

New data on cranial anatomy of the ceratopsian dinosaur *Psittacosaurus major*

HAI-LU YOU, KYO TANOUE, and PETER DODSON



You, H.-L., Tanoue, K., and Dodson, P. 2008. New data on cranial anatomy of the ceratopsian dinosaur *Psittacosaurus major*. *Acta Palaeontologica Polonica* 53 (2): 183–196.

An exceptionally preserved skull and mandible of ceratopsian dinosaur *Psittacosaurus major* revealed many anatomical details such as the existence of an elliptical median interpremaxillary foramen, a prominent neurovascular canal on the internal wall of the beak, long, slightly divergent basiptyergoid processes developed as vertical blades with a deep cleft between them, and horizontally oriented vomer. The new specimen shows two autapomorphies of *Psittacosaurus major*, the transversely narrow dorsal skull roof and very prominent dentary flanges, confirming the presence of two large-skulled psittacosaur species in the Lujiatun Bed of the Lower Cretaceous Yixian Formation in Beipiao City, western Liaoning Province, China, the long- and narrow-skulled *P. major*, and broad-skulled *P. lujiatunensis*.

Key words: Dinosauria, Ceratopsia, *Psittacosaurus*, Cretaceous, Yixian Formation, Liaoning, China.

Hai-Lu You [youhailu@gmail.com], Institute of Geology, Chinese Academy of Geological Sciences, 26 Baiwanzhuang Road, Beijing 100037, P.R. China;

Kyo Tanoue [tanoue@sas.upenn.edu], Department of Earth and Environmental Science, University of Pennsylvania, 240 S. 33rd Street, Philadelphia, PA 19104-6316, USA;

Peter Dodson [dodsonp@vet.upenn.edu], School of Veterinary Medicine and Department of Earth and Environmental Science, University of Pennsylvania, 3800 Spruce Street, Philadelphia, PA 19104-6045, USA.

Introduction

Psittacosaurus Osborn, 1923 is a genus of small bipedal ornithischian dinosaur from the Early Cretaceous of eastern Asia, especially Mongolia and China. It is one of the less celebrated fruits of the famed American Museum of Natural History Central Asiatic Expeditions of the 1920s. It was named by Osborn in 1923 (Osborn 1923), but it was not until the seminal work of Maryńska and Osmólska in 1975 (Maryńska and Osmólska 1975) that *Psittacosaurus* gained unequivocal membership as a basal member in the clade Ceratopsia by virtue of possessing a rostral bone. By 1990, more than 115 specimens were recognized in major collections (Sereno 1990a), and this number has been augmented in the past decade by literally scores of specimens from Liaoning Province, China. One specimen includes the skeletons of 34 babies along with one adult (Meng et al. 2004). *Psittacosaurus* is one of the most common of all dinosaurs (Dodson 1990). It would seem that its very commonness has bred contempt of sorts, and only recently has this genus drawn serious scientific attention, beginning with the Ph.D. dissertation of Paul Sereno in 1987. Until that time, there was a tendency to synonymize additional Chinese species of *Psittacosaurus* (i.e., *Psittacosaurus osborni* Young, 1931; *P. tingi* Young, 1931; *P. sinensis* Young, 1958; *P. youngi* Zhao, 1962; and *P. guyangensis* Cheng, 1982) with the type species, *P. mongoliensis* Osborn, 1923. Sereno (1987, 1990a, b) carefully reviewed all *Psittacosaurus* material described to date and concluded that of the historical “species”,

P. mongoliensis and *P. sinensis* were undoubtedly valid, *P. youngi* is a synonym of *P. sinensis*, and all other nominal species are synonyms of the type species, *P. mongoliensis*. Sereno himself described two new species, *P. xinjiangensis* (Sereno and Chao 1988) from northwestern China and *P. meileyingensis* (Sereno et al. 1988) from northeastern China. A number of new species have followed: *P. neimongoliensis* and *P. ordosensis* both from Inner Mongolia (Russell and Zhao 1996); *P. mazongshanensis* from Gansu (Xu 1997); *P. sibiricus* from West Siberia (Leschinskiy et al. 2000; Averianov et al. 2006); *P. lujiatunensis* from Liaoning (Zhou et al. 2006); and *P. major* from Liaoning (Sereno et al. 2007). Thus the geographic range of *Psittacosaurus* extends for more than 2000 km from east to west, and speciation is no more improbable over such a wide span of both geography and climatic conditions for *Psittacosaurus* than it would be for any vertebrate, especially a small one. Moreover, Lucas (2006) has posited that the temporal range of *Psittacosaurus* species is approximately 20 million years from the Barremian to the Albian stages of the Early Cretaceous. This is approximately three times the average duration of a genus of dinosaur (Dodson 1990), again suggesting the probability of multiple species (if not genera) of *Psittacosaurus*. Granted that not all of the named species are necessarily valid, it appears that a stronger case of multiple congeneric species can be made for *Psittacosaurus* than for almost any other dinosaur.

Another problem that has plagued the study of *Psittacosaurus* is poor preservation compounded by lack of thorough

preparation consistent with the perceived commonness and lack of value of individual specimens. It is not clear if the entire rich collection of specimens at the American Museum of Natural History includes a single completely prepared cranial specimen. Sereno (e.g., 1987, 1990a, b; Sereno and Chao 1988; Sereno et al. 1988) did not illustrate details of the palate and braincase but often showed the various apertures through which these structures might be observed. Likewise, descriptions allude to incomplete preparation and lost parts (Russell and Zhao 1996; Xu 1997). Ideally, skulls should contain no sediment inside, and the jaws should be removed from their natural articulation, permitting full access to the palate. Anything less constitutes incomplete preparation.

It is with some trepidation that we describe new specimen CAGS-IG-VD-004 of *Psittacosaurus major* Sereno, Zhao, Brown, and Tan, 2007 from the Lujiatun Bed of the Yixian Formation in the Lujiatun region of Beipiao City, Liaoning Province, northeastern China. However, the exceptional preservation and excellent preparation of the specimen seem to make this project worthwhile inasmuch as certain anatomical details are revealed for the first time. New discoveries of very large *Psittacosaurus* skulls (length 190 mm or longer) both from the Lujiatun region and from Sihetun now number at least six specimens, none of which were known prior to 2006 (Zhou et al. 2006; Lü et al. 2007; Sereno et al. 2007; H.-L. You, K. Tanoue, and P. Dodson, unpublished data).

Institutional abbreviations.—CAGS-IG, Chinese Academy of Geological Sciences, Institute of Geology, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LH, Long Hao Institute of Geology and Paleontology, Hohhot, China.

Description

The skull is large, mature, and very well preserved (Figs. 1, 2). It is complete in nearly every detail, excepted as noted in the description that follows. The skull is, however, somewhat sheared laterally, causing it to tilt to the right, as the right quadrate and cheek are displaced towards the midline. The left side is somewhat better preserved than the right. The skull measures 192 mm in basal length from the rostral to the occipital condyle, and 189 mm from the rostral to the left quadrate. It is thus about 25% larger than typical skulls of *Psittacosaurus mongoliensis* (Sereno 1987) and similar in size to the recently described *P. lujiatunensis* (Zhou et al. 2006), *P. sibiricus* (Averianov et al. 2006), and *P. major* (Sereno et al. 2007). Its appearance is typical of every skull of *Psittacosaurus*, with a high, short face, large orbits and temporal fenestrae, incipient parietal frill and prominent, laterally-flaring jugal horn cores. Features that draw attention are relatively large nares, circular on the left side but elliptical on the right, very prominent, laterally flaring palpebrals, and an infratemporal fenestra that is much narrower ventrally

than dorsally. In some skulls of *Psittacosaurus*, the breadth of the skull across the jugals is equal to or greater than the length of skull (e.g., *P. sinensis*, *P. lujiatunensis*); this is not true of the present specimen, even allowing for the effect of crushing (Fig. 1A).

Dermal skull roof.—The rostral bone, whose existence was tentatively acknowledged by Romer (1956) but generally doubted until Maryńska and Osmólska's (1975) study, is seen with exceptional clarity on this specimen. It is a tall element capping the premaxillae and forming almost half of the cutting edge of the edentulous beak in lateral view (Fig. 2A). The tip of the rostral is not deflected downward as it is modestly in *P. mongoliensis* and in most species of *Psittacosaurus*, or strongly pendent as it is in *P. sinensis*, but is nearly straight, and in any case well above the level of the maxillary teeth. In great contrast to *Neoceratopsia*, the front of the rostral is broad and smoothly rounded. The bone tapers dorsally almost to a point both in lateral and in rostral views, and likely contacts the nasals, although there is a gap of several mm now. The external surface of the rostral, particularly in its ventral half, shows a texture characterized by small vascular foramina, but the tapering dorsal half is smoothly textured. The prominent rostral-premaxillary suture is nearly vertical and widely open; the ventral last centimeter deflects caudoventrally to meet the cutting edge. In palatal view, a thin sharp edge is seen defining a horseshoe-shaped curve reminiscent not of a parrot's beak but of a goose's. Internally the rostral arches sharply dorsally to meet the palatine process of the premaxilla.

