0	0	1	1	1	1	1	1
5	0	0	1	1	1	1	1	1
6	0	0	1	1	1	0-1	1	1
7	0	0	1	1	1	1	1	1
8	0	0	1	1	0	0	0	0
9	0	0	1	1	0	0	0	0
10	0	0	1	1	0	0	0	0
11	0	0	1	1	?	?	0	0
12	0	0	0	0	1	1	1	1
13	0	0	0	0	1	1	1	1
14	0	0	0	0	1	1	1	1
15	0	0	0	-	1	-	1	1
16	0	0	0	0	1	1	1	1
17	0	0	0	0	1	1	1	1
18	0	0	0	0	1	1	1	1
19	0	0	0/1	0	1	?	1	1
20	0	0	0	0	1	?	1	1
21	0/1	0	0	0	1	?	1	1
22	0	0	0	0	1	1	1	1
23	0	0	0	0	0	1	1	1
24	0	0	0	0	0	1	1	1
25	0	?	0	0	0	1	1	1
26	0	0	0	0	0	1	1	1
27	0	0	0	0	0	?	1	1
28	0	0	0	0	0	?	1	1
29	0	0	0	0	0	?	1	1
30	-	0	0	0	0	0	1	1
31	0	0	0	0	0	0	1	1
32	0	0	0	0	0	0	1	1
33	0	0	0	0	0	0	1	1
34	0	0	0	1	0	0	1	1
35	0	0	0	0	0	0	1	1
36	0	0	0	0	0	0	1	1
37	0	0	0	0	0	0	1	1
38	0	0	0	0	0	0	1	1
39	0	0	0	0	0	0	1	1
40	0	0	0	0	1	0	1	1
41	0	0	0	0	0	0	1	0
42	0	0	0	0	0	0	1	0
43	-	0	0	0	0	0?	1	0
44	0	0	0	0	0	0	1	0
45	0	0	1	0	0	0	1	0
46	0	0/1	1	0	0/1	0	1	0
47	?	0	0	0	0	?	1	0
48	0	0	0	0	0	0	0	1
49	0	0	0	1	0	0	0	1
50	0	0	0	0	0	0	0	1
51	0	0	0	0?	0	0	0	1
52	0	0	0	0	0	0	0	1
53	0	0	0	0	0	0	0	1
54	0	0	0	0	0	0	0	1
55	0	0	0	0	0	0	0	1
56	0	0	0	1	0-1	0	0	1

indicate that the forelimb could be used, at least occasionally, as a weight-supporting organ. It can therefore be concluded that *Bactrosaurus johnsoni* was probably a "semibipedal" animal (*sensu* LEONARDI, 1987), as it seems to have been the norm in iguanodontids (NORMAN & WEISHAMPEL, 1990) and hadrosaurids (WEISHAMPEL & HORNER, 1990): a bipedal stance was adopted for fast locomotion, but the forelimbs might be placed on the ground during slow locomotion or when stationary.

PHYLOGENETIC RELATIONSHIPS OF *BACTROSAURUS JOHNSONI*

From the osteological analysis of *Bactrosaurus johnsoni* presented above, it appears that this ornithopod presents a mosaic of both iguanodontid and hadrosaurid characters. Moreover, as previously discussed by GILMORE (1933), MARYANSKA & OSMOLSKA (1981a) and WEISHAMPEL & HORNER (1986), it also presents an apparent mixing of so-called hadrosaurine and lambeosaurine characters. In order to clarify the phylogenetic relationships of *Bactrosaurus johnsoni*, a cladistic analysis of derived ornithopods is presented below. It is now demonstrated that the subfamilies Hadrosaurinae and Lambeosaurinae are monophyletic; moreover, the phylogenetic relationships of most North-American forms within both subfamilies seem currently well established (see WEISHAMPEL & HORNER, 1990 and WEISHAMPEL *et al.*, 1993, for examples). Therefore, as it is not the purpose of the present paper to present new phylogenetic informations about North-American hadrosaurs, it has been decided to consider the subfamilies Hadrosaurinae and Lambeosaurinae as taxonomic units in our cladistic analysis. The other taxa considered here are *Telmatosaurus transsylvanicus*, *Ouranosaurus nigeriensis*, *Iguanodon bernissartensis* and *I. atherfieldensis*. *Camptosaurus dispar* and *Hypsilophodon foxii* are used as successive outgroups. It would also have been very interesting to include the Chinese ornithopods *Probactrosaurus gobiensis*, *Gilmoreosaurus mongoliensis* and *Tanius sinensis* in this cladistic analysis, as they are probably also close to the "frontier" between advanced iguanodontids and primitive hadrosaurids. Unfortunately, the anatomy of these forms is too incompletely known: it awaits review and, above all, the discovery of new material. The characters used in the present analysis are chosen to best reflect the relative completeness of *Bactrosaurus johnsoni* and exclude autapomorphies. The polarity of each character is discussed in the osteological part of the article. The character/taxon matrix is presented in Table 1. These data were analysed using HENNIG 86 program (FARRIS, 1988) to retrieve the most parsimonious tree from the data at hand. A single 61-step most parsimonious tree was generated, with a consistency index of 0.90 and a retention index of 0.91.

The resulting cladogram is presented in Figure 38. On the basis of this analysis, the following classification can be proposed:

Node 1: "Ankylopollexia": *Camptosaurus* + higher ornithopods

For SERENO (1986: 540), the Ankylopollexia constitute a well-defined monophyletic subgroup of advanced ornithopods, which includes *Camptosaurus*, *Probactrosaurus*, *Iguanodon*, *Ouranosaurus* and hadrosaurs. This monophyletic group may be defined by 15 synapomorphies. For NORMAN (1990: 153), the status of this node is dubious and is probably more accurately portrayed as an unresolved trichotomy between the Dryosauridae, *Camptosaurus* and "higher" ornithopods. It is not the purpose of the present paper to discuss this problem, as *Camptosaurus* is only used in the present analysis as outgroup.

Node 2: Iguanodontidae + Hadrosauroidea

This monophyletic group is characterized, in this analysis, by the following synapomorphies:

1. Supraoccipital excluded from the margin of the foramen magnum.
2. Sternal bones with rod-shaped and caudolaterally directed processes
3. Olecranon process of the ulna well-developed.
4. Prepubis dorso-ventrally expanded; prepubic blade and neck distinctly separated.
5. Caudal ramus of the pubis reduced in length.
6. Femur nearly straight in lateral view (possible reversion in *Telmatosaurus transsylvanicus*).
7. Pes formula: 0, 3, 4, 5.

Node 3: Iguanodontidae

No consensus exists, at the present time, about the systematic status of the family Iguanodontidae. SERENO (1986) regards *Ouranosaurus nigeriensis* as the sister-group of the Hadrosauridae, on the basis of 17 synapomorphies. NORMAN (1990) disproves the validity of these characters and gathers *Ouranosaurus* with *Iguanodon* in the family Iguanodontidae, on the basis of five synapomorphies. Four of these characters are tentatively retained in the present analysis. The fifth character refers to the morphology of the quadratojugal; as its position is not clear in *Camptosaurus dispar*, *Bactrosaurus johnsoni* and *Telmatosaurus transsylvanicus*, it has not been retained in our cladogram.

8. Maxilla with a well developed jugal process that projects obliquely caudoventrally from the lateral body of the maxilla.
9. Prominent lacrimal process of the maxilla, forming the cranial margin of the antorbital foramen.
10. Lacrimal block-like, bearing a distinctive pattern of depressions on its internal surface and forming the lateral wall of the internal passage that leads to the antorbital fenestra.
11. Enlarged conical pollex ungual with first phalanx reduced to a flattened disk.

