

Cranial anatomy of the iguanodontoid ornithopod *Jinzhouosaurus yangi* from the Lower Cretaceous Yixian Formation of China

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The Yixian Formation (Lower Cretaceous) of Liaoning Province, China, is justifiably famous for its exceptionally preserved fauna, which includes a remarkable diversity of non-avian dinosaurs. Here, we provide the first detailed description of the cranial skeleton of the iguanodontian ornithopod *Jinzhouosaurus yangi*. Many previously unrecorded features have been recognised, permitting a new and more robust diagnosis for this taxon, which is based on a suite of autapomorphic features. *Jinzhouosaurus* and an unnamed sauropod represent the largest, but some of the least abundant, animals in the Jehol Biota, a situation that contrasts with many other Lower Cretaceous faunas in which large dinosaurs are common faunal components. This rarity may be due to either palaeoenvironmental constraints or taphonomic bias, although it is not possible to choose between these alternatives on the basis of current data.

Key words: Dinosauria, Ornithopoda, Iguanodontia; Jehol Biota; Aptian, Liaoning Province, China.

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Introduction

Iguanodontia is a clade of ornithischian dinosaurs that comprises the duck-billed hadrosaurids and a paraphyletic array of basal taxa, including *Iguanodon*, *Camptosaurus*, and *Ouranosaurus* (e.g., Sereno 1986, 1999; Norman 1990, 1998, 2002, 2004). Basal members of the clade exhibit a grade of organisation that can be defined on the basis of a suite of anatomical features that are intermediate between those of hadrosaurids and basal (non-iguanodontian) ornithopods (see Norman 2004). The earliest known iguanodontian is “*Callovosaurus* (= *Camptosaurus*) *leedsii*” from the middle Callovian of the UK (Galton 1980; Ruiz-Omeñaca et al. 2007), but the diversity of these taxa remained relatively low during the Late Jurassic and earliest Cretaceous. However, the group radiated rapidly from the Valanginian onward, with basal iguanodontians (i.e., non-hadrosaurids) reaching their acme in the Aptian and Albian stages of the Lower Cretaceous, at which time they were widely distributed throughout Europe, North America, Asia, and Africa (Weishampel et al. 2004). Several lineages of basal iguanodontians (e.g., rhabdodontids) persisted into the Late Cretaceous and they remained important faunal components in southern Europe until the end of the Maastrichtian (Norman 2004). In general, however, the diversity of basal iguanodontians declined during this interval and

they were eclipsed in terms of both species-richness and abundance by their relatives, the hadrosaurids.

The past decade has witnessed the description of many new basal iguanodontians, most of which have been recovered from late Early Cretaceous deposits in northern China. The first of these was “*Probactrosaurus*” *mazonshanensis*, which was named on the basis of a partial skull and postcranial skeleton collected from the Xinminbao Group (Aptian–Albian) of Gansu Province (Lü 1997). Although this species was referred to the Mongolian genus *Probactrosaurus*, it has been suggested that it does not pertain to the latter taxon and may be only distantly related (Norman 2002): further study of this specimen is needed. A second Gansu locality in the Middle Grey Unit of the Xinminbao Group yielded *Equijubus normani*, consisting of an almost complete skull and partial postcranial skeleton, which can be easily differentiated from closely related taxa on the basis of numerous cranial autapomorphies (You et al. 2003a). It has been proposed that *Equijubus* represents the basalmost member of Hadrosauroida (You et al. 2003a), but other phylogenetic analyses place this taxon much further down the iguanodontian tree (Norman 2004). *Nanyangosaurus zhugeii* is represented by a partial postcranial skeleton from the Sangping Formation (?Albian) of Henan Province and can be separated from the aforementioned taxa by manual charac-

ters (Xu et al. 2000). A preliminary phylogenetic study recovered *Nanyangosaurus* as the sister-taxon to the Hadrosauridae (Xu et al. 2000); however, this hypothesis requires confirmation as it is based on an analysis that only considered the interrelationships of a very small sample of iguanodontian taxa. Another putative sister-taxon to Hadrosauridae was described as *Shuangmiaosaurus gilmorei*, whose remains (an incomplete and deformed skull) were recovered from the late Early or early Late Cretaceous Sunjiawan Formation of Liaoning Province (You et al. 2003b). A fifth taxon, *Lanzhousaurus magnidens*, has been described from the Hekou Group (Lower Cretaceous) of Gansu Province on the basis of a partial skeleton: it has been identified as a basal iguanodontian that is only distantly related to *Equijubus* and *Probactrosaurus* (You et al. 2005). Finally, the holotype specimen of *Jinzhouosaurus yangi* was recovered from the Yixian Formation (lower Aptian) of Liaoning Province (Wang and Xu 2001a, b; Figs. 1–3). Although the original description of this taxon refers only to the skull, the postcranial skeleton of the holotype individual was also collected, but has only recently been prepared for study. Similarly, several juvenile specimens that are potentially referable to this taxon have also been excavated, but await full preparation and description (WX-L, unpublished data).

These new discoveries have significantly increased the overall diversity of basal iguanodontians and have also contributed to debates over iguanodontian phylogeny, the evolution and sequence of acquisition of hadrosaurid characteristics and iguanodontian palaeobiogeography (e.g., Xu et al. 2000; Norman 2002, 2004; You et al. 2003a, b, 2005). However, none of these phylogenetic studies have attempted to incorporate all of the Chinese taxa into an analysis with all other iguanodontians: consequently, the exclusion of different taxa from each analysis may have had significant effects on the topologies recovered.

Here, we provide new information on the holotype skull of *Jinzhouosaurus yangi* (IVPP V12691), supplementing the original brief description (Wang and Xu 2001a, b). The phylogenetic analyses of Norman (2004) suggest that *Jinzhouosaurus* is a member of Iguanodontoidea (the clade consisting of iguanodontians more closely related to *Iguanodon* and *Edmontosaurus* than to *Camptosaurus*; see Norman 2002: 138) and our comparisons encompass members of this clade and penecontemporaneous taxa from China. These comparisons indicate that *Jinzhouosaurus* can be distinguished all other iguanodontoids on the basis of several cranial autapomorphies (including many that were previously unrecognised). The postcranial skeleton and phylogenetic position of *Jinzhouosaurus* will be addressed elsewhere (WX-L, PMB, and RJB, unpublished data). For the sake of convenience, all non-hadrosaurid iguanodontoids will be termed “basal iguanodontoids” hereafter.

Institutional abbreviations.—IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NHM, The Natural History Museum, London, UK.

Systematic palaeontology

Ornithischia Seeley, 1887

Ornithopoda Marsh, 1881

Iguanodontia Sereno, 1986

Iguanodontoidea Cope, 1869 (sensu Norman, 2002)

Genus *Jinzhouosaurus* Wang and Xu, 2001a

Jinzhouosaurus yangi Wang and Xu, 2001a

Holotype: IVPP V12691, a largely complete individual comprising the skull and most of the postcranial skeleton.

Type locality: Baicaigou, Toutai, Yixian County, Liaoning Province, People's Republic of China.

Type horizon: Dakangpu Member (equivalent to the Dawangzhangzi Beds) of the Yixian Formation, lower Aptian (Lower Cretaceous) (Swisher et al. 1999).

Revised diagnosis (cranial features only).—Differs from all other iguanodontoid taxa in possessing the following features: lachrymal reduced in size with a sub-triangular outline; nasals terminate in a pointed, sub-triangular caudal process that overlaps the frontals; frontals fused; frontal unit with a “T”-shaped outline in dorsal view and prominent, distinct postorbital processes that are offset from the main body of the bone; laterodorsal surface of the frontal bears an elongate shallow depression.