The premaxilla in lateral view has the form of a broad plate that fills most of the face. It has a long, caudodorsally-sloping contact with the maxilla, broad contact with the lacrimal, and defines the ventral half of the external naris. As in other species of *Psittacosaurus*, a deep horizontal groove in the premaxillary-maxillary suture at the level of the maxillary ridge marks the beginning of an irregular, meandering groove in the premaxilla that trends rostradorsally to the level of the tip of the rostral, believed by some to represent the caudal edge of a horny sheath covering the beak (Sereno et al. 1988; Zhou et al. 2006). On the right side of the specimen, a broad, smooth, depressed area runs caudodorsally from the meandering groove to the external naris that is greater in area than the naris itself. It is not evident on the left side. Evidence for the lacrimal canal, as emphasized by (Sereno et al. 1988) is clear. On the left side, the surface of the premaxilla is somewhat fractured, and any unossified zones are not clearly demarcated; on the right side an irregular fractured zone on the premaxilla trends rostroventrally from the level of the lacrimal foramen for 20 mm. This may be an artifact, but it certainly exposes the nasolacrimal canal, which is filled with red sediment. Below the rostral end of the canal is a large foramen, and unrelated to it, is a large 5 mm wide foramen, found only on the right side. Unreported in other species, we believe it is an artifact. Extending 40 mm rostrally on a line with the external maxillary ridge is the cutting edge of the beak, formed in lateral view by equal contributions from the premaxilla and the

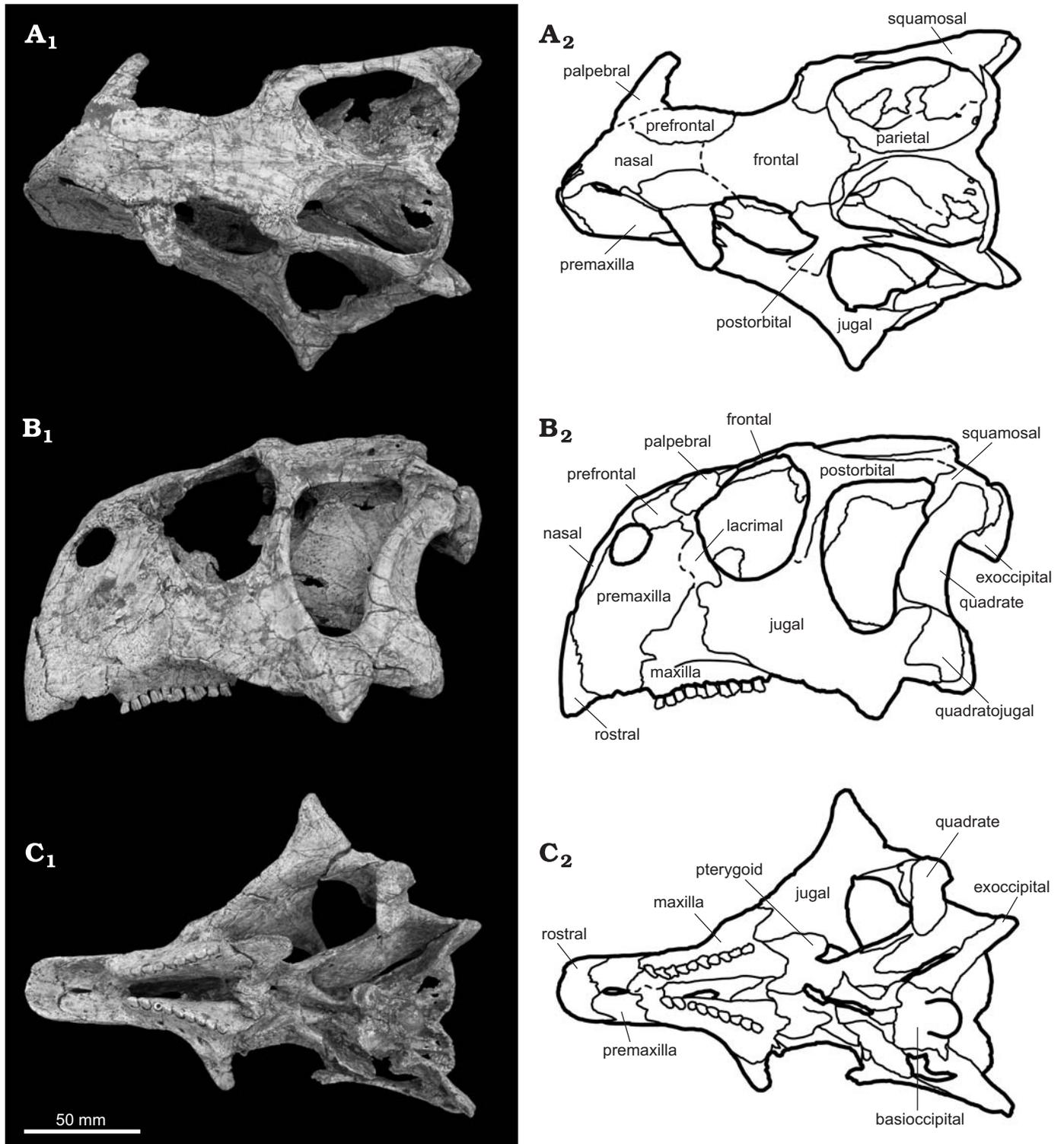


Fig. 1. Ceratopsian dinosaur *Psittacosaurus major* Sereno, Zhao, Brown, and Tan, 2007, new cranial specimen CAGS-IG-VD-004 from the Early Cretaceous Lujiatun Bed of Yixian Formation near Beipiao City, Liaoning Province, China, in dorsal (A), left lateral (B), and ventral (C) views. Photographs (A₁, B₁, C₁) and interpretive outlines (A₂, B₂, C₂).

rostral. The cutting edge of the premaxilla is thicker caudally and thins somewhat rostrally where it contacts the cutting edge of the rostral. The premaxilla arches strongly dorsally 12 mm to form the secondary palate, but fails to meet its fellow on the

midline except right at the rostral suture. A prominent elliptical median interpremaxillary foramen is formed that measures 10 mm in length and 3 mm in breadth (Figs. 1C, 3A). Although also seen in *Hongshanosaurus* (IVPP V 12617) and in

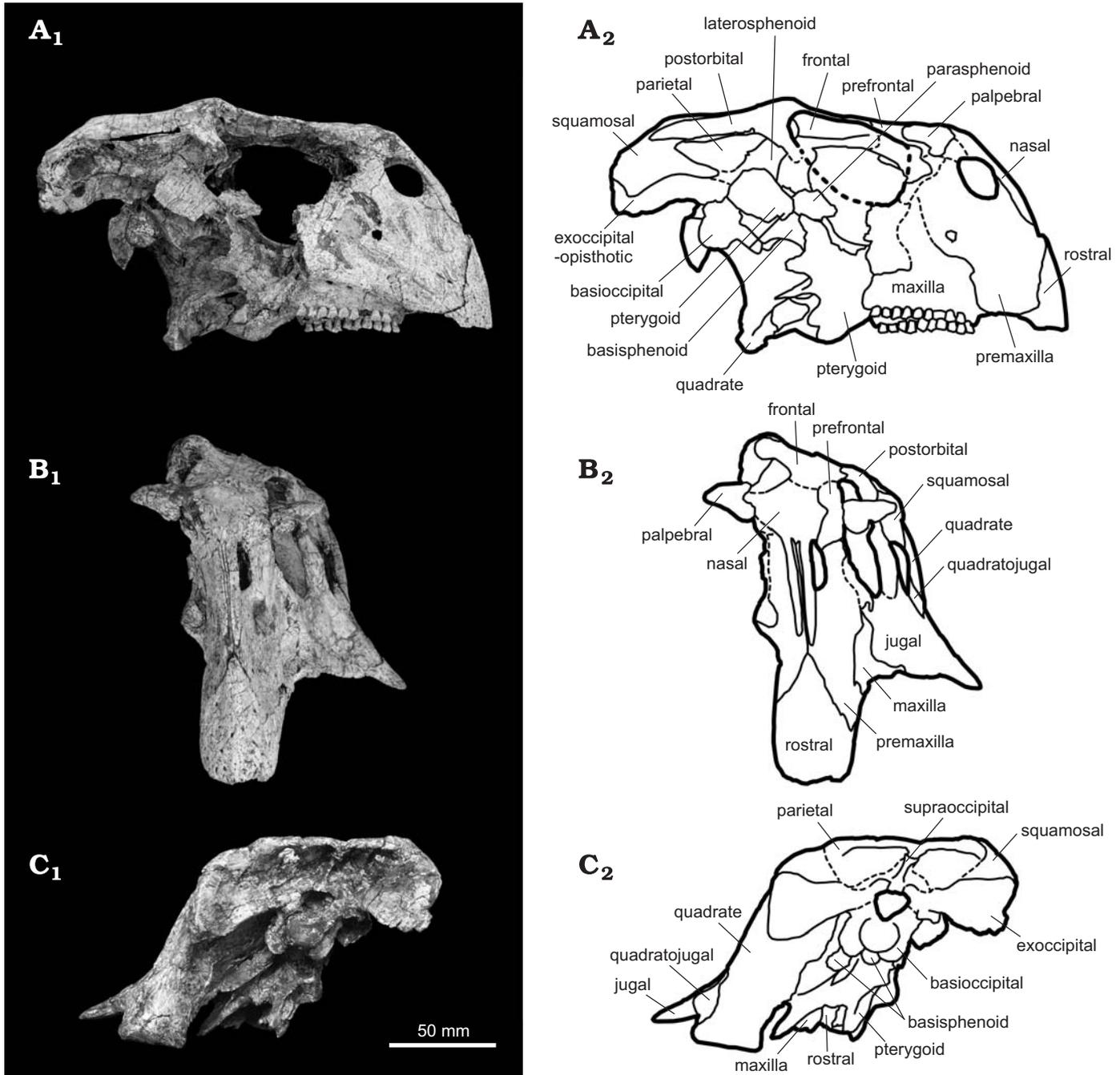


Fig. 2. Ceratopsian dinosaur *Psittacosaurus major* Sereno, Zhao, Brown, and Tan, 2007, new cranial specimen CAGS-IG-VD-004 from the Early Cretaceous Lujiatun Bed of Yixian Formation near Beipiao City, Liaoning Province, China, in right lateral (A), rostral (B), and caudal (C) views. Photographs (A₁, B₁, C₁) and interpretive outlines (A₂, B₂, C₂).

a juvenile specimen of *P. lujiatunensis* (CAGS-IG-VD-005), this foramen seems to have escaped detection until now. Each premaxilla meets the rostral in a gentle, rostrally-convex curve anchored at the midline.

