New psittacosaur occurrences in Inner Mongolia

Dale A. Russell and X.-J. Zhao

Abstract: Psittacosaur materials were collected from seven localities in the course of Dinosaur Project fieldwork in Inner Mongolia. Two new species of *Psittacosaurus* are recognized, bringing the number of well-defined species to six. One, based on a nearly complete skeleton, resembles *Psittacosaurus mongoliensis*, but is a smaller animal with a relatively larger head and longer tail. The other species possesses jugal horns, but exhibits a different combination of characters than *Psittacosaurus sinensis* and *Psittacosaurus xinjiangensis*. A larger matrix of taxa and characters than is presently available will be necessary to resolve adequately phylogenetic relationships within the genus. Psittacosaurs were small dinosaurs, the skeletons of which are preserved in unusual completeness in proximity to aeolian environments of deposition. Their small brain size relative to that of modern mammals of similar body size implies a relatively restricted behavioral repertoire.

Résumé : Lors des travaux sur le terrain du Projet dinosaurien, dans la région intérieure de la Mongolie, il y a eu sept localités qui ont livré des éléments de psittacosaure. Deux nouvelles espèces de *Psittacosaurus* ont été identifiées, ce qui porte à six le nombre d'espèces bien définies. Une nouvelle espèce, fondée sur un squelette presque complet, ressemble à *Psittacosaurus mongoliensis*, cependant c'est un animal plus petit avec relativement une tête plus grosse et une queue plus longue. L'autre nouvelle espèce est munie des cornes jugales, mais elle possède une combinaison de caractères différente de celles de *Psittacosaurus sinensis* et *Psittacosaurus xinjiangensis*. Il devient donc nécessaire d'élargir la matrice des taxons et des caractères disponible actuellement si on veut solutionner adéquatement la relation phylogénétique à l'intérieur de ce genre. Les psittacosaures étaient de petits dinosaures, leurs squelettes sont préservés dans un état exceptionnellement complet, et à proximité de milieux éoliens de sédimentation. Leur cerveau de petite dimension, comparativement au cerveau des mammifères actuels de taille similaire, implique un répertoire comportemental relativement restreint.
[Traduit par la rédaction]

内容提要

在中国内蒙进行的恐龙合作计划野外工作中，在七个地点采集到了鹦鹉嘴龙化石材料。这些标本中有两个鹦鹉嘴龙属 (*Psittacosaurus*) 新种，从而使本属中能被恰当定义的种上升为六个。新种之一是以一具几乎完全的骨架建立的；它与蒙古鹦鹉嘴龙 (*P. mongoliensis*) 相似，但不同之处在于它的个体较小、头颅较大、以及尾巴较长。另一新种具有颧骨角突，但在性征组合方面与中华鹦鹉嘴龙 (*P. sinensis*) 和新疆鹦鹉嘴龙 (*P. xinjiangensis*) 不同。目前本属的种数及其性征数据资料尚显太小而不足于妥善解决属内的亲缘关系。鹦鹉嘴龙是个体较小的种类，它们的骨架一般在近风成沉积环境下保存非常完好。它们与现代同等大小的哺乳类动物相比头颅显得较小，从而说明鹦鹉嘴龙的生活行为范围有较大的局限性。

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Реферат

Останки Psittacosaur были собраны в семи местах в процессе проведения полевых работ по проекту "Динозавр" во Внутренней Монголии. Выделены два вида Psittacosaurus, доведя число надежно

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определенных видов до шести. Один вид, на основании почти полностью сохранившегося скелета, напоминает P. mongoliensis, но это меньшее по размеру животное, с относительно более крупной головой и более длинным хвостом. Другой вид демонстрирует югумные рога, но другую комбинацию признаков в сравнении с P. sinensis и P. xinjiangensis. Более обширная матрица таксонов и характеристик, чем доступная в настоящее время, потребуется для адекватного решения вопроса о филогенетических взаимоотношениях внутри этого рода. Пситтакозавры были мелкими динозаврами, чьи скелеты сохранились в необычной полноте в близкой к эоловому осадконакоплению обстановке. Небольшой размер их мозга по сравнению с современными млекопитающими со сходными размерами тела указывает на относительно ограниченный репертуар поведения.

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Introduction

Psittacosaurus presently contains four relatively well known species of small (<1.5 m long), bipedal ceratopsians, all of which occur in China (Table 1). Their osteology has been well studied by Sereno and his collaborators (Sereno 1987, 1990*a*, 1990*b*; Sereno and Chao 1988; Sereno et al. 1988). Psittacosaur remains occur in continental strata of middle Cretaceous age throughout Central Asia, including Siberia and the Mongolian People's Republic, the People's Republic of China (Sereno 1987), and Japan (Manabe and Hasegawa 1991). *Psittacosaurus sattayaraki* is based upon a dentary from Thailand (Buffetaut and Suteethorn 1992). Additional material is needed to confirm its validity, and the species will not be considered here. *Psittacosaurus* is the smallest of only four dinosaurian genera known from more than 100 skeletons or skeletal fragments (others are *Coelophysis*, *Plateosaurus*, and *Maiasaura*; see data in Weishampel et al. 1990).

