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On Asian ornithopods (Dinosauria: Ornithischia). 3. A new species of iguanodontid dinosaur

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The holotype of the Mongolian species of ornithopod dinosaur *Iguanodon orientalis* from the Early Cretaceous (Barremian-Aptian of Khamarin Khural) has been shown to have been established on holotype material that is non-diagnostic, but appears to be closely similar osteologically to the Western European species *I. bernissartensis*. Additional material collected from the locality known as Khuren Dukh (Dornogov′, Mongolia), which had previously been referred to *I. orientalis* has been re-examined and shown to represent a new genus and species (***Altirhinus kurzanovi*** **gen.** et **sp. nov**) of ornithopod dinosaur from the Early Cretaceous (Late Aptian/Early Albian). The anatomy of this new ornithopod is described; it shows a number of similarities to the known species of *Iguanodon*, but also demonstrates features which are in some instances unique to this taxon, while others seem to be either convergent upon, or transformational with respect to, the more derived hadrosaurid ornithopods of the Late Cretaceous. Palaeogeographic evidence is corroborative in that it suggests contemporaneous, albeit episodic, links between the Northern Hemisphere landmasses during the Barremian-Albian interval; these explain the appearance of very 'European' large ornithopods (*Iguanodon*) in Asia in Barremian/Aptian times as a consequence of land-based dispersal. Subsequent isolation of Asia from the European 'domain' during the late Early Cretaceous (Albian) may be responsible for the appearance of derived forms such as ***Altirhinus***, and is suggestive of an Asian centre of origin for the family Hadrosauridae in middle Cretaceous times; this contradicts an earlier vicariance-biogeographic model of ornithopod evolution. The cranial anatomical modifications seen in this new taxon: vertical expansion of the dorsal nasal cavity, lateral expansion and lowering of the cropping beak relative to the jaw line, increase in the number of replacement teeth (but no significant miniaturization of the crowns) and the trend toward formation of a more integrated battery of cheek teeth, seen to varying degrees in several mid-Cretaceous ornithopods are commented upon; they can be interpreted within the context of an evolutionary trend culminating in the cranial complexity seen in the terminal lineage of ornithopods represented by the Late Cretaceous Hadrosauridae. Functionally, some of these changes can be correlated with what can be interpreted as 'improvements' to the efficiency of food gathering and processing which might represent increased niche partitioning and/or responses to increasingly tough and abrasive (xeric adapted) foliage; others, notably the modifications to the nasal cavity (perhaps associated with providing space for a counter-current moisture conserving turbinal system), are suggestive of a biological response to increasingly seasonal/xeric conditions in the middle of the Cretaceous Period or changes in the floral composition of these times.

ADDITIONAL KEY WORDS:—vertebrate – palaeontology – biogeography – Cretaceous – Ornithopoda – *Altirhinus* – systematics.

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INTRODUCTION

Following the early Soviet expeditions to Mongolia in the late 1940s (summarized by Rozhdestvensky, 1960), Rozhdestvensky (1952, 1966) identified the first iguanodontid dinosaur from Cretaceous deposits at the locality named Khamarin Khural in southern central Dornogov′ (East Gobi Province). The validity of this taxon was first questioned by Norman (1980). Revision of the holotype material (Norman, 1996) has revealed that the Barremian-Aptian aged Mongolian species named *Iguanodon orientalis* Rozhdestvensky, 1952 is not based on diagnosable material, but that which is preserved is indistinguishable from the much better known European species *Iguanodon bernissartensis* Boulenger, 1881. In the early 1980s collaborative expeditions organized by the Palaeontological Institute of the Soviet (later Russian) Academy of Sciences and the Geological Institute of the Mongolian Academy of Sciences resulted in the discovery in 1981 (by Dr S. M. Kurzanov) of more iguanodontid ornithopod material from Dornogov′, but this time from a locality named Khuren Dukh (Fig. 1) located approximately 200 km northeast of Khamarin Khural. This material includes skull and postcranial elements in a good state of preservation, and representative of a size range of individuals: the maximum body length of individuals from this sample is estimated to be in the range 7–8 metres.

A well-preserved skull of the new iguanodontid from Khuren Dukh has been referred to consistently as 'Iguanodon orientalis' (*vide* Norman, 1985; Norman & Weishampel, 1990) on the basis of comparison drawn with the teeth of the known Mongolian species *I. orientalis*. Re-study of the holotype of *I. orientalis* by Norman (1996) confirmed the suspected affinities (Norman, 1980) of this species with the western European genus *Iguanodon bernissartensis*, and demonstrated that the referred ornithopod material from Khuren Dukh did not belong to the same taxon.

Ornithopod dinosaur biogeography and evolution during the Cretaceous Period

are interesting because of the unusual distribution which these dinosaurs display in time and space, this prompted the suggestion that vicariance may be at the root of the phylogeny of iguanodontid and hadrosaurid ornithopods (Milner & Norman, 1984) rather than the normal dispersalist interpretations (Cox, 1974). The utility of Milner & Norman's work was that it was predictive of the distribution of these ornithopods in space and time, and suggested a research programme which concentrated on the problematic taxa (the ornithopods of the Late Cretaceous of Transylvania, and the early Late Cretaceous forms recorded from Asia). Work over the past few years has been focused on these problems in Transylvania (Weishampel, Grigorescu & Norman, 1991; Weishampel, Norman & Grigorescu, 1993; Norman & Weishampel, in prep).

Asian discoveries of large ornithopods are of considerable interest because they focus attention on the evolutionary pattern of appearance and replacement shown by two groups of ornithopods: the iguanodontids, which are predominantly Early Cretaceous in occurrence; and the hadrosaurids, which are exclusively Late Cretaceous. Gilmore (1933) described *Bactrosaurus* and *Mandschurosaurus* (= *Gilmoreosaurus*, Brett-Surman [1979] from Asia (see also Weishampel & Horner, 1986); and later Rozhdestvensky (1952, 1966, 1974) addressed this matter following the discovery of new ornithopod species belonging to the genera *Iguanodon* and *Probactrosaurus*, with the latter genus regarded as most nearly intermediate between iguanodontids and hadrosaurids. This interpretation was amplified by Taquet (1975) who derived hadrosaurids explicitly from the gracile species *Iguanodon atherfieldensis* (cf. Norman, 1986) via forms such as *Probactrosaurus*.

The phylogenetic speculations aroused by these (relatively) new discoveries is added to by the curiously changeable northern Hemisphere coastline geography of the middle (Barremian-Albian) Cretaceous (Smith, Smith & Funnell, 1994; Fig. 2) which suggest shallow marine isolation of North America, Europe and Asia followed by sequential contacts firstly between just Europe and Asia, followed by isolation of
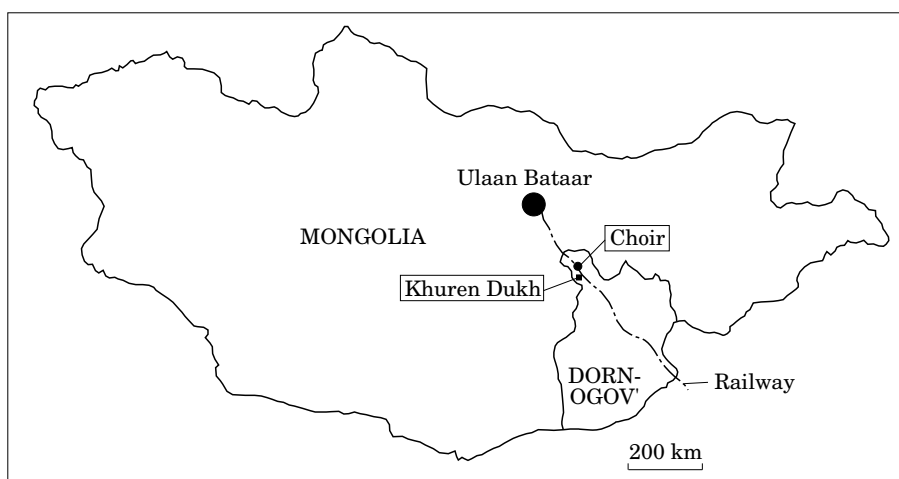

Figure 1. Outline map of Mongolia showing the approximate location of Khuren Dukh at which the holotype and referred material of ***Altirhinus kurzanovi*** **gen.** et **sp. nov.**, was collected.
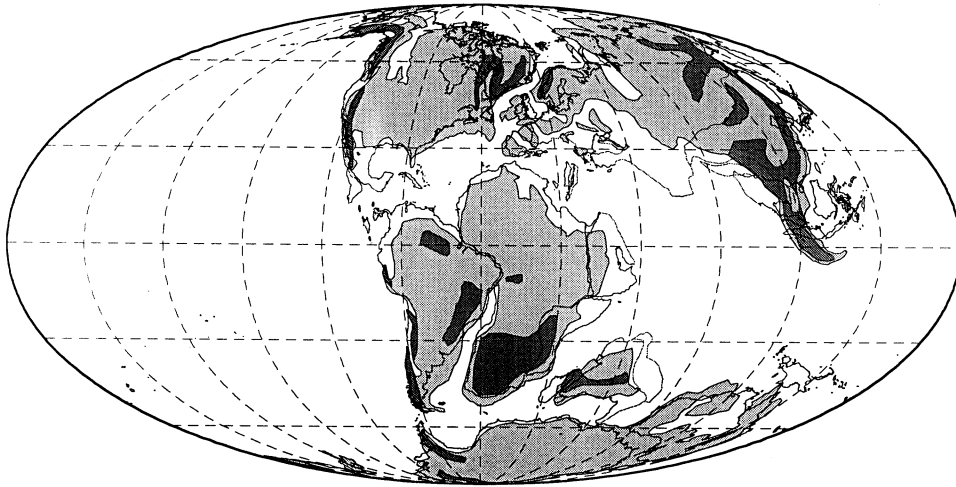
Figure 2. Palaeocoastline reconstructions of the Aptian Stage showing a land-based dispersal route for iguanodontian dinosaurs between Europe and Asia. (From Smith, Smith & Funnell, 1994).

Europe from North America and Asia, and persistent high latitude contact between Asia and North America via Beringia. Migration/dispersal patterns of large vertebrates will have been affected by, and reflect, such geographic changes (Russell, 1995), and their subsequent evolutionary history may be a direct consequence of these periods of either isolation or contact.

Re-study of previously described specimens (Norman, 1996; Norman & Kurzanov, 1997; Norman & Sues, in press); and examination of new material collected from the Aptian-Cenomanian beds of Mongolia (Norman, in prep.), will shed new light on the taxonomy, systematics and evolutionary history of these ornithopod dinosaurs. This subject is of particular evolutionary interest because along with the synapsids of the Late Paleozoic and the mammals of the Tertiary, dinosaurs show one of the most intense periods of terrestrial diversification in the fossil record of vertebrates; and, among dinosaurs, hadrosaurid ornithopods (cf. Weishampel & Horner, 1990; Weishampel & Norman, 1989) along with ceratopids (Dodson & Currie, 1990) show a spectacular degree of dominance in Late Cretaceous Northern Hemisphere terrestrial ecosystems.

This paper serves to describe the anatomy of a new iguanodontid from Mongolia, and to compare it with that of presently known species of iguanodontids. Larger questions relating to the systematic position of known iguanodontids are to be assessed in the light of this and further new material (Norman, in prep.) and the questions posed originally by Milner & Norman (1984), and Norman (1990). Preliminary observations are made concerning the systematics, phylogeny and underlying mechanisms of evolution operating on iguanodontid and hadrosaurid ornithopods.

Repository abbreviations. PIN – Palaeontological Institute Nauk (Moscow); BMNH – Natural History Museum (London); IRSNB – Institut Royal des Sciences Naturelles de Belgique (Brussels).

STRATIGRAPHIC AND GEOGRAPHIC CONTEXT

The stratigraphy of Mongolia during the Cretaceous and more specifically the stratigraphic correlation between localities within Mongolia are not fully resolved (D.A. Russell pers. comm., July 1996). The comments made below must therefore be regarded as tentative and open to subsequent revision.

The detailed stratigraphy of Mongolia is complicated by the existence of extensional faulting across the Gobi Basin that has produced a mosaic of grabens and semi-grabens which were filled by vertebrate-bearing strata. This structural complexity adds materially to the problems of historical interpretation of this part of the world and the evolution of its fauna with respect to adjacent land areas (principally North America and Western Eurasia). Preliminary attempts to correlate sites across Mongolia have been summarized by Jerzykiewicz & Russell (1991) who looked specifically at late Mesozoic sedimentation and stratigraphy. This work proposed that during Aptian times ('Shinkhudukian') Mongolian sedimentation was attributable to large perennial lakes, which were succeeded by a regime of vast, fluvially influenced plains with smaller lakes during Aptian-Albian ('Khukhtekian') time. They also noted that Early Cretaceous vertebrate assemblages were generally depauperate and exhibited strong endemism, but during the Khukhtekian the faunas became more diverse as a result of immigration from Europe and North America. This segment of time is of considerable interest because the taxon *Iguanodon orientalis* which has been recently redescribed (Norman, 1996) is suspected to be of Barremian-Aptian age, judged by comparison with the European fauna of dinosaurs which includes the apparently very similar form *I. bernissartensis*.

A Late Barremian/Early Aptian date for the European localities which have yielded *I. bernissartensis* (England – Norman, 1980; Belgium – Norman, 1980; Germany – Norman, 1987a; Spain – Sanz *et al.*, 1984), and for the Khamarin Khural locality in Mongolia (Norman, 1996) that has yielded the anatomically similar *I. orientalis* would thus be explicable in terms of a direct land connection between Europe and Asia in Early Aptian times (Smith, Smith & Funnell, 1994; Fig. 2). The latter locality was incorporated by Jerzykiewicz & Russell (1991) into a listing of localities of Khukhtekian 'Age' (Aptian-Albian) in Mongolia. The Khuren Dukh locality, first reported by Martinsson (1982) was similarly placed in the Khukhtekian 'Age' designation, but the fauna collected from various sites within this locale is clearly distinct. The new iguanodontid described below is anatomically more derived (and therefore presumably geologically younger) than that which was collected from the locality 200 km further south (Khamarin Khural). In the absence of reliable chronostratigraphic information it will be taken as a working hypothesis that, on the basis of the iguanodontid fauna, Khuren Dukh is of a stratigraphic age equivalent to the Late Aptian/Early Albian (110–100 million years ago).

A Late Aptian/Early Albian age for the Khuren Dukh locality, if taken in the context of the palaeocoastline maps of Smith, Smith & Funnell (1994) provides the unifying interpretation that the subsequent isolation of western Europe from Asia in Late Khukhtekian time (Early Albian) may well explain the derived features seen in the Khuren Dukh iguanodontid remains described below.

SYSTEMATIC PALAEONTOLOGY

Classification

Order: Ornithischia (Seeley, 1887)
    Suborder: Ornithopoda (Marsh, 1881)
        Infraorder: Euornithopoda (*sensu* Weishampel, 1990)
            Family: Iguanodontidae Cope, 1869
                Genus ***Altirhinus*** novum

Derivation of name. 'Alti-' L. *altus* = high, and 'rhinus' Gr. *rhinus* = the nose. In recognition of the highly arched nasal bones of the skull which give the snout of this animal a distinctively elevated profile.

Diagnosis. As for species.

Type-species. **A. kurzanovi sp. nov.**, by monotypy.

Stratigraphic age. Early Cretaceous: Late Aptian/Albian; 'Khukhtekian' age (Jerzy-kiewicz & Russell, 1991).

Locality. Khuren Dukh (Xypeh Dyx), northwestern Dornogov′ (East Gobi Province), Mongolia (approximately 30 km South of the town of Choir [Choyr]).

A. kurzanovi sp. nov

Derivation of name. For the collector of this new species, Dr Sergei M. Kurzanov of the Palaeontology Institute of the Russian Academy of Sciences, Moscow, who is renowned for his collecting prowess, and for his work on a wide variety of Mongolian fossil vertebrates.

Diagnosis. Euornithopod dinosaur, up to 8 metres long (on current evidence). *Cranial*: rostral tip of nasals strongly arched; external surface of nasals smooth, with no depression on lateral surface for extension of a (presumed) extra-narial pouch; midline internasal groove; rostral portion of premaxilla downcurved; lateral flaring of premaxilla (to widen the oral cavity) not bounded by a raised rim; no antorbital fenestra; lacrimal articulates with a finger-shaped dorsal process of the maxilla; large curved palpebral (1) articulates with prefrontal; quadrate (paraquadratic) foramen present between quadratojugal and quadrate; rostral end of jugal tapers to a point; jugal articulates with a caudolaterally directed finger-like process on the maxilla; postpalatine foramen present; surangular with two lateral foramina; downcurved rostral end to dentary; two replacement crowns in deeper (caudal) portions of maxillary and dentary dentitions. *Postcranial*: (manus proportions strongly resemble those of *Iguanodon* spp.); large, conical, but laterally compressed ungual phalanx of manus digit I; carpus well ossified, but not co-ossified into two discrete blocks, as seen in *Camptosaurus*, *Iguanodon* spp. and *Ouranosaurus*; digit IV of manus with an apparently short hoof-like ungual; ilium with sinuous dorsal margin, large anterior process, everted dorsal ridge, no brevis shelf; shaft of ischium straight, parallel-sided and with an axial twist, form of distal end unknown at present; shaft of femur curved rostrally; large, finger-shaped lesser trochanter (not flattened and appressed to the anterolateral margin of the greater trochanter).

PIN numbers. The numbering system appears to reflect a locale number, i.e. Khuren Dukh (3386) followed by a more specific excavation site (e.g. 3386/1,2, etc). Unfortunately the numbering system is clearly not used entirely consistently through-out the collections of PIN (the Palaeontological Institute of the Russian Academy

of Sciences) and appears to have been abbreviated in some instances, as indicated below.

Holotype

PIN 3386/8 (some numbered 3388). *Cranial*: much of the left side of the skull well preserved, right side of skull crushed and damaged and represented by isolated bones (right nasal, dentary, predentary, pterygoid fragments, quadrate, squamosal, postorbital, jugal, surangular, angular, prearticular, paroccipital wing). *Axial skeleton*: left and right atlas neural arches. No vertebrae. *Appendicular skeleton*: scapula (l), coracoid (l), sternals (r & l), pubis (r), ischia (r & l), manus digit V, ungual of manus IV, III, three pedal phalanges including one ungual.

Paratypes

PIN 3386/7 (3387). *Cranial*: dentary (l & r), predentary, surangular (l & r), angular, splenial, prearticular, maxilla (l & r), premaxilla, jugal, palpebral, prefrontal, frontals, lacrimals, quadrate (r & l). Pterygoid, palatine, ?vomers. 10 isolated teeth. *Axial skeleton*: left atlas neural arch, fragmentary vertebrae (cervical and dorsals), many ribs. *Appendicular skeleton*: manus (metacarpals, phalanges and unguals); sternal bones, coracoids, humerus, radius, ulna.

PIN 3386/9 (3389). *Appendicular skeleton*: scapula (l & r), coracoid (l), sternal (l & r), humerus (l & r), radius (l & r), ulna (r). Manus (r): metacarpals II, III, IV, V. Ungual of pollex, all phalanges of digits II, III & IV, phalanges 1, 2 of digit IV, and 1, 2 of digit V; manus (l): metacarpals II, III, IV, V, pollex spine, digits II, III and IV complete, one phalanx of V. Isolated carpal bones. Pubis (r & l), femur (l), tibia (r), fibula (l & r), astragalus (l & r), two sets of metatarsals, all first phalanges, second phalanges on right and left digits II & III and two lateral unguals. Axial: set of 34 caudal vertebrae.

PIN 3390. Small ornithopod skeleton. Broken limb and girdle bones of a small ornithopod, with some neural arch and jaw fragments. Isolated dentary tooth.

PIN 3391. Small ornithopod skeleton. Partial left pes. tibia, 4 vertebral centra, small fragments.

