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Taxonomy, Cranial Morphology, and Relationships of Parrot-Beaked Dinosaurs (Ceratopsia: *Psittacosaurus*)

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IN 1922, WELL-PRESERVED FOSSILS of the first parrot-beaked dinosaur were discovered in Early Cretaceous horizons in the Gobi Desert of Mongolia. Now referred to a single species, *Psittacosaurus mongoliensis,* these remains include a growth series from hatchlings to adults. In subsequent years, 15 species have been added to the genus *Psittacosaurus* and a second genus, *Hongshanosaurus,* was recently described, all from Early Cretaceous rocks in Asia. Although the second genus and about one-half of the species attributed to *Psittacosaurus* are potentially invalid, *Psittacosaurus* remains the most species-rich dinosaurian genus, with interspecific variation concentrated in the skull and dentition. This paper reviews evidence differentiating the named genera and species of psittacosaurs, outlines major cranial changes in a growth series from hatchling to adult in *Psittacosaurus mongoliensis,* and provides evidence of two species groups within the genus.

Introduction

Exceptional psittacosaur skeletons were discovered in 1922 as the first major paleontological find of the Asiatic Expeditions led by Roy Chapman Andrews of the American Museum of Natural History (Andrews 1932). Now attributed to a single species, *Psittacosaurus mongoliensis,* this material includes complete skulls and skeletons of hatchlings as well as adults (Coombs 1980, 1982). For many years, Osborn's two brief notes on *P. mongoliensis* (Osborn 1923, 1924) and a description of *P. sinensis* (Young 1958) provided most of the information available on psittacosaur morphology.

Recent Work. Sereno (1987) provided an overview of psittacosaur morphology. Portions of this dissertation were published, including the description of two new species (*P. meileyingensis, P. xinjiangensis;* Sereno and Zhao 1988; Sereno et al. 1988), the synonomy of several poorly known species (Sereno 1990a), and an overview of the morphology of the clade Psittacosauridae (Sereno 1990b). Although most of this overview can be found in You and Dodson (2004), reference is made only to the original source (Sereno 1990b).

Russian psittacosaurs, including a partial skull first reported by Rozhdestvensky (1955, 1960) at Shestakovo in Siberia, became the subject of a dissertation by Xijin Zhao under his direction. Renewed work at Shestakovo in 1994 has yielded more complete skeletal remains described as *P. sibiricus* (Averianov et al. 2006).

In China, *P. meileyingensis* (Sereno et al. 1988) was the first dinosaur described from the mid-Cretaceous Jehol fauna in the Yixian and Jiufotang Formations of Liaoning Province (Xu and Norell 2006). In subsequent years, scores of non-avian dinosaurs and basal avians have been described, including two new species of *Psittacosaurus, P. lujiatunensis* (Zhou et al. 2006b) and *P. major* (Sereno et al. 2007), and a new genus and species, *Hongshanosaurus houi* (You et al. 2003; You and Xu 2005).

FIGURE 2.1. Paleogeographic distribution of psittacosaurids and location of particularly fossiliferous or singular localities. Locality abbreviations, 1: Shestakovo (Siberia); 2: Delunshan (Xinjiang); 3: Bulasutuin; 4: Ondai Sair; 5: Khobur; 6: Oshih; 7: Ulan Osh; 8: Khuren Dukh; 9: Sharalin Ula; 10: Tsakurt; 11: Kharmin Us; 12: Suhongtu (Inner Mongolia); 13: Haratologay (Inner Mongolia); 14: Guyang (Inner Mongolia); 15: Hangginqi (Inner Mongolia); 16: Laiyang (Shandong); 17: Meileyingzi, Shangyuan (Liaoning). Four localities have yielded contemporaneous psittacosaur species: 12: *P. mongoliensis, P.* sp.; 15: *P. neimongoliensis, P. sinensis* (= *P. ordosensis*); 17 (Meileyingzi): *P. meileyingensis, P. mongoliensis;* 17 (Shangyuan): *P. lujiatunensis, P. major.*

Finally, a new species, *P.* sp., was discovered in 2001 in the Bayan Gobi Formation of the Inner Mongolia Autonomous Region (Fig. 2.1, locality 12; Fig. 2.2; Sereno et al. in review).

In recent years hundreds of specimens of *Psittacosaurus* have been collected in the vicinity of the type locality Oshih in Mongolia, and perhaps thousands more have been collected from the Lujiatun Beds of the Yixian Formation in Liaoning Province in China (Xu and Norell 2006). Among the many specimens from the Lujiatun Beds is a nest of hatchlings with an adult (Meng et al. 2004), a juvenile social group (Qi et al. 2007), and an adult preserving integumentary bristles (Mayr et al. 2002).

Psittacosaur "Biochron." The genus *Psittacosaurus* is so common in mid-Cretaceous vertebrate faunas of northern and central Asia that a "psittacosaur" fauna (Dong 1973) or "biochron" (Lucas 2006) has been proposed, beginning in the mid-Barremian (ca. 125 Ma) and extending to the mid-Albian (ca. 105 Ma; Lucas 2006), for a duration of about 20 million years. The interval with abundant psittacosaurs, however, may only have been half as long as previously reported. New radiometric dates from Liaoning Province (He at al. 2006; Zhou et al. 2007) confirm that the lowermost beds of the Yixian Formation (Lujiatun, Jianshangou), which include the oldest psittacosaurs, are no older than 123–125 Ma, straddling the Barremian-Aptian boundary (Gradstein et al. 2004). The youngest psittacosaurs in Liaoning (*P. mongoliensis, P. meileyingensis*) lie below the Aptian-Albian boundary (ca. 112 Ma), about 13 million years later.

Taxonomic Issues. Two genera and 17 species have been named over the years, all from Lower Cretaceous rocks in Asia

Table 2.1. Psittacosaurid Genera and Species

Taxon	Author	Skull	Skeleton	Senior synonym
Taxa regarded as valid				
Psittacosaurus sp.	Sereno et al. in review	√	√	
Psittacosaurus lujiatunensis	Zhou et al. 2006b	√	√	
Psittacosaurus major	Sereno et al. 2007	√	√	
Psittacosaurus meileyingensis	Sereno et al. 1988	√	–	
Psittacosaurus mongoliensis	Osborn 1923	√	√	
Psittacosaurus neimongoliensis	Russell and Zhao 1996	√	√	
Psittacosaurus sibiricus	Averianov et al. 2006	√	√	
Psittacosaurus sinensis	Young 1958	√	√	
Psittacosaurus xinjiangensis	Sereno and Zhao 1988	√	√	
Junior synonyms				
Protiguanodon	Osborn 1923			*Psittacosaurus*
Hongshanosaurus	You et al. 2003			*Psittacosaurus*
Protiguanodon mongoliense	Osborn 1923			*P. mongoliensis*
Psittacosaurus Protiguanodonensis	Young 1958			*P. mongoliensis*
Psittacosaurus youngi	Zhao 1962			*P. sinensis*
Psittacosaurus osborni	Young 1931	–	–	*P. mongoliensis*
Psittacosaurus guyangensis	Cheng 1983	–	–	*P. mongoliensis*
Nomina dubia				
Hongshanosaurus houi	You et al. 2003	√	–	? *P. lujiatunensis*
Psittacosaurus mazongshanensis	Xu 1997	√	–	?
Psittacosaurus ordosensis	Russell and Zhao 1996	√	√	? *P. sinensis*
Psittacosaurus tingi	Young 1931	–	–	?
Psittacosaurus sattayaraki	Buffetaut and Suteethorn 1992	–	–	Ceratopsia, incertae sedis

Note: The quality of cranial and postcranial remains for a given species is indicated by a checkmark for a relatively complete skull or articulated postcranial skeleton or a dash for more fragmentary material.

(Table 2.1). As I will argue below, more than one-half of these are junior synonyms, the principal taxonomic shortcomings being four in kind:

1. Fragmentary holotypic material that is difficult to assess
2. Immature material that may not yet have acquired species-specific cranial proportions or full development of processes and horns
3. Character states presented as diagnostic that have a multi-species distribution
4. Character states presented as diagnostic that are incompletely formulated or clearly correlated with other character states

Nothing can be done about problem 1, except to realize in future taxonomic work that the proper identification of most psittacosaur species requires relatively complete, well-prepared holotypic specimens for taxonomic resolution. For example, *P. guyangensis* (Cheng 1983) and *P. mazongshanensis* (Xu 1997) suffer from fragmentary holotypic specimens that allow only a limited number of comparisons. Unless there is a compelling reason, future holotypic material within *Psittacosaurus* should be limited to relatively complete skulls or skulls with associated skeletons.

Problem 2 is well exemplified by a new genus and species, *Hongshanosaurus houi* (You et al. 2003; You and Xu 2005). Based on a compressed, immature, isolated skull that is approximately one-fourth adult size, *H. houi* is difficult to validate as a taxon or to serve as the basis for referral of additional specimens. The solution to this problem is to identify post-hatching features that appear with maturity, down-weighting their absence in material that is clearly immature. In this review, I attempt to establish the outlines of post-hatching cranial transformation in *Psittacosaurus mongoliensis,* in order to identify relative shape or other changes that may have been misinterpreted as taxonomic signal in immature specimens.

Future holotypic referral should avoid specimens that are clearly immature, because many of the nuanced features that distinguish species, such as raised edges, eminences, flanges, and horns, appear late in post-hatching growth.

Problem 3 requires review, as in Xu and Zhao (1999) and in the present work, in order to better understand character distributions. In several instances in this review, we do not have enough comparative information to decide with confidence whether several features currently functioning as species differentia, such as the width of the distal end of the ischium in *P. neimongoliensis,* are truly diagnostic or just further examples of individual or size-related variation.

Problem 4 requires a more diligent, guarded approach to the formulation of characters. Sereno (1987: table 18), for example, listed a "dorsally positioned" external naris as a synapomorphy for *Psittacosaurus*. This has been classified as a "relative-geometric" character by Sereno (2007), because it draws attention to the dorsal position of the external naris relative to some other feature. That other feature, however, is not specified in the character, although that specification is key to its evaluation in any terminal taxon. A complete character can be constructed from associated text (Sereno 1987: 254), which pinpoints the ventral margins of the external naris and orbit as the relative relationship of interest (Table 2.2, character 2). A more considered (or complete) formulation of the character in this case makes it possible for another taxonomist to evaluate and score the condition among specimens.

The second aspect of problem 4, character correlation, violates character independence, an underlying assumption for character data under a parsimony criterion (Sereno 2007). Averianov et al. (2006: 363), for example, listed "skull width exceeds skull length" as well as "premaxilla length to height ratio less than 60%" as derived character states for two characters in *P. sibiricus*. The premaxilla in this species is particularly short anteroposteriorly. This condition, however, also results in a proportionately shorter skull, the postorbital portion of which then appears proportionately wider. Premaxilla length and skull length in this case appear to be dependent.

Present Approach. The approach to generic and species taxonomy in the present work acknowledges the utility of a differential diagnosis (Mayr et al. 1953), which lists both autapomorphies as well as particular feature combinations that differentiate species. Listing numerous symplesiomorphies in a species diagnosis as if it were a taxonomic key, however, is not illuminating or effective (Sereno 1990c: 16). In the diagnoses in their review of psittacosaur species, for example, Xu and Zhao (1999) mix together unique features with others that have limited distribution among psittacosaurs and still others that might characterize ceratopsians. In this review, I enumerate the most diagnostic features that are either unique or thought to be derived for the species at hand. These are often followed by other features that help to distinguish the species that have a limited distribution within *Psittacosaurus*. The characters in this paper that were compiled above the species level (Tables 2.2, 2.3) were formulated and edited with standards for completeness, testability, and independence in mind (Sereno 2007).

Institutional Abbreviations. AMNH: American Museum of Natural History, New York; BNHM: Beijing Natural History Museum, Beijing; CAGS-IG: Chinese Academy of Geological Sciences, Institute of Geology, Beijing; GI SPS: Geologic Institute, Section of Paleontology and Stratigraphy, Ulan Bator; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; JZMP: Jingzhou Museum of Paleontology, Jingzhou; LH: Long Hao Institute for Stratigraphic Paleontology, Hohhot; PIN: Paleontological Institute, Moscow; PKUP: Peking University Paleontological Collections, Beijing; PM TGU: Paleontological Museum, Tomsk State University, Tomsk; UCRC: University of Chicago Research Collection, Chicago; UGM: Urümqi Geological Museum, Urümqi; ZMNH: Zhejiang Museum of Natural History, Hangzhou.

Anatomical Abbreviations. +: positive sclerotic plate; −: negative sclerotic plate; 1–12: tooth or vertebral number; I–IV: quadrants I–IV in a sclerotic ring; a: angular; ac: acromion; ai: atlantal intercentrum; almf: anterolateral maxillary foramen; alp: alveolar pedestal; ana: atlantal neural arch; apd: articular surface for the predentary; apmf: anterior premaxillary foramen; aqj: articular surface for the quadratojugal; ar: articular; ari: attachment ridge; bo: basioccipital; bp: basal plate; bpt: basipterygoid process; bs: basisphenoid; bt: basal tubera; C: cervical vertebra; c: coronoid; ce: centrum; ci: crista interfenestralis; cnIII–XII: cranial nerves III–XII; co: coracoid; cof: coracoid foramen; d: dentary; D: dorsal vertebra; de: denticle; den: denticule; df: dentary flange; ec: ectopterygoid; emf: external mandibular fenestra; en: external naris; eo: exoccipital; f: frontal; flc: fenestra of the lacrimal canal; fm: foramen magnum; fob: fossa for the olfactory bulb; gl: glenoid; ic: intercoronoid; if: incisive foramen; imf: internal mandibular fenestra; j: jugal; jfo: jugal fossa; jh: jugal horn; k: keel; l: lacrimal (or left); lc: lacrimal canal; lf: lacrimal foramen; lhv: lateral head vein; lpmf: lateral premaxillary foramen; ls: laterosphenoid; m: maxilla; mfo: maxillary fossa; mp: maxillary protuberance; mpmf: medial premaxillary foramen; n: nasal; na: neural arch; ncr: nuchal crest; nsu: nasal sulci; oc: occipital condyle; od: odontoid; ofo: occipital fossa; op: opisthotic; p: parietal; pap: palpebral; pd: predentary; pl: palatine; pm: premaxilla; pmri: premaxilla-maxilla ridge; po: postorbital; pocr: postorbital crest; poh: postorbital horn; pojcr: postorbital-jugal crest; pojfo: postorbital-jugal fossa; pojh: postorbital-jugal horn; popr: paroccipital process; ppf: postpalatine foramen; pr: prootic; pra: prearticular; prf: prefrontal; prfcr: prefrontal crest; pri: primary ridge on crown; ps: parasphenoid; psqs: parietosquamosal shelf; pt: pterygoid; ptfo: pterygoid fossa; ptmr: pterygoid mandibular ramus; q: quadrate; qf: quadrate foramen; qj: quadratojugal; qjp: quadratojugal protuberance; r: rostral (or right); rf: replacement foramen; rp: retroarticular process; sa: surangular; saf: surangular foramen; sc: scapula; scb: scapular blade; scr: sclerotic ring; sh: shaft; so: supraoccipital; sp: splenial; sq: squamosal; st: stapes; stf: stapedial footplate; stp: sternal plate; sts: stapedial shaft; sym: symphysis; ts: triturating surface; v: vomer.

Systematic Paleontology

Dinosauria Owen 1842
Ornithischia Seeley 1888
Ceratopsia Marsh 1890
Psittacosauridae Osborn 1923

Phylogenetic Definition. The most inclusive clade containing *Psittacosaurus mongoliensis* Osborn 1923 but not *Triceratops horridus* Marsh 1889 (Sereno 2005; Sereno et al. 2005).

Diagnosis. Same as *Psittacosaurus.*

Included Genera. Psittacosaurus.

Remarks. Sereno (2005) provided the first phylogenetic definition for this taxon, when it appeared there were two genera of psittacosaurs (*Psittacosaurus, Hongshanosaurus*). With *Hongshanosaurus* reduced to a junior synonym of *Psittacosaurus* (see below), the familial taxon is redundant with the genus *Psittacosaurus*. "Psittacosauridae" and its vernacular "psittacosaurid" thus are not used in the remainder of this paper but could become "active" (Sereno et al. 2005) if additional genera allied with *Psittacosaurus* are described in the future.

***Psittacosaurus* Osborn 1923**

Synonomy. Protiguanodon, Hongshanosaurus.

Protiguanodon (Osborn 1923). The second genus and species described by Osborn (1923), *Protiguanodon mongoliense,* has been both regarded as a junior synonym of *P. mongoliensis* (Rozhdestvensky 1955, 1977; Coombs 1982) and referred to a new species, *Psittacosaurus protiguanodonensis* (Young 1958). Osborn's reasons for distinguishing these two Mongolian taxa were reevaluated by Sereno (1987, 1990a, b), and the two holotypic skeletons were found to lie within the variation present in the large collection of *Psittacosaurus mongoliensis* discovered by the American and Soviet-Mongolian expeditions. *Protiguanodon* and *Psittacosaurus protiguanodonensis* thus are regarded as junior synonyms of *Psittacosaurus* and *P. mongoliensis,* respectively (Table 2.1).

Hongshanosaurus (You et al. 2003). The genus *Hongshanosaurus* was erected on the basis of a dorsoventrally crushed, immature skull (IVPP V12704) about 35 mm in length. An adult skull over 150 mm in length was subsequently described and referred to the same genus and species (You and Xu 2005; IVPP V12617). The latter specimen clearly exhibits many of the derived features common to all psittacosaurs in the genus *Psittacosaurus* (Table 2.2). Only one feature was cited to support their phylogenetic interpretation of *Hongshanosaurus loui* as the sister taxon to all known species of *Psittacosaurus*—preorbital snout length approximately 50% of skull length (You and Xu 2005: 172). In other psittacosaurs the snout is proportionately shorter, measuring 40% or less of skull length.

Anteroventral crushing of the cranium in both specimens of *Hongshanosaurus houi* (You et al. 2003; You and Xu 2005), however, brings into question the supposedly longer snout proportions, as well as the additional features (oval shape of the external naris, orbit, and laterotemporal fenestra) cited as autapomorphies. In the better-preserved adult skull, the anterior end of the lower jaw protrudes slightly beyond the upper jaw (You and Xu 2005: fig. 1a); the upper portion of the cranium thus has been displaced posteroventrally, lowering its profile and lengthening the distance anterior to the orbit. Major cracks in this specimen course posterodorsally at a right angle to the direction of compression.

Overlooked in the description of *H. loui* is the presence of autapomorphies subsequently used to differentiate another psittacosaur species from the same horizon, *Psittacosaurus lujiatunensis* (Zhou et al. 2006b). These include the narrow prefrontal width (relative to nasal width) and the apparent contact between the jugal and quadrate (You et al. 2003; You and Xu 2005). Shared derived features between *H. houi* and *P. lujiatunensis* include the absence of an external mandibular fenestra and, as preserved in the adult skulls of both taxa, the presence of a prominent dentary flange with a squared anterior corner. It seems quite likely that these specimens pertain to the same species of psittacosaur, the most common dinosaur found in the Lujiatun Beds of the Yixian Formation. Distortion of cranial remains from this horizon is well known, as can be seen by comparison of the holotypic and paratypic skulls attributed to *P. lujiatunensis* (Zhou et al. 2006b). Why these similarities were not mentioned by Zhou et al. (2006b) in their description of *P. lujiatunensis* is not clear, as elsewhere many of the same authors criticized the adequacy of the holotypic skull of *H. houi* (Zhou et al. 2006a).

If these specimens pertain to the same species, as seems possible, a case could be made that *P. lujiatunensis* (Zhou et al. 2006b) is the junior synonym of *Psittacosaurus* (= *Hongshanosaurus*) *houi* (You et al. 2003). Reevaluation of the material, however, favors the course taken here, which is to regard *Hongshanosaurus* as a junior synonym of *Psittacosaurus* and *P. houi* as a nomen dubium. The immaturity of the holotypic skull of *H. houi* undermines any significance given to the absence of features that appear with age, such as the prominence of the jugal horn or presence of a dentary flange.

Several of the features linking *H. houi* and *P. lujiatunensis,* furthermore, are not uniformly present in their respective holotypic specimens. The prefrontal, for example, is proportionately narrow in the holotypic specimen of *H. loui* (You et al. 2003; IVPP V12704) but is subequal in width to the nasal in the referred adult skull (You and Xu 2005; IVPP V12617). In *P. lujiatunensis,* the prefrontal is shown as narrow relative to the nasal only in the paratypic skull (PKUP V1054); the nasal-prefrontal suture does not appear to be preserved in the holotypic skull (Zhou et al. 2006b; ZMNH M8137). Thus it is not clear if this feature is variable, or if the apparent variability is simply an artifact of preservation. The thin medial edge of the prefrontal overlaps the nasal and is often partially broken away in specimens of *P. mongoliensis,* giving the prefrontal a proportionately narrower appearance. Finally, jugal-quadrate contact is an autapomorphy of *P. lujiatunensis* preserved in both holotypic and paratypic skulls (Zhou et al. 2006b). Such contact may occur in the holotypic specimen of *H. loui* (You et al. 2003), although the posterior end of the bone is not well preserved. Jugal-quadrate contact is shown only on one side of the referred skull of *H. loui* (You and Xu 2005). The variability of this feature, thus, may also be a consequence of preservational factors.