Comments.—The postcranial skeleton of the holotype specimen was unprepared at the time of the initial description; consequently, the original diagnosis was based solely on cranial characters (Wang and Xu 2001a, b). However, most of the features listed by Wang and Xu (2001a, b) have a much wider distribution among iguanodontoids, including: a long preorbital region; triangular maxilla in lateral view with elongate rostral process; absence of an external antorbital opening; exclusion of frontals from the dorsal orbital margin; curved quadrate shaft; long axis of supratemporal fenestra oriented anterolaterally; presence of 16 dentary teeth; and dentary teeth become larger in the caudal part of the tooth row (see Taquet 1976; Norman 1980, 1986, 1998, 2002; Lü 1997; Kobayashi and Azuma 2003; You et al. 2003a). An additional character (weakly bilobate ventral process of the prementary) appears to be absent (see below). However, the presence of several autapomorphic features and the unique combination of character states in the skull strongly supports the retention of *Jinzhouosaurus* as a valid taxon. Paul (2008) proposed an emended diagnosis of this genus, but none of the features he listed are autapomorphic for *Jinzhouosaurus* and many are in error. These issues are discussed in more detail in the Discussion (below).

Description

The skull appears to be essentially complete and articulated, but has been mediolaterally compressed, resulting in some crushing, cracking and distortion (Fig. 1). It is partially embedded in a slab of matrix that obscures most of the right mandible and the right side of the skull: the rostral margin of the

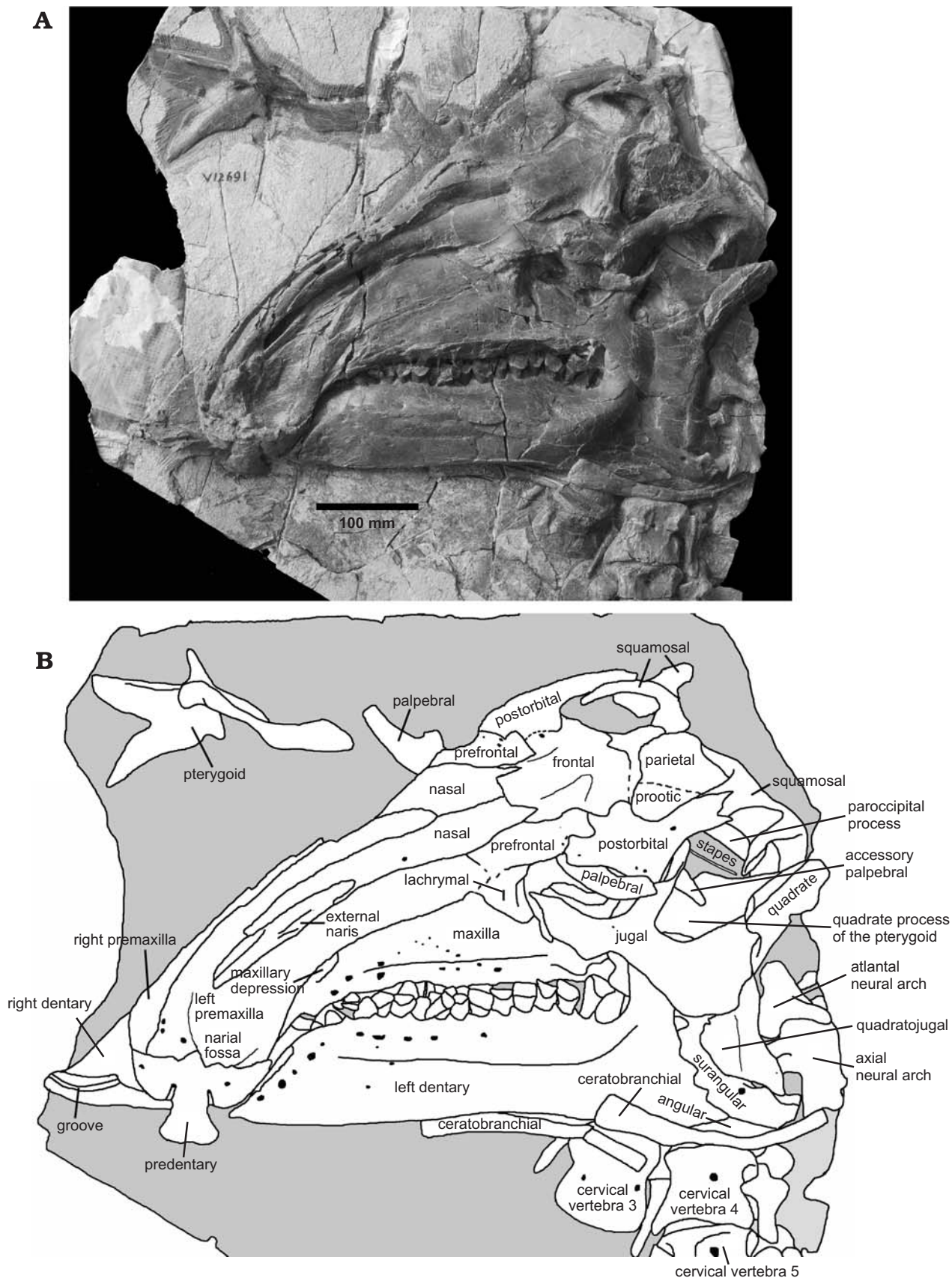


Fig. 1. Holotype skull of the iguanodontoid ornithomorph *Jinzhousaurus yangi* Wang and Xu, 2001a (IVPP V12691) from the lower Aptian (Lower Cretaceous) Dakangpu Member of the Yixian Formation of Baicaigou, Liaoning Province, People's Republic of China. Photograph (A) and interpretative drawing (B) of the skull in left lateral view.

right dentary and right premaxilla are partially visible. However, the left side of the skull and the left mandible are fully exposed. The entire skull roof is available in dorsal view, but most of the palate and neurocranium are occluded by other elements. Additional preparation carried out subsequent to the initial description has revealed the presence of the right palpebral and right pterygoid (Figs. 1–3); the latter is isolated from the rest of the skull, suggesting that the embedded right side of the skull may be badly damaged. Some of the sutures between individual cranial elements are difficult to determine and a few (e.g., the interfrontal suture) have become indistinguishably fused, suggesting that this represents an adult individual. In most cases, individual elements are only visible in one or two views, restricting the amount of anatomical information that can be extracted from the specimen. Comparisons with other taxa are based on personal observations of *Iguanodon*, *Mantellisaurus* and hadrosaurid material housed in the collections of NHM (e.g., *Mantellisaurus atherfieldensis* NHM R5764 and R11521; *Edmontosaurus* sp. NHM R3637, R4862, and R8927; *Lambeosaurus* sp. NHM R9527, R9528, and on published descriptions of *Altirhinus* (Norman 1998), *Dollodon* (Norman 1986), *Eolambia* (Kirkland 1998; Head 2001), *Equijubus* (You et al. 2003a), *Fukuisaurus* (Kobayashi and Azuma 2003), *Iguanodon* (Norman 1980), *Lanzhousaurus* (You et al. 2005), *Mantellisaurus* (Hooley 1924; Norman 1986), *Ouranosaurus* (Taquet 1976), *Probaetrosaurus* (Norman 2002), “*Probaetrosaurus*” *mazongshanensis* (Lü 1997), *Protohadros* (Head 1998), *Shuangmiaosaurus* (You et al. 2003b) and hadrosaurids (Ostrom 1961; Horner 1992; Horner et al. 2004; Evans and Reisz 2007; Gates and Sampson 2007; Gates et al. 2007).

General skull proportions are very similar to those of *Dollodon*, *Iguanodon*, and *Mantellisaurus*, with an elongate preorbital region that accounts for approximately 64% of total skull length (525 mm as measured from the caudal margins of the parietals to the tip of the snout). The external narial fossa is dorsoventrally narrow but rostrocaudally elongate, accounting for approximately 43% of preorbital skull length, which is considerably larger than in *Dollodon*, *Iguanodon*, *Mantellisaurus* or *Ouranosaurus* (approximately 30% in the former three taxa and 18% in *Ouranosaurus*), but shorter than that of *Altirhinus* (approximately 57% of preorbital skull length). Its caudal portion extends over the rostral part of the maxillary tooth row, as occurs in all but the most basal iguanodontians (e.g., *Dryosaurus*: Galton 1983). Although the circumorbital bones are slightly distorted, it appears that the orbit was small and circular in outline. As in *Altirhinus*, *Equijubus*, *Protohadros*, and hadrosaurids, there is no indication of an external antorbital fossa or fenestra in *Jinzhousaurus*. In dorsal view, the supratemporal fenestrae are sub-triangular in outline, with the apex of the triangle directed medially (Figs. 1, 2). They are longer rostrocaudally than they are wide transversely. The left infratemporal fenestra has an elliptical outline, with its long axis directed caudodorsally. The lower jaw lacks an external mandibular fenestra. In contrast to many of the other dinosaur specimens

from the Dawangzhangzi Beds of the Yixian Formation (e.g., *Sinosauropteryx*, *Caudipteryx*, *Protarchaeopteryx*: Xu and Norell 2006), the holotype specimen of *Jinzhousaurus* lacks any preserved soft-tissues.