OSTEOLOGICAL DESCRIPTION

Cranial anatomy

For purposes of pure descriptive osteology the terms rostral (=anterior) and caudal (=posterior) will be used as standard (following Weishampel, Dodson & Osmolska, 1990); for more general anatomical description, the terms anterior and posterior will be used for reasons of common sense. Comparisons have been drawn primarily with the derived iguanodontid ornithopods: *Iguanodon atherfieldensis*, *I. bernissartensis* and *Ouranosaurus nigeriensis*; as well as with the serially more derived members of the ornithopod Family Hadrosauridae (including the non-crested or solid-crested members of the Subfamily Hadrosaurinae (hadrosurines) and the (generally) tubular crested members of the Subfamily Lambeosaurinae (lambeosaurines)—see Weishampel, Norman & Grigorescu [1993] for further information).
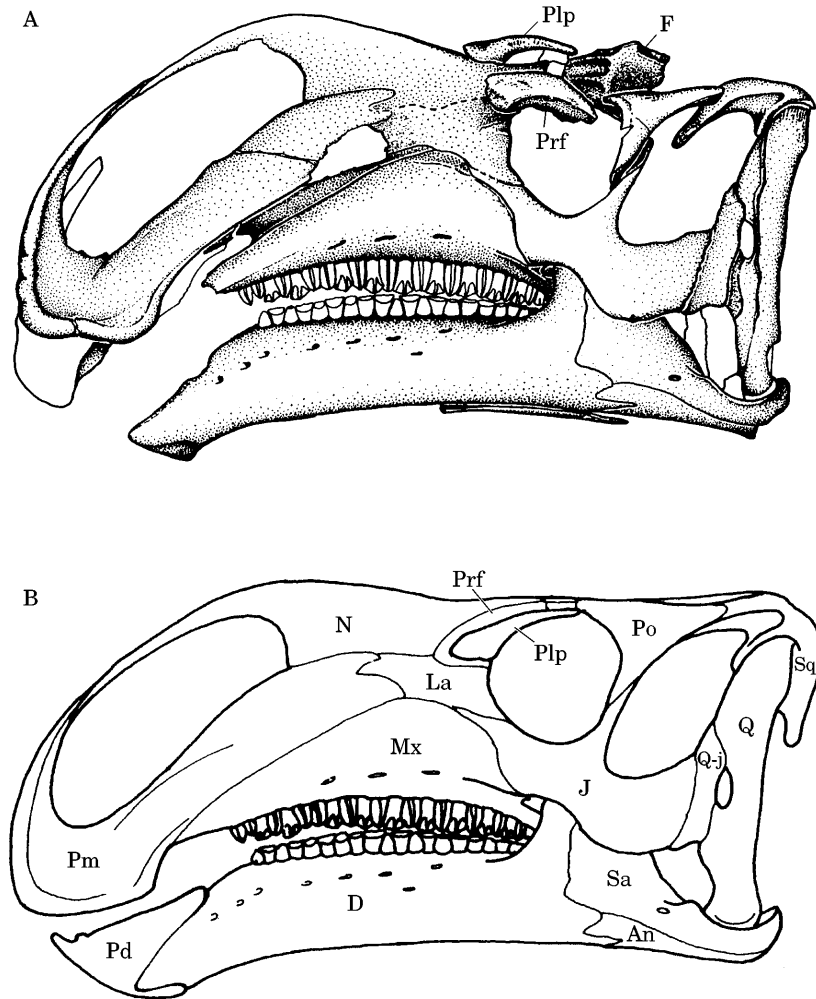
Figure 3. *Altirhinus kurzanovi* **gen.** *et* **sp. nov.** A, skull in lateral view, based on PIN 3386/8 (holotype). Total length as preserved: 760 mm. B, reconstruction of the skull in lateral view. Abbreviations: An – angular; D – dentary; F – frontal; J – jugal; La – lacrimal; Mx – maxilla; N – nasal; Pd – predentary; Plp – palpebral; Po – postorbital; Prf – prefrontal; Q – quadrate; Q-j – quadratojugal; Sa – surangular; Sq – squamosal.

General observations

The general proportions of the skull (Fig. 3A,B) give a superficial resemblance to that of the hadrosaurine (*sensu* Weishampel & Horner, 1990) ornithopod *Brachylophosaurus* (Fig. 4B), insofar as the front part of the snout bears an elevated, arched nasal region and ventrally offset, moderately flared premaxillary beak. The remainder of the skull, although constructed on a general osteological framework common to most ornithopod dinosaurs, is not typical of members of the Hadrosauridae; the detailed anatomical characters displayed by the individual bones are most similar to those of the ornithopod family Iguanodontidae (Norman, 1980, 1986, 1990).
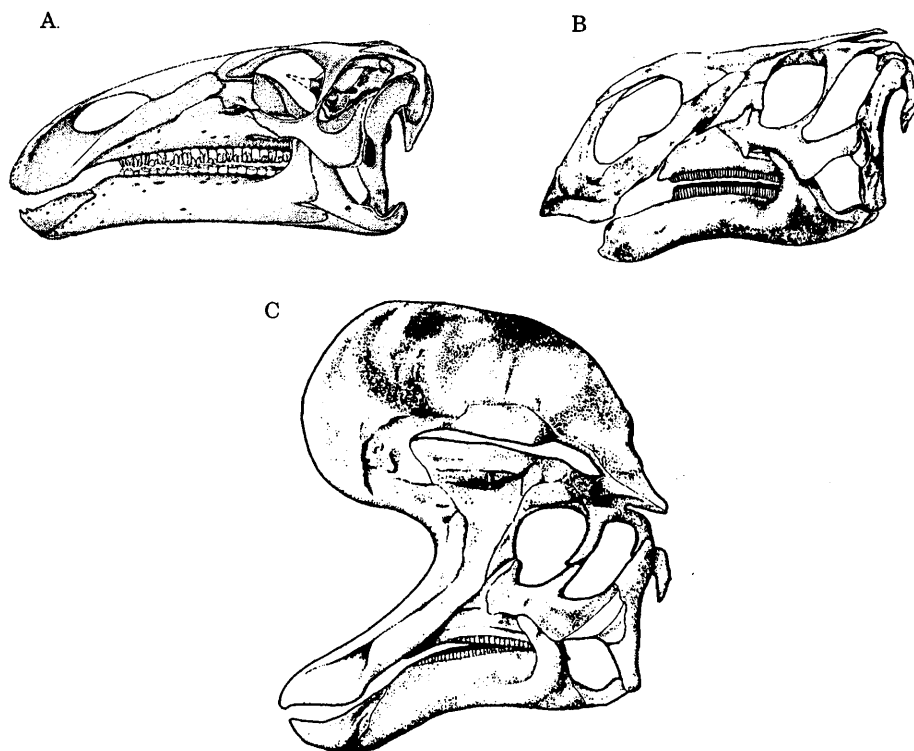
Figure 4. Lateral views of the skulls of: A, *Iguanodon atherfieldensis*; B, hadrosaurine *Brachylophosaurus canadensis*; C, lambeosaurine *Lambeosaurus magnicristatus* (B, C, from Weishampel & Horner, 1990).

Facial skeleton
Premaxilla. The oral portion of the premaxilla (Fig. 3) projects considerably below the horizontal level of the maxillary tooth row, and gives to the whole of the anterior facial region a curious and notable downward inflection which is similar to that seen in many Hadrosauridae (Fig. 4B,C) and corresponds with the downward deflection of the anterior portion of the mandible. The oral margin is expanded laterally to form a relatively modest 'beak' which is not edged by a thickened and raised rim as seen in hadrosaurines (Fig. 4B), but more nearly resembles the sloping lower narial depression seen in lambeosaurines and *Iguanodon* (Fig. 4A,C). The oral margin which supported the keratinous rhamphotheca (beak) is relatively smoothly contoured but immediately behind the oral margin there is a median and a lateral indentation (Fig. 5) which correspond to prominent median and lateral 'cusps' on the opposing margin of the predentary (Fig. 15); these indicate the occlusal relations between these bones during feeding/cropping.

Medially the premaxilla forms a thickened rostral plate which supports the internarial septum; the latter spans the area beneath the medial dorsal (nasal) spine and the portion of the premaxilla which roofs the extreme rostral part of the buccal cavity. The outer surface of the premaxilla is slightly ridged and roughened, reflecting the attachment area of a rhamphotheca. The medial dorsal spine arches caudally delimiting the external narial chamber and tapers rapidly as it approaches the anterior tip of the nasal bone; there is a shallow facet running along the ventrolateral
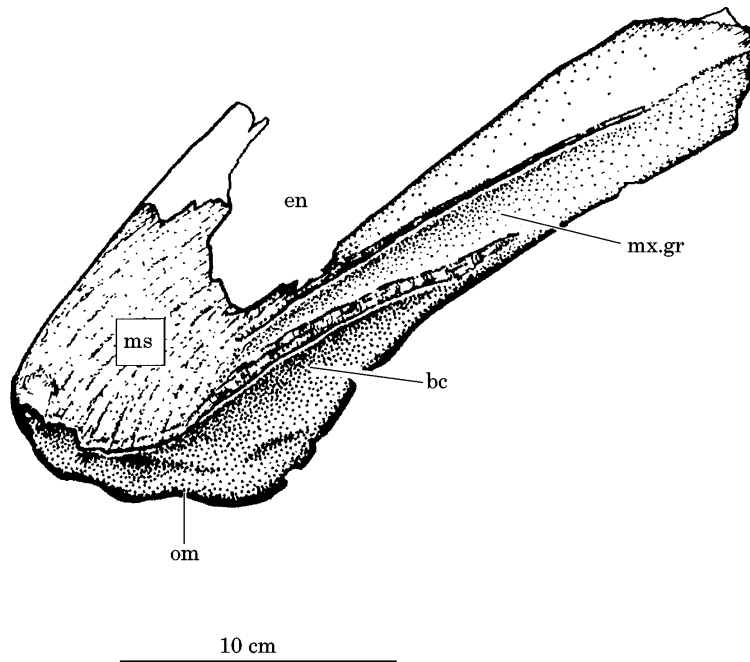
Figure 5. **A. kurzanovi sp. nov.** Premaxilla (PIN 3386/7) in medial view. Abbreviations: bc – buccal cavity; en – external naris; ms – median sutural surface for adjacent premaxilla; mx.gr – groove for rostral process of maxilla; om – oral margin of premaxilla.

edge of the premaxilla which indicates the facet for the nasal; these two bones overlap approximately midway along the external narial opening. The paired premaxillae meet the nasals such that the premaxillae wedge out in a median groove above the nasals.

A large lateral process projects backward and obliquely upward from the beak and lays in a trough present on the rostrodorsal surface of the maxilla (see Fig. 3A); this process forms the lower border of the external naris. The process is approximately triangular in cross-section rostrally, but progressively thins and its external surface slopes ventrolaterally forming what is in effect an extension of the lower narial depression seen above the rhamphothecal region up the side of the face. Caudally the premaxilla forms an extensive overlapping suture with the lacrimal (Fig. 3) and provides a ridge along its dorsal edge upon which sits the nasal. The medial surface of the premaxilla (Fig. 5, ms) is ridged and scarred by ligaments reflecting a firm but unfused sutural attachment to its neighbour—clearly post-mortem movements have separated the premaxillae in the holotype skull (Fig. 3); there is also an oblique groove (functionally a median fossa when the premaxillae are articulated in life position) which appears to have accommodated the median dorsal spine of each maxilla (Fig. 5, mx.gr) an arrangement which is seen in *Hypsilophodon* (Galton, 1974a, b, and pers. obs.); this 'groove' is bounded below by a suturally scarred edge, which formed the medial portion of the roof of the anterior buccal cavity, and above by a raised horizontal ridge which forms the midline floor of the narial cavity.

Maxilla. The external appearance of the maxilla is well shown in the holotype skull PIN 3386/8 (Fig. 3) and two disarticulated, incomplete maxillae (PIN 3386/7 –
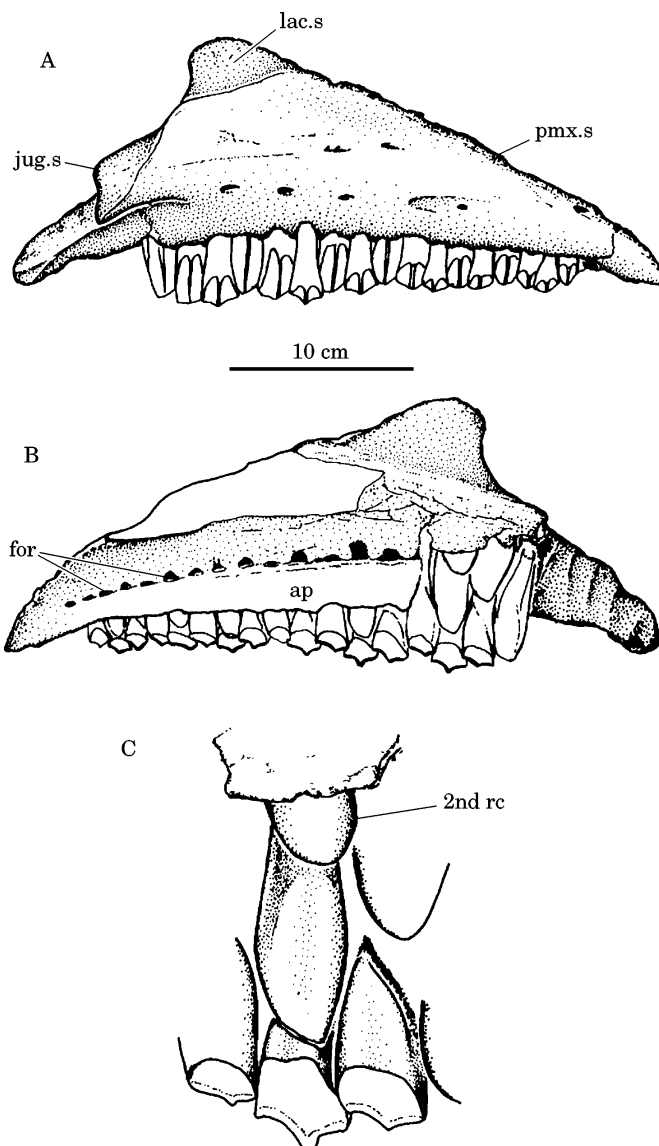
Figure 6. **A. kurzanovi sp. nov.** Maxilla (incomplete PIN 3386/7) in lateral (A) and medial (B) view. (C) shows enlargement of the medial view to show replacement teeth *in situ*. Abbreviations: 2nd rc – second replacement crown; ap – alveolar parapet; for – special foramina; lac.s – sutural surface for lacrimal; jug.s – sutural surface for jugal bone; pmx.s – sutural surface for premaxilla.

Fig. 6). The maxilla is the most robust of the facial bones and has a somewhat lopsided triangular outline in lateral view. There are 21 vertical tooth rows on the right maxilla of PIN 3386/7 (Fig. 6).

Rostrally the maxilla is wedge-shaped, tapering to a ventrally deflected point which underlies the lateral portion of the premaxilla; the dorsal surface of this rostral end has an oblique, dorsolaterally directed flange against which articulated the

caudolateral extension of the premaxilla. It is evident from the holotype skull (PIN 3386/8 – Fig. 3) that the sutural surface between the maxilla and premaxilla was relatively weak (in mechanical terms) in that it had apparently permitted (postmortem) the rostrum to be shunted caudally relative to the remainder of the skull. The nature of the premaxilla–maxilla suture is best shown in the holotype skull, and an additional feature of this suture is also seen, which is the existence of a medial dorsal process of the maxilla; this latter projects rostrally, medial to the lateral process of the premaxilla, and would appear to have engaged in a recess on the medial surface of the latter (Fig. 5, mx.gr). The area immediately beneath this medial process is a vertical wall which marks the inner surface for attachment of the premaxilla and appears to be an integral part of the pleurokinetic hinge seen generally in iguanodontian ornithopods. A very similar structure has been described in the genus *Iguanodon* (Norman, 1980, 1986) and is also present in the genus *Ouranosaurus* (personal observation—*contra* Horner, 1988, 1990).

The dorsal margin of the maxilla continues to rise to its highest point about two-thirds of the distance toward the caudal end of the bone. In this area there is a complex suture with the lacrimal, which includes (judged by the shape of the medial surface of the lacrimal) a dorsal, flattened projection which serves as the main support of the lacrimal, but the rostroventral margin of the lacrimal appears also to be wedged along a ledge developed from the dorsal surface of the maxilla. There is no convincing evidence for an antorbital fenestra at the junction between the lacrimal and maxilla (compare Figs 3 & 4A) as seen in *Camptosaurus* (Gilmore, 1909), *Iguanodon* (Norman, 1980, 1986) and *Ouranosaurus* (Taquet, 1976). Lateral and ventral to the lacrimal attachment area, there is a ventrolaterally directed (jugal) process; the external surface of this process is marked by a sinuous line which delineates the ventral extent of the suture with the rostral process of the jugal. The remainder of the jugal process is enveloped by the rostral portion of the jugal, a very similar anatomical configuration has been described in *Iguanodon* (Norman, 1986).

Lacrimal. An isolated dorsal half of the left lacrimal is preserved in PIN 3387 (Fig. 7A,B). This shows the position of the lacrimal duct and the relationship between the lacrimal and ventral portion of the prefrontal. It is clear from this fragment, and from the holotype skull that the lacrimal was a quite extensive bone on the side of the face. Medially a portion of the suture with the dorsal process of the maxilla is preserved (cf. *I. atherfieldensis*, [1986; fig. 12]). And from the rostral process of the jugal it is clear that there was a substantial lower portion of the bone which formed the lower front quadrant of the orbital cavity. The rostroventral portion of the lacrimal contacted the premaxilla, and was probably wedged in position by thin laminae developed from the dorsal edge of the maxilla.

The holotype skull, despite the disruption caused by *postmortem* displacement, shows no evidence for the presence of an antorbital fenestra between the lacrimal and maxilla as seen in other non-hadrosaurid iguanodontians (Norman, 1986).

Prefrontal. An isolated partial left prefrontal is preserved in PIN 3387 (Fig. 7C) in addition to what can be observed in the holotype (Fig. 3) where telescoping of the muzzle against the skull roof has caused the prefrontal to be displaced across the orbit. The isolated fragment consists of a roughly oblong bone, flattened transversely. The upper portion has a small elevated knob against which the palpebral appears to have articulated; beneath this surface there is another raised area which may
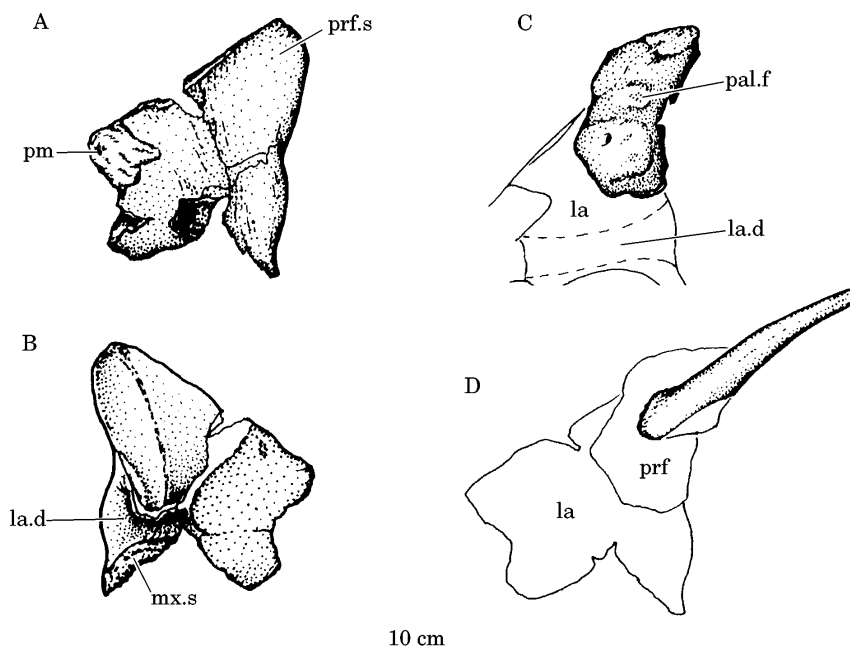
Figure 7. *A. kurzanovi.* **sp. nov.** Lacrimal (partial) in lateral (A) and medial (B) view (PIN 3387). The rostral portion of this bone is missing though a small fragment of the premaxilla appears to be attached to the rostral margin. (C) Prefrontal (PIN 3387) in lateral view placed on an outline of the restored lacrimal. (D) Palpebral (PIN 3387) in lateral view placed on outline of prefrontal/lacrimal. Abbreviations: la – lacrimal; la.d – lacrimal duct; mx.s – maxillary suture; pal.f – palpebral facet; pm – premaxilla; prf – prefrontal; prf.s – prefrontal suture.

well have served for the attachment of the remainder of the baseplate of the palpebral. This bone appears to have had an extensive (but relatively loose) overlapping suture with the lacrimal, the medial surface of the prefrontal has a shallow depressed surface which fits extremely snugly against the lateral surface of the lacrimal (Fig. 7C).

Palpebral (supraorbital). A displaced left palpebral is preserved on the holotype skull (PIN 3386/8 – Fig. 3A) and an isolated, but slightly damaged left palpebral is preserved among the skull fragments associated with PIN 3387 (Fig. 7D). This bone is remarkably similar to that described in *I. atherfieldensis* (Norman, 1986; fig 16). The base of the bone is expanded, faces medially and is slightly concave; it rested on the lateral surface of the prefrontal and there is a slight lip, that fits into a small notch on the prefrontal margin which, no doubt, helped to secure it in position. The distal portion of the bone is curved and tapering, ending at a blunt and slightly rugose point, and follows the dorsal border of the orbital cavity parallel to the prefrontal and frontal bones. The outer surface of the bone is dorsoventrally convex and slightly rugose in texture, and the medial surface is a relatively acute edge. It is not possible to be certain whether a 2nd palpebral existed as is the case in *I. bernissartensis* (Norman, 1980) and has been reported in some better preserved hadrosaurids (Maryanska & Osmolska, 1981).
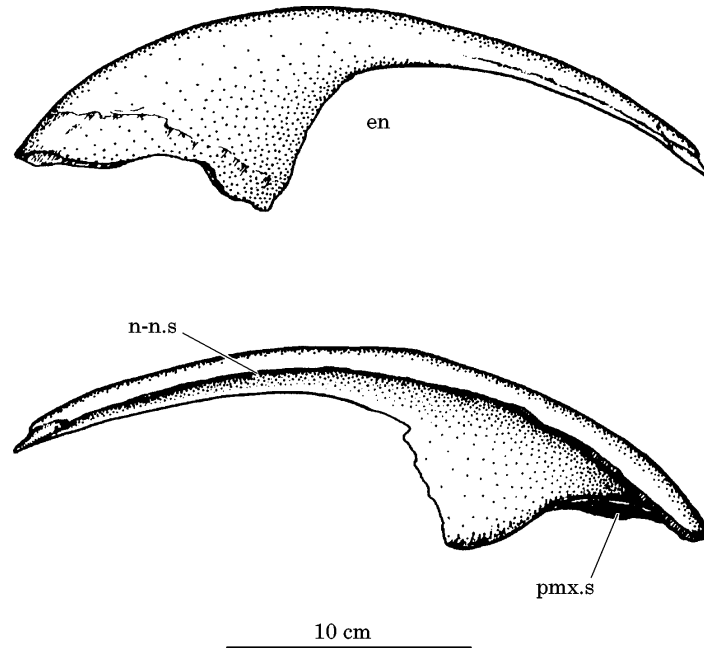
Figure 8. *A. kurzanovi* **sp. nov.** Nasal bone (partial PIN 3386/8) in lateral (A) and medial (B) view. Abbreviations: en – external naris; pmx.s – premaxillary suture; n-n.s – nasal–nasal suture.