Given the tremendous abundance of psittacosaur remains that were available by 2003 from the Lujiatun Beds of the Yixian Formation, it is unfortunate that *Hongshanosaurus loui* and *Psittacosaurus lujiatunensis* were not established on the basis of mature, well-prepared skeletons with complete skulls as in *P. major* (Sereno et al. 2007). If *Hongshanosaurus loui* and *Psittacosaurus lujiatunensis* represent the same species within *Psittacosaurus,* the latter would be a junior synonym of the former. It seems most prudent, however, to tentatively recognize the species *P. lujiatunensis* on the basis of its more complete, more mature, and less distorted holotypic and paratypic skulls (ZMNH M8137, PKUP V1054). Following this course, the species *H. loui* is here regarded as a nomen dubium, because of the crushed, immature state of the holotypic specimen. It seems likely that the referred adult skull can be shown to pertain to *P. lujiatunensis*.

Known Distribution. Psittacosaur distribution is currently limited to northeast Asia, with specimens found as far north as Siberia, as far east as Japan, as far west as Xinjiang, and as far south as Shandong (Fig. 2.1; Lucas 2006). Poorly preserved jaw fragments from Thailand (Buffetaut and Suteethorn 1992) are not regarded here as referable to the genus *Psittacosaurus* (see "Systematic Paleontology").

Diagnosis. Ceratopsian dinosaurs with (1) preorbital skull less than 40% of skull length, (2) external naris with ventral margin dorsal to that of the orbit, (3) nasal internarial process extending ventral to external naris, (4) rostral-nasal contact present, (5) premaxilla dorsolateral process maximum width subequal to dorsoventral orbital diameter, (6) premaxilla-prefrontal contact present, (7) premaxilla-jugal approximation or contact present, (8) maxillary fossa, (9) maxillary protuberance, (10) fenestra of the lacrimal canal, (11) antorbital fenestra and fossa absent, (12) postorbital posterior process extends along the entire supratemporal bar, (13) end of squamosal anterior process situated on the dorsal aspect of the postorbital, (14) pterygoid with neomorphic palatal lamina forming the basal plate, (15) pterygoid with hypertrophied mandibular ramus, (16) medial quadrate condyle planar, (17) laterally divergent palpebral with transverse posterior margin, (18) predentary with very short, tongue-shaped ventral processes, (19) predentary with semicircular anterior margin, (20) dentary with ventral ridge or flange, (21) articular with planar surface for quadrate condyles, and (22) dentary teeth with bulbous cone-shaped primary ridge with secondary ridging (see Table 2.2).

***Psittacosaurus* sp. Sereno et al. (in review)**
Figure 2.2

Holotype. LH PV2, skull and articulated skeleton.

Type Horizon and Locality. Bayan Gobi Formation (Aptian); N 40° 59′ 42.4″, E104° 3′ 53.8″, southwest of Suhongtu, Nei Mongol Autonomous Region, People's Republic of China (Fig. 2.1, locality 12).

Diagnosis. Psittacosaur characterized by autapomorphies including (1) pyramidal horn on the postorbital bar composed almost entirely of the postorbital, (2) postorbital-jugal fossa, (3) minimum width of the postorbital bar approximately 50% the width of the base of the process, (4) retroarticular process deflected posteromedially at an angle of 40° from the axis of the mandible.

Other features with limited distribution among psittacosaur species include preorbital snout length 35% the length of the skull, a ventrolaterally projecting pyramidal jugal horn, a low quadratojugal eminence, no development of dentary flanges or an external mandibular fenestra, and maxillary and dentary tooth rows limited to eight teeth.

Remarks. The holotypic specimen of *P.* sp. is a fully mature individual showing complete fusion at the mandibular symphysis and within the axial column (Fig. 2.2A). The skull is slightly fractured and twisted in dorsal view but otherwise superbly preserved. The skeleton is preserved in three-dimensions, including a fully articulated ribcage with a gastrolith mass. The specimen is thus well preserved for identifying species-level features. The pyramidal postorbital horn is preserved on both sides (Fig. 2.2B) and differs in shape and composition from that in *P. sinensis,* where the horn is more elongate and split between the postorbital and jugal. Just dorsal to the horn, the postorbital bar is very narrow. The posterior process of the postorbital is deeply emarginated and rather narrow in lateral view as a result. The edge of the emargination terminates as a straight, horizontal crest positioned below the center of the body of the postorbital.

P. sp. constitutes yet another pattern of character states not

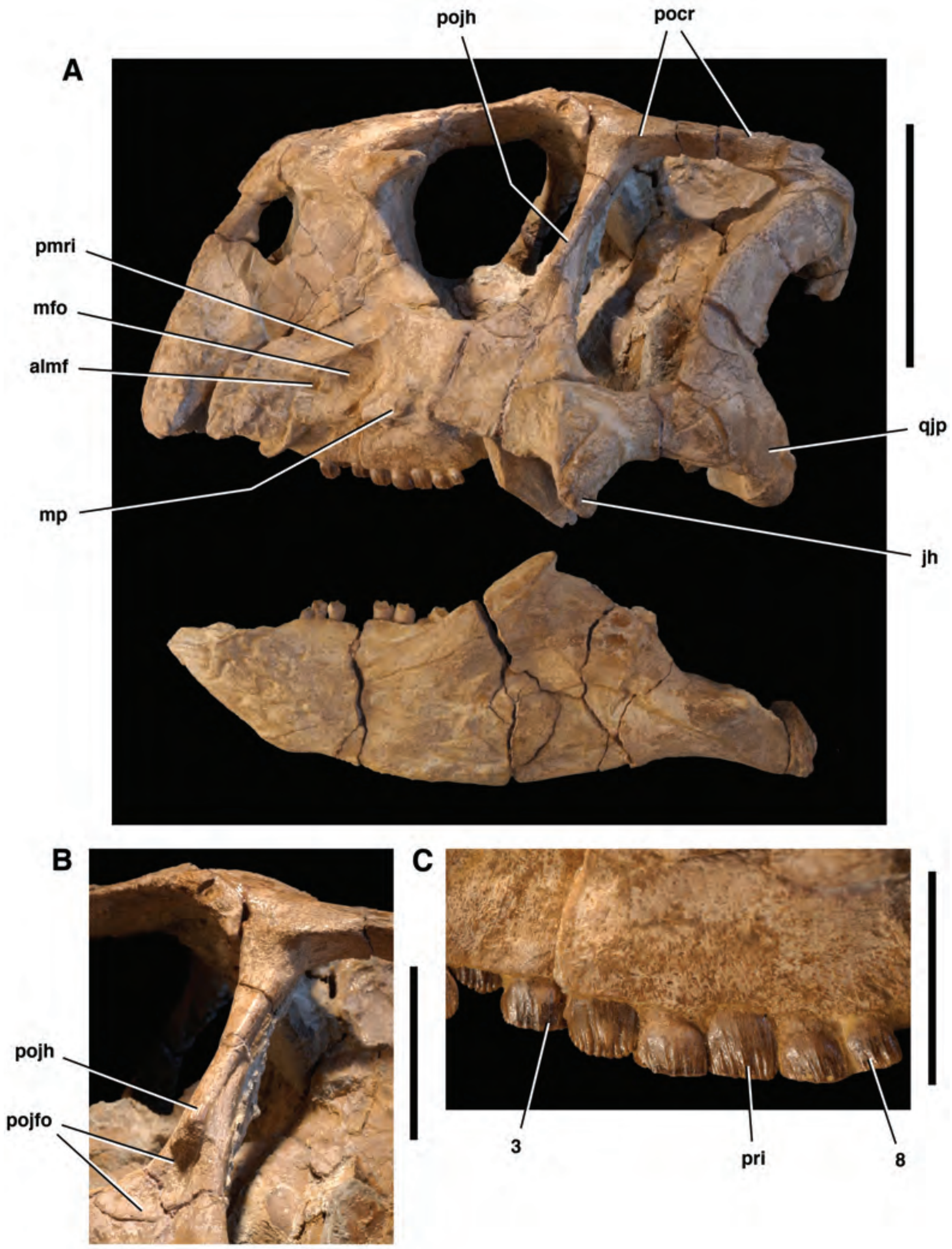


FIGURE 2.2. *Psittacosaurus* sp. (LHPV2). Skull in (A) lateral view; (B) enlarged view of postorbital-jugal horn in lateral view; (C) enlarged view of maxillary crowns in lateral view. Scale bars are (A) 4 cm; (B) 2 cm; (C) 1 cm. Reproduced in color on the insert.

previously reported within *Psittacosaurus* (Sereno et al. in review). The three autapomorphies listed above seem to be uniquely expressed in *P.* sp. The pyramidal horn on the postorbital bar has a rather smooth surface and is constructed solely of the postorbital, rather than a combination of the postorbital and jugal as in *P. sinensis*. The straight crest on the body of the postorbital (Fig. 2.2B) contrasts with the arched crest in *P. mongoliensis* and *P. sinensis*. The strong medial deflection of the retroarticular process is also unique among psittacosaur species. All of these features are preserved on both sides of the skull.

A relatively small-bodied species, *P.* sp. has skull and skeletal lengths comparable to those of *P. sinensis* (Young 1958; Sereno 1987). The skull, in addition, has a preorbital length of about

35% of skull length, a postorbital horn and associated jugal fossa, and low quadratojugal eminence. There is no development of a dentary flange, and only eight teeth in maxillary and dentary tooth rows (Fig. 2.2C). These features more closely resemble the condition in *P. sinensis* than in *P. mongoliensis* or *P. lujiatunensis*. However, *P.* sp. more closely resembles *P. mongoliensis* than *P. sinensis* in other regards, such as the lack of shortening of the lower jaw relative to the upper jaw, maxillary and jugal fossae, a ventrolaterally projecting jugal horn, and an arched crest on the body of the postorbital.

Psittacosaurus lujiatunensis **Zhou et al. 2006b**

Holotype. ZMNH M8137, skull with lower jaws (Zhou et al. 2006b: fig. 2).

Paratypes. ZMNH M8138, skull with jaws and cervicals 1–3; PKUP, V1053, juvenile skull with fragmentary lower jaws (Zhou et al. 2006b: fig. 4); PKUP V1054, adult skull with lower jaws, proatlas and atlas (Zhou et al. 2006b: fig. 3).

Type Horizon and Locality. Lujiatun Beds, lowermost Yixian Formation (late Barremian or earliest Albian); Lujiatun (near Beipiao), Liaoning Province, People's Republic of China (Fig. 2.1, locality 17).

Revised Diagnosis. Psittacosaur characterized by autapomorphies including (1) prefrontal width less than 50% that of the nasal, (2) quadratojugal-squamosal contact along anterior margin of quadrate shaft, and (3) jugal-quadrate contact posteroventral to the laterotemporal fenestra.

Other features with limited distribution among psittacosaur species include preorbital snout length equal to 35% skull length, a ventrolaterally projecting pyramidal jugal horn, absence of a horn on the postorbital bar, a central jugal fossa, a low quadratojugal eminence (paratypic skulls; PKUP V1053, V1054), strong dentary flange with anterior corner, external mandibular fenestra closed, and maxillary and dentary tooth row limited to eight teeth.

Remarks. The revised diagnosis emphasizes three autapomorphies that were cited in the original diagnosis but mixed with features that have a much broader distribution, such as closure of the mandibular fenestra (Zhou et al. 2006b). One feature is shared only with *P. major,* a fossa on the broad anterior ramus of the jugal, here termed the central jugal fossa. Another feature, a ridge ascending from the maxillary protuberance, is present in two other species, *P. major* and *P. meileyingensis*. *P. lujiatunensis* lacks the very narrow nasal and frontal proportions and the elongate basipterygoid processes in *P. major* (Sereno et al. 2007). *P. lujiatunensis* is probably closest to *P. major,* both of which come from the Lujiatun Beds of the Yixian Formation. Future comparative study of additional skulls and skeletons will either verify their distinguishing features or suggest that they represent variants of a single species.

Psittacosaurus major **Sereno et al. 2007**

Figures 2.3–2.6

Holotype. LH PV1, skull and skeleton (Sereno et al. 2007).

Notable Referred Specimens. JZMP-V-11, skull and skeleton (Lü et al. 2007); CAGS-IG-VD-004, partial skull (You et al. 2008).

Type Horizon and Locality. Lujiatun Beds, lowermost Yixian Formation (late Barremian or earliest Albian); Lujiatun (near Beipiao), Liaoning Province, People's Republic of China (Fig. 2.1, locality 17).

Revised Diagnosis. Psittacosaur characterized by autapomorphies including (1) maximum width across nasals and interorbital frontal width subequal to maximum width of the rostral, (2) tall subtriangular laterotemporal fenestra with anteroposterior width of the ventral margin approximately 25% of dorsoventral height, (3) anterior ramus of jugal convex (best seen in dorsal view), (4) elongate basipterygoid processes subequal in length to the body of the basisphenoid as measured from the notch between the processes to the basal tubera, (5) hypertrophied dentary flange with anterior corner approximately 30% of the depth of the dentary ramus and with only a short gap to the predentary, and (6) seven sacral vertebrae (addition of one dorsosacral).

Other features with limited distribution among psittacosaur species include preorbital snout length 33% of skull length, a ventrolaterally projecting pyramidal jugal horn, closure of the external mandibular fenestra, and maximum depth of the angular greater than that for the surangular. Sereno et al. (2007) listed among diagnostic features the relative size of the skull, which is approximately 40% of trunk length (Lü et al. 2007). This proportion, however, characterizes several psittacosaur species, including cf. *P. lujiatunensis* (Mayr et al. 2002), *P. xinjiangensis* (Sereno and Zhao 1988), and *P. sinensis* (Young 1958). *P. mongoliensis,* with a skull length only 30% of trunk length, is either primitive among psittacosaurs or has reverted back to a proportion common to many other small-bodied ornithischians. You et al. (2008: 195) also noted the narrow width of the ventral portion of the laterotemporal fenestra as characteristic of *P. major.* They proposed, in addition, that the maximum length of the skull exceeds its width across the jugal horns in this species. This proportion, however, is often subject to postmortem distortion and also changes with growth (the skull increasing in relative width). These two dimensions, furthermore, are subequal in the skull they referred to *P. major* (You et al. 2008: fig. $1C_2$).

Remarks. *P. major* and *P. lujiatunensis,* named independently from the same formation (Zhou et al. 2006b, Sereno 2007), are large-bodied psittacosaurs with adult skull length in excess of 200 mm, matched in size only by *P. sibiricus* (Averianov et al. 2006). Only a few of the many hundred specimens of *P. mon-*

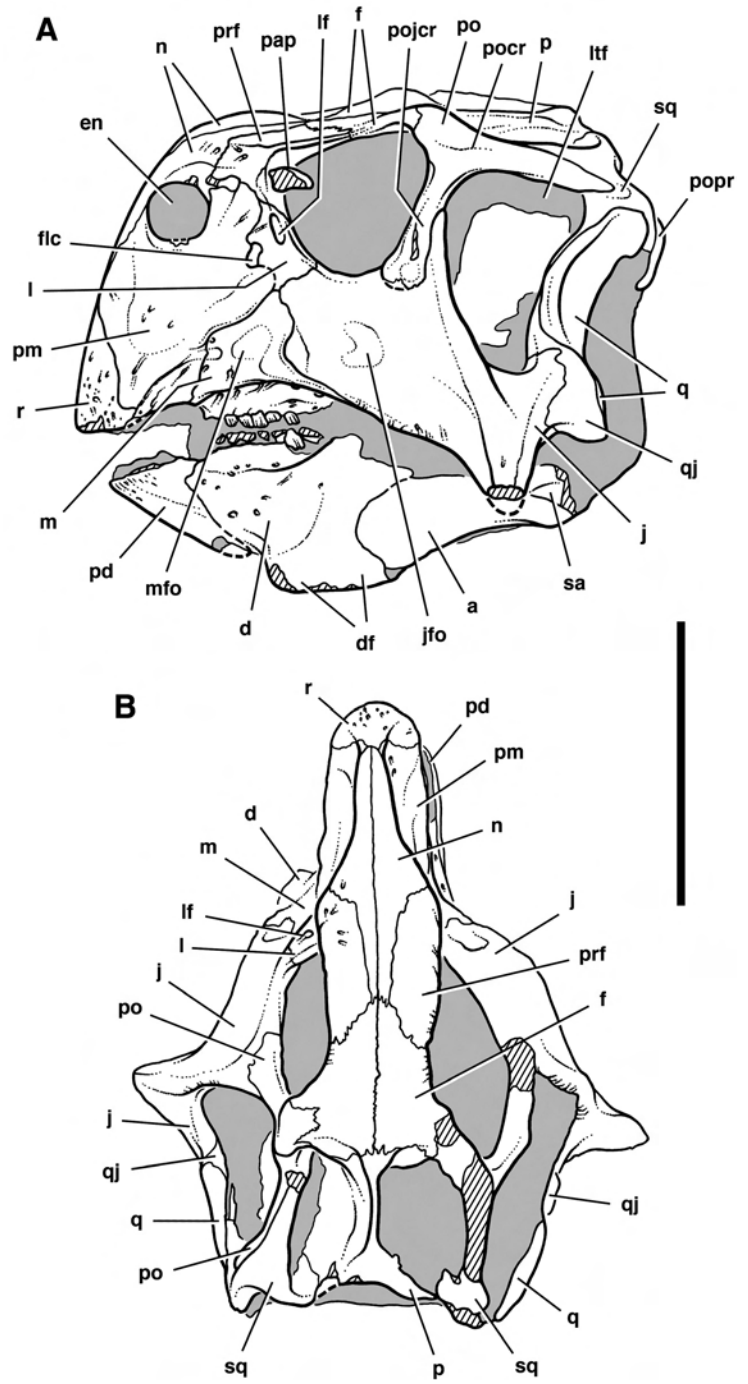


FIGURE 2.3.
Psittacosaurus major (LH PV1). Skull in (A) lateral view; (B) dorsal view. See text for abbreviations. Grey tone indicates matrix; cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 10 cm.

goliensis approach the size of these taxa (Sereno 1987). *P. major* is distinguished by the proportions of the nasal and frontal, which are narrower in *P. major* than in any other psittacosaur; by the narrow ventral margin of the laterotemporal fenestra that gives it a subtriangular shape in lateral view; by the convexity of the broad anterior ramus of the jugal that appears to have accommodated enlarged adductor musculature en route to the dentary; by basipterygoid processes that are approximately twice as long as in other psittacosaurs; by the extreme depth and anterior extension of the dentary flange, which approaches the predentary; by the narrow width of the prefrontal; and by the absence of jugal-quadrate and quadratojugal-squamosal contact, which is present in *P. lujiatunensis*. The presence of seven sacral vertebrae in *P. major,* one more than recorded in other psittacosaurs, cannot be assessed in *P. lujiatunensis* from published information.

