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

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ABSTRACT—A new species of psittacosaur, *Psittacosaurus xinjiangensis*, is based on one articulated skeleton and additional disarticulated material from several individuals. Diagnostic features of the species include an anteriorly flattened jugal horn, an unusually high denticle count on maxillary and dentary crowns, a proportionately narrow iliac postacetabular process, and ossified tendons that extend along the tail.

INTRODUCTION

Psittacosaurus were first discovered in Lower Cretaceous beds in Outer Mongolia (Mongolian People's Republic) by the Central Asiatic Expeditions of the American Museum of Natural History (Osborn 1923, 1924). Since that time, psittacosaur fossils have been discovered to the south in China (Inner Mongolia, Shandong, Liaoning; Young, 1931, 1958; Chao, 1962; Cheng, 1983; Sereno et al., 1988) and to the north in Siberia (Rozhdestvensky, 1955).

Recently Dong (1973b) mentioned the discovery of psittacosaur remains in the Junggar Basin of the Xinjiang Uygur Autonomous Region in western China. He identified the material as an indeterminate species of *Psittacosaurus*, noting similarities to *Psittacosaurus mongoliensis* in the dentition and in adult body size. Other faunal tabulations, however, have assigned the material to *Psittacosaurus mongoliensis* (Dong, 1973a: 4, fig. 2; Cheng, 1983:134). In the following report, we describe these skeletal remains as a new species in the genus *Psittacosaurus*.

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

MATERIAL

The fossil remains of the new species were collected in 1964 by the Xinjiang Expedition of the Institute of Vertebrate Paleontology and Paleoanthropology at Delunshan, a locality in the Junggar Basin of the Xinjiang Uygur Autonomous Region in western China (Fig. 1). The psittacosaur fossils were discovered in the Lower Cretaceous Tugulu Group, a sequence of terrestrial mudstones and sandstones that attain a thickness of approximately 180 meters at Delunshan. A diverse, but poorly known, fauna associated with the new psittacosaur species includes ornithopods, coelurosaurs,

carnosaurs, pterosaurs, and chelonians (Chao Shichin, pers. obs.). However, allocation of the fossil-bearing horizons to the Lower Cretaceous and correlation with fossiliferous Lower Cretaceous strata near Wuerho is tentative (Dong, 1973a).

All material of the new species is housed in the IVPP collections.

SYSTEMATIC PALEONTOLOGY

Suborder CERATOPSIA Marsh, 1890
Genus *PSITTACOSAURUS* Osborn, 1923

PSITTACOSAURUS XINJIANGENSIS, sp. nov.
(Figs. 2–8)

Type Specimen—IVPP V7698 (Figs. 2, 3, 4F, 6), articulated subadult skeleton including the crushed posterior portion of the skull, but lacking both carpi, the right and most of the left manus, both hind limbs beyond the proximal ends of the tibiae, and most of the tail. The matrix surrounding the skeleton is a soft beige mudstone.

Locality and Horizon—Delunshan, Junggar Basin, Xinjiang Uygur Autonomous Region; Tugulu Group.

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

Diagnosis—Psittacosaur with anteriorly flattened jugal horn and maxillary crowns with denticulate margin curving posteromedially onto the side near the crown base. Postcranial characters include proportionately elongate iliac postacetabular process and posterior extension of ossified epaxial tendons onto the anterior half of the tail.

Psittacosaurus xinjiangensis lacks diagnostic features of other psittacosaur species such as the subtriangular antorbital fossa of *P. mongoliensis*, the quadratojugal boss and strongly emarginated quadrate shaft of *P. meileyingensis*, and the curved tooth row and postorbital-jugal horn core of *P. sinensis*.

Referred Specimens—IVPP V7701 (Fig. 7), fragmentary right ilium, left pubis, and distal right and left

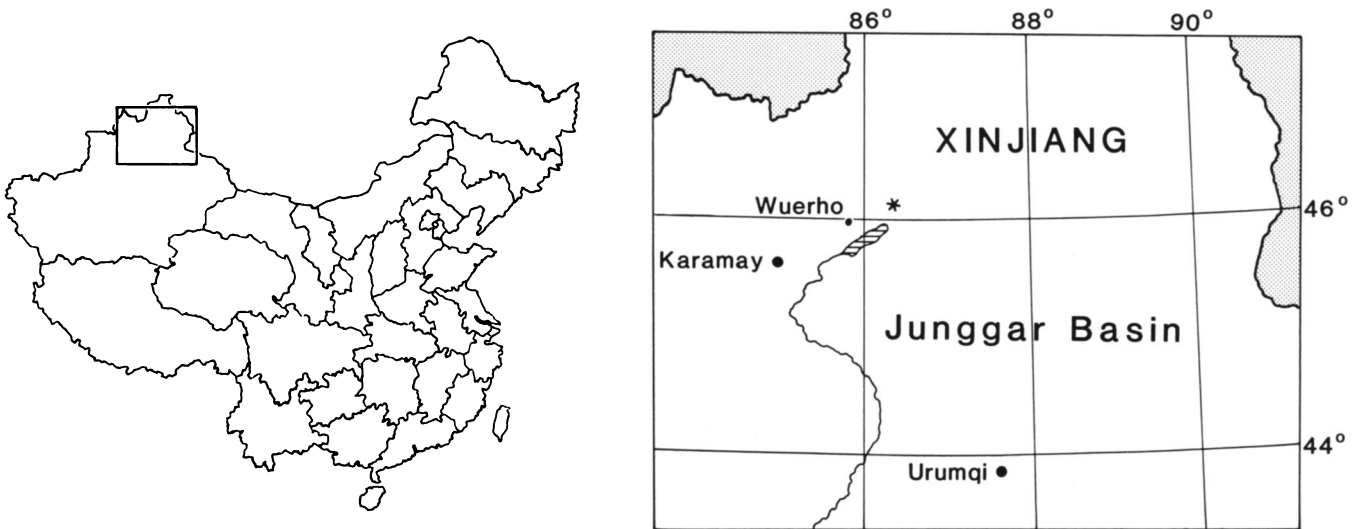


FIGURE 1. Map of type locality in the Junggar Basin of the Xinjiang Uygur Autonomous Region of western China. * = Delunshan.

fibulae of possible association, a second individual represented by a pair of fragmentary fibulae, and vertebrae from several individuals; IVPP V7702, right and left maxillary fragments each with five teeth (Fig. 5A), and an anterior right dentary fragment (similar size, but association unknown); IVPP V7703, left maxillary fragment with unworn replacing crown (Fig. 5B) and an anterior right dentary fragment (similar size, but association unknown); IVPP V7704, complete right maxilla with eight alveoli (Fig. 4A, B) and left dentary fragment (no association) with single, erupting dentary crown (Fig. 5C, D); IVPP f.n. 64047-6, fragmentary postcrania of several individuals; IVPP f.n. 64047, skeletal fragments of several individuals including two maxillae with teeth, nine jugal horns (Fig. 4D, E), an articulated basioccipital, basisphenoid, and ventral exoccipital fragment (Fig. 4C), dorsal and caudal vertebrae, nine proximal scapulae, six distal scapulae, five coracoids, 12 distal humeri, two distal ulnae, one distal radius with articulated radiale, nine proximal femora (Fig. 8A), five distal femora, nine proximal tibiae (Fig. 8B), nine distal tibiae (two with articulated astragali and two with articulated astragali and calcanea; Fig. 8D), a right astragalus (Fig. 8E), and two right calcanea.

DESCRIPTION

The collection of isolated skeletal elements indicates that *P. xinjiangensis* attained an adult body size comparable to *P. mongoliensis*. The subadult status of the articulated holotype skeleton (IVPP V7698; Fig. 2) is inferred from its smaller size as well as the lack of a sagittal crest on the fused parietals and the disarticulation of the predentary from the lower jaw. The parietal in adult specimens of other psittacosaur species bears a low sagittal crest, and the predentary is joined

firmly, or is coossified with, the dentaries in other mature ceratopsians.

Skull

The skull of *Psittacosaurus xinjiangensis* is known primarily from the type skeleton, which preserves only the posterior dermal skull roof, occiput, left palpebral, parts of both mandibular rami, and a fragmentary prementary (Figs. 2, 3). Cranial fragments of other individuals consist almost entirely of jaw fragments and jugal horns (Fig. 8).

Maxilla—The maxilla of *P. xinjiangensis* is subtriangular in shape, as shown by an isolated right maxilla, the most complete example (IVPP V7704; Fig. 4A, B). The anterior and posterodorsal edges are finished and form a continuous sutural margin for adjacent dermal elements of the lateral face, indicating that the antorbital fenestra was closed; there is no smooth, non-sutural margin on the maxilla that could form the border of a patent antorbital fenestra. The antorbital fossa, however, is retained in *P. xinjiangensis* as a shallow depression confined to the dorsal portion of the maxilla (Fig. 4A), similar to that of *P. meileyingensis* (Serenio et al., 1988) and intermediate in form between the deep, clearly defined fossa of *P. mongoliensis* and the extremely weak fossa of *P. sinensis* and *P. youngi*.