Premaxilla.—Both premaxillae are present and the left premaxilla is generally well preserved. The right premaxilla is partially obscured by its antimere, but its rostral margin is visible and portions of its medial surface can be seen through the left external naris (Fig. 1). Both narial processes are extensively cracked. The exact shape of the snout cannot be determined with certainty due to crushing of the specimen; however, it seems likely that the premaxillae would have flared at least slightly laterally, as occurs in many other basal iguanodontoids (e.g., *Dollodon*, *Equijubus*, *Iguanodon*, *Mantellisaurus*, and *Probaetrosaurus*), but would have lacked the stronger expansion seen in *Protohadros* and hadrosaurids.

In lateral view, the premaxilla consists of a sub-quadrate plate that supports two elongate, caudodorsally extending processes: a rostradorsally situated narial process and a caudodorsally positioned maxillary process. Rostrally, the margin of the premaxillary body is rugose and forms a narrow raised platform relative to the rest of the lateral surface. This platform bears three small circular foramina: two are positioned close to the rostral margin of the bone and the third is positioned on the caudal margin of the raised area. Caudal to this, the main body of the premaxilla is shallowly excavated to form a broad smooth narial fossa that surrounds the ventral and caudoventral margins of the external naris. Unfortunately, the ventral margins of both premaxillae are obscured by the presence of the prementary, so it is not possible to determine if the premaxilla was crenulate or edentulous. The rostral end of the premaxilla is strongly down-turned and extends for a significant distance ventral to the dentary tooth row, as also occurs in *Altirhinus*, *Equijubus*, *Protohadros*, and hadrosaurids, although this has been slightly accentuated by crushing.

The narial and maxillary processes form the rostroventral and caudoventral margins of the external naris. The narial process is gently curved, rostrocaudally narrow and tapers caudally. Its ventral margin forms an extensive overlapping contact with the nasal and the latter element excludes the premaxilla from the caudodorsal margin of the external naris. The lateral surface of the narial process is strongly convex rostrocaudally. The opposing narial processes meet along the midline in a straight suture and their apices intervene between the rostral margins of the nasals, forming “V”-shaped contacts. It should be noted that in our interpretation, these processes extend much further caudally than shown in the figure accompanying the original description (Wang and Xu 2001b: fig. 2).

In lateral view, the surface of the maxillary process is gently convex to planar along its entire length; this surface is separated from the depressed narial fossa by a blunt dorsoventrally extending ridge of bone. The ventral margin of the process forms a long sloping articular contact with the maxilla, while its dorsal margin forms most of the caudoventral bound-

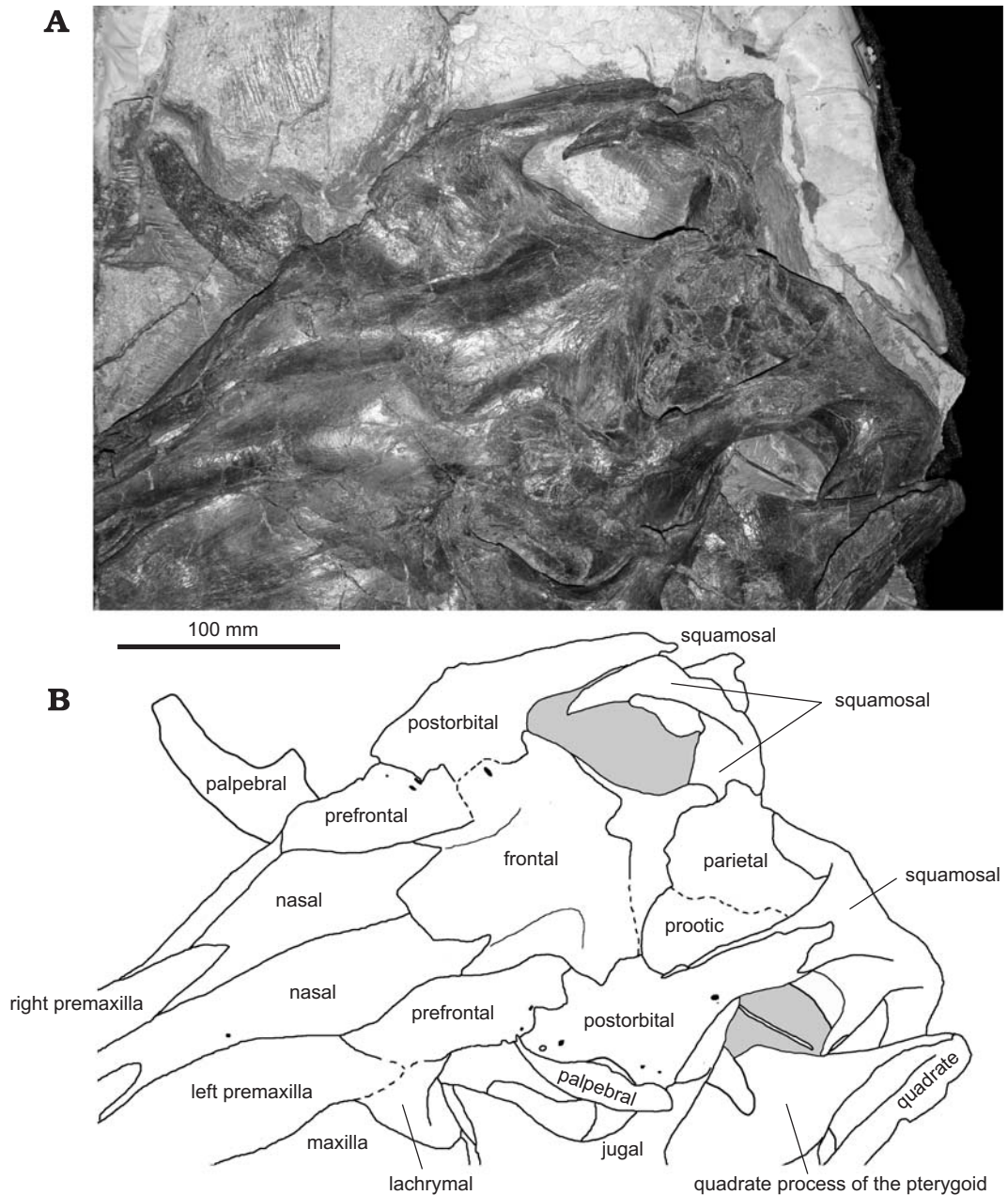


Fig. 2. Skull roof of the iguanodontoid ornithomimid *Jinzhousaurus yangi* Wang and Xu, 2001a (IVPP V12691) from the lower Aptian (Lower Cretaceous) Dakangpu Member of the Yixian Formation of Baicaigou, Liaoning Province, People’s Republic of China. Photograph (A) and interpretative drawing (B) of the skull in left lateral view.

ary of the external naris. The maxillary process increases in dorsoventral depth caudally, reaching its maximum depth at a point just rostral to its apex. This is similar to the condition seen in *Altirhinus*, *Eolambia*, *Ouranosaurus*, and *Probactrosaurus*, but contrasts with that seen in other basal iguanodontoids (e.g., *Dollodon*, *Equijubus*, *Iguanodon*, and *Mantellisaurus*), in which the maxillary process is much more slender and tapers distally. The caudal end of the maxillary process is fractured and a flake of bone in this area that was previously interpreted as the rostral end of the lachrymal (Wang and Xu 2001a, b) is regarded here as part of the premaxilla. This reinterpretation results in the presence of a broad contact between

the premaxilla and prefrontal, as occurs in *Dollodon*, *Equijubus*, *Iguanodon*, *Mantellisaurus*, and some hadrosaurids (but not in basal iguanodontians, *Altirhinus* or *Ouranosaurus*); the caudoventral part of the maxillary process still contacts the lachrymal, but this articulation is smaller than previously suggested. Medially (visible on the right premaxilla only), the maxillary process bears a series of longitudinal ridges that presumably form part of an articular surface for the rostromedial portion of the maxilla.