Nasal. The nasal (Figs 3, 8) forms a considerable proportion of the roof of the muzzle; it bridges the region between the median dorsal premaxillary spine rostally and the frontals caudally, and with the premaxilla completely encloses the external naris through its contact with the lateral posterior premaxillary process; it also contacts the medial edge of the prefrontal, and whether it has a sutural relationship with the lacrimal is impossible to decide from the known material.

The nasal is strongly arched rostro-caudally, and rostrally it tapers to a point which lies alongside the medial process of the premaxilla and attaches to a shallow, relatively smooth, sutural surface, and the tapering premaxillary process rests in a channel which lies above the nasal–nasal suture (Fig. 8). The medial nasal–nasal suture is depressed below the dorsal margin of the nasal such that there was a midline channel extending down the centre of the nasal portion of the snout. Laterally the edge of the nasal forms a sharp margin to the dorsal external naris, which leaves the ventral surface of this process also vaulted, while the external surface has a line of small foramina which run parallel to the narial margin. The ventral edge of the nasal is sharp and curves downward to meet the premaxilla and form the caudal margin of the external naris. Where it meets the premaxilla, the nasal is thickened transversely and has a ventral recess, the side walls of which clamp around the dorsal margin of the premaxilla.

The caudal section of the nasal is less well known. On the holotype skull (PIN 3386/8) the left nasal appears to show a sinusoidal outline in lateral view, reversing the arching of the rostral region so as to be able to meet and overlap the frontals in the horizontal plane; the nasal–frontal suture is partly preserved on an isolated skull roof (Fig. 11). Laterally the nasal probably formed a diagonal suture with the
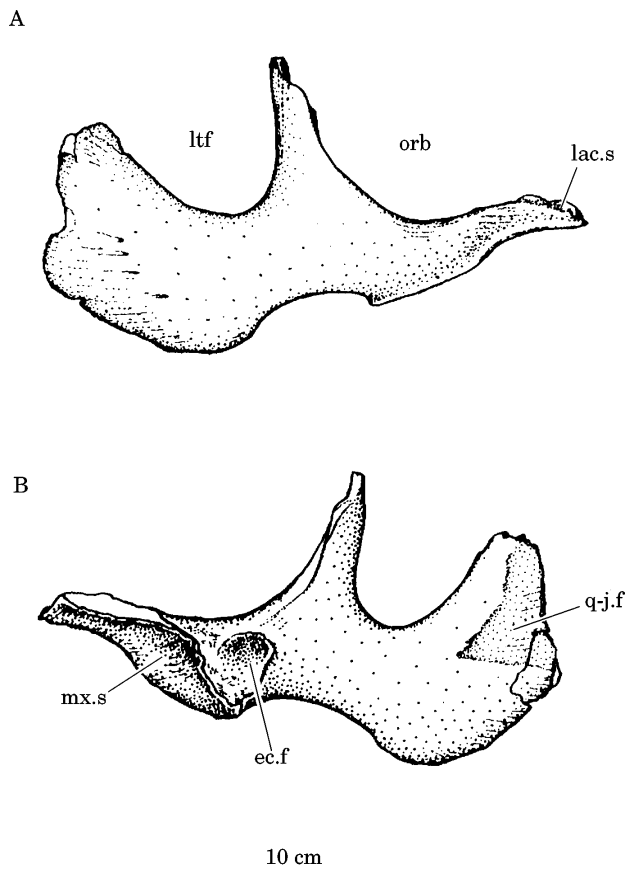
Figure 9. *A. kurzanovi* **sp. nov.** Jugal in lateral (A) and medial (B) view. PIN 3387. Abbreviations: ec.f. – facet for the ectopterygoid; lac.s – suture for lacrimal bone; ltf – lateral temporal fenestra; mx.s – sutural surface for finger-like projection from maxilla; orb – orbital cavity; q-j.f – facet for the rostral process of the quadratojugal.

prefrontal, although the precise relationship between these bones in this pre-orbital area has been somewhat disturbed by the rearward shunting of the premaxilla and nasal unit (relative to the remainder of the skull) which has occurred in the holotype (Fig. 3A).

Jugal. The external appearance of the jugal is well shown in the holotype skull (Fig. 3) and in the isolated element (PIN 3387 – Fig. 9). The rostral extremity of the jugal pinches out between the maxilla and lacrimal just rostral to the anterior margin of the orbital cavity. The lateral surface of the rostral process is smooth and flattened, highlighted by a few radiating striae (Fig. 9A) and forms a thin wall of bone with a ventral margin which is limited by a shallow sinuous edge which fits neatly against a complementarily shaped ledge on the external surface of the maxilla (Figs 3, 6). Medial to this lateral wall, the internal and ventral portion of the rostral process is deeply excavated to form a recess into which slots the jugal process of the maxilla (Fig. 9B); immediately caudal to the recess for the maxilla there is a relatively smooth, thumb-print depression on the medial wall of the jugal, which marks the

sutural surface for the ectopterygoid. (Fig. 9B, ec.f). The dorsal surface of the rostral process is marked by a facet for the attachment of the lacrimal; the latter overlaps the extreme tip of the jugal, and makes it appear as though it tapers to a point between the maxilla and lacrimal.

Immediately behind the lacrimal sutural surface the upper edge of the jugal is smoothly curved where it forms the lower margin of the orbital cavity; rising to above half the height of the orbit it produces a rostrocaudally flattened (concave transversely) postorbital process, which underlaps the descending process of the postorbital. The postorbital process of the jugal descends steeply before curving caudally and rising again steeply toward the upper portion of the quadrate to form the lower half of the lateral temporal fenestra. The caudal part of the jugal is laterally compressed and expanded dorsoventrally; its caudal margin is irregular along its upper half where it forms an overlapping suture with the quadratojugal; the latter fits into a recess on the medial wall of the jugal (Fig. 9B, q-j.f). The lower half of the caudal border is free and overlaps the coronoid process of the lower jaw and curves forward (convex ventrally) before rapidly inflecting and arching (concave ventrally) to meet the base of the rostral process at the ectopterygoid facet. The external surface of the jugal is smooth, though its lower (free) caudal margin is marked by low-relief striations, and some small foramina.

Quadratojugal. The quadratojugal is not well known, though its general features can be seen in the holotype skull (PIN 3386/8) where the quadratojugal and jugal are slightly separated. The quadratojugal appears to have been laterally flattened and approximately triangular in outline, with the apex projecting rostrally and lying in a shallow recess on the medial surface of the jugal (Fig. 9B, q-j.f). The lateral surface is recessed to receive the jugal (Fig. 3A) and its posterior border overlaps the upper part of the jugal wing of the quadrate (above the quadrate foramen), spans the anterior margin of the quadrate foramen and overlaps the lower part of the jugal wing of the quadrate (Fig. 10).

Quadrate. The quadrate is a slightly curved, pillar-like bone forming the rear border of the cheek (Figs 3, 10). The upper end of the quadrate has a relatively small articular head which fits into a deep recess in the squamosal and is clamped (at least partially) by a rostroventrally directed, finger-like process of the squamosal. Caudal to and beneath the articular head there is an essentially vertical buttress (Fig. 10); ventral to the buttress, the body of the quadrate curves smoothly toward the lower (articular) condyle; rostral to the main shaft of the quadrate two wings of bone are produced: one a rostrally directed thin sheet (jugal wing) whose anterior margin is interrupted by an embayment for the quadrate (paraquadratic) foramen (Fig. 10); the edges of the jugal wing immediately adjacent to the embayment are marked by sutural attachment areas for the quadratojugal (Fig. 10, q-j.s); the other (pterygoid) wing is rostromedially directed, and, though not well preserved in this material, undoubtedly overlapped the caudal wing (posterior alar projection) of the pterygoid. The articular condyle is rostrocaudally convex, and medially expanded.

Squamosal. The squamosal is not fully preserved (Fig. 3). As usual for ornithopod dinosaurs this bone caps the quadrate, whose head is located in a deep pocket on the ventral surface of the squamosal. A finger-shaped process is directed rostroventrally from the socket for the quadrate and runs along the rostral margin of the jugal wing of the quadrate. Above the socket for the quadrate, the squamosal
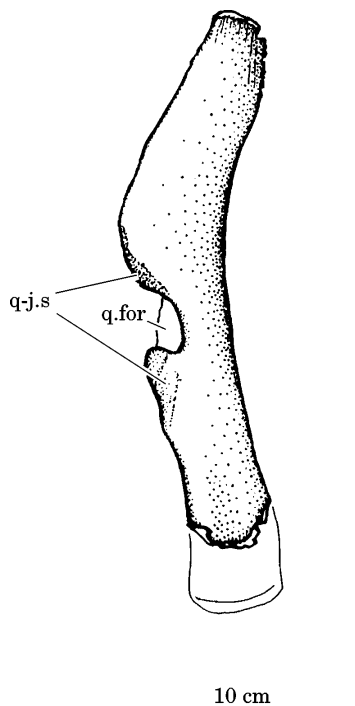
Figure 10. *A. kurzanovi* **sp. nov.** Quadrate (partial left) in lateral view (PIN 3387). Abbreviations: q-j.s – facets for attachment of the quadratojugal; q.for – embayment for the quadrate (paraquadratic) foramen. Length 23.6 cm.

produces a rostrally directed process with an external ledge; the ledge is continuous with the caudal process of the postorbital, and the two bones overlap and thereby enclose the lateral temporal fenestra, and simultaneously form an internally vaulted lateral border of the upper temporal fenestra. The details of the contact between the squamosal and the paroccipital process and roofing of the braincase are not preserved in this material; and the caudal process, which would have been expected to partially back the quadrate and its buttress, is not preserved either.

Postorbital. In lateral view (Fig. 3), the postorbital has a tri-radiate structure. Rostro-ventrally the postorbital is embayed where it forms the dorsocaudal quadrant of the orbital cavity; the smooth contour of this surface is contrasted by the irregularly scarred and pitted external surface of the postorbital dorsally. Ventrally the postorbital produces a tapering (jugal) process which backs the outer part of the orbital cavity and more distally overlaps the jugal in a comparatively weak ligamentous suture. The caudal (squamosal) process overlaps the squamosal. Rostrally the postorbital meets the frontal along the orbital margin and the suture between these two bones extends mediocaudally in a long curve in a coarse, lapped sutural surface and appears to terminate at its junction with the parietal medially (Fig. 11).

Frontals. The frontals are displaced and exposed in ventral view on the holotype skull (Fig. 3). An isolated portion of the skull roof (PIN 3386/7 – Fig. 11) shows the form of the frontal and its relationship with adjacent bones clearly. The frontals are not fused in this specimen, though this may well be an immature individual, and
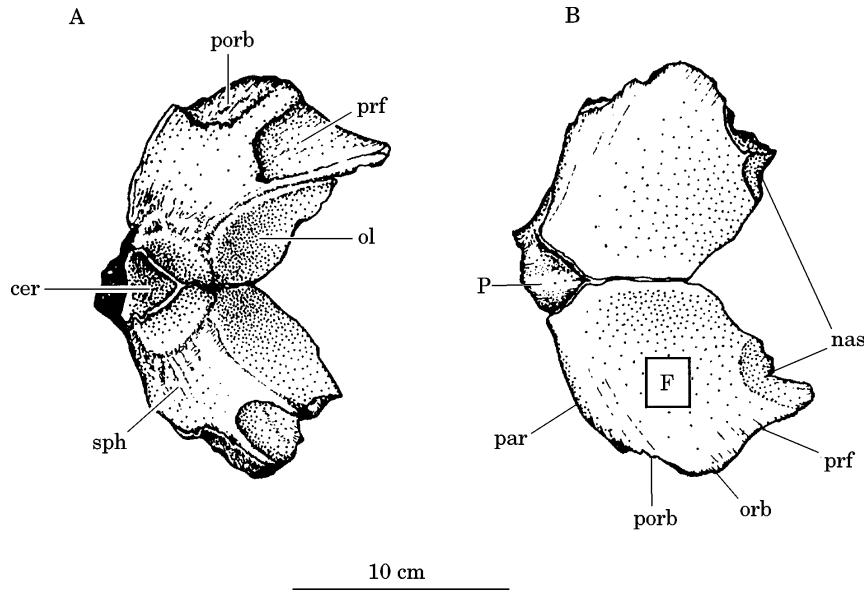
Figure 11. **A. kurzanovi sp. nov.** Skull roof (PIN 3387) in dorsal (A) and ventral (B) views. Abbreviations: cer – roof of cerebral cavity; F – frontal; nas – sutures for nasal bones; ol – roof of olfactory cavity; orb – orbital margin; P – parietal; par – parietal suture; porb – postorbital suture; prf – prefrontal suture; sph – sphenethmoid contact.

each is roughly pentagonal in plan view; they meet in a slightly raised butt-jointed suture sagitally. The dorsal surface (Fig. 11B) is slightly concave and relatively featureless. Rostrally the frontal has an oblique, sharp-edged margin which diverges from its neighbour and this may well have marked the position of a temporary fronto-nasal fontanelle. Laterally the dorsal surface has a shallow depression, which marks the overlapping suture with the caudal edge of the nasal bone (nas). Lateral and caudal to the nasal suture the margin of the frontal is somewhat irregular and roughened—this marks the attachment area for the prefrontal (prf); caudal to this suture there would appear to have been a short exposure of the frontal along the dorsal orbit margin (orb) before the curved sutures for the postorbital (porb) and parietal (par) bones. A small fragment of the parietal is attached to the frontals.

In ventral view (Fig. 11A) the frontal has a complex set of indentations and grooves corresponding to attachment areas for adjacent bones of the skull roof and neurocranium, or the roof of channels associated with cranial cavities. Rostrally and medially a broad domed area corresponds to the olfactory lobes (ol); immediately behind this area the skull roof is constricted and this is followed by a small midline domed area, which marks the most anterior portion of the cerebral part of the endocranial cavity (cer). The recesses for the prefrontals, which were bound to the frontals by well-developed tongue and groove sutures and for the postorbital bones, which were of similar form, are well shown. Ridging on the ventral surface of the frontals lateral to the cerebral vaulting probably marks the attachment area for the sphenethmoid portion of the braincase (sph).
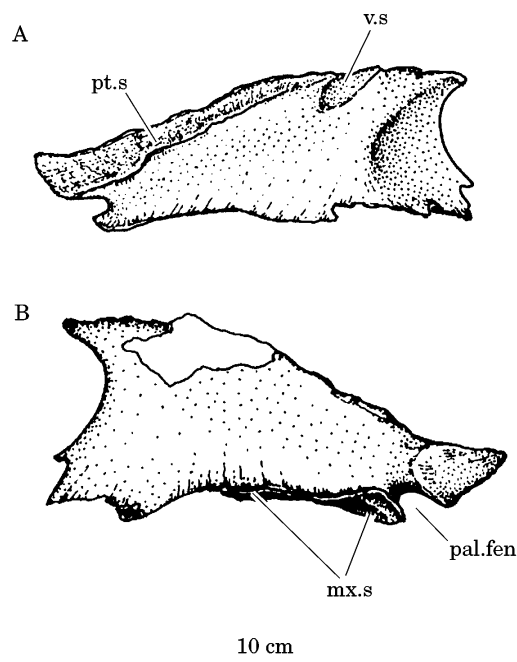
Figure 12. *A. kurzanovi* **sp. nov.** Palatine in medioventral (A) and dorsolateral (B) views (PIN 3386/7). Abbreviations: mx.s – sutural surface for maxilla; pal.fen – palatine fenestra; pt.s – pterygoid sutural surface; vs – vomerine sutural facet. Length 10 cm.

Neurocranium

Parietal. The braincase and much of the associated skull roof is missing from the holotype and all the referred material. A small fragment of the parietal is preserved attached to the isolated frontal plate (PIN 3387 – Fig. 11) but, apart from showing the form of the rostral part of the cerebral cavity, this is of no material value for descriptive purposes.

Palate

PIN 3386/7 includes disarticulated parts of the palatal region of the skull and forms the basis of the description below. The holotype skull does not preserve any of this region of the skull, apart from a broken part of a pterygoid and what appears to be the rostral tip of the ectopterygoid (Fig. 3).

Palatine. The left palatine is preserved and appears to be almost complete (Fig. 12). It is very approximately wedge-shaped in profile and has a broad and recessed base which is corrugated, forming a strong sutural surface which wraps around much of the medial caudodorsal edge of the maxilla. When positioned on the maxilla the palatine faces obliquely medioventrally, arching over the rear part of the combined nasobuccal cavity. The laterodorsal surface of the palatine is smooth and slopes dorsomedially thereby forming at least part of the lower and inner wall of the orbital cavity. The anterior margin of the palatine is concave and marked by a small projection near its lower border; the free (dorsomedial) edge of the palatine curves rostrally and ends in a rough, blunt point. Caudal to the rostral tip the upper edge

of the palatine is rough and rather irregular and develops an extensive, stepped and irregular surface on its ventromedial edge, which marks the sutural attachment area for the rostral (palatine ramus) of the pterygoid (Fig. 14A). The medial surface of the palatine is smooth and concave. The anterior part of the medial wall of the palatine is strengthened by a thick, curved ridge.

Caudally the palatine has an extensive overlapping suture against the pterygoid; immediately below (and lateral to) the suture for the pterygoid, the caudal border has a smooth notch where it forms the anterior wall of a reduced palatal fenestra (Fig. 12, pal.fen). Such fenestrae are reduced in ornithischian dinosaurs generally (Romer, 1956 and *Scelidosaurus*, pers. observ.) and are clearly absent from hadrosaurids (Heaton, 1972), but appear to be present in ornithopods more generally (*Hypsilophodon*). Closure of the palatal fenestra may be a unique trait within the hadrosauridae among ornithopods.

Pterygoid. A partial left pterygoid is preserved with the palatine in PIN 3386/7 (Fig. 13); it appears to be lacking a part of its rostral tip (adjacent to the palatine) and much of the deep and thin quadrate wing, but retains most of the salient characters of this bone. The only adequate description of ornithopod pterygoid bones is to be found in Heaton (1972) based as it was on the extremely well-preserved pterygoids of hadrosaurid dinosaurs. Comparison is made with the work of Heaton, in particular with respect to those of the hadrosaurines (*sensu* Weishampel & Horner, 1990) *Edmontosaurus* and *Brachylophosaurus*.

The rostral portion (=palatine ramus) of the pterygoid comprises a dorsally inclined, essentially horizontally flattened plate (slightly arched inferiorly – Fig. 13C) which meets the medial edge of the palatine in a strong, stepped suture, visible in lateral view (Fig. 13A); these two bones form a broad shelf separating the roof of the nasobuccal cavity from the floor of the braincase (Fig. 14A). At the base of the rostral process the pterygoid forms a thickened and complex central plate. The base only of the dorsal and caudal portion of this central plate is preserved, but undoubtedly developed into an extensive and thin wing of bone (=posterior alar projection) which overlapped, on its medial side, the pterygoid wing of the quadrate; the lower and more substantial portion of this wing (=postero-inferior projection) is preserved and shows a thickened medial, horizontal ledge (=buttressing flange) which widens as it merges with the central plate to form the area of the basal articulation (Fig. 13B,D, b.art). Beneath the shelf for the basal articulation there is a crescentic ridge (=bifurcating flange) behind which there is a foramen/fossa, the latter having been noted in *I. bernissartensis* (Norman, 1980: fig. 14); this ridge curves ventrally and buttressed the pterygoid/ectopterygoid flange (=ectopterygoid ramus). In lateral view (Fig. 13A) the ectopterygoid ramus can be seen to bear a well-marked scarred area for the attachment of the ectopterygoid as well as the maxilla.