The maxilla is a triangular bone whose base constitutes the toothrow, and whose apex over the middle of the toothrow reaches a near four-way junction with the premaxilla, lacrimal and jugal (Fig. 1B). The apex of the maxilla appears to taper to a point rather than having a trapezoidal form as in *P. lujiatunensis*, *P. neimongoliensis*, and *P. meileyingensis* (Zhou et al.

2006). It is not, however, low, as the apex is slightly above the ventral border of the orbit. The maxilla has a prominent depression dorsal to the horizontal external maxillary ridge that defines the dorsal edge of the deep buccal emargination. The depression, also prominent in *P. mongoliensis* and *P. lujiatunensis*, does not have the triangular form characteristic of that of *P. mongoliensis*, (resembling instead the impression of a finger pressed into heavy clay), and is emphatically not to be considered as an antorbital fossa, which has been lost in psittacosaurus (Sereno 2000).

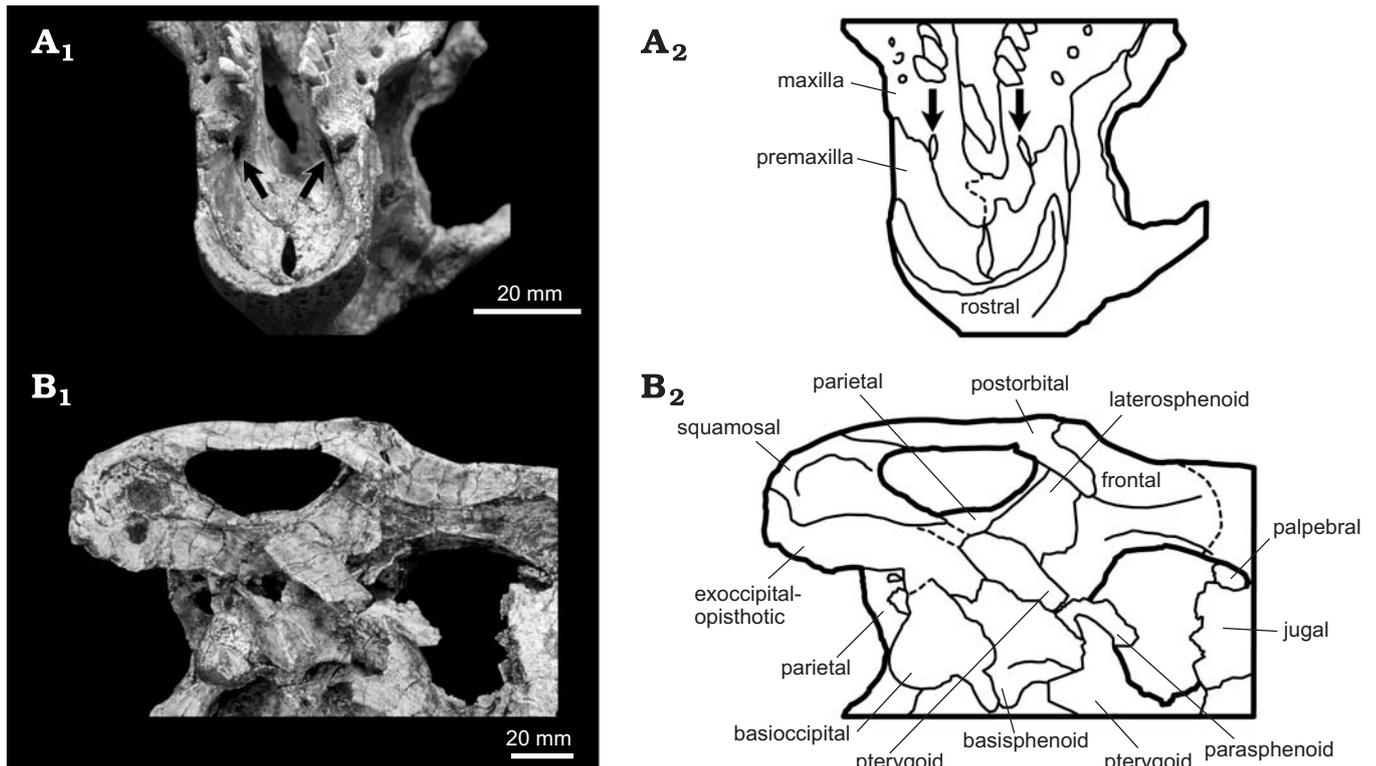


Fig. 3. Ceratopsian dinosaur *Psittacosaurus major* Sereno, Zhao, Brown, and Tan, 2007, new cranial specimen CAGS-IG-VD-004 from the Early Cretaceous Lujiatun Bed of Yixian Formation near Beipiao City, Liaoning Province, China, in palatal view (A) (with arrows indicating the neurovascular openings in the secondary palate formed by the rostral-premaxilla-maxilla complex), and right lateral and ventral view (B) of the caudodorsal portion of the skull, showing the internal (ventral) surface of the frontal and the quadrate cotyla of the squamosal. Photographs (A₁, B₁) and interpretive outlines (A₂, B₂).

The maxillary-jugal suture runs directly ventrally from the apex of the maxilla until it reaches the external maxillary ridge, then it bends abruptly to run caudoventrally, as the jugal overlaps the maxilla for several centimeters until the latter terminates. At the bend, there is a slight but not especially noteworthy blunt prominence; the same site is highly prominent in *P. mongoliensis* and other species, but it lacking in *P. sinensis* and *P. neimongoliensis* (Zhou et al. 2006). Our specimen appears to agree with the latter two species in this character. There is a series of prominent ventrally-directed neurovascular foramina beneath the external maxillary ridge; these number four on the left side and three on the right side. The caudal foramen is the largest of these, measuring 5 or 6 mm in long axis. In palatal view, strong premaxillary processes of the maxillae join the secondary palate in fused symphysis behind the premaxillae. The curved premaxillary-maxillary suture is visible, but the flat intermaxillary suture, extending for 19 mm caudal to the premaxilla, is not. On the internal wall of the beak, rostradorsal to the first maxillary tooth, a prominent neurovascular canal, probably carrying terminal branches of the maxillary branch of the trigeminal nerve and maxillary branches of the carotid artery, passes between the premaxillary process of the maxilla and the premaxilla itself (Fig. 3A). The size of the foramen suggests that the oral mucosa of the beak was well supplied and possibly fleshy. The medial surface of the maxilla is flat and high. Caudally between the pterygoid symphysis and a cau-

dally convex suture between the maxilla and mandibular ramus of the pterygoid, there is a small cleft in the maxilla measuring about 6 mm in length for a neurovascular foramen. The position is close to that of the palatine foramen, identified in basal neoceratopsians as an opening for palatine branches of the maxillary artery and nerve (Brown and Schlaikjer 1940). Ventral to the palatine foramen the maxilla overlaps the pterygoid with a shallow convex tab. For an alternate description, see the palatine below.

The lacrimal is typical of that of psittacosaurids, and forms the rostral border of the orbit and prominently displays the orbital opening of the nasolacrimal duct. It is not especially well preserved in the present specimen, although it is better on the left than on the right side. It is overlapped on its rostral edge by the premaxilla.

The nasal forms the rostromedial part of the skull roof, and then flexes rostroventrally above the caudal end of the external naris to form the internarial bridge. The nasal forms the dorsal border of the external naris and continues rostroventrally past the naris to meet or almost meet the rostral as a slender, tapering rostral process. The rostral process of the nasal appears to sandwich the premaxillae, uniquely barely visible on the midline from the external naris down to the rostral. The external nares are large, nearly circular on the left side and measure 23 mm by 20 mm in horizontal and vertical axes respectively, and are elliptical on the right side, measuring 26 mm by 15 mm in long and short axes, respec-

tively. Due to the maturity of the specimen, the internasal and nasal-frontal sutures are hard to discern. In many specimens of *Psittacosaurus* (e.g., Sereno et al. 1988; Russell and Zhao 1996; Zhou et al. 2006), there is a swelling or tumescence of either the nasals or prefrontals on the skull roof between the orbits and the external naris, and the abrupt narrowing of the snout at the level of the caudal end of the external nares coincides with the nasal flexure. Consequently, psittacosaurus have a blunt-nosed appearance, perhaps most extreme in *P. lujiatunensis* (Zhou et al. 2006) and *P. sibiricus* (Averianov et al. 2006). In the present specimen there is little if any such swelling, and the skull roof tapers smoothly from the rostror-dorsal region of the nares to the internarial bridge, as in *P. major* (Sereno et al. 2007). The nasals are comparatively narrow, and are squeezed caudally between the prefrontals. The combined width of the nasals at the narrowest (10 mm) is less than that of either prefrontal measured at the same point (14 mm left, 15 mm right). This is in great difference from *P. lujiatunensis*, in which the nasals are twice as wide at the prefrontals (Zhou et al. 2006).