Maxilla.—The maxilla is a rostrocaudally elongate element with a low triangular outline in lateral view, with its apex po-

sitioned at the junction of the maxilla, premaxilla, prefrontal and lachrymal. Its rostral tip is strongly down-turned, forming a sub-vertical articulation with the premaxillary body and paralleling the morphology of the latter element. The rostradorsal margin of the maxilla forms a long, straight sloping contact with the maxillary process of the premaxilla, while the dorsocaudal maxillary margin incorporates a short articulation for the lachrymal (dorsally) and a more extensive jugal contact (ventrally).

The dorsal part of the lateral surface is relatively flat, but exhibits small, irregular concavities and convexities. In addition, numerous small foramina are present in this area: these all have sub-circular outlines and open in a rostralateral direction. They are irregularly distributed, but appear to be concentrated on the rostral half of the element: they are not as numerous or as well-developed as those that occur in *Equijubus* (You et al. 2003a). There is no evidence for an antorbital opening. Ventrally, a well developed, acute and rostrocaudally extending ridge defines the dorsal boundary of a deep buccal emargination. Beneath this ridge the lateral surface of the maxilla is bevelled ventromedially and extends toward the midline resulting in a deeply inset tooth row. The buccal emargination increases in depth caudally, reaching its maximum depth at the end of the tooth row. Several larger, elliptical foramina (all of which open rostralaterally) lie within the buccal emargination, forming a linear series that is positioned at a point approximately halfway between the buccal ridge and the tooth row. At the caudal end of the maxilla, the ridge defining the buccal emargination is extended into a hook-like jugal process (absent or reduced in *Equijubus* and *Fukuisaurus*, but present in *Altirhinus*, *Eolambia*, *Iguanodon*, *Mantellisaurus*, and *Ouranosaurus*), which overhangs the caudalmost part of the buccal emargination and bears a ventral sulcus.

A small shallow fossa is present on the rostralateral surface of the maxilla, adjacent to the premaxillary suture (Fig. 1B). This fossa does not penetrate the body of the maxilla and its caudal border is sharply defined by a raised lip of bone. It is elliptical in outline with the long axis orientated caudodorsally: this feature does not appear to be present in *Altirhinus*, *Dollodon*, *Eolambia*, *Equijubus*, *Fukuisaurus*, *Iguanodon*, *Ouranosaurus*, *Protohadros*, or *Shuangmiaosaurus*, but a similar structure is visible in some individuals of *Mantellisaurus* (NHM R11521: although it appears to be absent in others, such as NHM R5764) and is variably developed in hadrosaurids (Jason Head, personal communication 2008). Most of the maxillary teeth are almost completely obscured by the dentary teeth, so it not possible to determine the exact number of tooth positions. However, some teeth are partially exposed allowing their size and arrangement to be observed (see Fig. 3C); on this basis it is estimated that 15–16 teeth were present.

Nasal.—In dorsal view, the nasals are elongate strap-like elements that meet each other at a simple midline articulation. They are widest at a point level with the caudal margin of the maxillary process of the premaxilla and taper in width

rostrally. The dorsal surface of each nasal is mediolaterally convex: this results in the presence of an elongate sagittal depression that extends caudal to the termination of the narial process of the premaxilla. Although this feature is genuine, it has been accentuated by deformation. The caudal margin of the nasal extends as a sub-triangular process that overlaps the rostradorsal corner of the frontal (Figs. 1B, 2): this differs slightly from a previous description (Wang and Xu 2001a, b), in which the nasofrontal joint is shown to be transversely straight as also occurs in *Dollodon*, *Iguanodon*, and *Ouranosaurus*. The prefrontal articulation is situated on the caudolateral margin and forms a straight rostrocaudally oriented joint.

In lateral view, the nasal is gently arched along its entire length. Caudally, its lateral margin has an extensive contact with the maxillary process of the premaxilla. Rostrally, the nasal divides into two processes: a slender and elongate anteromedial process, which comprises the majority of the rostral portion of the element, and a very small, sub-triangular anterolateral process. The lateral margin of the anteromedial process forms the dorsal margin of the external naris, whereas its medial margin is overlapped by the narial process of the premaxilla. The anterolateral process forms the caudalmost border of the external naris: this process is absent in *Dollodon*, *Equijubus*, *Iguanodon*, and *Mantellisaurus*, but is present in *Altirhinus* and hadrosaurids. A small circular foramen is present close to the lateral margin of the nasal, near to the apex of the maxilla.

Prefrontal.—The prefrontal is sub-rectangular in dorsal view and is approximately three times longer than wide, with its long axis directed rostrocaudally. Its dorsal surface is rostrocaudally concave, but this probably represents an artefact of compression. Several small foramina are present on the posterolateral corner of the dorsal surface close to its caudal margin. One of these is positioned close to the orbital margin and is sub-circular in outline; two larger elliptical foramina are situated caudomedial to the first. Rostrally, the medial surface of the prefrontal contacts the nasal, but caudally it articulates with the frontal. The caudal margin of the element is reduced in transverse width and forms a sub-triangular process that articulates with the postorbital: this postorbital/prefrontal articulation excludes the frontal from the dorsal margin of the orbit. Consequently, the prefrontal forms the rostradorsal margin of the orbit in lateral view. Its orbital (lateral) margin is thickened dorsoventrally and is rugose, as also occurs in *Protohadros*. Together with a depression on the caudodorsal margin of the lachrymal, a roughened surface on the rostralateral corner of the prefrontal forms the articular surface for the palpebral. The rostralateral part of the prefrontal contacts the maxillary process of the premaxilla (contra Wang and Xu 2001a, b: see above). In the English translation of the original description, it is noted that “the prefrontal is large ... accounting for about 60% of the length of the skull” (Wang and Xu 2001b: 1671): however, this appears to be a translation error and the element referred to in this statement is actually the premaxilla.