A complete skull and skeleton that appears to be referable to *P. major* was published independently by Lü et al. (2007:

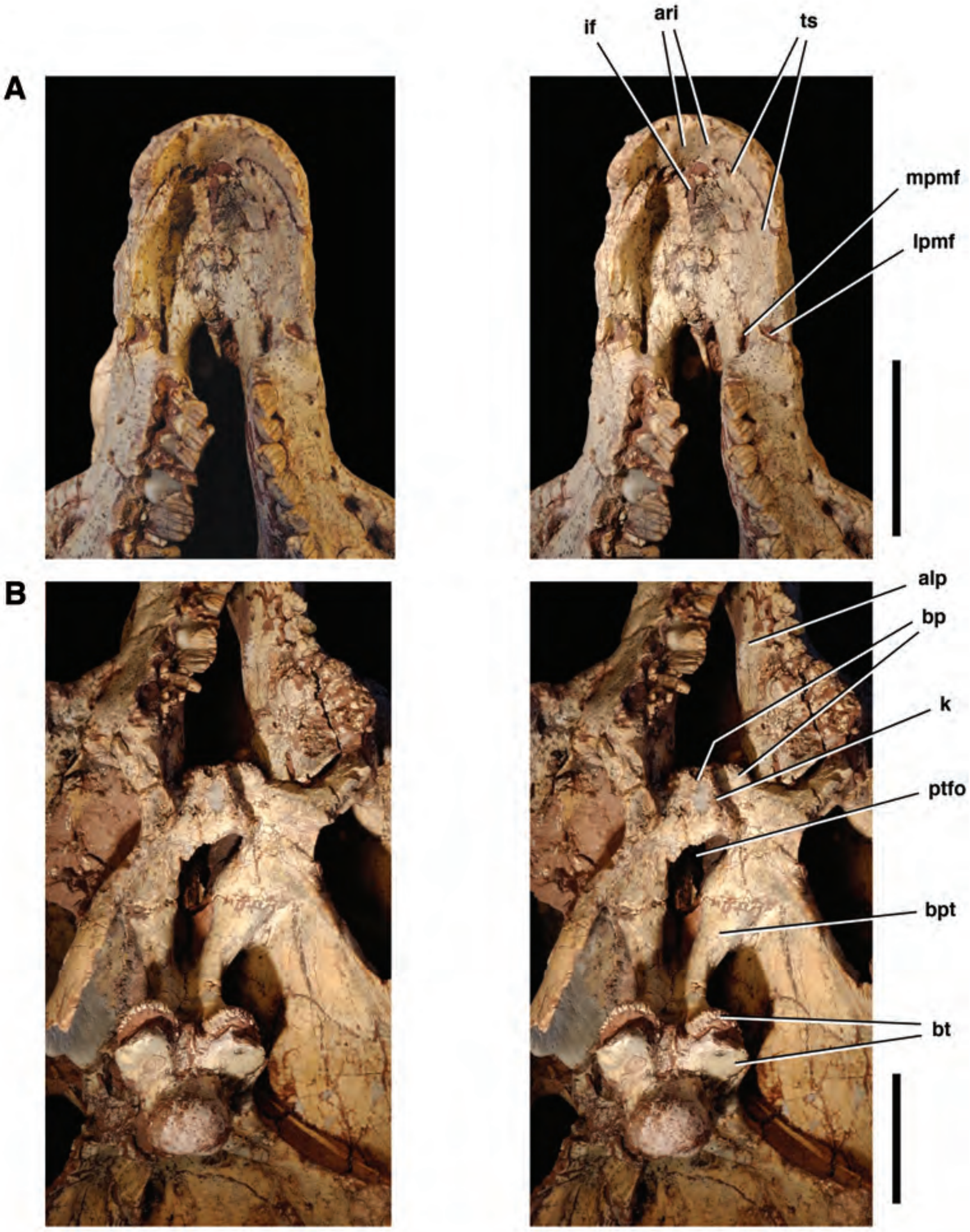


FIGURE 2.4. *Psittacosaurus major* (LH PV1). (A) Stereopairs of anterior palate in ventral view; (B) stereopairs of posterior palate and braincase in posteroventral view. See text for abbreviations. Scale bars are 3 cm. Reproduced in color on the insert.

figs. 1, 2). It shows similar development of head-trunk proportions, hypertrophy and anterior extension of the dentary flange, and absence of quadratojugal-squamosal contact. The jugal approaches and may contact the quadrate in this specimen. At least one trunk vertebra is missing, and the anteriormost sacral rib to the additional dorsosacral appears to have been broken (Lü et al. 2007: fig. 1).

P. major and *P. lujiatunensis* are differentiated based on skulls of mature individuals. The difference in the length of the basipterygoid processes is significant. The feature most likely attributable to preservational factors is the narrow width of the prefrontal in *P. lujiatunensis,* which may be due to breakage along its thin medial edge and is well documented only in a single paratypic skull (Zhou et al. 2006b: fig. 3). Similarly, the novel sutural contacts of the jugal and quadratojugal dorsal to the jaw articulation in *P. lujiatunensis* may be subject to variation; in *P. major* these bones are separated by only a narrow margin. These sutural contacts, however, have not been demonstrated to occur in other species. The condition in other well-preserved adult skulls and description of postcranial re-

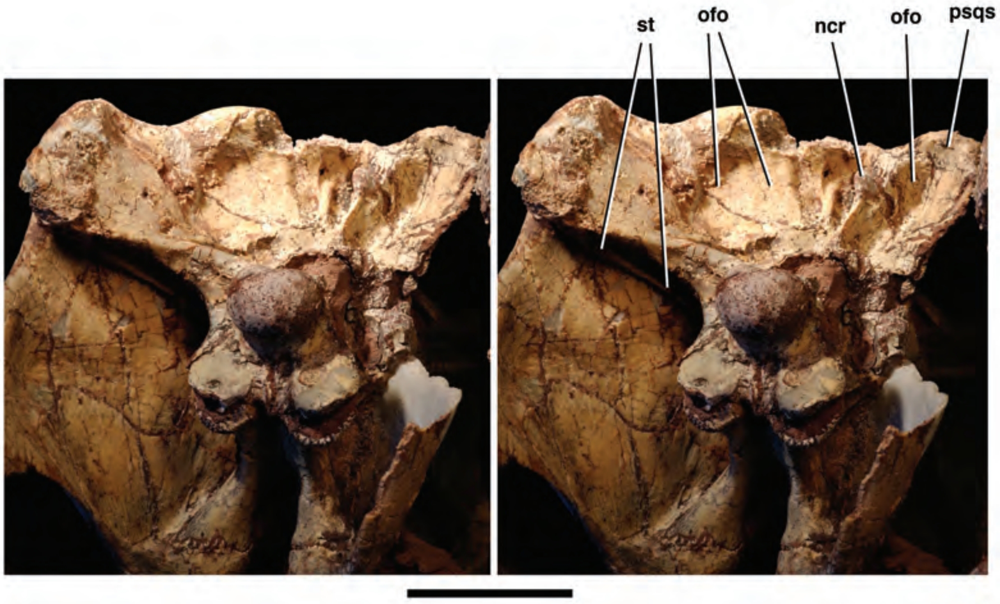


FIGURE 2.5. *Psittacosaurus major* (LH PV1) stereopairs of occiput in posteroventral view. See text for abbreviations. Scale bar is 3 cm. Reproduced in color on the insert.

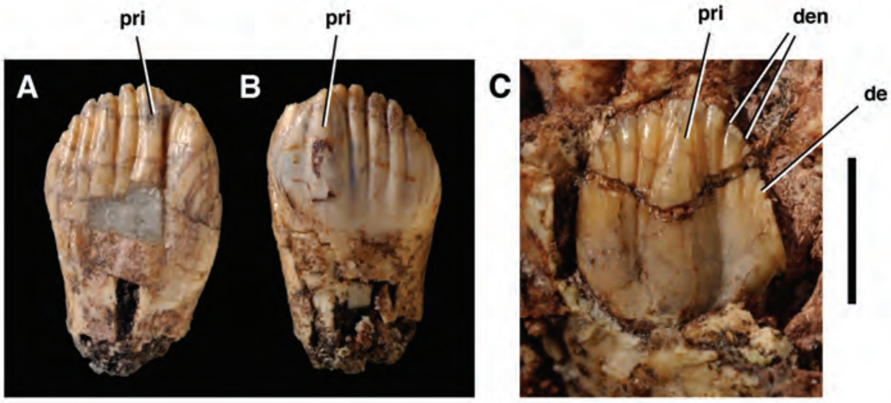


FIGURE 2.6. *Psittacosaurus major* (LH PV1). Maxillary crown in (A) lateral and (B) medial views; (C) dentary crown in medial view. Scale bar is 5 mm. Reproduced in color on the insert.

mains from the Lujiatun Beds are needed to verify the distinction between these two large psittacosaurs.

Psittacosaurus meileyingensis Sereno et al. 1988

Holotype. IVPP V7705, skull with jaws lacking the jugal horns and central body of the premaxilla (Sereno et. al. 1988: figs. 2, 3).

Notable Referred Specimens. CAGS-IG V330, adult skull lacking the anterior end of the snout and partial postcranial skeleton (Sereno et. al. 1988: figs. 8D, 9).

Type Horizon and Locality. Meileyingzi Beds, Jiufotang Formation (Aptian); Beipiao, Liaoning Province, People's Republic of China (Fig. 2.1, locality 17).

Diagnosis. Psittacosaur characterized by autapomorphies including (1) preorbital length only approximately 30% of skull length, (2) subtriangular orbit with acute ventral corner, and (3) rugose quadratojugal eminence.

Other features with limited distribution among psittacosaur species include a ridge ascending from the maxillary protuberance, a strong dentary flange, and a small external mandibular fenestra.

Remarks. *P. meileyingensis* was described on the basis of two adult skulls, one with a partial postcranial skeleton. As with *P. major* and *P. lujiatunensis* from the Yixian Formation, *P. mongoliensis* has been recovered along with *P. meileyingensis* in the overlying Jiufotang Formation (Sereno et al. 1988). In the case of the latter species, however, there is no question regarding its distinction.

Psittacosaurus mongoliensis

Figure 2.7

Synonomy. P. tingi, P. osborni, P. guyangensis (Table 2.1). Young (1958) regarded *P. tingi* (Young 1931) as a junior synonym of *P. osborni* (Young 1931), both species based on immature, fragmentary specimens from the Inner Mongolia Autonomous Region (Sereno 1987, 1990b). You and Dodson (2004: table 22.1, 490) listed *P. osborni* as a valid species, although it was not among the valid species cited in the text. In the partial skull referred to *P. osborni* (Sereno 1990a: fig. 15.5), the shallow angular and open external mandibular fenestra favors synonomy with *P. mongoliensis* (Sereno 1987, 1990b; Xu and Zhao 1999), although these features may occur in juvenile specimens of other species. Because several psittacosaur species have been recorded from Inner Mongolia (*P. mongoliensis, P. neimongoliensis, P. ordosensis, P. mazongshanensis*), reference to *P. mongoliensis* remains tentative.

Psittacosaurus guyangensis is based on the anterior portion of a skull (CAGS-IG V351), which is about two-thirds the size of the holotypic skull of *P. mongoliensis*. Disarticulated postcranial remains of several individuals of varying maturity were referred to this taxon from the same locality (Cheng 1983). In the skull piece, a maxillary fossa and pendant maxillary protuberance are present, the predentary extends to the anterior end of the snout, and there are at least nine teeth in the maxillary series (Cheng 1983: fig. 30). These features are consistent with *P. mongoliensis,* to which it was tentatively referred (Sereno 1987, 1990b; Xu and Zhao 1999) (Table 2.1). As with *P. osborni,* You and Dodson (2004: table 22.1, 490) listed *P. guyangensis* as a valid species, although it was not among the valid species cited in the text.

Holotype. AMNH 6254, skull that includes the right sclerotic ring, left stapes, and ceratohyals, and an articulated skeleton lacking only several anterior caudal vertebrae and most of the right hind limb (Sereno 1990b: fig. 15.2).

Notable Referred Specimens. AMNH 6253, fragmentary skull with articulated postcranial skeleton with gastrolith mass (holotype of *Protiguanodon mongoliense*) (Sereno 1990b: fig. 15.3); AMNH 6257, fragmentary vertebrae, distal left humerus, and the left carpus and manus lacking only the ulnare and terminal phalanx of digit IV; AMNH 6260, partial skull and skeleton with complete carpus and manus and skin impressions on metatarsus; AMNH 6534, skull with lower jaws and hyoids (Colbert 1945: fig. 5B), atlas and three anterior caudal vertebrae, fragmentary ribs, right scapulocoracoid, fragmentary right ilium, right femur, and the phalanges of right pes digit I; AMNH 6535, hatchling skull with jaws and partial skeleton including the atlas, dorsal vertebrae, ribs, both sternals, both scapulae, and both coracoids (Coombs 1982: fig. 4, pl. 14); AMNH 6536, crushed skull with lower jaws, sclerotic ring, atlas and axis, and articulated and disarticulated postcrania pertaining to many juvenile individuals including vertebrae, numerous partial and complete girdle elements, limb bones, an articulated hind limb and tail, and a partial left pes (Coombs 1982: figs. 1, 2, 5, 6).

Type Horizon and Locality. Khukhtek Formation (Aptian-Albian); Oshih, Ovorkhangai, Mongolian People's Republic (Fig. 2.1, locality 6; Lucas 2006).

Diagnosis. Psittacosaur characterized by autapomorphies including (1) a raised lip on the orbital margin of the prefrontal and (2) transverse expansion of the distal end of the ischial blade to approximately twice its width at mid-shaft.

Other features with limited distribution among psittacosaurs include the presence of a maxillary fossa, maxillary protuberance, and low dentary flange. The raised lip on the prefrontal appears among juveniles less than one-half adult size, and may show some variation in adults. It cannot be considered a mark of immaturity, however, as it is present in several adults in which many of the elements of the skull roof are coossified (e.g., AMNH 6254, 6534).

Remarks. *P. mongoliensis* has slightly longer preorbital proportions than any other psittacosaur species, usually measuring 37% rather than 30–35% of skull length. This proportional difference is subtle and is highly dependent on skull orientation and choice of relative metric, as discussed below (see description, general adult skull shape). For the measurements in this paper, the skull is oriented with the maxillary tooth row held horizontal.

Psittacosaurus neimongoliensis Russell and Zhao 1996

Holotype. IVPP 12-0888-2, articulated skeleton with skull (Russell and Zhao 1996: figs. 1, 3, 4)

Notable Referred Specimens. IVPP 12-0888-3, right side of skull and anterior portion of skeleton; IVPP 07-0888-11, partially disarticulated skull.

Type Horizon and Locality. Ejinhoro Formation (Aptian-Albian); 80 km west of Dongshen, Ordos Basin, Nei Mongol Autonomous Region, People's Republic of China (Fig. 2.1, locality 15; Dong 1993).

Diagnosis. Psittacosaur characterized by autapomorphies including (1) posterior end of the nasal contacting its opposite in the midline (not separated by the frontal), (2) frontal interorbital width approximately 30% of frontal length, and (3) postorbital extending along the margin of the orbit (rather than inset from the margin by the frontal in dorsal view).

Other features with limited distribution among psittacosaur species include skull length approximately 40% of trunk length, preorbital snout length approximately 35% the length of the skull, and absence of the external mandibular fenestra. The upper temporal bar angles posterolaterally, a condition

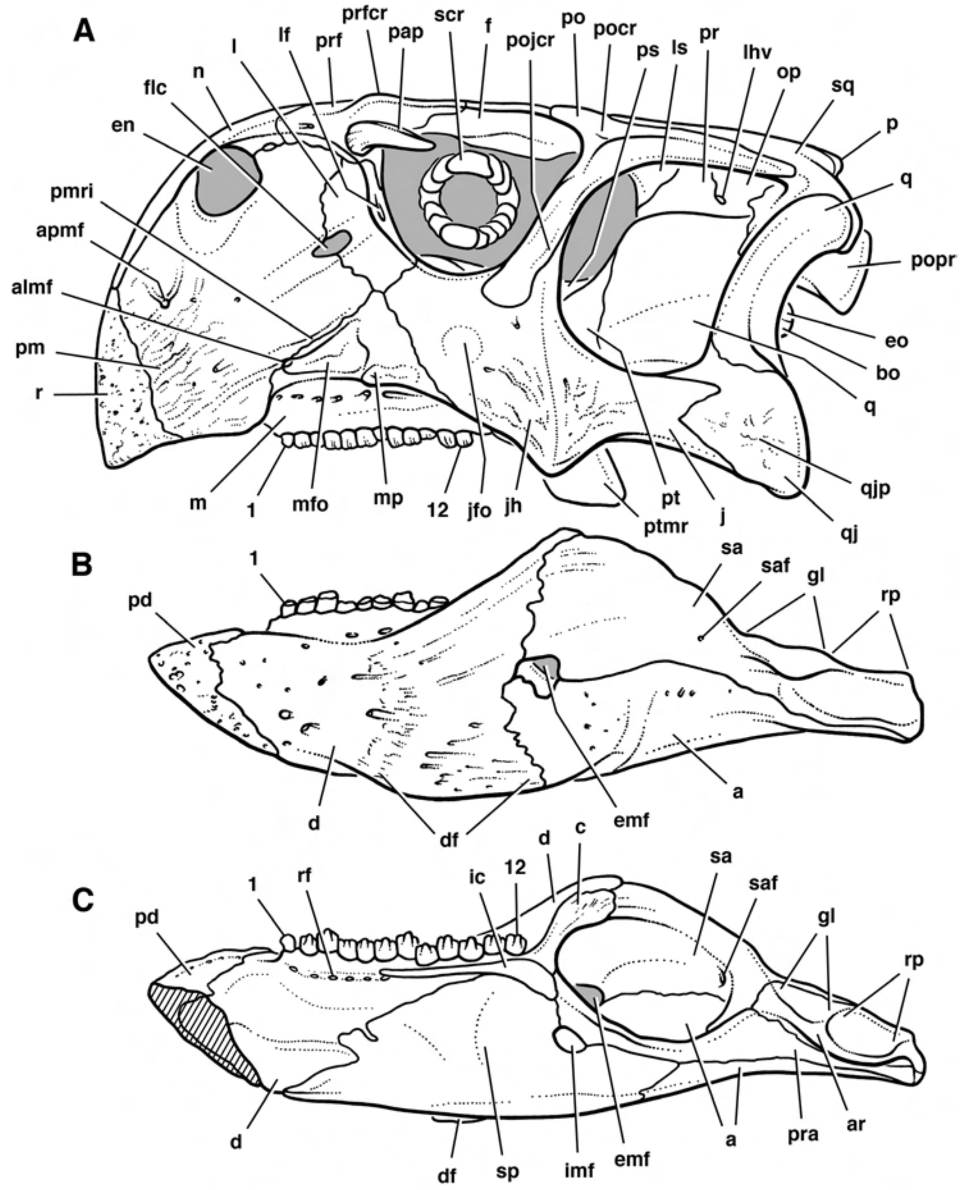


FIGURE 2.7. *Psittacosaurus mongoliensis* skull reconstruction based on the holotype (AMNH 6254) and referred skulls (AMNH 6534, PI/3779/10, 3779/12, 3779/20; IVPP V7668). (A) lateral view; (B) lower jaw in medial view. Cross-hatching indicates section through bone. See text for abbreviations.

similar to that in *P. sinensis,* although this may be due to damage to the posterior skull table.

Remarks. P. neimongoliensis appears to be most closely related to *P. mongoliensis.* There is no development of a postorbital-jugal horn, and the dentary flange is modestly developed. Unlike *P. mongoliensis,* however, the skull is large relative to the trunk, as in all other species. The preorbital portion of the skull, in addition, is less than 35% of skull length, the prefrontal does not have a raised lateral edge, the anterior process of the squamosal stops short of the body of the postorbital, the external mandibular fenestra is closed, and the distal end of the ischial blade is not broadened. The lack of maturity of the holotype is potentially problematic regarding a few of these features, such as the short preorbital proportions of the skull and the raised prefrontal lip. These features may only appear late in growth in *P. mongoliensis,* a species that is also present in similar-age rocks elsewhere in Inner Mongolia.

In addition to the second autapomorphy cited above, Russell and Zhao (1996) cited as diagnostic characters the length of the ischium (longer than the femur), its proportionately narrow distal end, and the shorter length of the squamosal anterior process. The former may be an artifact of measurement;

when ischial length is measured from the acetabulum to the distal end, its length in *P. neimongoliensis* is comparable to that in several other psittacosaurs including *P. mongoliensi*s (just longer than the femur). The other two features are plesiomorphic within *Psittacosaurus*. The diagnostic features of the species are currently limited to minor sutural variation and proportional differences on the skull table. More information is needed on the morphology of the holotype and referred specimens of *P. neimongoliensis* to confirm the distinctiveness of this species.

Psittacosaurus sibiricus **Averianov et al. 2006**

Holotype. PM TGU 16/4-20, articulated skeleton with skull (Averianov et al. 2006: fig. 2).

Notable Referred Specimens. PM TGU 16/4-21, skull with articulated postcranial skeleton; found with holotypic skeleton.

Type Horizon and Locality. Ilek Formation (Aptian-Albian); Shestakovo 3, Shestakovo, Kemerovo Province, Russia (Fig. 2.1, locality 1).

Diagnosis. Psittacosaur characterized by autapomorphies including (1) laterotemporal fenestra subequal in maximum height and anteroposterior length, (2) postorbital ventral process with subvertical orientation set at an angle of approximately 95° to the posterior process, (3) postorbital with small dorsal horn, (4) enlarged palpebral subequal in transverse width to the adjacent skull roof, (5) palpebral posterior margin nearly straight and angled anterolaterally, (6) predentary dorsoventrally compressed with a wedge-shaped profile with external margins set at approximately 30°, (7) angular with arcuate ventral extension of the dentary flange, (8) angular process projecting laterally at posterior end of the ventral flange of the mandible, and (9) 14 dorsal vertebrae (one added).

Other features with limited distribution among psittacosaur species include preorbital snout length 35% the length of the skull, a ventrolaterally projecting pyramidal jugal horn, and no development of a maxillary protuberance, maxillary fossa, or external mandibular fenestra.

Remarks. The holotypic specimen of *P. sibiricus* is a fully mature individual with coossification of several of the cranial sutures (Averianov et al. 2006). A distinctive species, *P. sibiricus* is characterized by a suite of autapomorphies. Of the 9 listed above, Averianov et al. (2006) either listed them as autapomorphies (1, 8, and 9) or described them in the text. I modified the first autapomorphy, which describes the shape of the laterotemporal fenestra, to avoid the use of skull length as a relative measure, the preorbital portion of which is subject to change in other species. I also combined the reorientation and straightness of the posterior margin of the palpebral, considering both of these to describe its altered shape. Finally, I excluded three autapomorphies listed by Averianov et al. (2006: 363) as too vaguely expressed to adequately test. These include the deep proportions of the premaxilla, the short medial process of the postorbital, and the deep cleft in the posterior ramus of the jugal. The first two cannot be evaluated in the articulated skull as the sutures are not shown. The edges of these bones may well have been subject to breakage when disarticulated, especially the thin edges of the premaxilla, but breakage is not indicated in available views of these bones. The posterior cleft in the jugal is difficult to differentiate from several other species on available evidence. Thus, further information is needed to shore up these features as viable autapomorphies.

