

Psittacosaurus amitabha, a New Species of Ceratopsian Dinosaur from the Ondai Sayr Locality, Central Mongolia

JAMES G. NAPOLI,^{1, 2} TYLER HUNT,³ GREGORY M. ERICKSON,³
AND MARK A. NORELL^{1, 2}

ABSTRACT

Psittacosaurus is the most speciose nonavian dinosaur genus, represented by at least 10 (and possibly as many as 19) species uncovered over a wide geographic range. Here, we report a new species of large-bodied *Psittacosaurus* from the Ondai Sayr locality in central Mongolia, which has hitherto produced only one other *Psittacosaurus* specimen. This new species is characterized by: (1) an elongate snout, with a gently inclined rostronasal margin, (2) a cranium dorsally convex rather than flat, (3) a subtemporal length less than 40% of total skull length, (4) a maxillary lamina that cups the posterior tooththrow, (5) five premaxillary foramina arrayed in an arc, (6) an antorbital fossa as long as it is wide, and (7) a palpebral with a well-developed posterior tonguelike process. *Psittacosaurus amitabha* is resolved as the most basal member of the genus *Psittacosaurus* in our phylogenetic analysis. This taxon expands our knowledge of the already-speciose genus *Psittacosaurus* as well as our understanding of the Ondai Sayr fauna, which is poorly known in comparison to other Mongolian Early Cretaceous localities.

¹ Richard Gilder Graduate School, American Museum of Natural History.

² Division of Paleontology, American Museum of Natural History.

³ Department of Biological Science, Florida State University.

INTRODUCTION

Since its original description by Osborn (1923), the genus *Psittacosaurus* has become the most well-known of all non-avian dinosaur genera, with hundreds to thousands of specimens discovered in China, Mongolia, Russia, and perhaps Thailand (Serenó, 2010). An exceptionally preserved, but contentious specimen of dubious legality in the Senckenberg Museum (SMF R 4970) (see Dalton, 2001) has revealed much regarding the integument of this taxon, such as the presence of a row of keratinous quills on the tail that may be homologous with avian feathers (Mayr et al., 2002, 2016) and countershading camouflage coloration across the rest of the body (Vinther et al., 2016). The extensive number of *Psittacosaurus* fossils also provides insights into individual species life history; for instance, juvenile-only assemblages of *Psittacosaurus* sp. suggest that the juveniles were gregarious, and formed mixed-age flocks (Meng et al., 2004; Zhao et al., 2013). The juveniles grew at a rate comparable to similarly-sized nonavian dinosaurs (Erickson et al., 2009; Bo et al., 2016) and were prey for contemporary predatory mammals such as *Repenomamus giganticus* (Hu et al., 2005).

With so many specimens spread across a broad geographic region, it is unsurprising that many species of *Psittacosaurus* have been recognized since the initial description of the genus. With his description of *Psittacosaurus mongoliensis*, the type species (from the Oshi locality; see Berkey and Morris, 1927), Osborn (1923) also reported a specimen from the Ondai Sayr locality (AMNH FARB 6253) that he dubbed *Protiguanodon mongoliense*. Initially, he placed *Protiguanodon* separately from *Psittacosaurus*, as a basal “Pro-Iguanodontia type”; however, he soon recognized the similarity of the two specimens and placed them as members of Psittacosauridae (Osborn, 1924). Two new species—*Psittacosaurus osborni* and *Psittacosaurus tingi*—followed in the next decade (Young, 1931). Later, Young (1958) also described another new species, *Psittacosaurus sinensis*, shortly followed by *Psittacosaurus youngi* (Zhao, 1962). In the 1980s, three additional species were described—*Psittacosaurus guyangensis*, *Psittacosaurus xinjiangensis*, and *Psittacosaurus meileyingensis* (Cheng, 1983; Sereno and Chao, 1988; Sereno et al., 1988). Cumulatively, in the past 30 years, 11 potential new species have been described, bringing the total number of proposed *Psittacosaurus* species to 19 (Serenó, 2010).

The taxonomy of *Psittacosaurus* species has a long history of synonymization. Sereno (1987) synonymized *Psittacosaurus youngi* with *Psittacosaurus sinensis*, and united *Psittacosaurus osborni* and *Psittacosaurus guyangensis* with *Psittacosaurus mongoliensis*. Furthermore, on the basis of extreme postcranial similarity, Sereno proposed *Protiguanodon* as a junior synonym of *Psittacosaurus*, referring AMNH FARB 6253 to *Psittacosaurus mongoliensis*. It is worth noting, however, that most of the “*Protiguanodon*” holotype (AMNH FARB 6253) skull weathered away before collection, leaving only a partial mandible and skull table for study (Osborn, 1923). Sereno (2010) extensively revised the taxonomy of *Psittacosaurus*, finding that nine of the proposed species were valid: *Psittacosaurus mongoliensis* (Osborn, 1923), *Psittacosaurus sinensis* (Young, 1958), *Psittacosaurus xinjiangensis* (Serenó and Chao, 1988), *Psittacosaurus meileyingensis* (Serenó et al., 1988), *Psittacosaurus neimongoliensis* (Russell and Zhao, 1996), *Psittacosaurus sibiricus* (Averianov et al., 2006), *Psittacosaurus lujiatunensis* (Zhou et al., 2006), *Psittacosaurus major* (Serenó et al., 2007), and *Psittacosaurus gobiensis* (Serenó et al., 2010). Recently, *P. lujiatunensis* and *P. major*,

both of which are known from the Lujiatun beds of the Yixian Formation, were found to form one morphometric cluster using 3D geometric morphometrics (Hedrick and Dodson, 2013), leading the authors to pronounce *P. major* a junior synonym of *P. lujiatunensis*. There are several problems with this analysis. The authors did not retrodeform the specimens, incorporated juveniles and adults in the same dataset, and did not reference the range of intraspecific variation present among modern animals. Therefore, we consider their argument for synonymizing these species inconclusive and continue to treat them as separate taxa in this study.

Here we describe a new species of *Psittacosaurus*, based on a well-preserved skull found in association with fragmentary postcrania. This specimen is notable for: (1) its large size (only matched by *Psittacosaurus major* and *Psittacosaurus sibiricus*), (2) its nearly complete and undistorted braincase, and (3) being the first specimen of the genus *Psittacosaurus* recovered from the Ondai Sayr locality since AMNH FARB 6253 nearly 100 years ago.

INSTITUTIONAL ABBREVIATIONS

AMNH FARB	American Museum of Natural History Fossil Amphibians, Reptiles, and Birds, New York
AMNH FF	American Museum of Natural History Fossil Fish, New York
AMNH FI	American Museum of Natural History Fossil Invertebrates, New York
CAGS-IG	Chinese Academy of Geological Sciences, Institute of Geology, Beijing
IGM	Mongolian Institute for Geology, Ulaanbaatar, Mongolia
LH	Long Hao Institute for Stratigraphic Paleontology, Hohhot, China
SMF	Forschungsinstitut Senckenberg, Frankfurt am Main, Germany
ZMNH	Zhejiang Museum of Natural History, Hangzhou, China

SYSTEMATIC PALEONTOLOGY

Dinosauria Owen, 1842

Ornithischia Seeley, 1888

Ceratopsia Marsh, 1890

Psittacosauridae Osborn, 1923

Psittacosaurus Osborn, 1923

***Psittacosaurus amitabha*, sp. nov.**

ETYMOLOGY: The celestial Amitabha Buddha is the Buddha of infinite light, and one of his attributes is extreme longevity (fig. 1). Amitabha is the principal Buddha of Pure Land Buddhism and is highly venerated in Mongolia.



FIGURE 1. A 19th-century Mongolian depiction of the Amitabha Buddha.

TABLE 1. Select measurements of IGM 100/1132.

Element	Measurement	mm
Skull	Basal length	152
	Width over quadrates	107
	Height	90
Mandible (partial)	Length	103
Metatarsal I (left; partial)	Length	28
	Width at distal end	16
	Anteroposterior diameter at proximal extent	12
Metatarsal II (left; partial)	Length	57
	Width at distal end	19
	Anteroposterior diameter at proximal extent	11
Metatarsal III (left; partial)	Length	61
	Width at distal end	20
	Anteroposterior diameter at proximal extent	10
Metatarsal IV (left; partial)	Length	53
	Anteroposterior diameter at proximal extent	7
Metatarsal IV (right; partial)	Length	49
	Width at distal end	16
	Anteroposterior diameter at proximal extent	7
Phalanx I-1	Length	33
	Width	20
Phalanx I-2	Length	37
	Width	15
Phalanx II-1	Length	30
	Width	20
Phalanx II-2	Length	27
	Width	18
Phalanx II-3	Length	39
	Width	17
Phalanx III-1	Length	28
	Width	23
Phalanx III-2	Length	25
	Width	20
Phalanx III-3	Length	23
	Width	17
Phalanx III-4	Length	36
	Width	16
Caudal vertebra 3	Length of centrum	25
	Width of centrum	24
	Height	61
	Width over transverse processes	79
	Total length (prezygapophyses-neural spine)	37



FIGURE 2: Map of Mongolia, showing the location of the Ondai Sayr locality from which IGM 100/1132 was recovered.

HOLOTYPE: IGM 100/1132, a nearly complete, undistorted skull with an associated partial mandible and fragmentary postcranial elements. The specimen was discovered by M.A. Norrell and J.M. Clark. All elements represented in IGM 100/1132 are listed in appendix 1, and select measurements are given in table 1.

TYPE LOCALITY: Ondai Sayr, Ussuk, Tsaagan Nor basin, Central Mongolia (fig. 2). The Ondai Sayr locality has also been considered the Andakhuduk Formation (Jerzykiewicz, 2000). The age of the locality is generally considered to be Barremian (Jerzykiewicz and Russell, 1991). Other dinosaurian remains have been found at this locality, including juvenile specimens of *Psittacosaurus* (Coombs, 1982), but vertebrate fossils are extremely rare (M.A.N., personal obs.). A list of all American Museum of Natural History specimens from the Ondai Sayr locality is presented in appendix 2.

DESCRIPTION

The skull of IGM 100/1132 (figs. 3–5) is nearly complete and three-dimensionally preserved, with only minor distortion to the left side. The jugal horns are missing, interpreted here as the result of postmortem scavenging by larval arthropods (fig. 3). The cranial sutures are nearly obliterated, suggesting this is a fully mature individual (but see

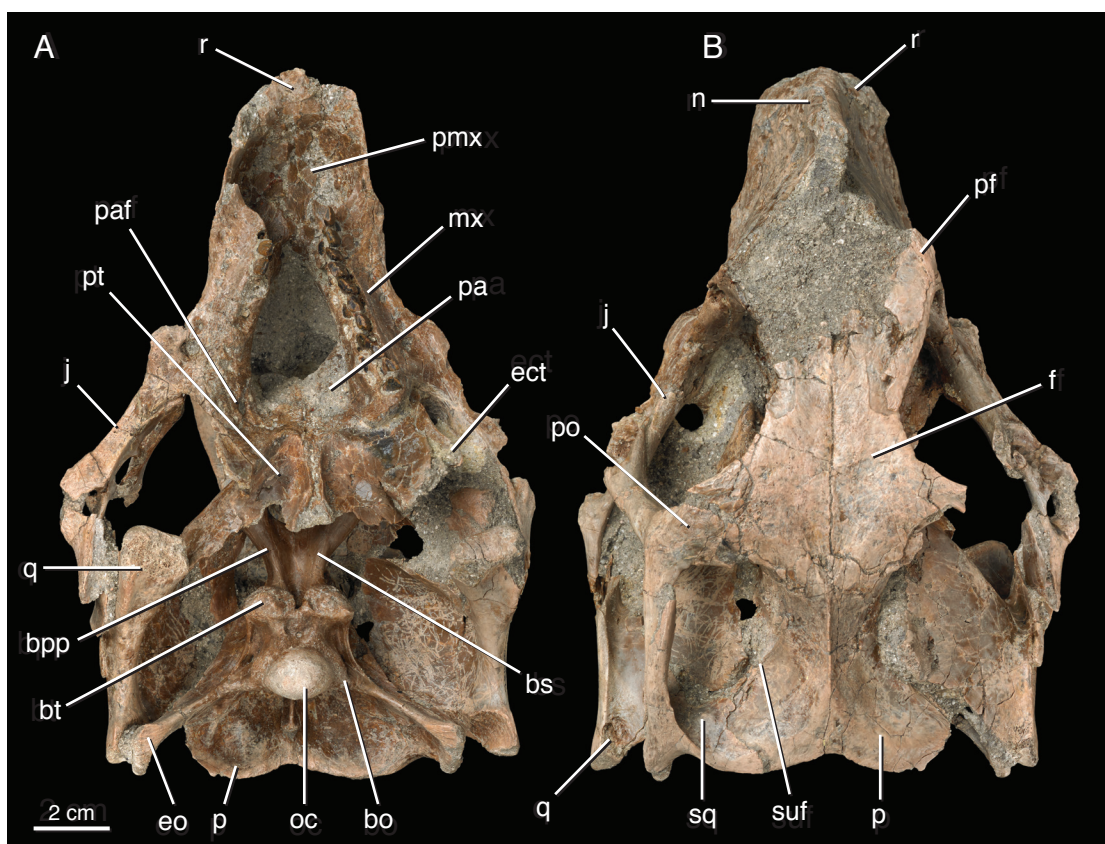
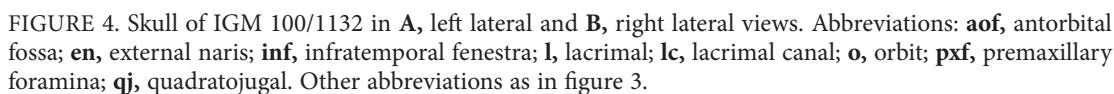