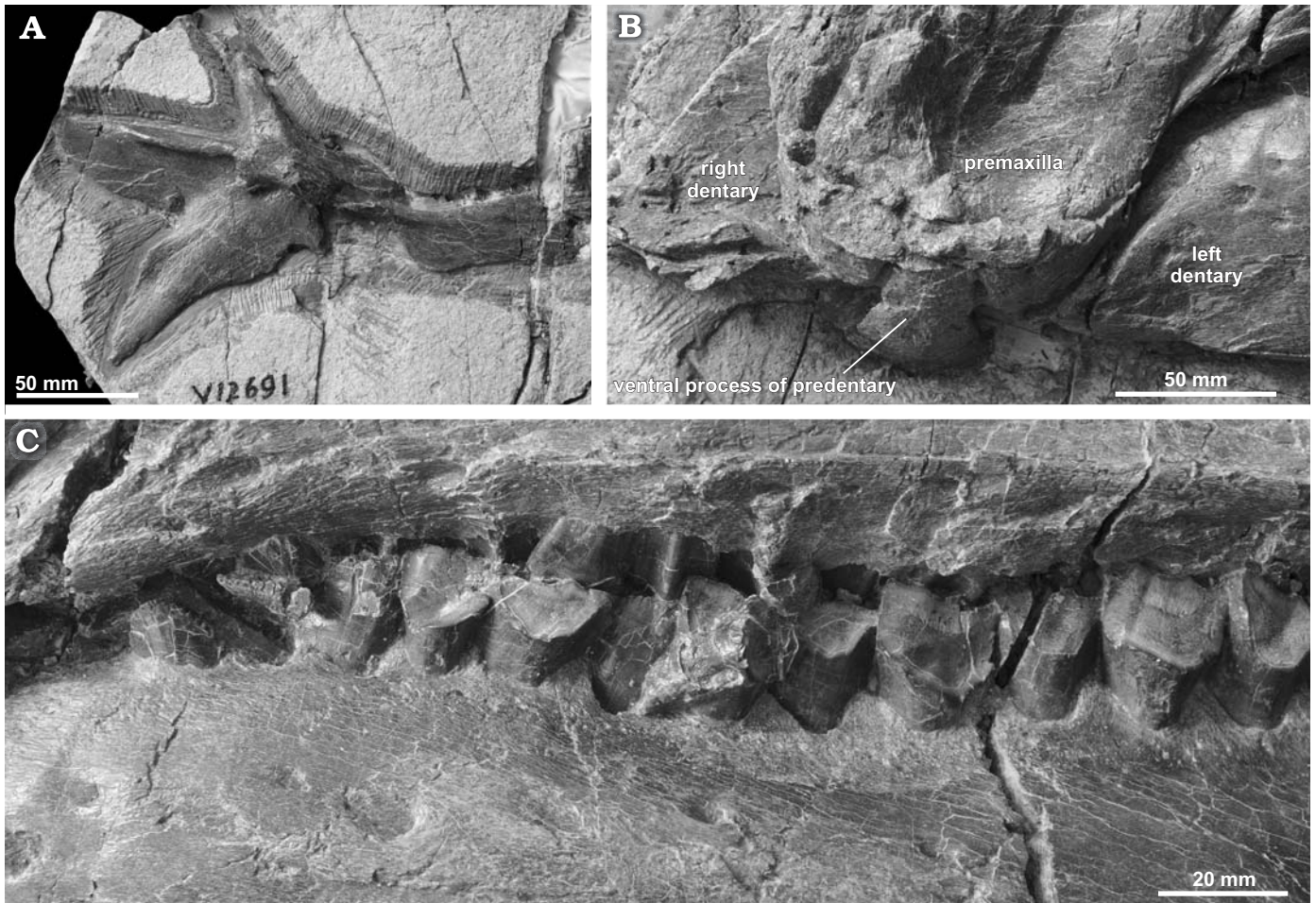


Fig. 3. Cranial elements of the iguanodontoid ornithomimid *Jinzhousaurus yangi* Wang and Xu, 2001a (IVPP V12691) from the lower Aptian (Lower Cretaceous) Dakangpu Member of the Yixian Formation of Baicaigou, Liaoning Province, People's Republic of China. Right pterygoid in medial view (A), premaxilla and snout (B), and maxillary and dentary tooth rows (C) in labial view (rostral is to the left).

Lachrymal.—In lateral view, the lachrymal is a small sub-triangular element that forms the rostral margin of the orbit. Its rostradorsal margin contacts the prefrontal along most of its length, but rostrally it has a small contact with the premaxilla. The ventral margin abuts the maxilla, but breakage of the specimen prevents determination of its relationship with the jugal. Its caudal border is pierced by a large foramen at approximately mid-height. The lateral surface of the element is strongly rugose and textured and bears an articular surface for the palpebral. In other iguanodontoids, including *Altirhinus*, *Dollodon*, *Equijubus*, *Iguanodon*, *Mantellisaurus*, *Ouranosaurus*, and hadrosaurids, the lachrymal is a relatively larger element and has a sub-quadrangular outline. The lachrymal does not contact the nasal (contra Wang and Xu 2001a, b; contra Paul 2008; Figs. 1B, 2).

Jugal.—In lateral view, the jugal consists of three main processes: a rostrally directed maxillary process, a caudodorsally directed postorbital process, and a caudally situated quadratojugal process. These three processes converge to meet in a dorsoventrally narrow main body that forms part of the caudo-

ventral border of the skull. The maxillary process is sub-triangular in outline and tapers in height anteriorly: its ventral margin articulates with the maxilla and its dorsal margin forms the ventral border of the orbit. It is not possible to determine the exact nature of the lachrymal articulation due to poor preservation. This morphology differs substantially from the condition in *Equijubus*, in which the maxillary process is exceptionally elongate and possesses a peg-like projection that originates from its dorsal margin (You et al. 2003a). The lateral surface of the maxillary process is gently convex dorsoventrally. The base of the maxillary process is slightly waisted, such that its dorsal and ventral margins converge before expanding again to merge with the main body of the bone. There is a distinct change in slope of the surface at this point and the surface of the jugal main body is more strongly convex than that of the maxillary process. The ventral margin of the jugal is stepped in lateral view, with an angle of approximately 120° separating the ventral margins of the maxillary and quadratojugal processes. A very small foramen is present on the main body, situated at the junction of the maxillary and postorbital processes.

The postorbital process is significantly longer than the maxillary process, is rostrocaudally narrow and tapers dorsally. It is mediolaterally expanded, producing a sub-triangular to sub-rectangular transverse cross-section, and its rostral margin bears a deep groove for the reception of the postorbital. In lateral view, the postorbital process forms the caudoventral margin of the orbit and the rostroventral margin of the lower temporal fenestra. It forms an angle of approximately 100° with the maxillary process. Finally, the quadratojugal process is greatly expanded relative to the main body of the bone and has a dorsoventrally elongate caudal margin, resulting in a fan-like outline in lateral view. Its rostradorsal margin, together with the dorsal margin of the main body, forms the ventral and caudoventral margins of the infratemporal fenestra.

Quadratojugal.—The quadratojugal is a flat, plate-like element that has become disarticulated and has shifted from its original position to lie ventral to the jugal and cover the ventral half of the quadrate. It is sub-crescentic in outline, with the length of the caudal margin exceeding that of the rostral margin. The rostral margin is dorsoventrally convex in lateral view, whereas the caudal margin is broadly concave and forms the rostral margin of the paraquadratic foramen. The rostral portion of the lateral surface is slightly depressed relative to the rest of the bone, forming the articular surface for the jugal. This articular surface accounts for approximately 50% of the rostrocaudal length of the element, suggesting that a large part of the caudal portion of the quadratojugal would have been exposed in lateral view when in life position, in contrast to the condition in *Iguanodon*, *Mantellisaurus* and some hadrosaurids in which only a thin portion of the element is visible. The exposed area would have been ventrally broad, narrowing dorsally, and is weakly convex rostrocaudally and shallowly concave dorsoventrally. It is likely that the quadratojugal made a small contribution to the caudoventral margin of the infratemporal fenestra, as also occurs in *Altirhinus* and *Ouranosaurus*.

Pterygoid.—The right pterygoid has become separated from the rest of the skull and is visible in medial view (Fig. 3A). Other small portions of the palate are visible through the left orbit and left infratemporal fenestra, but these cannot be identified with confidence. The pterygoid is a tetradial element consisting of four processes that radiate from a central plate. These four processes are: the palatal ramus, which extends anteriorly and a little dorsally; the ectopterygoid ramus, which extends ventrally and formed part of the pterygoid flange; and the inferior and superior parts of the quadrate ramus, which both articulate with the pterygoid wing of the quadrate, and extend caudally and caudodorsally, respectively. The rostral-most part of the palatine ramus consists of a vertically oriented flat sheet of bone. Distally, this sheet contracts dorsoventrally into a rod like structure that continues as a prominent ridge that traverses the main body of the bone. This ridge merges with and extends over much of the central plate, and terminates in a knob-like buttress. The palatine ramus forms an angle of approximately 120° with the short ectopterygoid ramus; the lat-

ter is a stout sub-triangular process whose dorsal surface forms a low ridge that merges with the knob-like buttress on the central plate.

The inferior quadrate ramus is separated from the ectopterygoid ramus by an angle of approximately 60° . This process has a sub-triangular outline and is flat and plate-like for most of its length; however, the rostral part of its ventral margin is thickened to form an extensive buttress that merges with the other ridges and buttresses that converge on the central plate of the pterygoid. The buttress along the ventral surface of the inferior quadrate ramus is slightly recurved to form a long shallow sulcus opening dorsally; this sulcus and the knob-like buttress together probably form the region for the basal articulation. The superior part of the quadrate ramus is also a flat triangular sheet of bone that is separated from the inferior part of the quadrate ramus by an angle of approximately 60° . It bears a very low central eminence that extends towards the central plate, but this eminence is not developed into a distinct ridge. Part of the central plate between the superior quadrate ramus and the palatine ramus appears to be missing, and the superior part of the quadrate ramus is separated from the palatine ramus by an angle of approximately 120° .