The antorbital fossa of other archosaurs, in contrast, is shared by both the maxilla and lacrimal, and often the jugal as well. *P. xinjiangensis* and other psittacosaurids retain the fossa despite complete closure of the antorbital fenestra. Closure of the antorbital fenestra in other archosaurs, in contrast, is always accompanied by loss of the antorbital fossa.

As in other psittacosaur species, a rounded maxillary

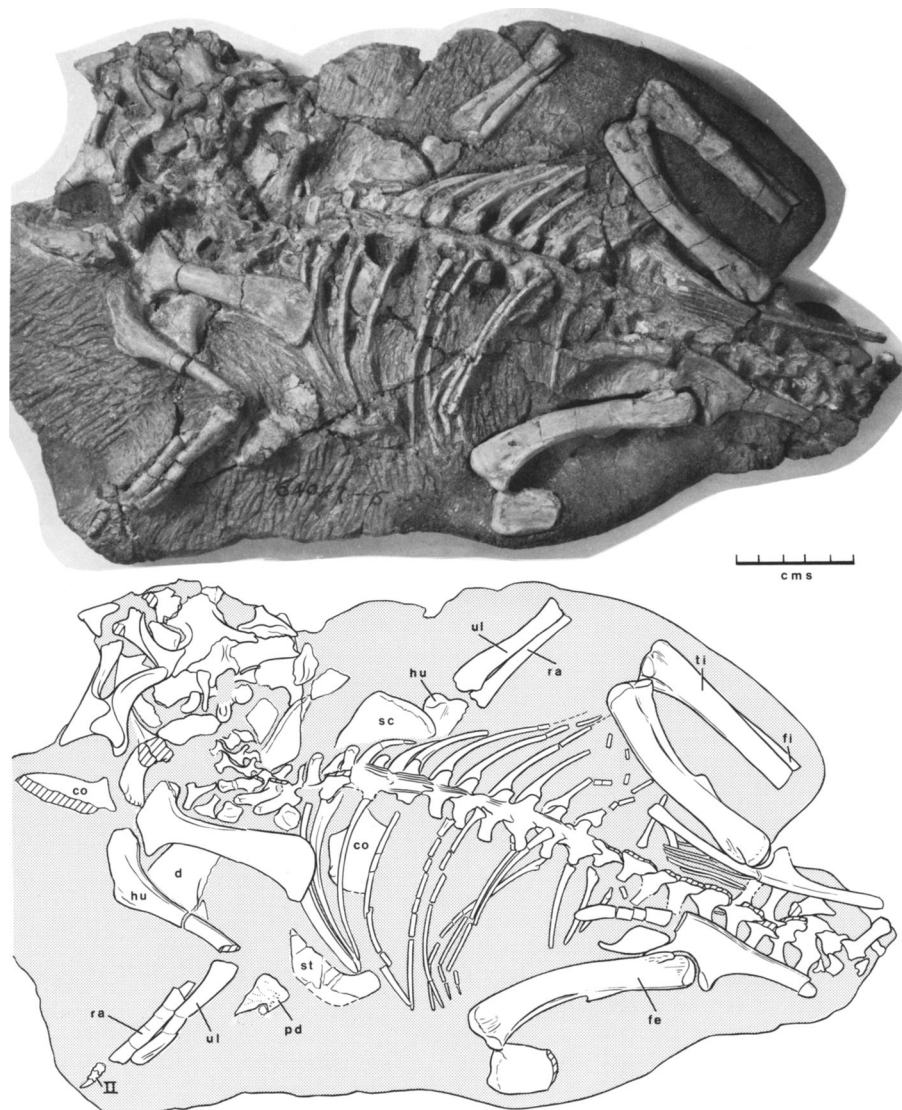


FIGURE 2. *Psittacosaurus xinjiangensis* (IVPP V7698). Dorsal view of the holotype skeleton. Abbreviations: II, manual second digit; co, coracoid; d, dentary; fe, femur; fi, fibula; hu, humerus; pd, predentary; ra, radius; sc, scapula; st, sternal; ti, tibia; ul, ulna.

process projects laterally from the rim of the cheek emargination on the posterior half of the maxilla (broken away in IVPP V7704; Fig. 8A). The process, the functional significance of which remains unknown, is a characteristic feature of the psittacosaur maxilla.

Parietal—The fused parietal is preserved only in the type skull and is damaged along the posterior margin (IVPP V7698; Fig. 3). The form and extent of the overhanging parietal shelf, therefore, cannot be determined. The parietal does form the majority of the posterior margin of the skull roof as in all other ceratopsians. The absence of a sagittal crest on the parietal of the type skull is probably a juvenile characteristic, as observed in the growth series of *P. mongoliensis*. The sagittal crest is present in adult skulls of *P. mongoliensis*, *P. sinensis*, *P. youngi*, and *P. meileyingensis*

(Sereno et al., 1988) and may well have been present in mature individuals of *P. xinjiangensis*.

Postorbital—The slender, triradiate postorbital is preserved only on the left side of the type skull (Fig. 3). In *P. sinensis* and *P. youngi* the lateral surface of the posterior ramus is strongly excavated. A raised edge along the dorsal margin of the excavation curves ventrally across the central body of the postorbital (*P. sinensis* Young, 1958: fig. 51). As in *P. mongoliensis* (Sereno et al., 1988: fig. 5), ornamentation of the postorbital is absent or very weak in *P. xinjiangensis*, although confirmation is needed from an adult skull of the latter.

Squamosal—Partially preserved on both sides of the type skull, the squamosal is quadriradiate, with anterior, posterior, ventral, and medial processes (Fig. 3).

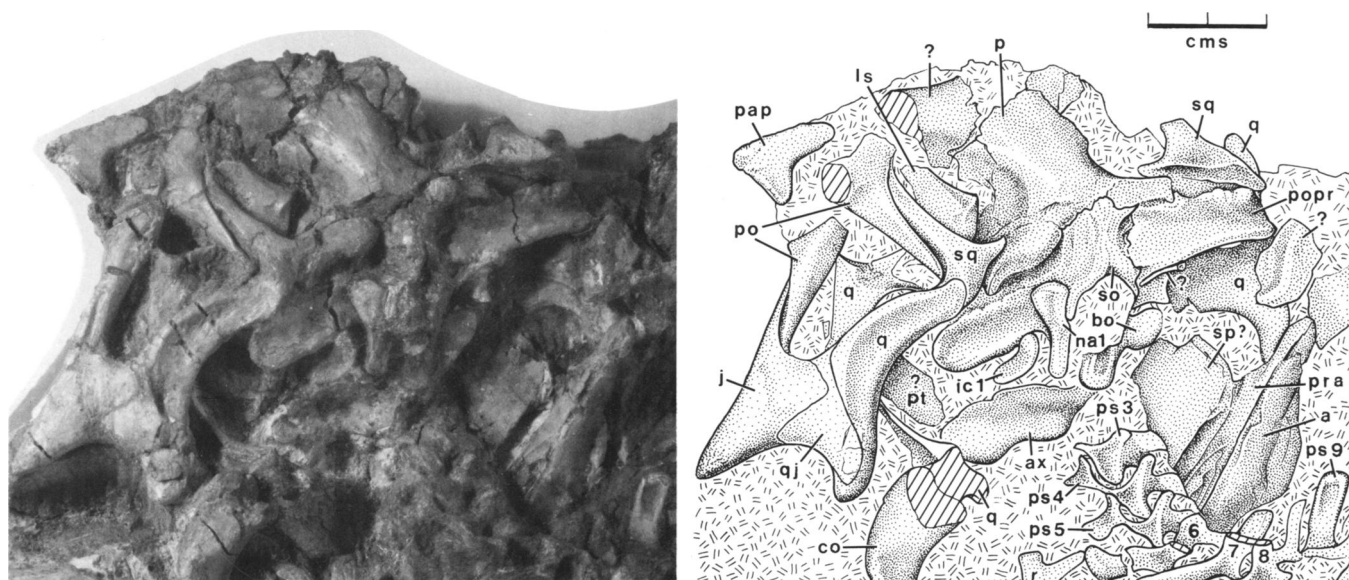


FIGURE 3. *Psittacosaurus xinjiangensis* (IVPP V7698). Dorsal view of the holotype skull. Abbreviations: a, angular; ax, axis; bo, basioccipital; co, coracoid; ic, intercentrum; j, jugal; ls, laterosphenoid; na, neural arch; p, parietal; pap, palpebral; po, postorbital; popr, paroccipital process; pra, prearticular; ps, presacral vertebra; pt, pterygoid; q, quadrate; qj, quadratojugal; r, rib; so, supraoccipital; sp, splenial; sq, squamosal.