FIGURE 3. Skull of IGM 100/1132 in A, ventral and B, dorsal views. Abbreviations: **bo**, basioccipital; **bpp**, basipterygoid process; **bs**, basisphenoid; **bt**, basal tuber; **ect**, ectopterygoid; **eo**, exoccipital-opisthotic; **f**, frontal; **j**, jugal; **mx**, maxilla; **n**, nasal; **oc**, occipital condyle; **p**, parietal; **pa**, palatine; **paf**, palatal foramen; **pf**, prefrontal; **pmx**, premaxilla; **po**, postorbital; **pt**, pterygoid; **q**, quadrate; **r**, rostral; **sq**, squamosal; **suf**, supra-temporal fenestra.

histology section below). A partial mandible and fragmentary postcrania were associated with the skull. The skull measures 182 mm long from the tip of the snout to the posterior margin of the paroccipital processes, 168.5 mm from the snout to the distal end of the basioccipital condyle, 107 mm wide across the quadrates and 90 mm high from the ventral margin of the pterygoid wings to the dorsal margin of the frontal. The basal skull length (from the tip of the rostral to the posterior margin of the quadrate condyles) is 152 mm. There is no trace of the vomer, but all other bones of the skull are present. The mandible is primarily represented by the dentary and possibly the angular; the prementary, surangular, splenial, coronoid, and articular are absent.

The preorbital region is 73 mm in length. The anterior margins of the rostral and nasals are inclined more posterodorsally than in other *Psittacosaurus*, where this margin is almost vertical. The skull roof is gently arched, reaching an apex over the middle of the orbits; this contrasts to the flattened skull roofs seen in other *Psittacosaurus*. The orbit is roughly circular,



Comparisons below are primarily drawn to *Psittacosaurus mongoliensis* (AMNH FARB 6254 and AMNH FARB 6253) and *Psittacosaurus major* (LHPV 1 and CAGS-IG-VD-004), with other specimens referenced where appropriate. Select measurements of preserved elements are presented in table 1. STL files of the specimen's skull, mandible, left pes, and caudal vertebrae are available as supplementary material (<https://doi.org/10.5531/sd.sp.34>). Our phylogenetic matrix, modified from Han et al. (2018), is available on MorphoBank (Project 3377).

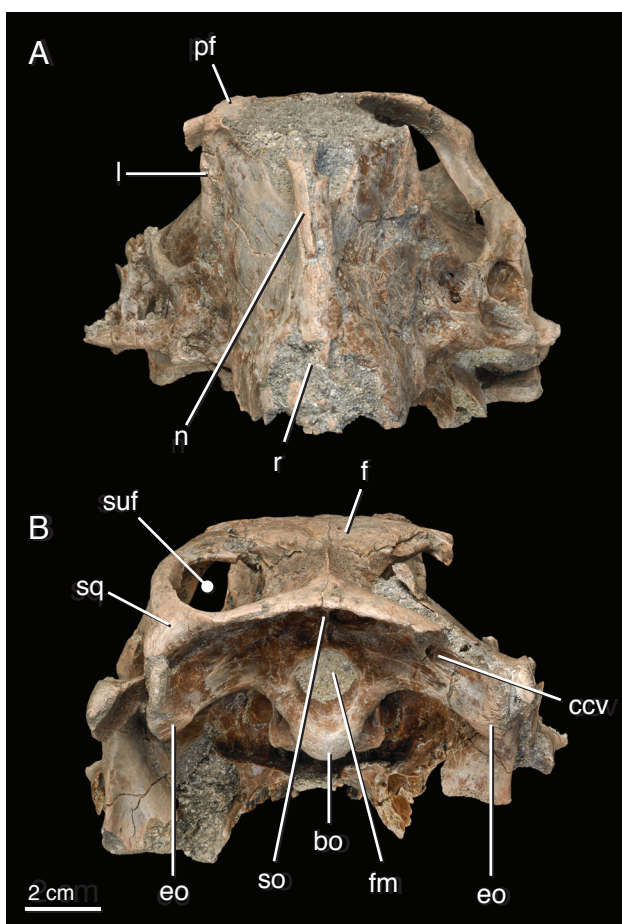


FIGURE 5. Skull of IGM 100/1132 in **A**, anterior and **B**, posterior views. Abbreviations: **ccv**, foramen for caudal middle cerebral vein; **fm**, foramen magnum; **so**, supraoccipital. Other abbreviations as in figures 3 and 4.

ROSTRAL

The anteroventral part of the rostral is eroded, as is most of the triturating margin. As in *Psittacosaurus mongoliensis*, *P. meileyingensis*, *P. gobiensis*, *P. major*, *P. neimongoliensis*, and *P. ordosensis* (Osborn, 1923; Sereno et al., 1988, 2007, 2010; Russell and Zhao, 1996; You et al., 2008), the apex of the rostral abuts the descending rostral processes of the nasals. Unlike in *P. sinensis* and *P. lujiatunensis*, the apex of the rostral does not extend between the rostral processes of the nasal (fig. 5A; Young, 1958; Zhou et al., 2006). In anterior view, the rostral is subtriangular (fig. 5A). Unlike in other *Psittacosaurus* species, the rostral does not uniformly taper to its apex. Instead, it narrows sharply at about two-thirds its height (fig. 5A). In lateral view, the rostral-premaxilla suture is sinuous (fig. 4). Dorsally, it is anteriorly convex and gently curved. At about half its height, the suture becomes strongly arched and anteriorly concave. The suture then trends anteroventrally to its ventral margin, in contrast to the condition seen in all other *Psittacosaurus* species (fig. 4). The surface of the rostral is pitted and striated, as in

other *Psittacosaurus* species and was likely covered with a keratinous beak in life (Osborn, 1923; Sereno et al., 1988, 2010). The rostral's anterior margin is gently curved, and does not recurve posteriorly as in *Psittacosaurus mongoliensis* (fig. 4; Osborn, 1923; Sereno, 1987, 2010).

PREMAXILLA

The premaxillae are tall and broad in lateral view, as in other species of *Psittacosaurus* (fig. 4). Near the rostral, the lateral surfaces of the premaxillae bear a rugose texture like that of the rostral, suggesting that the keratinous beak was not confined to the rostral. The posterior expansion of the posterolateral process of the premaxilla excludes the maxilla from the external nares, which are bounded solely by the nasals and premaxillae. This is diagnostic of Ornithischia and like the condition found in all other *Psittacosaurus* species (Sereno, 1987; Russell and Zhao, 1996; Averianov et al., 2006; Zhou et al., 2006; Sereno et al., 2007, 2010). The external nares are oval and posterodorsally inclined, unlike the near-vertical condition found in *P. meileyingensis*, *P. gobiensis*, *P. neimongoliensis*, *P. ordosensis*, and *P. lujiatunensis*, and unlike the circular nares found in *P. mongoliensis*, *P. major*, *P. sibiricus*, and *P. sinensis* (fig. 4; Osborn, 1923; Young, 1958; Sereno, 1987; Sereno et al., 1988; Russell and Zhao, 1996; Averianov et al., 2006; Zhou et al., 2006; Sereno et al., 2007, 2010). Like in all other *Psittacosaurus* species, the lateral surfaces of the premaxillae are broadly concave (Sereno, 1987). Just posterior to the apex of the rostral, the premaxillae bear five foramina arranged in an arc (fig. 4). The two posteriormost foramina open posterodorsally and on both sides merge into a single hourglass-shaped opening. The next two foramina open dorsally and the anteriormost foramen opens anteriorly, toward the rostral. These foramina are interpreted as neurovascular foramina, like those present in *P. mongoliensis* and *P. gobiensis* (Sereno, 1987; Sereno et al., 2010), but are more numerous than described in any known species of *Psittacosaurus*. Neurovascular grooves are faint but can be discerned from several of the foramina on each side of the skull. The premaxillae lack fenestrated lacrimal canals, as in *P. mongoliensis*, *P. major*, and *P. meileyingensis* (Osborn, 1923; Sereno, 1987; Sereno et al., 2007). The premaxillae contact the prefrontals and lacrimals posteriorly, and the maxilla ventrally; the contact with the maxilla is marked by a raised ridge, as in *P. mongoliensis* (see Sereno, 1987). Ventrally, the premaxillae expand medially, joining with the rostral and maxillae to form an arched secondary palate at the front of the upper jaw (fig. 3A). As in all other *Psittacosaurus* species, the premaxillae are edentulous.

MAXILLA

The maxillae are subtriangular in lateral view (fig. 4). The premaxilla-maxilla suture is marked by a distinct ridge, which forms the anterior boundary of a triangular maxillary fossa as in most other *Psittacosaurus* species, with the exception of *P. sinensis* and *P. neimongoliensis* (Young, 1958; Russell and Zhao, 1996). This fossa is not considered homologous to the antorbital fossa where the antorbital fenestra occurs in other archosaurs

(Serenio, 2000, 2010; You et al., 2008). The posterior sutural contacts of the maxilla are not visible due to presumed fusion, but the bone obviously contacts the jugal and seems to have a narrow contact with the lacrimal, as in most *Psittacosaurus* species but unlike *P. sinensis* and *P. gobiensis* (Serenio, 1987; Serenio et al., 2010). The maxilla is strongly emarginated, displaying the medially inset toothrow characteristic of ornithischian dinosaurs (fig. 3A). Approximately six foramina open ventrolaterally from under the buccal emargination, as in *P. mongoliensis* (Serenio, 1987). The dentition in the left maxilla is complete, bearing 11 teeth. The teeth are heavily worn; the labial surfaces in the least-worn teeth bear a central primary ridge, flanked by two secondary ridges anterior and posterior to the primary ridge, forming five cusps in total. The lingual surfaces of the maxillary teeth are smooth, but the five cusps are discernible at the margin of the crown.

Anteriorly, the maxillae show projecting anteromedial processes that form the posterior end of the secondary palate (fig. 3A). Posteriorly, the tooth-bearing pedestal of the maxillae turns inward, forming a cupped lamina that is anteriorly concave. The posterior aspect of this cupped lamina abuts the pterygoid; this is in contrast to the condition in *P. mongoliensis* where the tooth-bearing pedestal contacts the pterygoid without a distinctive cupped lamina.

PALATINE

The posterior portions of both palatines are preserved (fig. 3A). They contact the pterygoid and ectopterygoid posteriorly and the maxilla laterally. The contact with the maxilla is antero-posteriorly extensive, running to approximately the middle of the toothrow via a long narrow processes of the palatine. Medially, the palatines vault dorsally, creating a raised palate over the posterior maxillary toothrow, as in other *Psittacosaurus* specimens. Together with the maxilla and the pterygoid, the palatine forms the palatal foramen common to all ceratopsians for the passage of the maxillary branch of the trigeminal nerve (Brown and Schlaikjer, 1940; You and Dodson, 2004).