Quadrate.—Only the dorsal portion of the left quadrate is visible: its ventral part is obscured by the quadratojugal and jugal. This interpretation differs from that of Wang and Xu (2001a, b), who identified the caudal part of the quadratojugal as the ventral part of the quadrate. The quadrate is a vertically oriented columnar element that is bowed rostrally, with a concave caudal margin. The quadrate shaft supports two rostrally directed rami: the quadratojugal and pterygoid wings. In lateral view, there is a prominent notch in the rostral margin of the quadratojugal wing that marks the position of the paraquadratic foramen. Dorsal to this notch, the rostral margin of the quadratojugal wing bears a deep groove with sharp, acute margins. The ventral part of this groove probably accommodated the dorsal part of the quadratojugal and part of the quadratojugal process of the jugal. The remainder of the groove is separated from the ventral section by a distinct break in slope: the dorsal part of the groove would have received the rostroventral process of the squamosal. The head of the quadrate is poorly preserved, but may have been slightly offset from the rest of the shaft. It has a sub-triangular cross section as preserved. The pterygoid wing is visible through the infratemporal fenestra. It is large and sheet like, but has been distorted and cracked. Together with the quadratojugal wing, it defines a deep sulcus on the rostral surface of the quadrate for the origin of the M. adductor posterior.

Squamosal.—The squamosal consists of a small main body that supports four processes: a rostral process that contacts the postorbital; a medial process that contacts the parietal; a ventral process that articulates with the quadrate; and a caudoventral process that articulates with the quadrate and paroccipital process. The squamosal forms the caudodorsal corner of the infratemporal fenestra and the caudolateral corner of the supratemporal fenestra.

In lateral view, the rostral and ventral processes are separated from each other by an angle of approximately 45°. Much of the lateral surface of the bone is excavated to form a deep sub-triangular sulcus that would have housed the origin of the *M. adductor externus superficialis*. The rostral process of the left squamosal is largely obscured by the postorbital, but that of the right squamosal is more accessible: this process tapers rostrally and its lateral surface bears a deep “V”-shaped groove for the reception of the postorbital. The ventral process is relatively short and has a sub-crescentic transverse cross-section: its rostral margin is transversely convex, while the caudal margin is transversely concave. A groove on the caudal margin of the ventral process would have formed an articular surface for the rostral margin of the quadrate. The ventral process was not long enough to have contacted either the jugal or quadratojugal. Together with the caudoventral process, the ventral process forms the articular surface for the head of the quadrate. The ventral and caudoventral processes extend almost parallel to each other and are similar in length, but it is likely that the caudoventral process has been crushed and is not in its correct orientation. In dorsal view the medial process forms an angle of approximately 45° with the rostral process and tapers rostrally towards its contact with the parietal. In caudal view, the medial processes of the squamosals approach each other closely, but do not contact one another (contra Wang and Xu 2001a, b; contra Paul 2008; Figs 1, 2).

Postorbital.—The postorbital is a triradiate element consisting of three processes that converge to form a centrally positioned, sub-triangular main body. These processes extend rostrally, rostroventrally and caudally, respectively. The rostral process contacts the prefrontal, excluding the frontals from the orbital margin. In dorsal view, this process is bifid and the caudal process of the prefrontal intervenes between these two branches. The lateral branch of the rostral process forms the dorsolateral margin of the orbit and articulates solely with the prefrontal, whereas the medial branch articulates with both the frontal and prefrontal. In lateral view, the orbital margin is thick and strongly rugose, which may be correlated with the presence of an accessory palpebral (see below). Similar rugosities are present in this position in *Altirhinus* and *Probactrosaurus*, but are absent in *Dollodon*, *Iguanodon*, *Mantellisaurus*, and *Ouranosaurus*. The dorsal surface of the rostral process bears several small sub-circular foramina and is very gently convex rostrocaudally. The lateral surface of the process is slightly offset from the rest of the postorbital lateral surface by a distinct ridge. There may be a point contact with the parietal but this is difficult to establish.

The ventral (jugal) process is largely obscured, but is strongly curved rostrally. Ventrally, it tapers both rostrocaudally and mediolaterally, producing a sub-triangular transverse cross-section, and terminates in a sharp point. Although this morphology is similar to that in the majority of other basal iguanodontoids it differs markedly from the con-

dition present in *Equijubus*, the postorbital of which lacks a well-developed ventral process. In *Jinzhousaurus*, the caudal process is damaged distally, but is parallel-sided for most of its length. A small foramen is present on the central part of this process, which forms the rostrolateral margin of the supratemporal fenestra. The process forms an elongate tongue-in-groove joint with the squamosal.

Frontal.—The frontals are indistinguishably fused to each other and the midline suture has been completely obliterated. This appears to be unique among iguanodontoids for which appropriate material is known and is proposed as an autapomorphy of *Jinzhousaurus*; an interfrontal suture is still visible in *Altirhinus*, *Dollodon*, *Eolambia*, *Iguanodon*, *Mantellisaurus*, *Ouranosaurus*, *Probactrosaurus*, “*Probactrosaurus*” *mazonshanensis*, *Protohadros*, and hadrosaurids. Taken together, the frontals form a broad sub-triangular, almost “T”-shaped, unit in dorsal view that extends to a point level with the rostral margin of the orbit (Figs. 1, 2). As in lambeosaurine and some hadrosaurine hadrosaurids, the frontals do not contribute to the orbital margin. This is in marked contrast to the condition present in other non-hadrosaurid iguanodontoids (e.g., *Altirhinus*, *Iguanodon*, *Ouranosaurus*, *Probactrosaurus*, and *Protohadros*), in which the frontal makes at least a small contribution to the orbital fenestra. The caudolateral corner of each frontal expands laterally to form a stout postorbital process that is distinctly offset from the main body of the bone. As a result, the greatest transverse width of the frontal lies close to its caudal border, across the postorbital processes. Again, this differs from the morphology seen in the majority of basal iguanodontoids, which have frontals with an elliptical outline in dorsal view and lack a prominent postorbital process. The maximum length of the frontals is approximately equal to their combined maximum width across the postorbital processes.

In dorsal view, the central portions of the frontals are transversely convex but are nearly straight anteroposteriorly. Lateral to the midline convexity, a prominent depression extends along the rostrolateral margins of the bone. These depressions lie medial to, and merge with, the prefrontal/frontal articulation. Other basal iguanodontoids appear to lack these features (e.g., *Dollodon*, *Iguanodon*, *Mantellisaurus*, and *Ouranosaurus*) and they may represent an autapomorphy of *Jinzhousaurus*. Rostrally, the frontal has a straight transverse margin, but the rostradorsal surface bears a sub-triangular facet for articulation with the caudal processes of the nasal. Similarly, the postorbital process bears a small notch for the reception of the postorbital. Caudally, the frontals contact the parietal along a weakly interdigitate suture. However, near the midline, the caudal border of the fused frontal unit is notched to form a “V”-shaped articular surface for the parietals: the latter elements form a distinct triangular process that intervenes between the frontals for a short distance. A similar feature is present in *Altirhinus*, but is absent in *Dollodon*, *Iguanodon*, *Ouranosaurus*, and “*Probactrosaurus*” *mazonshanensis*. However, some individuals referred

to *Probactrosaurus* appear to possess an incipient version of the condition present in *Altirhinus* and *Jinzhou-saurus* (see Norman 2002: fig. 8C). Finally, the frontals of *Jinzhou-saurus* form the rostral border of the supratemporal fenestra, but are not excavated by supratemporal fossae.