Psittacosaurus sinensis **Young 1958**

Figures 2.8–2.10

Synonomy. P. youngi. From the same beds and near the localities of the holotypic specimen of *P. sinensis,* a second species was described, *P. youngi* (Zhao [Chao] 1962), based on a partial skeleton with a well-preserved skull (BNHM BPV149; Fig. 2.10). The diagnosis, however, included no autapomorphies to distinguish the specimen, which has more recently been referred to *P. sinensis* (Table 2.1; Sereno 1987, 1990a, b).

Holotype. IVPP V738, articulated skeleton of an adult individual; skull virtually complete, lacking only the palpebrals and the distal tip of the left jugal horn; postcranium lacking only the distal radius and ulna, carpus, manus, distal tarsals on both sides, and the distal three phalanges of digit III of the right pes; parts of the skeleton obscured by matrix include the occiput, vertebral centra, cervical ribs, coracoids, sternals, pubes, ischia, and most of the phalanges of the right pes (Young 1958: figs. 50–52, pls. 4, 5).

Notable Referred Specimens. IVPP V739 (Young 1958: fig. 54), partial articulated adult skeleton including the posterior dorsal vertebrae, sacrum, anterior caudal vertebrae, ribs, both ilia, proximal right ischium, femora, tibiae and fibulae; IVPP V740-1 (Young 1958: fig. 53), partial articulated adult skeleton including 15 articulated vertebrae (10 dorsal and 5 sacral vertebrae), left and fragmentary right scapulocoracoids, distal left humerus, both ilia lacking the postacetabular processes, proximal ischia, both pubes lacking only the distal portion of the prepubic process, right femur and right proximal fibula, and complete left hind limb lacking only the distal phalanges; IVPP V742, fragmentary skull with maxillary teeth; IVPP V743, maxilla with four teeth; several isolated teeth possibly representing more than one individual; IVPP V743a, fragmentary teeth and postcrania; IVPP V744 (Young 1958: fig. 55), anterior portion of a skull and fragmentary postcrania; IVPP V745, maxilla with four teeth and one isolated tooth; IVPP V749 (Young 1958: figs. 56, 57), skeleton with disarticulated skull elements including both maxillae and nasals, left jugal and exoccipital, supraoccipital, predentary, and articulated postcrania including 12 presacral vertebrae, right atlantal rib, posterior cervical and dorsal ribs, left sternal, both scapulocoracoids, right humerus, left ulna,

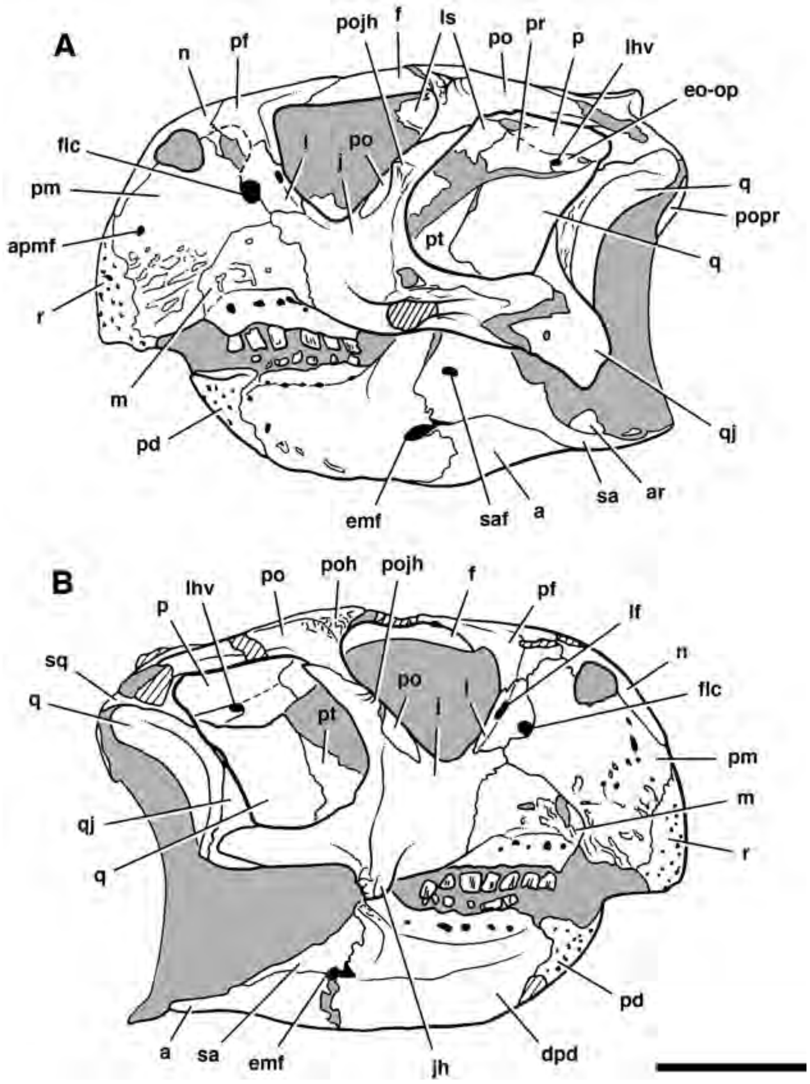


FIGURE 2.8.
Psittacosaurus sinensis (IVPP V738) skull in (A) left lateral view; (B) right lateral view. See text for abbreviations. Grey tone indicates matrix; cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 3 cm.

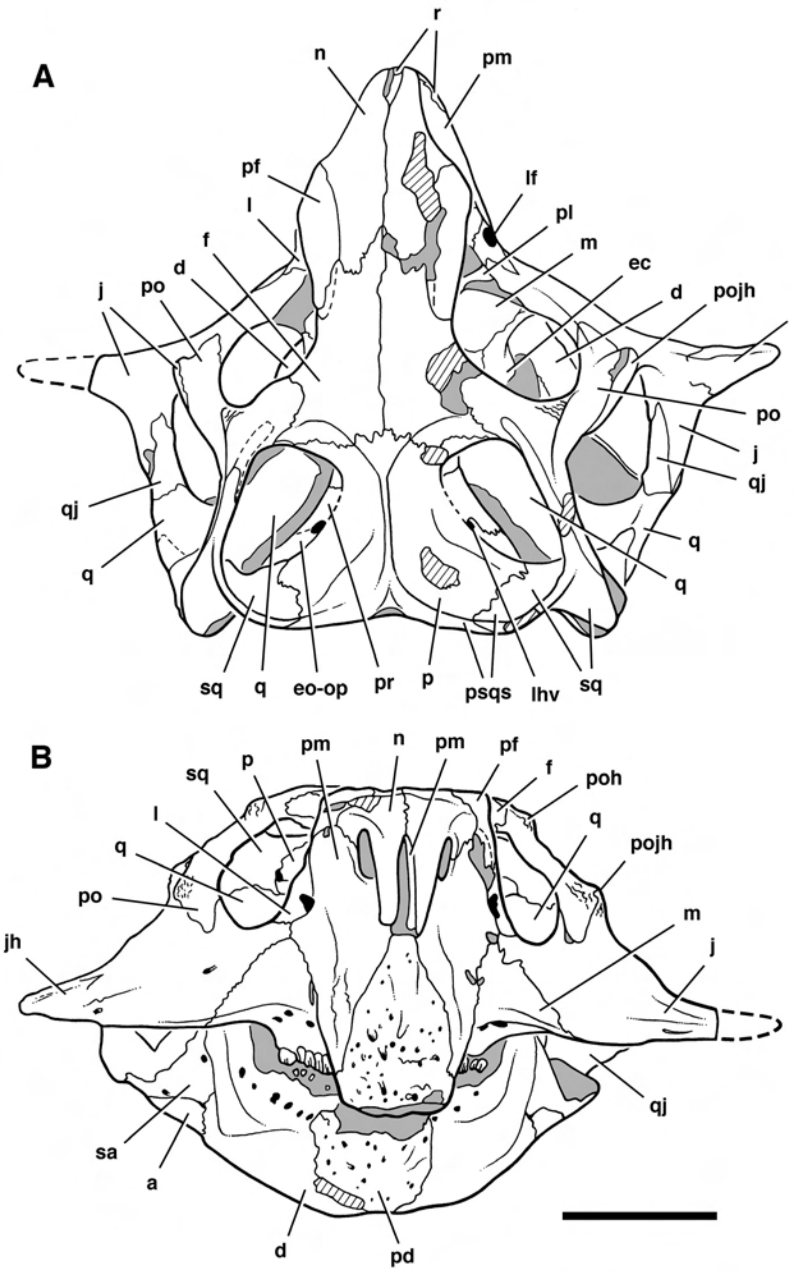
and partial right manus; associated disarticulated postcrania including the sacrum, fragmentary right ilium, both pubes, right humerus, right radius, right femur, right fibula, and partial pes; IVPP V750, series of dorsal ribs; IVPP V752, maxilla with five teeth, partial sacrum, and two distal femora; IVPP V753, internal skull mold; BNHM BPV149 (type of *Psittacosaurus youngi* Zhao 1962; Fig. 2.10), complete skull with fragmentary postcranium including the vertebral column from the posterior cervical to the anterior caudal vertebrae, fragmentary dorsal ribs, left ilium, proximal left ischium, and a fragment of the left pubis; CAGS-IG V808, two subadult skulls with articulated lower jaws; CAGS-IG unnumbered, excellent adult skull with articulated lower jaws and cervical vertebrae; CAGS-IG unnumbered, fragmentary skull with lower jaws.

Type Horizon and Locality. Qingshan Group, Doushan Formation; Doushan village, 5 km northwest of Laiyang, Shandong Province (Fig. 2.1, localities 15, 16).

Diagnosis. Small-bodied psittacosaur with cranial autapomorphies including (1) pendant rostrum that positions the ventral edge of the rostral bone below the level of the maxillary tooth row, (2) anteroventral processes of the nasal separated in the midline by a narrow gap, (3) short lower jaw that positions the anterior margin of the predentary in opposition to the premaxilla rather than the rostral, (4) posteriorly flaring skull roof with postorbital-squamosal bars diverging at an angle of approximately 30°, (5) absence of the maxillary fossa, (6) absence of the maxillary protuberance, (7) vertically elongate horn on the postorbital bar split between jugal and postorbital, (8) frontal participation in the supratemporal fossa, (9) ectopterygoid far removed from postpalatine foramen by broad maxilla-pterygoid contact, (10) internal mandibular fenestra reduced to a foramen, (11) absence of ossified tendons, (12) prepubic and postpubic processes transversely broad throughout their length (transversely wider than dorsoventrally tall), and (13) prepubic process projecting anteriorly as far as the preacetabular process of the ilium.

Remarks. The small-bodied *Psittacosaurus sinensis,* based on

FIGURE 2.9.
Psittacosaurus sinensis (IVPP V738) skull in (A) dorsal view; (B) anterior view. See text for abbreviations. Grey tone indicates matrix; cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 3 cm.



an articulated skeleton (Young 1958: fig. 52), is known from considerable skeletal material. Previous diagnoses for this species originally were short and sometimes inaccurate. Gastralia are not present in *P. sinensis* (contra Steel 1969: 39), and it is not plausible that *P. sinensis* be reduced to a junior synonym of *P. mongoliensis* (Rozhdestvensky 1955; Coombs 1982). The pendant form of the rostral in the holotypic skull is less apparent because the ventral tip of the rostral is broken away (Fig. 2.8). When reconstructed, it would extend below the level of the tips of the maxillary crowns, as in a referred skull (Fig. 2.10). *P. sinensis* shares several features with one or more additional species, including preorbital skull length of approximately 30% of skull length, the absence of an external mandibular fenestra or mandibular flange, and a short prepubic process.

Psittacosaurus xinjiangensis Sereno and Zhao 1988

Holotype. IVPP V7698, posterior portion of the skull including the jugal horn and palpebral and articulated skeleton lacking distal limb bones and tail (Sereno and Zhao 1988: figs. 2, 3, 4F, 6).

Notable Referred Specimens. IVPP V7702, jaw fragments of unknown association including right and left maxillae preserving five teeth and an anterior dentary fragment (Sereno

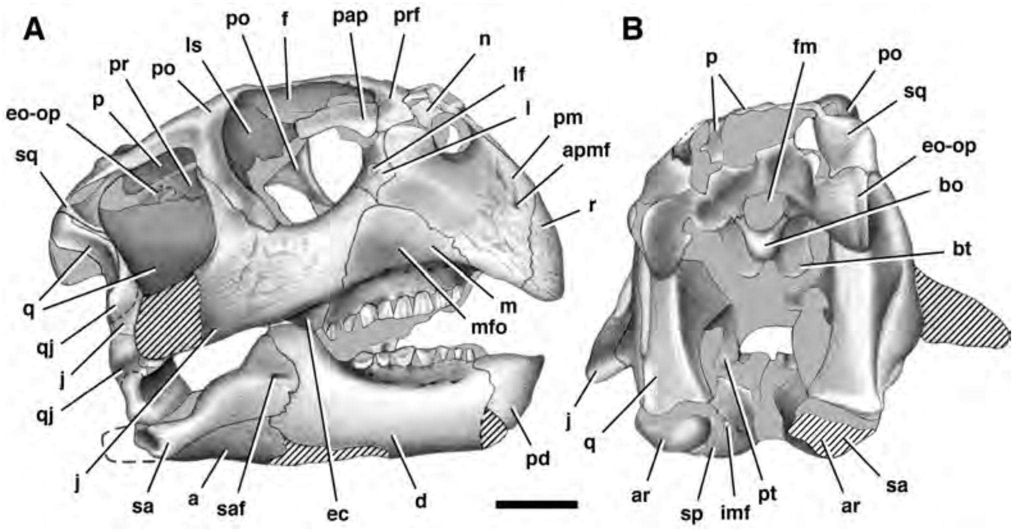


FIGURE 2.10. *Psittacosaurus sinensis* (BNHM BPV149) skull in (A) right lateral view; (B) posterior view. See text for abbreviations. Grey tone indicates matrix; cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 2 cm.

and Zhao 1988: fig. 5A); IVPP V7704, complete right maxilla with eight alveoli and left dentary fragment with erupting crown (Sereno and Zhao 1988: figs. 4A, B, 5C, D); IVPP field number 64047, fragmentary bones of several individuals including portions of the jugal, basioccipital and basisphenoid and an articulated series of mid-caudal vertebrae with ossified tendons (Sereno and Zhao 1988: figs. 4C–E, 8F); UGM XG94Kh201, skull fragments and partial articulated skeleton lacking the tail (Brinkman et al. 2001: figs. 3–7).

Type Horizon and Locality. Tugulu Group (Aptian), Delunshan, Junggar Basin, Xinjiang Uygur Autonomous Region, People's Republic of China (Fig. 2.1, locality 2).

Revised Diagnosis. Psittacosaur characterized by autapomorphies including (1) hook-shaped palpebral with V-shaped posterior margin, (2) dentary teeth with as many 21 denticles in the posterior center of the tooth row, (3) ossified tendons extending into mid-caudal vertebrae, and (4) narrow iliac postacetabular process with height at midlength less than 25% of the length of the process (as measured from the posterior edge of the ischial peduncle to the distal tip of the process).

Although relative preorbital skull length is not known, other features with limited distribution among psittacosaur species are discernable from preserved portions of the skull, including the absence of a quadratojugal eminence and dentary flange. Maxillary and dentary tooth rows appear to be limited to eight teeth.

Remarks. The denticle count of 21 in a dentary tooth of *P. xinjiangensis* is high compared to the figured crowns of other psittacosaurs. Caution is warranted in assessing this feature, as denticle count increases with maturity and varies according to tooth position. The highest denticle counts occur in crowns of mature individuals from the posterior center of the tooth rows, where they tend to reach maximum size. The ossified tendons are preserved in an isolated series of mid-caudal vertebrae.

The absence of ossified tendons in the mid- and distal tail in other psittacosaurs is based on well-preserved specimens of *P. mongoliensi*s (Sereno 1987), cf. *P. lujiatunensis* (Mayr et al. 2002), and *P. sinensis* (Young 1958).

The holotypic specimen of *P. xinjiangensis* appears to be a subadult individual. A referred adult individual form Urho (= Wuerho) in the Junggar Basin not far from the holotypic locality (Brinkman et al. 2001) has a femur length of 153 mm, or approximately one-third greater than that of the holotype (105 mm). Thus, some caution is in order regarding features observed in the holotype that may owe their lack of expression to immaturity, such as the absence of a quadratojugal eminence. The elongate postacetabular process of the ilium appears to be diagnostic, a process that has a height of at least 30% or more of its length in *P. mongoliensis* (Osborn 1924), *P. major* (Lü et al. 2007), *P. sinensis* (Young 1958), and *P. sibiricus* (Averianov et al. 2006). The more slender curved, or hooklike, shape of the prefrontal seems to be a good character, because the shape of this bone is broader in immature specimens of *P. mongoliensis*. A similar hooklike shape, however, may occur in juvenile specimens referred to *P. lujiatunensis* (P. Makovicky pers. com.). The holotype of *P. xinjiangenesis,* nevertheless, has reached adult size, as shown by a second specimen of similar size with fused sacral vertebrae (Brinkman et al. 2001).

The revised diagnosis excludes two characters previously listed by Sereno and Zhao (1988), the anteriorly flattened jugal horn and the curved distal end of the denticulate margin on the maxillary crowns, characters that appear elsewhere. The jugal horn, in particular, has a sharp edged anterior face in fully mature specimens of *P. mongoliensis, P. lujiatunensis,* *P. major,* and probably other species as well. The diagnosis, on the other hand, includes the unusual shape of the palpebral in the holotypic specimen, which has an unusually concave, or V-shaped, posterior margin (Sereno and Zhao 1988: fig. 4F). The palpebral varies considerably in shape among species but does not appear to undergo marked shape transformation during growth. Averianov et al. (2006) noted a size differential in the palpebral of *P. sibiricus* but did not note any shape differential. The occipital condyle in *P. xinjiangensis* appears small in both the holotype and a referred specimen, its transverse width less than one-half the width of the basal tubera (Sereno and Zhao 1988; Brinkman et al. 2001). In other species the condyle is usually more than one-half the width of the basal tubera, although this character may be influenced by exactly how the condyle is oriented and circumscribed.

NOMINA DUBIA

Psittacosaurus mazongshanensis. *P. mazongshanensis* is based on a fragmentary specimen preserving the lower jaws and portions of the maxilla (Xu 1997: fig. 3; IVPP V12165). The skull is preserved upside down, the dorsal skull roof eroded away, crushed, or covered by the lower jaws. The ventral margins of the dentaries are broken, eliminating the chance to determine the presence or strength of a dentary flange. Xu (1997) emphasized the strong development of the maxillary protuberance, the high number of denticles, the length of the secondary ridges in the dentary crowns, and the Y-shape and potential length of the snout. An exact denticle count, however, was never specified, and the figured crowns appear truncated by wear (Xu 1997: fig. 4). Denticle count varies along the tooth row in other psittacosaur species and is not sufficiently high in this case for distinction. Sereno (2000) questioned the validity of this species, as none of the features listed in the original diagnosis are unique. Averianov et al. (2006) reiterated the "Y-shaped lower jaw" as a diagnostic feature, although this appears to be an artifact of preservation (Zhou et al. 2006b). Zhou et al. (2006b: 112) regarded the pendant form of the maxillary protuberance to be a distinguishing feature, although this process is also pendent to some degree in *P. mongoliensis, P.* sp., and other species. Unfortunately, it is no longer possible to investigate these potential distinguishing features, as the maxillary protuberance and all of the teeth in the holotype have been lost (Zhou et al. 2006b). As none of these features are sufficiently documented for comparison, *Psittacosaurus mazongshanensis* is here considered a nomen dubium (Table 2.1).

Psittacosaurus ordosensis. The holotypic specimen of *P. ordosensis* (IVPP 07-08888-1) includes the ventral one-half of a skull and partial hind limb, although additional unprepared specimens were noted to exist (Russell and Zhao 1996). The limited information available is insufficient to distinguish this material from that of *P. sinensis* (Sereno 2000). Outstanding features shared by both include small body size (skull length approximately 100 mm), pendant anterior end of the upper jaw, short lower jaw with predentary tip opposing the premaxilla, a rudimentary maxillary fossa, and tooth rows limited to eight teeth. The tooth rows were described as straight in *P. ordosensis* by Russell and Zhao (1996) rather than concave as reported in *P. sinensis* (Sereno 1990b). In *P. sinensis,* however, the curvature is often very subtle (Young 1958: fig. 57). Furthermore, it is clear that the tooth rows in all psittacosaurs are laterally concave, such as those in *P. mongoliensis* and the recently described skull of *P. sibiricus* (Averianov et al. 2006: fig. 10A).