The prefrontal is a somewhat L-shaped bone, forming the rostror-dorsal rim of the orbit on the skull roof, and then bending rostroventrally onto the side of the face to meet the lacrimal and premaxilla. The prefrontals taper caudolaterally and terminate in the middle of the dorsal rim of the orbit.

The triangular palpebrals are very prominent in this specimen, articulating broadly with the prefrontal at the rostror-dorsal corner of the orbit. In dorsal view, the palpebral projects directly caudolaterally; for the better preserved left palpebral, the length of the base is 23 mm and the height of the apex of the triangle is 26 mm. The rostral edge of the palpebral is rolled ventrally into a flange at right angles to the body of the bone, so that viewed rostrally, the bone is also triangular, measuring 15 mm in thickness at its base (on the right side), tapering to 5 mm in thickness at the apex. The triangular flange evidently necessitates lateral flaring of the palpebral, causing effective shielding of the corner of the eyeball at least.

The frontal is a large central element of the skull roof that forms the caudodorsal part of the rim of the orbit. It extends from the nasals and prefrontals rostrally to the parietal and postorbital caudally. The frontal measures 33 mm in breadth at its narrowest between the orbits. Its length is less certain due to the problem of determining its rostral and caudal limits, but appears to be about 55 mm. The caudolateral part of the frontal forms part of the shallow rim that marks the rostral end of the supratemporal fenestrae. The interfrontal suture cannot be detected, but a low median ridge plainly reveals its position. The central region of the frontal is shallowly depressed relative to the lateral edge, and the frontal reaches its highest relief (of 3 or 4 mm) caudolaterally at the thickened caudodorsal edge of the orbit, where it contacts the postorbital.

The internal (ventral) surface of the frontal clearly shows the hourglass-shaped trace of the rostral regions of the brain, defined by scars that must trace the attachment of a cartilaginous orbitosphenoid (Fig. 3B). The scar is 9.5 mm wide at its narrowest, nearly twice the width reported by Russell and

Zhao (1996) for the same measurement in *P. neimongoliensis* (4.7 mm), the skull of which measures 132 mm in length. The frontal is thickest over the brain (ca. 9.6 mm), and tapers to a thin edge at the orbital rim (3 mm), the bevel conforming somewhat to the globe of the eyeball.

The bony orbit is very large, measuring 55 mm in length and 61 mm in height. The eyeball itself must have been only a modest fraction of that size due to the narrowness of the interorbital space. The distance between the dorsal orbital rim and the orbitosphenoid scar on the frontal bone is only 13 mm, and the distance between the ventral rim of the orbit and the palatine is about 22 mm. Thus, the maximum conceivable diameter of the eyeball would be 44 mm, assuming a ventral position in the orbit; the minimum 26 mm; and the reasonable intermediate estimate, placing the eyeball more or less in the middle of the orbit, is 35 mm, leaving a generous space of roughly 10 mm all around the eyeball for the adnexa. Put another way, the eyeball fills only about 35% of the area of the orbit. If allowance be made for crushing of the skull, the dorsal measurement is unaffected but the ventral measurement might be increased to 30 mm, allowing for an eyeball 60 mm in diameter, which is too great for the horizontal measure of the orbit. The intermediate value is 43 mm. In this case, the eyeball occupies 55% of the surface area of the orbit, and leaves a rim of 6 to 9 mm around the socket. Such an eyeball would have been somewhat exophthalmic, especially dorsally, giving its bearer a slightly bug-eyed appearance.

The parietal is the most caudal element of the central skull roof. It bounds the supratemporal fenestrae both medially and caudally, and along with the frontal and postorbital, participates in the formation of the rostral boundary of the fenestra. The orientation of the parietal is predominantly horizontal, although the sagittal crest is convex dorsally and in lateral view stands above the temporal bar formed by the postorbital and squamosal. The parietal fans out caudally into a frill that overhangs the occiput. Although all psittacosaurus show this frill, it is particularly strongly developed in the present specimen, with a length (measured parasagittally because of the sagittal emargination) of 30 to 33 mm, and a breadth of 69 mm. The gently biconvex caudal margin of the frill has a cardioid shape and is strongly emarginated on the midline. Moreover, and apparently uniquely among psittacosaurus, the caudal edge of the parietal has the form of a thickened bar, contrasting with the extremely thin web of the parietal fan. The bar is thicker on the right side than on the left, and measures up to 9 mm in thickness. These precocious characters are reminiscent of the frills of certain Canadian Late Cretaceous centrosaurine (Dodson and Currie 1990) and chasmosaurine (Godfrey and Holmes 1995) ceratopsids, albeit in miniature. The caudal edge of the frill is horizontal in caudal view. The supratemporal fenestrae are large and elliptical, and their long axes are parallel to the long axis of the skull. The left and right supratemporal fenestrae measure 61 mm and 57 mm in length, and 34 mm and 34 mm in width, on the left and right sides, respectively.

The postorbital is a three-pronged bone that contributes to the skull roof, to the temporal bar, and to the postorbital

bar-jugal bar that separates the orbit from the infratemporal fenestra. The postorbital achieves little presence on the skull roof, as the caudolateral corner of the frontal apparently occupies a more lateral position than in the other species of *Psittacosaurus* (Serenó et al. 1988; Russell and Zhao 1996; Zhou et al. 2006). However, there is a modest prominence above the caudodorsal corner of the eye where the postorbital meets the frontal, and the orbital rim is 12 mm thick here. The postorbital-jugal bar is surprisingly thin, only 8 mm wide in lateral view opposite the most rostral extent of the infratemporal fenestra, but twice that figure ventrally. The jugal process of the postorbital is long and slender, overlapping the jugal and forming most of the caudal border of the orbit. There is a modest smooth eminence on the postorbital near its lower end, no doubt marking the position where the elaborate jugal “horn” (more reasonably, jugal eminence) of *P. sinensis* begins (Serenó et al. 1988). There is also a laterally-directed modest prominence in the middle of the three-way junction of the three prongs of the postorbital, rostradorsal to the adjacent corner of the infratemporal fenestra, but no ridges run either caudally or ventrally from this eminence as in other species (Serenó et al. 1988; Zhou et al. 2006). The squamosal process of the postorbital overlaps the postorbital process of the squamosal and forms the entire dorsal border of the infratemporal fenestra in lateral view, as expected.

The squamosal provides the cotyla for the dorsal end of the quadrate, contributes to the temporal bar separating the temporal fenestrae, forms much of the lateral border of the supratemporal fenestra and also the caudolateral corner, and anchors the caudolateral edge of the parietal frill. A stout medially-directed process marks the squamosal contribution to the parietal frill, although the parietal-squamosal suture cannot be determined. The entire frill is situated rostral to the dorsal end of the quadrate, and a slight dorsal orientation of the medial process of the squamosal elevates the caudal margin of the frill above the level of the temporal bar, making it visible in lateral view. The rostradorsal end of the quadrate is well supported by the squamosal, which sends a tapering process ventrally down the rostral edge of the quadrate. The process is fan-shaped proximally, and is supported by the pterygoid wing of the quadrate. The quadrate process extends ventrally for 22 mm and then is apparently truncated by a fracture. There is a 25 mm hiatus between the ventral process of the squamosal and the dorsal process of the quadratojugal. It is possible that they contacted each other as in *P. lujiatunensis*, but this cannot be determined. The squamosal terminates caudally as a broad, thin tab applied to the rostralateral surface of the paroccipital process of the exoccipital. On the right side of the specimen, the cheek unit, consisting of the quadrate, quadratojugal and jugal have been removed, exposing the quadrate cotyla of the squamosal with exceptional clarity (Fig. 3B). It is clear that the caudolateral orientation of the planar surface so formed provides little restriction or provides little caudal bracing for the head of the quadrate.

The jugal is one of the most distinctive bones of the entire psittacosaur skull. It runs from the maxilla and lacrimal

rostrally to the quadratojugal caudally, it forms the ventral borders of the orbit and the infratemporal fenestra, and it bears the ventrolaterally-flaring jugal horn that is the hallmark of ceratopsians generally and of *Psittacosaurus* specifically. The lateral flare of this specimen is comparatively modest. The width between jugal horns is estimated at 160 mm, only about 85% of basal skull length; in *P. sinensis*, *P. lujiatunensis*, and *Hongshanosaurus* the width of the skull exceeds skull length (Serenó 1990a; Zhou et al. 2006; You and Xu 2005). The jugal overlaps the maxilla in lateral view along the external maxillary ridge as far caudally as the distal end of the toothrow, and then it forms a lateral flange that overhangs the mandible, terminating in the jugal horn. The jugal is modestly thickened at the suborbital margin (5.5 mm), at the rostral base of the lateral flange (7 to 8 mm), and along the rostroventral edge of the infratemporal fenestra. The central suborbital portion of the jugal is somewhat thin. There appears to be a low diagonal ridge running caudoventrally from the region of the jugal-lacrimal-maxillary junction to the rostral edge of the jugal flange. Another ridge runs from the rostroventral edge of the infratemporal fenestra ventrally to the apex of the jugal horn; this is one of the defining features of the genus (Serenó 1987). The jugal horn core itself measures about 25 mm in length and 27 mm across its base. The right horn is the more robust, measuring 19 mm in thickness at its base, compared to only 12 mm on the left side. The lateral surface shows coarse vascular grooves cited as evidence for the keratinous sheath, but the ventral surface of the horn core is smooth. Caudoventrally the jugal divides into two short prongs into which the quadratojugal slots. The larger dorsal prong forms a small part of the caudal border of the infratemporal fenestra, and lies as a tab on the surface of the quadratojugal. The ventral process underlies that bone.