A socket for the head of the quadrate faces ventrally at the juncture of the four processes. The tapering anterior process overlaps the postorbital medially to form a narrow posttemporal bar. As in other psittacosaurids, the medial process of the squamosal forms only a minor portion of the free posterior margin of the skull roof. The posterior process forms a thin, posterovertrally projecting plate that intervenes between the head of the quadrate and the distal end of the paroccipital process. Judging from the left squamosal of the type skull, the posterior squamosal process of *P. xinjiangensis* does not completely separate the quadrate head and paroccipital process, similar to the configuration in *P. sinensis* (IVPP V738). In *P. mongoliensis*, in contrast, the squamosal completely separates the quadrate head and paroccipital process (IVPP V7668; PI 3779/10).

Jugal—The jugal (Figs. 3, 4D, E) is preserved on the left side of the type skull and is well represented in the isolated, fragmentary cranial elements of larger individuals (IVPP f.n. 64047). The orbital ramus of the jugal shows characteristic ceratopsian proportions; it is greater in dorsoventral height than the jugal ramus under the laterotemporal fenestra.

The shape and size of the jugal horn varies among psittacosaur species and is the most important cranial element for their taxonomy. In all psittacosaurids a ridge passes ventrally from the postorbital bar to a prominent point on the ventral margin of the jugal, dividing the lateral surface of the jugal into two planes. All psittacosaurids exhibit some thickening of the midsection of the jugal. In *P. mongoliensis* (Sereno et al., 1988: fig. 5), the moderately developed horn is formed by

the lateral prominence and ventral extension of the ridge. In *P. sinensis*, *P. youngi*, and *P. xinjiangensis*, the prominent horn projects laterally, rather than ventrolaterally, and is distinct from the remainder of the jugal, particularly along the base on the posterior side of the horn.

Several characteristics of the jugal horn are peculiar to *P. xinjiangensis* (Fig. 4D, E). The anterior surface of the jugal horn, which is bounded by sharp dorsal and ventral edges, is exceptionally flat and covered by fine, radiating grooves. The dorsal and ventral horn surfaces, on the other hand, are characterized by a raised layer of porous bone with impressions of vascular channels. Shallow vascular channels also occur on the horn and adjacent surfaces of the jugal in other species of *Psittacosaurus*, suggesting a horny covering in life. Judging from surface texture on the jugal of *P. xinjiangensis*, the horny covering may have been better developed and restricted to a surface encompassing only the jugal horn.

Quadratojugal—The quadratojugal is preserved only on the left side of the type skull (Fig. 3). The quadratojugal overlaps the lateral surface of the quadrate shaft as a thin plate, bordering the laterotemporal fenestra ventrally. The lateral surface of the quadratojugal is preserved well enough to demonstrate the absence of a horn, the presence of which is diagnostic for *P. meileyingensis* (Sereno et al., 1988).

Quadrate—The quadrate is preserved, though fractured, on both sides of the type skull (Fig. 3). For purposes of description, the bone can be divided into two parts—the expansive, thin, anteromedially directed pterygoid ramus, and the narrow, anterolaterally

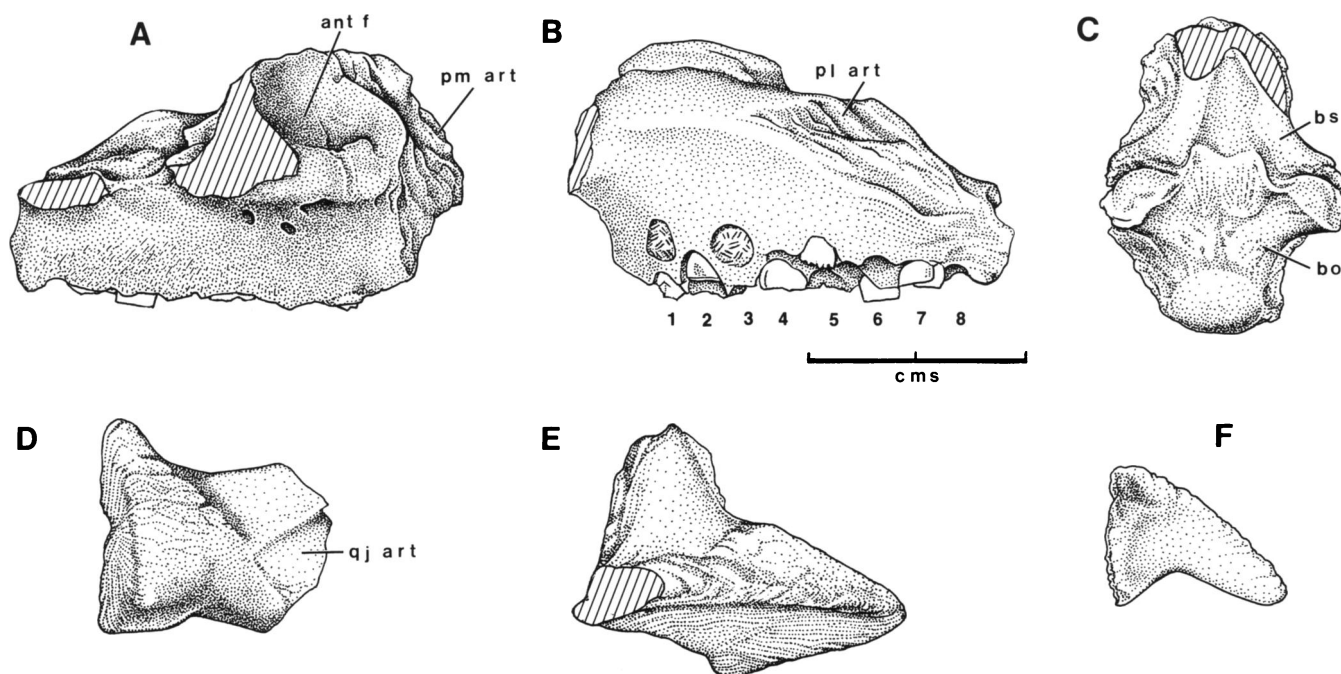


FIGURE 4. *Psittacosaurus xinjiangensis*. A, lateral and, B, medial views of the right maxilla with tooth positions numbered (IVPP V7704); C, basioccipital-basisphenoid fragment in ventral view (IVPP f.n. 64047); D, lateral and, E, anterodorsal views of the right jugal (IVPP f.n. 64047); F, left palpebral in ventral view (anterior toward top; IVPP V7698). Abbreviations: **ant f**, antorbital fossa; **bo**, basioccipital; **bs**, basisphenoid; **pl art**, articular surface for the palatine; **pm art**, articular surface for the premaxilla; **qj art**, articular surface for the quadratojugal.

directed shaft. The pterygoid ramus is very deep dorsoventrally. The cranioquadrate passage (the space between the pterygoquadrate wing and the sidewall of the braincase) is consequently reduced to a narrow slit (*P. mongoliensis* PI 3779/10; *P. sinensis* IVPP V738; *P. youngi* BNHM BPV.149). In *P. xinjiangensis* (IVPP V7698), the deep pterygoid ramus is partially exposed on the right side in posterior view.

The quadrate shaft arches from the posterolateral corner of the skull roof and the transversely expanded quadrate condyles at the jaw articulation below. The quadrate shaft of *P. xinjiangensis*, as preserved on the left side (IVPP V7698), is only moderately arched in lateral view, similar to that observed in *P. mongoliensis* (AMNH 6254, IVPP V7668) but in contrast to the more strongly arched condition in *P. sinensis* (IVPP V738), *P. youngi* (BNHM BPV.149), and *P. meileyingensis* (Sereno et al., 1988). Likewise, the posterior margin of the quadrate shaft is only lightly excavated as in *P. mongoliensis* (AMNH 6254, IVPP V7668, PI 3779/10, PI 3779/12) but in contrast to the deep excavation of the margin in *P. sinensis*, *P. youngi*, and *P. meileyingensis* (Sereno et al., 1988). The head of the quadrate in *P. xinjiangensis* contacts the squamosal dorsally and the paroccipital process posteriorly, which can be seen in situ on the left side of IVPP V7698.

Occiput—There is no trace of any exoccipital-opisthotic suture in the flattened occiput of the type skull (Fig. 3). This compound element joins the supraoccipital and basioccipital around the foramen magnum, all

three contributing approximately equally to the border of the foramen magnum (IVPP V7698, IVPP f.n. 64047).

An isolated basioccipital-basisphenoid-ventral exoccipital fragment (IVPP f.n. 64047; Fig. 4C) preserves the transversely broad, platelike basal tubera, which are separated by a median cleft. The tubera extend slightly below the level of the occipital condyle.