Xu and Zhao (1999: 80) added several other cranial features to the diagnosis of *P. ordosensis* such as an "eminence on caudal frontal" and "posterodorsal corner of the skull depressed." The dorsal aspect of the skull, however, is not preserved in the holotype specimen (Russell and Zhao 1996: fig. 5), and no other specimens are cited or figured. Additional study of the holotype and referred material may eventually show that diagnostic features do exist, or, at least, a diagnostic combination of features. For the time being, *P. ordosensis* is regarded as a nomen dubium.

Psittacosaurus sattayaraki. *P. sattayaraki* is based on a right dentary about 50 mm in length (TF 2449a), to which was referred another jaw fragment possibly pertaining to a maxilla (presumably TF 2449b; Buffetaut and Suteethorn 2002). Initially referred to *Psittacosaurus* without specific attribution (Buffetaut et al. 1989), the dentary was later made the holotype of a new species, *P. sattayaraki* (Buffetaut and Suteethorn 1992). Although these fragments add tantalizing information to the still poorly known terrestrial Cretaceous faunas of southeast Asia, assigning the holotypic dentary to Ceratopsia incertae sedis based on its stout proportions may be the most specific assignment possible (Sereno 2000). Unsatisfied with that reassessment, Buffetaut and Suteethorn (2002) have continued to claim that *P. sattayaraki* is a valid species referable to the genus *Psittacosaurus* and that the upper jaw fragment collected later at the site is properly referred to the species.

First, there is no basis for reference of the additional upper jaw fragment to the taxon, which was established on a dentary. The additional jaw fragment is very poorly preserved and figured (Buffetaut and Suteethorn 1992: fig. 2A, B). The authors are unsure whether it represents a right or left jaw fragment and leave open the possibility that some of its teeth were blunted by wear. They claimed that a "loose replacement tooth" from this specimen has a "strong primary ridge" (Buffetaut and Suteethorn 1992: 805). Unfortunately, there is no documentation of this crown in their papers, its possible wear facets, the described angle between crown and root, or any other feature beyond its comparable size and site of origin to justify their interpretation that this specimen might pertain to the same taxon, much less the same individual, as the holotype.

Second, their description of the "bulbous" primary ridge and "incipient" dentary flange in the holotype is poorly preserved on the original specimen and appears to be enhanced in their figures. The specimen was acid-etched, rather than mechanically prepared, and basal portions of the two most acomplete replacement crowns appear to have dissolved away. The bulbous form of the primary ridge is based on two partial crowns in the third and fifth alveoli. The more anterior of the two preserves only the apical margin and cannot establish the form of the primary ridge. Two drawings of this crown edge have been published (Buffetaut and Suteethorn 1992: fig. 3B; Buffetaut and Suteethorn 2002: fig. 1b), neither of which appears to precisely match the available photograph of the crown (Buffetaut and Suteethorn 1992: fig. 2C). The latest interpretation depicts the apical denticle above a widening primary ridge (Buffetaut and Suteethorn 1992: fig. 3B; b), but this drawing appears to show more of the crown than is actually preserved. The upper one-half of the more posterior crown is preserved and has also been depicted in two ways. The first drawing shows secondary ridges extending farther down the crown than the primary ridge (Buffetaut and Suteethorn 1992: fig. 3B). The most recent interpretation shows an asymmetrical, primary ridge that broadens toward the middle of the crown, although much less than is typical in psittacosaurs, in which the ridge is very prominent and occupies the middle section of the crown. The broadening of this ridge, in addition, cannot be verified in the only available photograph (Buffetaut and Suteethorn 1992: fig. 3B). The primary ridge may expand basally to some degree, although this should be documented with a properly lit, enlarged image or stereophotograph.

The "incipient" dentary flange, likewise, is not apparent in the only available photograph (Buffetaut and Suteethorn 1992: fig. 2E). The ventral contour of the dentary does not match their drawing, which depicts a discrete ridge toward the rear of the dentary ramus (Buffetaut and Suteethorn 1992: fig. 3C). The psittacosaur dentary flange, furthermore, is not developed in this way, as a posteriorly located ridge that increases in strength posteriorly. The flange is deepest anteriorly under the anterior end of the tooth row. In species with a reduced flange, such as *P.* sp., the flange is located more anteriorly and is swollen and strongest anteriorly.

Third, the features listed in the diagnosis of *P. sattayaraki* (incipient dentary flange, strongly convex alveolar edge, five denticles to each side of the apical denticle) are not unique and also vary during growth in psittacosaurs. Nothing in the additional defense of this species (Buffetaut and Suteethorn 2002) alters the fact that these poorly documented features are not unique. Post-hatching growth witnesses an increase in tooth and denticle counts, and the medial convexity of the tooth row in many psittacosaurs is often stronger than that shown in the Thai dentary.

Fourth, the broad dorsoventral proportion of the anterior end of Meckel's canal and near vertical dentary symphysis are not present in any other psittacosaur species and do not closely resemble the condition in hatchlings (contra Buffetaut and Suteethorn 2002: 73). Although the specimen could have been diagnosed on these grounds, its apparent immaturity and uncertain generic affinity mitigate against erecting a new taxon. Xu and Zhao (1999) listed *P. sattayaraki* as a junior synonym of *P. mongoliensis* without comment, although there appears to be no justification for such an attribution. Averianov et al. (2006) supported recognition as a new species of *Psittacosaurus* but did not offer any unique features. Contrary to Buffetaut and Suteethorn (1992) and Averianov et al. (2006), the tooth row in *P. sattayaraki* is not straight but rather is gently medially convex in dorsal view as in all psittacosaurs (see Buffetaut and Suteethorn 1992: fig. 2D). The basis for referral to *Psittacosaurus* rests entirely on the bulbous form of the primary ridge in the dentary teeth, which is not well established. Ceratopsia, incertae sedis, may be the best tentative assignment for this fragmentary, albeit interesting, dentary (Table 2.1).

Cranial Morphology

SKULL ORIENTATION AND PREORBITAL LENGTH

The shape and measurement of the skull in psittacosaurs are very sensitive to the orientation of the cranium. If the dorsal skull roof is positioned so that it is horizontal, for example, the anterior margin of the snout assumes a nearly vertical orientation and appears particularly short in dorsal view.

In orthogonal views in this paper, the cranium is oriented with the maxillary tooth row positioned along a horizontal. Similarly, the lower jaw in disarticulation is oriented with the dentary tooth row positioned along a horizontal. With the cranium in this registration, the postorbital portion of the skull roof in all species is tilted slightly posteroventrally in lateral view, and the tapering anterior process of the nasal is exposed in dorsal view. From this horizontal axis, perpendicular lines are established to the anterior margin of the rostral and the anterior rim of the orbit. The distance between these perpendiculars is a measure of *preorbital length,* which is compared to *skull length,* as measured from the anterior margin of the snout to the posterior margin of the quadrate. Using this posterior landmark for skull length reduces variation from crushing and breakage that often occurs along the posterior margin and corners of the skull. When measured consistently in this manner, all psittacosaurs have a relatively short preorbital skull segment that is less than 40% of skull length.

ADULT SKULL SHAPE AND FORM

The following is a brief summary of adult skull shape in psittacosaurs highlighting the most unusual and variable features. Various terms have been used to describe osteological features that are present primarily in psittacosaurs. A specialized terminology, introduced in italics below, is developed to encourage terminological uniformity. The description is based on firsthand examination of *P.* sp., *P. major, P. meileyingensis, P. mongoliensis, P. neimongoliensis, P. sinensis and P. xinjiangensis* (Sereno 1987; Sereno and Zhao 1988; Sereno et al. 1988) as well as reference to descriptive accounts of *P. lujiatunensis* (Zhou et al. 2006b), *P. neimongoliensis* (Russell and Zhao 1996), and *P. sibiricus* (Averianov et al. 2006).

General Skull Shape. The psittacosaur cranium, as its name suggests, resembles that in parrots in several regards (Zusi 1993). The bill-sheathed snout is short, deep, and narrow and constructed primarily of the expansive posterolateral process of the premaxilla. The preorbital segment of the psittacosaur skull is less than 40% of skull length, shorter than in nearly all other ornithischians. Preorbital length in *P. mongoliensis* is approximately 37% of skull length, or slightly greater than that in other species (30–35% of skull length). Because preorbital skull length increases somewhat during growth, species comparisons are most useful when using the skulls of mature individuals.

A proportionately deep median rostral bone caps the snout anteriorly. The snout sidewall lacks any sizeable openings, given the high position of the external naris and absence of an antorbital fenestra. The nasal, unlike that in any other dinosaur, extends below the external naris, its anteroventral tips resting against the dorsal end of the rostral bone. The internarial bar, as a consequence, is constructed from the nasal alone, rather than a composite strut formed by processes of the nasal and premaxilla. The sutureless internarial bar and rostral-nasal contact in psittacosaurs further strengthens the anterior margin of the snout, which is loaded by compressive forces from the upper bill.

As in other ceratopsians, the skull roof is subtriangular in dorsal view, reaching its greatest breadth across the jugals just posterior to the orbit. In all species of *Psittacosaurus,* the ventral margin of the skull narrows in width from the jugal horn to the quadrate condyle (also *Chaoyangsaurus;* Zhao et al. 1999). The skull in other neoceratopsians, in contrast, does not show similar narrowing along the ventral margin (e.g., *Yinlong,* Xu et al. 2006; *Liaoceratops,* Xu et al. 2002). As in all ceratopsians, the frontoparietal roof is relatively narrow, broadly exposing both the orbit and laterotemporal fenestra in dorsal view.

Dorsal Skull Roof. The psittacosaur rostral is broadly arched transversely and is relatively thin, despite a wedge-shaped appearance in lateral view. Ventrally it occludes with the broadly arched edge of the predentary and lacks the derived anterior keel and recurved ventral tip that are present in neoceratopsians. The palatal surface of the rostral is crescent-shaped and angles anteroventrally at approximately 60° from the horizontal plane of the skull. A rounded, U-shaped *attachment ridge* occupies the middle one-third of this surface and extends between the palatal processes of the premaxillae (Fig. 2.5). This ridge, which is well exposed in *P. mongoliensis, P. major* and *P.* sp., presumably served to anchor the upper bill, reinforcing the central portion of the rostral.

The premaxilla is edentulous, expansive, and polygonal in shape, forming most of the vertical wall of the tall psittaciform rostrum. The majority of the bone is composed of a hypertrophied posterolateral process, which in most ornithischians is a small triangular process tapering between the maxilla and nasal. The posteromedial or internarial process, in contrast, is reduced to a small spur that forms the anteroventral corner of the external naris. The premaxillary foramen pierces the lateral wall near the anterior end of the premaxilla well below the small external naris. The lateral wall of the lacrimal canal is incompletely ossified in *Psittacosaurus,* leaving an oval *fenestra of the lacrimal canal* between the premaxilla and lacrimal, a condition unique to the genus. Premaxillary, maxillary, lacrimal, and jugal sutures converge toward a point on the posterior snout, the exact pattern at their junction showing some variation. The premaxilla joins the maxilla along a rugose, akinetic suture that protrudes laterally as an anteroventrally sloping *premaxilla-maxilla ridge* (Fig. 2.2A). The attachment surface for the keratinous upper bill clearly extended beyond the rostral bone and onto the premaxilla.

The relatively small, subtriangular maxilla has a distinctive subtriangular depression above the buccal emargination here termed the *maxillary fossa* (Figs. 2.2A, 2.3A, 2.7A; "secondary depression," Sereno 1990b: 583; "antorbital fossa," Zhou et al. 2006b: 105). The maxillary fossa is not a pneumatic depression and has no relation to the antorbital fossa (Sereno 1990b, 2000). In hatchling psittacosaurs, the maxillary fossa is present (see below), although at no point is there any trace of an antorbital opening or any other connection between the maxillary fossa and the nasal cavity, a necessity were it to be considered a pneumatic structure. Of several neurovascular foramina that open within, or on the rim of, the maxillary fossa, the largest is located near, or along the suture with the premaxilla. Here termed the *anterolateral maxillary foramen,* it opens anterolaterally into an impressed vessel tract that passes anteroventrally to the edentulous margin of the premaxilla (Fig. 2.2A). The ventral margin of the maxillary fossa forms the dorsal edge of the buccal, or cheek, emargination. A characteristic process, here termed the *maxillary protuberance* ("maxillary boss," Sereno, 1987: 76; "maxillary process," Sereno et al. 1988; "protuberance," Zhou et al. 2006b: 105) is present on the posterior end of the rim of the cheek emargination near the maxilla-jugal suture. The maxillary fossa and protuberance are poorly developed in some species (*P. neimongoliensis, P. sinensis, P. sibiricus*).

The buccal emargination, or cheek, is deeply inset. The lateral wall of the cheek is nearly flat and inclined at approximately 45° medioventrally. The opposing surface within the palate that borders the internal nares is nearly vertical as seen in palatal view (Fig. 2.4A). As a result, there is a dorsally thickening wedge of bone above the maxillary tooth row, here referred to as the *alveolar pedestal,* which thins abruptly to a vertical plate in the region of the maxillary fossa.

One of the hallmarks of the skull of *Psittacosaurus* is the pyramidal *jugal horn,* which sometimes shows impressed vascular grooves indicative of a keratinous sheath. Although the jugal horns in adult *P. sinensis* appear to be the most laterally prominent, the size and lateral prominence of the horns appear to increase during growth in many species and are easily altered by postmortem distortion. Distinguishing species on the basis of jugal horn size, form, and orientation is fraught with uncertainty.

The central body of the postorbital and the midpoint of the postorbital bar are also raised as keratin-covered protuberances, although neither reaching the size of the jugal horn. In most species, the protuberance on the central body of the postorbital is developed only as a ridge, here termed the *postorbital crest,* which extends posteriorly along the lateral side of the posterior process (Fig. 2.2A). In *P. sibiricus,* however, the portion of the protuberance on the central body is raised as a blunt, dorsolaterally projecting *postorbital horn* (Averianov et al. 2006). The second crest or horn, here termed the *postorbital-jugal crest* or *horn,* occurs more ventrally on the postorbital bar. In *P. mongoliensis* and *P. major* it is developed only as the everted posterior edge of the ventral process of the postorbital. In other species such as the new species from Inner Mongolia and *P. sinensis,* it is raised as a smooth pyramidal horn mainly on the postorbital or a more rounded horn with rugose texture split between the postorbital and jugal (Figs. 2.2B, 2.9).

Finally, there is a *quadratojugal protuberance* on the central body of the quadratojugal that is best developed as a discrete rugosity in *P. meileyingensis*. In most other species, this area is raised only as a smooth eminence (Fig. 2.2A).

Variably developed depressions, or fossae, besides the maxillary fossa are located near the orbit and include the *postorbital-jugal fossa* just below the postorbital-jugal horn (Fig. 2.2B) and the *jugal fossa* located on the jugal below the orbital margin (Fig. 2.3A).

A *parietal-squamosal shelf* projects posteriorly over the occiput as a transversely broad, anteroposteriorly narrow, horizontal sheet. Often referred to as a "frill," the shelf neither projects posterodorsally nor varies significantly in anteroposterior length, as occurs in neoceratopsians presumably in response to a display function. Smooth depressions on the ventral aspect of the shelf, here termed the *occipital fossae,* are present in all species to either side of the prominent keel-shaped nuchal crest (Fig. 2.5). These fossae may have functioned primarily as an expanded area of attachment for depressor mandibulae musculature.

Palate. The secondary palate, the majority of which is formed by the premaxilla in all species (contra Zhou et al. 2006b: fig. 4), is subcircular in ventral view and arches high above the bony edge of the upper bill. In the midline, a large slit-shaped *incisive foramen* opens onto the premaxillary palate from the nasal cavity (Fig. 2.4A; "median notch," Sereno 1987: 75; "interpremaxillary foramen," You et al. 2008: 185). To each side of this foramen, the anteroventral edge of the premaxilla projects from the palatal surface to form what appears to be a narrow triturating surface inset within the upper bill for the lower bill (Fig. 2.4A). This edge is well preserved in *P.* sp., *P. major,* and *P. mongoliensis* (Fig. 2.4A, ts). Two large foramina, here termed the *medial* and *lateral premaxillary foramina* ("neurovascular canal," You et al. 2008: 187), probably provided the primary vascular support for the internal aspect of the upper bill (Fig. 2.4A). They open anteriorly from the anterior end of the maxilla, the medial foramen is slit-shaped and located medial to the bill margin and the lateral foramen is subcircular and located lateral to the bill margin at the anterior extremity of the buccal emargination. Posteriorly the premaxilla is rigidly sutured to the anteromedial process of the maxilla, which meets in the midline and excludes the premaxilla from the footplate of the vomera and border of the internal nares. The vomera are strongly arched dorsally in lateral view such that the ventral edges are located just below the ventral orbital margin as in *Protoceratops* (Sereno 2000).

Although it appears that psittacosaurs lack an interpterygoid vacuity, a gap is present separating most of the original, or primary, palatal rami. The primary palatal ramus is exposed only in dorsal view within the orbit, where the distal margins of the steeply angled palatal rami join in the midline, pinching the vomera anteriorly and the parasphenoid posteriorly. A pterygoid vacuity separates the posterior portions of the primary palatal rami but is obscured in ventral view by a secondary, or neomorphic, lamina of the pterygoid. This secondary lamina contacts its opposite in the midline to form what has been termed the *basal plate,* the median suture of which in adults is fused and raised into a low median crest (Sereno

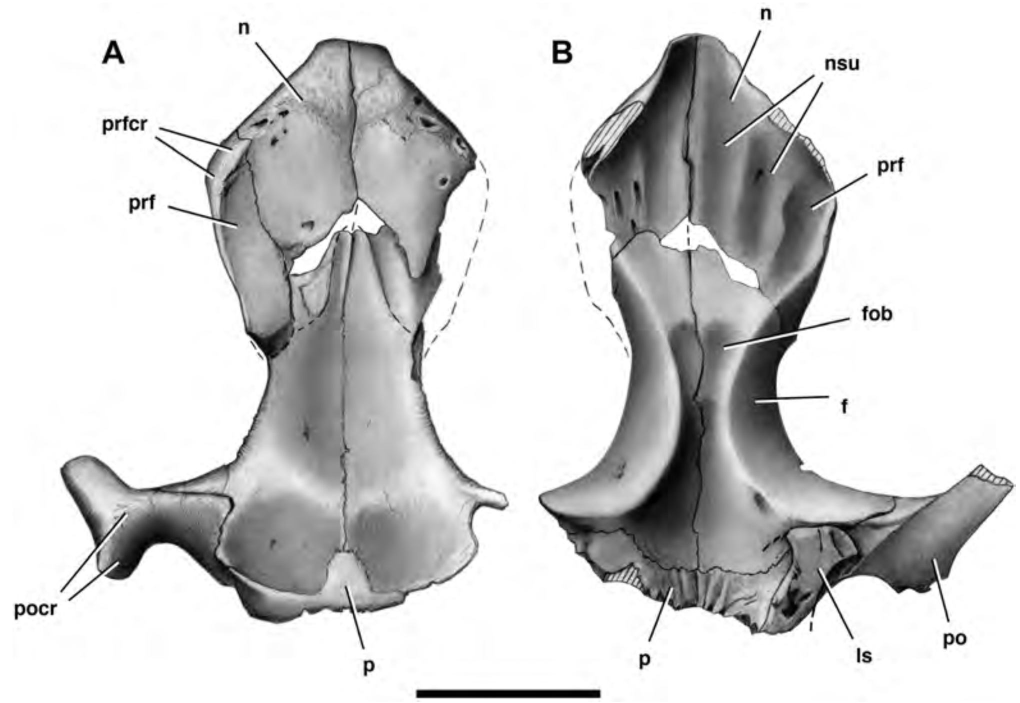


FIGURE 2.11. *Psittacosaurus mongoliensis* (PI 3779/20) skull table in (A) dorsal view; (B) ventral view. Cross-hatching indicates broken bone; dashed line indicates estimated edge. See text for abbreviations. Scale bar is 3 cm.

1987). In ventral view of the palate, the vomera and the secondary palatal laminae form the vaulted posterior palate, which slopes posteroventrally at about 45°. The basal plate forms a secondary palatal surface ventral to the primary palatal rami, between which is a blind pocket of pyramidal shape. Termed the *pterygoid fossa,* this pocket opens posteriorly between the basipterygoid articulations (Fig. 2.4B). Only psittacosaurs have this reinforced, akinetic palatal structure, which is designed to withstand unusually high bite force.

Braincase. The subrectangular occipital surface is divided in the midline by a vertical keel-shaped nuchal crest, the expanded dorsal end of which approaches but does not contact the overlying parietal-squamosal shelf (Fig. 2.5). The paroccipital process extends laterally, expanding gradually to a subquadrate distal end. There is no development of a ventral hook-shaped process for attachment of jaw-opening musculature as in ornithopods. Rather that anchoring role may have been played by the parietosquamosal shelf, as indicated by the *occipital fossae* on its ventral surface. These fossae, which are invariably present in psittacosaurs and easily observed in the largest species (e.g., *P. major*), extend ventrally onto the paroccipital processes (Fig. 2.5). The occipital condyle, basal tubera and basipterygoid processes lie roughly in the same horizontal plane, the latter processes noticeably longer in *P. major* (Fig. 2.5).