The quadratojugal lies between the lower end of the quadrate and the jugal, and is wedge-shaped in caudal view, broadest ventrally and tapering dorsally. It is partially covered in lateral view by the dorsal prong of the jugal which divides the bone into two parts, as in *P. lujiatunensis* (Zhou et al. 2006) but unlike the other species of *Psittacosaurus* (Serenó et al. 1988; Russell and Zhao 1996). The quadratojugal wraps rostradorsally around the shaft of the quadrate, and forms the caudal border of the infratemporal fenestra for 20 mm or so. It tapers dorsally and may be broken, so its full dorsal extent cannot be determined. There is a noticeable prominence on the prong situated near the caudal base of the jugal horn, but it is not as pronounced as in *P. sinensis* and *P. meileyingensis* (Serenó et al. 1988; Zhou et al. 2006).

The infratemporal fenestra measures 77 mm in height. As in *P. lujiatunensis* and *P. major*, it narrows ventrally, from a dorsal width of 52 mm to a ventral width of 20 mm. In other species of *Psittacosaurus* it is rectangular and unreduced ventrally.

Palatoquadrate complex.—The components of the palate, from rostral to caudal, consist of the premaxilla, the maxilla, the vomer, the palatine, the ectopterygoid and the pterygoid.

The vomer is preserved only as a single fragment. Similarly, the palatines are mostly missing except for caudal fragments. These have already been well described elsewhere (Serenó et al. 1988; Zhou et al. 2006).

The vomer is not well preserved in this specimen, but several observations are offered anyway. It forms a median bar separating the choanae and runs between the maxillary symphysis and the pterygoids. It is universally described as arched (Serenó 1990; Serenó et al. 1988; You and Xu 2005; Zhou et al. 2006), although this term is unexplained. It is rarely figured, but when figured it appears in palatal view (You and Xu 2005; Zhou et al. 2006) in which neither a longitudinal nor a transverse arch could in principle be seen. In some specimens, including CAGS-IG-VD-005 and *Hongshanosaurus houi* (You and Xu 2005), the vomer is primarily horizontal in orientation and is not at all arched. The vomer attaches to the dorsal surface of the maxillary symphysis, at a level well dorsal to the external maxillary ridge, in the vicinity of the ventral rim of the circumnarial depression. It does not form part of the secondary palate as it does in basal neoceratopsians. This is similar to the level of the vomerine prominence of the palatine process of the pterygoids. Thus the vomer is horizontal in orientation in psittacosaur; it does not arch caudodorsally as in basal neoceratopsians (Osmólska 1986). The choanae of psittacosaur are large and open ventrally onto the roof of the oral cavity in a more or less horizontal plane.

The palatine is discerned with difficulty, and does not appear to be very prominent in the present specimen. Possibly lateral crushing has destroyed important parts. In broad-snouted specimens such as CAGS-IG-VD-005, the palatines are more prominent, both rostrocaudally and mediolaterally. In CAGS-IG-VD-005, they are broadly applied to the side of the pterygoid, but do not rise as far dorsally as the vomerine prominence. The rostral edge is directed transversely in a saddle-like lateral slope that ends as a thickened buttress on the medial surface of the jugal at a four o'clock position in the right orbit or eight o'clock position in the left orbit. This corresponds to the transverse palatine wing of Osmólska (1986). The transverse saddle defines the caudal border of the choana, which appears to be very capacious. The choana is bordered rostrally by the maxillary symphysis, medially by the vomer, and caudally by the pterygoid. In CAGS-IG-VD-004, the orbital buttress of the palatine can be discerned on the left side, slightly more ventral (closer to the 7 o'clock position) than in CAGS-IG-VD-005, on a level with the seventh maxillary tooth. The palatine is applied to the medial surface of the maxilla caudally. Due to uncertainty, two alternate descriptions are presented. One interpretation of the palatine is that it forms the caudoventral edge applied to the maxilla as far ventrally as the dental foramina, covers the maxilla opposite the last two teeth, forms a rounded tab-like process that overlaps the rostromedial medial base of the mandibular process of the pterygoid, and is cleft dorsal to this to form a palatine foramen. The rostral border would ascend as a thin irregular edge dorsal to the penultimate maxillary tooth. Dorsal to the maxilla the

palatine contacts the palatine process of the pterygoid, but the thin lamina cannot be followed. The alternate interpretation is that the palatine is entirely dorsal to the palatine foramen (see maxilla above). In any case, the choana appears to extend from the level of the first maxillary tooth to the level of the seventh maxillary tooth.

Both ectopterygoids are poorly preserved, and can be identified as only as fragments on the caudodorsal bases of the left and right mandibular processes of the pterygoids. They are directed rostrolaterally across the caudal edge of the maxilla dorsal to the last tooth, and meet the medial surface of the maxillary-jugal ridge. The ectopterygoid contacts the jugal as in other specimens (Serenó 1987; Serenó et al. 1988; Zhou et al. 2006).

The complex, three-dimensional pterygoids are well preserved, and consist of quadrate, mandibular and palatine rami and a central plate, all well exposed. The pterygoids are separated along the caudal midline by a cleft that continues rostrally for 19 mm (combined length of cleft including both basisphenoid plus pterygoid components is 37 mm) and then forms a symphysis resulting in a short central plate at the level of the caudal end of the maxilla. The quadrate ramus of the pterygoid is very thin and overlaps the pterygoid wing of the quadrate medially. In ventromedial view it can be seen as far caudoventrally as about three-quarters of the distance between the central plate of the pterygoid and the quadrate condyle, and from there the caudal margin meanders rostradorsally to the vicinity of the rostral end of the cranioquadrate passage. The irregularity of the course suggests loss of thin bone by breakage or flaking. A thickened ridge curves caudoventrally from the basiptyergoid process to the ventral edge of the quadrate ramus. In so doing, a distinctive pocket is formed on the medial surface of the quadrate ramus, the thickness of which reflects the breadth of the strong basiptyergoid processes. The mandibular ramus of the pterygoid lightly overlaps the caudolateral aspect of the maxilla immediately caudal to the tooththrow and the adjacent palatine, and forms a strong pendant process that defines the ventral medial edge of the mandibular adductor fossa. This fossa is bounded laterally by the medial surface of the jugal, and rostrally by the ectopterygoid. The process measures 26 mm in length (measured medially from the maxillary suture to the broad rounded tip), 17 mm in breadth at its base, and only 4 mm in thickness. The palatine rami of the pterygoids ascend steeply rostradorsally from the central plate at an angle of about 60°, and remain closely appressed to each other on their rostral aspect. They form a rounded process expanded in lateral view on the midline almost at the level of the lacrimal canal in the rostral edge of the orbit. Here they would be expected to embrace the vomers, which are not preserved. From the caudal edge of the vomerine prominence, thin laminae of the pterygoid descend caudoventrally towards the basiptyergoid processes; the profile of the dorsal edge corresponds more or less with the ventral rim of the orbit. The space between the laminae, open dorsally, forms an interptyergoid vacuity, which is floored rostroventrally by the

pterygoid symphysis (central plate plus palatine rami) and is continuous caudally with the basisphenoid-pterygoid cleft. In some specimens, including CAGS-IG-VD-005 and *Hongshanosaurus houi* (You and Xu 2005), a median bar connects the parasphenoid to the vomerine prominence of the pterygoid, but no such connection is preserved in the present specimen.

The quadrate is tall in lateral view, gently convex rostrally and concave caudally. Only the condyles and a small caudal edge are visible ventrally, but in *P. mongoliensis* none of the quadrate is visible ventrally (Serenó et al. 1988). Dorsal to the quadratojugal, the quadrate is visible for the remainder of its course. The left quadrate measures 88 mm in height, the right quadrate 100 mm. The left mandibular condyle is well preserved, and measures 31 mm in width and 14 mm in length. The transverse axis of the mandibular condyle is approximately at 90° to the long axis of the skull. The broad, egg-shell-thin pterygoid wing of the quadrate is typical in its development, and completes the medial wall of the infratemporal fossa as far rostrally as the postorbital bar. The pterygoid wing is bowed slightly laterally, creating a space between it and the prootic-opisthotic, called the cranioquadrate passage by Sereno (1987). It contacts the former on a small thickening or prominence at the rostral end of the horizontal crista prootica. The pterygoid wing of the quadrate and its complement on the pterygoid form a curtain of bone that obscures the ventral portions of the braincase in lateral view, including most of the cranial nerve foramina. Fortunately, these bones are broken away on the right side of the skull, providing lateral access to some of these structures. Otherwise, deep braincase structures are typically visible only through the orbit (e.g., Sereno 1987; Zhou et al. 2006), or in palatal view.

Braincase.—On the occipital surface, the visible structures include the basioccipital, exoccipitals, and supraoccipital, as well as the parietal and squamosals. The fused occipital condyle, which measures 18 mm in diameter, reveals no sutures by which the basioccipital and exoccipital components can be discerned, although other specimens of less maturity show it to be composed primarily of the basioccipital. The condyle is about 25% smaller in diameter than the 25 mm reported for the skull of *Psittacosaurus lujiatunensis*, which is of similar size (Zhou et al. 2006). The condyle forms a good smooth hemisphere, mounted on a very short pedestal, which is angled somewhat caudoventrally. The pendent basioccipital tubera hang beneath the condyle, and are heavy, with a broad median cleft between them, unlike the solid plate of bone in basal neoceratopsians (e.g., You and Dodson 2003; You et al. 2005). They span a width of 33 mm, almost twice that of the condyle itself, and hang 26 (left) to 29 (right) mm below the level of the exoccipitals.