Palpebral—The disarticulated left palpebral of the type skull is exposed in ventral view (Fig. 4F). As in other primitive ceratopsians, the palpebral is short, relative to the diameter of the orbit, and flattened dorsoventrally. It articulates freely against the anterodorsal margin of the orbit. The palpebral of *P. xinjiangensis* is L-shaped, closely resembling the palpebral in *P. youngi* (BNHM BPV.149) and *P. meileyingensis* (Sereno et al., 1988). The ventral surface of the palpebral is gently concave immediately adjacent to the articular corner.

Lower Jaw—Little can be said about the lower jaw except to note the general proportions of the more completely exposed elements, the dentary and predentary. Relative to the length of the dentary, the tapering coronoid process is moderate in size (IVPP V7698, left dentary), and a ventral flange does not appear to have been developed along the ventral margin of the ramus. As in other psittacosaur species, the predentary is large relative to the length of the dentary (IVPP V7698, disarticulated; Fig. 2).

Dentition—Because the premaxilla is not known in

P. xinjiangensis, the presence or absence of premaxillary teeth cannot be determined. An isolated right maxilla from a subadult individual preserves a complete alveolar margin with broken roots or sockets for eight teeth (IVPP V7704; Fig. 4A, B). By comparison to the growth series of *P. mongoliensis*, a fully mature maxillary tooth row of *P. xinjiangensis* would probably not exceed eight to 10 teeth. The number of teeth in the dentary tooth row is unknown but would probably be very close to the count for the maxillary tooth row.

Both maxillary and dentary tooth rows are inset from the lateral surface of the snout and lower jaw, respectively, along their entire lengths. The buccal recess lateral to the tooth rows (Galton, 1973) occurs in all ornithischians except *Lesothosaurus*. In apical view, the tooth rows are nearly straight as in *P. mongoliensis* (AMNH 6254, 6534). The tooth rows in *P. sinensis* and *P. youngi*, on the other hand, are laterally concave. As characterizes all primitive ornithischian dentitions, the crowns of both upper and lower tooth rows are set in an imbricate arrangement along the tooth row, such that the anterior edge of each crown is offset to the medial side of the posterior edge of the next anterior crown (IVPP V7702).

The anteriormost and posteriormost one or two maxillary teeth are smaller than teeth in the center of the row (IVPP V7702, V7704). An increase in tooth size, therefore, occurs toward the center of the tooth row rather than toward either end, a shared derived character for the Ornithischia (Sereno, 1986).

Unequal thickness of enamel on opposing crown surfaces has been reported in primitive ornithopods (Crompton and Charig, 1962) and many other ornithischians (Sereno, 1986:245). *P. xinjiangensis* also has an asymmetrical distribution of enamel in both maxillary and dentary crowns; the enamel on the lateral side of the maxillary crown and the medial side of the dentary crown is two to three times thicker than on the opposite crown surface. Enamel thickness can be observed along the perimeter of wear facets or fracture surfaces that transect the crown (IVPP V7702, V7704, maxillary crowns; IVPP V7704, dentary crown).

Tooth-to-tooth wear in *P. xinjiangensis* and other psittacosaur produces broad wear facets (Fig. 5B). The thickly enamelled crown surface forms the leading edge of each facet (IVPP V7702). Wear facets are developed individually and the occlusal surface along the tooth row is discontinuous. The wear facets, however, lie in nearly the same plane of orientation at an angle of about 60 degrees to the vertical axis of the crown. On close inspection, wear surfaces on some maxillary crowns are actually a composite of two intersecting wear facets, which were produced by adjacent, opposing dentary crowns (e.g., IVPP V7702, left maxilla). Thus, a single crown often occludes against more than one opposing crown, but not in any precise pattern. Consistent alternate occlusion does not appear to have been developed.

As in ornithischians primitively, a vertical tooth column consists of two teeth at most, one functional tooth

above one replacement tooth. A single replacement foramen is located under each alveolus at an even distance from the alveolar margin. The alveolar border above the replacement foramen is very thin and is resorbed during eruption of the replacement tooth (IVPP V7702, V7704). The pattern of replacement in *P. xinjiangensis* is not well established. There is only one tooth row with a complete set of tooth positions (IVPP V7704, Fig. 4B). The crowns of the functional teeth are broken. Posterior waves of replacement are manifest, but the pattern is not consistent at the anterior end. The replacement teeth, at equivalent stages of eruption, are in positions 2, 4, and 7 in a row of eight maxillary teeth. The replacement teeth in positions 5 and 8 are at an earlier stage of eruption, and the replacement tooth in position 6 has only initiated eruption, with an intact alveolar border. Thus, posteriorly replacing Zahnreihen include crowns 4, 5, and 6, and more posteriorly, crowns 7 and 8. For the anterior three teeth to conform to this pattern, the tooth in position 1 should be moving into a functional position on the edge of the alveolus, with no visible replacement crown. The first tooth, however, fully occupies the first alveolus with a small replacement crown visible below. Other jaw fragments are too incomplete to establish a consistent pattern.

Complete **maxillary crowns** in *P. xinjiangensis* can be distinguished from those in other psittacosaur. The maxillary crowns in *P. xinjiangensis* (Fig. 5B; IVPP V7703, erupting left maxillary crown) are proportionally broader than those of other psittacosaur (Sereno et al., 1988: fig. 5A, B). In lateral or medial view, an unworn maxillary crown in *P. xinjiangensis* is subcircular, whereas the maxillary crowns in other psittacosaur are oval, with the long axis vertical (Fig. 7A, B). Tooth wear quickly obscures original crown proportions by truncating the apical portion of the crown (Fig. 5A). Although maxillary crowns in *P. sinensis* (IVPP V738) have been shown with nearly square proportions in the center of the tooth row (Young, 1958: fig. 51), the straight apical margin strongly suggests truncation by wear. The shape of an unworn maxillary crown in *P. sinensis* remains unknown.

The presence of 14 denticles along the apical margin of an unworn maxillary crown of *P. xinjiangensis* is more than in maxillary crowns of any other psittacosaur. *P. mongoliensis* (Sereno et al., 1988; PI 3779/20, 3779/24, 3779/28) and *P. sinensis* (IVPP V738) have between eight and 11 denticles on maxillary crowns from the center of the tooth row (denticle number in *P. sinensis* is estimated from the number of ridges near the tip of the crown). Unfortunately, denticle number varies among the outgroups to *Psittacosaurus*, and, therefore, it is not clear what number of denticles represents the primitive condition. In *P. xinjiangensis* the posterior four denticles curve onto the medial side near the base of the crown (Fig. 5B; IVPP V7703, V7704), an unusual feature that is diagnostic for the species.

The lateral surface of the maxillary crown is convex anteroposteriorly but relatively flat dorsoventrally (Fig.