The dorsal skull roof preserves shallow fossae for the forebrain as well as two smaller oval fossae for the olfactory bulbs (Fig. 2.11B). More anteriorly, there is a pair of shallow sulci on the ventral aspect of the nasals, which are clearly positioned anterior to the endocranial volume (Fig. 2.11B). The lateral nasal sulcus was misinterpreted recently as an enlarged fossa for an olfactory bulb (Zhou et al. 2007: fig. 2B).

Accessory Dermal Elements. The palpebrals in psittacosaurs and other ceratopsians are subtriangular rather than elongate as in most other ornithischians. In all species of *Psittacosaurus,* in addition, the palpebrals project laterally from the anterodorsal corner of the orbit, extending laterally to a width equal to that of the posterior skull table (Fig. 2.12). In basal neoceratopsians, in contrast, the palpebrals curve posteriorly.

A sclerotic ring is composed of a series of thin, oval overlapping plates that compose a ring of relatively modest size in *Psittacosaurus* (Fig. 2.13). The circular sclerotic ring is relatively small, the maximum outside diameter (18 mm) about one-half of the maximum diameter of the orbit (38 mm). Positive plates are located at the top and bottom of the ring, but only one negative plate is present on the anterior side of the ring. Given the circular geometry of the sclerotic ring, the number of positive plates must equal the number of negative plates. Another negative plate, therefore, must have been present on the damaged posterior side of the ring. Thus there

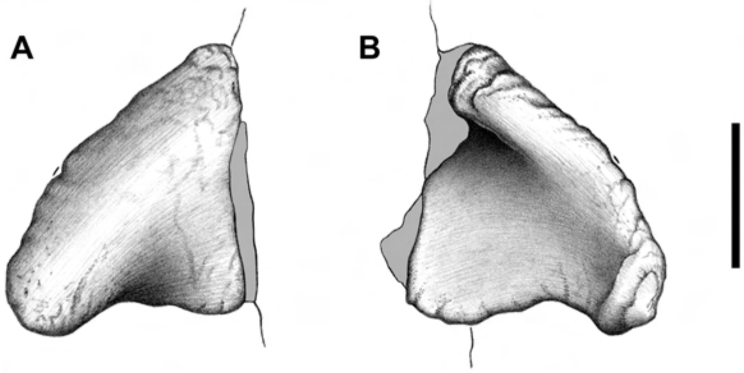


FIGURE 2.12.
Psittacosaurus mongoliensis (IVPP V7668) left palpebral in (A) dorsal view; (B) ventral view. Grey tone indicates matrix. Scale bar is 1 cm.

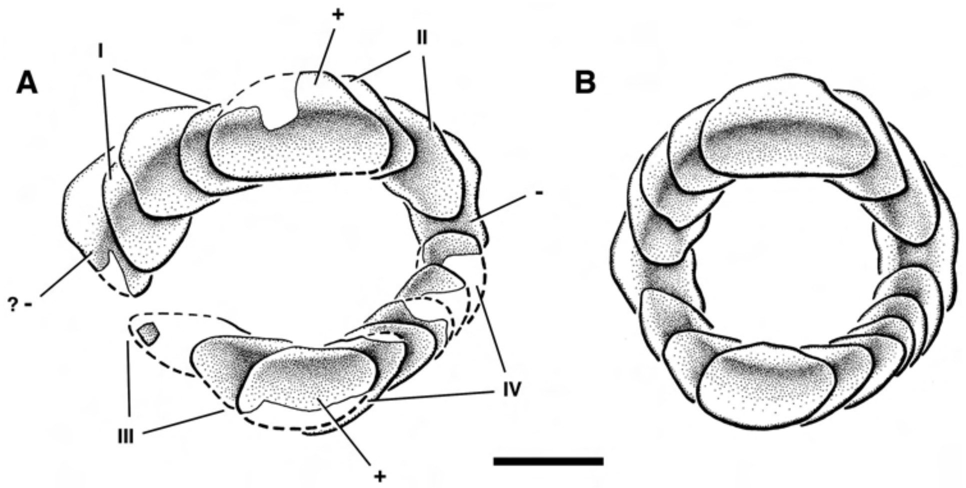


FIGURE 2.13.
Psittacosaurus mongoliensis (AMNH 6254) right sclerotic ring in (A) lateral view; reconstruction of right sclerotic ring in (B) lateral view. See text for abbreviations. Dashed line indicates estimated edge. Scale bar is 5 mm.

are at least 15 plates in the sclerotic ring of *P. mongoliensis,* 14 of which are preserved, and at least 1 missing negative plate (Sereno 1987).

Lower Jaw. The lower jaw fuses at the mandibular symphysis with maturity, uniting the dentaries (including their tooth rows) and the predentary as an akinetic unit. A pendant *dentary flange* ("ventral flange," Sereno 1987: 134; "dentary flange," Zhou et al. 2006b: 110; "ventrolateral flange," You et al. 2008: 192) projects ventrolaterally from the dentary ramus in *P. lujiatunensis, P. meileyingensis, P. major,* and *P. sibiricus*. The dentary flange is low in *P. mongoliensis* and represented only by rugosities in some other species. Both coronoid and intercoronoid ossifications are present, the latter a delicate strap-shaped bone currently preserved only in *P. mongoliensis* (Fig. 2.14). The jaw joint, which is similar in all species, allowed rotary as well as anteroposterior movement. Rounded, poorly divided quadrate condyles articulate against a broad, flat *articular platform* composed mostly of the articular (Fig. 2.14). A robust retroarticular process extends posterior to the jaw articulation, unlike the very short process in neoceratopsians.

Stapes and Hyoid. The slender columelliform stapes is preserved in *P. mongoliensis, P. lujiatunensis* (Zhou et al. 2006b), and *P. major* (LH PV1). In the last individual the stapes is preserved in natural articulation, the slender columnar shaft extending toward the otic notch between the quadrate head and paroccipital process (Fig. 2.15). The slightly expanded distal section of the ossified shaft nearly reaches the presumed position of the tympanum.

A pair of rods identified as ceratohyals are preserved in *P. mongoliensis, P. sibiricus* and *P. sinensis* (Colbert 1945, Sereno 1987, Averianov et al. 2006). Approximately one-third as long as the skull, two specimens preserve the ceratohyal between the mandibular rami, demonstrating that the flattened end of the shaft is positioned anteriorly and the cylindrical end posteriorly (*P. mongoliensis* PI 3779/17; *P. sinensis* IVPP V738). The anterior end is transversely compressed and the shaft curves posterolaterally toward the mandibular rami, a configuration similar to that in other ornithischians such as *Edmontosaurus* (Versluys 1923) and *Corythosaurus* (Ostrom 1961).

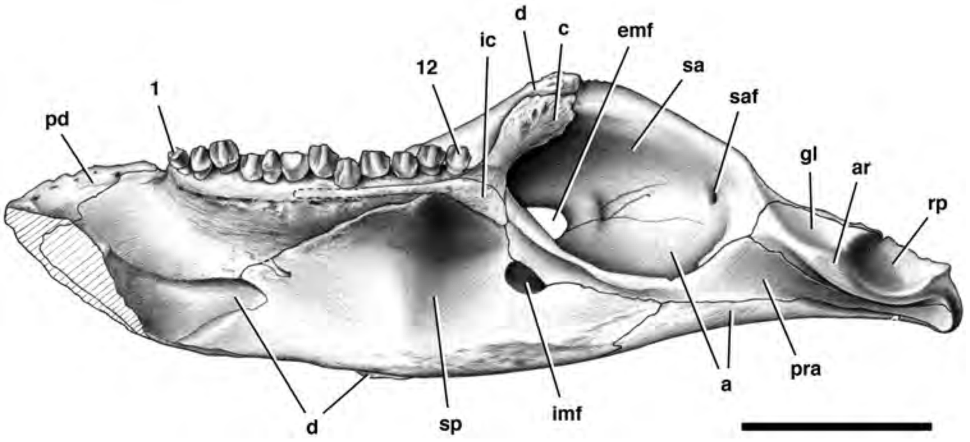


FIGURE 2.14. *Psittacosaurus mongoliensis* (AMNH 6534) right lower jaw in medial view. See text for abbreviations. Cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 3 cm.

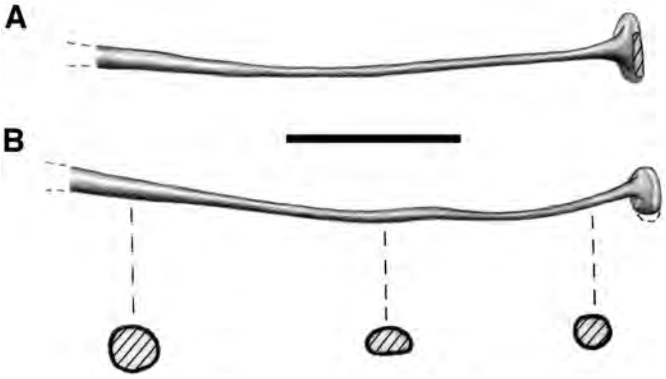


FIGURE 2.15. *Psittacosaurus mongoliensis* (AMNH 6254) right stapes in (A) presumptive lateral view; (B) presumptive ventral view with three cross sections of the stapedial shaft at four times magnification. Cross-hatching indicates bone section. Scale bar is 1 cm.

Dentition. The psittacosaur dentition is limited to a dozen or less teeth in the maxillary and dentary that remain structurally simple, with one functional and one replacement tooth per alveolus. Tooth number increases with age, ranging in adults between 10 and 12 for large species and 9 and 10 for smaller species. The tooth rows of all species are equal in length and diverge posteriorly, the posteriormost tooth in each tooth row separated from its opposite in the midline by approximately three times the distance of the anteriormost pair (Figs. 2.4, 2.9B).

Enamel is always present on both sides of the crown (contra You et al. 2008: 194), although it is thicker on the lateral and medial aspects of maxillary and dentary crowns, respectively (Fig. 2.6). The most characteristic feature of the dentition is the bulbous primary ridge on the dentary crowns (Fig. 2.6C). Tooth-to-tooth wear facets, which are evident shortly after hatching, truncate upper and lower crowns at approximately 20° from the vertical. There are clear traces of crown-to-crown wear in several species that indicate that the power stroke is nearly straight and draws the mandibles posterodorsally at 30° from the horizontal (Fig. 2.16). Tooth wear in psittacosaurs thus is neither orthal nor propalinal (contra Norman and Weishampel 1991: fig. 11). Rather psittacosaurs employed a unique masticatory cycle involving posteriorly divergent, akinetic upper and lower jaws and an isognathus posterodorsal power stoke. The resulting high-angle, tooth-to-tooth wear facets resemble those in other ornithischians that have kinetic upper and lower tooth rows and an orthal power stroke.

NEONATE SKULL TRANSFORMATION

Material. In 1922 the Third Asiatic Expedition collected a number of immature individuals along with the adult holotypic skeleton of *Psittacosaurus mongoliensis* (Osborn 1923, 1924) from the Khukhtek Formation (= Oshih or Ondai Sair Formations, Tevsh svita) on the northern flank of Arts Bogd in an east-west graben known as Oshih (locally as “Osh”; Rougier et al. 2001). The juvenile material includes three partial skulls of different age (AMNH 6535, 6536, 6540), several partial skeletons as well as disarticulated postcrania (Sereno 1987). The smallest individual (AMNH 6535; Figs. 2.17–2.19) was identified as the partial skeleton of a “tiny dinosaur” by Walter Granger in his field notes in 1922 and later described as a psittacosaur in passing by Andrews (1932: 223). The abundance and similar size of much of the postcranial material suggests that a nest of hatchlings may have been inadver-

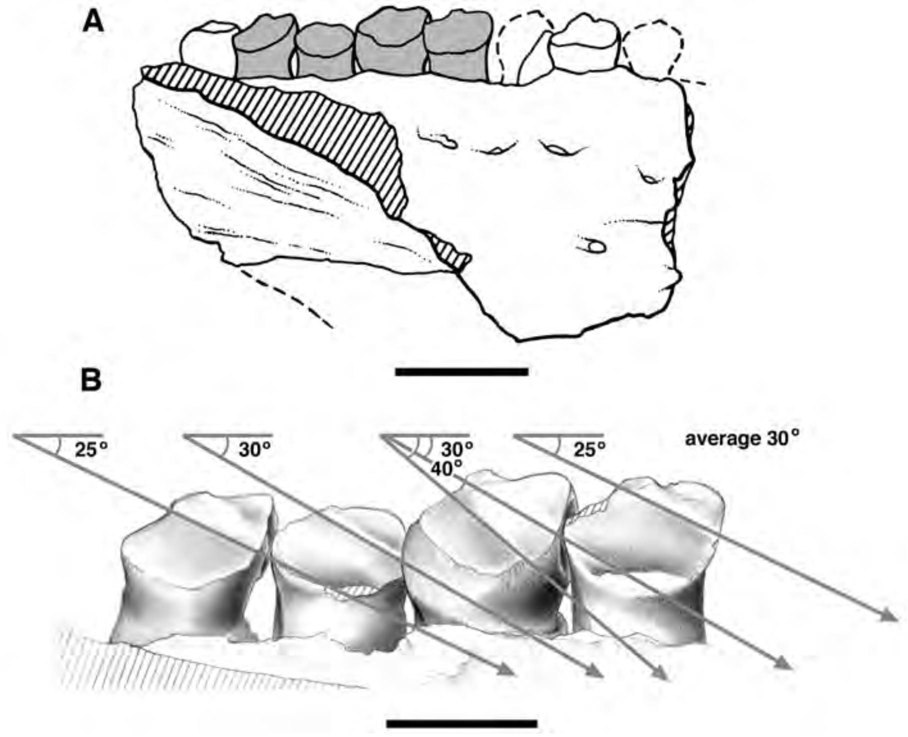


FIGURE 2.16.
Psittacosaurus mongoliensis (PI 698/1-3). (A) Posterior portion of the right dentary with posteriormost eight tooth positions in lateral view; (B) close-up of four worn teeth (shaded in A) showing mesowear in lateral view. Cross-hatching indicates broken bone; arrows show the angle of passage of individual teeth in the maxillary tooth row across the dentary tooth row. Scale bar is 1 cm.

tently collected, which would have been the first to have been encountered by paleontologists.

The juvenile material was first studied by Coombs (1980, 1982), who described the two smallest skulls (AMNH 6535, 6536) as well as postcranial material assigned arbitrarily to the larger specimen (AMNH 6536) (Figs. 2.17–2.22). By that time, the postcranial bones belonging to the smallest skull (AMNH 6535) had become disassociated from the skull (Fig. 2.17). Subsequently this partial, articulated skeleton was located and reunited with the skull by the author (Sereno 1987). On the basis of the skull alone, Coombs (1980: 380, fig. 2) estimated its body length between 230 and 250 mm with a skull approximately 50% of its trunk length. The postcranial skeleton preserves most of an articulated trunk and pertains to a hatchling that was probably less than 200 mm in length. Its skull length is approximately 70% of the estimated length of the trunk (Fig. 2.17A).

Now fully prepared, the two smaller skulls are figured in detail (Figs. 2.18–2.22). The smallest skull (AMNH 6535) has a length of 27.5 mm, or about 20% of adult skull length. The skull is preserved without distortion or flattening. The left stapes is preserved in two pieces on the left side of the braincase (Fig. 2.20A). Most of the rostral, all of the predentary, and both postorbitals and squamosals are eroded away. There are no palpebrals or sclerotic rings, although these are present in nestlings that are slightly larger (skull length approximately 35 mm; Meng et al. 2004) and so were probably lost to erosion. The second smallest skull has a length of about 40 mm, or about 30% of adult skull length, and is smaller than juveniles found recently in association (skull length approximately 57 mm; Qi et al. 2007). The skull is flattened exposing the dorsal skull roof in right lateral view (Figs. 2.21B, 2.22B). The right palpebral and left sclerotic ring are preserved (AMNH 6536; Fig. 2.22). The palpebral is subtriangular rather than elongate as in many other ornithischians; Coombs (1982: fig. 3) mistakenly interpreted a section of the pterygoid as the posteriorly elongate shaft of the palpebral.

Both skulls of *P. mongoliensis* are associated with the anteriormost cervical vertebrae and were presumably originally articulated with postcranial skeletons. The trunk of the smaller individual is preserved. The association of postcrania with the larger individual cannot be established, although the presence of multiple individuals of comparable size suggests that nestlings may have been collected.

General Skull Shape. Skull form and sutural pattern in even the smallest individual are remarkably similar to that of an adult. General shape changes in the skull during growth include many of those expected in any diapsid, such as reduction in the size of the orbit and braincase and development of a rim on the supratemporal fossa and sagittal crest (Coombs 1982). Rounded anterodorsal and posterodorsal skull margins become squarer as the skull table flattens. Preorbital skull length increases from approximately 30% of total skull length in the smallest individual to 35% in the slightly larger skull,

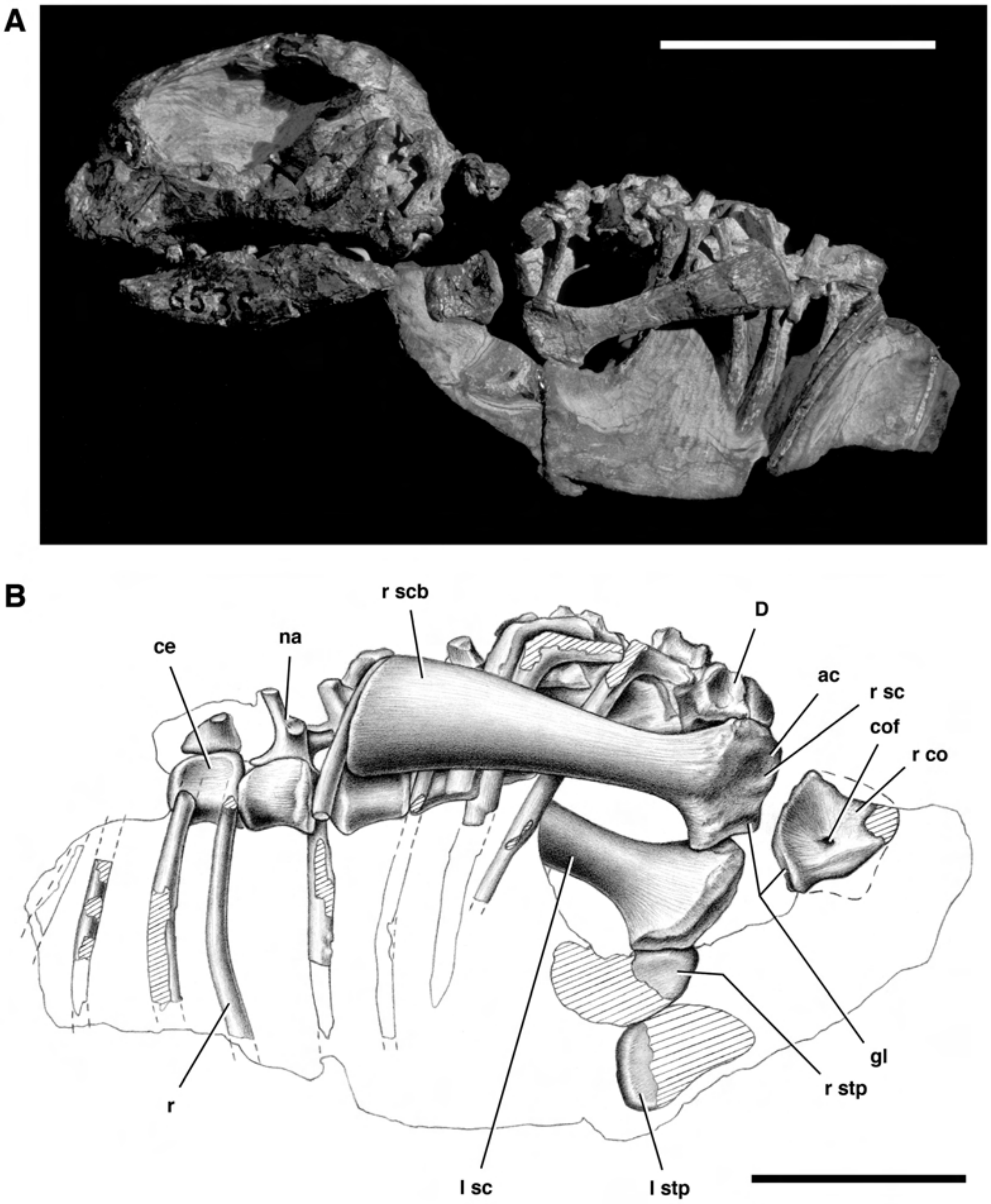


FIGURE 2.17. *Psittacosaurus mongoliensis* (AMNH 6535) hatchling skull and partial skeleton in (A) left lateral view; partial postcranial skeleton in (B) right lateral view. See text for abbreviations. Cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bars are (A) 2 cm; (B) 1 cm.

with most adult skulls still slightly longer at about 37%. Thus most of the lengthening of the preorbital portion of the skull occurs at very small size. The laterotemporal fenestra increases in anteroposterior length from about 45% of its height in the smallest skull to about 70% in an adult. The parietal-squamosal shelf is not well preserved in the hatchling skulls, so how it changes with growth is uncertain.