During the summers of 1988 and 1990, *Psittacosaurus* remains, including those of two additional species described below, were recovered in abundance in Inner Mongolia by field parties of the Dinosaur Project.

Abbreviations

AMNH, American Museum of Natural History, New York; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

Systematics

Suborder Ceratopsia Marsh, 1890
Family Psittacosauridae Osborn, 1923
Genus *Psittacosaurus* Osborn, 1923

Psittacosaurus neimongoliensis, new species

Type

IVPP 12-0888-2, nearly complete skeleton lacking much of braincase and distal caudal vertebrae (for measurements see Table 2).

Etymology

The species name refers to the Inner Mongolia Autonomous Region (Nei Mongol Zizhiqu) in which the type locality occurs.

Referred specimens

IVPP 07-0888-11, partially disarticulated skull. IVPP 12-0888-1, centra from 1 dorsal, 6 sacral, and 17 associated caudal vertebrae, fragments of ilia, right ischium, most of right and parts of left hind limb. IVPP 12-0888-3, right lateral margin of skull and mandible, and anterior portion of skeleton. Three unprepared specimens.

Locality

Ejinhoro Formation (Dong 1993, p. 2175), on east–west-trending ridge of greenish-yellow siltstones intercalated with reddish, locally chaotically bedded, ledge-forming sandstones; 1 km southeast of Yangpo village, 10 km north of main east–west highway, 80 km west of Dongsheng, and 63 km east of Hangginqi, in Ordos region of Inner Mongolia. Strata do not appear to conform to characterization of Ejinhoro Formation as "brick red with greyish green clastics" (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region 1991, map 1).

Associated fauna

Vertebrate fossils include the seven specimens of *Psittacosaurus neimongoliensis* cited above, a partial skeleton of a stegosaur (*Wuerhosaurus ordosensis* Dong, 1993), sauropod teeth (cf. *Chiayusaurus* sp.), and pterosaur bones.

Diagnosis (differentia)

Frontal narrow (broad in *Psittacosaurus meileyingensis*, *Psittacosaurus mongoliensis*), ischium distinctly longer than femur (shorter than or approximately equal to femur in *P. mongoliensis*), distal end of ischium not horizontally flattened (horizontally flattened in *P. mongoliensis*), anterior ramus from squamosal does not reach anterior wall of supratemporal fenestra (reaches anterior wall in *P. mongoliensis*, *Psittacosaurus sinensis*, *Psittacosaurus xinjiangensis*).

Table 1. *Psittacosaurus* occurrences in China.

***Psittacosaurus mongoliensis* Osborn, 1924**
(A) Liaoning, from red clays, sandstones, and conglomerates near the base of the Binggou Formation (X.-J. Zhao quoted in Yu et al. 1986; Sereno et al. 1988)
(B) Including *Psittacosaurus guyangensis* (Sereno 1987, p. 53), Inner Mongolia, Lisangou Formation, north of Hohehut
(C) Including *Psittacosaurus osborni* and *Psittacosaurus tingi* (Sereno 1987, pp. 51–52), Inner Mongolia, Tebch (Haratologay), near Urad Houqi, in sediments of Barremian–Aptian age (Eberth et al. 1993)
(D) Inner Mongolia, Hulanhushu (Sereno 1987, pp. 466, 492)

***Psittacosaurus sinensis* Young, 1931**
(A) Shandong Province, Qingshan Formation (including *Psittacosaurus youngi*, Sereno 1987, p. 58); the red clastics have also yielded *Peishanemys testudiformis*, which occurs in strata of Khukhtykian (Aptian–Albian age in Mongolia) (Nessov and Verzilin 1981; Jerzykiewicz and Russell 1991)
(B) Inner Mongolia, Hulanhushu (Sereno 1987, pp. 466, 499)

***Psittacosaurus xinjiangensis* Sereno and Chao, 1988**
Xinjiang, Junggar Basin near Wuerhe, Tugulu Group

***Psittacosaurus meileyingensis* Sereno, Chao, Cheng, and Rao, 1988**
Liaoning, from red clays, sandstones, and conglomerates near the base of the Binggou Formation (X.-J. Zhao quoted in Yu et al. 1986; Sereno et al. 1988)

