PSITTACOSAURUS MEILEYINGENSIS (ORNITHISCHIA: CERATOPSIA), A NEW PSITTACOSAUR FROM THE LOWER CRETACEOUS OF NORTHEASTERN CHINA

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ABSTRACT—A new psittacosaur species, Psittacosaurus meileyingensis, is based on a well preserved skull with referred cranial and postcranial remains. The skull is tall relative to its length and has a subcircular profile. Distinctive characteristics of the new species include a low horn on the quadratojugal and a prominent ventral flange on the dentary.

The discovery of both Psittacosaurus meileyingensis and Psittacosaurus mongoliensis in the same formation strongly suggests their coexistence.

INTRODUCTION

Psittacosaurs are known exclusively from Lower Cretaceous deposits in Asia. These early ceratopsians, first discovered in Outer Mongolia, are now known from several widespread localities in China and Siberia (Young, 1931, 1958; Rozhdestvensky, 1955; Chao, 1962; Cheng, 1983; Sereno and Chao, 1988). We report here on the discovery of a new psittacosaur, Psittacosaurus meileyingensis, from several closely situated localities in the Jiufotang Formation near the town of Meileyingzi in Liaoning Province, northeastern China.

Abbreviations—AMNH = American Museuum of Natural History, New York; **BNHM** = Beijing Natural History Museum, Beijing; **IG** = Institute of of Geology, Beijing; **IVPP** = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; **PI** = Paleontological Institute, Moscow.

MATERIAL

The finely preserved type skull of Psittacosaurus meileyingensis (IVPP V7705) was recovered in 1973 by Chao Shichin (Institute of Vertebrate Paleontology and Paleoanthropology). In 1977 Cheng Zhengwu collected the skeleton of a smaller individual (IG V.330) in the vicinity of the type locality. Revisiting the area in 1982, Rao Chenggang and Han Zhoukuan (Beijing Natural History Museum) collected two fragmentary adult skulls (BNHM BPV.399, BPV.401) and one juvenile skull (BNHM BPV.400) of the new species. They also received an adult skull of Psittacosaurus mongoliensis (BNHM BPV.398) that had been collected by locals in the vicinity.

The fossil remains of the new species are housed in the IVPP, IG, and BNHM collections.

SYSTEMATIC PALEONTOLOGY

Suborder CERATOPSIA Marsh, 1890
Genus PSITTACOSAURUS Osborn, 1923

PSITTACOSAURUS MEILEYINGENSIS, sp. nov.
(Figs. 2–4, 8, 9)

Type Specimen—IVPP V7705 (Figs. 2, 3, 4, 8), nearly complete skull with articulated lower jaws and anterior three cervical vertebrae.

Locality and Horizon—Meileyingzi, approximately 60 km southwest of Chaoyoung, Liaoning Province; Jiufotang Formation.

Etymology—Specific name refers to the geographic region that includes the type locality.

Diagnosis—Psittacosaur with unusually tall cranial proportions and subcircular profile. Other derived cranial features include transversely broad postorbital region, subtriangular orbit with acute ventral corner, quadratojugal rugosity, quadrate shaft with strong posterior emargination, quadrate shaft angled anterolaterally, anteromedially canted quadrate condyles, and prominent ventral dentary flange.

A distinct primary ridge on the lateral maxillary crown surface is a distinguishing, but variable, characteristic. Preserved portions of the postcranium do not exhibit diagnostic features for the species. Psittacosaurus meileyingensis lacks the diagnostic features of other psittacosaur species, such as the laterally prominent jugal horn in P. sinensis and in a new species from northwestern China, and the subtriangular antorbital fossa in P. mongoliensis.

Referred Specimens—BNHM BPV.399 (Fig. 8C), fragmentary adult skull lacking most of the skull roof and snout, but preserving articulated lower jaws and the axis; BNHM BPV.400, weathered juvenile skull
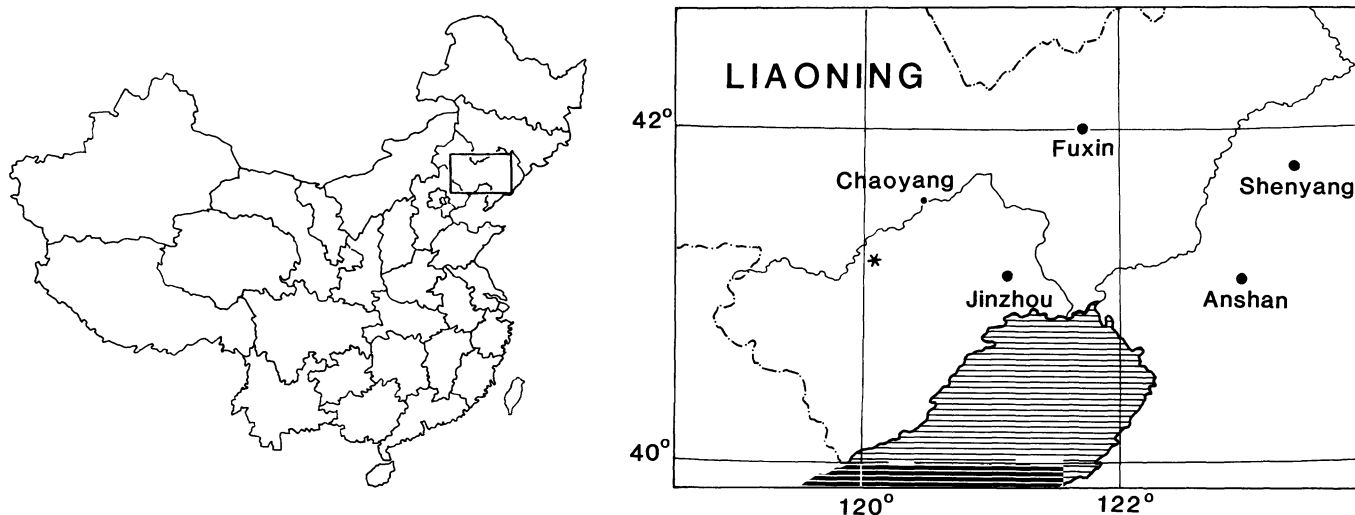
FIGURE 1. Map of type locality in Liaoning Province, northeastern China. * = Meileyingzi.

with articulated lower jaws; BNHM BPV.401, very fragmentary, disarticulated, adult skull; IG V.330 (Figs. 8D, 9), adult skull lacking the anterior snout, postero-lateral corner of the skull roof, posterior right jugal, and left maxilla; right and left mandibular rami dis-articulated, lacking the symphyseal region and pre-dentary (about 30 percent smaller than type skull); associated postcrania including two sacral centra, eight articulated caudal vertebrae with chevrons, proximal left scapula, left coracoid, right scapular blade, nearly complete left ilium, right ilium lacking the ischiac pe-duncle and postacetabular process, proximal left is-chium, proximal left femur, left distal tibia, left prox-imal and distal tarsals, and left metatarsals 1–4.