Other changes include the absence or rudimentary form of what may be interpreted as secondary sexual characteristics, which here include the various horns, rugose eminences and upturned edges that appear to be ornamental rather than serving as sites for muscle attachment. The jugal horn and mandibular flange are rudimentary, and there is no development of the maxillary protuberance or upturned lip of the prefrontal. Other features that change with growth but also have been cited as differences among species include relative preorbital skull length, relative size of the occipital condyle, relative position of the posterior margin of the secondary palate, and

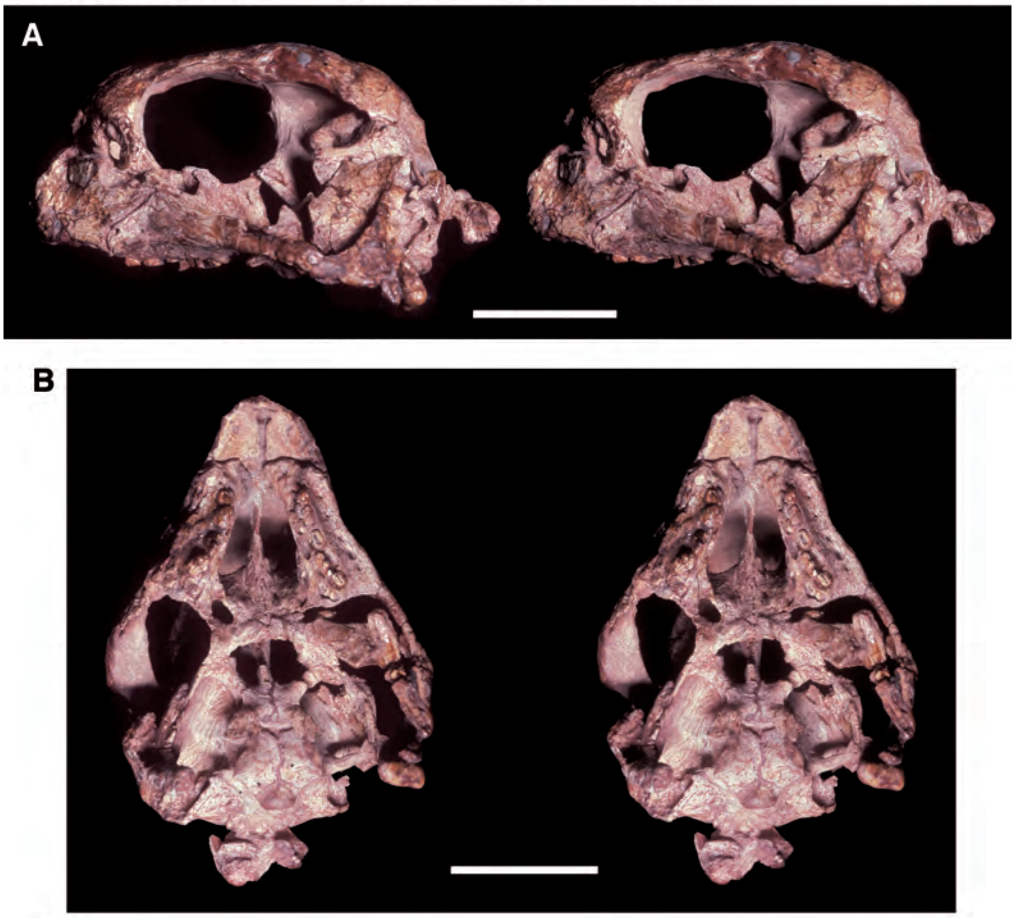


FIGURE 2.18. *Psittacosaurus mongoliensis* (AMNH 6535) stereopairs of hatchling cranium in (A) left lateral view; (B) ventral view. Scale bars are 1 cm. Reproduced in color on the insert.

number of teeth in the maxillary and dentary tooth rows. Demonstrating maturity is important, especially when these features are invoked as species differentia.

Dorsal Skull Roof. In both skulls the premaxilla has a large foramen near its anterior margin and distinct depressions posterior to the rostral and ventral to the prefrontal as in the adult (Figs. 2.19A, B, 2.22). The premaxilla-maxilla suture is elevated as a ridge with a large vascular foramen at its anteroventral extremity. A maxillary fossa with foramina is located posteroventral to the ridge. An antorbital fenestra, thus, is absent in the smallest individual, and the external fossa on the maxilla must be a secondary feature unique to *Psittacosaurus*. It is not a pneumatic depression, judging from the absence of any communication with the nasal passage and presence of foramina and surface texture in adults. As will be explored below, to the contrary, it appears to be an attachment feature related to the unusually expanded jaw musculature in psittacosaurs.

In both skulls the free ventral margin of the premaxilla separates the rostral and maxilla (contra Coombs 1982: 100, fig. 7A, B), and the sutures of the premaxilla, maxilla, lacrimal, and jugal converge on a point as in the adult. In AMNH 6540, the bony platform for the bill and the vascular foramina and impressed channels supplying the keratinous bill are already established as in the adult. The sutures on the sidewall of the snout and vascular supply to the bill are similar to that of an adult.

In lateral view of the smallest skull, the jaw articulation is located below the level of the maxillary tooth row, the quadrate shaft arches posteriorly to its head, the maxillary and dentary buccal emargination and coronoid process are well developed, and a well-developed mandibular flange is present in the smaller hatchling skull (Coombs 1982; Fig. 2.19F). On the left side, the lacrimal canal is exposed as often occurs in adults. In dorsal view the orbit and laterotemporal fenestra are exposed lateral to the skull table. In ventral view, the maxillary tooth rows are gently laterally concave to either side of a strongly arched palatal septum, and a subrectangular mandibular flange projects ventrolaterally posterior to the maxillary tooth row. The quadrate condyle also can be seen to angle anteromedially rather than having a transverse orientation. The predentary-dentary suture is open in both skulls (contra Coombs 1982), fusing later in growth in adult mandibles.

Palate. The palate shows a number of changes during

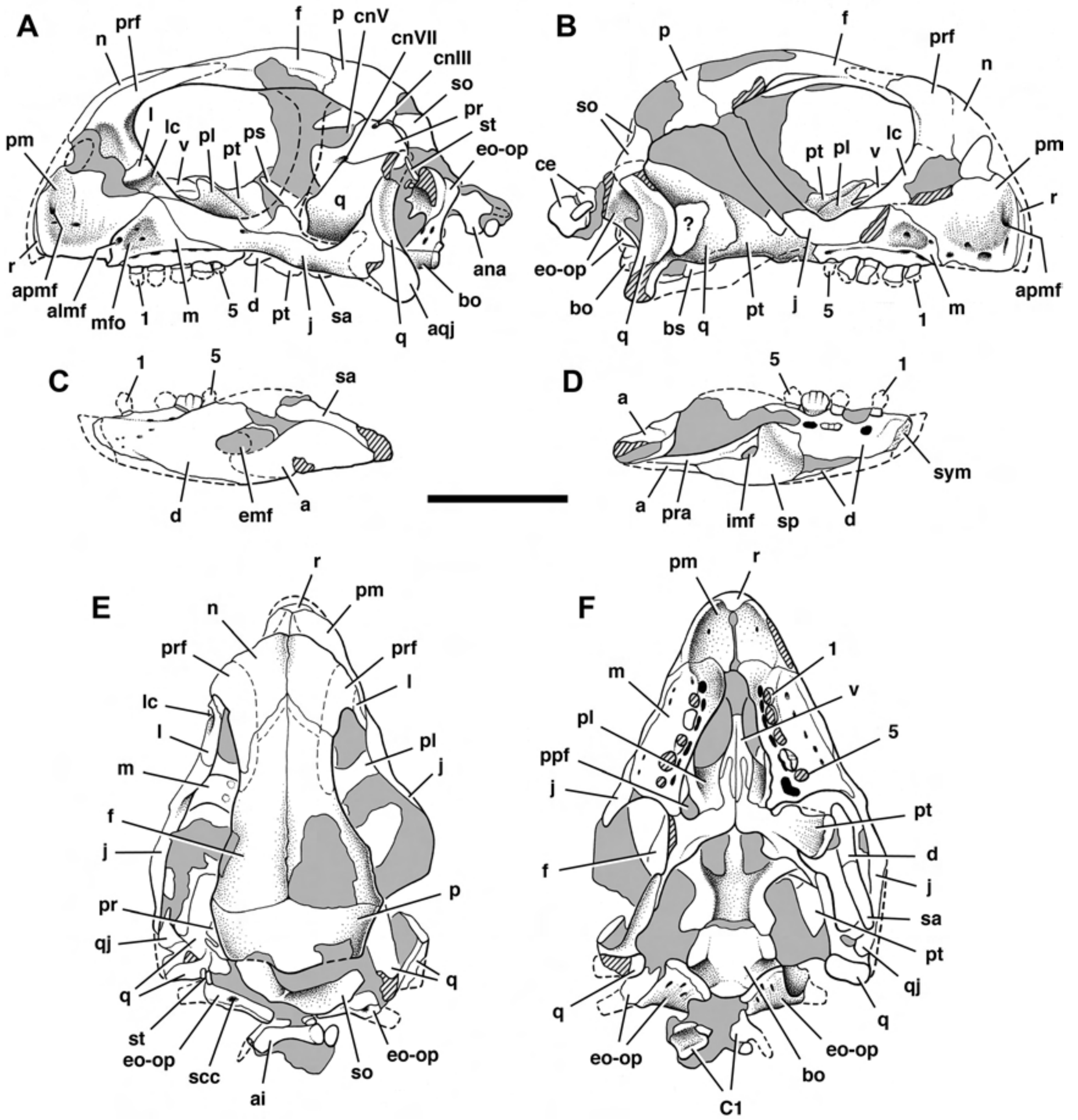


FIGURE 2.19. *Psittacosaurus mongoliens*is (AMNH 6535). Hatchling cranium in (A) left lateral view; (B) right lateral view; (E) dorsal view; (F) ventral view. Left lower jaw in (C) lateral view; (D) medial view. See text for abbreviations. Grey tone indicates matrix; cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 1 cm.

growth. The premaxillary palate, which is well preserved and exposed on the smallest skull (Figs. 2.19F, 2.20B), becomes more deeply vaulted with maturity. The posterior edge of the secondary palate, located anterior to the tooth rows in the smallest skull, extends farther posteriorly to a position even with the tooth rows in adults. The unusual structure of the posterior palate, in which a neomorphic process of the pterygoid extends to the midline as a horizontal basal plate, is in place in the smallest hatchling. The basal plate is preserved as a horizontal shelf between the pendant, well-developed mandibular rami of the pterygoids, and it encloses a pterygoid fossa under the tent-shaped palatal rami of the pterygoids (Figs. 2.4B, 2.20B).

Braincase. The braincase decreases in size with growth. In both skulls, the basioccipital forms the majority of a small occipital condyle. Apparently unlike *Protoceratops* (Brown and Schlaikjer 1940), however, the exoccipitals form the lateral corners of the condyle even in the smallest skull (Fig. 2.20B). The basal tubera are developed as parasagittal ridges that do not extend toward the midline. The pedicel of the exoccipital faces posterolaterally in the smallest skull and reorients to face laterally in the adult (Fig. 2.20B). The exoccipital and

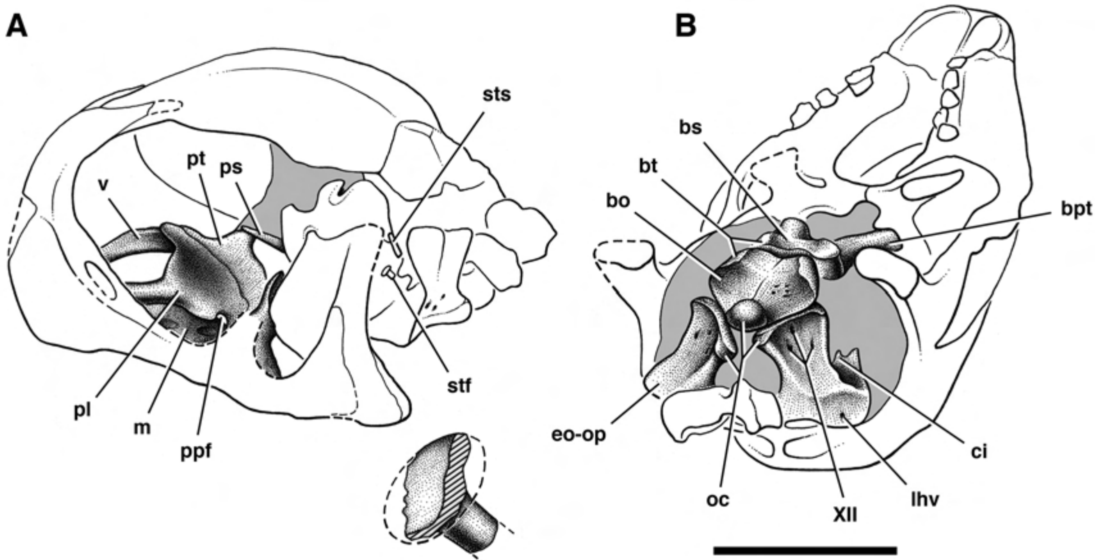
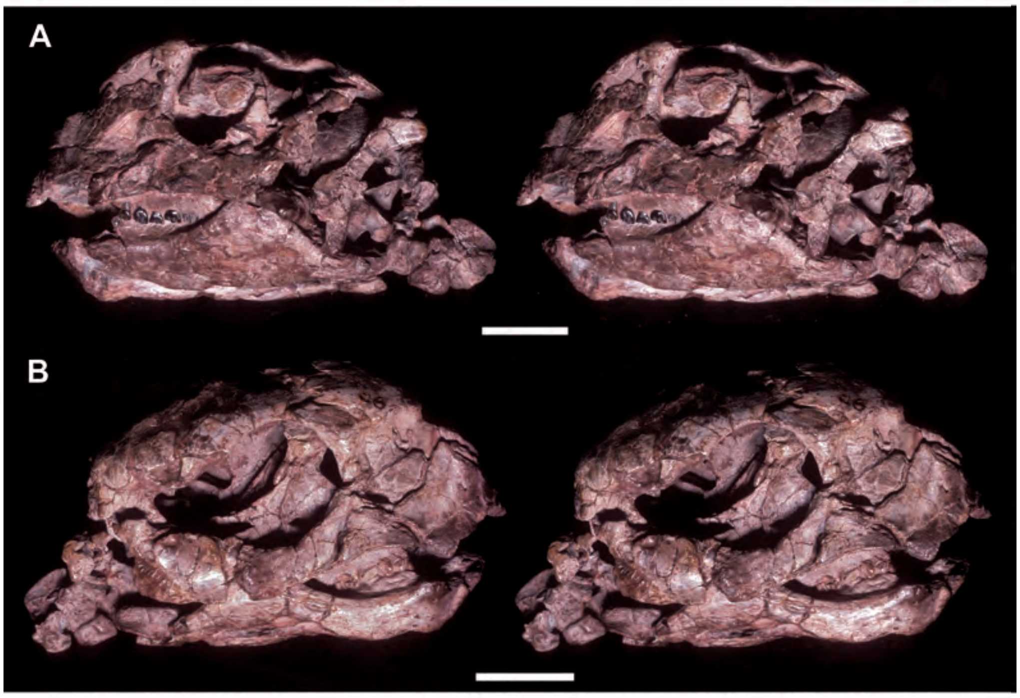
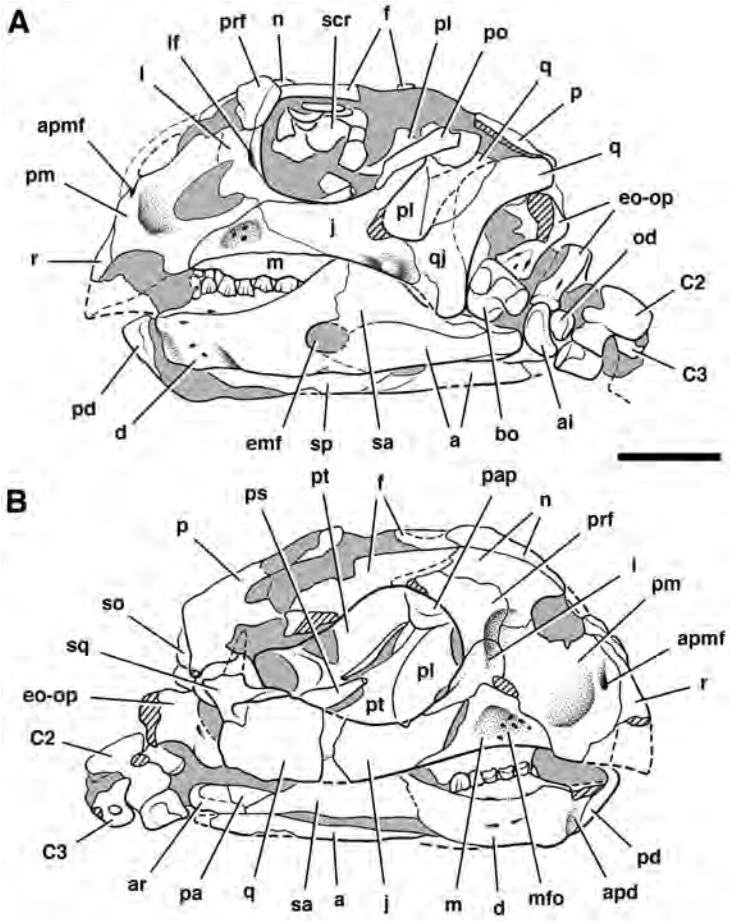


FIGURE 2.20. *Psittacosaurus mongoliensis* (AMNH 6535) hatchling cranium in (A) posterodorsolateral view showing palate and an enlarged view of the stapedial footplate; (B) posteroventrolateral view of 0braincase. See text for abbreviations. Grey tone indicates matrix; cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 1 cm.



.**FIGURE 2.21.** *Psittacosaurus mongoliensis* (AMNH 6536) stereopairs of hatchling skull and anterior cervical vertebrae in (A) left lateral view; (B) right lateral view. Scale bars are 1 cm. Reproduced in color on the insert.

FIGURE 2.22.
Psittacosaurus mongoliensis (AMNH 6536) hatchling skull and anterior cervical vertebrae in (A) left lateral view; (B) right lateral view. See text for abbreviations. Grey tone indicates matrix; cross-hatching indicates broken bone; dashed line indicates estimated edge. Scale bar is 1 cm.



opisthotic are fully coossified, which must occur prior to hatching.

Lower Jaw. In the lower jaw, the predentary is well preserved, uniting the ends of the dentaries in the slightly larger juvenile (AMNH 6540; Fig. 2.22). The predentary and dentary fuse late in ontogeny but can remain suturally distinct or disarticulated in subadults. The bone is initially crescentic in dorsal view but becomes more strongly U-shaped in the adult. In anteroventral view, the predentary is subquadrate with a weakly divided posterior margin, the remnants of the bifid ventral process in neornithischians. The lateral process in the juvenile is poorly developed, whereas in the adult it extends posteriorly as a raised edge to join the lateral margin of the dentary buccal emargination. A mandibular flange is present on the dentary of the larger hatchling skull and increases in prominence, extending posteriorly as a ridge onto the angular in the adult. The external mandibular fenestra decreases in size, and the surangular decreases in depth compared to the angular.

Stapes. The stapes is preserved in the smallest skull, the footplate broken away from most of the shaft, at least a section of which is ossified (Fig. 2.20A). The relative diameter of the footplate of the stapes decreases with growth, and the shaft becomes relatively much longer in the adult (AMNH 6254).

Dentition. Maxillary and dentary tooth count also increases from 5 in AMNH 6535 to 7 in AMNH 6536 to 10–12 teeth in adults (Sereno 1987). The teeth of both hatchling skulls exhibit wear facets, as noticed by Coombs (1982). Well-developed, high-angle wear facets truncate several crown tips as in adults. As mentioned above, many aspects related to mastication are in place in the smallest hatchling skull, including the inset of the tooth row, the presence of both anterior bill-bearing bones, and the position and form of the lower jaw joint (Fig. 2.20). These hatchlings, thus, were not only precocial feeders (Coombs 1982), but the masticatory apparatus appears to have sliced vegetation in a manner identical to that in the adult.