PTERYGOID

The pterygoids are fused along the midline. As in other *Psittacosaurus*, they form a horizontal basal plate at the posterior end of the palate, which projects the palatal, mandibular, and quadrate rami of the pterygoid (fig. 3A). The palatal ramus is not exposed, but clearly articulated with the palatine to form a vaulted posterior palate. The interpterygoid space described by Serenio (1987) is not visible. The mandibular rami are thin but mediolaterally broad, passing posteroventrally to form the flanges for attachment of the *M. pterygoideus* jaw adductor musculature. The anteromedial part of this ramus contacts the cupped posterior lamina of the maxilla.

Posteriorly, the basal plate and mandibular rami grade into the quadrate ramus, a large sheet that in this specimen has fused with the pterygoid ramus of the quadrate to form a solid sheet of bone between the adductor chamber and the braincase (fig. 3A). The quad-

rate ramus also forms an anteriorly facing articular facet to receive the basiptyergoid processes of the basisphenoid. This articulation is not visible in ventral view, a condition similar to that in *Psittacosaurus mongoliensis*, though in this case it is not due to the development of a posterior tablike process of the quadrate ramus (which is not preserved in this specimen), but rather to the overall posterior extent of the quadrate ramus and basal plate.

ECTOPTYERGOID

The left ectoptyergoid is present dorsal and lateral to the left pterygoid flange, running along the length of the flange to contact the maxilla and jugal anteriorly (fig. 3A). The ectoptyergoid-ptyergoid articulation takes the form of an elongate scarf joint. The ectoptyergoid is excluded from the palatal foramen by the maxilla and pterygoid. The right ectoptyergoid is not present.

NASAL

The majority of the nasals are eroded, however the rostral processes on both sides are preserved, the right more completely than the left (figs. 3B, 5A). The rostral processes abut the ascending process of the rostral bone, and overlay the anterior margin of the premaxilla between the rostral and the external nares. The eroded region of the specimen suggests that the external nares were framed equally by the premaxillae ventrally and the nasals dorsally. The dorsal surface of the nasals is completely eroded, and their width at the midline and contacts to the prefrontals and frontals cannot be discerned. In overall form, however, it is clear that the nasals were less strongly flexed than in other species of *Psittacosaurus*; combined with an anteroventrally projected rostral, this gives the snout of *Psittacosaurus amitabha* a more elongate appearance than even that of the notably long-snouted *Psittacosaurus mongoliensis* (fig. 4; Sereno, 2010).

PREFRONTAL

Portions of the right and left prefrontals are preserved, with the right element being more complete (fig. 3B). The prefrontal-lacrimal suture is completely obliterated, so the details of this contact cannot be discerned; however, it is clear that the anterodorsal quadrant of the orbit was framed by the prefrontal. The prefrontal portion of the orbital rim is textured, indicating ligamentous attachment to the palpebral. There is a raised lip or “prefrontal crest” on the orbital margin of the prefrontal, as seen in *Psittacosaurus mongoliensis* (fig. 5A; Sereno, 1987, 2010). The posterior ramus of the prefrontal contacts the frontal in a broad scarf joint, as evidenced by broad flat articular facets on the anterodorsal frontal. The posterior terminus of these processes are squared off, and the bone appears to have expanded anteriorly, making it somewhat roughly teardrop shaped in dorsal view.

PALPEBRAL

Part of the right palpebral is present, but disarticulated from the rest of the skull. The palpebral is markedly distinct from that of other *Psittacosaurus*, where the palpebral is subtriangular in dorsal view, extending through only the anterior one-third of the orbit. The palpebral of IGM 100/1132 is posteriorly expanded into a distinct tongue, extending more than half the length of the orbit in life position. The posterior tongue deflects dorsally, slightly overlapping the frontal. The ventral surface of the bone bears a distinct striated surface that likely served as insertion for the ligament attaching it to the prefrontal. The anterior region of the element is broken, but appears to have been subtriangular, as in other *Psittacosaurus*. In its anteroposterior extent, the palpebral is similar to the element in basal ornithopods such as *Haya griva* (Makovicky et al., 2011). However, in *H. griva* the posterior extension of the palpebral is on the lateral side, whereas the posterior tongue in IGM 100/1132 is on the medial side, articulating with the rest of the skull (Barta and Norell, in review).

LACRIMAL

Both lacrimals are present; though their sutural contacts are fused, they appear to have contacted the prefrontals, premaxillae, maxillae, and jugals (fig. 4). Lacrimal-premaxilla contact varies among *Psittacosaurus* species; *Psittacosaurus mongoliensis* and *Psittacosaurus major* both have limited contact between these bones, while *Psittacosaurus sinensis* does not (Young, 1958; Sereno, 1987, 2010; Sereno et al., 2007). The lacrimal frames the anteroventral quadrant of the orbit in *Psittacosaurus*. The lacrimal bears a large foramen allowing neurovascular passage via the lacrimal canal from the orbit to the rostrum. The neurovascular occupants of this canal likely passed through the premaxillary foramina to supply and innervate the rostrum. The lacrimal canal does not appear to be laterally fenestrated, as in most *Psittacosaurus* (fig. 4). Sereno (2010) claims that this fenestra indicates incomplete ossification of the lacrimal canal at the premaxilla-lacrimal suture; however, the bone is very thin (as evidenced by bilateral damage on this specimen), suggesting that the “fenestra of the lacrimal canal” may simply be a region of thin and easily broken bone. This would explain the wide distribution of this structure and its irregular, often subrectangular shape.

FRONTAL

The paired frontals are both preserved completely, joined at the midline by a straight suture (fig. 3B). Anteriorly, they contacted the prefrontals and nasals via flattened scarf joints. While the anterior extent of the frontals is partially eroded, the nasal contacts appear to have formed a zigzag anterior margin that was laterally confluent with a straight, posteriorly extending contact with the prefrontal that deflects laterally at about the middle of the orbit. Medial to the prefrontal facet, the frontals have a striated texture (fig. 3B). The frontal forms a part of the dorsal orbit, between the prefrontals and postorbitals. The postorbital-frontal suture is broad, and W-shaped in dorsal view. Posteriorly, the frontals contacted the parietal in a sinuous suture. Two small but

distinct fossae are present on each side of the midline, just anterior to the parietal contact, uniting to form a posteriorly angled triangular depression about the midline (fig. 3B). These fossae are absent on AMNH FARB 6253, which instead displays a prominent frontal contribution to the supratemporal fossae (Osborn, 1924). In IGM 100/1132, the frontals are nearly excluded from the supratemporal fenestrae, but do form a small portion of the rim between the parietal and postorbitals, and do not contribute to the supratemporal fossa (fig. 3B).

POSTORBITAL

The postorbital is a triradiate bone forming approximately one-third of the dorsal margin and all the posterior margin of the orbit. The right postorbital is disassociated from the remainder of the skull, but the entire left postorbital is present in its original position (fig. 3, 4). The anterior ramus of the postorbital is dorsoventrally flat and anteroposteriorly wide, broadly contacting the frontal (see above), and narrowly contacting the parietal at the anterior rim of the supratemporal fenestra (fig. 3B). The body of the postorbital is swollen into a rugose boss that may have borne a small keratinous sheath, similar to that inferred by Sereno et al. (2010) for *Psittacosaurus gobiensis*. The posterior ramus of the postorbital is long and thin, forming a long scarf joint with the anterior ramus of the squamosal; the postorbital's posterior ramus is so long that it nearly contacts the head of the quadrate. This ramus forms the dorsal margin of the infratemporal fenestra, nearly excluding the squamosal from this opening (fig. 3B). The ventral ramus of the postorbital frames the posterior rim of the orbit and the anterior margin of the infratemporal fenestra. This ramus is thicker than the posterior ramus, and roughly cylindrical in cross section. The ventral ramus contacted the jugal; however, postmortem scavenging (probably by arthropods) and sutural fusion make the details of this contact difficult to discern. It does seem that the ventral ramus of the postorbital laterally overlaid the postorbital process of the jugal in a scarf joint. The region of the postorbital-jugal contact bears a distinct laterally directed eminence that represents a postorbital-jugal crest, which is known from most *Psittacosaurus*, and may have also borne a keratinous sheath (fig. 4A; Sereno, 2010; Sereno et al., 2010).

JUGAL

The jugals have been mostly destroyed by postmortem scavenging (figs. 3–5). The jugal horns are notably missing, preventing comparison of this important structure with other species of *Psittacosaurus*. Sutural fusion has also made most of the contacts of the jugal difficult to discern. However, the jugal obviously contacts the lacrimal, maxilla, postorbital, and quadratojugal, and forms the ventral rim of the orbit and infratemporal fenestra. The jugal also seems to share a limited contact with the pterygoid, via a thin process intervening between the pterygoid and maxilla (fig. 3A). The quadratojugal process of the jugal does not appear to be forked (as in other species of *Psittacosaurus*), overlaying the quadratojugal as a simple tongue-shaped process (fig. 4).

QUADRATOJUGAL

The quadratojugal is subtriangular and mediolaterally flattened. The right quadratojugal is present, and the left is not preserved; however, the articular surface of the left quadratojugal is clearly preserved (fig. 4). The posterior margin of the bone is sinuous, posteriorly concave dorsally and posteriorly convex ventrally. It overlays the quadrate in a scarf joint along their entire contact and is similarly overlain by the jugal anteriorly. Unlike most *Psittacosaurus* species (but similar to CAGS-IG-VD-004, a specimen referred by You et al. [2008] to *Psittacosaurus major*), the quadratojugal does not extend posteriorly to cover the entire ventrolateral aspect of the quadrate in lateral view. No quadratojugal foramen is present.

QUADRATE

Both quadrates are preserved. As in all *Psittacosaurus* species and dinosaurs generally, they can be partitioned into two divisions—a broad, sheetlike pterygoid ramus and a vertical shaft (Sereni, 1987). The pterygoid ramus forms an anteriorly convex shield that, in life, would have intervened between the temporal fenestrae and the braincase, obscuring the braincase from lateral view (fig. 4). Anteriorly, this ramus contacts the pterygoid just anterolateral to the juncture of the pterygoid and basipterygoid processes. The suture continues ventrally before deflecting sharply to project posteriorly to the posterior extent of the quadrate process of the pterygoid (fig. 3A).

The quadrate shaft is mediolaterally compressed for its dorsal half, expanding ventrally to become subrectangular in cross section (fig. 5B). The dorsal head of the quadrate shaft sits in a glenoid cup within the squamosal. A medial lamina of the squamosal glenoid prevents the quadrate head from contacting the paroccipital process (figs. 4A, 5B). The quadratojugal overlaps the quadrate laterally via a broad scarf joint (see above). A posteriorly directed crest sits on the lateral margin of the lower half of the quadrate shaft; this crest terminates just dorsal to the articular condyles (fig. 5B). The ventral margin of the condyles is roughly horizontal, and the lateral condyle larger than the medial. In lateral view, the quadrate shaft is strongly flexed anteriorly for its dorsal half, and forms most of the posterior boundary of the infratemporal fenestra.

SQUAMOSAL

The left squamosal is present in its original position; the right is dissociated from the cranium and is missing part of the postorbital ramus. The squamosal is triradiate in dorsal view, with a long barlike postorbital ramus, a short stout posterior ramus, and a flattened parietal ramus that contributes to the squamosal-parietal shelf overhanging the occiput (fig. 3B). A thin lamina descends along the anteroposterior axis of the postorbital ramus, forming a groove for the squamosal ramus of the postorbital. This lamina gives rise to an anteroventrally directed prong at its posterior extent (fig. 4A). At the origin of the prong lies a small fossa, interpreted as the attachment site for *M. adductor mandibulae externus superficialis* (Han et al., 2018). Posterior to this prong, the quadrate glenoid occurs within the body of the squamosal, without its own distinct process; this glenoid is framed posteriorly by another thin lamina that com-

pletely excludes the quadrate from the paroccipital processes, as in *Psittacosaurus mongoliensis* (fig. 3B; Sereno, 1987). In dorsal view, the squamosal expands posteriorly, with the parietal ramus contacting the parietal in a broad scarf joint to frame the posterolateral quadrant of the supratemporal fenestra (fig. 3B). Ventrally, this ramus also contacts the dorsal surface of the pterygoid ramus of the quadrate, contributing to the continuous sheet of bone separating the braincase from the temporal fenestrae. Overall, the squamosal is similar to that of AMNH FARB 6253 being distinguished by the lack of an invagination between the posterior and parietal rami of the squamosal in IGM 100/1132.