DESCRIPTION

Skull

The general form and sutural pattern of the skull remains relatively uniform among psittacosaur species. All species have a parrotlike rostrum capped anteriorly by a tall, wedge-shaped rostral bone. The external naris is dorsally positioned, the antorbital fossa reduced, and the antorbital fenestra completely closed.
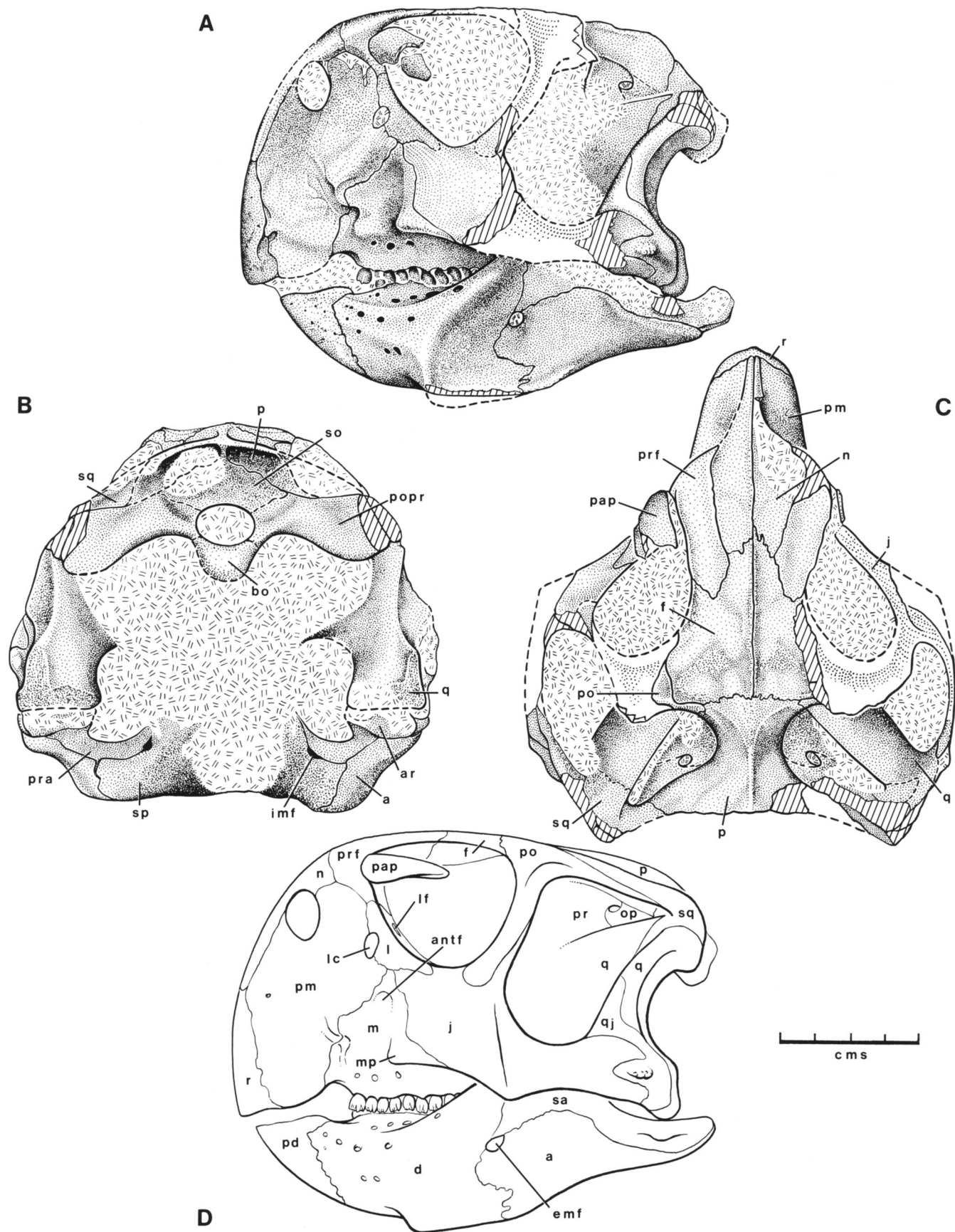
Psittacosaurus meileyingensis presents a slight vari-ation on this theme. The skull is very tall relative to its anteroposterior length. The relatively short antero-posterior proportions of the skull are particularly no-ticeable in the snout. As a result, the skull has an oval or subcircular profile, in marked contrast to the sub-rectangular profile in *P. mongoliensis* and *P. sinensis*. In dorsal view the postorbital segment of the skull is very broad transversely. Anteriorly the skull tapers in width from the orbital region to the narrow snout. In lateral view the posterodorsal corner of the skull is depressed, such that the squamosal is positioned below the level of the central body of the postorbital. The occiput, in consequence, is low dorsoventrally but broad

transversely. The contour of the orbit is characteris-tically subtriangular, due to the tight arc of the ventral orbital margin, in contrast to the gentle arc of the same margin in *P. mongoliensis* and *P. sinensis*.

Dermal Skull Roof (Figs. 2, 3, 4A)—The *rostral* is vertically tall and broadly rounded ventrally, as in oth-er psittacosaurs. In *Psittacosaurus* there is minimal development of the posterolateral processes along the ventral margin, in contrast to other ceratopsians. As in *P. mongoliensis* and *P. sinensis,* the narrow dorsal portion of the rostral is wedged between the ventral tips of the nasals.

The *premaxilla* is an expansive bone, forming most of the lateral snout surface and contacting the rostral, maxilla, nasal, lacrimal, and prefrontal. The premax-illa–maxilla suture in *P. meileyingensis* follows the crest of a low ridge, which runs from the alveolar margin posterodorsally. Anteroventral to the orbit, the pre-maxilla, maxilla, lacrimal, and jugal nearly converge to a point—a characteristic psittacosaur sutural pattern (Fig. 2A, D). At the sutural junction in *P. meiley-ingensis,* the premaxilla and jugal are separated by a narrow maxilla–lacrimal contact, a configuration sim-ilar to *P. mongoliensis* (Fig. 5) but different than *P. sinensis,* in which a narrow premaxilla–jugal contact separates the maxilla from the nasal.

A horny bill sheathed the rostral and anteroventral portions of the premaxilla and maxilla in life. In *P. meileyingensis* a sinuous groove courses across the ven-tral portion of the premaxilla and anterior tip of the maxilla, marking the posterior margin of the sheath (Fig. 2A). The snout surface anterior to this groove is rugose with anastomosing vascular impressions. Pos-terior to this groove, an unossified gap on the lateral surface of the lacrimal exposes the lacrimal canal on the side of the snout. The unossified gap, preserved on both sides of the type skull (IVPP V7705; Fig. 2A, D), is bordered anteriorly by the premaxilla. This unos-
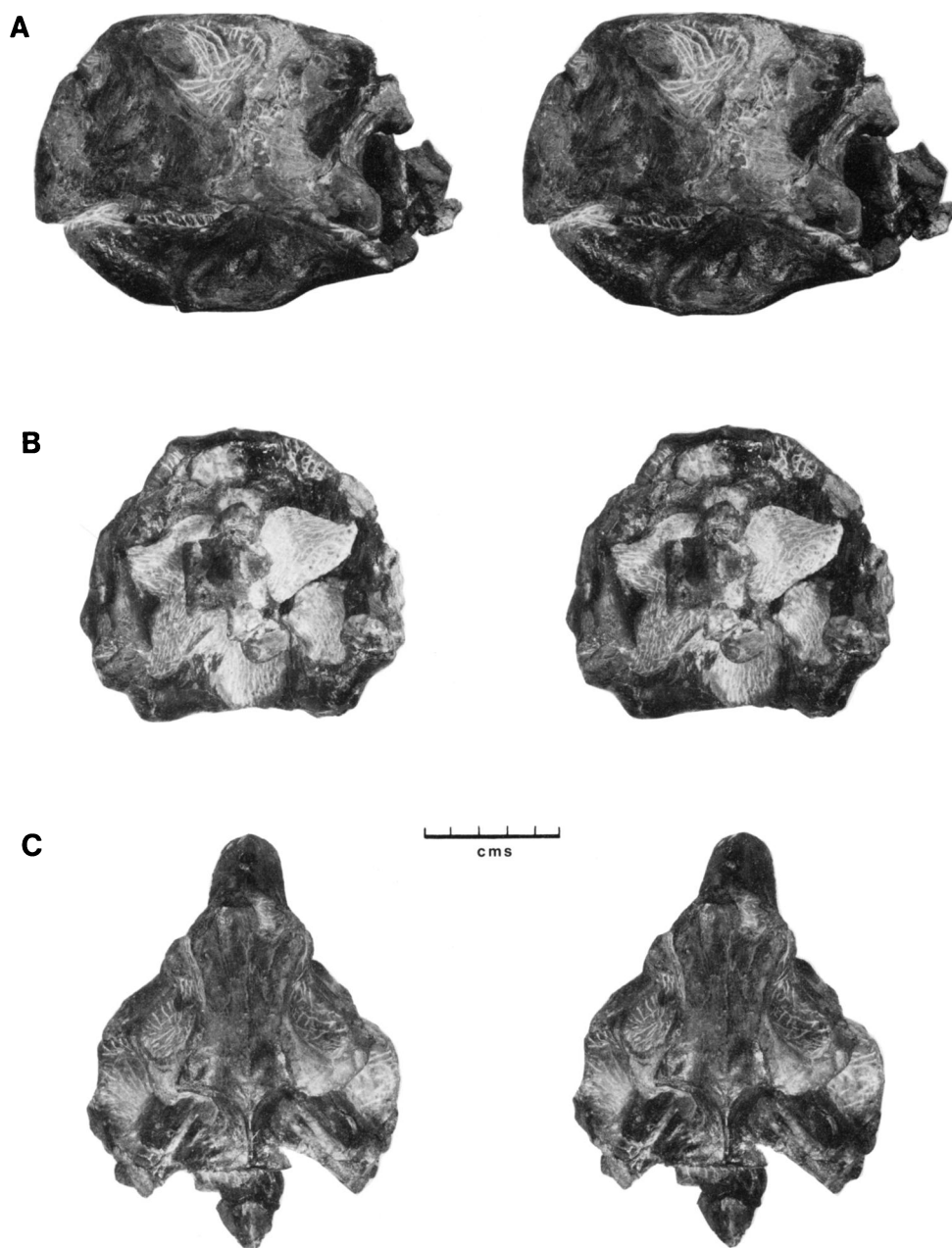
FIGURE 3. *Psittacosaurus meileyingensis* (IVPP V7705). Stereopairs of the skull. **A**, left lateral view; **B**, posterior view; **C**, dorsal view.