The exoccipitals form wing-like, caudolaterally-directed paroccipital processes that contribute indirectly to the support of the dorsal end of the quadrate by supporting the caudal extremity of the squamosal. The distal ends of the paroccipital processes are dorsoventrally expanded and project caudally

beyond the quadrate (forming the extremity of the skull in lateral view) and also hang well below the head of the quadrate, forming an ample tympanic recess between it and the concave caudal edge of the quadrate. The paroccipital process supports the squamosal dorsally and, at mid-length, the parietal frill. The better-preserved left paroccipital process measures 58 mm in length from the foramen magnum to the tip. The dorsoventrally expanded tip measures 32 mm in width.

The supraoccipital forms a sharp sagittal ridge or septum that runs from the foramen magnum to the ventral surface of the parietal. Dorsally the septum expands to form a shelf or pedicle that supports a ventral sagittal process of the parietal. The septum divides the occipital surface into left and right compartments for the insertion of cervical epaxial muscles. The supraoccipital-exoccipital suture cannot be determined.

The basisphenoid shows two major features in ventral view. The first are paired plate-like processes that conform in general size and shape to the basal tubera of the basioccipital, from which they are separated by a shallow transverse groove. The second feature consists of long, rostrally-projecting basiptyergoid processes, which are received in pockets on the medial surfaces of the pterygoids near the level of the caudal end of the orbit in lateral view. The basiptyergoid processes are strongly separated from each other, continuing rostrally the channel that divides the basal tubera. On the right side of the skull, the wings of the quadrate and pterygoid are broken away, exposing this region with exceptional clarity. In ventral view the basiptyergoid processes seem to be rods, but in lateral or oblique view, it is seen that they are vertical blades measuring 12 mm in height. The basiptyergoid processes diverge only slightly in the present specimen, but in a small specimen of *P. lujiatunensis* (CAGS-IG-VD-005) that measures 77 mm in length, the processes diverge from each other at an angle of almost 60°. The basiptyergoid processes measure 30 mm in length from the basioccipital-basisphenoid suture to the pterygoids, and appear to be much longer than those in *P. lujiatunensis* (Zhao et al. 2006: figs. 2F, 3D). Between the processes is a deep cleft, which is continuous caudally with the cleft between the basal tubera and rostrally with a cleft between the pterygoids. Nothing like this is seen in basal neoceratopsians such as *Archaeoceratops* (You and Dodson 2003) or *Auroraceratops* (You et al. 2005). In CAGS-IG-VD-005, which is relatively low, the basiptyergoid processes are oriented horizontally, but in CAGS-IG-VD-004 the processes are shallowly declined, and the basisphenoid-pterygoid articulation is located slightly below the level of the occipital condyle.

Situated dorsally on midline above and between the basiptyergoid processes is a median rostrum, the parasphenoid, a vertical blade with an expanded rostral tip, which is readily seen through the orbit projecting rostral to the pterygoid processes of the quadrate. The dorsal edge of the parasphenoid is concave, leaving an important recess between it and the laterosphenoids above.

The rostr dorsally-ossified element of the braincase is the laterosphenoid. It sits on the basisphenoid, and forms a strong pillar that curves rostr dorsolaterally underneath the rostro-

medial corner of the supratemporal fenestra to contact the skull roof at the caudodorsal edge of the orbit. The laterosphenoid is supported dorsally by the parietal, and fits into a cotyla on the ventral surfaces of the frontal and postorbital. As is generally the case in archosaurs, the joint is a synovial not a fibrous one. The rostroventral edge of the laterosphenoid that supported the mid and rostral portions of the brain due to breakage is very thin, friable, and incomplete. Some of it has clearly been lost due to breakage, but almost certainly this region was continued rostrally by an unossified orbitosphenoid. The laterosphenoid forms the rostral and a short part of the rostromedial wall of the mandibular adductor chamber ventral to the supratemporal fenestra. A prominent crack in the rostral part of the adductor chamber lines up with the trigeminal foramen ventrally, and this is tentatively accepted as the laterosphenoid-prootic junction.

The prootic and opisthotic are situated caudal to the laterosphenoid, and form the medial wall of the adductor chamber ventral to the parietal, but are not suturally distinct from each other. The crista prootica is a long horizontal ridge that more or less marks the dorsal extent of the pterygoid wing of the quadrate. Dorsal to this, the surface of the prootic is smooth, providing a surface for origin of the jaw adductor musculature. The crista prootica may be seen in ventral view as a sharp, curled ridge directed caudolaterally more or less parallel to the ventral edge of the paroccipital process. It thus defines the medial edge of the cranioquadrate passage and the rostrolateral edge of the tympanic canal, which measures nearly 7 mm in width. The stapes would be situated here if it was present, but none was preserved.

The cranial nerve foramina are not well preserved. A major landmark is the trigeminal foramen, situated ventrally between the laterosphenoid and the prootic. On the right side of the present specimen there is a fractured area just dorsal to the basisphenoid that measures 10 mm in width. The trigeminal foramen is visible on the left side situated on the level of the rostrorodorsal corner of the infratemporal fenestra. It measures about 4 mm in diameter, is situated in a pit, and directs the course of the trigeminal nerve ventrolaterally. On the right side, the trigeminal foramen is less distinct, but several grooves course rostrorodorsally along the ventral edge of the laterosphenoid. At least one of these seems to correspond to the groove reported for cranial nerve III, the oculomotor nerve, in *P. lujiatunensis* (Zhou et al. 2006). A pit ventral and slightly caudal to trigeminal foramen on the left side may correspond to the foramen for cranial nerve VII, the facial nerve. On the ventrolateral aspect of the paroccipital process there is a triangular depression defined by two ridges, one running dorsolaterally from the occipital condyle, and one caudodorsally from the basioccipital. In this depression are three foramina, representing the exits for cranial nerves IX, X, XI, and XII, the glossopharyngeal, vagus, accessory and hypoglossal nerves, respectively.

Mandible.—Both mandibles are preserved. The mandible is long and deep in lateral view and slender in dorsal view. The

left mandible measures 188 mm in length and 68 mm in height. The existence of an external mandibular foramen is uncertain since the portion including the dentary-surangular-angular junction is missing. The mandibular ramus is nearly straight in dorsal view. A distinctive flange is developed ventrolaterally from the middle one third of the mandible. The jaw articulation is approximately 10 mm lower than the base of the tooth row. The following description of the mandibular elements is based mainly on the better preserved left mandible (Fig. 4).

The prementary caps the dentaries rostrally. Its length is 36 mm, width 39 mm and height 41 mm. Possibly due to the compression of the rostral bone, it is wider than the rostral. In lateral view, it is short and deep as in *P. lujiatunensis*, *P. meileyingensis*, *P. neimongoliensis*, and *P. sinensis*, and it differs from relatively long and shallow prementary of *P. mongoliensis* and *P. sibiricus* (Young 1958; Sereno 1987; Sereno et al. 1988; Russell and Zhao 1996; Averianov et al. 2006; Zhou et al. 2006). It is triangular in lateral view and semicircular in rostral view. It forms most, if not all, of the cutting edge of the edentulous lower beak. In dorsal view, the cutting edge is horseshoe-shaped as in the opposing rostral. The right dorsal process, which is approximately 10 mm long articulates dorsally with the rostrorodorsal margin of right dentary. The ventral process extends caudoventrally in lateral view tapering distally. The dorsal one-third of its external surface and most of the dorsal surface except for the small area immediately rostral to mandibular symphysis are pitted. In contrast, the ventral two-thirds of the rostral surface is mostly characterized by a smooth texture, but there also are shallow grooves. In dorsal view, the caudal margin of its dorsal surface is composed of caudally concave two arches, which receive the rostrally convex ends of dentaries, anchored at the midline.

The dentary fills nearly half of the mandible in lateral view. Its rostral end is covered by the caudal margin of prementary, with the prementary-dentary suture running caudoventrally in lateral view. The dentary measures 87 mm in length and 68 mm in height. Medially, the rostral ends of the dentaries contact with each other at the symphysis. The caudodorsal portion of the dentary rises to form the rostral half of the coronoid process including its apex. On both lateral and medial sides of the apex, striations for pseudotemporalis muscle attachment run caudodorsally (Ostrom 1964). Slightly rostrally from the midpoint of the ventral margin stretches the rostral end of the unusually strong ventrolateral flange, which is present to some degree in most psittacosaurids. *P. sinensis* and *P. neimongoliensis* do not possess this flange (Sereno et al. 1988; Russell and Zhao 1996). The flange reaches the middle of the ventral margin of angular. In medial view, the ventrolateral flange extends ventral to splenial. The dentary is widest opposite the rostral end of the flange in dorsal view, reaching the width of 22 mm including the flange. A prominence extending across the lateral surface from the coronoid process to the rostral corner of the flange noted in *P. meileyingensis*, *P. mongoliensis*, and *P. lujiatunensis* (Sereno 1987; Sereno et al. 1988; Zhou et al. 2006) is poorly developed.