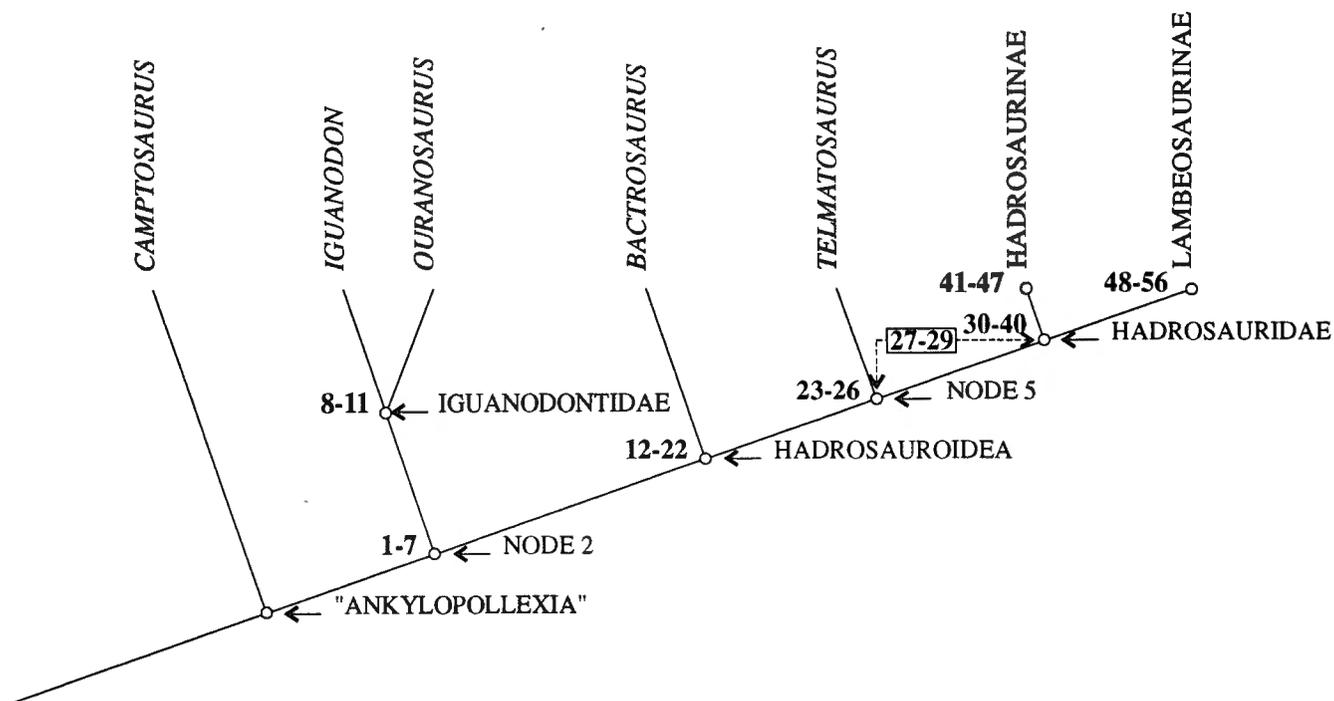


Fig. 38 – Phylogenetic relationships of *Bactrosaurus johnsoni*, from the Iren Dabasu Formation. For the signification of the character numbers, see text.

WEISHAMPEL *et al.* (1993) place *Ouranosaurus*, *Iguanodon* and Hadrosauridae (including *Telmatosaurus transsylvanicus*) in an unresolved trichotomy: this constitutes a compromise between SERENO'S (1986) and NORMAN'S (1990) positions.

As previously described by TAQUET (1976), NORMAN (1990) and WEISHAMPEL *et al.* (1993), *Ouranosaurus nigeriensis* developed several derived characters paralleling those observed in "true" hadrosaurs: the presence of a diastema in the mandible is a synapomorphy of the clade Hadrosauridae, the lateral expansion of the rostrum also characterizes the clade Hadrosaurinae, the presence of a broad solid crest on the nasal can also be observed, within the Hadrosaurinae, in the small clade *Maiasaura peeblesorum* + *Brachylophosaurus canadensis*, the shortening of the parietal and the great development of the neural spines also appeared independently in the Lambeosaurinae. On the other hand, *Iguanodon* also developed characters paralleling those observed in more derived hadrosaurs: the angle between the root and crown of dentary teeth $< 130^\circ$ and the caudal sacral centra are grooved, like in Hadrosaurinae. However, it has been shown that the latter character is very variable, in non-hadrosaurid "Ankylopollexia".

For HORNER (1990), *Ouranosaurus nigeriensis* must be placed with the Lambeosaurinae (his "Lambeosauridae") in a clade Lambeosauria, whereas *Iguanodon* and the Hadrosaurinae (his "Hadrosauridae") form the clade Hadrosauria. The characters supporting this hypothesis have been discussed in the osteological part of the present paper. This hypothesis is not retained because it would require too many parallelisms and/or reversions.

Node 4: Super-family Hadrosauroidea

This clade includes *Bactrosaurus johnsoni*, *Telmatosaurus transsylvanicus* and the Hadrosauridae. It is characterized by the following synapomorphies:

12. More than one replacement tooth in each tooth position; crowns firmly cemented together to form a rigid battery.
13. Articular surface of the occipital condyle vertical.
14. Basipterygoid processes long and slender, projecting more ventrally than the occipital condyle.
15. Presence of fontanelles on the skull of younger specimens.
16. Absence of surangular foramen.
17. Miniaturization of the maxillary teeth.
18. Single large carina on the maxillary teeth.
19. Preacetabular process of ilium very deflected ventrally (convergently acquired in *Iguanodon bernisartensis*).
20. Antitrochanter of ilium developed.
21. Obturator foramen of pubis fully open.
22. Transverse widening of the tibial proximal head extending on the diaphysis.

Node 5: *Telmatosaurus transsylvanicus* + *Hadrosauridae*

Telmatosaurus transsylvanicus shares several synapomorphies, not observed in *Bactrosaurus johnsoni*, with the Hadrosauridae:

23. Migration of the antorbital foramen along the upper reaches of the premaxillary articular surface of the maxilla.

24. More than 30 maxillary and 29 dentary tooth positions.
25. Absence of paraquadrate foramen.
26. Absence of caudal secondary ridge on the dentary teeth.

The polarity of the following characters is unknown in *Telmatosaurus transsylvanicus*. Therefore, in the current state of our knowledge, it cannot be decided if these synapomorphies characterize node 5 or node 6:

27. Supraorbital fused with the prefrontal.
28. Pubic peduncle of ilium reduced in size.
29. Ischial peduncle of ilium formed by two small protrusions.

Node 6: Family Hadrosauridae:

This family regroups the subfamilies Hadrosaurinae and Lambeosaurinae. This clade can be characterized by the following synapomorphies:

30. Reduction of the denticulations on the oral margin of the premaxillae and of the prementary.
31. Narrow and sub-hemispherical mandibular condyle.
32. Caudal border of the skull not indented.
33. Medial rami of the paired squamosals nearly in contact.
34. Diastema in mandible (convergently evolved in *Ouranosaurus nigeriensis*).
35. Coronoid process of the dentary inclined forwards.
36. Dentary teeth miniaturized.
37. Dentary teeth not recurved.
38. Large single carina on dentary teeth.
39. Odontoid process free from the axis.
40. Angular deltopectoral crest (convergently evolved in *Bactrosaurus johnsoni*).

Node 7: Subfamily Hadrosaurinae:

The subfamily hadrosaurinae includes the following genera, mainly discovered in the Campanian-Maastrichtian of North-America and Asia (WEISHAMPPEL & HORNER, 1990): *Gryposaurus*, *Hadrosaurus*, *Aralosaurus*, *Maia-saura*, *Brachylophosaurus*, *Saurolophus*, *Prosaurolophus*, *Lophorhothon*, *Anatotitan*, *Edmontosaurus* and *Shantungosaurus*. This clade is characterized by the following synapomorphies:

41. Reflected premaxillary lip.
42. Enlarged external nares: up to 40% of the basal skull length (reversal in *Maia-saura peeblesorum*).
43. Maxilla symmetrical in lateral view.
44. Circumnarial depression extending on the nasal.
45. Angle between the crown and root of dentary teeth < 130° (convergently evolved in *Iguanodon*).
46. Caudal sacral centra grooved (convergently evolved in *Iguanodon*).
47. Ischial shaft tapering distally.

Node 8: Subfamily Lambeosaurinae

The family Lambeosaurinae includes the following genera, from the Campanian-Maastrichtian of North-America: *Lambeosaurus*, *Parasaurolophus*, *Corythosaurus* and *Hypacrosaurus*, but also several incompletely known taxa from Kazakhstan, Mongolia and Japan (WEISHAMPPEL & HORNER, 1990). This clade can be characterized by the following characters:

- 48: Frontal entirely excluded from the orbital rim.
- 49: Parietal shortened (convergently evolved in *Ouranosaurus nigeriensis*).
- 50: Lacrimal laterally "lapped" by the maxilla.
- 51: Maxillary shelf.
- 52: Hollow supracranial crest.
- 53: External naris completely surrounded by the premaxilla.
- 54: Truncated and rounded rostral process of the jugal.
- 55: Absence of premaxillary foramen.
- 56: Very tall neural spines (convergently evolved in *Ouranosaurus nigeriensis*).

From that cladogram, it is clear that *Bactrosaurus johnsoni* occupies a very basal position in hadrosaur phylogeny, in accord with its presumed early stratigraphical distribution. It also appears that this species cannot be included within the family Lambeosaurinae, as previously asserted by numerous authors (GILMORE, 1933; STEEL, 1969; BRETT-SURMAN, 1979; MARYANSKA & OS-MOLSKA, 1981a; WEISHAMPPEL & HORNER, 1986, 1990). The latter hypothesis would imply the reversion of at least 18 characters in *Bactrosaurus johnsoni*. In fact, this animal shares a list of plesiomorphic characters with, on one hand, the Hadrosaurinae and, on the other hand, the Lambeosaurinae; some characters also appear to have evolved convergently in *Bactrosaurus johnsoni* and in representatives of these two subfamilies. This can easily explain the apparent mixing, in *Bactrosaurus johnsoni*, of lambeosaurine and hadrosaurine characters that intrigued so many palaeontologists.

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Caption of the plates

PLATE 1

- Fig. 1 – Portion of the bone-bed discovered in Quarry 95E5, Iren Dabasu Formation, including ischia, ilia, pubes, humerus, vertebrae and ribs of *Bactrosaurus johnsoni*. Scale bar = 20 cm.
- Fig. 2 – Caudal vertebrae in connection of *Bactrosaurus johnsoni* (SBDE 95E5/28), from the Iren Dabasu Formation. Scale bar = 10 cm.