sified gap also occurs in *P. mongoliensis* (Fig. 5) and *P. sinensis,* but is relatively smaller in the latter.

Although the antorbital fenestra is closed, it appears that a remnant of the primitively broad antorbital fossa is retained as a shallow depression above the buccal recess on the *maxilla* (Fig. 2A, D). The shallow antorbital fossa, which compares closely with that in *P. xinjiangensis* (Sereno and Chao, 1988), is approxi-

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FIGURE 2. *Psittacosaurus meileyingensis* (IVPP V7705). Skull. **A**, left lateral view; **B**, posterior view; **C**, dorsal view; **D**, reconstruction in left lateral view (based on IVPP V7705, IG V.330, BMNH BPV.399). Abbreviations: **a**, angular; **antf**, antorbital fossa; **ar**, articular; **bo**, basioccipital; **d**, dentary; **emf**, external mandibular foramen; **f**, frontal; **imf**, internal mandibular foramen; **j**, jugal; **l**, lacrimal; **lc**, lacrimal canal; **lf**, lacrimal foramen; **m**, maxilla; **mp**, maxillary process; **n**, nasal; **op**, opisthotic; **p**, parietal; **pap**, palpebral; **pd**, predentary; **pm**, premaxilla; **po**, postorbital; **popr**, paroccipital process; **pr**, prootic; **pra**, prearticular; **prf**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **r**, rostral; **sa**, surangular; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal.
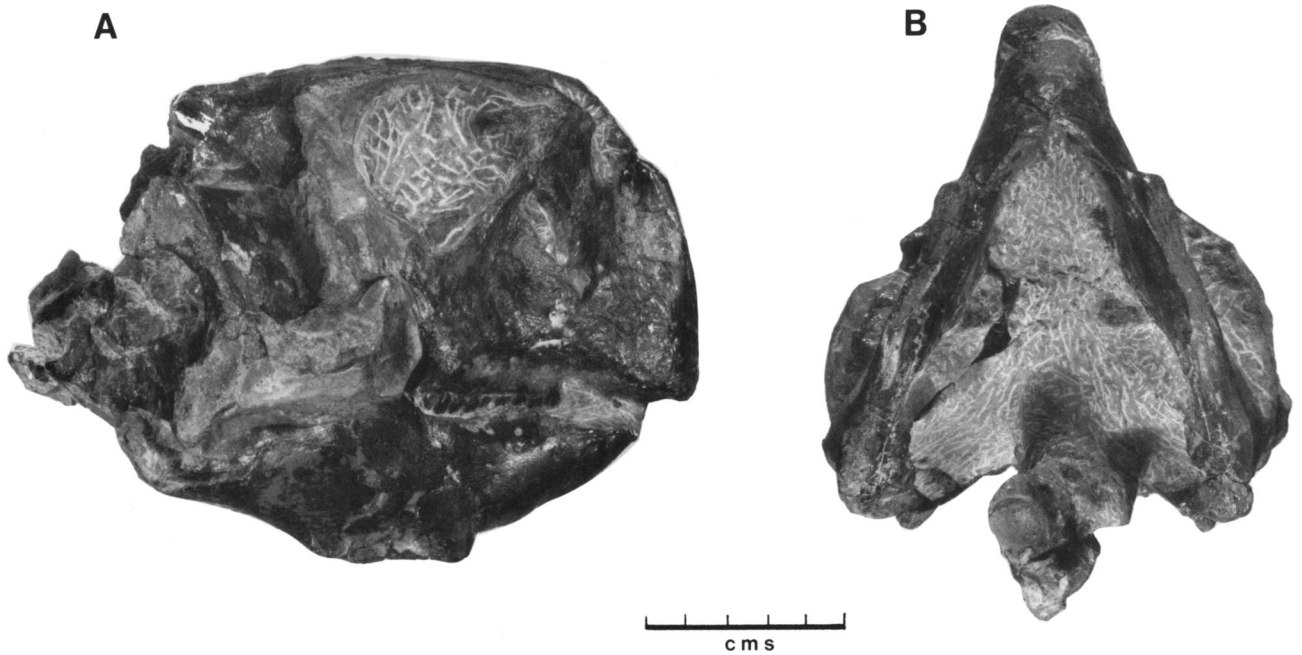
A   **B**

FIGURE 4.   *Psittacosaurus meileyingensis* (IVPP V7705). Skull. **A**, right lateral view; **B**, ventral view.

mately intermediate in depth between the distinct triangular fossa of *P. mongoliensis* (Fig. 5) and the extremely shallow fossa of *P. sinensis* (Young, 1958: fig. 51) and *P. youngi* (Chao, 1962: fig. 1). A protuberance, located in the same position in all psittacosaurs, projects laterally from the rim of the deep cheek emargination on the maxilla just anterior to the maxilla–jugal suture (Figs. 2A, D, 3A).

The *lacrimal* and *prefrontal* are very similar in shape and sutural relations to the same elements in other psittacosaurs. The lacrimal foramen is exposed only in a referred skull (IG V.330). The lacrimal canal passes anteroventrally from the lacrimal foramen to the narial passage, but also opens on the lateral side of the snout through an unossified gap in the lateral wall of the lacrimal (IG V.330; IVPP V7705, Fig. 2A, D). In dorsal view the prefrontal is subrectangular and flat, lacking the raised lateral edge characteristic of *P. mongoliensis* (Fig. 6).

In contrast to *P. sinensis* and *P. youngi,* the *frontal* approaches, but does not participate in, the formation of the supratemporal fossa. The dorsal surface of the frontal is restricted to the flat interorbital portion of the skull roof. The *parietal* is a fused median element in all ornithischians. In *P. meileyingensis* the parietal is short anteroposteriorly relative to the total length of the skull roof and bears a low sagittal crest. The free posterior shelf of the parietal, or the parietal frill, measures approximately 1.5 cm in the midline in IVPP V7705, which has a total skull length of 13.7 cm. Relative to total skull length, the frill in *P. meileyingensis* is more rudimentary than in any other psittacosaur. The maximum anteroposterior length of the frill occurs in the midline, where the frill is inclined horizontally.