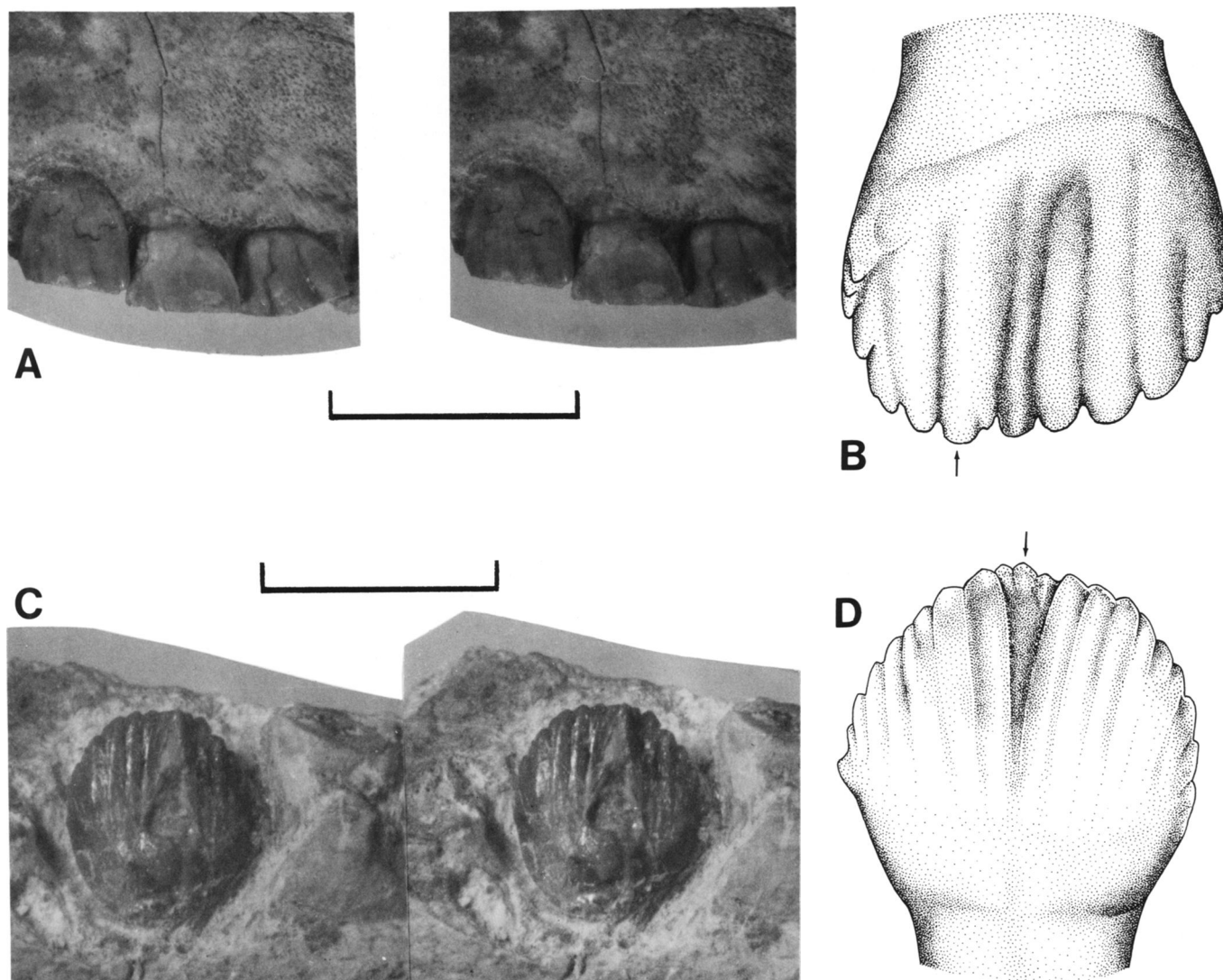


FIGURE 5. *Psittacosaurus xinjiangensis*. A, left maxillary teeth (IVPP V7702) in lateral view (stereopair); B, left maxillary tooth in medial view, based on IVPP V7703; C, left dentary tooth (IVPP V7704) in medial view (stereopair); D, reconstruction of a left dentary tooth in lateral view, based on IVPP V7704. Arrows indicate the apex of the primary ridge. Scale = 5 mm.

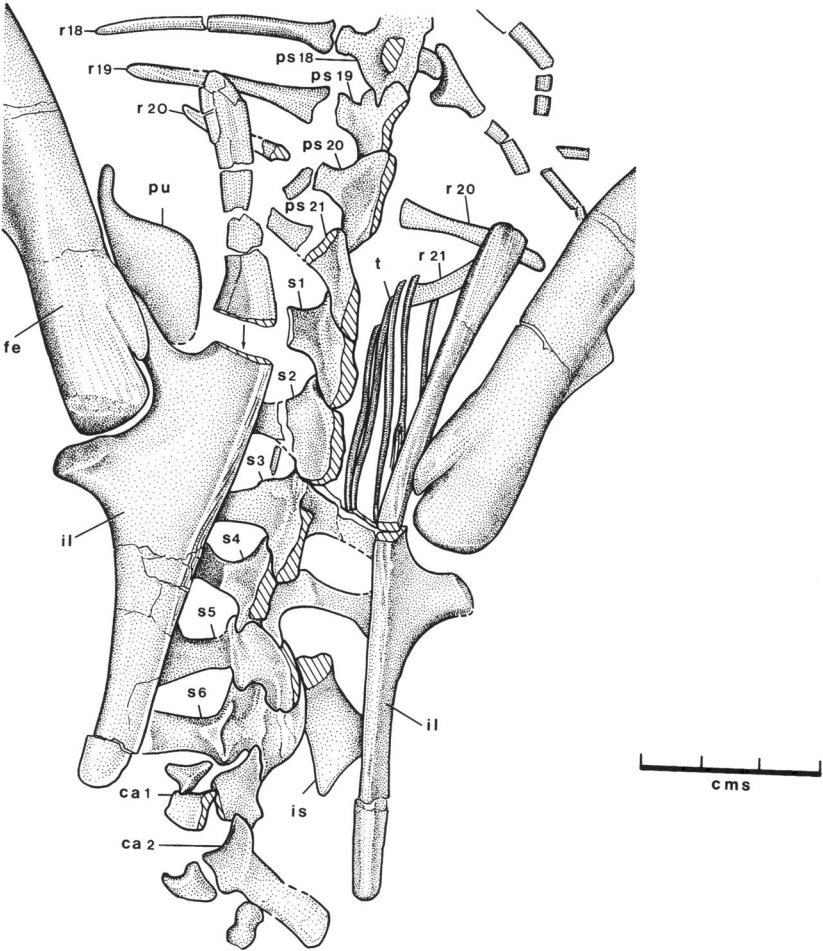
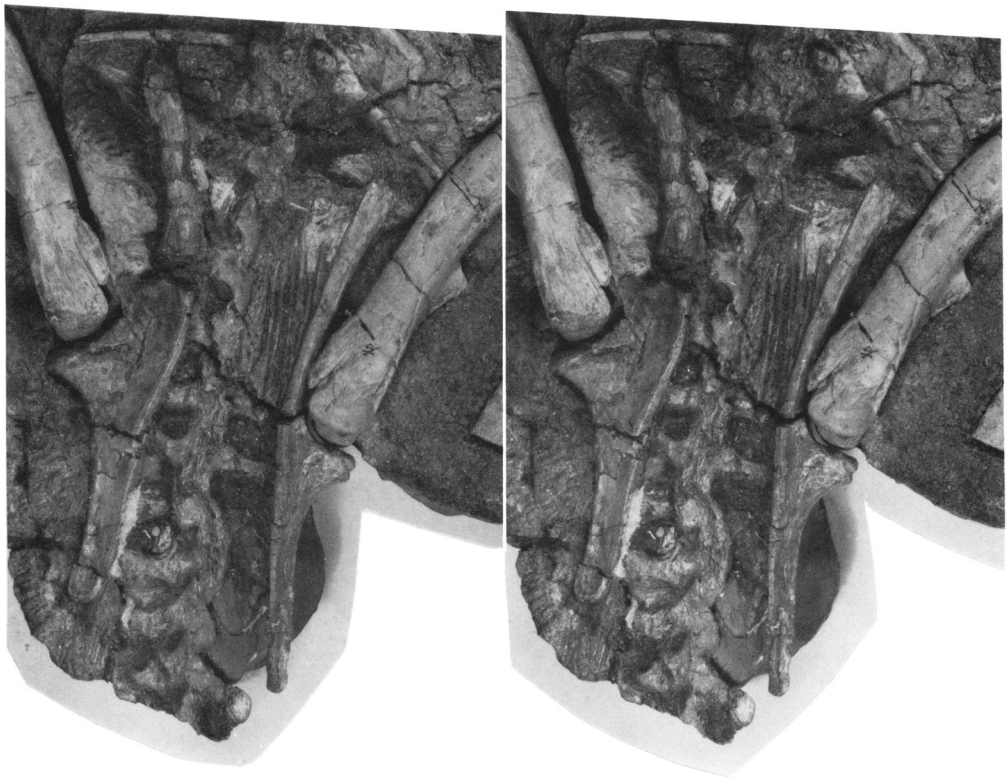
5A). The lateral crown surface is divided weakly into three lobes: a broad anterior lobe, a posteriorly angling central lobe, and a narrow posterior lobe. The anterior lobe is nearly flat, the central lobe weakly convex anteroposteriorly, and the posterior lobe markedly convex anteroposteriorly.

The posteriorly angling central lobe in *P. xinjiangensis* is very similar to that in *P. mongoliensis* and *P. meileyingensis*. In complete crowns of the latter two species, the central lobe tapers to the apex as a weak primary ridge in unworn crowns. This is very probably the condition in *P. xinjiangensis*, in which the tips of all available maxillary crowns exposed in lateral view are truncated by wear. It is also probable, therefore, that the apex of maxillary crowns in *P. xinjiangensis* is posteriorly offset as in the other species. The beginnings of secondary ridges are present on several max-

illary crowns in *P. xinjiangensis* just below the wear surface. As in other psittacosaur, the secondary ridges dissipate at midcrown and are absent in the basal portion of the crown.

The medial surface of the maxillary crown is anteroposteriorly and dorsoventrally convex (IVPP V7703; Fig. 5B). Rounded secondary ridges extend ventrally from the denticles over most of the crown surface, with the central ridge the widest anteroposteriorly. Similar low secondary ridges are present on the medial surface of the crowns in *P. mongoliensis* (PI 3779/24-1, 3779/28; Sereno et al., 1988: fig. 7B) and in *P. meileyingensis*. The medial surface is not exposed for comparison in *P. sinensis*.