PLATE 2

- Fig. 1 – Supraoccipital of *Bactrosaurus johnsoni* (SBDE 95E5/29), from the Iren Dabasu Formation - A: caudal view; B: rostral view. Scale bar = 2 cm.
- Fig. 2 – Basioccipital - basisphenoid of *Bactrosaurus johnsoni* (SBDE 95E5/1), from the Iren Dabasu Formation - A: lateral view; B: dorsal view. Scale bar = 2 cm.
- Fig. 3 – Partial braincase of *Bactrosaurus johnsoni* (SBDE 95E5/30), from the Iren Dabasu Formation - A: caudal view; B: lateral view; C: dorsal view; D: ventral view. Scale bar = 2 cm.

PLATE 3

- Fig. 1 – Parietal of *Bactrosaurus johnsoni* (SBDE 95E5/2), from the Iren Dabasu Formation - A: dorsal view; B: ventral view. Scale bar = 2 cm.
- Fig. 2 – Left frontal of *Bactrosaurus johnsoni* (SBDE 95E5/3), from the Iren Dabasu Formation - A: dorsal view; B: ventral view. Scale bar = 2 cm.
- Fig. 3 – Parietal - left frontal in connection of *Bactrosaurus johnsoni* (SBDE 95E5/2-3), from the Iren Dabasu Formation - dorsal view. Scale bar = 2 cm.
- Fig. 4 – Premaxillae of *Bactrosaurus johnsoni* (SBDE 95E5/4-4bis), from the Iren Dabasu Formation - A: dorsal view; B: ventral view; C: lateral view of the right premaxilla; D: medial view of the right premaxilla. Scale bar = 2 cm.

PLATE 4

- Fig. 1 – Right maxilla of *Bactrosaurus johnsoni* (SBDE 95E5/31), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 5 cm.
- Fig. 2 – Left jugal of *Bactrosaurus johnsoni* (SBDE 95E5/32), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 5 cm.
- Fig. 3 – Right nasal of *Bactrosaurus johnsoni* (SBDE 95E5/33), from the Iren Dabasu Formation - A: dorsal view; B: ventral view; C: lateral view. Scale bar = 5 cm.

PLATE 5

- Fig. 1 – Right quadrate of *Bactrosaurus johnsoni* (SBDE 95E5/8), from the Iren Dabasu Formation - A: rostral view; B: caudal view. Scale bar = 5 cm.
- Fig. 2 – Right squamosal of *Bactrosaurus johnsoni* (SBDE 95E5/9), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 2 cm.
- Fig. 3 – Right prefrontal of *Bactrosaurus johnsoni* (SBDE 95E5/11), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 2 cm.
- Fig. 4 – Right postorbital of *Bactrosaurus johnsoni* (SBDE 95E5/34), from the Iren Dabasu Formation - A: dorsal view; B: lateral view. Scale bar = 2 cm.
- Fig. 5 – Left supraorbital of *Bactrosaurus johnsoni* (SBDE 95E5/35), from the Iren Dabasu Formation - lateral view. Scale bar = 2 cm.

PLATE 6

- Fig. 1 – Left dentary of *Bactrosaurus johnsoni* (SBDE 95E5/12), from the Iren Dabasu Formation - A: dorsal view; B: lateral view; C: medial view. Scale bar = 5 cm.
- Fig. 2 – Prementary of *Bactrosaurus johnsoni* (SBDE 95E5/36), from the Iren Dabasu Formation - A: dorsal view; B: caudal view; C: ventral view; D: rostral view. Scale bar = 5 cm.

PLATE 7

- Fig. 1 – Left surangular of *Bactrosaurus johnsoni* (SBDE 95E5/13), from the Iren Dabasu Formation - A: lateral view; B: medial view; C: ventral view; D: dorsal view. Scale bar = 2 cm.
- Fig. 2 – Dentary teeth of *Bactrosaurus johnsoni* (SBDE 95E5/12), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 2 cm.
- Fig. 3 – Atlas of *Bactrosaurus johnsoni* (SBDE 95E5/37), from the Iren Dabasu Formation - A: cranial view; B: ventral view; C: dorsal view; D: caudal view. Scale bar = 2 cm.
- Fig. 4 – Axis of *Bactrosaurus johnsoni* (SBDE 95E5/14), from the Iren Dabasu Formation - A: cranial view; B: lateral view; C: caudal view. Scale bar = 5 cm.

PLATE 8

- Fig. 1 – Cranial cervical vertebra of *Bactrosaurus johnsoni* (SBDE 95E5/16), from the Iren Dabasu Formation - Cranial view. Scale bar = 5 cm.
- Fig. 2 – Caudal cervical vertebra of *Bactrosaurus johnsoni* (SBDE 95E5/17), from the Iren Dabasu Formation - Cranial view. Scale bar = 5 cm.
- Fig. 3 – Dorsal vertebra of *Bactrosaurus johnsoni* (SBDE 95E5/38), from the Iren Dabasu Formation - A: cranial view; B: lateral view. Scale bar = 5 cm.
- Fig. 4 – Cervical vertebrae in connection of *Bactrosaurus johnsoni* (SBDE 95E5/39), from the Iren Dabasu Formation - Dorsal view. Scale bar = 5 cm.
- Fig. 5 – Proximal caudal vertebra of *Bactrosaurus johnsoni* (SBDE 95E5/20), from the Iren Dabasu Formation - A: caudal view; B: lateral view. Scale bar = 5 cm.
- Fig. 6 – Distal caudal vertebrae in connection of *Bactrosaurus johnsoni* (SBDE 95E5/28), from the Iren Dabasu Formation - Lateral view. Scale bar = 5 cm.

PLATE 9

- Fig. 1 – Sacrum of *Bactrosaurus johnsoni* (SBDE 95E5/39), from the Iren Dabasu Formation - A: dorsal view; B: ventral view; C: left lateral view; D: right lateral view. Scale bar = 10 cm.
- Fig. 2 – Left dorsal rib of *Bactrosaurus johnsoni* (SBDE 95E5/41), from the Iren Dabasu Formation - cranial view. Scale bar = 5 cm.

PLATE 10

- Fig. 1 – Left scapula of *Bactrosaurus johnsoni* (AMNH 6553), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 10 cm.
- Fig. 2 – Left sternal of *Bactrosaurus johnsoni* (SBDE 95E5/23), from the Iren Dabasu Formation - caudal view. Scale bar = 5 cm.
- Fig. 3 – Right coracoid of *Bactrosaurus johnsoni* (SBDE 95E5/22), from the Iren Dabasu Formation - medial view. Scale bar = 5 cm.
- Fig. 4 – Right humerus of *Bactrosaurus johnsoni* (SBDE 95E5/24), from the Iren Dabasu Formation - A: cranial view; B: caudal view. Scale bar = 5 cm.

PLATE 11

- Fig. 1 – Left ulna of *Bactrosaurus johnsoni* (SBDE 95E5/42), from the Iren Dabasu Formation - A: medial view; B: cranial view; C: lateral view; D: caudal view. Scale bar = 5 cm.

Fig. 2 – Left radius of *Bactrosaurus johnsoni* (SBDE 95E5/43), from the Iren Dabasu Formation - A: medial view; B: cranial view; C: lateral view; D: caudal view. Scale bar = 5 cm.

PLATE 12

Fig. 1 – Right ilium of *Bactrosaurus johnsoni* (SBDE 95E5/25), from the Iren Dabasu Formation - A: medial view; B: lateral view. Scale bar = 10 cm.

Fig. 2 – Right ischium of *Bactrosaurus johnsoni* (SBDE 95E5/26), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 10 cm.

Fig. 3 – Right pubis of *Bactrosaurus johnsoni* (SBDE 95E5/43), from the Iren Dabasu Formation - A: lateral view; B: medial view. Scale bar = 10 cm.

PLATE 13

Fig. 1 – Right femur of *Bactrosaurus johnsoni* (AMNH 6577), from the Iren Dabasu Formation - A: caudal view; B: lateral view; C: cranial view; D: medial view. Scale bar = 5 cm.

Fig. 2 – Right tibia of *Bactrosaurus johnsoni* (AMNH 6577), from the Iren Dabasu Formation - A: lateral view; B: cranial view. Scale bar = 5 cm.

Fig. 3 – Right fibula of *Bactrosaurus johnsoni* (SBDE 95E5/44), from the Iren Dabasu Formation - A: medial view; B: lateral view. Scale bar = 5 cm.

PLATE 14

Fig. 1 – Right astragalus of *Bactrosaurus johnsoni* (AMNH 6577), from the Iren Dabasu Formation - A: dorsal view; B: cranial view. Scale bar = 3 cm

Fig. 2 – Right calcaneum of *Bactrosaurus johnsoni* (AMNH 6577), from the Iren Dabasu Formation - A: dorsal view; B: medial view. Scale bar = 3 cm.

Fig. 3 – Left metatarsus of *Bactrosaurus johnsoni* (AMNH 6553), from the Iren Dabasu Formation - A: dorsal view; B: plantar view. Scale bar = 5 cm.

Fig. 4 – Proximal phalanx of *Bactrosaurus johnsoni* (SBDE 95E5/45), from the Iren Dabasu Formation - dorsal view. Scale bar = 3 cm.