The form of the lateral portion of the frill differs from that in other psittacosaurs. In posterior view the frill margin is arched with the lateral portions of the frill curving ventrally; the lateral portions of the frill taper in anteroposterior length away from the midline and are inclined posterodorsally rather than horizontally. In *P. mongoliensis, P. sinensis,* and *P. youngi,* in contrast, the frill overhangs the occiput as a horizontal shelf.

Only fragments and impressions of the *postorbital* are preserved in the type skull (IVPP V7705) and in an adult skull of a second individual (BNHM BPV.399). Both postorbitals, however, are complete in a smaller individual (IG V.330). Three processes radiate from the central body of the postorbital: a short, broad medial process, and longer ventral and posterior processes.

All psittacosaurs have at least a rugosity or low ridge running across the lateral surface of the central body of the postorbital. In *P. meileyingensis* the ridge originates on the dorsal portion of the posterior ramus and curves ventrally, terminating along the anterior edge of the ventral process (Fig. 2D). Ventral to the ridge, the surface is concave. Both the ridge and concavity are more pronounced than in *P. mongoliensis* (Fig. 5; AMNH 6254, 6534) but less so than in *P. sinensis* (IVPP V738). In *P. sinensis* the lateral surface of the posterior process is concave along its entire length.

The short, blunt medial process (Fig. 2D) contributes to the dorsal margin of the orbit as in *P. sinensis* (Young, 1958: fig. 51). In *P. mongoliensis,* in contrast, a narrow posterior extension of the frontals laterally overlaps the medial postorbital process along the orbital margin (Fig. 2).
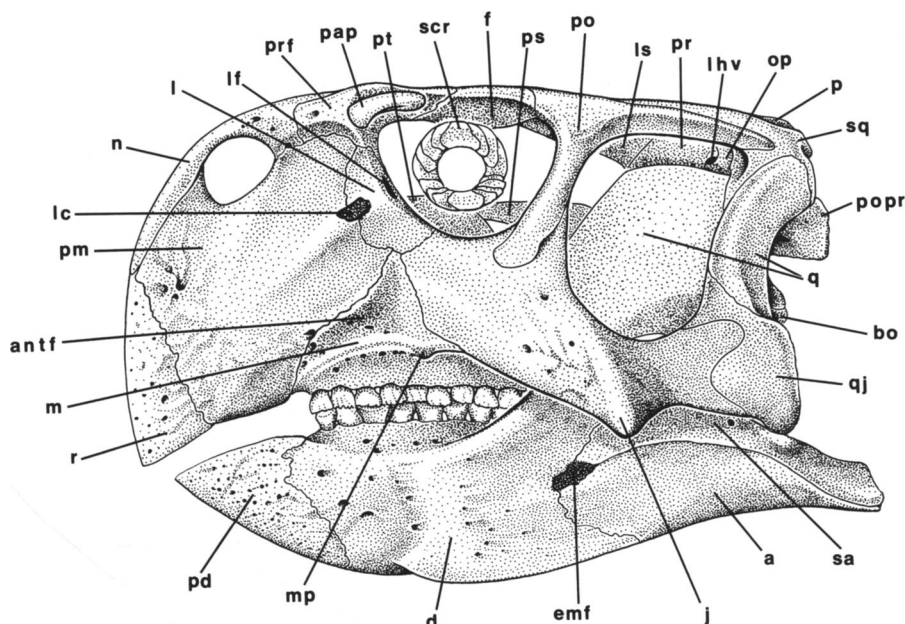
FIGURE 5. *Psittacosaurus mongoliensis* skull reconstruction in lateral view. Abbreviations: **a**, angular; **antf**, antorbital fossa; **bo**, basioccipital; **cqp**, cranioquadrate passage; **d**, dentary; **ect**, ectopterygoid; **emf**, external mandibular foramen; **f**, frontal; **j**, jugal; **l**, lacrimal; **lc**, lacrimal canal; **lf**, lacrimal foramen; **lhv**, lateral head vein; **ls**, laterosphenoid; **m**, maxilla; **mp**, maxillary process; **n**, nasal; **op**, opisthotic; **p**, parietal; **pal**, palatine; **pap**, palpebral; **pd**, predentary; **pm**, premaxilla; **po**, postorbital; **popr**, paroccipital process; **pr**, prootic; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal; **r**, rostral; **sa**, surangular; **scr**, sclerotic ring; **sp**, splenial; **sq**, squamosal.

The distal end of the ventral process is slightly expanded anteroposteriorly and is very thin (IVPP V7705, BNHM BPV.399). The postorbital–jugal suture is raised as a low crest midway along the postorbital bar (BNHM BPV.399). A prominent tuber occupies the same position in *P. sinensis* (IVPP V738; Young, 1958: fig. 51) and *P. youngi* (BNHM BPV.149; Chao, 1962: fig. 1).

Only a fragment of the left **squamosal** is preserved in the type skull (IVPP V7705; Fig. 2). Both right and left squamosals are present in a smaller skull (IG V.330). As in other psittacosaurs, the spatulate ventral and medial processes overlap the pterygoid wing of the quadrate and the lateral parietal frill, respectively. In both IVPP V7705 and IG V.330, the posterior process of the squamosal does not completely separate the quadrate head from the paroccipital process, which is also the situation in *P. sinensis* (IVPP V738) and *P. xinjiangensis* (IVPP V7698; Sereno and Chao, 1988).

The orbital ramus of the **jugal** is broader dorsoventrally than the posterior ramus beneath the laterotemporal fenestra, a derived character for the Ceratopsia (Sereno, 1986). The sutural contacts of the jugal include the maxilla, lacrimal, postorbital, and quadratojugal. A narrow maxilla–lacrimal contact separates the jugal from the premaxilla as in *P. mongoliensis*. Relative to the jugal bone as a whole and the adjacent elements of the dermal skull roof, the jugal horn in *P. meileyingensis* is smaller than in any other psittacosaur, although the horn in the former species is not preserved in its entirety in any single individual (IVPP

V7705, BNHM BPV.399). A low rounded ridge originates on the dorsal ramus of the jugal and continues posteroventrally to the horn tip, effectively dividing the lateral jugal surface into two planes—one anterior and one posterior to the ridge. In all other psittacosaurs, the ridge on the jugal is stronger and the horn more prominent laterally.

In contrast to other psittacosaurs, the **quadratojugal** of *P. meileyingensis* incompletely overlaps the lower half of the quadrate in lateral view (IVPP V7705, BNHM BPV.399). Anterior to the jaw articulation, only a narrow band of the quadratojugal separates the jugal and quadrate (Fig. 2A, D).

A very distinctive feature of *P. meileyingensis* is the presence of a rugose prominence in the center of the lateral surface of the quadratojugal (Fig. 2A, D). The elevated rugosity is preserved, although incompletely, in the type skull (IVPP V7705) and in a referred skull (BNHM BPV.399). Whether or not the quadratojugal rugosity was covered with a horny sheath in life cannot be determined from available material.