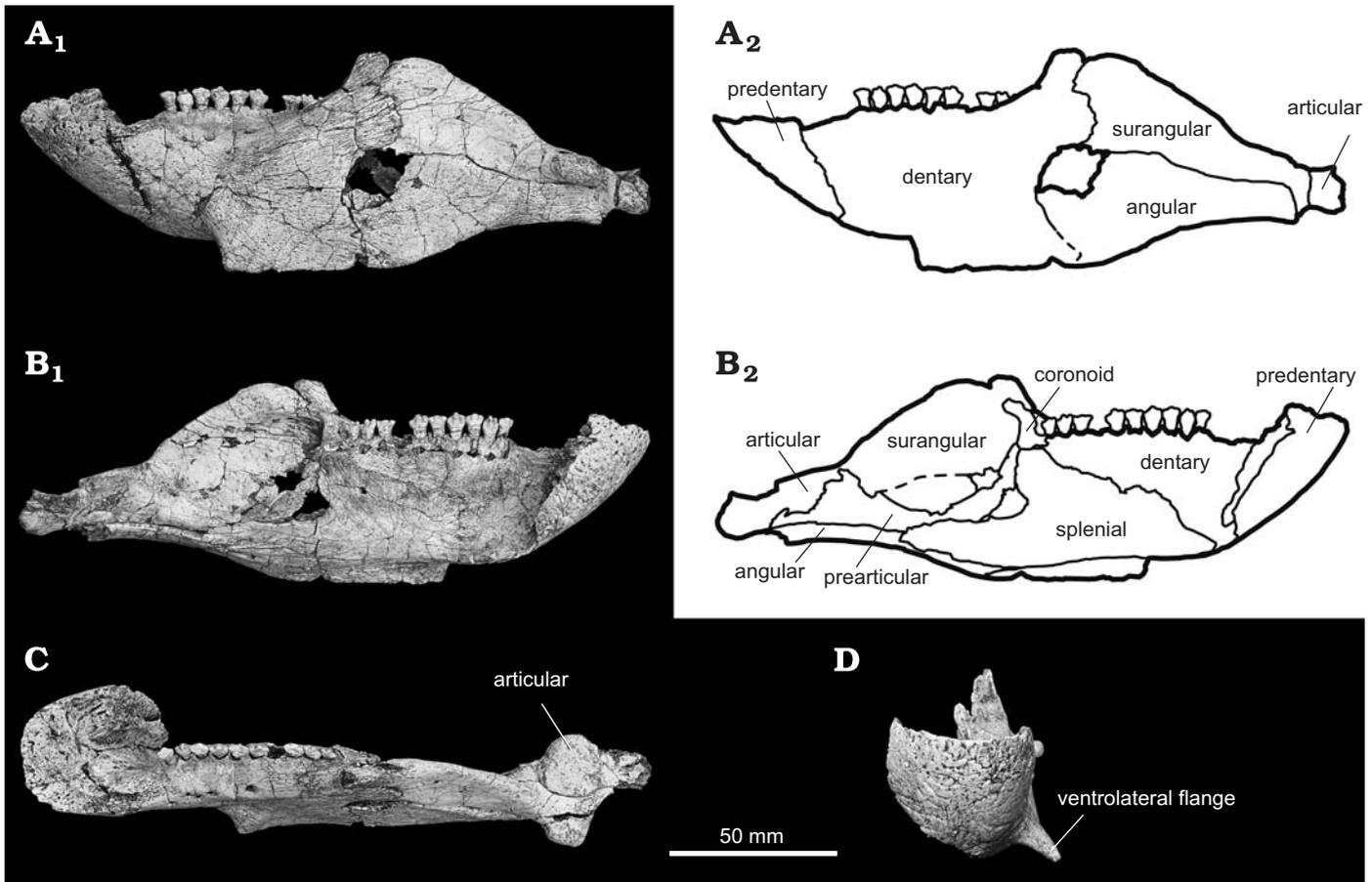


Fig. 4. Ceratopsian dinosaur *Psittacosaurus major* Sereno, Zhao, Brown, and Tan, 2007, new cranial specimen CAGS-IG-VD-004 from the Early Cretaceous Lujiatun Bed of Yixian Formation near Beipiao City, Liaoning Province, China. Left mandible in lateral (A), medial (B), dorsal (C), and rostral (D) views (A₁, B₁, C, and D are photographs and A₂ and B₂ are interpretive outlines).

The surangular is a large bone forming most of the upper half of the caudal third of the mandible. It is bounded by the dorsal half of the dentary rostrally, the angular ventrally and the articular caudally. In lateral view, it is subtriangular, tapering caudoventrally. It is 65 mm long and 38 mm high. The rostradorsal corner of the surangular contributes the caudal half of the coronoid process. In dorsal view, it is mostly slender. However, at its caudal end, it bears a lateral projection slightly tilting laterally. Together with the medially projecting articular, the left and right mandibles have their greatest widths of 30 mm and 34 mm, respectively, at the point of the projections. The projection is lateral to and co-planar with the glenoid surface of the articular, thus participating in jaw articulation.

The angular forms most of the ventral half of the caudal third of the mandible. It contacts the ventral half of dentary rostrally, the surangular dorsally and the articular caudally. It is slightly larger than surangular. In lateral view, it is a subtriangular element tapering caudally and roughly symmetrical to the surangular across the surangular-angular suture. Its length measures 76 mm and height 34 mm. In medial view, it is overlapped by the prearticular and partially by caudal end of the splenial. The suture between the surangular and the angu-

lar is ambiguous in medial view. The ventrolateral flange of the mandible ends at the middle of the angular.

The splenial covers the midsection of the medial side of the mandible. It is bounded by the dentary rostradorsally, the coronoid dorsally, the prearticular caudally and the angular caudoventrally. Its length is 78 mm and height 29 mm. The rostral end along the ventral margin is located immediately caudal to the predentary. From the rostral end, the rostradorsal margin of the splenial stretches caudodorsally to the rostroventral end of the coronoid. The rostral half of the ventral margin is nearly horizontal, whereas the caudal half is ventrally convex, reaching the middle of the angular. The caudodorsal margin is convex rostroventrally, forming the rostral and ventral walls of the Meckelian foramen.

The coronoid is the smallest element of the mandible contributing to the medial side of the coronoid process. It contacts the dentary rostrally and dorsally, the splenial ventrally, the prearticular caudoventrally and the surangular caudally. Its rostrocaudal length measures 11 mm and height 12 mm. Only the left coronoid is preserved in this specimen. In medial view, it is L-shaped with its dorsal portion curved caudally. The rostral process extending from the ventral portion of the vertical shaft is just ventral to the caudal end of the

tooth row. In this specimen, the coronoid does not reach the dorsal end of the coronoid process of the dentary. The dorsal end of coronoid is possibly missing.

The prearticular consists of a thin strip on medial side of the caudal portion of the mandible. It is bounded by the splenial rostrally, the coronoid rostradorsally, the articular caudodorsally and the angular ventrally. It is 75 mm long and 22 mm high. The rostral half of the prearticular is thinner than its caudal half and it stretches rostradorsally. The ventral margin of the rostral half composes the dorsal and caudal wall of the Meckelian foramen. The caudal half of prearticular is horizontal, with a dorsal projection just rostral to the articular in medial view. It does not reach the caudal end of the mandible along with articular.

The articular constitutes the dorsal side of the caudalmost portion of the mandible. The rostral portion of the articular is a very unusual flat, disk-shaped articular surface, which receives the quadrate of the skull. The medial half of the articular surface extends medially as a projection. The left articular surface is 21 mm in length and 19 mm in width. The length and width of the right articular surface are both 19 mm. There is a slender retroarticular process stretching caudally from the disk-shaped articular surface, reaching the caudal end of the mandible.

Dentition.—There are ten and nine teeth in left and right maxillary tooth rows, respectively. The tooth rows are nearly straight in ventral view. The left tooth row is 52 mm long and the right tooth row 49 mm (Fig. 5A). In ventral view, the crowns are aligned at a shallow angle to the tooth row. The mesial end of each crown lingually overlaps the distal end of the preceding crown as in *P. meileyingensis* (Serenio et al. 1988). Although one replacement tooth each for the 9th left maxillary tooth and the 8th right tooth are present, the outlines of the two unworn maxillary tooth crowns are not fully exposed. The crowns of the functional teeth are approximately 4 to 6 mm long mesiodistally and 3 to 4 mm wide linguolabially. In labial view, two deep and long grooves separate the primary ridge from the mesial and distal lobes. In some maxillary teeth, these grooves and primary ridges are poorly developed. Separated by shallow grooves, some ridges are developed in both lobes. The mesial lobe is relatively flat and long, whereas the distal lobe is convex and short. The details of the lingual surface are obliterated by tooth wear. The enamel layer can be observed on the labial side of the crown, but not on the lingual side.

On both dentaries, there are 10 teeth in the tooth rows. The tooth row is nearly straight. The left tooth row is 50 mm long and the right tooth row 54 mm (Fig. 5B). The last two teeth are located medial to the rostral slope of the coronoid process. However, the caudalmost tooth is rostral to the apex of the coronoid process unlike ceratopsids, in which the tooth row extends caudal to the apex. Replacement teeth are present for first, third, and fifth dentary teeth on both right and left tooth rows. As in the maxillary teeth, there is only one replacement tooth for each tooth position. The crowns of re-

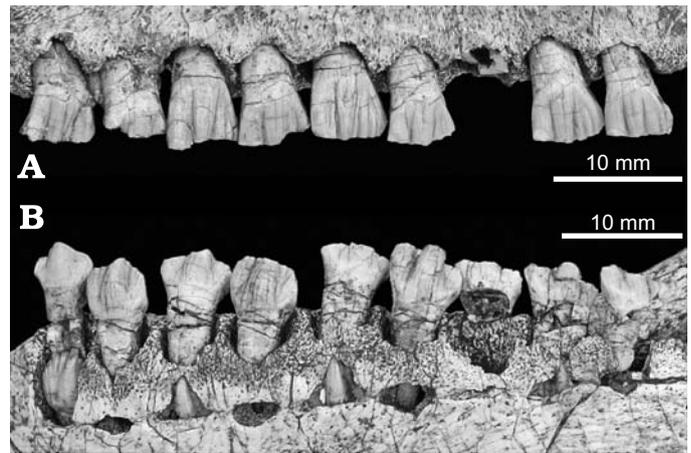


Fig. 5. Ceratopsian dinosaur *Psittacosaurus major* Sereno, Zhao, Brown, and Tan, 2007, new cranial specimen CAGS-IG-VD-004 from the Early Cretaceous Lujiatun Bed of Yixian Formation near Beipiao City, Liaoning Province, China. **A.** Right maxillary tooth row in labial view. **B.** Right dentary tooth row in lingual view.

placement teeth for both left and right first dentary teeth are well exposed, showing circular to subcircular outlines. The crowns of functional teeth are approximately 5 to 6 mm long mesiodistally and 3 to 4 mm wide linguolabially. On the lingual view of the functional tooth, the primary ridge is more prominent than that of maxillary tooth, both in width and height. Rostral and caudal lobes are of about the same size. The rostral lobe is more convex than the caudal lobe. There is an enamel layer on lingual side, but not on the labial side.