Discussion and Conclusions

TAXONOMY AND SPECIES RELATIONSHIPS

Psittacosaurus. The lone genus *Psittacosaurus* is characterized by 21 synapomorphies, about 40% of which are new to this

Table 2.2. Cranial Characters with Derived States in Well-Known Species of *Psittacosaurus*

Synapomorphy	Original author	1	2	3	4	5	6
1. Preorbital skull length: more (0), or less than (1), 40% of skull length (rostral to quadrate condyle).	Sereno 1987	1	1	1	1	1	0
2. External naris, ventral margin, location relative to the orbital ventral margin: ventral (0); dorsal (1).	Sereno 1987	1	1	1	1	1	0
3. Anterior tip of the nasal internarial process, location: dorsal (0), or ventral (1), to the external naris.	Sereno 1987	1	1	1	1	1	0
4. Rostral-nasal contact: absent (0); present (1).	Sereno 1987	1	1	1	1	1	0
5. Premaxilla, dorsolateral process, maximum width: less (0), or subequal to (1), dorsoventral orbital diameter.	Sereno 1987	1	1	1	1	1	0
6. Premaxilla-prefrontal contact: absent (0); present (1).	this paper	1	1	1	1	1	0
7. Premaxilla-jugal approximation or contact: absent (0); present (1).	Sereno 1987	1	1	1	1	1	0
8. Maxillary fossa: absent (0); present (1).	this paper	1	1	1	1	1	0
9. Maxillary protuberance: absent (0); present (1).	Sereno 1987	1	1	1	1	1	0
10. Lacrimal canal fenestra: absent (0); present (1).	Sereno 1987	1	1	1	1	1	0
11. Antorbital fenestra and fossa: present (0); absent (1).	Sereno 1987	1	1	1	1	1	0
12. Postorbital posterior process, extension along supratemporal bar: partial (0); complete (1).	this paper	1	1	1	1	1	0
13. Squamosal, end of anterior process, position on postorbital: lateral (0); dorsal (1).	this paper	1	1	1	1	1	0
14. Pterygoid basal plate (secondary lamina): absent (0); present (1).	this paper	1	1	1	1	1	0
15. Pterygoid mandibular ramus, length: short process (0); pendant process projecting into the adductor fossa (1).	Sereno 1987	1	1	1	1	1	0
16. Quadrate medial condyle: convex (0); planar (1).	this paper	1	1	1	1	1	0
17. Palpebral, orientation of posterior (medial) margin: posterolateral (0); transverse (laterally divergent) (1).	this paper	1	1	?	1	1	0
18. Predentary ventral process(es), shape: longer than broad (0); broader than long (1).	this paper	1	1	?	1	1	0
19. Predentary anterior margin, shape (dorsal view): V-shaped (0); semicircular (1).	this paper	1	1	1	1	1	0
20. Dentary flange: absent (0); present (1).	Sereno 1987	1	1	1	1	1	0
21. Articular, surface for quadrate condyles: concave (0); planar (1).	this paper	1	1	1	1	1	0
22. Dentary teeth, primary ridge, shape: narrow, smooth (0); cone-shaped (approximately 1/3 crown face) with secondary ridging.	Sereno 1987	1	1	1	1	1	0

Note: The best known species of *Psittacosaurus* as well as the basal neoceratopsian *Liaoceratops yanzigouesis* (Xu et al. 2002) are scored. The basal neoceratopsian *Chaoyangsaurus youngi* (Zhao et al. 1999) also exhibits the derived state of characters 1 and 9, rendering the outgroup condition ambiguous for *Psittacosaurus*. Species abbreviations, 1: *P. mongoliensis;* 2: *P. lujiatunensis;* 3: *P. major;* 4: *P.* sp.; 5: *P. sinensis;* 6: *Liaoceratops yanzigouesis*.

analysis (Table 2.2). Preorbital skull length is very short, less than 40% skull length (as measured from the tip of the premaxilla to the posterior aspect of the quadrate condyle at the jaw articulation). Basal neoceratopsians such as *Liaoceratops, Archaeoceratops,* and *Protoceratops* have preorbital lengths ranging from about 45 to 55% (Sereno 2000; Xu et al. 2002; You and Dodson 2003). Although *Yinlong* appears to be particularly short-snouted (about 24% skull length), the holotype and only known skull is from a juvenile, and its particularly short snout is attributable to immaturity (Xu et al. 2006).

The tall snout, its sutural pattern, the dorsal position of the external naris, and the unusual structure of the internarial bar are all features unique to psittacosaurs among dinosaurs (Table 2.2, characters 2–7). Three other features, the premaxilla-maxilla ridge, the maxillary protuberance, and the construction of the supratemporal bar, may well be attachment sites for enhanced jaw musculature (Table 2.2, characters 8, 9, 12, 13).

A unique fenestra is nearly always present over the lacrimal canal, an opening that is unrelated to the antorbital fossa or fenestra, which are absent (Table 2.2, characters 10, 11). The posterior palate is reinforced with an additional bony plate to resist transverse compression as well as a pendant mandibular process to provide attachment for enhanced pterygoideus musculature (Table 2.2, characters 14, 15). Those muscles may have pulled the lower jaw forward, taking advantage of the flat jaw articulation (Table 2.2, character 16).

The palpebral projects strongly laterally in all species, a de-

Table 2.3. Variable Features among Species of *Psittacosaurus*

Autapomorphy	Author	1	2	3	4	5	6	7	8	9
1. Skull length relative to trunk length: approximately 30% (0); 40–45% (1).	A	0	1	1	1	1	1	1	1	1
2. Preorbital skull length relative to total skull length: 40–36% (0); 35–30% (1).	modified from B	0	1	1	1	1	1	?	1	1
3. External mandibular fenestra: present (0); absent (1).	B	0	1	1	1	1	1	?	1	1
4. Dentary flange, prominence: rugosity (0); low crest (1); prominent flange with anterior corner (2).	B	1	2	2	2	1	0	?	0	0
5. Jugal fossa: absent (0); present (1).	C	0	0	1	1	0	0	?	0	0
6. Postorbital-jugal ornamentation: ridge (0); horn (1).	B	0	0	0	0	1	1	?	1	1
7. Maxillary crowns, maximum width relative to height: 75% (0); subequal (1).	A	0	0	0	0	0	1	1	1	1
8. Premaxilla-jugal contact: absent (0); present (1).	B	0	0	0	0	?	1	?	0	1
9. Supratemporal bar, orientation (dorsal view): parasagittal (0); posteriorly divergent at an angle of approximately 15° (1).	B	0	0	0	0	0	0	?	1	1
10. Lower jaw length: long, predentary opposes rostral and premaxilla (0); short, predentary opposes premaxilla and anterior maxillary teeth (1).	A	0	0	0	0	0	0	?	1	1

Note: Original author abbreviations for characters that unite species groups, A: this paper; B: Sereno (1987); C: Zhou et al. (2006b). Character 4 is ordered. Species abbreviations, 1: *P. mongoliensis*; 2: *P. meileyingensis*; 3: *P. lujiatunensis*; 4: *P. major*; 5: *P. sibiricus;* 6: *P.* sp.; 7: *P. xinjiangensis*; 8: *P. neimongoliensis*; 9: *P. sinensis*.

rived feature of unknown function (Table 2.2, character 17). The predentary and dentary are firmly united, reinforcing the rounded bill margin at the anterior end of the lower jaw and providing direct attachment for jaw musculature (Table 2.2, characters 18, 20). The jaw articulation is flat for the most part, allowing posterior displacement of the lower tooth row during jaw closure (Table 2.2, characters 16, 21). Finally the dentary teeth have a bulbous primary ridge, the shape and prominence of which characterize the genus (Table 2.2, character 22).

Psittacosaur species. Sereno (1987) listed some 35 cranial characters that characterized, or varied among, the four species of *Psittacosaurus* then known (*P. mongoliensis, P. meileyingensis, P. xinjiangensis, P. sinensis*). The present review recognizes nine species using approximately 40 cranial characters. *Psittacosaurus* remains the most speciose dinosaurian genus, despite inflation of species numbers with taxa that now appear poorly justified. Differentiation among several species of *Psittacosaurus* is subtle and requires continuing review of current collections, which contain many new specimens. Such review must carefully consider the maturity of specimens under comparison and use dental features that are understood in the context of variation along a tooth row.

A Basal Species. The interrelationships of psittacosaurs were first addressed by Sereno (1987: table 19) using six characters scored in the four species that were regarded as valid at that time (*P. mongoliensis, P. meileyingensis, P. xinjiangensis, P. sinensis*). Only one of the six characters was scored as informative (lateral projection of the jugal horn in *P. xinjiangensis* and *P. sinensis*), a character subject to considerable developmental and individual variation as well as postmortem distortion. Subsequently, Russell and Zhao (1996), Xu (1997), and Averianov et al. (2006) have presented quantitative cladistic analyses of psittacosaur relationships, using 13, 17, and 31 characters, respectively. Recently You et al. (2008) added *P. lujiatunensis* and *P. major* to the data matrix in Averianov et al. (2006).

There is little consensus between these analyses regarding character data or results. Reanalysis of the data matrix of Russell and Zhao (1996) shows that 12 of 13 characters are informative, which yield 9 most parsimonious trees (23 steps; CI = 0.61; RI = 0.50). A strict consensus tree has one internal node uniting *P. ordosensis, P. neimongoliensis* and *P. sinensis* on the basis of the relative width of the postorbital region of the skull (broad versus narrow), a relative-linear character that is difficult to evaluate as stated (missing relative measure; Sereno 2007). With one additional step in length, all phylogenetic structure within *Psittacosaurus* breaks down (Fig. 2.23A). The analysis of Xu (1997) is based on Russell and Zhao (1996), although he excluded the new species *P. neimongoliensis* and *P. ordosensis* and included *P. mazongshanensis,* a species the validity of which has been questioned above (Fig. 2.23B). Xu (1997) added several characters, although the data matrix in some cases does not match the number of characters or states in the character list as mentioned by Averianov et al. (2006).

Reanalysis of the data matrix in Averianov et al. (2006) shows that 30 of 31 characters are informative (Fig. 2.23C), which yield seven most parsimonious trees as reported (58 steps; CI = 0.54; RI = 0.58). Although three internal nodes are present as indicated by Averianov et al. (2006), this data has little more phylogenetic structure than that in Russell and Zhao (1996; Fig. 2.23A). With one additional step in length, all phylogenetic structure within *Psittacosaurus* breaks down

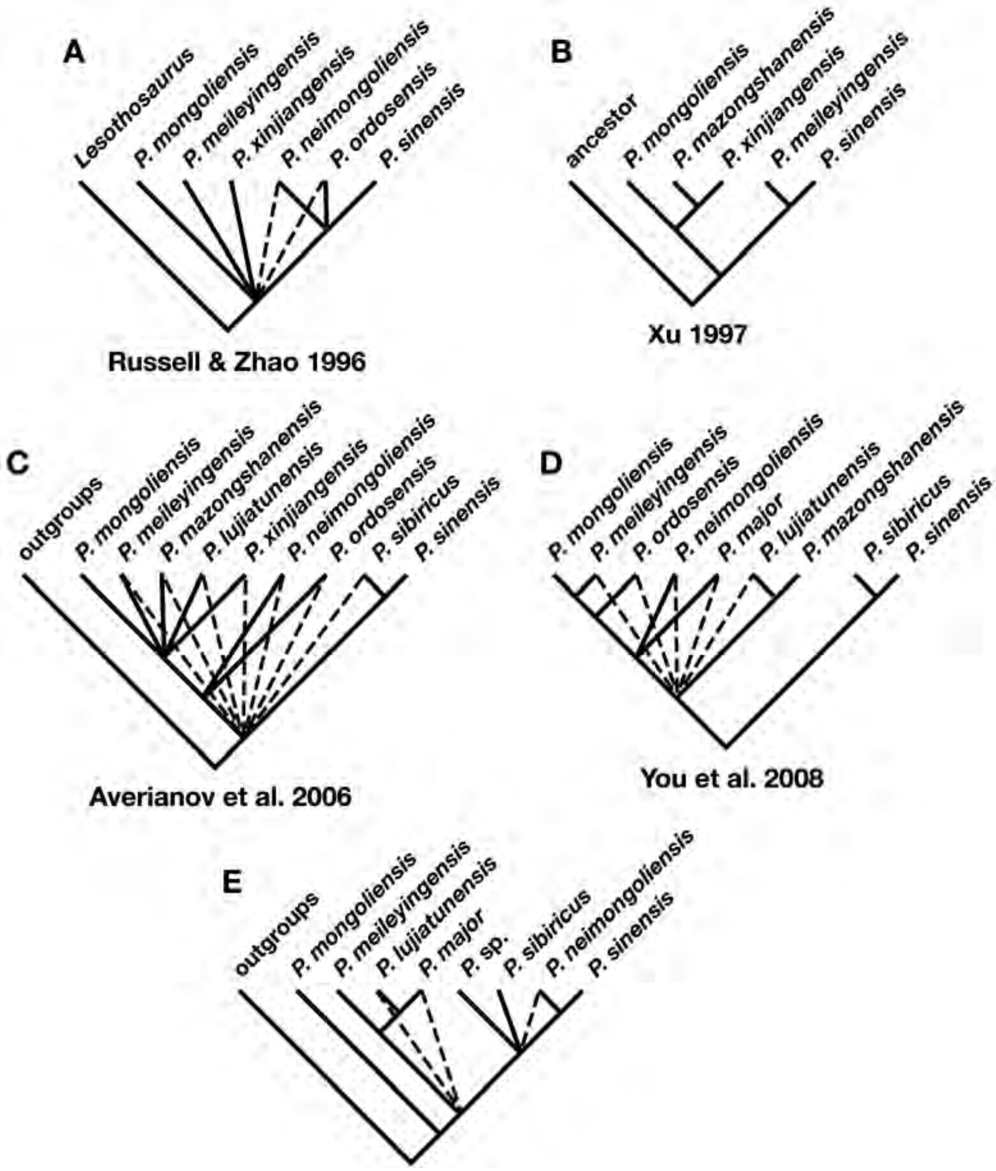


FIGURE 2.23. Previous phylogenetic hypotheses for psittacosaur species. (A) Consensus tree based on data in Russell and Zhao (1996); (B) tree given by Xu (1997); (C) consensus tree based on data in Averianov et al. (2006); (D) consensus tree based on data in You et al. (2008); (E) present phylogenetic hypothesis for psittacosaur species. Dashed lines indicate loss of resolution when considering trees one step longer than minimum length.

(Fig. 2.23C). Likewise, when a single species with the most missing data (*P. xinjiangensis*) is removed and the data reanalyzed, all phylogenetic structure within *Psittacosaurus* breaks down. When the species of questionable validity is removed (*P. mazongshanensis*), only one subclade remains (*P. mongoliensis, P. meileyingensis, P. xinjiangensis*). This trio of species, however, breaks down with one additional step in length. When the unnamed species from the Yixian Formation (*Psittacosaurus* sp.; Xu and Wang 1998) is removed, only a single pair of species remain (*P. sibiricus, P. sinensis*). In this case, two additional steps in tree length are required before all phylogenetic structure breaks down.

Recently, You et al. (2008) used the data matrix of Averianov et al. (2006), adding *P. major* and replacing "*Psittacosaurus* sp.," which is based on an incomplete specimen from the Yixian Formation (Xu and Wang 1998), with *P. lujiatunensis*. That replacement should have been further explained, as approximately two-thirds of the character states for *P. lujiatunensis* differ from those given for *P.* sp. by Averianov et al. (2006). Yu et al. (2008: fig. 6) presented a single fully resolved tree of 58 steps, although reanalysis of their data yields 3 trees at that length (Fig. 2.23D, consensus tree). As with Averianov et al. (2006), only one pair of species remains (*P. sibiricus, P. sinensis*) when considering trees one step longer, and this species pair breaks down with two additional steps in tree length.

The present phylogenetic assessment is based on a smaller set of characters in what are viewed as the least controversial species (Fig. 2.23E). Only 10 cranial characters are scored in 8 species (Table 2.3). Using *Yinlong, Liaoceratops,* and *Protoceratops* as outgroups and removing the poorly known species *P. xinjiangensis* (which can only be scored for two of the characters), a parsimony analysis yields 3 trees of 11 steps (CI = 0.91; RI = 0.93). *P. mongoliensis* is positioned as the sister taxon to other psittacosaurs.

One character that supports this conclusion, skull length relative to trunk length, is new to the analysis. In *P. mongoliensis* the skull is proportionately larger than in other psittacosaur species, varying between about 40–45% of trunk length (Table 2.3, character 1). Trunk length in this regard equals the length of the presacral vertebral column or, if the vertebrae are not exposed, the length from the back of the skull roof to the middle of the preacetabular process of the ilium. These proportions are known in most species, with proportions for *P. lujiatunensis* inferred from other specimens from the Lujiatun Beds (Xu and Wang 1998; Mayr et al. 2002). Skull length in *P. mongoliensis,* in contrast, is only approximately 30% of trunk length, as best preserved in the holotype skeleton (Osborn 1924; Sereno 1990b). The major question here involves the outgroup condition, because neoceratopsians also have skulls that are 40% or more of trunk length (Sereno et al. 2007). The Late Jurassic ceratopsian *Yinlong downsi* (Xu et al. 2006), however, resembles *P. mongoliensis* with a skull length only approximately 30% of trunk length. Because the holotype of *Y. downsi* is a subadult, furthermore, its skull proportion is likely to decrease slightly with maturity. More remote nonceratopsian ornithischians have skull lengths comparable to *P. mongoliensis* and *Y. downsi,* which are usually less than 30% and always less than 40% of trunk length.

Another feature suggesting that *P. mongoliensis* is basal to other species is the preorbital length of the skull (Table 2.3, character 2). The length of the preorbital segment of the skull—when measured in adult skulls with uniform registration of the cranium as discussed above (see discussion, general adult skull shape)—is approximately 30–35% of skull length in all psittacosaur species except *P. mongoliensis,* where it averages about 37%. Preorbital length in both *Chaoyangsaurus* and *Yinlong,* however, is short (approximately 30%) as well. Other basal neoceratopsians such as *Archaeoceratops* (You and Dodson 2003), in contrast, have preorbital lengths approximately 40% of skull length. The basal condition for Ceratopsia thus is not settled.

Lastly, the external mandibular fenestra is open in *P. mongoliensis* but closed in other species (Table 2.3, character 3). *P. mongoliensis* is the only psittacosaur with a substantial external mandibular fenestra in fully mature individuals (e.g., AMNH 6234). The basal neoceratopsian *Yinlong* (Xu et al. 2006) also has an open fenestra, although this varies among basal neoceratopsians (e.g., small in *Chaoyangsaurus* and closed in some other neoceratopsians).

Two Clades. Some character evidence suggests that psittacosaur species other than *P. mongoliensis* can be divided into two groups, here termed the "*P. major*" and "*P. sinensis*" clades, which is maintained with one additional step in tree length (Fig. 2.23E). The *P. major*-clade is characterized by hypertrophy of the dentary flange with development of a marked anterior corner and a fossa centered on the jugal (Table 2.3, characters 4 and 5). This psittacosaur subclade, however, breaks down with a single additional step in tree length.

The *P. sinensis*-clade is characterized by a postorbital-jugal horn (Table 2.3, character 6). Species in this group that are more advanced than *P. sibiricus* have sutural contact between the premaxilla and jugal and have reduced the dentary flange to a ridge (Table 2.3, characters 4 and 7). Finally, *P. neimongoliensis* and *P. sinensis* have posteriorly divergent supratemporal bars (diverging posteriorly at an angle of 30° from an apex a short distance anterior to the rostral) and a lower jaw that is noticeably shorter than the upper jaw (Table 2.3, characters 8 and 9). The short lower jaw is not an artifact of preservation or movement relative to the cranium. Its shorter length is preserved in natural articulation in the holotypic skull of *P. sinensis* (Fig. 2.8). The short length of the lower jaw positions the predentary posterior to the rostral in opposition to the premaxilla and anteriormost maxillary teeth. In the original reconstruction of *P. neimongoliensis* (Russell and Zhao 1996: fig. 1B), the lower jaw was shifted forward relative to the cranium, such that the quadrate condyle is positioned over the retroarticular process. When the jaw joint is realigned, *P. neimongoliensis* also has the very short lower jaw. In other species such as *P. mongoliensi*s, it is impossible to slide the lower jaws posteriorly into this position.

Ceratopsian Roots. There has yet to be found a truly transitional form to *Psittacosaurus* that would help to polarize characters within the genus, which is restricted to a relatively narrow temporal interval within the Early Cretaceous. Recently other ceratopsians have been discovered in beds of similar age (Xu et al. 2002) and in earlier horizons of Late Jurassic age (Xu et al. 2006). Most notable among these finds are *Chaoyangsaurus* (Zhao et al. 1999) and *Yinlong* (Xu et al. 2006), which have been placed in some arrangements outside other ceratopsians including psittacosaurs (Xu et al. 2002, 2006). In skull structure and masticatory function, however, the psittacosaur pattern described in this account differs in many ways from these ceratopsians, which are characterized by a narrow hooked upper beak, deep supratemporal bar, markedly divergent tooth rows, and very short retroarticular process. These neoceratopsian features may point to an early divergence from psittacosaurs during the Jurassic, a hypothesis that awaits a rigorous test from new character data on early ceratopsians.

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