The **dentary teeth** in *P. xinjiangensis* are known from a single erupting crown (IVPP V7704; fig. 5C, D). The crown is comparable in size to maxillary and dentary



crowns in adult individuals of other psittacosaur species. In medial view the crown is circular with 21 denticles, significantly more than dentary teeth of equal size in any other psittacosaur. The denticles are symmetrically distributed, 10 to each side of the apical denticle. Secondary ridges extend only a short distance from the denticles, and as in *P. mongoliensis* the anterior and posterior margins of the crown are not prominent (AMNH 6253; Osborn, 1923: fig. 5, 1924: fig. 3B, misidentified as a maxillary crown). A well defined, ventrally tapering median depression, descending from the top three denticles, characterizes the lateral crown surface, which is only partially exposed in IVPP V7704 (Fig. 5D). As on the medial side, secondary ridges descend only a short distance from the denticles but are weaker and more rounded.

Postcranium

The postcranium of *P. xinjiangensis* is known from the type skeleton (IVPP V7698; Figs. 2, 6) as well as disarticulated, fragmentary bones pertaining to many individuals and a range of body sizes (IVPP V7701, f.n. 64047; Figs. 7, 8). The axial column of the type skeleton is present from the atlas to the anterior caudals and includes several fragmentary cervical ribs, most of the dorsal ribs, and a fragmentary left sternal. A proatlas is not preserved. The appendicular skeleton is incomplete distally, lacking both carpi and most of each manus, the tarsi, and both pedes.

Vertebral Number—The vertebral column of IVPP V7698 preserves 29 consecutive vertebrae, the anterior 21 of which constitute the presacral division (Figs. 2, 6). Although the cervical region of the column is flexed and fractured, a reliable count of the vertebrae can be derived from transverse processes and neural spines. At the posterior end of the presacral division, the rib of the 20th presacral extends laterally beyond the preacetabular process on both sides and clearly does not articulate at its tip with the ilium (Fig. 6). The 21st presacral rib, which is slightly shorter than the 20th, is overlapped entirely at its distal end by the preacetabular process. Due to the compression of the pelvis and ribcage, the exact relationship between the 21st rib and the ilium cannot be determined. The position of this rib and its relative length compare closely to the 21st, or last, presacral rib in *P. mongoliensis* (AMNH 6253, 6254, GI SPS 100/606) and *P. sinensis* (IVPP V738). Poor exposure of the neural arch and centrum prevents subdivision of the presacral column into cervicals and dorsals.

The transverse process of the first sacral, exposed on the left side, is directed at the base of the preacetabular process of the ilium (Fig. 6). The posterior sacral ar-

ticulations with the ilium are exposed on the left side. Given the correct identification of the first sacral, there are six sacrals in the type skeleton, which is similar to that recorded in *P. mongoliensis* (AMNH 6253, GI SPS 100/606), *P. sinensis* (IVPP V739, V740-1), and *P. youngi* (BNHM BPV.149).

Vertebral Morphology—The crescentic atlas intercentrum and L-shaped left atlas neural arch have been displaced behind the left paroccipital process of the crushed skull (IVPP V7698; Fig. 3). The anterior surface of the intercentrum is cup-shaped to accommodate the occipital condyle. The rounded pedicels on each side of the intercentrum articulate with the separate, paired neural arches (IVPP f.n. 64047). The atlas neural arch has an elongate epiphysis, at the base of which is located the postzygapophysis. The morphology of the atlas is very similar in *P. mongoliensis* (AMNH 6254, PI 3779/11, 3779/26) and *P. sinensis* (IVPP V738, V749; Young, 1958: figs. 52, 56).

The axis of *P. xinjiangensis*, preserved only in the type skeleton, has rotated to the left and lies perpendicular to the remainder of the column (Fig. 3). It has been strongly flattened, preserving little detail except the outlines of a well developed neural spine. The neural spines of the fourth to the sixth cervicals are higher and more pointed than in *P. sinensis* (IVPP V738, V749) but have similar proportions to those in *P. mongoliensis* (AMNH 6254, PI 2860/1).

The dorsal vertebrae are poorly preserved in the type skeleton and are described from isolated dorsals of referred adult individuals (IVPP f.n. 64047). In ventral view the centra of the anterior dorsals are transversely constricted with rounded ventral keels. The anterior face of the centrum is subtriangular with the apex pointing ventrally. The contour of the posterior face is more rounded. In mid-dorsal vertebrae, a pocket is developed on the posterior side of the base of the transverse process. The depression is walled medially by a thin posteriorly projecting lamina, which forms the posterior margin of the neural arch. A similar pocket is present on dorsal vertebrae in *P. mongoliensis* (PI 3779/11) and *P. sinensis* (IVPP V740-1). The parapophysis and diapophysis coalesce in the posterior dorsals and, therefore, would articulate with single-headed ribs (IVPP f.n. 64047). The posteriormost three dorsals appear to have single-headed ribs in the type skeleton (IVPP V7698).

Isolated anterior caudal vertebrae have transversely constricted centra and ventral keels (IVPP f.n. 64047). Posterior caudals (Fig. 8F) have spool-shaped centra similar to those of *P. mongoliensis* (AMNH 6253, 6254).

Ribs and Sternales—The ribs of the type skeleton are poorly preserved, particularly in the cervical region.

←

FIGURE 6. *Psittacosaurus xinjiangensis* (IVPP V7698). Stereopair and illustration of the sacrum and pelvic girdle of the holotype skeleton. Abbreviations: ca, caudal vertebra; fe, femur; il, ilium; is, ischium; ps, presacral vertebra; pu, pubis; r, rib; s, sacral vertebra; t, tibia.

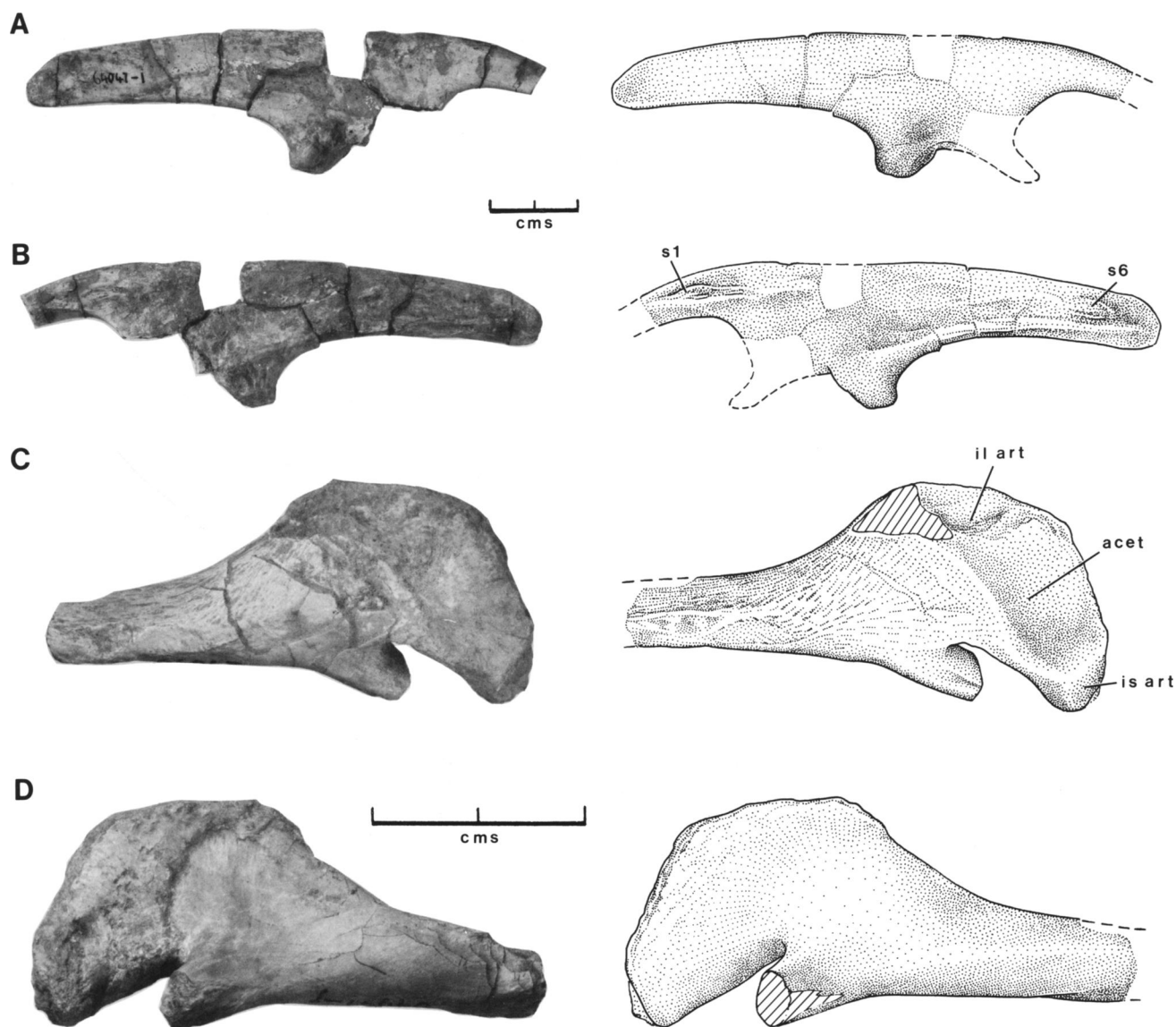


FIGURE 7. *Psittacosaurus xinjiangensis* (IVPP V7701). A, lateral and, B, medial views of the right ilium; C, lateral and, D, medial views of the left pubis. Abbreviations: **acet**, acetabulum; **il art**, articular surface for the ilium; **is art**, articular surface for the ischium; **s**, articular area for sacral vertebra.