SUPRAOCCIPITAL

The supraoccipital is diamond shaped in posterior view and is wider than it is tall (fig. 5B). It narrowly contributes to the dorsal border of the foramen magnum. From the medial apex of the supraoccipital to its center, a mediolaterally thin posteriorly directed process arises and underlaps the parietal-squamosal shelf, forming a lamina between the right and left sides of the dorsal occiput. This platelike process was identified by Sereno (1987) as the attachment point for the nuchal ligament.

EXOCCIPITAL-OPISTHOTIC

As in most archosaurs and all species of *Psittacosaurus*, the exoccipitals and opisthotics are completely fused (Sereno, 1987). These elements form the posterolaterally directed paroccipital processes, which in *Psittacosaurus amitabha* terminate with a distinct boot-shaped expansion (fig. 5B). In contrast, the paroccipital processes of AMNH FARB 6253 do not expand at their lateral ends (Osborn, 1924). The posterodorsal aspects of the paroccipital processes bear a marked depression that is confluent with a posterolaterally directed foramen that passes antero-medially into the braincase (fig. 5B). This is likely the entrance of the caudal middle cerebral vein (Witmer and Ridgely, 2009; Bever et al., 2013). They share an extensive dorsal contact with the supraoccipital, parietal, and squamosal, from medial to lateral; the parietal contact is comparatively brief. As noted above, a lamina of the squamosal intervenes between the quadrate and the paroccipital processes. As in *Psittacosaurus mongoliensis*, the exoccipital-opisthotic frames the posterior margin of the fenestra ovalis (fig. 6; Sereno, 1987).

The exoccipital-opisthotics form part of the dorsal and most of the lateral margins of the foramen magnum. Ventrally, they contact the basioccipital on a distinct peduncle. This peduncle houses the foramina of three cranial nerves, arranged so they form an inverted triangle in lateral view (fig. 6). From anterior to posterior, these foramina were occupied by: (1) the jugular canal (containing the glossopharyngeal [IX], vagus [X], and accessory [XI] nerves, as well as the jugular vein), (2) branches 1 and 2 of the hypoglossal nerve (XII), and (3) branch 3 of the hypoglossal nerve (Sereno, 1987; Averianov et al., 2006). Sereno (1987) further suggests that the anterior foramen provided passage for the glossopharyngeal nerve (IX) and the jugular vein. A lateral crest arises from the anterior extent of the exoccipital-opisthotic peduncle,



FIGURE 6. Detail of braincase of IGM 100/1132 in posterolateral view. Abbreviations: **fo**, fenestra ovalis; **jc**, jugular canal; **V**, trigeminal foramen; **VII**, foramen for facial nerve; **XII-1, 2**, foramen for first and second branches of the hypoglossal nerve; **XII-3**, foramen for third branch of the hypoglossal nerve.

passing ventrally to merge with the basioccipital part of the basal tuber. Unlike in *Psittacosaurus mongoliensis*, the posterolateral edge of the peduncle does not bear a distinct ridge framing the three cranial nerve foramina.

BASIOCCIPITAL

The basioccipital frames the ventrolateral and ventral margins of the foramen magnum, forming the single ball-shaped occipital condyle (fig. 5B). The occipital condyle does not feature a midline excavation in posterior view as figured by Osborn (1924) for AMNH FARB 6253. It contacts the exoccipital-opisthotics dorsally and the basisphenoid anteriorly. The latter suture is almost completely fused and is difficult to discern. The basioccipital contributes extensively to the basal tubera, forming the posterior 65% of their length. Along the midline, between the basal tubera and the occipital condyle, is a small foramen that would have entered the posterior floor of the braincase (fig. 3A). This structure is situated within a small heart-shaped fossa, and is not noted in the braincase descriptions of Sereno (1987), Averianov et al. (2006), or You et al. (2008), and may therefore be autapomorphic for this taxon. Zhou et al. (2006) note a small oval fossa between the occipital condyle and basal tubera in *Psittacosaurus lujiatunensis*, which may correspond to this foramen; however, it is more likely homologous to the fossa in which the foramen is situated.

BASISPHEOID

The basisphenoid is well-preserved, but the basisphenoid rostrum is notably missing. This bone contacts the basioccipital posteroventrally and the exoccipital-opisthotics and prootics dorsally (figs. 3A, 6). Anteriorly, the bone projects out two stout bar-shaped basiptyergoid processes, which articulate with the pterygoids. Posteriorly, it forms the anterior portions of the basal tubera. The anterior faces of the basal tubera give rise to thin anteriorly directed laminae; these merge with laminae that arise from the basisphenoid-prootic contact to form the basiptyergoid processes (fig. 3A). The tuberal laminae and basal tubera themselves frame a deep invagination on the ventral aspect of the basisphenoid that does not communicate with the endocranial cavity (Sereno, 1987). The lateral space between these laminae frame the foramen for the passage of the internal carotid artery into the pituitary fossa (Sereno, 1987), which opens anterodorsally from the anterodorsal aspect of the basisphenoid and in life would have been confluent with the endocranial cavity. The posterodorsal corner of the basisphenoid contributes to the margin of the fenestra ovalis (fig. 6).

PROOTIC

Both prootics are preserved, though their sutures to the exoccipital-opisthotics and basisphenoid are nearly obliterated by fusion (fig. 6). They are taller than wide in lateral view, with prominent posterodorsal processes overlapping the lateral face of the paroccipital processes.

They contact the basisphenoid ventrally, exoccipital-opisthotics posteriorly, the parietal dorsally, the laterosphenoids anteriorly and the broad pterygoid ramus of the quadrate laterally. The prootics form part of the lateral wall of the endocranial cavity. This bone forms most of the anterior margin of the fenestra ovalis; anterior to the fenestra ovalis, it is punctured by another foramen for the facial nerve (VII; Sereno, 1987). The prootic also frames the posterior margin of the trigeminal foramen, which is visible on both sides (fig. 6).

LATEROSPHEOID

The laterosphenoids are partially preserved, with only their posterior regions present (figs. 4B, 6). They contact the prootics posteriorly and the parietal, postorbitals, and frontals dorsally defining the anterolateral wall of the braincase. While the anterior region is missing on both sides, it is likely that the bone would be visible through the orbit when complete, as in other species of *Psittacosaurus*. The trigeminal foramen is visible on both sides, opening laterally for the passage of branches 2 and 3 of the trigeminal nerve (V). It is framed mostly by the laterosphenoid, with less than half of the posterior opening framed by the prootic.

MANDIBLE

The mandible of IGM 100/1132 is highly fragmentary, missing the entire prementary, surangular, splenial, coronoid, and articular (figs. 7, 8). The angular may be partially present, but the preservation is so poor that it is impossible to state this for certain; thus, the mandible is primarily represented by the dentary. The articular facet for the prementary is clearly demarcated as a shallow rugose fossa with numerous neurovascular foramina. The lateral rami of the prementary are less than half the length of the descending process and are lateral to the first dentary tooth. This represents an autapomorphy of this taxon, because in other *Psittacosaurus* the first dentary tooth is separated from the lateral ramus of the prementary by a short diastema. Most of the dentary toothrow is missing, so the number of dentary teeth cannot be determined. The anterior portion of the right coronoid process is present, arising as a gentle incline from the body of the dentary and laterally displaced from the toothrow (figs. 7, 8).

POSTCRANIA

The atlantal intercentrum, as in other dinosaurs, is broad and U-shaped, with an anterior concavity to receive the occipital condyle (Sereno, 1987). These bones fit together tightly when manually articulated, confirming the identity of this fragmentary vertebral element. As in *Psittacosaurus mongoliensis*, there are two ventrolaterally projecting tab-shaped processes that would have articulated with the cervical ribs of the atlas (Sereno, 1987). There is an elliptical depression in the middle of the intercentrum, visible in dorsal view.

The two well-preserved dorsal ribs both come from the left side (fig. 9). The articular facets of the capitula and tubercula are elliptical in shape, dorsoventrally taller than anteroposteriorly



FIGURE 7. Mandible of IGM 100/1132 in **A**, dorsal and **B**, ventral views. Abbreviations: **cp**, coronoid process; **dt1**, first dentary tooth; **pdl**, facet for lateral ramus of predentary; **pdv**, facet for ventral ramus of predentary.

wide. The proximal neck of the ribs is roughly cylindrical in cross section, thinning mediolaterally to the ventral extent of the rib. The anterior face of the neck has a striated strip, running ventrally from the anterior aspect of the tuberculum and eventually fading as the rib flattens ventrally. This structure is present on both ribs and may represent a scar from the intercostal musculature. The posterior face of the rib has a long costal groove that begins just ventral to the tuberculum. The medial and lateral ridges bounding this groove become more closely appressed ventrally, uniting and terminating the groove when the rib becomes maximally flattened. A nutrient foramen is present on the posterior aspect of the capitulum, just dorsal to the tuberculum, in both well-preserved dorsal ribs.

The right pes is represented by 13 elements, including portions of all four metatarsals and nine phalanges (fig. 10). Digits I–III are complete on the right pes. The left pes is represented by the distal ends of metatarsals II–IV and phalanx III-1. Generally, the lateral condyles of the pedal elements extend farther distally than the medial condyles, which are larger and more bulbous in appearance. Metatarsal I is flattened laterally to receive the medial surface of metatarsal II. Phalanx I-1 is elongate compared to the other nonungual phalanges and has a poorly developed intercondylar groove at its distal end. The extensor tendon pits on each condyle are

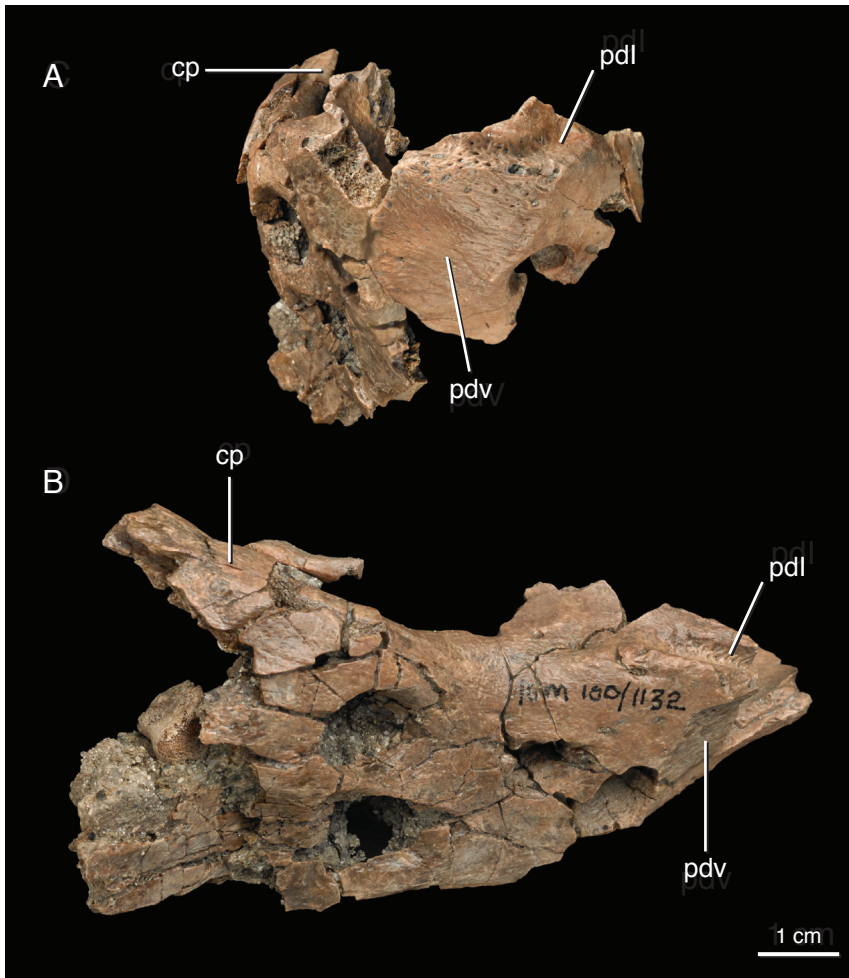


FIGURE 8. Mandible of IGM 100/1132 in A, anterior and B, right lateral views. Abbreviations follow those in figure 7.

well developed. Phalanx I-2 is an ungual—like all other unguals in this specimen, it is gently bowed and rounded on its dorsal aspect, but flattened ventrally. Unlike the other unguals, it is flattened on its medial surface, suggesting that in life the animal bore weight on the ventromedial surface of phalanx I-1, not the ventral surface as in the other three digits. Its medial and lateral sides bear grooves, probably for the passage of the blood vessels that supplied the keratinous sheath it would have borne in life. The lateral vascular groove is flanked by a medial ridge of bone, giving the ungual a spade-shaped appearance in dorsal or ventral view.