Fig. 5 – Ungual phalanx of *Bactrosaurus johnsoni* (SBDE 95E5/46), from the Iren Dabasu Formation - A: dorsal view; B: plantar view. Scale bar = 3 cm.

PLATE 1



1



2

PLATE 2

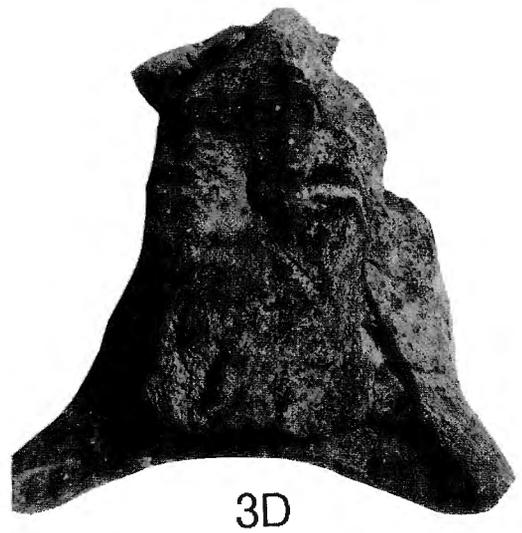
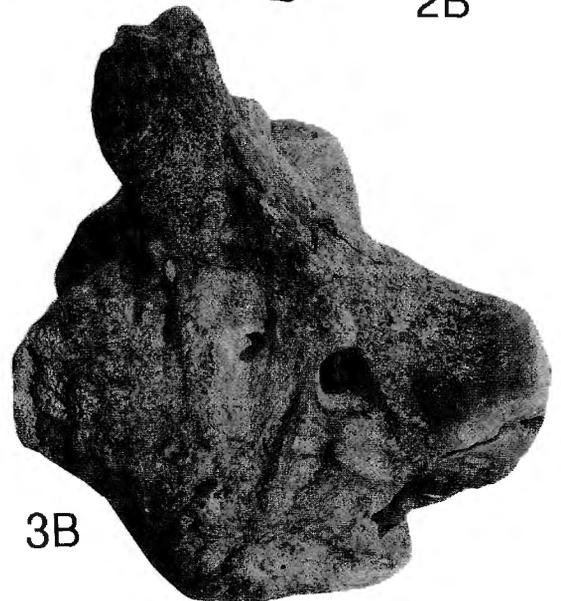
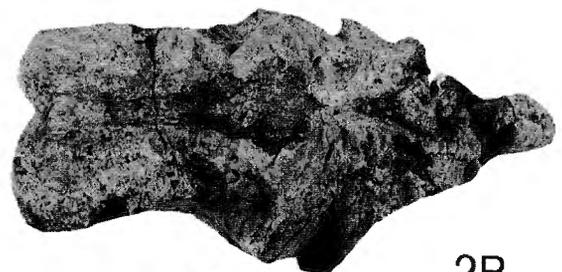
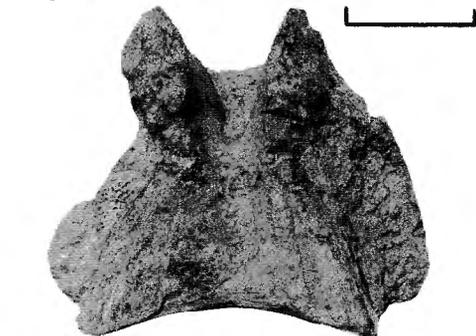


PLATE 3

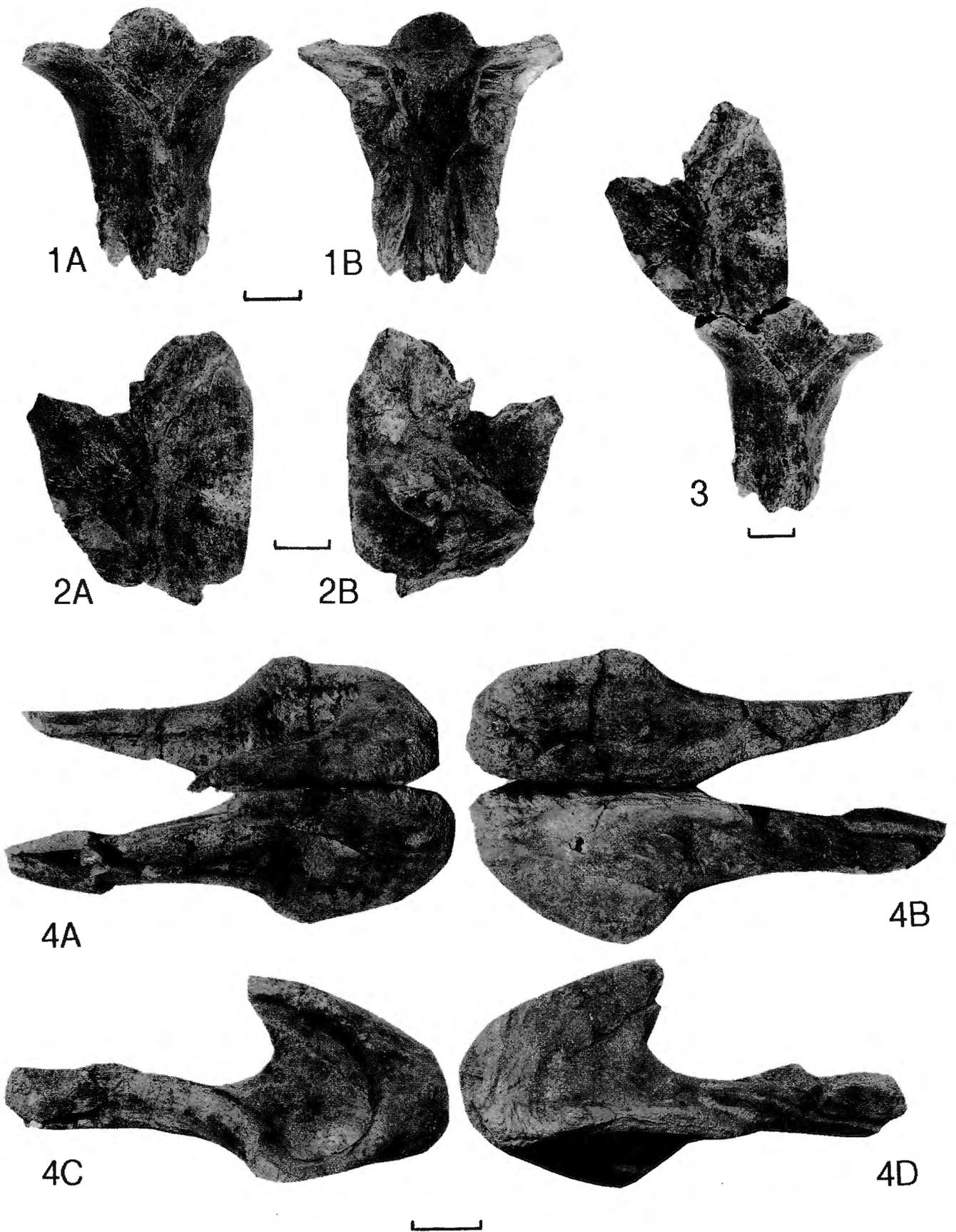
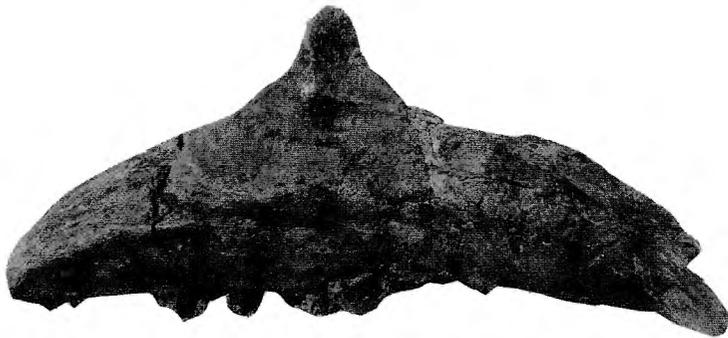


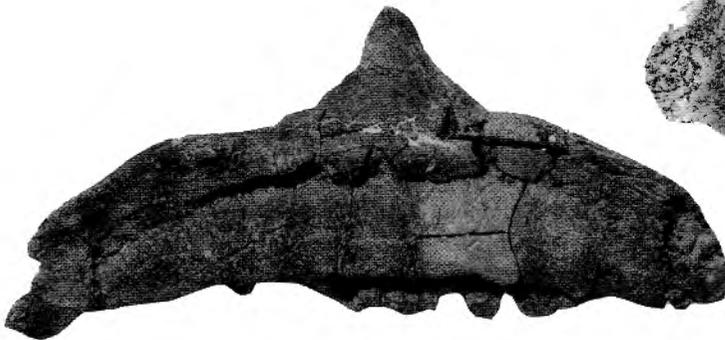
PLATE 4



1A



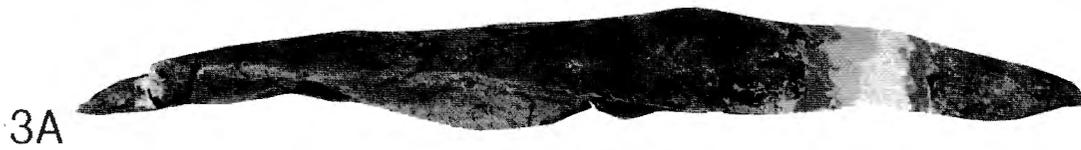
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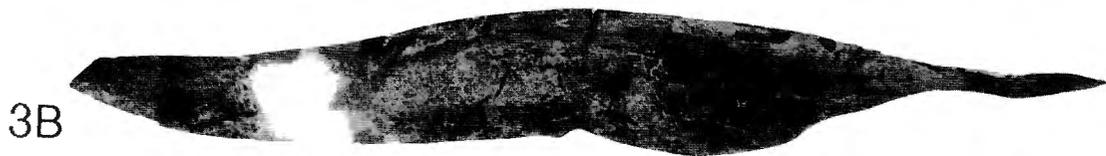
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2B