The subtriangular **palpebral** articulates exclusively with the prefrontal in the anterodorsal corner of the orbit. Both right and left palpebrals are preserved in the type skull but have rotated somewhat from their natural positions (Fig. 2). The flat surfaces of the palpebral are oriented horizontally in natural articulation, with a thickened, rounded edge forming the external margin. The medial edge of the palpebral is noticeably shorter than the external margin as in *P. youngi* (Chao,
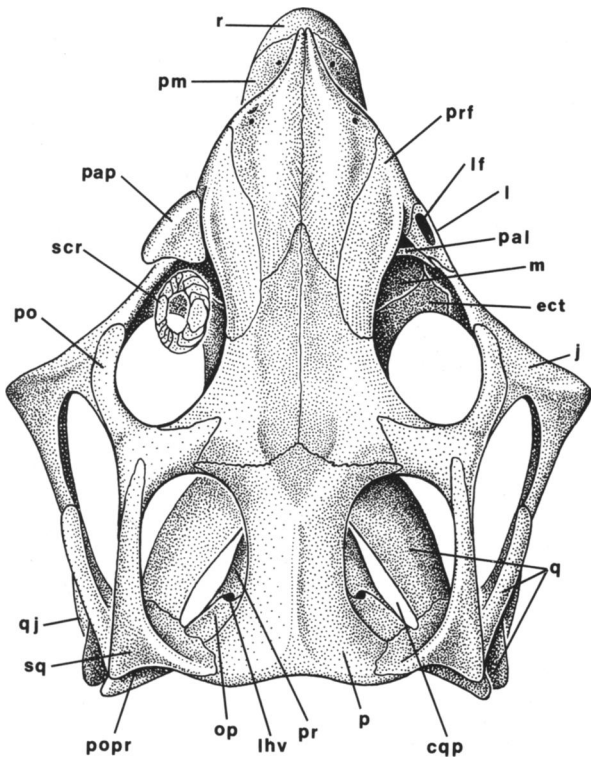
FIGURE 6. *Psittacosaurus mongoliensis* skull reconstruction in dorsal view (see Fig. 5 for abbreviations).

1962) and *P. xinjiangensis* (Sereno and Chao, 1988), in contrast to the condition in *P. mongoliensis* in which these edges are subequal in length (Fig. 6).

Palate (Fig. 4B)—In *P. meileyingensis* the sutural contacts of the **quadrate** include the squamosal, quadratojugal, pterygoid, and paroccipital process. In lateral view, the dorsal half of the quadrate shaft arches posteriorly, and the head is rounded and slightly expanded. The shaft is rotated strongly anterolaterally, almost at 45 degrees to the sagittal plane of the skull, and is noticeably excavated along its posterior margin (Fig. 2A, D; IVPP V7705, BNHM BPV.399). The ventral end of the quadrate shaft expands transversely to form a broad condylar surface, the axis of which is angled anteromedially at approximately 60 degrees from the anteroposterior axis of the skull. The condylar surface in both *P. mongoliensis* and *P. sinensis,* in contrast, are oriented perpendicular to the skull axis.

The pterygoid ramus of the quadrate is expansive, and, as a result, the cranioquadrate passage between the pterygoquadrate wing and the sidewall of the braincase is correspondingly narrow, as in other psittacosaurs (Fig. 2C).

The **pterygoid** is composed of three principal rami: a posterolaterally directed quadrate ramus, a posteroventrally directed mandibular ramus, and an anterodorsally directed palatal ramus. The quadrate ramus is poorly exposed in available material.

The long mandibular ramus is joined laterally by the ectopterygoid and extends posteroventrally from the lateral side of the palate toward the mandibular fossa of the lower jaw. Both right and left mandibular rami are broken distally in IG V.330, but the distal tip of the left side is exposed in IVPP V7705 (Fig. 4B). The unusual straplike proportions of the mandibular ramus constitute one peculiarity of the psittacosaur palate that does not occur elsewhere among dinosaurs.

The palatal ramus projects anterodorsally forming the steep posterior portion of the palatal vault. Right and left palatal rami suture at the midline, eliminating the interpterygoid vicinity. The postpalatine foramen is situated posterolaterally (IG V.330), as in *P. mongoliensis.*

Relative to skull length, the **vomer** is short anteroposteriorly. In lateral view the paired vomers arch from their posterior suture with the pterygoid palatal rami to the maxillae anteriorly, where they fuse to form a single median strut (IG V.330). The anterior footplate of the vomers anchors between the anteromedial processes of the maxillae; the vomers do not contact the premaxillae, which are excluded from the anterior border of the internal nares as in *P. mongoliensis.*

Braincase (Figs. 2, 3)—The occiput is broad transversely and low dorsoventrally. The foramen magnum is bounded by the supraoccipital, basioccipital, and the exoccipitals (IVPP V7705).

The sutural boundaries of the diamond-shaped **supraoccipital** are only partially exposed (IVPP V7705). As in *P. mongoliensis,* a thin, platelike nuchal crest extends dorsally in the midline from the rim of the foramen magnum across the supraoccipital to the parietal shelf (IG V.330).

The **basioccipital** forms the majority of the occipital condyle. A sizeable median cleft separates the basal tubera, which extend ventrally below the level of the occipital condyle as in *P. youngi* (Chao, 1962: fig. 4). The transversely compressed basipterygoid processes of the basisphenoid are similar in all psittacosaurs and are directed anterolaterally, with only a shallow ventral inclination (IG V.330). Posteriorly the basipterygoid processes are continuous with parasagittal prominences that cross the ventral surface of the basisphenoid to respective basal tubera.

Portions of the **prootic** and **opisthotic** are exposed in lateral view of the braincase, suturing dorsally to the parietal (IVPP V7705). As in *P. sinensis* (IVPP V738), *P. youngi* (BNHM BPV.149) and *P. mongoliensis* (Fig. 5), a foramen for the lateral head vein pierces the lateral wall of the braincase between the prootic and opisthotic (IVPP V7705). The contour of the lower edge of each paroccipital process follows a gentle sigmoid curve in the type skull (IVPP V7705), but the same edge is straight in a smaller referred skull (IG V.330). The **laterosphenoid** arches from the sidewall of the braincase to the lateral skull roof, contacting the ventral surface of the parietal, frontal, and postorbital.

Lower Jaw (Figs. 2–4)—The following description is based primarily on the articulated lower jaws of the type skull (IVPP V7705). As in *P. mongoliensis,* in-

ternal and external mandibular fenestrae are present, the former bounded by the dentary, angular and surangular, and the latter by the splenial and prearticular. As preserved in IVPP V7705, the lower jaws are displaced posteriorly a short distance from their natural articulation with the cranium (see Fig. 2A, D).

The *predentary* is subtriangular in lateral and ventral views, with short, weak lateral processes and a broad ventromedian process. The roughened and pitted surface, doubtless, supported a horny bill in life that opposed a similar bill attached to the anterior snout. Unlike most ornithischians, the predentary in adult *P. meileyingensis* and other ceratopsians is bound tightly to the mandibular symphysis, forming a strong immobile joint (Sereno, 1986).

The *dentary*, the dominant structural element of the mandibular ramus, extends from the symphysis to the top of a moderately sized coronoid process. The dentary, not the surangular, forms the top of the coronoid process, as is characteristic of all ornithischians (Sereno, 1986). The most unusual feature of the lower jaw is the presence of a well developed flange projecting from the ventral margin. Composed almost entirely by the dentary, the flange dissipates posteriorly as a low ridge on the angular. The flange does not project directly ventrally but rather curves ventrolaterally.

A rounded prominence arches across the lateral surface of the dentary from the coronoid process, dorsally, to the prominent anterior corner of the flange, ventrally. The flange and rounded prominence are present, although much less prominent, in *P. mongoliensis* (Fig. 5), and are absent altogether in *P. sinensis* (Young, 1958: fig. 51). The dentary symphysis is spout-shaped as in nearly all ornithischians (Sereno, 1986).

On the medial side of the mandibular ramus, the long dorsoventrally deep *splenial* extends from the mandibular fossa to very near the dentary symphysis, as in *P. mongoliensis* and *P. sinensis*. The narrow *prearticular* (Fig. 2B) forms the ventral margin of the mandibular fossa and the dorsal margin of the internal mandibular fenestra (IVPP V7705).

The posterior elements of the lower jaw are preserved only in the type skull (IVPP V7705). Broadly exposed on the posterior mandible, the *surangular* and *angular* extend past the jaw articulation onto the retroarticular process. The *articular* forms the cotylus for the quadrate condyle, although the surangular may have contacted the lateral edge of the quadrate.