Digit II is represented by the left and right metatarsal and the right phalanges. The metatarsal bears well-developed extensor pits on each condyle, and is tightly appressed to metatarsals I and III in life position (fig. 10). The lateral condyle extends further distally than the medial. The phalanges are hourglass shaped, with equally wide proximal and distal ends but



FIGURE 9. Left dorsal ribs of IGM 100/1132 in posterior view. **A**, most complete rib and **B**, second most complete rib. Abbreviations: **ca**, capitulum; **gr**, costal groove; **nf**, nutrient foramen; **tb**, tuberculum.

appressed in the middle. They are roughly as wide as long and possesses a well-developed intercondylar groove and extensor pits (fig. 10). The dorsal intercondylar processes of the phalanges are well developed into a posterior tongue.

Digit III is represented by a left and right metatarsal, all four right phalanges, and left phalanx III-1. The metatarsal shaft is straight and roughly square in cross section, with flattened edges contrasting the more sinuous and cylindrical shafts of the other three metatarsals. The distal end is medially deflected, as in *Psittacosaurus mongoliensis*. These phalanges resemble the phalanges of digit II in having deep intercondylar grooves, prominent extensor pits, and tonguelike dorsal intercondylar processes (fig. 10). The extensor pits are particularly prominent on phalanx III-3. The ungual bears lateral ridges on both sides, framing the edges of the vascular groove, making the bone spade shaped in ventral view (fig 10).

Digit IV is represented by the left and right metatarsals but no phalanges (fig. 10). The shaft is closely appressed to that of metatarsal III, with the head deflected slightly laterally. *Psittacosaurus mongoliensis* has five phalanges on digit IV (Sereno, 1987), and it seems likely that *Psittacosaurus amitabha* had the same number in life.

The isolated chevron is highly fragmentary, representing only a portion of the proximal region of the element. The left pedicle is intact, possessing a circular articular facet for contact with the caudal centrum. The right pedicle is broken at about one quarter its height. While it impossible to confidently assign the position of this chevron in the caudal series, its relatively large size implies that it was associated with one of the large anterior caudals.

The 21 caudal vertebrae form a continuous series. Unlike the opisthocoelous caudals of *Psittacosaurus mongoliensis*, these caudals are amphicoelous, with both ends of the centrum concave. *Psittacosaurus* generally possesses 43 caudal vertebrae, so this series likely represents about half of the total caudal number (Sereno, 1987). The presence of well-developed chevrons associated with almost every vertebra strongly suggests that the preserved caudals are caudals 2–22 (as the first chevron in *Psittacosaurus* occurs between

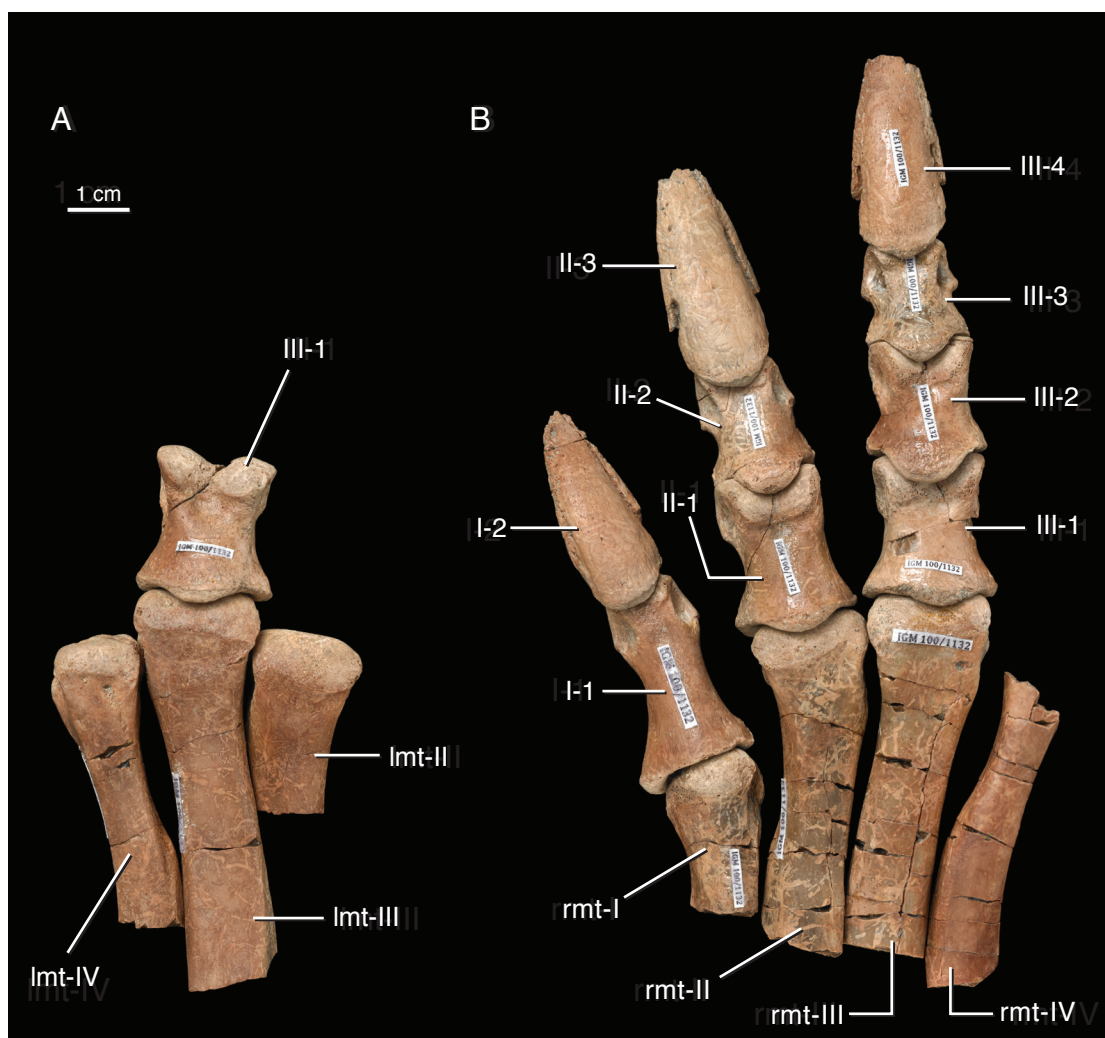


FIGURE 10. **A**, left and **B**, right pes of IGM 100/1132. Abbreviations: **lmt**, left metatarsal; **rmt**, right metatarsal. Roman numerals denote digit number, and Arabic numerals denote phalanx number within each digit.

caudals 2 and 3). The most proximal caudal (interpreted as caudal 2) is not associated with a chevron, and thus likely paired with the large, very fragmentary chevron described above. Caudals 3–14 and 16–22 are all associated with chevrons; caudal 15 is therefore the only element in the series that cannot be paired with a chevron. The vertebrae vary in their preservation; caudal 3 (fig. 11) is the best preserved, with an almost complete neural arch and two intact fused transverse processes (Sereno, 1987). Caudal 12 is the most poorly preserved, having split in half down the sagittal plane such that only the right side is represented. All other caudals, though generally well preserved, are missing part or all of the neural arch and transverse processes. The right transverse process is usually the better preserved; only caudal 4 preserves a left transverse process without the right. The caudal centra range in length from 23 mm (caudal 3) to 15 mm (caudal 22).

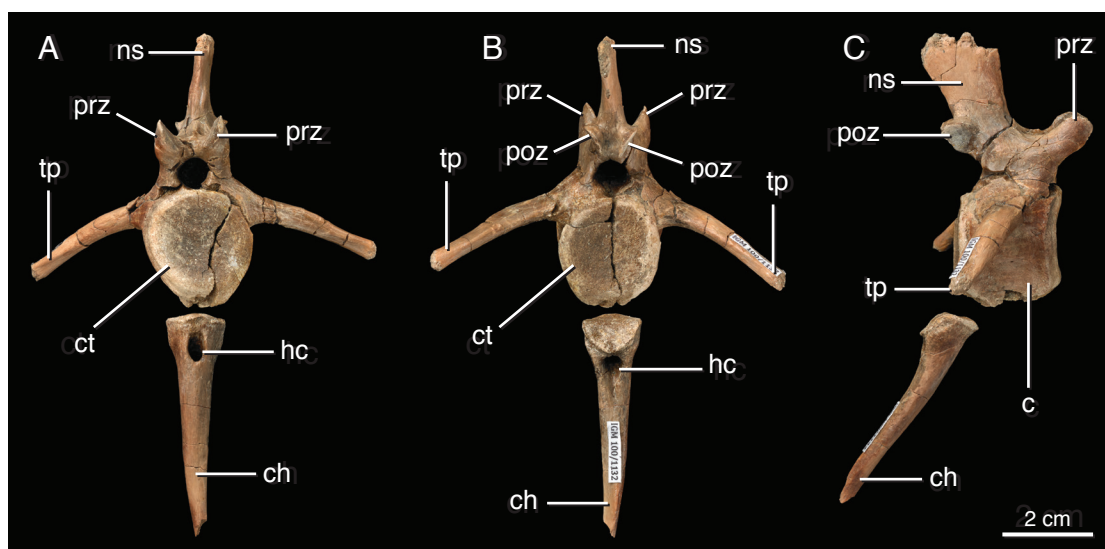


FIGURE 11. Third caudal vertebra of IGM 100/1132 in **A**, anterior, **B**, posterior, and **C**, right lateral views. Abbreviations: **ch**, chevron; **ct**, centrum; **hc**, hemal canal; **ns**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis; **tp**, transverse process.

Moving posteriorly down the series, the centra become longer anteroposteriorly than tall. All caudals have some degree of ventral keeling, which is most pronounced in caudals 7–15. The anterior neural arches project dorsally, shifting to a more posterodorsal orientation in the more posterior caudals. The chevrons shrink dramatically to half their maximum length after caudal 15. The prezygapophyses are almost vertical in the anterior caudals, with facets directed mostly medially and slightly dorsally. These facets point increasingly medially in the progressively more posterior caudals, orienting the prezygapophyses increasingly vertically. The postzygapophyses complement their articular mates. The anterior caudals have mostly laterally and slightly ventrally directed postzygapophyses. These facets reorient more dorsally in the more posterior caudals, but distinct postzygapophyses do not occur past caudal 15.

GASTROLITHS

Nine small gastrolith fragments representing seven gastroliths were found with the skeleton (fig. 12). They are of varying sizes and lithologies, but all are rounded with a weathered surface texture. The largest gastrolith is 24.5 mm long, 19.4 mm wide, and 10.5 mm thick. The smallest is 12.6 mm long, 9 mm wide, and 7.2 mm thick.

ENDOCRANIAL CAST

The well-preserved and undistorted braincase enables the generation of an endocranial cast, visualizing the brain, several cranial nerve buds, and the inner ear (fig. 13). To accommodate the missing anterior laterosphenoids, we set a conservative boundary between remain-



FIGURE 12: Gastroliths of IGM 100/1132.

ing sections of braincase to avoid estimating the cerebrum beyond the evidence present in the specimen. Foramina were followed to their opening, giving many nerve buds the appearance of a flattened expansion at their most distal extent; this is an artifact of the endocasting process and is not interpreted as the true anatomy of the organism.