3A



3B



3C

PLATE 5

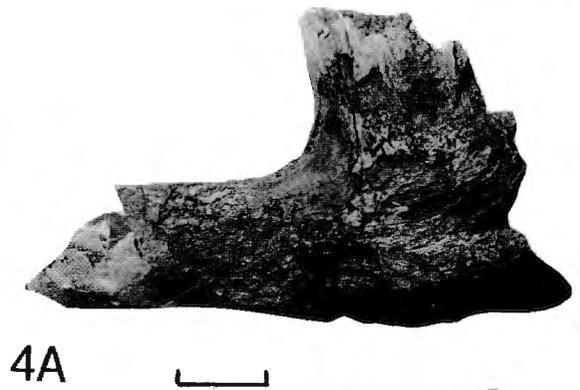
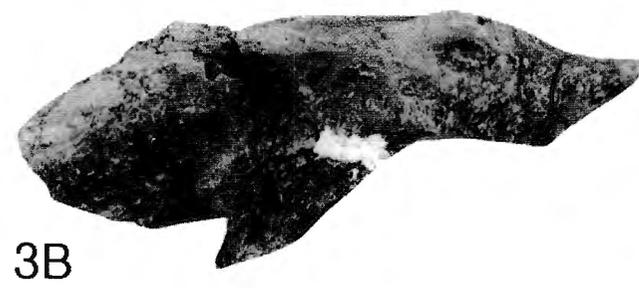
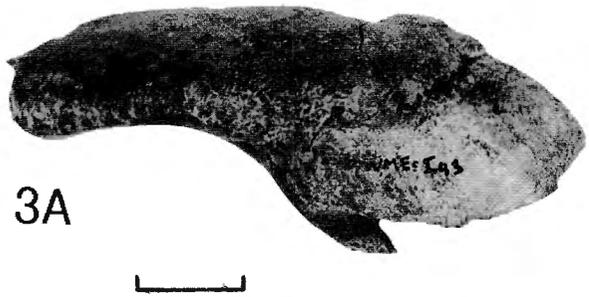
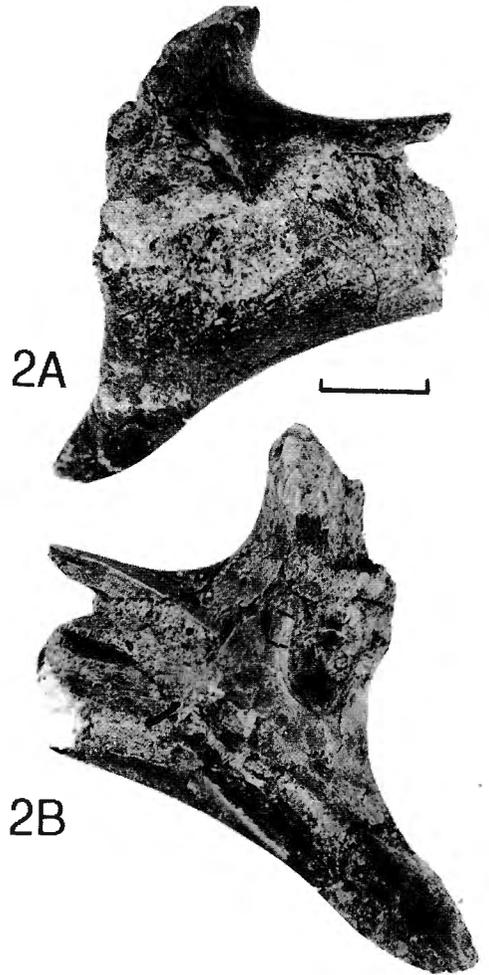
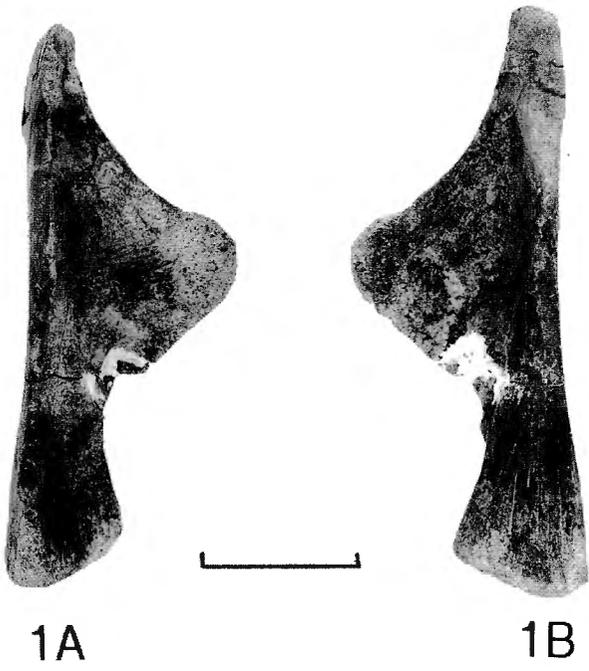


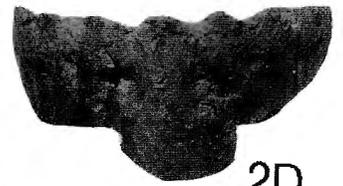
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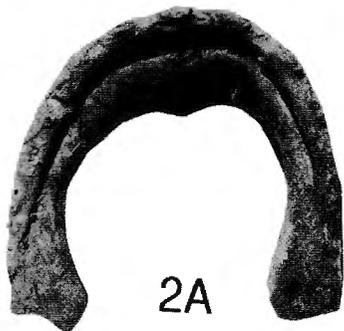
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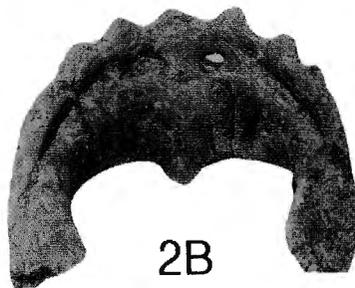
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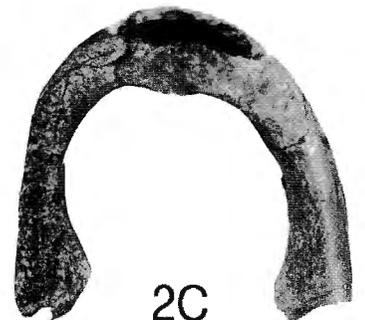
2D