Dentition (Figs. 8, 9A)—Premaxillary teeth are absent in *P. meileyingensis* and other psittacosaurs. Both maxillary and dentary tooth rows are inset from the lateral surface of the snout, creating a buccal recess, or cheek, lateral to the dentition. The tooth rows are nearly straight, and the teeth are tightly packed with only small spaces between the crowns and the alveolar border. Individual crowns are set at an angle to the axis of the tooth row, such that the anterior edge of a given crown overlaps medially the posterior edge of the next most anterior crown (Fig. 8A, B).

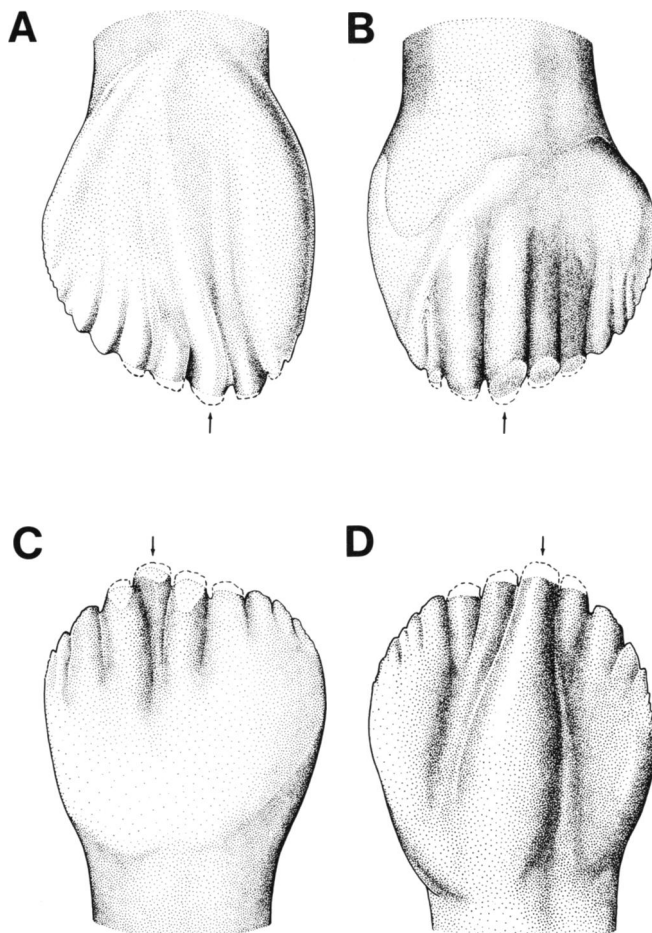The crowns of unworn cheek teeth are oval in lateral

FIGURE 7. *Psittacosaurus mongoliensis.* Maxillary and dentary teeth. **A**, left maxillary tooth in lateral view (PI 3779/24-1); **B**, left maxillary tooth in medial view (PI 3779/24-1); **C**, right dentary tooth in lateral view (PI 3779/24-2); **D**, right dentary tooth in medial view (PI 3779/24-2). Arrows identify the primary ridge denticle.

view, although nearly all available crowns are worn at their tips. Tooth wear quickly obliterates the distinguishing characteristics of the distal crown. Active tooth replacement is well exposed in IG V.330 and involves a maximum of two teeth in a single vertical tooth column—one active tooth and one replacement. No consistent replacement pattern along the tooth row can be established in the available dentitions of *P. meileyingensis.*

The maxillary crowns are set at an angle to the axis of the roots (Fig. 8C). As a result, the apices of the maxillary crowns point more directly toward the occlusal plane than the opposing dentary crowns. The enamel is distributed asymmetrically, a thicker layer present on the lateral side of the maxillary crowns and on the medial side of the dentary crowns.

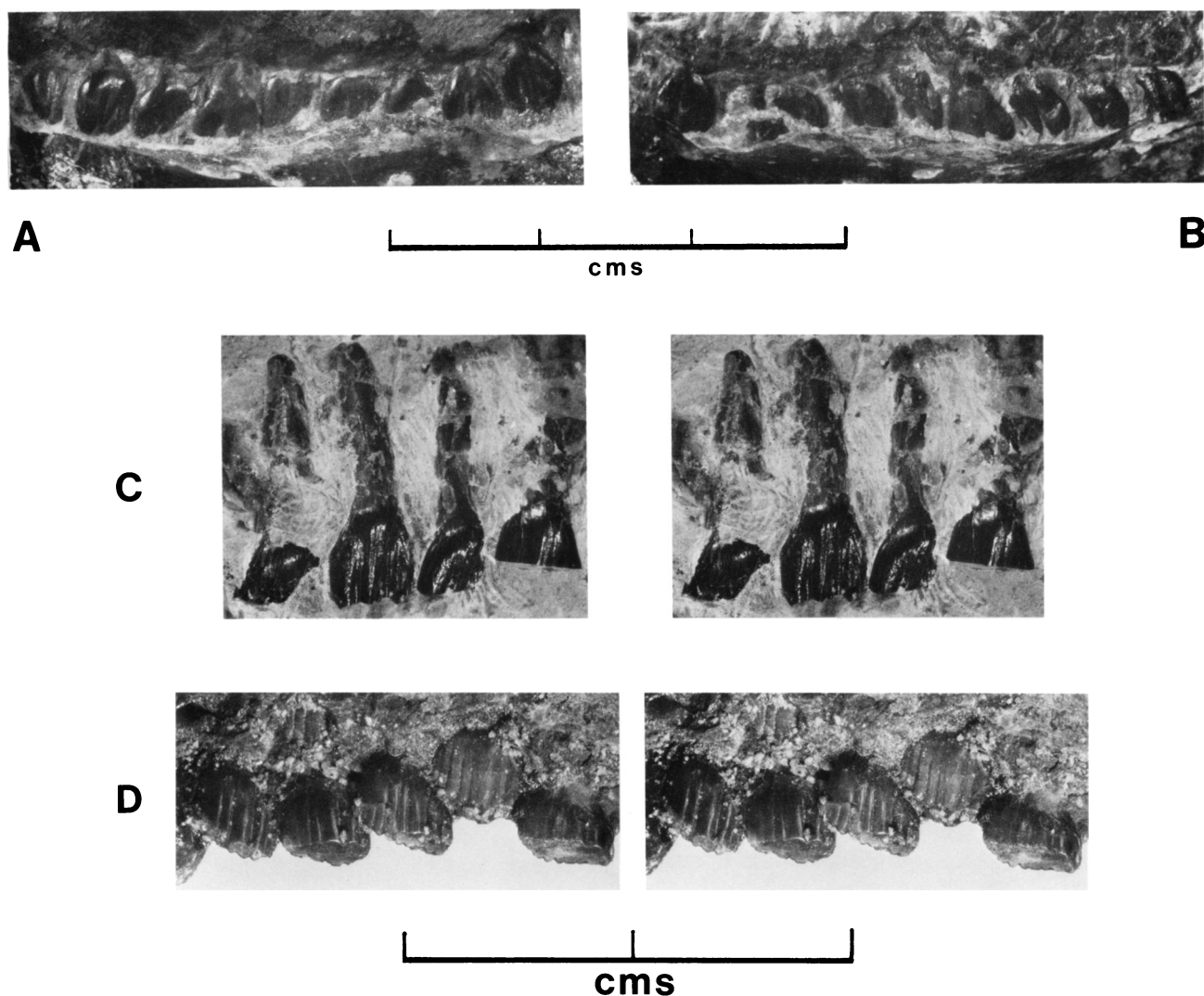Nine *maxillary teeth* constitute the complete maxillary tooth rows in both the type skull (IVPP V7705)

FIGURE 8.   *Psittacosaurus meileyingensis*. Maxillary teeth. **A**, right maxillary tooth row in lateral view (IVPP V7705); **B**, left maxillary tooth row in medial view (IVPP V7705); **C**, stereopair of right maxillary teeth in lateral view (BNHM BPV.399); **D**, stereopair of right maxillary teeth in medial view (IG V.330).

and a somewhat smaller skull (IG V.330), but only seven are present in the maxillary tooth rows of a juvenile (BNHM BPV.400). An increase in tooth number during growth is expected and has been documented in *P. mongoliensis* (AMNH 6535, 6536, 6524, 6534; Coombs, 1982; Sereno, 1987).