The overall form of the endocast is highly reminiscent of the brain of *Alligator mississippiensis* (e.g., Watanabe et al., 2018) as well as that of *Psittacosaurus lujiatunensis* (Zhou et al., 2007). The olfactory tracts are long and hourglass shaped, extending along the ventral aspect of the frontal past the orbits, presumably to contact the nasal mucosa. The olfactory tracts grade into the cerebrum. Due to the partial laterosphenoids, the lateral extent and general form of the cerebrum are unclear; however, it was certainly small relative to the enlarged cerebrum seen in coelurosaurian theropods (Brusatte et al., 2009; Witmer and Ridgely, 2009; Bever et al., 2013). The optic lobes and cerebellum are similarly unexpanded. The posterodorsal corner of

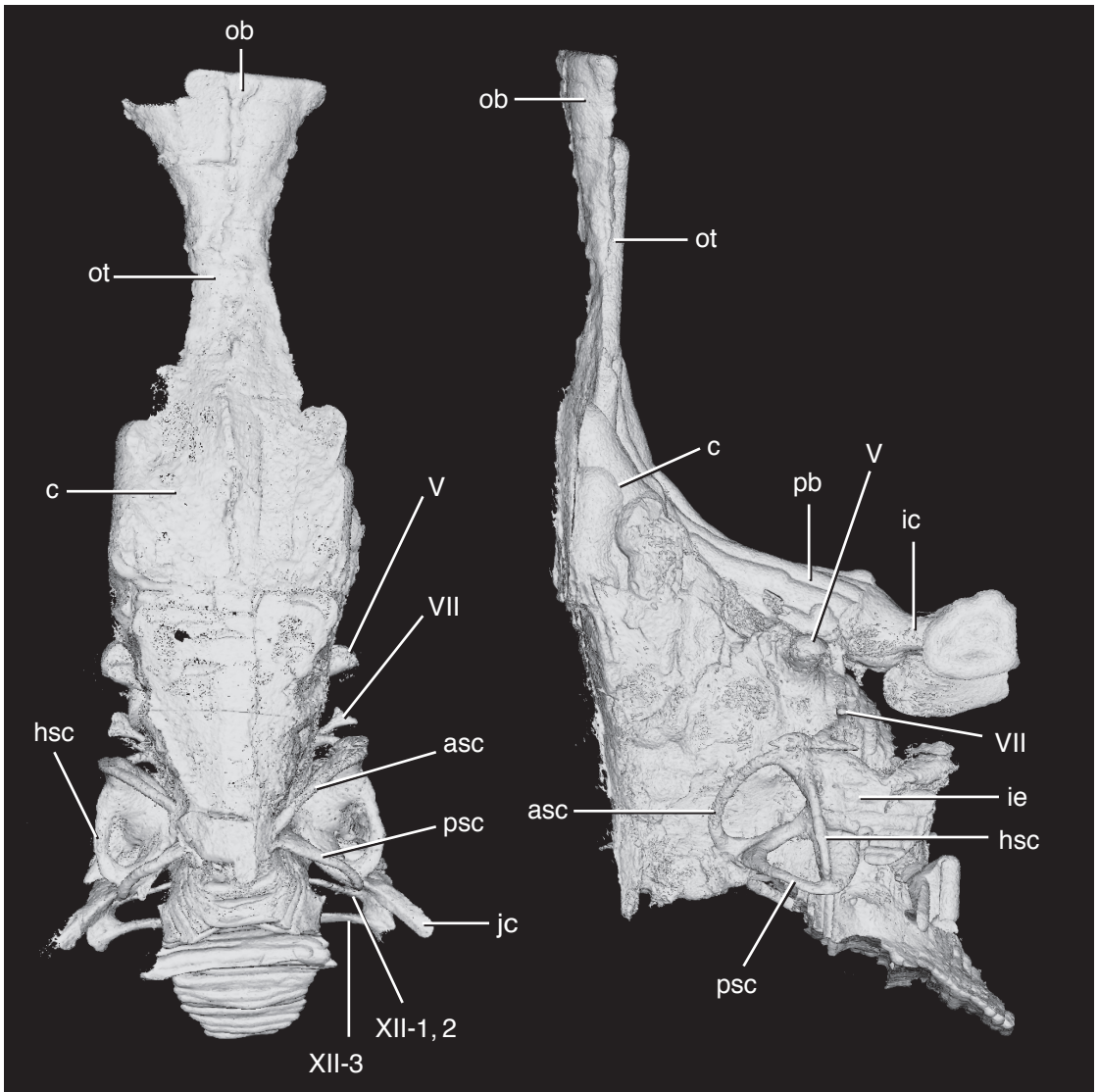


FIGURE 13: Endocranial cast of the skull of IGM 100/1132, in **A**, dorsal and **B**, right lateral view. Abbreviations: **asc**, anterior semicircular canal; **c**, cerebrum; **hsc**, horizontal semicircular canal; **ic**, internal carotid artery; **ie**, inner ear; **jc**, jugular canal; **ob**, olfactory bulb; **ot**, olfactory tract; **pb**, pituitary body; **psc**, posterior semicircular canal; **V**, trigeminal nerve; **VII**, facial nerve; **XII 1, 2**, first and second branches of hypoglossal nerve; **XII-3**, third branch of hypoglossal nerve.

the endocast displays a dorsal peak, corresponding to the dural sinus (Witmer and Ridgely, 2009; Bever et al., 2013). The pituitary extends from the midline, under the presumed location of the optic lobe; the internal carotid arteries travel dorsomedially into the pituitary fossa from below. A series of cranial nerve buds are visible; from anterior to posterior, they are interpreted as the buds of V, VII, X/XI (the jugular canal), and branches 1 and 2 of XII (fig. 13).

The most notable feature of the endocast is the inner ear; particularly conspicuous are the robust semicircular canals. The lateral semicircular canal is oriented slightly anterodorsally, implying that at rest, the animal's head was slightly downturned (Witmer et al., 2003; Brusatte et al., 2009). The same condition is seen in *Psittacosaurus lujiatunensis* (Zhou et al., 2007), the endocast of which is extremely similar to that of *P. amitabha*.

OSTEOHISTOLOGIC ANALYSIS

We histologically sampled an incomplete (76.0 mm TL) distal metatarsal from IGM 100/1132 to provide an independent assessment of the animal's ontogenetic status. The element was sectioned in the transverse plane 61.1 mm from the distal end of the bone at or near the middiaphysis. The dimensions at the region of sectioning are 16.4 mm mediolaterally and 11.4 mm anteroposteriorly. The element shows a hollow medullary cavity that is 7.2 mm wide mediolaterally and 3.3 mm in diameter anteroposteriorly. Petrographic microscopy was used to visualize and document the osseous microstructure. The terminology utilized by Francillon-Vieillot et al. (1990) and Cormack (1987) was adopted to describe the microstructure.

The cross section shows three distinct regions: (1) a trabeculated inner spongiosa; (2) a highly vascularized inner cortex; and (3) a less vascularized laminated outer cortex (fig. 14). The spongiosa is composed of woven-fibered bony trabeculae, some of which show isolated secondary osteons (SO; fig. 14). The inner cortex is composed of primary reticular fibro-lamellar bone.

The outer cortex consists of three annuli composed of parallel fibered bone (PFB; fig. 14), some that contain primary or short, obliquely oriented primary osteons. The annuli bound two layers composed of fibro-lamellar tissue with primary osteons oriented either longitudinally or obliquely in circular rows (FLB; fig. 14). The periosteal surface of the outermost annuli includes incompletely formed primary osteons (IPO; fig. 14).

Collectively, the development shift from fairly well-vascularized and relatively rapidly forming primary reticular fibro-lamellar bone (inner cortex) to more slowly deposited tissues (i.e., less vascularized cyclically deposited parallel-fibered bone and less-vascularized fibro-lamellar tissue; Castanet et al., 1996) indicates the animal's growth was slowing at the time of death. The finding of incompletely formed primary osteons at the periosteal surface supports this conclusion, as does the absence of signs of somatic maturity such as lines of arrested growth (LAGS) and external fundamental structuring (closely packed LAGS).

The histological assessment based on metatarsal histology suggests IGM 100/1132 was nearing somatic maturity but was still showing modest growth at the time of its demise. In other words, it had the potential to become a somewhat larger animal. Given the already large size of the skull, *Psittacosaurus amitabha*, when fully grown, may have been nearly as large as *Psittacosaurus major* and *Psittacosaurus sibiricus*, the two largest members of the genus known to date. However, the skull of IGM 100/1132 is 20 mm shorter than that found in *P. major* and *P. sibiricus*, so it is unlikely that this individual could have reached an even larger size.

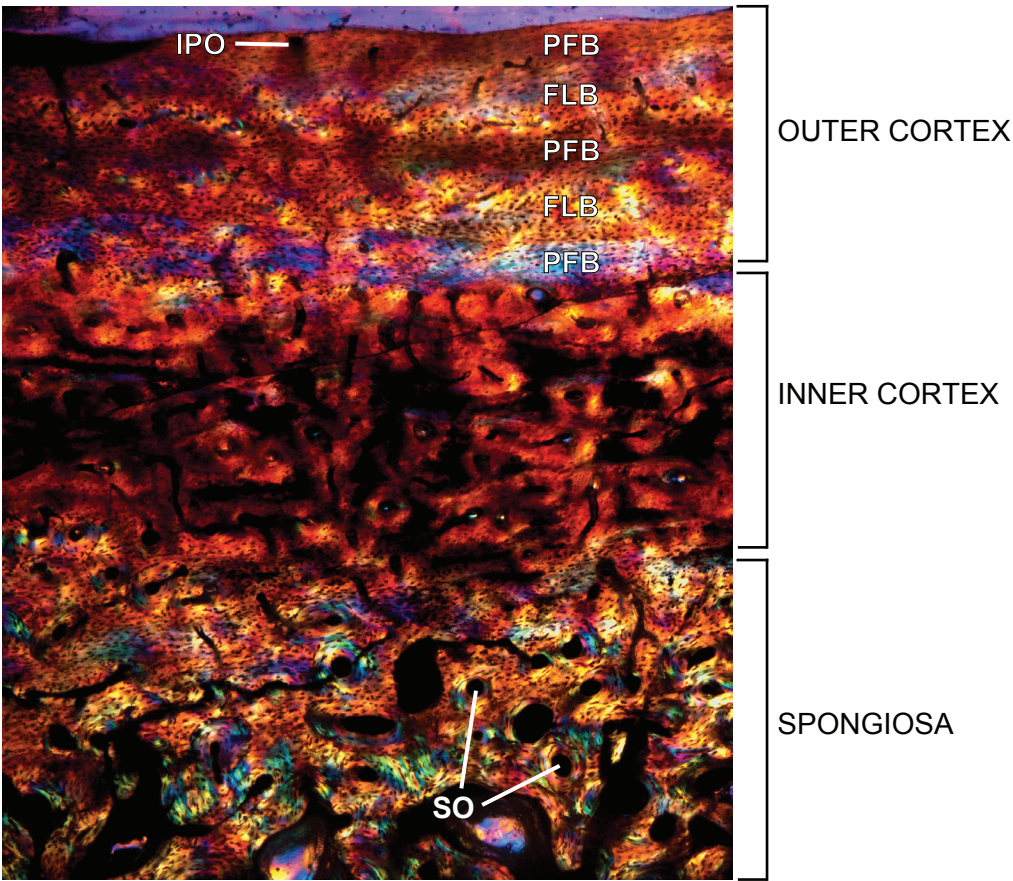


FIGURE 14: Osteohistological section of left metatarsal III. Abbreviations: **FLB**, fibro-lamellar bone; **IPO**, incomplete primary osteons; **SO**, secondary osteons; **PFB**, parallel-fibered bone.

PHYLOGENETIC ANALYSIS

We scored IGM 100/1132 in the character matrix of Han et al. (2018) to demonstrate its affinities relative to other *Psittacosaurus* species. On the basis of size, the only possible previously described species this specimen could belong to is *Psittacosaurus major*, known from several specimens of similar size (Serenó et al., 2007; You et al., 2008); the only other species of similar size, *Psittacosaurus sibiricus*, is distinguished by many morphological characters not present in IGM 100/1132. We scored LH PV-1 (Serenó et al., 2007) and CAGS-IG-VD-004 (You et al., 2008; the holotype and a major referred specimen of *Psittacosaurus major*) from the literature to test whether this specimen formed a clade of large-bodied *Psittacosaurus* with *Psittacosaurus major*, and if it should be referred to this taxon. We also scored ZMNH M18137—the holotype of *Psittacosaurus lujiatunensis*, as described by Zhou et al. (2006)—as a further comparison and to assess the synonymy of this taxon with *Psittacosaurus major* proposed by Hedrick and Dodson (2013).

In addition, we scored AMNH FARB 6254—the holotype of *Psittacosaurus mongoliensis*, the type species of this genus—and LH PV2 (the holotype of *Psittacosaurus gobiensis*) to assess the relationship of this taxon with other *Psittacosaurus* from the Gobi region. AMNH FARB 6253—the only other *Psittacosaurus* known from the Ondai Sayr Formation—has a skull too fragmentary to include in the matrix; however, given its referral to *Psittacosaurus mongoliensis*, close identity between this taxon and the new specimen would support a close relationship between the Ondai Sayr *Psittacosaurus* specimens.