2A



2B



2C

PLATE 7

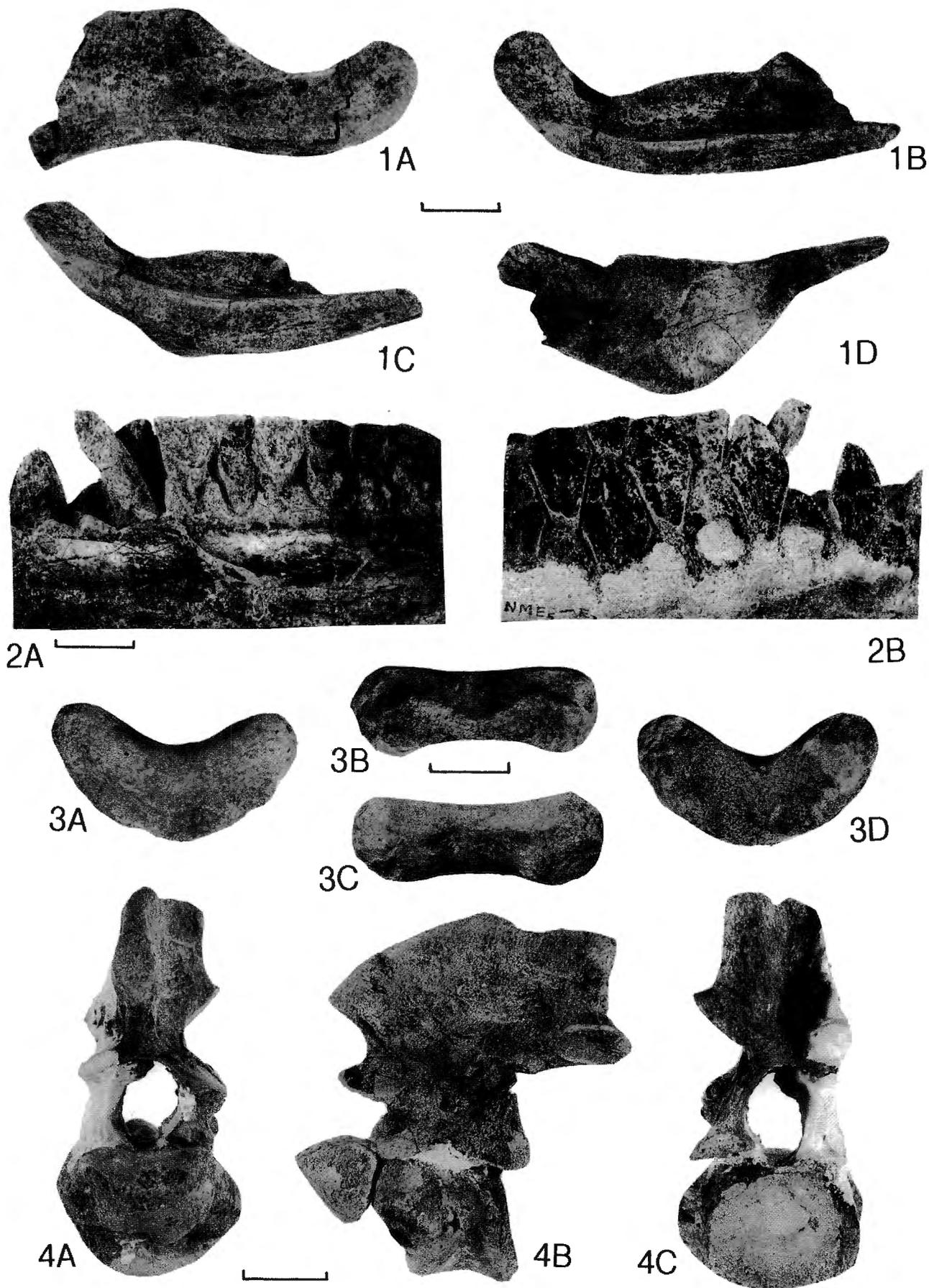


PLATE 8

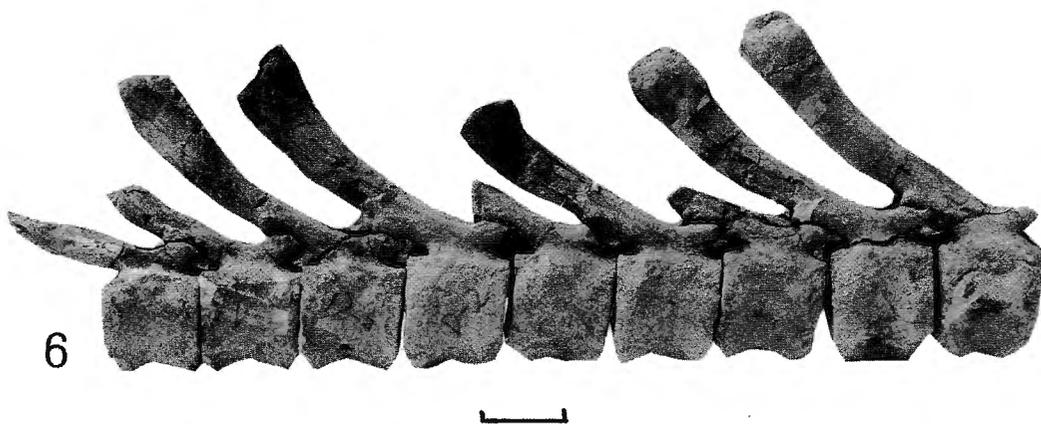
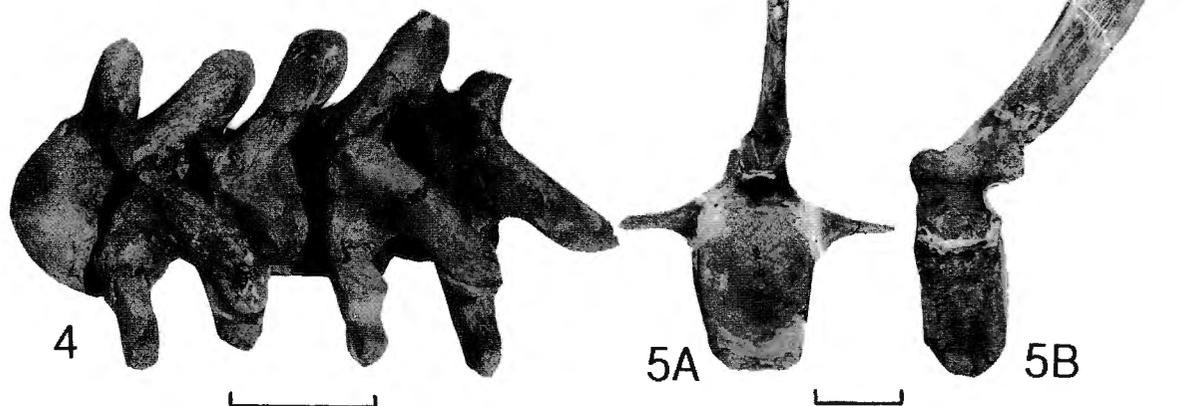
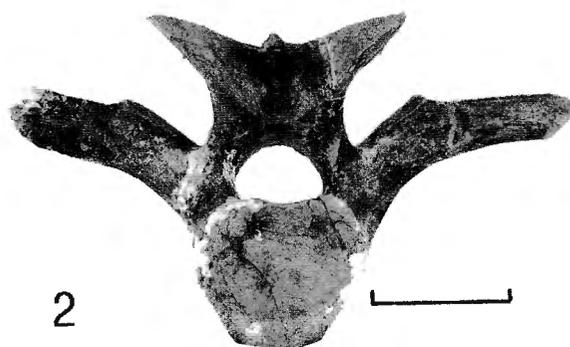
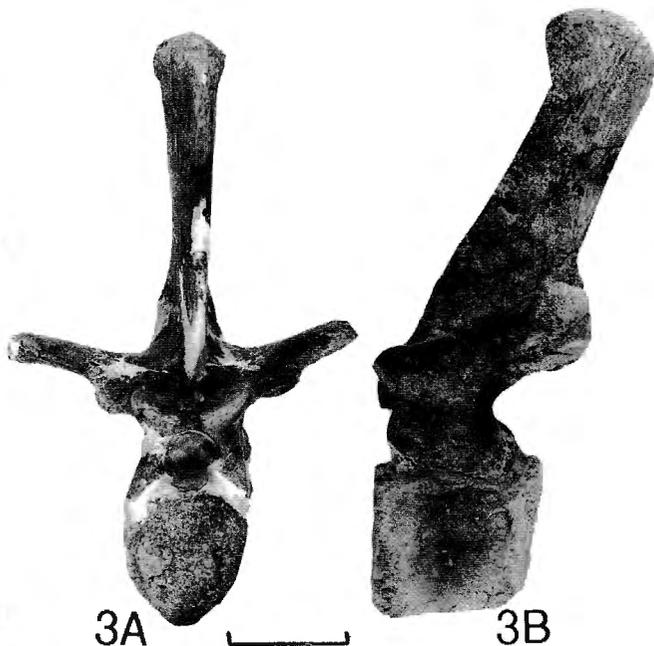
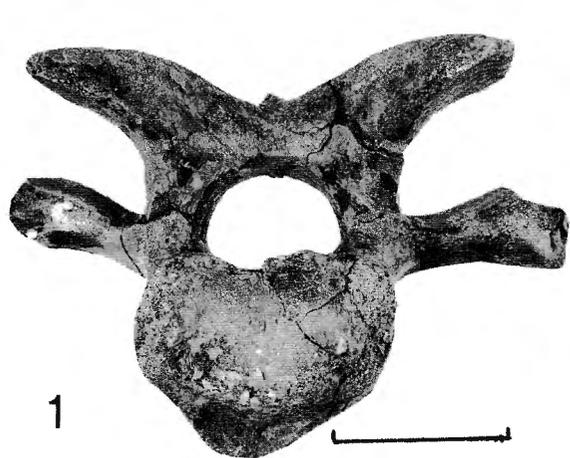