The posterior dorsal ribs are short and appear to be single-headed. A fragmentary left sternal is exposed in ventral view in the type skeleton. As in *P. mongoliensis* (PI 3779/28) and *P. sinensis* (IVPP V749; Young, 1958, labeled exoccipital), the sternal is a crescentic plate with a thickened lateral margin but very thin medially (Fig. 2). In *P. xinjiangensis* the portion of the sternal that articulates with the rib cage is narrow and more elongate than in *P. mongoliensis* and *P. sinensis*.

Ossified Tendons—Ossified tendons are present between the transverse processes and neural spines of the ninth presacral to the first caudal in IVPP V7698. Importantly, ossified tendons are also present on an articulated series of three small caudal vertebrae (IVPP f.n. 64047; Fig. 8F). The low neural spine of these

caudals compares closely with the reduced neural spines of mid-caudal vertebrae (CA24–CA25) in *P. mongoliensis*. In well preserved skeletons of *P. mongoliensis* (AMNH 6253, 6254, PI 3779/11) and *P. sinensis* (IVPP V738), ossified tendons do not extend beyond the anteriormost caudal vertebrae. In *P. xinjiangensis*, in contrast, ossified tendons appear to have extended distally along at least half the length of the tail. The single-stranded ossified tendons in *P. xinjiangensis* are preserved in an epaxial position on each side of the neural arch.

Pectoral Girdle—The tab-shaped acromion and distal expansion of the scapular blade (Fig. 2) are similar to those in *P. mongoliensis* and the new species from Chaoyoung, in contrast to the narrow, elongate blade

in *P. sinensis* (IVPP V740-1, V749; Young, 1958: fig. 53).

The coracoid forms approximately half of the glenoid. The lateral surface of the coracoid is divided by a crest into anterior and posterior portions. The posterior portion faces laterally, whereas the anterior portion faces ventrolaterally and curves ventromedially toward the sternum. The angle between the two portions of the coracoid is noticeably sharper in *P. sinensis* (IVPP V740-1; Young, 1958: fig. 53) than in other psittacosaur species (*P. xinjiangensis* IVPP f.n. 64047; *P. mongoliensis* AMNH 6534; Sereno et al., 1988).

Forelimb—The preserved portions of the forelimb are very similar in all species of psittacosaur. The broadly expanded deltopectoral crest gives the proximal end of the humerus a rectangular shape. Distally, the medial condyle is larger and extends farther distally than the lateral condyle. The ulna is very similar to that of *P. mongoliensis*, with a short, rounded olecranon process and gentle sinuous curve in the shaft in lateral view (IVPP V7698; Fig. 2). The distal end is slightly expanded and rotated relative to the long axis of the proximal end. The critical parts of the radius are not preserved well enough in *P. xinjiangensis* for comparison.

A radiale is preserved in articulation with a distal radial fragment (IVPP f.n. 64047). Disc-shaped with two rounded protuberances on the ventral edge, the radiale is identical to that in *P. mongoliensis* (AMNH 6257).

The manus in *P. xinjiangensis* is known from only three articulated phalanges, probably the distal three phalanges of digit II, which are preserved in place at the distal end of the left forelimb of the type skeleton (Fig. 2). The ungual is sharper than in *P. mongoliensis* (AMNH 6253, 6254, 6257) and *P. sinensis* (IVPP V740-1; Young, 1958: fig. 56), although this may be related to the smaller size of IVPP V7698.

Pelvic Girdle—The postacetabular process, preserved on both sides of the type skeleton and in an adult specimen (IVPP V7701), is particularly long relative to its height, a distinguishing characteristic of the species (Figs. 6, 7). The ischia are very poorly known. The pubis, preserved on the left side of the type skeleton and in the disarticulated material (Figs. 6, 7), is indistinguishable from that of *P. mongoliensis* (AMNH 6253, PI 2860/3, 3779/23; Osborn, 1924: fig. 8). As in ornithischians primitively, the pubis in psittacosaur has a very small articular surface for the ischium, a surface of moderate size for the ilium, and a broad surface for the acetabulum. The prepubic process is twisted gently along its length; the plane of flattening rotates from a vertical orientation at the base to a ventrolateral-dorsomedial orientation at the distal extremity. The postpubic process joins the body of the pubis on the ventromedial side.

Hind Limb—The hind limb of *P. xinjiangensis* does not differ significantly from other psittacosaur species. The bowed shaft of the femur exhibits a pendant fourth trochanter on its proximal half, a finger-like lesser tro-

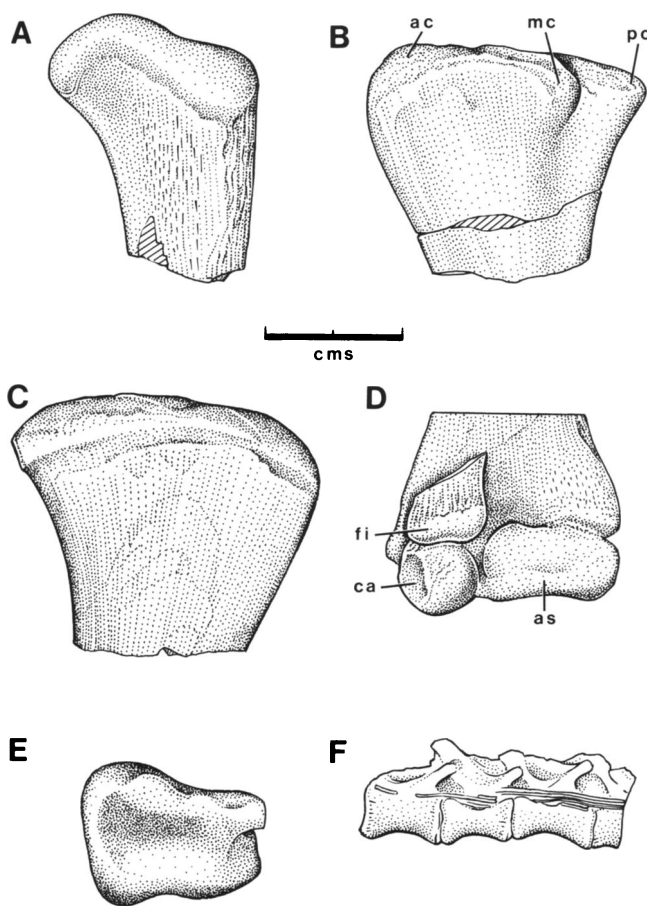


FIGURE 8. *Psittacosaurus xinjiangensis* (IVPP f.n. 64047). A, proximal right femur in posterior view; B, proximal left tibia in lateral view; C, proximal left tibia in medial view; D, right distal crus and proximal tarsus in anterior view; E, right astragalus in dorsal view (anterior toward top); F, three midcaudal vertebrae with ossified tendons in right lateral view. Abbreviations: ac, anterior condyle; as, astragalus; asc pr, ascending process of the astragalus; ca, calcaneum; fi, fibula; mc, medial condyle; pc, posterior condyle.

chanter that extends to the dorsal edge of the greater trochanter, and shallow anterior and deep posterior intercondylar grooves. The greater trochanter in the femora of the type skeleton is not as broadly expanded as in larger individuals, and the lesser trochanter does not attain the height of the greater trochanter (Figs. 2, 6, 8A). These differing proportions may be attributable to the subadult status of the type skeleton. Antero-posterior expansion of the greater trochanter also occurs during growth in *P. mongoliensis* (Coombs, 1982: fig. 5).

The proximal and distal ends of the tibia are well represented (Fig. 8B, C, D). Comparison of subadult (IVPP V7698) to adult elements (IVPP f.n. 64047) indicates a change in proportion of the ends of the tibia with age. The proximal end of the tibia is subdivided into three condyles: anterior, posterior, and medial. The medial condyle is proportionally smaller and the

TABLE 1. Distribution of diagnostic characters for new psittacosaur species among psittacosaur and representative outgroup taxa. + = present; - = absent; () = probable character state; ? = unknown.