Fortunately, a single erupting maxillary crown preserves an unworn apex in medial view (Fig. 8D; IG V.330); all other available maxillary crowns are truncated distally by wear. The unworn maxillary crown is oval with a ventral apex offset slightly posteriorly as in *P. mongoliensis*. There are at least six or seven denticles anterior to the apical denticle, with fewer, probably two or three, posterior.

The ornamentation of the lateral side of the maxillary crown in *P. meileyingensis* is very similar to that in *P. mongoliensis* and *P. xinjiangensis* (Sereno and Chao, 1988). A posteriorly angling primary ridge orig-

inates near the base of the crown, where it is broadest, and tapers ventrally to form a ridge, which terminates in the apical denticle (Fig. 8C). A sharp, well defined primary ridge is found only in *P. meileyingensis* (IVPP V7705, BNHM BPV.399) but exhibits some variability; in one individual (IG V.330) the primary ridge is poorly developed and indistinguishable from the condition that occurs in *P. mongoliensis* (PI 3779/24, 3779/28) and *P. xinjiangensis* (IVPP V7704; Sereno and Chao, 1988).

As in *P. xinjiangensis* (Sereno and Chao, 1988), the lateral surface of the maxillary crown in *P. meileyingensis* is divided into two lobes, one on each side of the primary ridge: a broad, relatively flat anterior lobe and a narrow, anteroposteriorly convex posterior lobe. Low secondary ridges flank the primary ridge and extend dorsally beyond midcrown on each lobe. At least three or four secondary ridges ornament the anterior

lobe and at least two are present on the posterior lobe. The posteriormost secondary ridge, which forms the posterior crown margin, equals the primary ridge in prominence and width.

The medial surface of the maxillary crown is exposed only in IG V.330 (Fig. 8D). As in *P. mongoliensis* and *P. xinjiangensis*, the surface is anteroposteriorly and dorsoventrally convex. Low rounded ridges extend from the denticles nearly to the base of the crown as in *P. xinjiangensis* (Sereno and Chao, 1988: fig. 5B). In the new species, the median ridge is wider than the others.

There are nine **dentary teeth** in the only completely exposed dentary tooth row (IG V.330, left dentary), which equals the number of teeth in the maxillary tooth row (IVPP V7705, IG V.330). The medial side of the dentary crown in all psittacosaurs is dominated by a bulbous median primary ridge, and the new species is no exception (Fig. 9A; IG V.330, BNHM BPV.399). There are approximately five denticles with descending secondary ridges to each side of the primary ridge, as preserved in a single unworn dentary crown (Fig. 9A). The secondary ridges are confined to the dorsal half of the crown and are eventually obliterated by tooth wear. A heavily worn dentary crown, therefore, has a simple tri-lobed appearance in medial view: a central lobe, which constitutes the base of the primary ridge, and a lobe to each side, which represent the smooth, convex crown base ventral to the secondary ridges.

The lateral side of the dentary crown is strongly convex anteroposteriorly and dorsoventrally, but details of ornamentation are poorly known. All laterally exposed dentary crowns are heavily worn except one crown, which is lacking only the extreme tip (IG V.330). Low rounded ridges extend across at least the dorsal third of the crown. A median ridge is not present, but the crown is not preserved well enough to determine if a median groove was present, as is the case in *P. mongoliensis* (Fig. 7C) and *P. xinjiangensis* (Sereno and Chao, 1988: fig. 5D).

The dentary crowns of *P. meileyingensis* lack the broad anteroposterior proportions of the dentary crowns in *P. sinensis* and the high denticle dentary crowns of *P. xinjiangensis*. As currently understood, however, the dentary crowns of *P. meileyingensis* and *P. mongoliensis* cannot be distinguished.

Postcranium

The postcranium of *P. meileyingensis*, known from a single individual with a partial skull, includes a series of caudal vertebrae, fragmentary pectoral and pelvic girdles, and a left hind limb (IG V.330).

The **axial skeleton** is represented by two sacral centra and an articulated series of eight anterior caudal vertebrae with chevrons. Because the first two caudal centra in the series lack facets for chevrons, the vertebral series probably represents caudals 1 through 8 by comparison with *P. mongoliensis* (Sereno, 1987). Chevrons articulate with all remaining centra. The centra of the

anterior caudals are transversely compressed and display a rounded ventral keel. In lateral view, the rectangular neural spines are twice as tall as wide. Well developed transverse processes arch horizontally from the sides of the neural arches.

Only the base of the anteriormost chevron is preserved, articulating between the third and fourth caudals of the series. The shaft of the next posterior chevron, articulating between the fourth and fifth caudals of the series, is rodlike, in contrast to the transversely compressed, bladelike chevrons located more posteriorly. As in *P. mongoliensis* (AMNH 6253, 6254) and *P. sinensis* (IVPP V738), the absence of any trace of ossified tendons along the caudal series suggests that *P. meileyingensis* may have had a flexible, rather than rigid, tail as occurs in *P. mongoliensis* (AMNH 6253, 6254).

The principal element of the **pectoral girdle**, the robust scapula shares equally with the coracoid in the glenoid fossa. The acromion is very well developed in *P. meileyingensis*, extending as a rounded tab dorsal to the margin of the adjoining coracoid (Fig. 9C). The distal expansion of the scapular blade is moderate, closely resembling the proportions of the blade in *P. mongoliensis* (Osborn, 1924) and *P. xinjiangensis* (Sereno and Chao, 1988) rather than the narrow proportions of the blade in *P. sinensis* (Young, 1958).

The coracoid is pierced laterally by the coracoid foramen (Fig. 9C), which opens near the coracoid suture medially. A crest divides the lateral surface of the coracoid into anterior and posterior portions. The anterior portion faces ventrolaterally and curves ventromedially toward the sternum, whereas the posterior portion faces laterally. The angle between the two portions of the coracoid is less than 90 degrees, which differs from the strongly flexed coracoid of *P. sinensis* (Young, 1958). The ventral edge anterior to the glenoid is broadly arched, which resembles that of *P. mongoliensis* and *P. xinjiangensis* (Sereno and Chao, 1988) but differs from the sharply arched ventral margin of *P. sinensis*.