PLATE 9

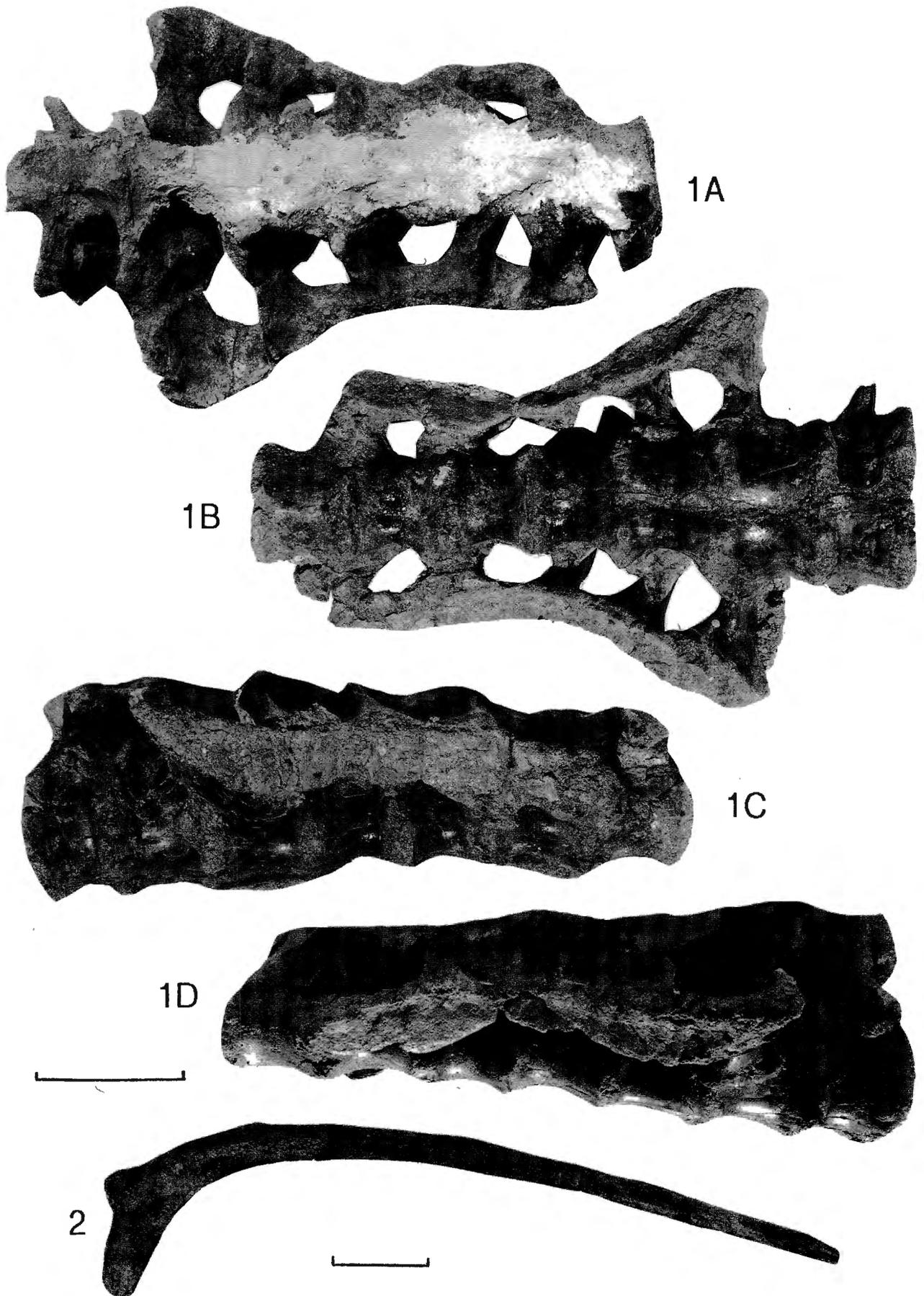
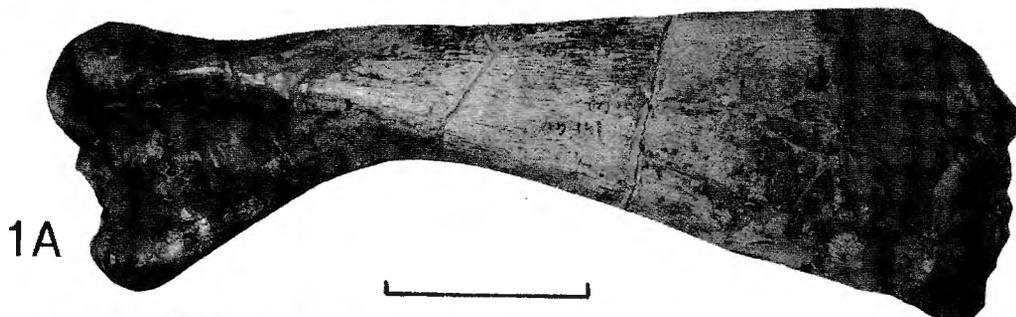
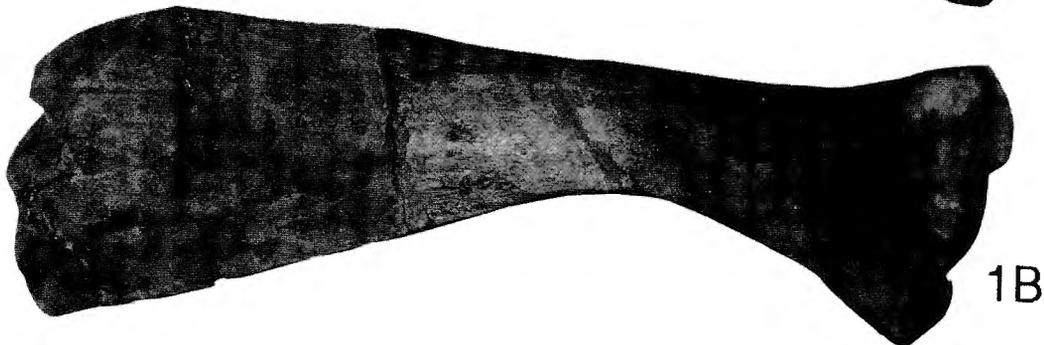


PLATE 10



1A



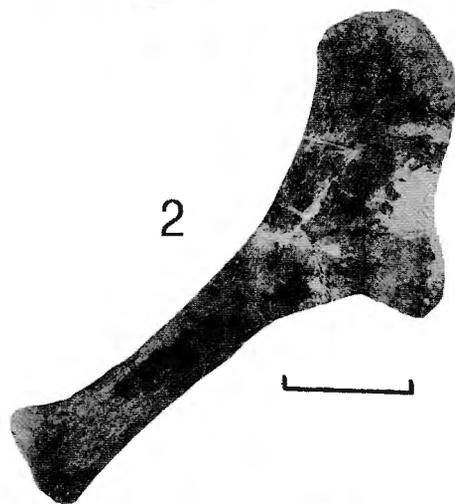
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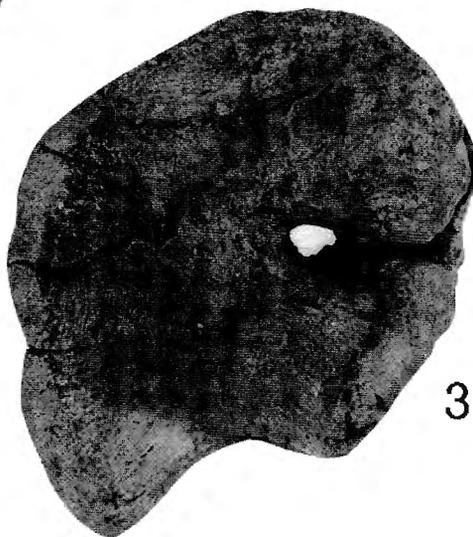
4A