Discussion

Psittacosaurus is a well defined clade, and includes perhaps as many as 10 species: *Psittacosaurus mongoliensis* (Osborn 1923), *P. sinensis* (Young 1958), *P. meileyingensis* (Serenio et al. 1988), *P. xinjiangensis* (Serenio and Chao 1988), *P. neimongoliensis* (Russell and Zhao 1996), *P. ordosensis* (Russell and Zhao 1996), *P. mazongshanensis* (Xu 1997), *P. sibiricus* (Leschinskiy et al. 2000; Averianov et al. 2006); *P. lujiatunensis* (Zhou et al. 2006), and *P. major* (Serenio et al. 2007). Among them, four have been discovered from the Lower Cretaceous Jehol Group in western Liaoning Province, China: two (*P. lujiatunensis* and *P. major*) from the Yixian Formation near the Town of Shangyuan, and the other two (*P. meileyingensis* and *P. mongoliensis*) from the overlying Jiufotang Formation near the Town of Shengli. These two localities are about 80 km apart, and both in the vicinity of Chaoyang City, Liaoning Province. Historically, many described species of *Psittacosaurus* are based on single specimens and/or very incomplete material, a practice that needs to change as progress is made in understanding *Psittacosaurus*. *Psittacosaurus* is one of the most abundant dinosaurs known (Dodson 1990; Sereno 1990a; Russell and Zhao 1996). Juvenile specimens are very common (e.g., Meng et al. 2004). Despite a history of

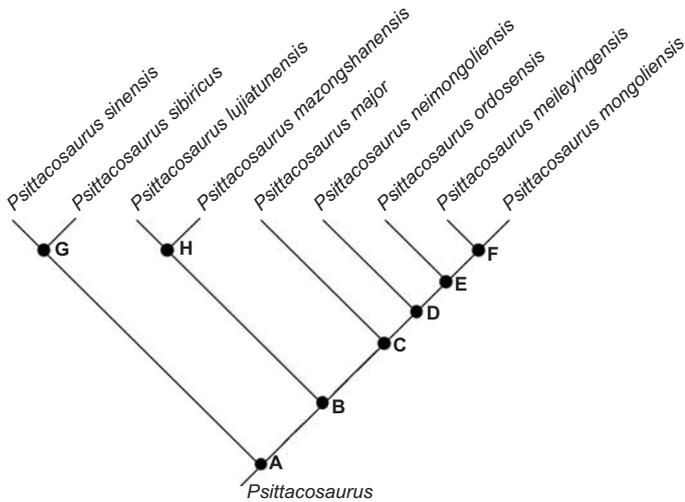


Fig. 6. The most parsimonious tree (length 58, consistency index 0.534, retention index 0.603) of *Psittacosaurus* obtained using the implicit enumeration option of the T.N.T. software (Goloboff et al. 2007). The data matrix of Averianov et al. (2006) was supplemented by coding 31 characters for *Psittacosaurus major* and *P. lujiatunensis* (see Appendix 1). *P. xinjiangensis* and *Psittacosaurus* specimen L0001 from the Yixian Formation of Liaoning (Xu and Wang 1998) were excluded due to large amount of missing data. Nodes are supported by the following unambiguous synapomorphies (in parenthesis are character numbers from Averianov et al.'s (2006) matrix). Node A: preorbital segment less than 40% of skull length (1), nasal extends ventrally beyond the external naris (5), ventral border of external naris is dorsal to the maxillary dorsal end (6), premaxillary teeth absent (8), and premaxilla-lacrimar contact present (9). Node B: lateral surface of the mandible straight (21). Node C: skull profile rounded (2). Node D: no synapomorphies. Node E: ventral margin of premaxilla-maxilla contact incised (11) and external mandibular fenestra present (20). Node F: "maxillary process" of maxilla present (14) and primary ridge on maxillary teeth caudoventrally angled (25). Node G: skull width exceeds skull length (3), premaxilla contacts jugal caudally (10), ventral postorbital horn present (15), rostral ramus of squamosal extends as far as to rostral wall of the supratemporal fenestra (17), quadrate shaft strongly arched in lateral view with caudal margin deeply excavated (19), and primary ridge on maxillary teeth weakly developed or absent (24). Node H: "maxillary process" of maxilla present (14) and denticles number on maxillary teeth equal to or more than 14 (26).

study stretching back more than 80 years, it is only in the past year (Zhou et al. 2006; Averianov et al. 2006; Sereno et al. 2007) that giant specimens of *Psittacosaurus* have been discovered. There are skulls of 190 mm in length or more, compared to 150 mm for a typical skull of *Psittacosaurus* (i.e., *P. mongoliensis*, *P. sinensis*, *P. neimongoliensis*, *P. meileyingensis*). Not only is absolute skull size very large, but Sereno et al. (2007) have demonstrated that skull size relative to body size is enlarged in *P. major*.

Several features of CAGS-IG-VD-004 support its placement in *P. major*. According to Sereno et al. (2007), *P. major* is diagnosed by its large skull relative to its postcranial skeleton, transversely narrow dorsal skull roof, very prominent dentary flange, ventrolaterally projecting jugal horn, absence of the external mandibular fenestra, and seven sacral vertebrae. CAGS-IG-VD-004 has a large skull, which is 192 mm long (203 mm in LH PV1, the holotype of *P. major*); however,

the relative length of its skull compared to the postcranial skeleton is unknown. Nevertheless, large skull size seems to be a feature shared by *P. major*, *P. lujiatunensis*, and *P. sibiricus*. CAGS-IG-VD-004 also has a transversely narrow dorsal skull roof as in *P. major*, in striking contrast to the condition in *P. lujiatunensis* and *P. sibiricus*. In *P. lujiatunensis*, the nasal is transversely wide, about twice the width of its prefrontal. As in *P. major*, CAGS-IG-VD-004 has a prominent dentary flange about one-third the depth of the mandibular ramus. Dentary flanges also exist in *P. lujiatunensis*, *P. sibiricus*, and *P. meileyingensis*, but they are not as prominent as in *P. major*. We do not consider the ventrolaterally projecting jugal horn in *P. major* a reliable feature, because the jugal horn always projects laterally in *Psittacosaurus*; and the caudal and/or ventral components are easily affected by preservation. However, the position of the jugal horn is a worthy feature. As noticed by Zhou et al. (2006), the caudally-placed jugal horn on the infratemporal bar is diagnostic of *P. lujiatunensis*, and this is also present in *P. major*. Closure of external mandibular fenestrae is another feature of *P. major*, but its condition in CAGS-IG-VD-004 cannot be verified. The large openings where the external mandibular fenestrae should be in CAGS-IG-VD-004 may either be real or the result of breakage of thin bone. Therefore, two out of six of *P. major* features (Sereno et al. 2007) are uniquely shared by LH PV1 and CAGS-IG-VD-004: the transversely narrow dorsal skull roof and the very prominent dentary flanges. Other autapomorphies of *P. major* noticed here include skull longer than wide, and the ventrally narrowing infratemporal fenestra.

Our cladistic analysis of *Psittacosaurus* recovered *P. major* at the base of a clade including *P. neimongoliensis*, *P. ordosensis*, *P. meileyingensis*, and *P. mongoliensis*, while this clade is the sister group of *P. lujiatunensis* + *P. mazongshanensis*; they together in turn constitutes the sister group of *P. sinensis* + *P. sibiricus* (Fig. 6). Although both *P. major* and *P. lujiatunensis* are from the same stratigraphic horizon (Lujiatun Bed of Yixian Formation) and same locality (Town of Shangyuan), *P. major* represents a long and narrow-skulled psittacosaur, and *P. lujiatunensis* represents a large broad-skulled psittacosaur. Although some may doubt the need for a second species of large-skulled *Psittacosaurus* from the Lujiatun beds of the Yixian Formation, our study supports the validity of *P. major*. Additional specimens appear referable to *P. major*, including one recently described by Lü et al. (2007).

Acknowledgements

We are grateful to Qiang Ji (Chinese Academy of Geological Sciences, Beijing, China) for supporting the project, Yu-Qing Zhang (Chinese Academy of Geological Sciences, Beijing, China) for preparing the specimen, and Ke-Qin Gao and Chang-Fu Zhou (Peking University, Beijing, China) for arranging to access specimens at Peking University. Review comments from David Norman (Sedgwick Museum, Department of Earth Sciences, University of Cambridge, Cambridge, UK) and Donald Brinkman (Royal Tyrrell Museum of Palaeontology, Drumheller, Canada) improved the manuscript and are greatly appreciated. Funding was