Parietal.—The midline suture between the parietals has been obliterated and the combined parietal unit has been broken into two sections, one that is still in articulation with the frontals (rostral section) and a caudal section that has been displaced to partially overlap the rostral part of the unit. Each parietal consists of a central body with paired rostralateral and caudolateral processes. The former extend laterally towards the postorbitals; the latter extend caudolaterally to articulate with the squamosals. The rostralateral processes are elongate and well-developed. The main body is strongly vaulted, with a sharp sagittal ridge, and the lateral surfaces are steeply inclined to extend downward and form the sidewall of the braincase. The sagittal ridge bifurcates rostrally, with each branch of this ridge extending laterally to merge with the rostral margin of the supratemporal fenestra. Similar ridges are present in most other basal iguanodontoids, but in “*Probactrosaurus*” *mazonshanensis* the junction between the parietals is marked by a shallow groove (Lü 1997). On the rostral midline, a “V”-shaped projection extends between the frontals. Lateral to this projection, the parietal expands mediolaterally to form the rostralateral processes, which contact the posterior surface of the frontals below the level of the skull table. This articulation is not easy to determine in dorsal view, but can be seen in caudodorsal view: similar comments apply the parietal/postorbital articulation, which is visible through the supratemporal fenestra although the contact is small and its exact nature is difficult to determine. Caudally, the parietals narrow to form the medial margins of the supratemporal fenestra before expanding transversely for a second time to form the caudolateral processes. The latter are overlapped along their caudal surfaces by the medial processes of the squamosals. The parietal forms a small part of the skull margin in posterior view, excluding contact between the squamosals. The caudal part of the parietal was incorrectly identified as the paroccipital process by Wang and Xu (2001a, b).

Palpebrals.—A palpebral and accessory palpebral are present, as in *Iguanodon*. They were free elements and were not incorporated into the main orbital margin. The left palpebral is preserved in the left orbit, whereas the right element lies dorsal to the skull roof. Both are exposed in dorsal view. The palpebral is stout, rod-like and transversely expanded at its rostral end. It is weakly arched rostrocaudally in lateral view and bowed laterally in dorsal view. The dorsal and lateral surfaces are transversely convex. Small rugosities are situated on the lateral margin and the bone surface is roughly textured. The caudal end of the palpebral is squarely truncated and rugose, forming an articular surface for an accessory palpebral. Only the left accessory palpebral is preserved: it is a small sub-triangular element that is situated in the infratemporal fenestra.

Neurocranium.—A small portion of the braincase is present, but few details are available as it is badly damaged and largely obscured by other skull elements. A highly fractured section of bone ventral to the parietal probably represents the prootic, but no nervous or vascular foramina can be identified. Another small section of bone visible through the left infratemporal fenestra might represent part of the left paroccipital process. No other features can be determined.

Predentary.—The predentary is closely appressed to the ventral margin of the left premaxilla (Fig. 3B). In rostral view, the main body of the bone is crescentic and tapers caudolaterally to form the lateral processes. Its dorsal (oral) margin is crenulated and the most prominent denticle is situated on the midline. The elongate ventral process is not bifurcate (contra Wang and Xu 2001a, b), in contrast to those of *Altirhinus*, *Dollodon*, *Equijubus*, *Iguanodon*, *Protohadros*, and hadrosaurids, and expands transversely towards its caudal end, giving it a sub-trapezoidal outline in rostral or ventral view (Fig. 3B). Lateral to the base of the ventral process, deep grooves extend rostrally towards small circular foramina that open at a point approximately halfway along the dorsoventral height of the bone. These foramina, together with three or four smaller openings, form a row that extends parallel to the oral margin.

Dentary.—Both dentaries are present; the left dentary is visible in lateral view, but only the rostromedial part of the right dentary is exposed. The dentary is a robust, elongate element that comprises most of the length of the mandible: it is much more slender than the exceptionally deep dentary of *Fukuisaurus*. Its dorsal and ventral margins extend sub-parallel to each other along the entire length of the tooth row. As in *Dollodon*, *Equijubus*, *Fukuisaurus*, *Iguanodon*, *Lanzhou-saurus*, *Mantellisaurus*, and *Ouranosaurus*, the rostral end of the dentary is not significantly downturned, differing from the strongly deflected dentary symphysis present in *Altirhinus*, *Protohadros*, and many hadrosaurids. Rostrally, it contacts the predentary: caudally it contacts the angular and surangular. Caudodorsally, a prominent dorsally extending coronoid process is present, which is inclined at 90° to the long axis of the dentary. It is laterally offset with respect to the tooth row and the latter extends medial to the coronoid process. However, the process is not separated from the tooth row by an extensive horizontal shelf thereby differing from the condition present in *Lanzhou-saurus*, *Shuangmiaosaurus*, and hadrosaurids. The apex of the coronoid process is obscured by the jugal. The caudoventral margin of the dentary extends beyond the caudal margin of the coronoid process, forming a sub-triangular caudal process that overlaps the surangular and angular, as also occurs in *Altirhinus*, *Equijubus*, *Fukuisaurus*, *Lanzhou-saurus*, some individuals of *Mantellisaurus* (NHM R11521), and hadrosaurids: this feature is absent in *Dollodon*, *Iguanodon*, and *Probactrosaurus*. The lateral surface of this process is gently concave.

The main body of the dentary is dorsoventrally convex along most of its length; however, at the rostroventral end of the dentary the lateral surface is gently concave and the ven-

tral margin of the dentary is strongly in-turned to meet its antimere along a broad, spout-shaped symphysis. In medial view, this in-turned portion of the dentary has a prominent rostrocaudally extending groove on its ventral surface, which is delineated by sharp ridges, dorsally and ventrally. This groove accommodated the ventral process of the prementary. The articular groove for the lateral process of the prementary is visible on the rostral surface of the left dentary; this groove does not extend as far dorsally as the tooth row, so the oral margin of the prementary would have been positioned slightly ventral to the tooth row.

A well-developed buccal emargination is present: its boundaries are formed by the medially inset tooth row and a prominent, rostrally extending lateral ridge that merges with the margin of the coronoid process. The transverse width of the buccal emargination increases caudally. Seventeen tooth positions are present. The rostral end of the dentary is not down-turned relative to rest of the bone and there is a diastema (equivalent to the length of two alveoli) between the caudal margin of the prementary and the first dentary tooth. A row of sub-circular foramina traverses the lateral surface of the dentary. The rostralmost five foramina form a line parallel to the prementary while seven additional irregularly spaced foramina comprise a row that extends parallel to the tooth row. Several other foramina are present on the lateral surface of the dentary ventral to the buccal ridge, but these are much smaller in diameter.

Surangular.—The surangular has extensive contacts with the dentary (rostrally) and the angular (ventrally): unfortunately, several areas are obscured by the displaced quadratojugal. The surangular contributes to the caudal margin of the coronoid process, but the extent of this contribution is difficult to determine. At a point approximately level with the base of the coronoid process, a small embayment is present in the rostral margin of the surangular. A similar embayment is present in this position in *Altirhinus* and *Lanzhousaurus*, but is absent in *Dollodon*, *Equijubus*, *Fukuisaurus*, *Iguanodon*, *Mantellisaurus*, and *Protihadros*.

A large circular foramen pierces the lateral surface of the surangular close to the craniomandibular joint. Just caudal to this foramen a small sub-triangular process arises from the dorsal margin of the surangular to form part of the lateral margin of the jaw articulation. Caudal to this point, the surangular tapers in dorsoventral height to form a short, blunt-ended retroarticular process that is upturned dorsally at its caudal tip. A small section of the dorsal surface can be seen: the glenoid fossa is gently concave both rostrocaudally and transversely.

Angular.—The angular is a small strap-like element that articulates with the surangular dorsally and the dentary rostrally, forming the caudoventral margin of the mandible. No other details can be determined.

Dentition.—Few details of the dentition are visible: in general, the surfaces of the maxillary teeth are obscured by the dentary teeth, while the latter are heavily worn (Fig. 3C).

With the exception of one dentary tooth, whose lingual surface is partially exposed, all preserved teeth are visible in labial view only. A single replacement dentary tooth is visible in the sixth alveolus: no other details of tooth replacement can be determined. As far as can be ascertained, the mesially positioned teeth are the smallest in both the dentary and maxillary tooth rows: the crowns expanded mesiodistally, reaching their maximum width at a point approximately half-way along the tooth row. Distal to this point the teeth maintain similar widths until the end of the tooth row.