4B



2



3

PLATE 11

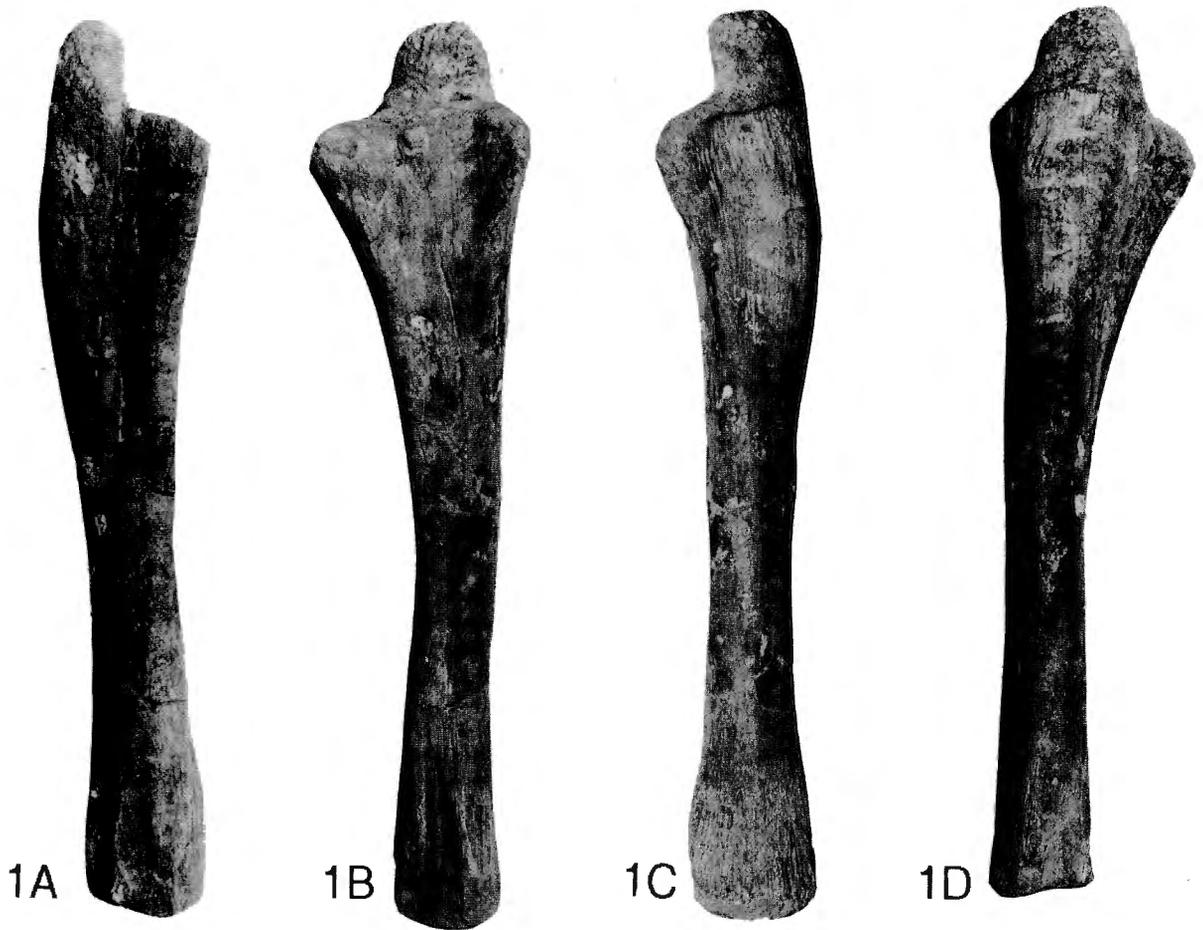


PLATE 12

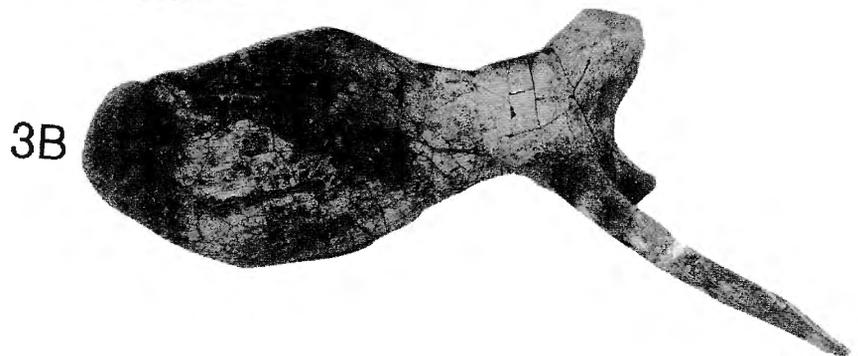
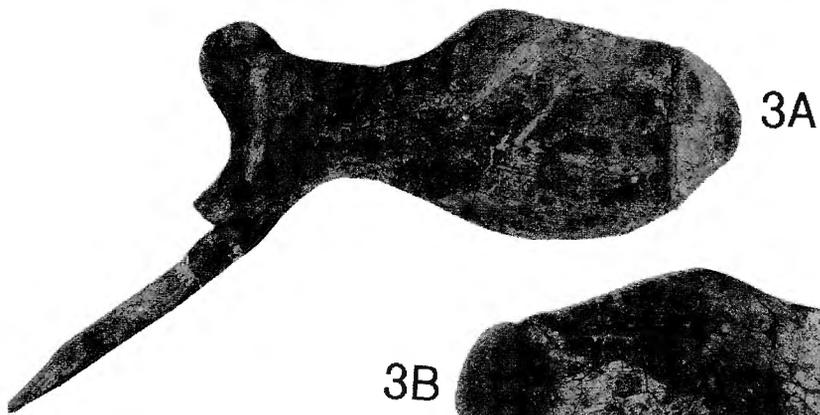
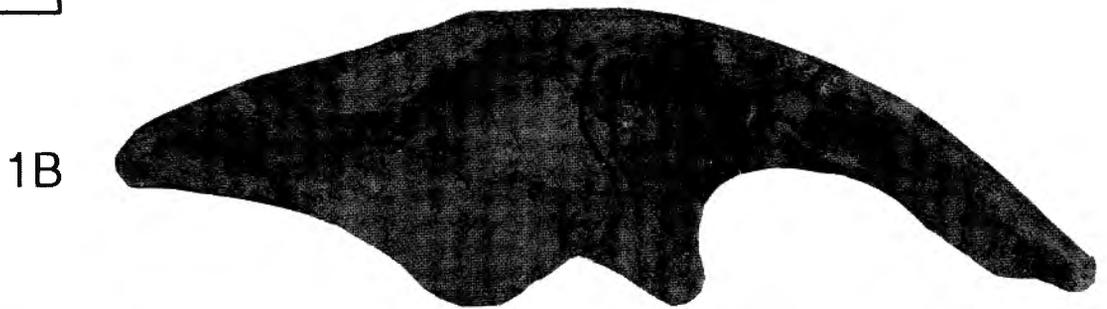
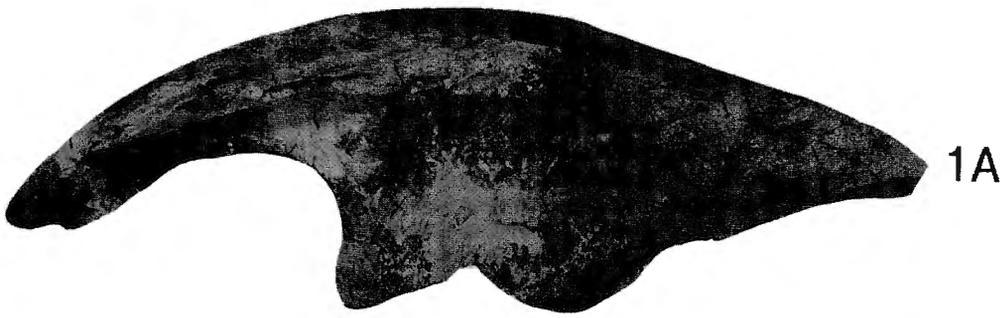


PLATE 13

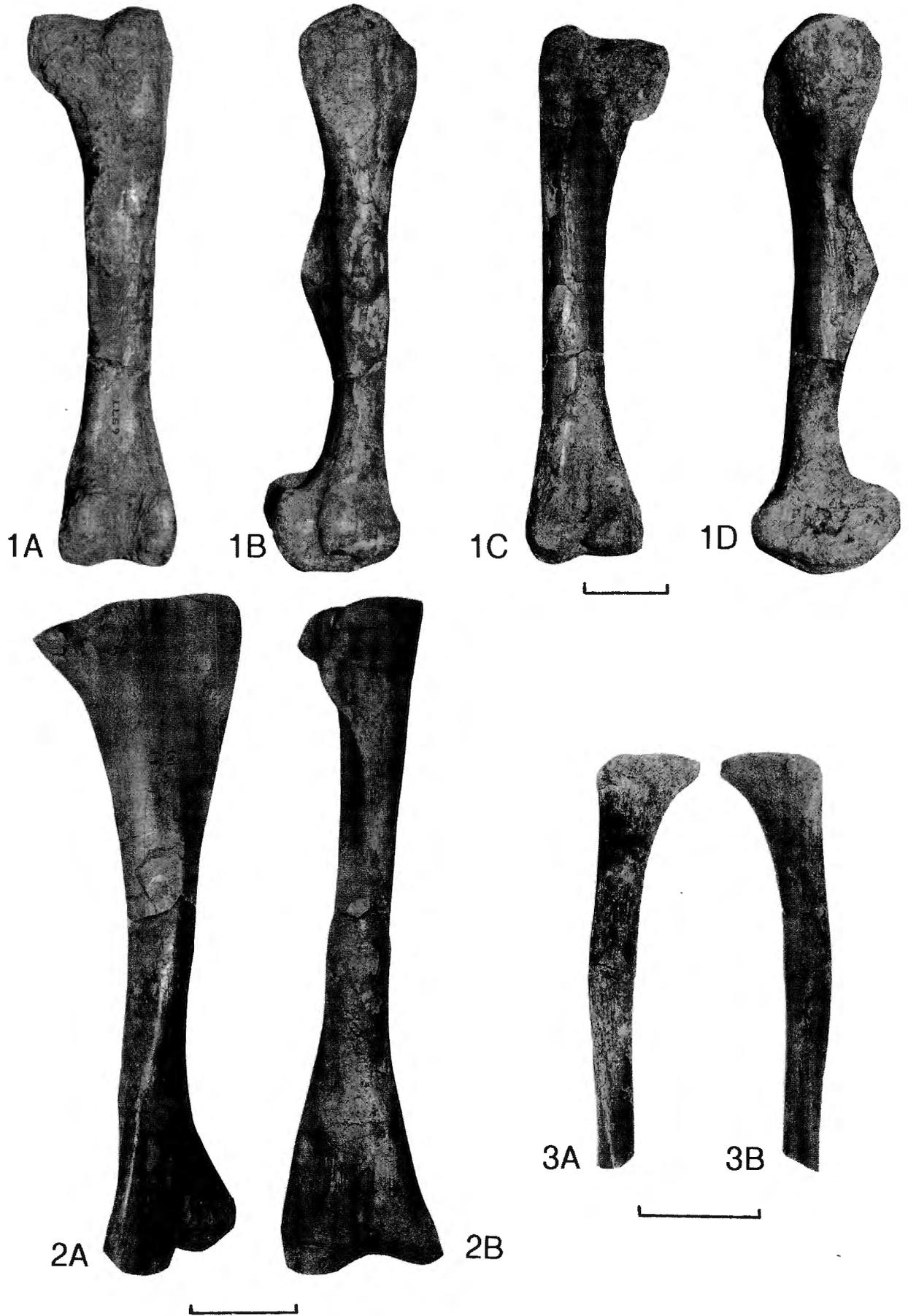


PLATE 14