Ectopterygoid. There is no evidence of the external shape of the ectopterygoid apart from the rostral tip which can be seen in the holotype skull. It is assumed to have been a strap-like element running from the articular socket on the medial surface of the jugal (Fig. 9) across the caudal part of the maxilla and on to the lateral surface of the pterygoid; a depressed area on the lateral surface of the pterygoid (Fig. 13) probably indicates the distal area of contact of the ectopterygoid. The ectopterygoid probably had an important function in helping to lock the pterygoid firmly against the caudal end of the maxilla.
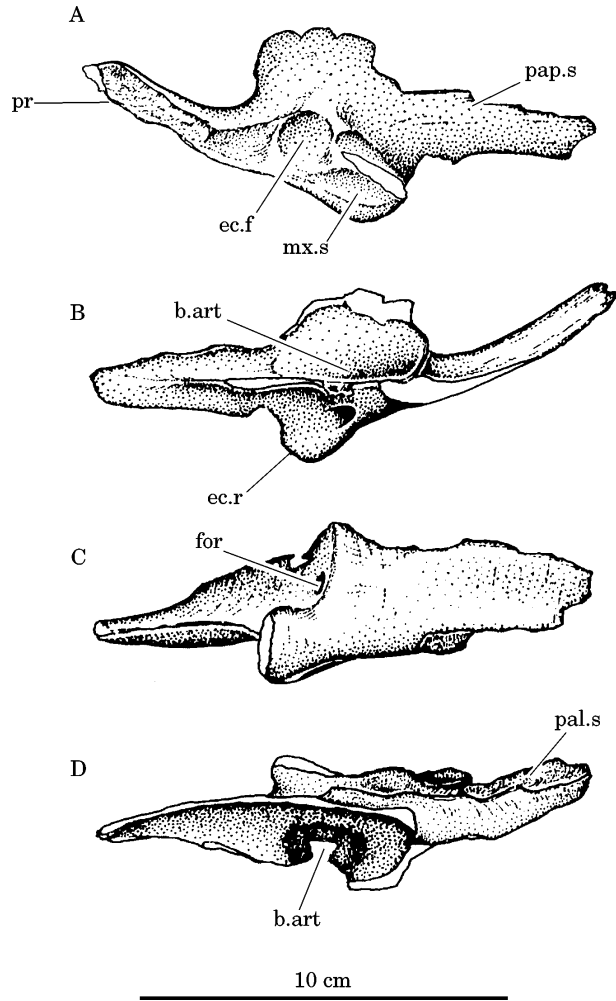
Figure 13. **A. kurzanovi sp. nov.** Pterygoid (incomplete – PIN 3386/7) in lateral (A), medial (B), ventral (C) and dorsal (D) views. Abbreviations: b.art – basal articulation; ec.f – facet for the ectopterygoid; ec.r – ectopterygoid ramus; for – foramen/fossa; mx.s – maxillary sutural surface; pal.s – palatine sutural surface; pap – posterior alar process. Length 13.3 cm.
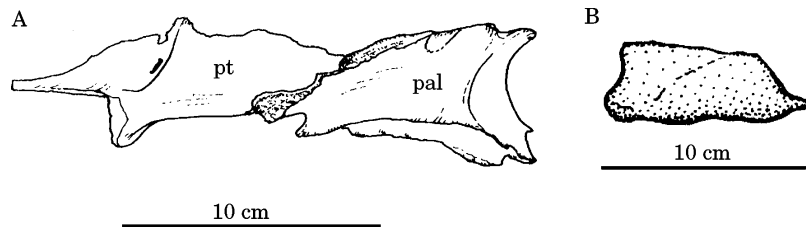

Figure 14. **A. kurzanovi sp. nov.** A, ventral aspect of pterygoid and palatine bones in articulation. B, partial vomer in lateral view (PIN 3386/7). Abbreviations: pal – palatine; pt – pterygoid.
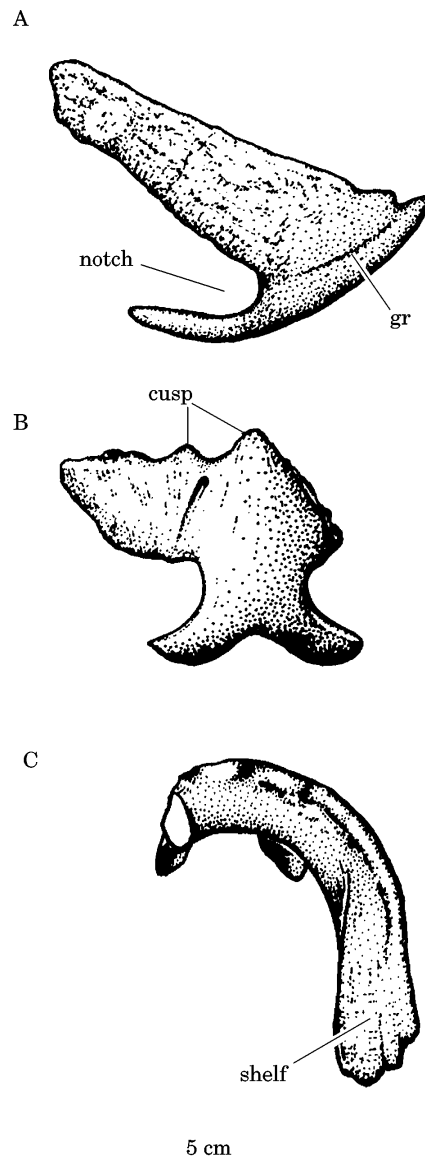
A

B

C

5 cm

Figure. 15. **A. kurzanovi sp. nov.** Predentary (incomplete – PIN 3386/7). In lateral (A); anterior (B); and dorsal (C) views. Abbreviations: cusp – denticulations on oral margin; gr – vascular groove; notch – recess to accommodate dentary; shelf – broad crushing surface of predentary beak.

Vomer. Two fragments, which may represent parts of the vomers are preserved along with the other palatal elements described above (Fig. 14B). They have the form of relatively thin, nondescript plates of bone, approximately triangular in lateral view. The curvature of the caudal margin and general form of these bones is indicative of their being parts of the vomers (cf. Norman, 1980, 1986; Heaton, 1972), but they do not add material evidence relating to the structure of the palate in this species.

Lower jaw
Predentary. This bone (PIN 3386/7) (Fig. 15) is very similar in general structure to
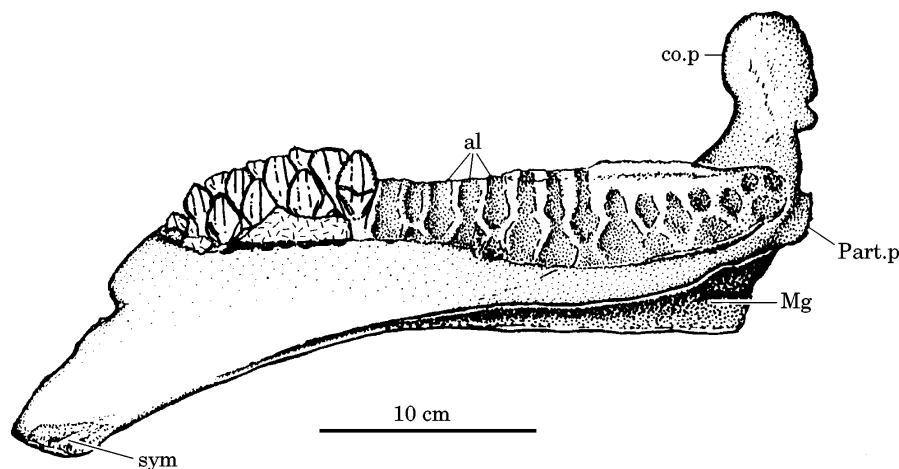
Figure 16. **A. *kurzanovi* sp. nov.** Dentary in medial view (PIN 3386/7). Much of the dental magazine has been broken away revealing the characteristic form of the lateral alveolar wall shaped by the erupting tooth crowns. Abbreviations: al – lateral alveolar wall; co.p – coronoid process; Mg – Meckelian groove; Part.p – prearticular process (broken off); sym – symphysis.

that of *Iguanodon* (Norman, 1980, 1986). In dorsal (occlusal) view (Fig. 15C) the bone is horse-shoe shaped and bears a graduated series of conical denticulations (cusps) arranged symmetrically either side of the largest midline cusp (Fig. 15B). Further laterally the denticulations cease and are replaced by a rounded ridge, which supported the cutting edge of the rhamphotheca, and curves caudally to the end of the bone lining up with the upper edge of the dentary. Lingual to the 'cutting edge' of the predentary there develops a shelf, which becomes increasingly broad caudally (Fig. 15C, shelf); a similar feature was noted in *Iguanodon* (Norman, 1980, 1986). The somewhat irregular caudal margin of this shelf rests on a notch on the adjacent inclined edge of the dentary. In lateral view (Fig. 15A), the predentary is wedge-shaped; the ventral margin angles rostroventrally and is broad and slightly recessed to fit against the dorsal margin of the dentary. A prominent rounded projection which forms the anterior tip of the dentary and lies immediately lateral to the symphysis, fits into a notch in the body of the predentary, and the predentary develops a pair of flaps which clamp against the under surface of the dentary, as also seen in hadrosaurids (Ostrom, 1961). The predentary, though incomplete is well preserved, and appears to show no evidence of a median caudal process immediately above the dentary symphsis. There are a number of vascular openings and grooves on the predentary which are presumed to be associated with support and growth of the rhamphotheca. A large vascular opening near the distal end of the dentary appears to be continuous with a foramen between the median and first lateral cusps, the two being connected via a groove on the external surface of the predentary (Fig. 15A, gr). An essentially similar arrangement of foramina and interconnecting groove is also seen in the jaw of *I. atherfieldensis* (pers. observ. – BMNH R. 11521), and may indeed by a widespread feature in ornithischians more generally.

Dentary. One right dentary (PIN 3386/7 – Fig. 16) is particularly well preserved. The rostral end of the dentary is relatively thin, curved downward and has a spout-like shape. The underside of the dentary lateral to the symphysis is marked by a

depression which represents the attachment area for the paired caudoventral processes of the predentary (Fig. 15C, shelf). From its lowest point: the dentary symphysis (sym) which is relatively small, oval and scarred by ligament attachment, the dorsal edge of the dentary curves laterally, and rises upward as a rounded edge to which the predentary was attached; this latter attachment area is terminated by a notch on the dorsal edge of the dentary, which marks the distal articulation of the dentary with the broad flattened caudal end of the predentary. Beyond this point the dentary margin continues to rise as a roughened edge (approximately in line with the occlusal margin of the predentary) for another 45 mm before the commencement of the dentition; this edge may have anchored an extension of the rhamphotheca. The bulk of the remaining ramus of the dentary is given over to accommodation for the dentition, the downward curvature notable in the rostral part of the ramus is lost and the dentary becomes progressively broader and deeper. At the rostral end of the dentition a row of dental foramina marking each of the vertical tooth families can be seen beneath the alveolar parapet which supports the dentition lingually. Caudally the teeth and parapet have been lost, but the impression of the tooth positions is left in the substance of the labial alveolar wall (Fig. 16, al), which is shaped to accommodate the functional and replacement crowns and roots of the teeth. Beneath the dentition on the lingual side of the dentary there is a vertical wall of bone which diminishes in height caudally and is terminated below by the channel formed by Meckel's canal (Mg); the latter curves laterally beneath the dentition forming a sleeve-like structure into which the lateral postdentary bones fitted and a tissue space which is continuous with the adductor fossa.

At the caudal end of the dentition the lingual surface of the dentary develops a caudoventrally directed spur (a remnant only of this remains) which supported the prearticular (Part.p) where it spanned the medial side of the adductor fossa. Dorsal to the support for the prearticular the dentary sweeps upward to form the robust labially offset coronoid process (co.p). The caudal margin of this is grooved to receive the dorsal process of the surangular, and the medial surface of the coronoid is scarred for the attachment of a small (presumably lozenge-shaped) coronoid bone. The dorsal edge of the coronoid process is somewhat expanded rostrocaudally. The base of the coronoid process is offset lateral to the dentition, and is supported by a curved buttress of bone which sweeps upward from a broad shelf labial to the dentition; this shelf diminishes rostrally as it runs parallel to the dentition forming the floor of the presumed cheek recess. The caudal portion of the dentary below the coronoid process follows an undulating margin where it overlaps the surangular, and then produces a caudally directed finger (Fig. 3) which overlaps the angular quite extensively (Fig. 20). The medial postdentary bones (splenial, prearticular) lie lingual to the dentary, while the lateral bones fit into the sleeve formed by the almost tubular external dentary wall.

Coronoid. This bone is not preserved in the collections, but is assumed to have lain on the medial side of the coronoid process where there is a facet for its attachment.

Surangular. This bone is well preserved in at least two examples (PIN 3386/7 – Fig. 17) and forms a substantial proportion of the external part of the rear of the lower jaw, contributing to the support of the coronoid process and a major part of the jaw joint. Rostrally the bone forms a curved and thin wall which slots inside the sleeve-like caudal part of the dentary. The dorsal part of this suture is more complex because the surangular produces a finger-like extension which fits into a slot on the
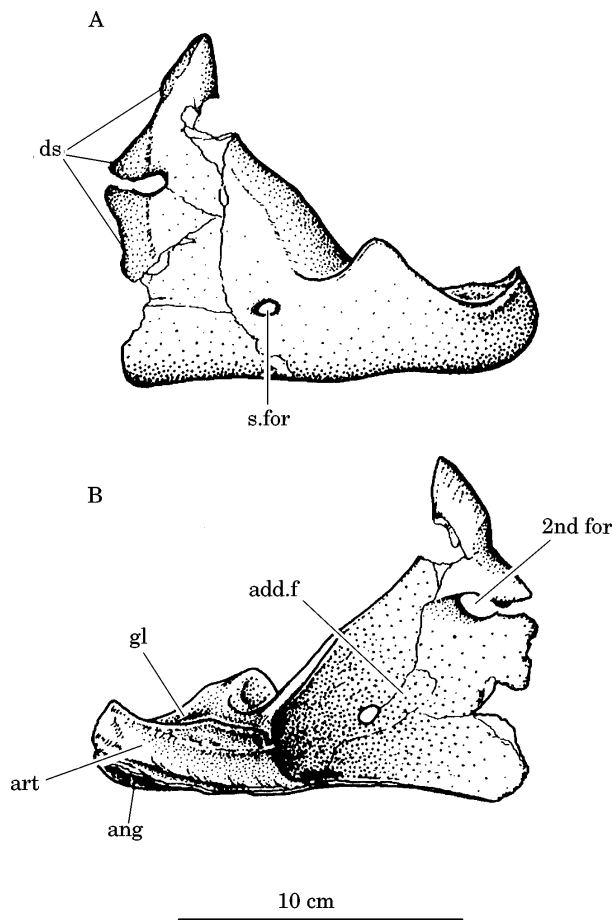
Figure 17. **A. kurzanovi sp. nov.** Surangular (PIN 3386/7). In lateral (A) and medial (B) views. Abbreviations: add.f – adductor fossa; ang – sutural contact with angular; art – sutural contact with articular; ds – dentary sutural surface; gl – lateral (glenoid) articulation for quadrate; s.for – surangular foramen; 2nd for – second foramen on surangular. Length 15 cm.

caudal edge of the coronoid process of the dentary; immediately beneath this process there is a well preserved foramen which is visible laterally (Fig. 17, 2nd for). This foramen lies in the same relative position as the 'large foramen' noted by Galton (1974a,b) on the surangular of *Hypsilophodon*. The external surface of the surangular is relatively smooth, and its caudal margin descends quite steeply toward the jaw articulation. Adjacent to the jaw articulation, the external surface of the surangular is everted to form a lip-like projection, which would appear to form the lateral margin of the quadrate cotylus and attachment area for the jaw joint ligaments. Rostroventral of the prominent lateral lip a prominent rounded surangular foramen is present, as seen in a variety of iguanodontian ornithopods, but absent in hadrosaurids. Immediately caudal to the quadrate cotylus the surangular is hooked upwards forming the lateral portion of the retroarticular process.

Medially (Fig. 17B) the surangular forms the lateral margin of a well developed adductor fossa (add.f) in the area immediately beneath and behind the coronoid
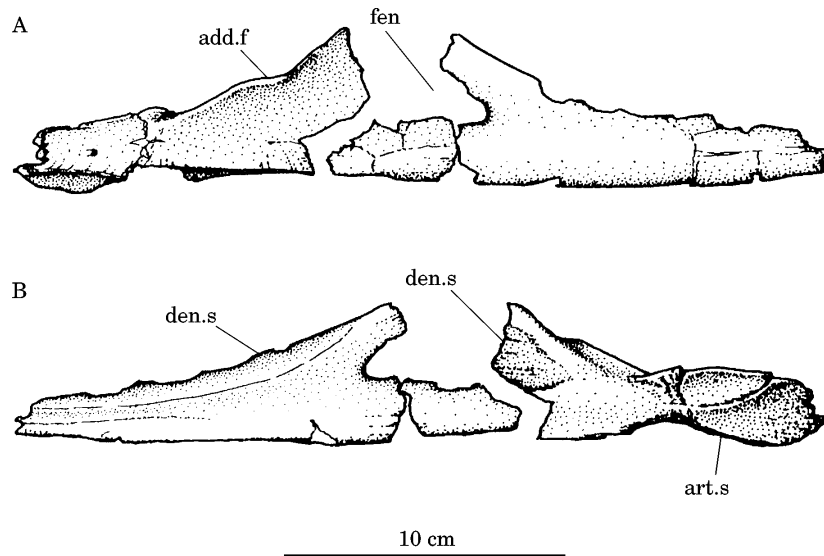
Figure 18. **A. kurzanovi sp. nov.** Prearticular (PIN 3386/7) in medial (A) and lateral (B) views. Abbreviations: add.f – medial margin of adductor fossa; art.s – contact area for articular bone; den.s – contact areas for the dentary; fen – Meckelian fenestra. Length c.29 cm.

process. In the area beneath and medial to the quadrate cotylus there is a horizontal recess which marks the area of attachment of the articular bone (art); the latter is presumed to have contributed to the medial part of the jaw joint, and the retroarticular process. Lying immediately beneath the presumed articular suture, there is another narrower and more ventrally positioned slot, which harboured the angular bone (ang).

Prearticular. The prearticular is a long, thin bone spanning much of the area of the dentary beneath the dental magazine, forming the medial wall of the adductor fossa, and clamping the medial side of the articular. A slightly broken, but well preserved left surangular is present in PIN 3386/7 (Fig. 18). The rostral process is long and thin and appressed to the medial wall of the dentary, covering Meckel's canal; there is a shallow recess showing where the dentary contracted the prearticular, above Meckel's canal, on the lateral surface of the prearticular (Fig. 18B). Caudally, the dorsal margin sweeps smoothly upward toward the coronoid process at the rear of the dentary, and there appears to have been a large Meckelian fenestra in the prearticular, which led through to the adductor fossa (a similar fenestra was noted in *I. bernissartensis* – Norman, 1980; pl. IV, and has now been observed in *I. atherfieldensis* BMNH R. 11321. This feature has not commonly been recorded in ornithopod dinosaurs, but this may well be a preservational bias). Beneath the coronoid process the dorsal edge of the prearticular descends gradually, forming the medial wall of the adductor fossa; this ends at a small raised area, which marks where the prearticular appears to have met the articular at the rostral edge of the quadrate cotylus. Caudal to this area the margin of the prearticular is sharp edged and tilted and twisted (to accommodate the articular bone which is wedged between the prearticular and surangular in this area) as it reaches its termination. Ventral to this region there is a bevelled edge which contacted the angular laterally.
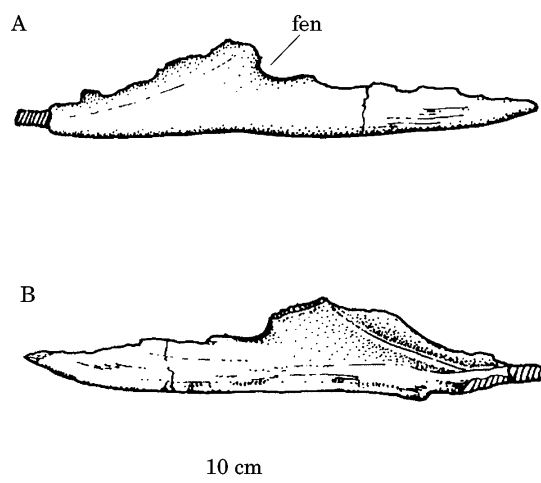
Figure 19. *A. kurzanovi* **sp. nov.** Splenial (partial PIN 3386/7) in medial (A) and lateral (B) views. Abbreviations; fen – Meckelian fenestra. Length 18 cm.

Splenial. The splenial (Fig. 19) is preserved as a slender piece of bone which lay against the prearticular and enclosed the rostral part of Meckel's canal; its precise relationships with the dentary and other postdentary bones are not clear. It would appear that it extended caudally to contribute to the Meckelian fenestra and that its caudal extremity lay alongside the mid-caudal section of the prearticular, but its rostral extent cannot be ascertained.

Angular. The left angular (PIN 3386/7, see Fig. 20, as well as the right PIN 3386/ 8) is well preserved, trough-like and occupied the lower edge of the lower jaw immediately behind the dentary and below the surangular. The bone is long and quite sinuous in shape. Externally the rostral part of the bone is overlapped extensively by the dentary, and its surface is scarred by this contact. Its upper edge is grooved to receive the lower edge of the surangular along a sinuous line, and beneath this edge there is an extensive overlap between these two bones, which undoubtedly strengthened the contact. The internal (dorsal) aspect of the bone is hollowed and at the rear forms a roughened ledge (probably for attachment of the articular); rostral to this area the surface bears a longitudinal ridge which may be associated with muscle attachment to the floor of the adductor fossa. The lower medial edge of the angular may have made contact with the prearticular.

Articular. This bone, which was small, lozenge-like and wedged between the surangular, prearticular and angular and contributed mostly to the retroarticular process, and very little (perhaps only a cartilaginous pad) to the medial portion of the articular glenoid for the quadrate; it is poorly ossified in *I. atherfieldensis* (BMNH R. 11520) and is not preserved in the collections of the PIN.

Dentition

Both the maxillary and dentary dentitions are preserved in the holotype and referred material, allowing a reasonable description of the form of the teeth and their arrangement in the dental apparatus. The replacement pattern, which is of
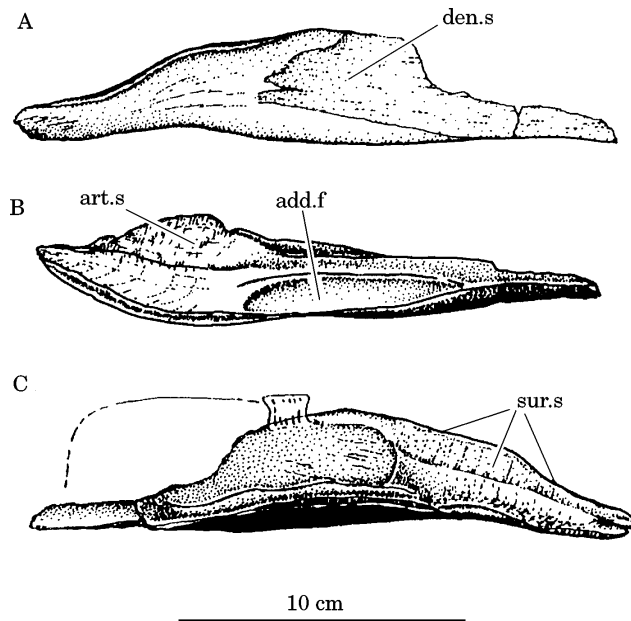
A

den.s

B   art.s   add.f

C   sur.s

10 cm

Figure 20. *A. kurzanovi* **sp. nov.** Angular (incomplete – PIN 3386/7). Lateral (A), dorsal (B) and medial (C) views. add.f – adductor fossa (deep portion); art.s – sutural surface for the articular; den.s – dentary sutural surface along the lateral face of the angular; sur.s – stepped suture for the surangular. Length 21 cm.

considerable interest because it appears to be intermediate between that seen in iguanodontids (*Iguanodon* and *Ouranosaurus*) and hadrosaurids, was not amenable to detailed study since the resources to do so were not available; however an outline of the pattern can be described on the basis of visual observation.