	<i>P. xinjiang-</i> <i>ensis</i>	<i>P. meiley-</i> <i>ingensis</i>	<i>P. mon-</i> <i>goliensis</i>	<i>P. sinensis</i>	<i>Proto-</i> <i>ceratops</i>	<i>Homalo-</i> <i>cephale</i>
<i>P. xinjiangensis</i>						
Jugal horn with flattened anterior face	+	-	-	-	-	-
Maxillary teeth with medially curving posterior dentical margin	+	-	-	-	-	-
Iliac postacetabular process narrow	+	-	-	-	-	-
Ossified tendons extending along proximal half of tail	+	(-)	-	-	-	-
<i>P. meileyingensis</i>						
Skull tall (relative to skull length)	?	+	-	-	-	(-)
Postorbital region of skull broad (relative to skull length)	(-)	+	-	-	-	(-)
Orbit subtriangular	?	+	-	-	-	-
Quadrate shaft strongly emarginated	-	+	-	-	-	-
Quadrate shaft strongly angled anterolaterally	?	+	-	-	-	-
Quadrate condylar surface oriented anteromedially	?	+	-	-	-	-
Quadratojugal boss	-	+	-	-	-	-
Prominent dentary flange	-	+	-	-	-	?

posterior condyle proportionally larger in an adult as compared to a subadult.

There are no differences in the fibula and proximal tarsals among the various species of psittacosaur. The fibula is broader proximally than distally (IVPP f.n. 64047; Fig. 8D). The distal shaft can be identified by its airfoil cross section; the thicker rounded medial margin tapers laterally to a sharp edge. The ventromedial corner has a rugose facet that butts against, or is adjacent to, the weakly developed ascending process of the astragalus.

The saddle-shaped astragalus is trapezoidal in proximal and distal views (Fig. 8E). The raised anterolateral corner of the astragalus forms a poorly developed ascending process that contacts the fibula, as preserved in two adult individuals (IVPP f.n. 64047; Fig. 8D). Approximately one-fourth the size of the astragalus, the calcaneum has four distinct surfaces, one nonarticular and three articular (Fig. 8D). The nonarticular lateral surface and the facet for the distal end of the fibula are concave. The convex distal surface is the greatest in area and articulates against the lateral distal tarsal, forming part of the mesotarsal ankle joint. In older individuals, partial fusion occurs between the astragalus, calcaneum, tibia, and fibula. In the collection of disarticulated elements, for example, five out of six astragali are preserved tightly bound to distal tibial fragments (IVPP f.n. 64047; Fig. 8D). Similarly, the calcaneum is most often found in articulation with the distal ends of the tibia and fibula.

DISCUSSION AND CONCLUSIONS

Most of the derived characters that unite psittacosaur as a monophyletic taxon are located in the skull. Although a complete skull is not yet available for the new species from Xinjiang, it clearly shows affinity with other species of psittacosaur. The preserved portions of the skull of *P. xinjiangensis* indicate that the antorbital fenestra was closed. The maxilla bears a

characteristic eminence on the dorsal rim of the buccal recess, and the primary ridge on the medial side of the dentary crowns is bulbous. These derived characters, as well as others, diagnose the genus *Psittacosaurus* and are absent in primitive members of the nearest outgroups, Neoceratopsia and Pachycephalosauria (Serenno, 1986, 1987). *Protoceratops* and *Homalocephale* are primitive members of the Neoceratopsia and Pachycephalosauria, respectively, and do not show any of the characteristics that diagnose *Psittacosaurus* or any of the included species (Table 1).

Psittacosaur constitute a small and early radiation of the Ceratopsia and do not diverge widely in morphology. Psittacosaur species can be distinguished largely by the shape of the jugal horn and the ornamentation in the dentition. The distribution of the diagnostic characters that distinguish the two new species from China, *P. xinjiangensis* and *P. meileyingensis* (Serenno et al., 1988), is shown in Table 1. Characters that diagnose *P. xinjiangensis* include the flat anterior face of the jugal horn, the peculiar curvature to the denticulate margin in the maxillary crowns, the proportionately narrow postacetabular process of the ilium and, possibly, the extension of ossified tendons along the anterior portion of the tail. These characters do not occur in other psittacosaur species nor in the nearest outgroups to *Psittacosaurus*. The sharply defined anterior face of the jugal horn, for example, does not occur elsewhere in the Ceratopsia. The broad surface of the horn in primitive Neoceratopsia, such as *Protoceratops*, faces anterolaterally, rather than anteriorly, and is not formed entirely by the jugal; the neoceratopsian horn is formed in large part by the epijugal, an accessory dermal element that does not occur among psittacosaur. The narrow iliac postacetabular process in *P. xinjiangensis*, which is over four times as long as high (at midlength), is proportionately longer than in any other ceratopsian or pachycephalosaur.

The available evidence relevant to psittacosaur in-

terrelationships is meager compared to the characters that diagnose the genus *Psittacosaurus* and several of its species. *P. xinjiangensis* does not share any derived characters with *P. mongoliensis* or *P. meileyingensis* but shares one conspicuous character with *P. sinensis* and its close relative *P. youngi*—the lateral orientation of the jugal horn. The lateral surface of the jugal in all ceratopsians is divided into two surfaces by a crest that runs ventrally from the postorbital bar, forming a horn of variable proportions. In *P. mongoliensis* and *P. meileyingensis* the horn is relatively small compared to the remainder of the skull and projects ventrolaterally at its tip. In *Protoceratops andrewsi* the jugal–epijugal horn projects posterolaterally. In *P. xinjiangensis*, *P. sinensis*, and *P. youngi*, in contrast, the jugal horn is developed as a distinct pyramidal mass that projects laterally at a right angle to the longitudinal axis of the skull. Based on this single character, we suggest tentatively that *P. xinjiangensis* may be more closely related to *P. sinensis* and *P. youngi* than to either *P. mongoliensis* or *P. meileyingensis*.

P. xinjiangensis was collected in strata of the Tugulu Group, which may be of Early Cretaceous age. Currently, meaningful biostratigraphic correlation with other psittacosaur species is not feasible.

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LITERATURE CITED

Chao S. 1962. New species of *Psittacosaurus* from Laiyang, Shantung Vertebrata Palasiatica 6:349–360. [in Chinese]

- Cheng Z. 1983. Reptilia; (Chapter 7) pp. 123–136 in Paleontology and Stratigraphy of the Mesozoic Coal-bearing Basin at Guyang, Nei Mongol Autonomous Region, China. Geology Press, Beijing.
- Coombs, W. P., Jr. 1982. Juvenile specimens of the ornithischian dinosaur *Psittacosaurus*. Paleontology 25:89–107.
- Crompton, A. W., and A. J. Charig. 1962. A new ornithischian from the Upper Triassic of South Africa. Nature 196:1074–1077.
- Dong Z. 1973a. Cretaceous stratigraphy of Wuerho district, Dsungar Basin. Reports of Paleontological Expedition to Sinkiang (II). Pterosaurian Fauna from Wuerho, Sinkiang. Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology 11:1–7.
- . 1973b. A vertebrate fauna from the Tugulo Series of Delunshan, Dsungar Basin. Cretaceous stratigraphy of Wuerho district, Dsungar Basin. Reports of Paleontological Expedition to Sinkiang (II). Pterosaurian Fauna from Wuerho, Sinkiang. Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology 11:53.
- Galton, P. M. 1973. The cheeks of ornithischian dinosaurs. Lethaia 6:67–89.
- Marsh, O. C. 1890. Additional characters of the Ceratopsidae, with notice of new Cretaceous dinosaurs. American Journal of Science, series 3, 39:418–426.
- Osborn, H. F. 1923. Two Lower Cretaceous dinosaurs from Mongolia. American Museum Novitates 95:1–10.
- . 1924. *Psittacosaurus* and *Protiguanodon*: two Lower Cretaceous iguanodonts from Mongolia. American Museum Novitates 127:1–16.
- Rozhdestvensky, A. K. 1955. New data on psittacosurs, Cretaceous ornithopods. Vorposy Geologii Azii 2:783–788. [in Russian]
- Sereno, P. C. 1986. Phylogeny of the bird-hipped dinosaurs (order Ornithischia). National Geographic Research 2: 234–256.
- . 1987. The ornithischian dinosaur *Psittacosaurus* from the Lower Cretaceous of Asia and the relationships of the Ceratopsia. Ph.D. dissertation, Columbia University, New York, 554 pp.
- , S. Chao, Z. Cheng, and C. Rao. 1988. *Psittacosaurus meileyingensis* (Ornithischia: Ceratopsia), a new psittacosaur from the Lower Cretaceous of northeastern China. Journal of Vertebrate Paleontology 8:366–377.
- Young, C. 1931. On some new dinosaurs from western Suiyan, Inner Mongolia. Bulletin, Geological Survey of China 11:159–226.
- . 1958. The dinosaurian remains of Laiyang, Shantung. Palaeontologia Sinica, New Series C, 16:1–138.

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