While we primarily relied on the Han et al. (2018) matrix in its original form, we made several modifications. Han et al. (2018) defined their character 19 as the presence or absence of an edentulous anterior region of the premaxilla; this character did not allow for a completely edentulous premaxilla. Han et al. (2018) defined their character 195 as the presence or absence of premaxillary teeth. We combined these characters into one, adding a third character state to character 19 to describe a fully edentulous premaxilla, and eliminating character 195. We felt that this would allow character 19 to better characterize the completely edentulous premaxillae of *Psittacosaurus* while not overweighting the absence of premaxillary teeth.

We also modified character 32, described by Han et al. (2018) as “Antorbital fossa (external antorbital fenestra): absent (0) or present (1).” These structures are distinct, and taxa such as *Psittacosaurus* have an antorbital fossa without an antorbital fenestra. While the *Psittacosaurus* antorbital fossa is likely a secondary trait not homologous to that of other dinosaurs (Serenó, 2000; You et al., 2008), the fossa is still present, and thus should be scorable in the matrix. To this end, we redefined character 32 as the presence or absence of an external antorbital fenestra and added a new character (char. 33) to describe the presence or absence of an antorbital fossa. The following characters describing the morphology of the antorbital fossa were scored for all *Psittacosaurus* in our analysis, having previously been scored as “not applicable.”

We performed our analysis using TNT 1.5 for Windows, run via Wine on a Mac OS X High Sierra operating system, and in R via RStudio (RStudio Team, 2015) using the packages “phangorn” and “TreeSearch” (Schliep, 2011; Brazeau et al., in press). All characters were weighted equally, and no characters were ordered. The TNT analysis was conducted following the procedure used by Han et al. (2018); maximum trees were set to 99,999; zero-length branches were collapsed and the search used 1000 tree bisection and reconnection (TBR) replicates holding 100 trees of each replicate. TBR was then used on all trees held in RAM. The R analysis first generated a neighbor-joining tree, which was used as the starting tree for a parsimony ratchet optimal tree search (Nixon, 1999). The two analyses yielded identical topologies within *Psittacosaurus*; the R results are presented here (fig. 15).

Psittacosaurus amitabha (IGM 100/1132) was recovered as the most basal of the *Psittacosaurus* specimens included in our phylogenetic analysis (fig. 15). LH-PV2 (*P. gobiensis* holotype) and ZMNH-M8137 (*P. lujiatunensis* holotype) formed successive outgroups to a clade containing *Psittacosaurus major* (LH-PV1 and CAGS-IG-VD-004) and *Psittacosaurus mongoliensis* (AMNH FARB 6254). Interestingly, *Psittacosaurus mongoliensis* and *Psittacosaurus lujiatunensis*, as originally scored by Han et al. (2018), form a sister clade to AMNH FARB 6254,

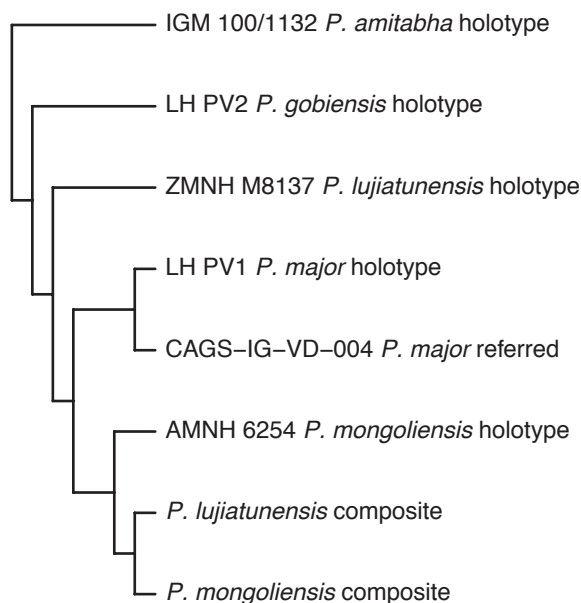


FIGURE 15: Phylogenetic interrelationships of IGM 100/1132 and other *Psittacosaurus* specimens. Composite specimens were those scored by Han et al. (2018); all others were scored for the present study, from the literature or firsthand observation of the specimens.

nested deeply within *Psittacosaurus*. No significant differences were observed in the broader tree topology compared to the results of Han et al. (2018).

According to our phylogenetic analysis, *Psittacosaurus amitabha* is the most basal of the *Psittacosaurus* species included in the present study. It did not resolve as phylogenetically close to *Psittacosaurus mongoliensis*. This result is unsurprising, given the poor development of the tall, steep rostrum characteristic of more derived *Psittacosaurus* species in *P. amitabha*. Our analysis is one of the first to study *Psittacosaurus* systematics at the specimen level; while this work is admittedly incomplete, given the large number of known *Psittacosaurus* specimens, it lays the groundwork for future resolution of psittacosaur interrelationships, and has allowed us to test hypotheses of species synonymy. Notably, our phylogenetic analysis does not recover any specimen of *Psittacosaurus lujiatunensis* as sister to any specimen of *Psittacosaurus major*. If *Psittacosaurus major* is a junior synonym of *Psittacosaurus lujiatunensis*, as suggested by Hedrick and Dodson (2013), the two should resolve as sister taxa. Therefore, we regard *Psittacosaurus major* as a valid taxon. While morphometrics has demonstrated utility in species assignment in the fossil record (Harvati, 2004; Polly and Head, 2004; Campione and Evans, 2011; Hansford and Turvey, 2018), the significant deformation of the specimens studied by Hedrick and Dodson (2013) probably biased their results. Methods to delimit species through shape-based methods warrant further development and integration with traditional phylogenetic methods.

In discussing the affinities of *Psittacosaurus lujiatunensis*, we must also consider the strange result of Han et al. (2018)'s coding, in which a specimen of *P. lujiatunensis* is sister to *P. mon-*

goliensis, forming a clade sister to the holotype of the latter (AMNH FARB 6254). While *P. mongoliensis* should resolve as sister to its own holotype (especially given that the holotype was one of the specimens examined by Han et al., 2018), *P. lujiatunensis* is far removed from its own. It is possible that this is an artifact of our scoring *P. lujiatunensis* from the literature instead of from firsthand observation. However, Han et al. (2018) used the same literature reference to score *P. lujiatunensis* as this study. It is alternatively possible that this reflects averaging of several *P. lujiatunensis* specimens into one composite operational taxonomic unit. It is additionally possible that some specimens currently assigned to *P. lujiatunensis* actually represent individuals of other species. Further work on the interrelationships of the many known *Psittacosaurus lujiatunensis* specimens will help resolve the differences between the present analysis and that of Han et al. (2018).

DISCUSSION

DIAGNOSTIC TRAITS

Psittacosaurus amitabha can be distinguished from other species of *Psittacosaurus* by the following characters: (1) a relatively longer snout than *Psittacosaurus mongoliensis*, with a less steeply inclined anterior rostronasal margin, (2) a cranium dorsally convex rather than flat, (3) a subtemporal length less than 40% of total skull length, (4) 5 premaxillary foramina arranged in an arc, (5) posterior lamina of the maxilla cupped around the toothrow, (6) an antorbital fossa as long as tall, and (7) a palpebral with a well-developed posterior tongue-like process. Furthermore, the presence of a well-developed rugose boss on the body of the postorbital and a prominent postorbital-jugal crest is not shared by all species of *Psittacosaurus*, while not autapomorphic to this new taxon. Zhou et al. (2006) did not note a postorbital boss in *P. lujiatunensis* and described a weaker postorbital-jugal crest than present in other species such as *P. sinensis*. Similarly, Sereno et al. (2007; 2010) do not describe well-developed postorbital bosses in *P. major* or *P. gobiensis*, noting the lack of a boss in the former and neglecting to mention the structure in the latter. In both taxa, the postorbital-jugal crest is present but more poorly developed than in *P. amitabha*. However, You et al. (2008) report a rounded boss on the postorbital of CAGS-IG-VD-004, another *P. major* specimen. *P. neimongoliensis* also appears to lack this structure, and to have a weak postorbital-jugal crest, which is described as rugose, in contrast to the texture found in *P. amitabha* (Russell and Zhao, 1996).

DISTINCTION FROM “*PROTIGUANODON MONGOLIENSE*”

Given that the only high-quality *Psittacosaurus* specimen from the Ondai Sayr locality for nearly a century was AMNH FARB 6253 (described as “*Protiguanodon mongoliense*” by Osborn [1924], synonymized with *Psittacosaurus mongoliensis* by Sereno [1987]), it is worth briefly considering whether IGM 100/1132 belongs to the same taxon. As described above, the sparse cranial material available for AMNH FARB 6253 differs from that of IGM 100/1132. The frontals of the former contribute to the supratemporal fenestra and do not display a midline trian-

gular fossa, the squamosal bears an invagination between the posterior and parietal rami, and the paroccipital processes do not terminate in a boot-shaped expansion. IGM 100/1132 is distinguishable by all the available cranial material and should be referred to a different taxon. This taxonomic decision is supported by the wide acceptance of the synonymy of "*Protiguanodon mongoliense*" and *Psittacosaurus mongoliensis* and our phylogenetic analysis. *Psittacosaurus amitabha* was recovered as basal to all other *Psittacosaurus* and distant from *Psittacosaurus mongoliensis*, which includes the only other known Ondai Sayr *Psittacosaurus*. Therefore, it seems that the Ondai Sayr locality hosted at least two *Psittacosaurus* species, similar to the situation in the Lujiatun locality of the Yixian formation, which hosted *Psittacosaurus lujiatunensis* and *Psittacosaurus major* (Zhou et al., 2006; Sereno et al., 2007; Hedrick and Dodson, 2013). Interestingly, both localities supported a small and large-bodied species, suggesting size as a mechanism of niche partitioning between the congeneric sympatric species.

CONCLUSIONS

Psittacosaurus is a ubiquitous member of the Asian Early Cretaceous Fauna. It is known from a plethora of specimens from many localities across substantial latitudinal range. Because it is known from so many specimens and from so many localities, it is unsurprising that the genus is very speciose, although there is significant taxonomic confusion. Here we report a new taxon, *Psittacosaurus amitabha*. Its type locality, Ondai Sayr has produced very few vertebrate fossils, so it is difficult to directly determine how similar the Ondai Sayr fauna is with presumed coeval beds like Oshii. Nevertheless, because *Psittacosaurus* is so densely sampled, it is unsurprising that there are numerous regional species that may reflect regional and temporal differences between localities.

ACKNOWLEDGMENTS

The authors thank Carl Mehling and Suzann Goldberg (AMNH) for access to specimens under their care, Carolyn Merrill (AMNH) for assistance in scanning, and Mick Ellison (AMNH) for photography of IGM 100/1132. This work was supported by a Richard Gilder Graduate School Graduate Fellowship (J.G.N.), the Macaulay family endowment, the Newt and Calista Gingrich endowment, and the Division of Paleontology at the American Museum of Natural History.

REFERENCES

- Averianov, A.O., A.V. Voronkevich, S.V. Leshchinskiy, and A.V. Fayngertz. 2006. A ceratopsian dinosaur *Psittacosaurus sibiricus* from the early cretaceous of West Siberia, Russia and its phylogenetic relationships. *Journal of Systematic Palaeontology* 4 (4): 359–395.
- Barta, D.E., and M.A. Norell. The osteology of *Haya griva* (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia. *Bulletin of the American Museum of Natural History*. In review.