Dentary teeth. There are 24 vertical tooth positions in the largest dentary (PIN 3386/7 – Fig. 16). Dentary teeth (Figs 16, 21A, 22) bear a strong similarity to those of *Iguanodon* sp; they have a mesiodistally expanded crown which, in lingual view, has the form of a slightly distorted trapezium, the long axis being inclined distal to the vertical (Figs 21A, 22). This fundamental asymmetry is betrayed in the positioning of the primary ridge (p), the slight difference between the lengths of the crenelated mesial and distal margins and the difference in the form of the lower margins of the crown (where they converge on the root).

Only the lingual surface of the crown, and mesial and distal edges which are ornamented with crenelations, are covered by a layer of enamel. The labial side of the crown has a dentine surface, which is smeared in places by a coating of cementum (cem). This latter surface is curved (concave vertically, convex horizontally) and smooth except at the mesial and distal edges adjacent to the lower (waisted) region of the crown as the crown merges with the root; in this area the surface is indented by a vertical depression which marks the position of adjacent successional crowns in the dentition.

The lingual surface of the crown is more complex, bearing a number of features which aid in identification. The surface is bisected unequally by a low but prominent (p – primary) ridge which extends from the base of the enamelled surface to the tip
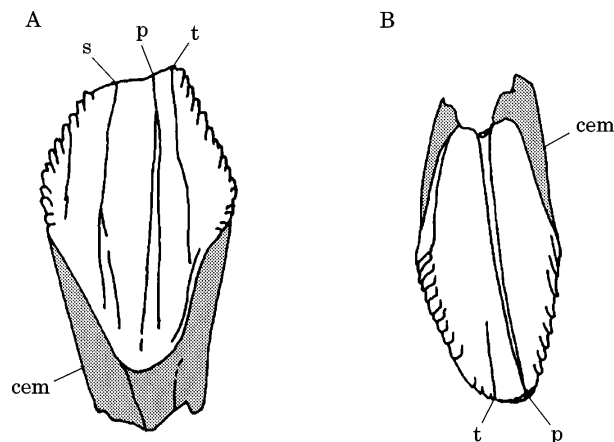
Figure 21. **A. kurzanovi sp. nov.** A, dentary tooth (slightly worn, distal part of root hollow and broken away, medial view); B, maxillary tooth (unworn, root not yet fully mineralized, lateral view). To show general characteristics and shape. Abbreviations: cem – cementum layer coating the root and lateral side of dentary crowns and medial side of maxillary crowns; p – primary ridge; s – secondary ridge; t – tertiary ridge. PIN 3386/7.
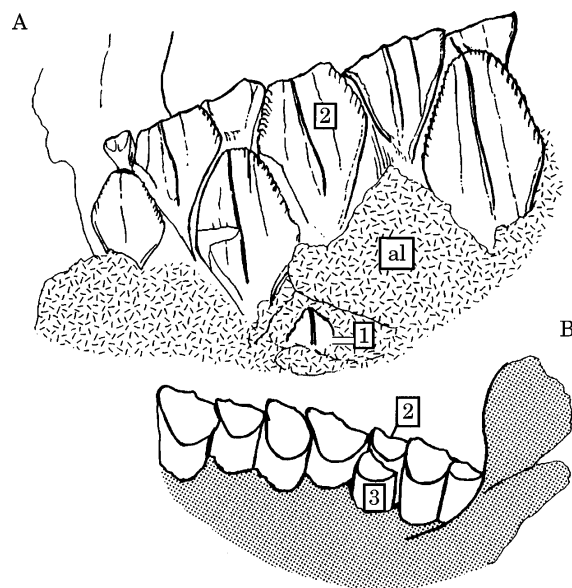

Figure 22. **A. kurzanovi sp. nov.** Dentary teeth (PIN 3386/7) from the left dentary ramus adjacent to the coronoid process in medial (A) and lateral (B) views, showing functional and replacement teeth in position and the presence of three teeth (1, 2, 3) in a vertical tooth position. Abbreviation: al – alveolar parapet.

of the crown. Mesial to the primary ridge the crown surface is further divided by a lower, but relatively prominent and broader (s – secondary) ridge which runs exactly parallel to the primary ridge and merges with the base of a denticle on the 'shoulder' of the mesial edge of the crown. A small number (1 or 2) of subsidiary ridges (t –

tertiary) may be found mesial to the secondary ridge in the form of wrinkles in the enamel which extend from the base of the mesial denticles and run parallel to the secondary ridge for some short distance. Distal to the primary ridge the crown surface is again subdivided (pretty consistently) by a low ridge which originates from the marginal denticles just distal to the apex of the tooth and extends down the crown diverging from the primary ridge, and approaching the inrolled shelf which forms immediately beneath the widest part of the crown.

The lower half of the enamelled surface contracts toward the midline of the crown. The mesial edge is roughly bevelled and this surface slightly overlaps the distal margin of the adjacent replacement crown. The distal edge is more prominent, and appears to show the marginal denticles inrolled to form an angled ledge; this corresponds to the presence of the slightly overlapping mesial edge of the adjacent successional crown in the dentition. The general shape of the crown and root therefore reflect the relatively dense packing of the teeth within the dentition to form a self-supporting magazine of teeth similar, though not one that is as functionally integrated as those seen in hadrosaurids (Ostrom, 1961). The presence of cementum on the labial surface of the crown indicates that adjacent and replacement crowns were anchored in place, and helped to support the functional crowns.

The marginal denticles are relatively large and coarse, having the form of short curved ledges which wrap around the edge (lingual to labial) of the crown and have an irregular edge to them. Between the shoulder and apex of the crown the denticles are smaller and more simple being conical in shape.

Maxillary teeth. A full maxillary dentition is not known (see Fig. 6), but since the maxillary crowns are narrower than the dentary crowns it would seem likely that there would have been about 26 vertical tooth positions in the maxilla which corresponds to the dentary (PIN 3386/7) containing 24. As with the dentary teeth, the similarity to those of *Iguanodon* is striking. The maxillary crowns are narrower and more lozenge-shaped in labial view than those of the dentary and less markedly asymmetrical (Fig. 21B).

The labial surface of the crown and its crenelated margins are coated with enamel, while the remainder of the crown and root are composed of dentine, with traces of a cementum coating (cem). The lingual surface of the tooth is relatively smooth, though the mesial and distal edges are channelled to accommodate the edges of adjacent replacement crowns (Fig. 6B,C).

The enamelled labial surface shows the distinctive features of such teeth. The crown is divided subequally by a very prominent (keel-like) primary ridge (p) which runs from the centre of the base of the crown to the apex. The slightly larger mesial surface of the crown is smooth and only interrupted by short subsidiary ridges (t, usually only one, frequently none) derived from the marginal denticles close to the apex. There is a slight shoulder to the mesial part of the crown margin, fringed by small simple apical denticles; beneath these, and along the remainder of the mesial margin lie a series of larger, ledge-like marginal denticles which are turned to project labially. Beyond the widest part of the crown, the mesial edge converges, as a thickened and somewhat wrinkled line, on the midline of the crown. The distal surface of the crown is smooth and unadorned by ridges; its margin consists of coarse, ledge-like denticles, which curve around on the lingual side of the crown margin, and the base of the crown converges on the midline as a mirror of the mesial edge.
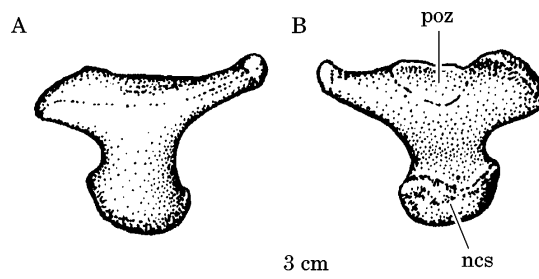
Figure 23. *A. kurzanovi* **sp. nov.** Atlas neural arch (left) in lateral (A) and medial (B) views. PIN 3386/8. Abbreviations: ncs – neurocentral suture; poz – posterior zygapophysis.

Placement. The dentary dentition has its teeth arranged in an inclined array (the long axis of the crowns inclined backwards rather than perpendicular to the long axis of the dentary—see Fig. 22). In addition there is a mild degree of overlap between adjacent crowns such that each crown is overlapped by the crown immediately behind it in the series. It is surmised that this had a mechanical function: lending additional support to adjacent crowns subjected to intense attrition during repetitive chewing (Norman, 1984; Norman & Weishampel, 1985). The maxillary dentition has its teeth arranged in a vertical array. The overlap between individual crowns also differs from that seen in the lower dentition in that the overlap is a repetitive one between adjacent teeth: the larger and more fully erupted teeth are found in alternate positions along the jaw and these occupy a slightly more labial position compared to the intervening crowns (Fig. 6A). This mechanical support system clearly assists in the ability of the dentition to resist the strong lateral reaction forces acting on the dentition during occlusion and the closer packing of the maxillary crowns.

Replacement. Evidence from the maxilla and dentary of this species shows that there were in some instances two successional crowns beneath the functional crown. A rudimentary crown is seen at the base of a replacement series in the right maxilla of PIN 3386/7 (Fig. 6B,C), and a partial dentary (Fig. 22) also shows evidence of a second replacement crown. In both instances these crowns are found in the deepest part of the jaw, and it seems likely that the second replacement crown appears by virtue of the space available within the alveolar tissue; in the shallower parts of the jaws it is likely that the 'normal' single replacement crown will be found.

This report is of interest because it appears to show an intermediate stage in tooth replacement between the conventional iguanodontian pattern (single replacement crown) and the multiple replacement crowns seen in hadrosaurids, without the notable crown miniaturization, which is a feature of hadrosaurid teeth.

Axial skeleton

The only parts of the axial skeleton which were collected by the Soviet-Mongolia expeditions were the atlas neural arch, some broken cervical and dorsal vertebral fragments and an articulated series of caudal vertebrae.

Atlas neural arch. A pair of these are preserved in the collections associated with PIN 3386/8 (Fig. 23). These bones have a standard form seen in all ornithopod dinosaurs.
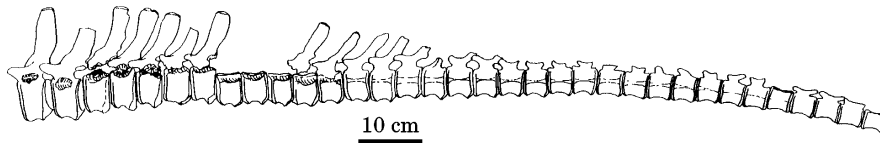
Figure 24. *A. kurzanovi* **sp. nov.** Caudal series of vertebrae, as preserved (PIN 3386/9).

The base is enlarged and attached via a cartilaginous pad to the atlas intercentrum, and the rostral edge contributed to the articulation with the occipital condyle. The arches curve over the neural canal and show a prominent rostral process (upon each of which sat a proatlas element), the arches approach each other in the midline but remained separated, and notched caudally where they articulated against the neural spine of the axis vertebra; beneath and lateral to this notch there are well marked postzygapophyses. The remainder of the neural arch consists of an oblique, blunt-ended transverse process.

Caudal vertebrae. An apparently articulated series of 34 caudal vertebrae (PIN 3389) were collected from Khuren Dukh (Fig. 24) and are representative of the majority of the tail of a relatively small individual; this is confirmed by the separation of neural arch from centrum in several examples and the absence of caudal ribs in the anterior members of the series.

The anterior caudals have a relatively deep amphiplatyan centrum, marked ventrally by prominent facets for the haemal arch (chevron bones). The caudal ribs are absent, but scars on the side of the neurocentral suture indicate their positions. The neural arch is low and arches across a relatively small neural canal. The anterior zygapophyses are long and finger-like, while the posterior are represented by small facets mounted on the base of the neural spine. The neural spine curves backwards, before rising vertically to a blunt apex and is about the same height as the centrum and neural arch combined. Succeeding vertebrae (numbered 33–29) show a progressive diminution of the height of the centrum and a slight decrease in the height of the neural spine (which takes on a more sloping shape). Between vertebrae 29 and 21 the caudal rib diminishes in size and finally disappears from the vertebra altogether. The vertebral centra become less high, and gradually take on a more hexagonal shape with the loss of the rib, and its replacement by a horizontal ridge on the side of the centrum, the posterior chevron facet also becomes much more prominent than the anterior one, and the neural spine become shorter and more inclined posteriorly. The remainder of the sequence shows the caudal becoming more angular-sided and shallower, with the neural arch declining in prominence as the neural spine disappears. The most distal members of the tail become more cylindrical and have in all probability lost the neural spine and the matching chevron bone. This general sequence of form change along the length of the tail is very consistent across most ornithopod dinosaurs.

Appendicular skeleton (forelimb)

The forelimb and shoulder girdle are well represented for this species, as is the pelvis, but the remainder of the hindlimb is rather sketchily represented.
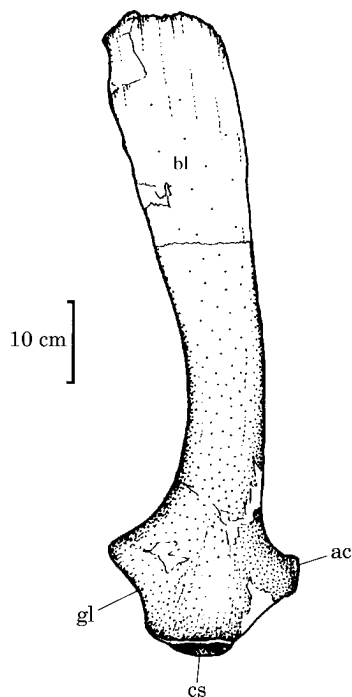
Figure 25. **A. kurzanovi sp. nov.** Scapula (left) in medial view (PIN 3388). Abbreviations: ac –
acromion process; bl – blade; cs – coracoid suture; gl – humeral glenoid. Length 79.5 cm.

Scapula. Represented by an almost complete left (PIN 3388 – Fig. 25) and a pair of
less perfectly preserved examples (PIN 3389) the blade is long, slender and curved
both medially to accommodate the curvature of the ribcage and along its leading
and trailing edges. The distal portion of the blade is laterally flat and the distal edge
thickened and rough for attachment of a presumed cartilaginous extrascapula.
Toward its proximal end the blade contracts rostrocaudally, and thickens transversely
before expanding again to produce the articular surface for the clavicle (cartilaginous),
coracoid and humeral glenoid. The rostral edge of the blade curves forward to
produce an acromion process which is supported externally by a buttress-like ridge
which curves distally before merging with the main scapular blade. Beneath the
acromion process the edge of the scapula is thickened and rugose and 'bi-facetted'
to where it is sutured to the coracoid. At the caudal end of the coracoid suture the
scapula is smoothly embayed for the humeral glenoid, which is supported by a
prominent and laterally everted shoulder of bone which forms the dorsal portion of
the glenoid. The external surface of the proximal end of the scapula is broadly
concave in the area between the acromial buttress and the everted shoulder above
the glenoid.

Coracoid. A left coracoid (PIN 3388) is very well preserved (Fig. 26A). It has the form
of a convexoconcave dish pierced by a foramen which is close to the junction
between the scapular suture and the humeral glenoid and is angled so that its medial
opening is along the edge of the coracoscapular suture. The scapular suture is
transversely expanded and rugose and has a marked angulation along its length
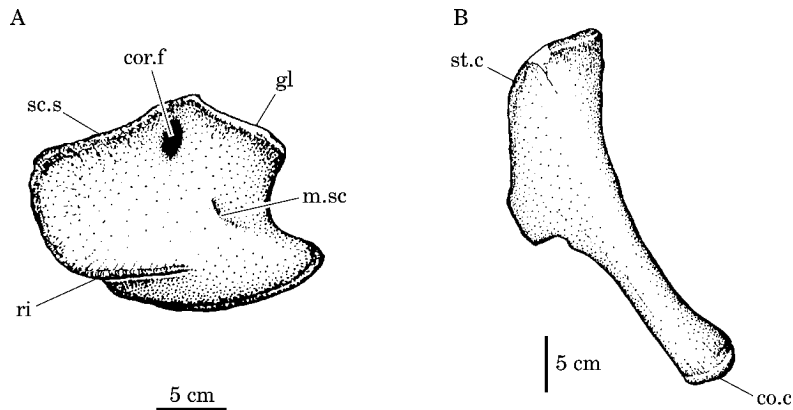
Figure 26. *A. kurzanovi* **sp. nov.** A, coracoid (left) in lateral view (PIN 3386/8). B, sternal bone in ventral view (PIN 3386/7). Abbreviations: cor.f – coracoid foramen; co.c – costal cartilage attachment; gl – humeral glenoid; m.sc – muscle scar; ri – ridge; sc.s – scapular suture; st.c – sternal cartilage attachment.

(which corresponds with the shape of the proximal end of the scapula). From the rostral end of the scapular suture the free edge of the coracoid follows a convex, curved course to the distal, hooked terminus; this edge is thickened and was presumably linked to the cartilaginous sternal sheet. From the distal point the caudal margin of the coracoid is embayed and expands transversely as it meets the thickened lip which forms the lower half of the humeral glenoid. The internal surface of the coracoid is dished and relatively smooth; the external surface is convex, and interrupted by a diagonal ridge (ri) which runs out and backward from the medial (free) edge.

Sternal. The sternal bones are typical of iguanodontians generally being 'hatchet-shaped'. As shown in Figure 2B the sternal (PIN 3388) has a broad medial, dorsoventrally flattened plate (thickening rostrally) which meets its opposite across the ventral median line; from this plate a caudolaterally directed (cross-sectionally round) process diverges and ends in a blunt, truncated tip, which presumably connected to the distal rib cartilages (co.c) of the anterior dorsal vertebrae. Similar sternals are found in *Iguanodon* (Norman, 1980, 1986), *Ouransaurus* (Taquet, 1976), *Probactrosaurus* (pers. obs.; Norman, in prep) and more generally in hadrosaurids (Lull & Wright, 1942).

Humerus. The humerus (Fig. 27) is well preserved and is a columnar bone with a sinusoidal curve. The proximal end is marked by a distinct articular head, which projects from the dorsal side and is flanked by 'shoulders' which also show a capping of articular cartilage. The lateral edge of the shaft descends vertically and develops into a thickened and anteriorly twisted deltopectoral crest (dpc), which extends to approximately half the length of the shaft, and accentuates the sinusoidal nature of the humerus, beneath the deltopectoral crest the shaft of the humerus narrows considerably before expanding again to form the distal condyles of the elbow joint. The medial edge of the humerus forms a more or less smooth concave curve as it descends to the distal condyle. The dorsal surface of the shaft is marked by a large depressed muscle scar (m.sc) which is positioned directly beneath the humeral head
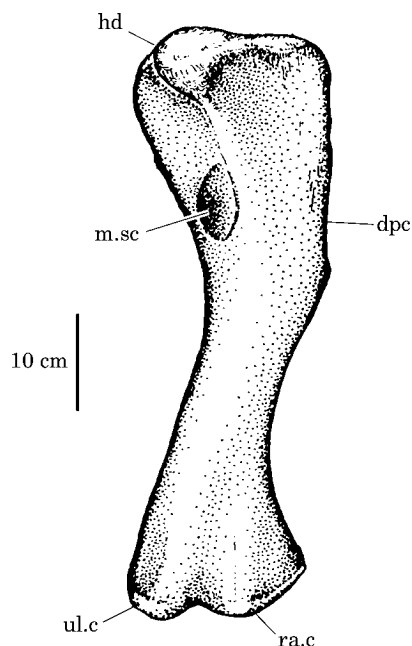
Figure 27. **A. kurzanovi sp. nov.** Humerus (right) in dorsal view (PIN 3386/8). Abbreviations: dpc – deltopectoral crest; hd – humeral head; m.sc – muscle scar; ra.c – radial condyle; ul.c – ulnar condyle. Length 59.5 cm.
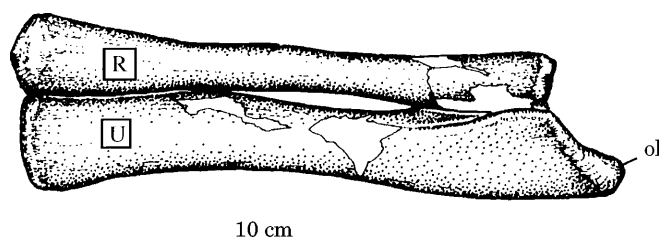

Figure 28. **A. kurzanovi sp. nov.** Radius and ulna (left) in lateral view. PIN 3386/8. Abbreviations: ol – olecranon.

and about a quarter of the way down the shaft. The long axis of the distal condyles is approximately in line with that head of the humerus and the lateral and medial condyles are separated by a modest intercondylar furrow. Just above the lateral condyle, on its ventral face, the surface of the shaft is depressed to accommodate the proximal end of the radius.

Radius. An apparently associated left radius and ulna (PIN 3386/8 – Fig. 28R) show that the radius is typical of that of iguanodontians generally. The proximal end is expanded and rounded in end view, with a 'flat' on the side which articulates against the ulna. The central portion of the shaft is narrower than the ends, and the distal end is expanded dorsoventrally and appears to have fitted obliquely against the distal end of the ulna (as described in *I. atherfieldensis*; Norman, 1986: fig. 49).