The **pelvic girdle** is known from overlapping parts from several individuals. The ilium is known from complementary fragments of the left and right sides (Fig. 9B). The left ilium is the most complete, lacking only the pubic peduncle and the distal end of the preacetabular process. The right ilium, preserving the portion missing on the left side, extends from the acetabulum anteriorly. Only the proximal half of the left ischium is preserved. In details and proportions, the ilium and ischium of *P. meileyingensis* are indistinguishable from that of *P. mongoliensis* (AMNH 6253, 6254; Osborn, 1924: figs. 8, 9). As in the latter, the iliac blade is moderately tall, narrowing along the postacetabular process. Preacetabular and postacetabular processes are approximately equal in length, and the pubic peduncle is narrower than the bulbous ischiac peduncle. The pubic peduncle of the ischium is subtriangular in cross section, and the broader iliac peduncle flares laterally to support the laterally prominent ischiac peduncle of the ilium. Distally, the ischial
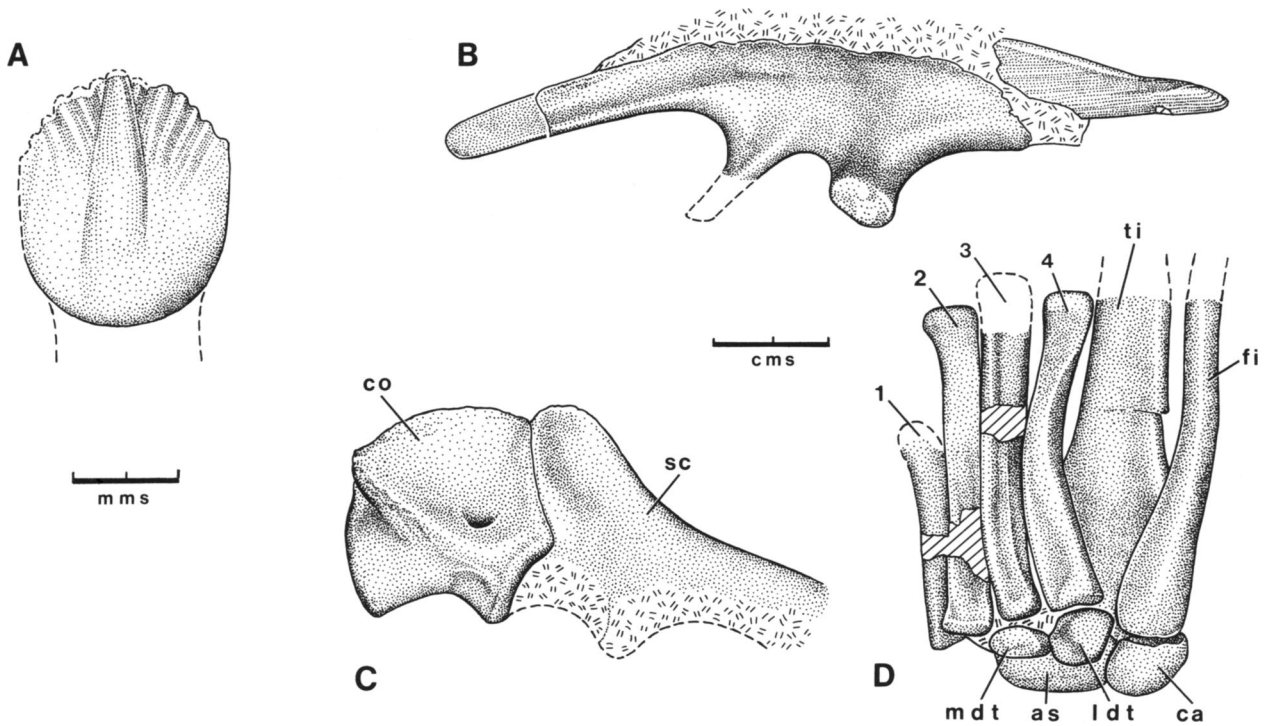
FIGURE 9. *Psittacosaurus meileyingensis* (IG V.330). **A,** partial reconstruction of the left dentary tooth in lateral view; **B,** left ilium (with distal preacetabular process of right ilium reversed) in lateral view; **C,** left scapulocoracoid in lateral view; **D,** left tarsus and pes in ventral view. Abbreviations: **as,** astragalus; **ca,** calcaneum; **co,** coracoid; **fi,** fibula; **ldt,** lateral distal tarsal; **mdt,** medial distal tarsal; **sc,** scapula; **ti,** tibia. Metatarsals are numbered.

shaft flattens into a ventromedially angling blade, similar in width and orientation to the corresponding mid-shaft region in *P. mongoliensis* (Osborn, 1924: fig. 9).

The **hind limb** is very similar in all psittacosaurs including *P. meileyingensis.* The proximal femur, distal tibia and fibula, tarsals, and metatarsals 1–4 are preserved on the left side.

The distal crus, tarsus, and pes are preserved in articulation. The ankle joint is hyperextended with the anterior surface of the crus and dorsal surface of the pes in apposition—the most common posture of the psittacosaur ankle when preserved in articulation (Fig. 9D; *P. mongoliensis* AMNH 6253, 6254, Osborn, 1924; *P. sinensis* IVPP V738, Young, 1958). In this state of preservation, the astragalus and calcaneum remain fixed to the ends of the tibia and fibula, and the distal tarsals remain in contact with the metatarsals.

Two distal tarsals are present, medial and lateral, both of which are similar in form and position to the distal tarsals of other ornithischians. The platelike medial distal tarsal articulates with the astragalus, proximally, and with metacarpal 3 and the lateral edge of metatarsal 2, distally. The thicker, blocklike lateral distal tarsal is concave proximaly for reception of the convex articular surface of the calcaneum. Distally, the lateral distal tarsal contacts only metatarsal 4. The relative metatarsal lengths in the left pes are primitive; metatarsal 3 is longest, metatarsals 2 and 4 subequal, and metatarsal 1 shortest. The metatarsals are compact

and the pes digitigrade. Metatarsal 4 exhibits the characteristic, primitive sigmoid curve in the shaft, which directs the distal condyles away from the axis of the pes. The absence of a fifth metatarsal may only reflect the incomplete nature of the remains.

DISCUSSION AND CONCLUSIONS

The close relationship of the new species to other members in the genus *Psittacosaurus* is immediately apparent. Derived characters that unite all species of psittacosaurs including the new species, *P. meileyingensis,* can be defined using other ceratopsians (Neoceratopsia) and pachycephalosaurs as succesive outgroups (Sereno, 1986). These characters include the anteroposteriorly short snout, dorsally positioned external naris, absence of an antorbital fenestra, elongate ventral process of the nasal, rostral–nasal sutural contact, expansive premaxillary contribution to the snout wall, maxillary eminence, elongate pterygoid mandibular ramus, and bulbous primary ridge on the medial side of the dentary crowns (Sereno, 1987).

The distinguishing features of *P. meileyingensis* are apparent in the proportions of the skull, which is tall relative to its length and transversely broad across the postorbital region. These proportions are distinctly different than those of other psittacosaur species, such as *P. mongoliensis* (Figs. 5, 6). The ornamentation of the quadratojugal and marked excavation along the pos-

terior margin of the quadrate shaft are also peculiar to *P. meileyingensis*. A prominent dentary flange hangs ventrally from the dentary and angular, marking the lower jaw of the new species. The distribution of these diagnostic characteristics within the genus and among the immediate outgroups is summarized by Sereno and Chao (1988: table 1).

Evidence for relationships among the species in the genus *Psittacosaurus* is scant. The immediate relationships of *P. meileyingensis*, in particular, are poorly established given available skeletal remains. The transverse width of the postorbital region of the skull increases toward the occiput in *P. meileyingensis, P. sinensis,* and *P. youngi* but remains uniform in width in *P. mongoliensis*, which suggests that the new species may be more closely related to *P. sinensis* and *P. youngi* than to *P. mongoliensis*. This character, however, occurs in primitive members of the nearest outgroup to *Psittacosaurus* (e.g., *Protoceratops*). An alternative character that may favor this subgroup of psittacosaur species is the rudimentary development of the antorbital fossa. The fossa, which is present in the outgroups, is somewhat better developed in *P. mongoliensis*.

The ventral dentary flange, however, suggests a different phylogenetic arrangement for psittacosaur species. Although a robust dentary flange is diagnostic for *P. meileyingensis*, a rudimentary flange occurs elsewhere only in *P. mongoliensis* (Sereno and Chao, 1988: table 1).

Psittacosaurus meileyingensis is known only from the type locality near Chaoyoung in Liaoning Province, northeastern China. As noted above, a relatively complete skull of *P. mongoliensis* was recovered in the vicinity of the type locality. The presence of *P. mongoliensis* in the same beds (Jiufotang Formation) and, apparently, very near the locality of *P. meileyingensis* suggests, but does not yet establish unequivocally, the coexistence of *P. mongoliensis* and *P. meileyingensis* in northeastern China during the Early Cretaceous.

ACKNOWLEDGMENTS

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The Bryan Patterson Prize of the Society of Vertebrate Paleontology recognizes outstanding student proposals for paleontological field work. The recipients of the 1988 Bryan Patterson Prize, each of whom received an award of $500, are: Greg Graffin (Department of Biology, University of California at Los Angeles), for his study "The oldest vertebrates: a new locality;" and Heather Wilson (Department of Zoology, Erindale College, University of Toronto), for her proposal entitled "Reconnaissance and collection of Lower Permian vertebrates at Richard's Spur, Oklahoma."