- Berkey, C.P., and F.K. Morris. 1927. Geology of Mongolia. Natural History of Central Asia, vol. 2. New York: American Museum of Natural History.
- Bever, G.S., et al. 2013. The braincase anatomy of the late Cretaceous dinosaur *Alioramus* (Theropoda: Tyrannosauroidae). *Bulletin of the American Museum of Natural History* 376: 1–72.
- Bo, Z., et al. 2016. Histologic examination of an assemblage of *Psittacosaurus* (Dinosauria: Ceratopsia) juveniles from the Yixian Formation (Liaoning, China). *Anatomical Record* 299: 601–612.
- Brazeau, M.D., T. Guillerme, and M.R. Smith. In press. An algorithm for morphological phylogenetic analysis with inapplicable data. *Systematic Biology*.
- Brown, B., and E.M. Schlaikjer. 1940. The structure and relationships of *Protoceratops*. *Annals of the New York Academy of Science* 40 (3): 133–266.
- Brusatte, S.L., T.D. Carr, G.M. Erickson, G.S. Bever, and M.A. Norell. 2009. A long-snouted, multihorned tyrannosaurid from the Late Cretaceous of Mongolia. *Proceedings of the National Academy of Sciences* 106 (41): 17261–17266.
- Campione, N.E., and D.C. Evans. 2011. Cranial growth and variation in edmontosaurs (Dinosauria: Hadrosauridae): implications for latest Cretaceous megaherbivore diversity in North America. *PLoS ONE* 6 (9).
- Castanet, J., A. Grandin, A. Abourachid, and A. de Ricqlès. 1996. Expression de la dynamique de croissance dans la structure de l'os périostique chez *Anas platyrhynchos*. *Comptes Rendus de l'Académie des Sciences de la Vie* 319: 301–308.
- Cheng, Z. 1983. Reptilia. In *The Mesozoic stratigraphy and paleontology of Guyang coal-bearing basin Nei Monggol Autonomous Region, China*: 123–136. Beijing: Geology Press.
- Coombs, W.P. 1982. Juvenile specimens of the ornithischian dinosaur *Psittacosaurus*. *Palaeontology* 25: 89–107.
- Cormack, D. 1987. *Ham's histology*. Philadelphia: Lippincott Williams & Wilkins.
- Dalton, R. 2001. Wandering Chinese fossil turns up at museum. *Nature* 414: 571.
- Erickson, G.M., P.J. Makovicky, B.D. Inouye, C.-F. Zhou, and K.-Q. Gao. 2009. A life table for *Psittacosaurus lujiatunensis*: initial insights into ornithischian dinosaur population biology. *Anatomical Record* 1521: 1514–1521.
- Francillon-Vieillot, H., V. de Buffrénil, J. Castanet, J. Géraudie, and F.J. Meunier. 1990. Microstructure and mineralization of vertebrate skeletal tissues. In J. G. Carter (editor), *Skeletal biomineralization: patterns, processes, and evolutionary trends*, vol. 1: 471–530. New York: Van Nostrand Reinhold.
- Han, F., C.A. Forster, X. Xu, and J.M. Clark. 2018. Postcranial anatomy of *Yinlong downsi* (Dinosauria: Ceratopsia) from the Upper Jurassic Shishugou Formation of China and the phylogeny of basal ornithischians. *Journal of Systematic Palaeontology* 16 (14): 1159–1187.
- Hansford, J., and S.T. Turvey. 2018. Unexpected diversity within the extinct elephant birds (Aves: Aepyornithidae), and a new identity for the world's largest bird. *Royal Society Open Science* 5:181295.
- Harvati, K. 2004. 3-D geometric morphometric analysis of temporal bone landmarks in Neanderthals and modern humans. In A.M.T. Elewa (editor), *Morphometrics: applications in biology and paleontology*: 245–258. Heidelberg: Springer-Verlag.
- Hedrick, B.P., and P. Dodson. 2013. Lujiatun psittacosaurids: understanding individual and taphonomic variation using 3D geometric morphometrics. *PLoS ONE* 8 (8): e69265.
- Hu, Y., J. Meng, Y. Wang, and C. Li. 2005. Large Mesozoic mammals fed on young dinosaurs. *Nature* 433: 149–152.
- Jerzykiewicz, T. 2000. Lithostratigraphy and sedimentary settings. In M.J. Benton, M.A. Shishkin, D.M. Unwin, and E. Kurochkin (editors), *The age of dinosaurs in Russia and Mongolia*: 279–296. Cambridge: Cambridge University Press.

- Jerzykiewicz, T., and D.A. Russell. 1991. Late Mesozoic vertebrates and stratigraphy of the Gobi Basin. *Cretaceous Research* 12 (4): 345–377.
- Makovicky, P.J., B.M. Kilbourne, R.W. Sadleir, and M.A. Norell. 2011. A new basal ornithopod (Dinosauria, Ornithischia) from the Late Cretaceous of Mongolia. *Journal of Vertebrate Paleontology* 31 (3): 626–640.
- Mayr, G., D.S. Peters, G. Plodowski, and O. Vogel. 2002. Bristle-like integumentary structures at the tail of the horned dinosaur *Psittacosaurus*. *Naturwissenschaften* 89: 361–365.
- Mayr, G., M. Pittman, E. Saitta, T.G. Kaye, and J. Vinther. 2016. Structure and homology of *Psittacosaurus* tail bristles. *Palaeontology* 59 (6): 793–802.
- Meng, Q., J. Liu, D.J. Varricchio, T. Huang, and C. Gao. 2004. Parental care in an ornithischian dinosaur. *Nature* 431: 145–146.
- Nixon, K.C. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* 15: 407–414.
- Osborn, H.F. 1923. Two Lower Cretaceous dinosaurs of Mongolia. *American Museum Novitates* 95: 1–10.
- Osborn, H.F. 1924. *Psittacosaurus* and *Protiguanodon*—two lower cretaceous iguanodonts from Mongolia. *American Museum Novitates* 127: 1–16.
- Polly, P.D., and J.J. Head. 2004. Maximum-likelihood identification of fossils: taxonomic identification of Quaternary marmots (Rodentia, Mammalia) and identification of vertebral position in the pipesnake *Cylindrophis* (Serpentes, Reptilia). In A.M.T. Elewa (editor), *Morphometrics: applications in biology and paleontology*: 197–221. Heidelberg: Springer-Verlag.
- RStudio Team. 2015. RStudio: integrated development for R. Boston: RStudio, Inc. Online resource (<http://www.rstudio.com/>).
- Russell, D.A., and X.-J. Zhao. 1996. New psittacosaur occurrences in Inner Mongolia. *Canadian Journal of Earth Sciences* 33: 637–648.
- Schliep, K.S. 2011. Phangorn: phylogenetic analysis in R. *Bioinformatics* 27 (4): 592–593.
- Sereno, P.C. 1987. The ornithischian dinosaur *Psittacosaurus* from the lower Cretaceous of Asia and the relationships of the Ceratopsia. Ph.D. dissertation, Columbia University, 554 pp.
- Sereno, P.C. 2000. The fossil record, systematics and evolution of pachycephalosaurs and ceratopsians from Asia. In M.J. Benton, M.A. Shishkin, D.M. Unwin, and E.N. Kurochkin (editors), *The age of dinosaurs in Russia and Mongolia*: 480–516. Cambridge: Cambridge University Press.
- Sereno, P.C. 2010. Taxonomy, cranial morphology, and relationships of parrot-beaked dinosaurs (Ceratopsia: Psittacosaurus). In M.J. Ryan, B.J. Chinnery-Allgeier, and D.A. Eberth (editors), *New perspectives on horned dinosaurs*: 21–58. Bloomington: Indiana University Press.
- Sereno, P.C., and S. Chao. 1988. *Psittacosaurus xinjiangensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of Northwestern China. *Journal of Vertebrate Paleontology* 8 (4): 353–365.
- Sereno, P.C., C. Shichin, C. Zhengwu, and R. Chenggang. 1988. *Psittacosaurus meileyingensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of Northeastern China. *Journal of Vertebrate Paleontology* 8 (4): 366–377.
- Sereno, P.C., Z. Xijin, L. Brown, and T. Lin. 2007. New psittacosaurid highlights skull enlargement in horned dinosaurs. *Acta Palaeontologica Polonica* 52 (2): 275–284.
- Sereno, P.C., Z. Xijin, and T. Lin. 2010. A new psittacosaur from Inner Mongolia and the parrot-like structure and function of the psittacosaur skull. *Proceedings of the Royal Society B: Biological Sciences* 277 (1679): 199–209.

Vinther, J., et al. 2016. 3D camouflage in an ornithischian dinosaur. *Current Biology* 26 (18): 2456–2462.

Watanabe, A., et al. 2018. Are endocasts good proxies for brain size and shape in archosaurs throughout ontogeny? *Journal of Anatomy* 234: 291–305.

Witmer, L.M., and R.C. Ridgely. 2009. New insights into the brain, braincase, and ear region of tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and behavior. *Anatomical Record* 292: 1266–1296.

Witmer, L.M., S. Chatterjee, and J. Franzosa. 2003. Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature* 425: 24–27.

You, H.-L., and P. Dodson. 2004. Basal Ceratopsia. In D.B. Weishampel, P. Dodson, and H. Osmólska (editors), *The Dinosauria*, 2nd ed. 478–493. Berkeley, CA: California University Press.

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

Young, C.C. 1931. On some new dinosaurs from western Suiyuan, Inner Mongolia. *Bulletin of the Geological Survey China* 2: 159–166.

Young, C.C. 1958. The dinosaurian remains of Laiyang, Shantung. *Palaeontologica Sinica* 142 C (16): 1–138.

Zhao, Q., M.J. Benton, X. Xu, and P.M. Sander. 2013. Juvenile-only clusters and behaviour of the Early Cretaceous dinosaur *Psittacosaurus*. *Acta Palaeontologica Polonica* 59 (4): 827–833.

Zhao, X. 1962. New species of *Psittacosaurus* from Laiyang, Shantung. *Vertebrata PalAsiatica* 6: 349–360.

Zhou, C.F, K.Q. Gao, R.C. Fox, and S.H. Chen. 2006. A new species of *Psittacosaurus* (Dinosauria: Ceratopsia) from the Early Cretaceous Yixian Formation, Liaoning, China. *Palaeoworld* 15 (1): 100–114.

Zhou, C.F, K.Q. Gao, R.C. Fox, and X.K. Du. 2007. Endocranial morphology of psittacosaur (Dinosauria: Ceratopsia) based on CT scans of new fossils from the Lower Cretaceous, China. *Paleoworld* 16 (4): 285–293.

APPENDIX 1

ALL ELEMENTS OF IGM 100/1132

Skull, nearly complete and undistorted	Phalanx II-1, left
Postorbital, right, disarticulated	Metatarsal III, left and right, distal half and distal end
Squamosal, right, disarticulated	Phalanx III-1, left
Palpebral, right, disarticulated	Phalanx III-2, left
Mandible, fragmentary	Phalanx III-3, left
Atlantal intercentrum	Phalanx III-4, left
Dorsal ribs, left, 3	Phalanx IV-3, left
Left ulna, fragmentary	Phalanx IV-4, left
Metatarsal I, left and right, incomplete	Phalanx IV-5, left
Phalanx I-1, left	Caudals 2–22, with associated chevrons
Phalanx I-2, left	Gastroliths, 10
Metatarsal II, left and right, distal half	Unassigned long bone fragments, 6

APPENDIX 2

AMERICAN MUSEUM SPECIMENS FROM THE ONDAI SAYR LOCALITY

Below is a list of fossil specimens that were recovered from the Ondai Sayr locality by the American Museum of Natural History Central Asiatic Expeditions, comprising a total of 30 specimens including dinosaurs, turtles, fish, and invertebrates.

Specimen number	Taxon
AMNH FARB 6243	" <i>Protiguanodon mongoliense</i> " holotype, articulated skeleton with fragmentary skull
AMNH FARB 6256	<i>Psittacosaurus</i> sp., left pes
AMNH FARB 6257	<i>Psittacosaurus</i> sp., left manus
AMNH FARB 6258	Saurischia, rib
AMNH FARB 6259	Small dinosaur, caudals and fragmentary pes
AMNH FARB 6664	Testudines, carapace and plastron fragments from several individuals
AMNH FF 8501–8504	<i>Asiatolepis fragilis</i>
AMNH FF 8542–8543	<i>Asiatolepis fragilis</i>
AMNH FI 39515–39517	<i>Ephemeropsis trisetalis</i>
AMNH FI 39518	<i>Estheria middenforffi</i>
AMNH FI 39519–39522	<i>Ephemeropsis trisetalis</i>
AMNH FI 39523	<i>Ephemeropsis melanurus</i>
AMNH FI 39524–29526	<i>Cymatophlebia?</i> <i>mongolica</i>
AMNH FI 39527	<i>Indusia reisi</i>
AMNH FI 39528	<i>Chironomopsis gobiensis</i>
AMNH FI 39529	genus and species indeterminate
AMNH FI 39530–39531	<i>Phyllocladites?</i> <i>morrisi</i>
AMNH FI 39532	Genus and species indeterminate

All issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Order printed copies on the web from:

<http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html>

or via standard mail from:

American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

Ⓒ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).