Ulna. The ulna is heavier and longer than the radius (Fig. 28U). Its proximal end is marked by the development of a knob-like olecranon process, distal to which the shaft of the bone is essentially triangular in section. The upper lateral portion distal to the olecranon provides a concavity in which articulates the proximal end of the radius, and there is a medial ridge, which runs for some distance down the shaft of the ulna and helped to secure the proximal end of the radius. The main shaft of the ulna contracts slightly, allowing for a shallow, but significant, gap between radius and ulna and therefore some limited ability for pronation/supination of the manus with respect to the upper arm. The distal end of the ulna is slightly dorsoventrally expanded.

The wrist and hand (Fig. 30) of this dinosaur show clear similarities to that which has been described in *Iguanodon* and *Ouranosaurus*. The first digit has an enlarged, probably divergent, spine-like ungual, the middle three digits form a compact unit which will allow for hyperextension of the hoof-like toes, and the fifth digit was probably long, flexible and opposable.

Carpus. Carpal elements have been preserved as separate elements in PIN 3389 (Fig. 29): these suggest that the carpal elements are robust and number at least seven, but, in this specimen which is of relatively large size, they are not coossified into two blocks as appears to have been the case in *Iguanodon* (Norman, 1980, 1986) and *Ouranosaurus* (Taquet, 1976, but illustrated proximodistally reversed). The individual carpals are illustrated and some attempt has been made to identify them by comparison with the carpals of *Iguanodon*, but these identifications are necessarily tentative.

Metacarpals. There is no evidence for a compressed and block-like metacarpal I capping the inner (dorsal) side of the carpus (despite the fact that one would be predicted, judged from the form of the ungual of digit I). Metacarpals II–V (Fig. 30) are well represented in the collections which include two more or less complete left manuses (PIN 3388 & 3386/9). *Metacarpal II* is slender and flattened laterally where it is appressed to MCII, its proximal end stands proud of the adjacent metacarpals and projected into a recess in the carpus as in *Iguanodon* (Norman, 1980). The distal end has a well-developed, oblique articular surface. *Metacarpal III* is the longest and most robust of the group the proximal and distal ends are expanded, and the shaft between but little contracted; the medial surface of the shaft is shaped for tight ligamentous attachment to MCII. The distal joint surface is well developed symmetrical and mildly trochlear. Laterally the shaft is rounded and bears scars for attachment to MCIV. *Metacarpal IV* is subsequent to MCIII in length and slightly less robust its proximal end is expanded, the shaft tapers and diverges slightly from MCIII when the two bones are articulated in life position. The distal articular surface is rounded, quite small and not trochlear. *Metacarpal V* is short, circular in section and rather block-like when compared to the previous examples. The proximal end is expanded and has a slightly concave proximal surface, its distal articular surface is similarly rounded and convex. Both of these articular joints (roughly ball-and-socket in character) suggest that the movement of this digit was not strongly constrained as may have been the case for digits II and III in particular.

Phalanges. A digit formula: 1:3:3:3:4 is most probable for this species (Fig. 30 shows those currently known). *Digit I.* No disc-like first phalanx was discovered beneath
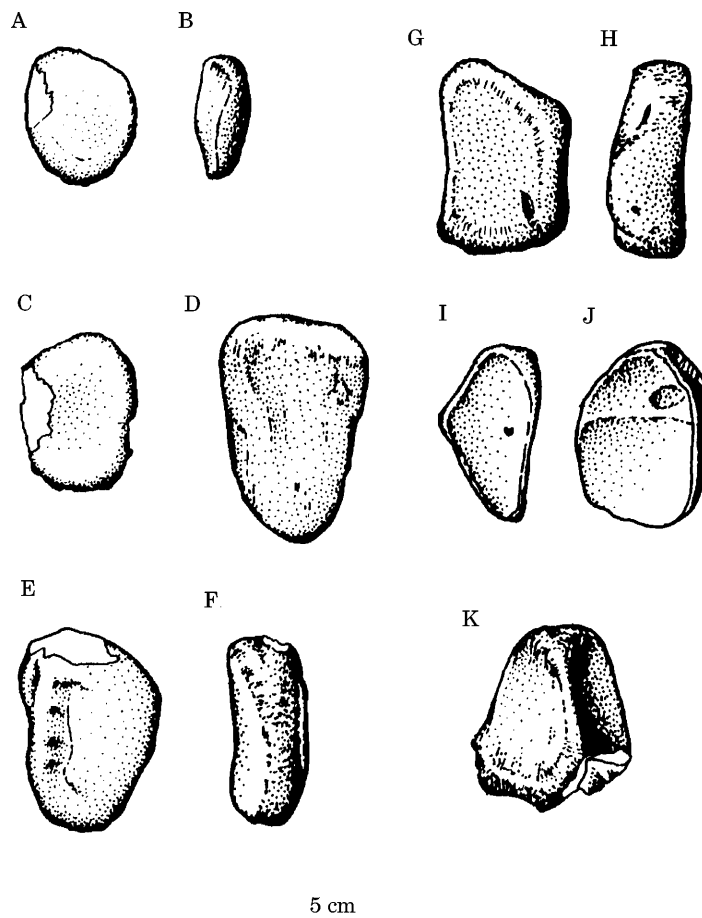
Figure 29. *A. kurzanovi* **sp. nov.** Isolated carpal bones (PIN 3386/9) as preserved. A & B, discoid (distal carpal 2?); C & D, discoid (distal carpal 3); D, ulnare; E & F, intermedium; G & H, radiale; I & J, distal carpal 5; K, distal carpal 4.

the ungual phalanx, as observed in *I. bernissartensis* (Norman, 1980), although it is possible that one of the small discoid elements associated with the other carpals (Fig. 29) is a first phalanx. The ungual is relatively large (slightly larger than the ungual of digit II) laterally compressed, but is straight and tapers to a blunt point (Figs 30, 31A–C); it also has a pair of quite well marked ungual grooves on either side of the (presumed) dorsal surface. This ungual bears a resemblance to the rather more conical pollex spike seen in *Iguanodon* (Norman, 1980, 1986) and reported in *Ouranosaurus* (Taquet, 1976). A smaller example of an apparently articulated right manus and forearm (PIN 3388, display mounted) shows a somewhat more conical shape, so the ungual may flatten during ontogeny. *Digit II.* There are three phalanges. The first phalanx is more slender and elongate than any of the others of the hand; its proximal end is expanded dorsoventrally and a little transversely, and the articular surface is concave dorsoventrally. The shaft of this phalanx is a little contracted and notably flattened laterally, where it lies adjacent to the distal portion of MCIII: the distal articular surface is characteristically twisted medially and has a shallow, but
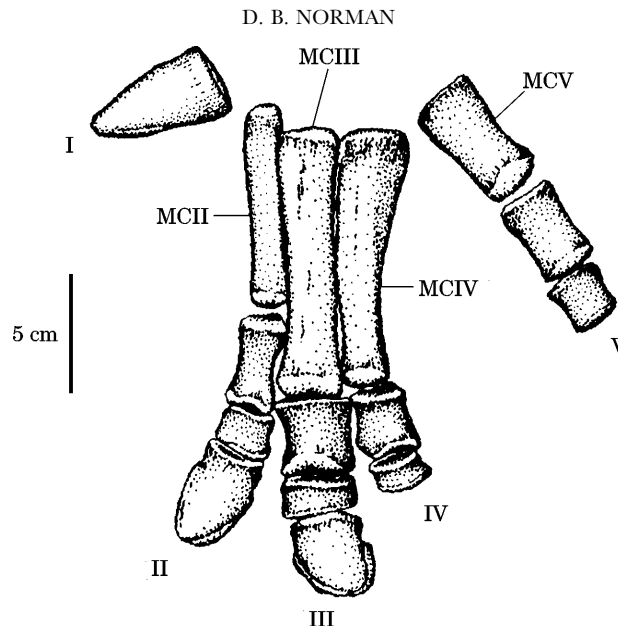
Figure 30. *A. kurzanovi* **sp. nov.** Manus (left) in dorsal view. Based on PIN 3389.
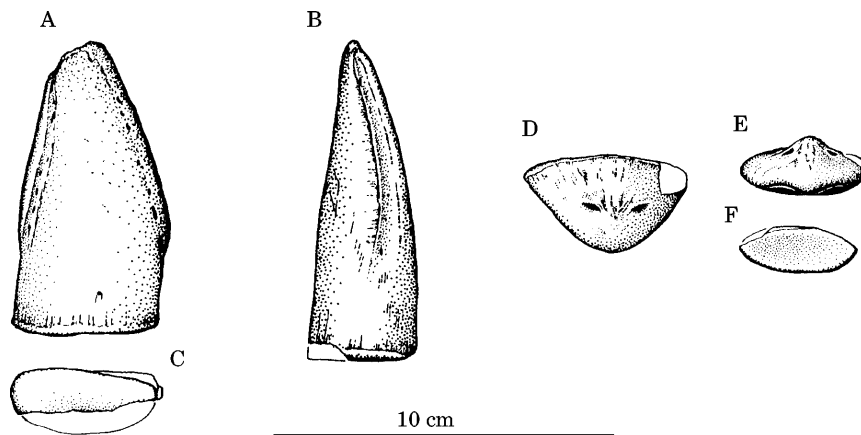

Figure 31. *A. kurzanovi* **sp. nov.** Phalanges of the manus. A–C, pollex ungual (PIN 3387), length 8.6 cm; D-F, tentative phalanx 3 of digit IV of the manus (PIN 3386/8), length 3 cm.

oblique trochlear surface. The second phalanx is shorter and more block-like, but also shows the asymmetry of its proximal and distal surfaces which allows this digit to diverge markedly from digit III. The ungual phalanx is large, flattened (generally hoof-like) and somewhat twisted medially along its length and has well marked claw grooves, particularly so along its lateral margin. *Digit III* has three phalanges. The first is large, symmetrical and block-shaped with a dorsoventrally concave proximal articular surface which is very slightly trochlear; the distal articular surface is more strongly trochlear. The second phalanx is very short and asymmetrical allowing the digit to diverge from digit II. The ungual phalanx is relatively shorter and broader

than that of digit II and is twisted laterally (away from) with respect to the latter digit; the claw grooves are well marked on medial and lateral edges of the ungual. *Digit IV* comprises at least two phalanges, and possibly a third. The first is similar in shape, though smaller, to the first phalanx of digit III, but its proximal articular surface is less clearly defined (suggesting less constraint on its movement on MCIV) and the distal surface is asymmetrical allowing the second phalanx to diverge from digit III. The second phalanx is smaller and more dorsoventrally flattened with slightly everted articular ends, the surfaces of which are dorsoventrally concave proximally and convex distally. A third phalanx of very similar form can be placed on the second (giving a digital form similar to that shown in *I. atherfieldensis* – Norman, 1986: figs 50, 51); however another element (Fig. 31D–F) associated with the collections labelled PIN 3386/8 has a structure which is suggestive of its having been the true ungual of digit IV. Norman (1980: figs 60, 61) was unable to demonstrate the presence of a terminal ungual on this digit in *I. bernissartensis*, even though the distal surface, of the second phalanx of digit IV appeared to be articular. This new element is triangular in plan view (Fig. 31D), its broad and dorsoventrally flattened base bearing a concave articular surface. The sides distal to the articular surface converge on a smoothly rounded tip which is slightly decurved, giving a convexity to the dorsal surface and a concavity to the ventral (flexor) surface. The dorsal surface is marked by the presence of two 'eye-like' depressions which are most probably abbreviated versions of the claw grooves in this short and very hoof-like ungual. *Digit V* comprises at least three phalanges. Unfortunately the disassociation of the known elements renders a complete formula for this digit impossible. The first phalanx is subcylindrical (slightly flattened on its ?flexor surface) with a concave proximal end and a convex distal surface the second and third phalanges would appear to be smaller versions of the first and more obviously dorsoventrally flattened. The third phalanx has a distal surface with evidence of a synovial joint so it would seem reasonable to presume that there was a fourth phalanx as demonstrated in *I. bernissartensis* (Norman, 1980: fig. 60).

Appendicular skeleton (hindlimb)

Elements of the hindlimb are neither well represented, nor very well preserved in the collections of the Palaeontology Institute Nauk, Moscow. Only a very general description will be provided.

Ilium. An isolated almost complete and undisorted small ilium (Fig. 32) is preserved in the collection from Khuren Dukh. It is unregistered, but was collected from the same localities which yielded the holotype and paratype specimens of this species (S.M. Kurzanov, pers. comm.). The ilium is 215 mm long, but is missing the rostral end of the anterior process (ap). In lateral view the dorsal edge has a notably sinuous line, with a quite strongly arched anterior process while the main body of the blade is slightly concave. The anterior process is particularly prominent and curves laterally along its length (swinging away from the posterior ribs) and is strengthened medially by a prominent ridge which is confluent with the ledge which forms above the sutural area for the sacral yoke. The dorsal margin of the ilium is smoothly rounded over the anterior process, but above the acetabulum develops a marked lateral lip (at), which develops into an everted facet above and behind the ischiadic peduncle
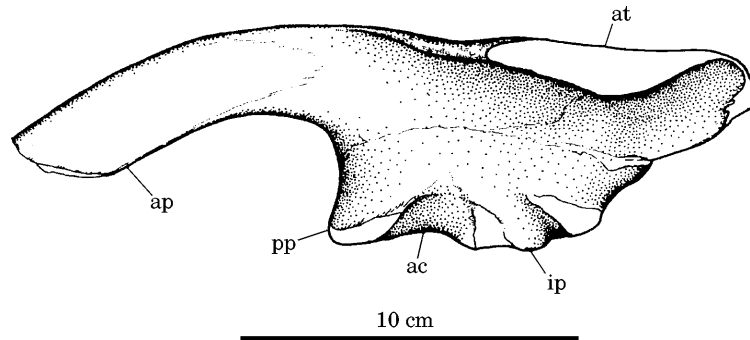
Figure 32. *A. kurzanovi* **sp. nov.** Ilium (left) in lateral view. Unregistered specimen of a juvenile individual associated with this species in collections from Khuren Dukh. 22 cm long. Abbreviations: ac – acetabular margin; ap – anterior process; at – antitrochanter; ip – ischiadic peduncle; pp – pubic peduncle.

(ip). The posterior part of the iliac blade is relatively short and curves downward to meet the ischiadic peduncle without the development of a significant 'brevis shelf.' The ischiadic peduncle is swollen laterally, but adjacent to the posterior part of the acetabulum (ac) has a bevelled surface. The acetabular margin is a shallow concavity, and the pubic peduncle (pp) is robust, with a triangular base with a deeply overhanging acetabular crest; only the base of the pubic peduncle is preserved.

In general the sinuous profile of the dorsal margin, prominent anterior process and everted (antitrochanter-like) posterior dorsal blade is reminiscent of that of hadrosaurids (Weishampel & Horner, 1990). In ornithopods such as *Camptosaurus* (Gilmore, 1909) *Iguanodon* (Norman, 1986) and *Ouranosaurus* (Taquet, 1976) and *Probactrosaurus* (pers. observ.; Norman in prep.) undistorted ilia have a less sinuous dorsal margin and a deeper, flatter posterior blade with a less strongly everted posterior dorsal margin.

Pubis. Two partial right pubes are preserved (PIN 3388, 3386/8). These (Fig. 33) are of typical iguanodontian form. The iliac peduncle is a triangular boss, beneath which is found an oblique concave area which forms part of the anterior margin of the acetabulum; this curves posteriorly, and diminishes in size, terminating in a small prong of bone which contacts the ischium along the ventral edge of the acetabulum. Beneath this 'prong' there is a notch which appears to represent the remnant of the obturator foramen, which was completed by contact with the ischium. Distal to this area the pubis has the form of a tapering rod, which lies parallel to the ischium but does not reach the end of the latter. The rostral blade of the pubis is deep and laterally compressed, the blade expands distally and somewhat ventrally deflected. The rostral blade strongly resembles that of *Iguanodon bernissartensis* (Norman, 1980) rather than the deeper and more flared type seen in *I. atherfieldensis* (Norman, 1986) and *Ouranosaurus* (Taquet, 1976).

Ischium. The only known ischium (PIN 3388 – Fig. 34) is from the left side, it is missing the articular portions of the proximal end and its distal end. The expansion of the proximal end indicates a perfectly normal relationship with the ilium and pubis in the acetabulum. Just distal to the pubic peduncle the ventral margin of the ischium is embayed and followed by a finger-like compressed flap of bone (obturator
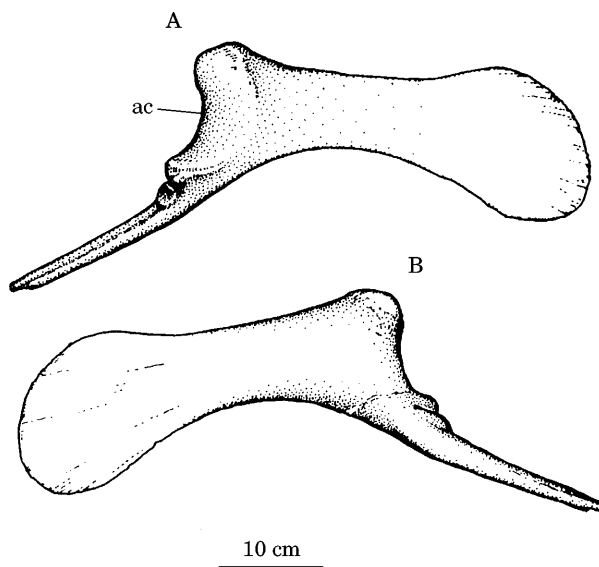
Figure 33. *A. kurzanovi* **sp. nov.** Pubis (right) in lateral (A) and medial (B) view. PIN 3386/8. Length 58.6 cm. Abbreviation: ac – acetabular margin.
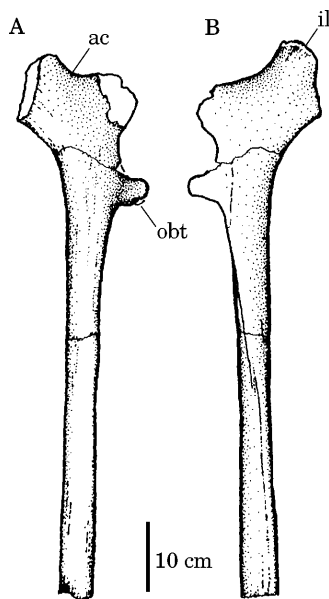
Figure 34. *A. kurzanovi* **sp. nov.** Ischium (right) in lateral (A) and medial (B) views. PIN 3388. Length 82.5 cm. Abbreviations: ac – acetabular margin; il – iliac peduncle; obt – obturator process.

process) which is set off on the medial side of the shaft, and offered some mechanical support to the thin pubic bone. The distal edge of the obturator process continues into the shaft as a prominent ridge, which curves around the axis of the shaft until it lies along the caudal margin; this gives the ischium a twisted appearance. The

ischium shows no sign of curvature along its length (normal in various medium-to-large ornithopods: *I. bernissartensis*, *Probactrosaurus gobiensis*, *Ouranosaurus nigeriensis*, *Camptosaurus dispar*) and there is no evidence either for or against an enlargement of the distal end. In the straightness, axial twist and parallel-sided nature of its ischial shaft *A. kurzanovi* resembles that of *I. atherfieldensis* (pers. observ.), Hadrosaurine ornithopods show an ischial shaft that tapers distally; and in hypsilophodontids the ischium tends to deepen and become laterally compressed. The distal end of the ischium is very slightly booted in *I. atherfieldensis* (pers. observ.).

Femur. A partial left femur (PIN 3388) which lacks much of both proximal and distal ends is preserved in the collections. The shaft appears to be curved (unlike the straight form seen in hadrosaurids) and the base of prominent lesser trochanter is present.

Tibia. An associated left tibia (PIN 3388) is a little better preserved and is typically ornithopod. The proximal end is expanded rostrocaudally and the cnemial crest is prominent and supported by a ridge which runs up the front of the tibial shaft. The distal end shows the typically offset inner and outer condyles for attachment of the astragalus (medially) and the calcaneum, and fibula laterally and rostrally respectively.

Fibula. An isolated complete fibula (not associated with the two previous bones—it is not commensurate) (PIN 3388) is again typically ornithopod, showing the broad and laterally compressed proximal end which tapers to the small and slightly everted distal termination; this latter rests on a facet on the calcaneum, and has a caudally flattened surface for attachment to the rostrolateral surface of the tibia.

Tarsus. No tarsal bones have been identified in the collections.

Metatarsals. Metatarsals II–IV are preserved (PIN 3388) and are identical to those of ornithopods generally. They differ in no significant respect from those described in *Iguanodon* (Norman, 1980, 1986). Metatarsals I and V are not preserved and their absence was probably real, but cannot be confirmed.

Digits. The phalangeal formula was probably: 0:3:4:5:0. *Digit II* (PIN 3388) comprises three phalanges which differ not at all from that described in *I. atherfieldensis* (Norman, 1986; figs 63, 64). *Digit III* appears to be complete in PIN 3391 and again differs in no significant respects from those of other ornithopods. *Digit IV*. All but one of the phalanges of this digit are preserved (PIN 3388).

<div align="center">DISCUSSION</div>

<div align="center">*The systematic position of* A. kurzanovi</div>

The anatomy of *A. kurzanovi* is broadly comparable to that of the ornithopod *Iguanodon* (Norman, 1980, 1986) ranging as it does from the general framework formed by the majority of the cranial bones, to many aspects of the postcranial skeleton (perhaps most notably, the form of the manus). However, systematic relationships between ornithopods of this general type and the younger hadrosaurids have been the subject of debate in recent years (Norman, 1984, 1986, 1990, in prep.; Norman & Weishampel, 1990; Sereno, 1986; Sues & Norman, 1990; Weishampel &

Heinrich, 1992; Weishampel, Norman & Grigorescu, 1993). There is not space to discuss these contributions in detail, but an outline of the systematic position of *Altirhinus kurzanovi* relative to other well-known euornithopods is necessary and will follow the summary of anatomical characters which have been used for systematic analyses. A data matrix and full systematic analysis will follow (Norman, in prep).