The maxillary tooth crowns are narrower mesiodistally than those of corresponding dentary teeth. In labial view, the maxillary crowns are lozenge-shaped and bear a strong, distally offset primary ridge. At least two, much weaker, secondary ridges are present mesial to the primary ridge: secondary ridges are also present on the maxillary teeth of *Altirhinus* (though they occur infrequently), *Dollodon*, *Equijubus*, *Iguanodon*, *Lanzhousaurus*, *Mantellisaurus*, and *Ouranosaurus*, but are absent in *Eolambia*, *Protihadros*, *Probactrosaurus*, “*Probactrosaurus*” *mazongshanensis*, *Shuangmiaosaurus*, and hadrosaurids. It cannot be determined if the crown margins are denticulate. Dentary tooth crowns are also lozenge-shaped, with their apices inclined labially. The mesial and distal margins of unworn dentary teeth are coarsely denticulate; individual denticles are mammillate. Denticles extend sub-parallel to the apicobasal axis of the crown. Most of the dentary teeth are worn and exhibit large steeply inclined apical wear-facets on their labial surfaces (Fig. 3C). In some cases, these wear facets appear to be continuous over adjacent teeth. The enamel is asymmetrically distributed and is thicker labially than lingually. Only one row of erupted teeth is in occlusion. The lingual surface of one dentary tooth is visible: there is a strong, distally offset primary ridge and at least one secondary ridge is positioned mesial to this; secondary ridges are also present on the dentary teeth of nearly all the above mentioned iguanodontoid taxa (with the addition of *Fukuisaurus* and lambeosaurine hadrosaurids: see Hall 1993), but are absent from the dentary dentitions of *Shuangmiaosaurus* and hadrosaurine hadrosaurids.

Stapes.—An elongate, narrow and cylindrical rod-like element visible through the infratemporal fenestra may represent the shaft of the stapes. No footplate is preserved.

Hyoid elements.—Two elongate rod-like elements that are preserved immediately ventral to the mandible represent the first ceratobranchials. Each is gently curved along its entire length and the rostral ends are slightly expanded relative to the rest of the element. A shallow groove extends along the distal surface of each element.

Discussion

Diagnosis of *Jinzhousaurus*.—Paul (2008) proposed an emended diagnosis of *Jinzhousaurus* that incorporates some of the features originally listed by Wang and Xu (2001a, b),

but includes many new characters. For the sake of consistency and clarity, these have been slightly reworded herein and include: (1) ratio between the preorbital skull length (premaxillary tip to rostral orbital margin) and caudal skull length (rostral orbital margin to paraoccipital process) ~ 1.25 ; (2) ratio of dentary length rostral to the coronoid process to minimum dorsoventral height of the dentary < 5 ; (3) rostrum subtriangular in lateral view; (4) premaxilla projects ventral to the level of the tooth rows; (5) maxillary process of premaxilla moderately deep; (6) dorsal apex of maxilla set caudally; (7) antorbital fenestra and fossa reduced; (8) lachrymal short; (9) lachrymal contacts nasal; (10) infratemporal fenestra small; (11) caudal portion of jugal short; (12) quadratojugal short; (13) quadrate moderately tall; (14) dorsocaudal buttress of quadrate small; (15) squamosals contact one another; (16) frontals do not contribute to orbital rim; (17) diastema absent; and (18) reduced tooth count.

With reference to the description presented above, characters 9 and 15 are in error and cannot be used in any diagnosis of *Jinzhousaurus*. Character 1 cannot be assessed as the distal ends of the paraoccipital processes are not visible and the caudal part of the skull is deformed and partially disarticulated, rendering accurate measurement of caudal skull length impossible. Character 3 is the result of plastic deformation and is of dubious validity, while character 10 is difficult to confirm due to distortion of the temporal region of the skull. Many other characters are vague, poorly defined and difficult to operationalise. For example, it is unclear what the term “quadratojugal short” (character 12) actually refers to: as currently defined it could apply to either the dorsoventral height or rostrocaudal width of the element in relation to either overall skull dimensions or the size of another cranial element. Similar comments apply to characters 8, 11, 13–14, and 18. In addition, it is not clear if character 17 is referring to a diastema between the rostral limit of the maxillary tooth row and the premaxilla, or that between the dentary tooth row and the prementary (both of which are features of some iguanodontians). In either case, a small diastema is present in both positions in *Jinzhousaurus*, rendering this character moot. The remaining features (characters 2–7 and 16) are found in variety of other iguanodontoids (see comparisons above) and are of limited taxonomic utility.

Although we agree with Paul (2008) that taxon diagnoses can be based on unique character combinations, we also advocate the primacy of autapomorphy-based diagnoses where possible. Autapomorphy based diagnoses, by definition, include only those features unique to a taxon: this emphasizes the distinctiveness of the animal in question and removes any ambiguity in its identification (the ultimate aim of the taxonomist). Paul (2008) notes that autapomorphy-based diagnoses can be undermined by the discovery of new taxa bearing these previously autapomorphic features. This issue has also been discussed in detail by Wilson and Upchurch (2003) who coined the term “obsolescent features” for characters originally deemed autapomorphic for a taxon that subsequently become recognized as more generally distributed within a

clade. Again, we agree with Paul (2008) that this situation can arise, but the same criticism can also be leveled at diagnoses based on unique character combinations: discoveries of new taxa and novel systematic analyses can significantly alter the phylogenetic and taxonomic distribution of any number of character states. In both cases it should be realized that diagnoses may need to be emended to accommodate new information and should evolve accordingly. As we have been able to identify several autapomorphies in the skull of *Jinzhousaurus* we refrain from providing a comparative diagnosis at present. None of the features proposed by Paul (2008) represent autapomorphies and all are excluded from our emended diagnosis.

Ecology of *Jinzhousaurus*.—The dinosaur fauna of the Jehol Biota is dominated by small-bodied taxa (< 3 m in body length), including a variety of coelurosaurian theropods, basal ceratopsians, the basal ornithomimid *Jeholosaurus* and the ankylosaur *Liaoningosaurus* (Xu and Norell 2006; Zhou 2006). Many of these taxa are known from multiple specimens and several different stratigraphic horizons: for example, hundreds (potentially thousands) of individuals of the basal ceratopsian *Psittacosaurus* have been recovered from the Yixian Formation. In contrast, remains of large dinosaurs are exceptionally rare: sauropods are represented by a handful of isolated teeth (Barrett and Wang 2007) and some undescribed cervical vertebrae (WX-L, unpublished data), while *Jinzhousaurus* is the only large ornithomimid and large theropods have yet to be identified. This situation is surprising and almost unique among dinosaur-bearing localities of Lower Cretaceous age, the majority of which yield abundant material of large-bodied iguanodontian ornithomimids, ankylosaurs, sauropods and allosauroid theropods (Weishampel et al. 2004).

Barrett and Wang (2007) proposed two hypotheses to account for this skewed body-size distribution: (1) genuine scarcity of large taxa, perhaps due to resource limitations or local physical conditions that created habitats inappropriate for large animals; and (2) presence of a taphonomic bias that precluded the preservation of large taxa. However, these explanations are not mutually exclusive. An analogous situation occurs in the Purbeck Limestone Formation (Berriasian) of England, which has yielded an exceptionally diverse fauna of small vertebrates but scant skeletal evidence of large-bodied taxa, although dinosaur footprints are abundant (Wright et al. 1998). In this case, the palaeoenvironments consisted of rapidly alternating freshwater to marginal marine settings under semi-arid conditions (Allen 1998), suggesting that there may have been both insufficient browse for a resident population of large dinosaurs and environmental conditions that would not be favourable to preservation of large skeletons (Norman and Barrett 2002). However, the sheer abundance of *Psittacosaurus* and other herbivores in the Jehol Group suggests that availability of suitable browse was not a limiting factor in this instance. Unfortunately, Jehol palaeoenvironments have yet to be studied in detail so

at present it is difficult to identify factors that may have influenced faunal composition. For example, palaeobotanical and sedimentological evidence provides conflicting evidence on the climate prevailing during deposition of the Jehol Group. Autochthonous floras are unknown and the mixture of floral taxa present may indicate either (i) a time-averaged flora representing a seasonal climate, with alternating semi-arid and mesic periods, or (ii) a chimaeric flora that includes plants from a broader region that comprised a range of different depositional environments, ranging from riparian channels to distal floodplains (Barrett and Hilton 2006). Additional work is urgently required to determine palaeoenvironmental conditions during Jehol times in order to examine how these may have influenced the composition and evolution of this unique biota.

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