The systematic revision of Sereno (1986) was critically reviewed, with respect to ornithopods, by Norman (1990); since that time new arrays of characters, or modifications to character-lists associated with ornithopods, have been offered by Forster (1990), Weishampel & Heinrich (1992). Weishampel, Norman & Grigorescu (1993), Coria & Salgado (1996) and Winkler, Murry & Jacobs (1997). A revised list of characters supporting the provisional cladogram (Fig. 35) is provided below. A synthesis of the lists of characters offered more recently by the authors above is presented in Appendix 1 and a classification based on the character lists in this section is to be found in Appendix 2. This subject will be covered in more depth (Norman, in prep.).

Overview. Altirhinus, although it bears some superficial resemblance to hadrosaurid dinosaurs (compare Figs 3, 4B) is here regarded as a derived member of the family Iguanodontidae (Fig. 35). Detailed similarities exist between *Iguanodon* spp., *Ouranosaurus* and the new species described here. Within the clade Dryomorpha extensive remodelling of the side of the face can be seen to be associated with the evolution of a powerful, yet stable pleurokinetic system and the teeth begin to form more stable arrangements, partly at least reflected in the moulding of the alveoli to the form of the emerging roots and crowns. Within iguanodontians as a whole the teeth begin to form integrated batteries (magazines) with a unified occlusal blade. This requires the teeth to be firmly, and consistently positioned in the jaws. It is not surprising to see the strong similarity that exists within the iguanodontids in the form of the dentary and maxillary teeth; their shapes interlock to form a partially self-supporting magazine. Associated with the flexure that occurs along the premaxilla-maxilla, the lacrimal is a key element forming a continuation of the premaxilla-maxilla hinge across the front margin of the orbit. The prefrontal typically has an overlapping, stepped suture with the lacrimal and the palpebral is removed from the lacrimal-prefrontal junction; in addition the lacrimal articulates very characteristically with the maxilla through a thumb-like process of the maxilla which fits against the medial wall of the lacrimal. The jugal also has a very distinctive tongue-in-groove sutural arrangement with the maxilla and ball-and-socket joint with the ectopterygoid, and this is again linked to provision of mobility with stability across the zygomatic arch. This functionally related complex associated with pleurokinesis is quite distinct from the path taken by hadrosaurs. The other most distinct feature of iguanodontids lies in the form of the manus, which is clearly highly specialized for a combination of weight-support (converging upon pedal morphology), prehension (hyperphalangy of digit V) and defence (the enormously enlarged pollex ungual); this has its origins in the facultatively bipedal camptosaurs of the Late Jurassic, which had relatively short and broad, but weight-supporting manuses.

Apomorphic traits seen in *Altirhinus* (expanded external nares and elevated nasals, diastema, ventral offset of the beak, increase in replacement teeth in maxillary and dental batteries) and [apparent] reduction in the co-ossification of the carpus are seen as convergent with the later hadrosaurids, rather than synapomorphies with the latter. As will be argued below, the changes in jaw morphology and nasal
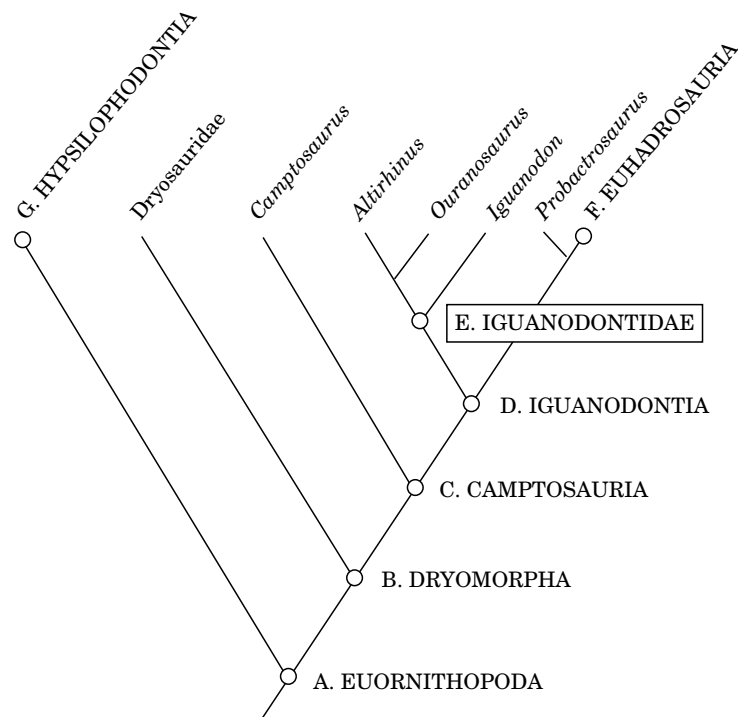
Figure 35. A cladogram of euornithopods supported by the characters listed below.

A. Euornithopoda (*sensu* Weishampel & Heinrich, 1992)
(1) Antorbital fenestra smaller in area than the antorbital fossa which it overlies. (2) Sinuous lower margin to the jugal arch. (3) Space separating the lower edge of the quadratojugal from the lateral margin of the jaw articulation. (4) Pleurokinetic hinge (lateral rotation of the cheek developed). (5) Anterior process of the pubis comparable in length to (or exceeds in length) the anterior process of the ilium. (6) Discrete, finger-shaped obturator process on the medioventral edge of the shaft of the ischium. (7) Shallow anterior intercondylar groove on distal end of femur. (8) ?The angle between anterior and posterior pubic ram <100°.

Tenontosauras as an hypsilophodontian
   The winnowed list of characters below has been used to support the inclusion of *Tenontosaurus* as the basal member of a clade including Dryomorpha+Camptosauria+Iguanodontia. This latter is the position supported by the majority of current workers in the field: Sereno (1986), Forster (1990), Coria & Salgado (1996) and Winkler, Murry & Jacobs (1997). However, see discussion in Appendix 1.
(1) Loss of premaxillary teeth (status: convergent: invalidated by *T. dossi* Winkler, Murry & Jacobs, 1997). (2) Oral margin of premaxilla everted and thickened (status: considered to be a size-related convergence within Euornithopoda). (3) Enlargement of external naris [to at least 20% of base skull length] (status: size-related convergence within Euornithopoda). (4) Circular or oval antorbital fenestra (status: widespread within Euornithopoda). (5) Denticulations on the oral margin of the predentary (status: considered size-related convergence within Euornithopoda). (6) Manus digit III has lost one phalanx (status: *consistent*, but rarely preserved in basal forms). (7) Humerus length equal to, or longer than, scapula (status: variable—probably locomotor-related proportions within Euornithopoda).

B. Dryomorpha (Dryosaurids+*Camptosaurus*+Iguanodontians)
(1) Paired ventrolateral processes on the predentary. (2) Lateral and medial rostral processes on the maxilla separated by an oblique channel for the caudolateral premaxillary process. (3) Teeth are also supported by the bone of the alveolus, which is moulded around each root and crown. (4) Development of specialized premaxilla–maxilla hinge (linked to two characters above) as part of the functional evolution of pleurokinesis. (5) Channel-like anterior intercondylar groove on femur. (6) Prominent articular head developed on the posterior side of the proximal end of the humerus. (7) Quadratojugal reduced to a small element separating the jugal and quadrate. (8) Quadrate with notch-like embayment in its lateral wing which forms the caudal margin of the quadrate (paraquadratic) foramen. (9) Close-packed teeth in the maxillary and dentary dentitions. (10) Width across the orbital region of the skull roof >the width across the occipital region. (11) Ischial shaft arched ventrally along its length. (12) Development of a small distal boot with a flat medial

surface on the ischium. (13) Obturator process positioned proximally on the shaft of the ischium (within 25% of the total length of the ischium).

C. Camptosauria (*Camptosaurus* + Iguanodontidae + *Probactrosaurus* + basal hadrosaurs)
(1) Prominent primary ridge on the labial surface of maxillary crowns. (2) Inrolling of the enamel on the lower half of the mesial edge of the crown (in lingual view) to form an oblique cingulum. (3) Maxillary crowns narrower and more lanceolate (when viewed labially) than dentary crowns (when viewed lingually). (4) Heavy ossification of the carpus. Metacarpal 1 shortened and incorporated obliquely into the carpus: consequent partial fusion of modified carpus into two blocks: (mc 1 + radiale + intermedium + adjacent distal carpals) and (ulnare + distal carpals 4 & 5). These two blocks articulate by means of broad concave facets with the distal ends of the radius and ulna. (5) Short, divergent digit 1 of manus (phalanx 1 block-shaped) and 'subconical manus digit 1 ungual' (Sereno, 1986, reporting the condition in *Camptosaurus*). (6) Digits II & III are dominant and end in dorsoventrally flattened unguals. (7) The digits display an ability to hyperextend and well-defined articular relationships, which indicate their use in weight support/locomotion. (8) Manus digit III has lost one phalanx (status: unknown in dryosaurids, but this feature is also recognized in *Tenontosaurus* and is either independently acquired in a weight-supporting manus, or supports the clade Iguanodontia *sensu* Sereno, 1986).

D. Iguanodontia (Iguanodontidae + *Probactrosaurus* + Euhadrosauria)
(1) Conical, pointed and strongly divergent ungual of digit I of manus. (2) Elongate and ligamentously bound ('bundled') metacarpals II–IV. (3) Metacarpals IV subequal in length to mc III and both are considerably longer than mc II. (4) Metacarpal II and its first phalanx are approximately equal in length to mc III. (5) Metacarpal II positioned proximal to mcs III & IV and projects into a recess on the distal surface of the carpus. (6) Flattened and distally rounded ungual phalanges on digits II & III. (7) Caudolateral process on the sternal bone. (8) Dorsoventrally expanded distal end of anterior pubic process. (9) Posterior pubic process shorter than ischium. (10) Pedal ungual phalanges of digits II–IV flattened and broad. (11) Lattice-like ossified tendons flank the dorsal, sacral and proximal caudal neural spines.

E. Iguanodontidae (*Iguanodon* spp., *Ouranosaurus*, *Altirhinus*)
(1) Dentary teeth broad and asymmetrical with a distally off-set but relatively low, primarily ridge, separated by a shallow trough from a parallel secondary ridge which meets the apex of the crown at a mesial 'shoulder'. A variable number of parallel tertiary ridges run down the crown surface taking their origin (usually) from the bases of the marginal denticles. (2) Dentary and maxillary teeth interlock through the shape of their adjacent crowns. Little evidence of cementum locking the crowns and roots of teeth into a battery (magazine). (3) Lacrimal is locked on to the finger-like process at the apex of the maxilla and is extensively overlain by the premaxilla and prefrontal. (4) Palpebral 1 (supraorbital) has a large base-plate which articulates loosely against the prefrontal alone. (5) Palpebral curves upward and backward following the line of the orbital margin (forming the equivalent of a prominent brow ridge) terminating near the postorbital and in some instances followed by a loose accessory palpebral (rarely preserved). (6) The jugo–maxillary suture is complex consisting of a finger-like caudolateral process of the maxilla which slots into a large recess on the medioventral surface of the jugal; the two meet in an externally sinuous sutural line. (7) The ungual phalanx of manus digit 1 is hypertrophied as a long, medially directed, robust conical spike, which articulated against its metacarpal via a flattened, disc-like 1st phalanx. The ungual may be subequal to, or exceed, the length of digit II of the manus. (8) Manus digit V shows evidence of hyperphalangy and diverges strongly from digits II–IV. (9) The carpal bones and metacarpal 1 are fused indistinguishably into two blocks of bone.

F. Euhadrosauria (Weishampel, Norman & Grigorescu, 1993)
(1) Miniaturization of maxillary crowns. (2) Cemented magazines of teeth. (3) Dentary alveoli form parallel-sided vertical furrows. (4) Localization of enamel to just the labial and lingual surfaces of the crowns of maxillary and dentary crowns respectively. (5) Near symmetry of lingual and labial aspects of dentary and maxillary crowns respectively. (6) Closure of mandibular and surangular fenestrae. (7) Complete loss of digit 1 of manus. (8) Reduction of carpus to two small elements. (9) Straight femoral shaft distal to fourth trochanter. (10) Anterior intercondylar groove on femur completely roofed over.

G. Hysilophodontia
(1) Maxillary teeth have the labial surface marked by low vertical striae and dentary teeth which have the lingual surface characterized by a sharp and prominent, approximately centrally positioned primary ridge. (2) Quadratojugal large and fenestrate. (3) Quadrate lateral wing has a large, shallow embayment for attachment of the quadratojugal. (4) Laterally compressed shaft to ischium, and which is straight and caudally directed (rather than curved ventrally). (5) Obturator process positioned near mid-length of ischium (between 30% and 50%). (6) Hypaxial ossified tendons.

passages can be linked to changing feeding style, which itself may be associated with either climatically induced floral change (increasingly abrasive, xerically adapted, plants) or niche partitioning among relatively abundant ornithopod herbivores. Other changes in cranial morphology (lengthening and broadening of the muzzle), and the elevation of the neural spines (possibly associated with support of an adipose heat shield) seen in *Ouranosaurus* can be interpreted similarly, and suggest a period of rapid diversification within iguanodontids in the mid-Cretaceous which, in this interpretation, presaged the rise of hadrosaurs in the early Late Cretaceous.

These iguanodontids however, despite the analysis of Sereno (1986), do not appear to be forms from which hadrosaurs were serially derived. Weishampel, Norman & Grigorescu (1993) demonstrate basal hadrosaur features in the relatively conservative, but paradoxically Late Cretaceous, ornithopod *Telmatosaurus*; and, perhaps more appropriately, similarly conservative features in cranial and postcranial anatomy are found in the enigmatic early Late Cretaceous ornithopod *Probactrosaurus* and *Gilmoreosaurus* (Norman, in prep.) and *Bactrosaurus* (Godefroit *et al.*, in press). The curious amalgam of characters in forms within the time interval (Barremian–Cenomanian) is suggestive of a mosaic acquisition of hadrosaur-like anatomy within several lineages of iguanodontian ornithopod (a process which might be termed 'hadrosaurization') driven, in part at least, by interrelated environmental, ecological and functionally driven factors. The alternative strategy exemplified by Sereno (1986) is to invoke parsimony and reduce these taxa to a step-wise series of character acquisitions along an Hennigian comb. This approach is beguiling in both its simplicity and logic, but may well not take account of trends within lineages and masks (as I believe it does) forms which exhibit convergence, of which *Tenontosaurus* and *Ouranosaurus* seem to be classic examples.

This approach does not conform to the reductionism implicit in pure cladistic systematics. Palaeobiological research programmes can also investigate details within a pattern of the history of life, and examine these assortments of bones as animals that had structures, functions and ecological interactions to contend with, not to mention their positions in a probably complex evolutionary history.

Late Early Cretaceous diversity of large ornithopod dinosaurs

The anatomy of *Altirhinus kurzanovi* adds to the diversity of medium-to-large (6–11 m long) sized ornithopods during mid-Cretaceous times. The diversity is represented by:

Iguanodon spp. By far the best known and most widespread form associated with the late Early Cretaceous (Barremian/Aptian) has been *Iguanodon*, which appears to have had a relatively conservative morphology (particularly of the skull). This genus has been reported from the Barremian of N. America (Weishampel & Bjork, 1989), the Barremian/Aptian of Europe (Norman, 1980, 1986, 1987a,b) and the Aptian of Asia (Rozhdestvensky, 1952; Norman, 1996).

Ouranosaurus nigeriensis and an unnamed species (Chabli & Norman, in prep.). Restricted so far to the Aptian of Africa, this ornithopod shows many similarities to *Iguanodon* in terms of the detailed anatomy of its skull and postcranial skeleton (Taquet, 1976). However, it also shows interestingly distinctive development of a longer and broader muzzle, with elevated nasal bosses which mimic those seen in

some later hadrosaurids. Postcranially its skeleton is conservative compared to that of *Iguanodon*, except for the pelvis and development of extremely elongate neural spines along the dorsal and anterior caudal series of vertebrae.

Tenontosaurus tilletti and *T. dossi*. From the Albian of North America, this form has been variously regarded as a morphologically oversized, derived hypsilophodontid (Dodson, 1980; Norman, 1984 and this account); or as a basal iguanodontian (*sensu* Sereno, 1986; Sues & Norman, 1990; Forster, 1990; Weishampel & Heinrich, 1992; Winkler, Murray & Jacobs, 1997). The cranial (Ostrom, 1970, Winkler, Murry & Jacobs, 1997)) and postcranial anatomy (Forster, 1990) of this taxon is very distinctive (and somewhat variable, see Winkler, Murry & Jacobs, 1997), and clearly sets it apart from *Altirhinus* (Appendix 2).

Muttaburrasaurus langdoni. A partial skeleton from the Albian of Queensland, Australia, this form is of large size (*c.* 10 m), and has been allied to the Iguanodontidae (Bartholomai & Molnar, 1981). The anatomy of this dinosaur is very interesting, and not consistent with that of a typical iguanodontid. There is a prominent nasal expansion, which might also show a circumnarial depression (similar to the condition seen in some hadrosaurine hadrosaurids); the maxillary dentition resembles that of more derived hypsilophodontids such as *Rhabdodon* (Norman & Weishampel, in prep.; Weishampel, Grigorescu & Norman, 1991) and the hypsilophodontian (or basal iguanodontian *sensu* Sereno) *Tenontosaurus* (Ostrom, 1970). The remainder of the postcranial skeleton, though imperfect, resembles that of hypsilophodontids (cf. Galton, 1974a,b) and *Tenontosaurus* (Forster, 1990). New material of this taxon has now been discovered (Bartholomai, pers. comm.) which, it is hoped, will help to clarify many aspects of both its anatomy and relationships.

The two new species of early Late Cretaceous ornithopod are shortly to be described (J. Kirkland, pers. comm., 1997; J. J. Head, in prep.) which may also add to this pattern of diversification.

Palaeobiogeography, dispersal and evolution of ornithopods in the mid-Cretaceous

Variable Mesozoic land geography had a large rôle to play in the distribution and evolution of dinosaurs through isolation (vicariance) and dispersal. Greater resolution of coastlines during this period of time is starting to make analyses of this type possible (Smith, Smith & Funnell, 1994). The period of time of greatest interest with respect to the evolution of large ornithopod dinosaurs is without doubt the Early Cretaceous. During Late Jurassic and Early Cretaceous times (Berriasian–Valanginian 138 Ma) western Europe and the entire North American landmass were fully linked permitting the spread of early iguanodontids (camptosaurs and iguanodonts) and hypsilophodontids; this link was cut during the subsequent Hauterivian (130 Ma) and was never re-established. It is not therefore particularly surprising to find that there are records of Lower Cretaceous *Iguanodon* spp. in North America (Galton & Jensen, 1975), but that by the Albian a distinctive fauna, dominated (cf. Forster, 1990) by the aberrant, large-bodied hypsilophodontian *Tenontosaurus*. At an equivalent time in western Europe the fauna was by contrast dominated by two species of *Iguanodon*: *I. atherfieldensis* and *I. bernissartensis* (Norman, 1980, 1986, 1987a,b). The tentative conclusion would appear to be that the common stock of

Euramerican ornithopods were segregated in mid-Early Cretaceous times and diverged taxonomically (and presumably ecologically) following isolation.

By contrast, western Europe, which had been isolated from the Asia land area by the Turgai Sea (Milner & Norman, 1984) since the Callovian (160 Ma) developed a dispersal route through to Asia during the Aptian (120 Ma – Fig. 2). Mongolian discoveries (Rozhdestvensky, 1952) tentatively dated at Barremian/Aptian (Norman, 1996) are strongly suggestive of dispersal of at least *Iguanodon* cf. *bernissartensis*. In addition a high latitude link between eastern Asia and North America may have allowed full Northern Hemisphere dispersal of this dinosaur species. The ornithopod identified as *Iguanodon lakotaensis* (Weishampel & Bjork, 1989) from the Aptian Lakota Formation of South Dakota is large and, from what has been described, generically and specifically indistinguishable from *I. bernissartensis*. A contemporary geographic link and consequent simple dispersal model would therefore explain the records of *Iguanodon* across the entire Northern Hemisphere.

The connection between Asia and North America from Europe proved transient and was apparently broken in the Albian (105 Ma), never to be re-established in the remainder of the Cretaceous. Isolated populations of iguanodontids persisted, but again it is perhaps not surprising to find increased generic and specific diversity in subsequent times. The closely related but distinct form *Altirhinus* is clearly suggestive of diversification from an ancestral population of *Iguanodon* spp., during Albian times. The appearance of basal hadrosaur-like ornithopods in Cenomanian deposits in Asia (Norman, in prep.) and North America (Head, 1996, and pers. comm.; Kirkland, pers. comm.) may thus be a product of isolation and diversification within ancestral populations of iguanodontids across the North American and Asia landmasses in the early Stages of the Late Cretaceous (Cenomanian–Coniacian).

Southern Hemisphere problematica. The discovery of the Aptian *Ouranosaurus* (Taquet, 1976, and a contemporary robust species, Chabli & Norman, in prep.) in Niger, and its positing as a sister-taxon to the Hadrosauridae (Sereno, 1986) is challenging. Despite the absence of clear palaeogeographic links during either the Late Jurassic or Early Cretaceous, it is evident that the dinosaur faunas of Africa and the Northern Hemisphere were in some contact (Galton & Jensen, 1975, 1979). It is thus possible that populations of iguanodontid dinosaurs were able to invade Africa in the Early Cretaceous and were able to evolve in relative isolation. *Ouranosaurus* appears to have converged anatomically with hadrosaurs in the elaboration of the beak and narial region. It is noteworthy that this species developed extraordinarily long neural spines on its dorsal, sacral and anterior caudal vertebrae; it has been claimed that these are synapomorphic with the elongate spines of lambeosaurines, but the spines in *Ouranosaurus* are so extreme (beyond anything seen in lambeosaurines) that it seems far more reasonable to suppose them to be an autapomorphy. Curiously the contemporary very large theropod *Spinosaurus* is also characterized by the development of enormously long neural spines. Such features have long been considered enigmatic, but the recent suggestion (J.B. Bailey, manuscript) that such spines supported an adipose hump (such 'humps' are similarly supported by elongate spines in mammals—bovids and camelids—today), which acted as a heat-shield, is worthy of consideration. These dinosaurs are found at very low latitude (within the Mesozoic Tropics) and may indeed have suffered significant heat loading at times of the year. This climatic regime (Wing & Sues, 1992) may in turn be related to changes in the skull (enlargement of the narial chamber to facilitate counter-current exchangers)

and feeding mechanism (relating to the quality of browse upon which *Ouranosaurus* fed).

Muttaburrasaurus from the ?Aptian of Queensland, Australia, is a geographically extremely remote outlier of large-bodied ornithopods. Anatomically it is still not well-known; however, it does appear to share some anatomical features in common with hypsilophodontids. Hypsilophodontids had a very wide geographic distribution throughout the late Mesozoic, ranging across Europe, North America, South America, Africa, Antarctica, Australia, and China. At present I consider it possible that *Muttaburrasaurus* represents an unusually large-bodied hypsilophodontid paralleling *Tenontosaurus* in the Northern Hemisphere (and possibly *Rhabdodon* – Norman & Weishampel, in prep.), which evolved in the absence of iguanodontids and converged on their body form. Enlargement of the nasal region in this species seems, yet again, to represent a puzzlingly common mid-Cretaceous theme.

Jaw function and feeding

Altirhinus is a conventionally pleurokinetic ornithopod, and differs in few respects from the generalized iguanodontid *Iguanodon*. Differences, and their potential implications, can be dealt with relatively succinctly:

(1) The enlargement and depression of the premaxillary and dentary beak in *Altirhinus* alters the mode of cropping and probably facilitated regular feeding on a diversity of low browse.

(2) The increase in the length of the diastema (relative to *Iguanodon*, though this is not as great as *Ouranosaurus*) facilitates a bi-modal jaw action, whereby the cropping action of the beak can operate without interfering with the normal chewing action (a feature common among herbivorous mammals today).

(3) The depth of the maxillary and dentary dentitions necessary to accommodate a 2nd replacement tooth is perhaps indicative of a more abrasive diet, but there are clearly limitations to this strategy since a 2nd replacement crown is only present in the deepest part of the jaw; the anterior, shallower part of the dentary appears to have a perfectly conventional replacement pattern with a single replacement crown beneath each functional tooth. There is no hint of miniaturization of the teeth in either jaw; in isolation the dentition is indistinguishable from that of *Iguanodon bernissartensis*.

(4) The remainder of the skull anatomy (excluding the expansion of the anterior nasal cavity) is relatively conservative, and closely comparable to that of *Iguanodon*.

REMARKS AND CONCLUSIONS

Altirhinus kurzanovi represents a new genus and species of iguanodontid ornithopod from the Aptian/Albian of Mongolia; it exhibits a number of derived anatomical features in the skull and postcranial skeleton which are convergent with the better known Late Cretaceous hadrosaurids.

This new species probably evolved from a widely dispersed stock of iguanodontids which appear to have developed a pan-Northern Hemisphere distribution during a brief interval in the late Early Cretaceous (Aptian).

The description of this new species offers an opportunity to re-examine the character-lists that have been generated in support of cladograms of Euornithopods (*sensu* Weishampel & Heinrich, 1992) in recent years. A revised cladogram is presented, and the supporting characters are listed.

It is suggested that the three taxa *Tenontosaurus*, *Ouranosaurus* and *Altirhinus* exhibit a number of convergent (homoplastic) features which have served (in the case of *Tenontosaurus* and *Ouranosaurus*) to mask their phylogenetic relationships. Homoplasy finds its origins in the trend toward large size seen pervasively within the Euornithopoda, in elaboration of the feeding apparatus for durophagy (separation of cropping action of the beak from chewing between the teeth by functional separation through the diastema), and in elaboration of the nasal tract, for respiratory turbinals to reduce water loss. The expansion of the narial cavity is commonly linked to the development of species-specific vocalization and/or visual recognition in euhadrosaurians and the water conservation model does not imply exclusion of these suggestions.

Tenontosaurus. It is argued here again (following Dodson, 1980; Norman, 1990) that *Tenontosaurus* is an unusually large hypsilophodontian, which has independently lost its premaxillary teeth: incidentally, Winkler, Murry & Jacobs (1997) indicate the presence of premaxillary teeth in *T. dossi*, the loss of which in *T. tilletti* thus becomes an independent autapomorphy within the subfamily Tenontosaurinae. The remaining characters (Forster, 1990): everted margin of the premaxilla (size-related), maxilla with paired rostral processes (incorrect), parallel dorsal and ventral borders of the dentary (variable in *T. dossi* and possibly autapomorphic to *T. tilletti*), leaf-shaped denticles on teeth (size variable feature), external opening of antorbital fossa small or absent (present in euornithopods), femur with shallow cranial intercondylar groove and deep caudal intercondylar groove (present in euornithopods). Two important features remain: denticulate predentary margin (which may be size-related, but this does not account for denticles on the predentary of *Dryosaurus* spp.), and manus digit III reduced to three phalanges (unfortunately the manuses of the majority of basal euornithopods, notably *Dryosaurus* and the variety of hypsilophodontids are unknown) this character is certainly consistent among camptosaurs and more derived forms.

Ouranosaurus. As argued earlier (Norman, 1990) the majority of the characters used by Sereno (1986) to characterize the Hadrosauroidea (*Ouranosaurus* + Hadrosauridae) are either unknown, repetitious of previous nodes, incorrect, or widely distributed among euornithopods. There is one potentially consistent feature: distal end of the paroccipital and accompanying squamosal process curve anteriorly, but this is insufficient to form the basis of such an important node, and is far more likely to be an autapomorphy of the species. The new character lists (Fig. 35) suggest that *Ouranosaurus* is nested within the Iguanodontidae and is supported by analysis using PAUP (Norman, in prep).

Altirhinus exhibits some features that are reminiscent of hadrosaurids, however these are regarded as convergent, the character lists support its placement within the Iguanodontidae.

Speculations about niche partitioning, trophic dynamics or floral dynamics and/or increasingly xeric conditions are at present just that: speculative. This style of changing environmental regime is consistent with recent multidisciplinary attempts at reviewing climate change across the Early Cretaceous of England (Allen *et al.*, in

prep.); however such interpretations are not yet possible in the Asian region which is the focus of this research.

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APPENDIX 1

Discussion of anatomical characters culled from the literature

1. Lateral expansion of the premaxillae. The maxillae of basal ornithopods are not laterally expanded (Weishampel & Heinrich, 1992) but broadening of the narial floor formed by the premaxillae occurs widely (*Tenontosaurus* Winkler, Murry & Jacobs, 1997, *Dryosaurus, Camptosaurus, Iguanodon* sp., *Ouranosaurus, Altirhinus,* Hadrosaurids). I have argued (Norman, 1990) that this may parallel and trend toward size increase, which is evident among the more derived ornithopods. Flaring of the lateral edge of the premaxilla is also seen in *Dryosaurus.*

2. Enlarged external narial fenestra. Weishampel & Heinrich (1992) have argued that all higher iguanodontians have an external narial fenestra that is at least 20% of base skull length. Careful measurement shows that this was also the case in *Dryosaurus.* Linkage between this character and the expansion of the premaxilla (1) is regarded as highly likely and reflects its exactly similar distribution among taxa. Additionally, extreme external naris expansion (40% of base skull length) is seen in Hadrosaurinae (Weishampel, Norman & Grigorescu, 1993), *Ouranosaurus* (*contra op. cit.*) and *Altirhinus.*

3. Denticulations on the oral margin of the predentary/premaxillae. This feature is found in *Dryosaurus, Tenontosaurus, Camptosaurus, Iguanodon* sp., *Ouranosaurus* and *Altirhinus.* The situation is less clear in Hadrosaurids, being apparently present in the basal hadrosaurid *Telmatosaurus* but 'not overtly denticulate' in Euhardrosaurians (Weishampel, Norman & Grigorescu, 1994).

4. Raised rim along the lateral margin of the premaxilla where it forms the lower edge of the external narial fenestra. The lateral rim above the oral margin of the premaxilla is reflected upward in *Ouranosaurus* (Taquet, 1976; *contra* Weishampel, Norman & Grigorescu, 1993) and Hadrosaurine hadrosaurids but, importantly, is not present in either *Telmatosaurus, Gilmoreosaurus* or Lambeosaurine hadrosaurids.

5. External narial fenestra completely surrounded by the premaxilla. Seen only in Lambeosaurine hadrosaurids (Weishampel, Norman & Grigorescu, 1993).

6. Circumnarial depression extending on to the external surface of the nasal. Modification of the premaxillae in lambeosaurines confines this feature to hadrosaurines alone.

7. Narrow solid crest. Confined to 'sauroloph' hadrosaurine hadrosaurids (Weishhampel & Horner, 1990).

8. Broad solid crest. The generalized condition shows no elaboration of the median dorsal skull roof of euornithopods (Weishampel, Norman & Grigorescu, 1993). The basal hadrosaurid *Telmatosaurus* shows the generalised condition, whilea solid crest is seen in 'maiasaurs' (Weishampel & Horner, 1990). *Ouranosaurus* also shows independent thickening of the caudal regions of each nasal at the front of the skull roof (Taquet, 1976).

9. Rostral process of the jugal tapers in lateral view. In the generalized condition (*Hypsilophodon, Tenontosaurus tilletti, Camptosaurus, Iguanodon, Altirhinus*) the rostral end of the jugal appears to taper to a point when viewed laterally; this reflects the fact that the tip forms a dorsoventrally compressed wedge which lies at least partly between the maxilla and lacrimal, and usually contacts the palatine medially. The derived state (shown particularly well in hadrosaurids) shows a broadly expanded rostral end to the jugal, which is applied to the lateral surfaces of the adjacent skull bones (maxilla and lacrimal). In *Ouranosaurus* the rostral process appears to be robust and broadly rounded in the illustrations from the original description (Taquet, 1976); careful examination of the specimen shows that the jugal is extremely similar to that of examples such as that of *Iguanodon* (Norman, 1980, 1986; fig. 15) with the expansion of the rostral end (which would appear to taper when in articulation) reflecting an exaggeration of the S-shaped ligature between the ventral edge of the jugal and the maxilla.

10. Tongue-and-groove articulation between jugal and maxilla. A finger-shaped process (jugal process) projects caudolaterally from the body of the maxilla and fits into a slot in the medioventral surface of the jugal. This feature is well shown in *Iguanodon* sp., *Ouranosaurus, Altirhinus* but is absent in all known hadrosaurids (including *Telmatosaurus*) where the jugal suture on the lateral surface of the maxilla forms a bevelled or strongly rugose area against which the broad, plate-like base of the jugal was firmly butted.

11. Rostral premaxilla–maxilla contact. In generalized ornithopods, exemplified by *Hypsilophodon* (Galton, 1974) the rostral tip of the maxilla is deflected medially, and fits into a median slot in the rear of the premaxilla where it not only meets its neighbour, but is wedged in place by vomers dorsally. In *Iguanodon* spp., *Ouranosaurus* (*contra* Weishampel, Norman & Grigorescu, 1993) and *Altirhinus*, as well as *Telmatosaurus* and hadrosaurines (*op. cit.*) there is a well-developed lateral rostral process of the maxilla, which tapers and is bevelled dorsally to support the caudolateral process of the premaxilla along the line of the pleurokinetic hinge (Norman, 1984); the medial process is retained and maintains a similar relationship with the premaxilla as in *Hypsilophodon*. The lateral rostral process is reported to be absent in lambeosaurines and the medial process is reduced to a curved in inclined wall which supports the premaxilla along its length.

12. Dorsal process of the maxilla. In *Iguanodon* spp., *Ouranosaurus*, and *Altirhinus*, (to be confirmed in *Camptosaurus*) the dorsal margin of the maxilla is marked by a relatively stout process at its apex; this apex is displaced caudally relative to the mid-length of the maxilla. The dorsal process anchors the lacrimal bone medially. Related to this, the lacrimals in *Iguanodon* sp. (Norman, 1986; fig. 12), *Ouranosaurus* (Taquet, 1976: fig. 23) and *Altirhinus* (Fig. 7A,B) are remarkably similar. In this latter respect there are a number of minor but important errors in the interpretation of the lacrimal of *Ouranosaurus* (Norman, in prep).

13. Antorbital fenestra. This feature, which is common (though variable within ornithischians generally) is consistent though variably expressed in basal ornithopods. The fenestra is absent (or has migrated dorsally) in hadrosaurids (see Weishampel, Norman & Grigorescu, 1993). It is clearly reduced in *Iguanodon* spp. and *Camptosaurus* and is also apparently absent in *Altirhinus* (an absence that does not correlate with the explanation given *op. cit.*) and may well have been occluded in *Ouranosaurus* (Norman, in prep).

14. Quadrate (paraquadratic) foramen. A foramen in the body of the quadratojugal arch is absent in the basal ornithischian *Lesothosaurus* and the basal ornithopod *Heterodontosaurus*. A foramen is present in the quadratojugal in *Hypsilophodon* and *Tenontosaurus*, and may be a derived feature of hypsilophodontids. A deep embayment in the lateral wing of the quadrate forms the caudal margin of the quadrate foramenl, the rostral margin of which is formed by the quadratojugal in *Iguanodon* spp., *Altirhinus*, and *Ouranosaurus*. There is no foramen in *Camptosaurus?*, *Dryosaurus?* or hadrosaurids.

15. Diastema. In *Iguanodon* spp., there is a relatively short gap (diastema) between the end of the

predentary and the first dentary tooth; this is also the case in *Tenontosaurus* and *Camptosaurus*. There is a longer diastema in *Ouranosaurus*, and *Altirhinus* and hadrosaurids generally, with the exception of the basal hadrosaurid *Telmatosaurus* (Weishampel, Norman & Grigorescu, 1993), *Gilmoreosaurus* (Norman, pers. observ.) and the problematic ornithopod *Probactrosaurus* (Norman, in prep.).

16. Angular visible on the lateral face of the mandible. This is the condition in non-hadrosaurid ornithopods such as *Iguanodon*, *Altirhinus* and *Ouranosaurus*. Medial migration (to occupy a uniquely ventromedial position) of the angular is reported in the basal hadrosaurid *Telmatosaurus* (Weishampel, Norman & Grigorescu, 1993).

17. The surangular foramen. Weishampel, Norman & Grigorescu (1993) cited the widespread presence of this feature in non-hadrosaurid ornithopods. This character is however more complex than implied. In the basal ornithischian *Lesothosaurus* a remnant of the mandibular fenestra is retained at the junction between the dentary and surangular. In *Heterodontosaurus* this fenestra is retained in the same topographic position, and a similar fenestra is shown between the surangular and dentary in *Hypsilophodon* with two smaller surangular foramina close to the jaw articulation.

Gasparinisaura shows a very large mandibular fenestra. *Tenontosaurus* appears to have a mandibular fenestra near the dentary suture with the surangular, and a surangular foramen close to the jaw joint, as do *Ouranosaurus* and *Altirhinus*; *Camptosaurus* has a mandibular fenestra, and *Iguanodon* has a well-developed surangular foramen. It seems likely that most ornithischians have a reduced mandibular fenestra at the junction between the surangular and dentary; the degree of overlap between these two bones may often obscure this fact. The surangular foramen is more variable (though it may be easily missed in smaller forms), but is well-developed in *Ouranosaurus*, *Iguanodon* and *Altirhinus*. No surangular foramen has been reported in hadrosaurids, although one is reported in a ?basal form (J. J. Head, pers. comm.).

18. Miniaturization of maxillary teeth. Non-hadrosaurid ornithopods have relatively broad, asymmetric crowns and tapering cylindrical roots which tend to be eroded from beneath. *Iguanodon*, *Ouranosaurus*, and *Altirhinus* conform to this model. Hadrosaurids, even basal forms such as Telmatosaurus exhibit pronounced miniaturization of the tooth crown, which becomes narrow, markedly lanceolate and almost completely symmetrical either side of a median ridge; in addition, the roots are angular-sided, reflecting the closer packing within the alveolar trough.

19. Miniaturization of the dentary teeth. Broad dentary crowns, which tend to be asymmetric are found among non-hadrosaurid ornithopods, though the patterns of ridging and grooving may vary between taxa (the crown form in *Ouranosaurus*, *Iguanodon* and *Altirhinus* is identical). The roots tend to be cylindrical, but have grooves mesially and distally beneath the shoulders of the crown to accommodate adjacent replacement crowns. Relatively broad dentary crowns are found in forms such as the basal hadrosaurid *Telmatosaurus*, *Gilmoreosaurus* and the enigmatic *Probactrosaurus*.

20. Single dominant carina on the enamel surface of the dentary crown. This feature is found in *Hypsilophodon*, *Tenontosaurus* and in a reduced form in *Dryosaurus* which have relatively broad crowns, and in all hadrosaurids except the basal form *Telmatosaurus*, *Gilmoreosaurus* and the enigmatic *Probactrosaurus* (Norman, in prep.). *Camptosaurus*, *Iguanodon*, *Ouranosaurus* and *Altirhinus* exhibit very similar broad dentary crowns whose medial surface is divided into three shallow, vertical channels by two subequal ridges.

21. Three or more dentary teeth in each alveolus. The generalized condition seen across the Ornithischia is for there to be single functional tooth and, at most, a single replacement crown in each alveolus. As reiterated by Weishampel, Norman & Grigorescu (1993) the presence of between 3 and 5 teeth in each alveolus has long been held as a synapomorphy of the hadrosaurids; the mode of tooth form and replacement pattern seen in Neoceratopids (Dodson, 1990) is clearly independently derived. *Altirhinus* shows the presence of 3 teeth in some its alveoli (Figs 6, 22).

Additional features cited below by Weishampel, Norman & Grigorescu (1993) have at best a dubious status.

Ventral groove in the sacrum. This character was regarded as important by Weishampel, Norman & Grigorescu (1993) as a means of distinguishing *Ouranosaurus* and lambeosaurines from all other ornithopods which are supposed to have ventrally ridged sacral vertebrae. However the sacrum of *Iguanodon atherfieldensis* is ridged and grooved (Norman, 1986: fig. 35) and the posterior sacrals of *I.*

bernissartensis have a broad sulcus (Norman, 1980). Thus, while this feature might be consistent within hadrosaurids, it is subject to parallelism among other non-hadrosaurid ornithopods.

Very tall neural spines. Weishampel, Norman & Grigorescu (1993) stated that this was a character shared (convergently) by *Ouranosaurus* and lambeosaurus. *Iguanodon atherfieldensis* (Norman, 1986) and *Iguanodon fittoni* (Norman, 1987) also display elongate neural spines. This character is also ill-defined and cannot be used objectively.

Reduced dorsal margin of the scapular blade. This character appears to be negated by the evidence shown in *Telmatosaurus*, and does not appear to be useful in this context.

Robust humerus. This is a very variable feature across ornithopods, and shows no consistency.

Angular deltopectoral crest. This feature is common to euhadrosaurids *sensu* Weishampel, Norman & Grigorescu (1993), and appears sporadically among more basal ornithopods.

Points of note:
(1) Ossified caudal hypaxial tendons have been identified in: *Hypsilophodon* (Galton, 1974a), *Tenontosaurus* (Ostrom, 1970), *Thescelosaurus* (Galton, 1974b), *Dryosaurus* (Galton, 1983), *Parksosaurus* (Weishampel, ms).
(2) Size-related trends explain the progressive increase in the number of vertebrae involved in the sacrum, migration of opisthocoely from the cervical series backward into the dorsal vertebral series, change in proportions of forelimb (relating to its use in locomotion), number of tooth families in the jaw, size of nasal openings and elaboration of the beak area, development of diastema.
(3) General trends include increasing size (Ornithischia) loss of digits I and V in pes (Ornithopoda, Marginocephalia and Stegosauria), loss of premaxillary teeth (general across Ornithischia).

APPENDIX 2

A classificatory hierarchy of related ornithopods based, in part, on the cladogram in Figure 35 is offered below.
Euornithopoda
    Hypsilophodontia
        Subfamily Tenontosaurinae
            Tenontosaurus tilletti
            T. dossi
        Tenontosaurus spp.
        Thescelosaurus spp.
        Rhabdodon spp.
        Family Hypsilophodontidae
            Hypsilophodon
            Othnielia
            Parksosaurus
            Agilisaurus
            Orodromeus
            Drinker
            Leaellynasaura
            Gasparinisaura
            Atlascopcosaurus
    Dryomorpha
        Family Dryosauridae
            Dryosaurus
            Valdosaurus

Camptosauria
    Family Camptosauridae
        Camptosaurus
        Cumnoria
        Callovosaurus
        Unnamed species from Portugal (Galton, 1980)
Iguanodontia (amended rank)
    Family Iguanodontidae
        Iguanodon spp.
        Ouranosaurus
        Unnamed species from Niger (Chabli & Norman,
        ***Altirhinus* gen. nov.**
Unnamed
    Probactrosaurus spp.
Euhadrosauria
    Telmatosaurus
    Hadrosauridae