***Psittacosaurus*, species undetermined**
(A) Hebei Province: several *Psittacosaurus* specimens have been recovered from fluvial sediments (Tujingzi Formation) of early Albian age (Dong 1987, p. 54; Gan and Zhang 1985)
(B) Ningxia (Inner Mongolia): a *Psittacosaurus* specimen with prominent jugal horns figured by Dong (1987, p. 53)

General description

The type skeleton was derived from a subadult animal, for sutures on the skull, between the presacral centra and neural arches, and between the scapula and coracoid are clearly visible but closed. The sacral centra are unfused. Evidence of pathology is present in infection-induced exostoses on the left transverse process of the 7th dorsal in front of the sacrum. The proximal end of the associated rib is also pathologically swollen and dorsoventrally pierced by a large oval foramen. Except where indicated, the following description is based upon the type specimen.

In lateral outline, the skull (Fig. 1) is intermediate between the relatively rectangular profile and elongated preorbital region of *P. mongoliensis* and the rounded profile and short preorbital region of *P. meileyingensis*. The skull and femur are about equal in length, unlike in *P. mongoliensis* where the skull is longer. The anterior and left lateral part of the skull is articulated. Separated elements include a right frontal, both quadrates, basisphenoid, left opisthotic–epoccipital, and right angular; the remainder are missing. Of the lower jaws, only the symphyseal region and left mandible are preserved.

The rostral (Fig. 1B) contacts the nasal on the dorsal midline of the skull. Ventral "nipping" edges of the rostral and premaxilla are edentulous and form a spoon-like structure 21 mm wide by 23 mm long. Dorsoposteriorly, a deep sulcus separates the infranarial ala of the premaxilla from the maxilla, but there is no clearly defined foramen between this ala and the lacrimal as in other psittacosaurs (Sereno et al. 1988). Unlike in *P. sinensis*, the premaxilla does not contact the jugal posteriorly, and the maxilla and lacrimal contact more broadly than in *P. meileyingensis* and *P. mongoliensis* (Sereno 1987; Sereno et al. 1988). There is no antorbital fossa.

A crest on the prefrontal anterodorsal to the orbit does not curl dorsally as in *P. mongoliensis* (Sereno 1987). The interorbital region of the frontal is narrower in IVPP 12-0888-2 and 07-0888-11 than in *P. mongoliensis*, *P. sinensis*, and *P. meileyingensis* (Sereno 1987). On the undersurface of the right frontal, sulci for the olfactory bulb, olfactory tract, and cerebral hemisphere are, respectively, 11.3, 4.8, and 8.7 mm wide. No sclerotic ossifications are preserved within the orbit. The frontoparietal suture is transversely oriented as in *P. sinensis* and *P. meileyingensis*, without the V-shaped anteromedian projection present in *P. mongoliensis*. A lamina of bone from the frontal underlies the medial process of postorbital, nearly separating it from the oribital margin. A small rugosity is present on the postorbital–jugal arch, in the position of the prominent "horn" in *P. sinensis*. The dorsolateral surface of the postorbital is traversed by a horizontal ridge. Medially, the anterior ramus of the squamosal is widely separated from the anterior wall of the supratemporal fenestra.

The flexure extending across the jugal from the postorbital bar to the tip of the jugal horn is less strongly developed than in *P. mongoliensis* (Sereno et al. 1988). The horn does not project laterally as do the pyramidal horns of *P. xinjiangensis* and *P. sinensis*. The lateral surface of the quadratojugal is smooth, as in *P. sinensis* and *P. xinjiangensis* (Sereno 1987); it bears a subtle prominence in *P. mongoliensis*, and is raised and textured in *P. meileyingensis*.

In posterodorsal aspect (Fig. 2A), the maxilla evidently separates the palatine from the ectopterygoid, as in *P. sinensis* (Sereno 1987), whereas in *P. mongoliensis* the palatine contacts the ectopterygoid. There is no postpalatine foramen. The parasphenoid rostrum is short, vertically broad, and transversely narrow (Fig. 2B). The basipterygoid process of the basisphenoid meets the pterygoid in a nearly immovable suture (Fig. 2B). There is no rounded transverse boss on the ventral surface of the bone as in *P. mongoliensis* (Sereno

Table 2. Measurements of IVPP 12-0888-2, the type specimen of *Psittacosaurus neimongoliensis* (in mm).

Skull	
Length of skull, premaxilla to quadratomandibular articulation	132
External naris, maximum diameter	12
Orbit, width	39
Orbit, height	40
Lateral temporal fenestra, height	46
Lateral temporal fenestra, width	28
Preorbital length skull	60
Length of lower jaw	124
Quadrate, height	59

Axial skeleton (width and height of centrum are measured from the posterior articular facet)

	Length of centrum	Width of centrum	Height of centrum	Height of vertebra
Presacrals				
Axis	17	14	15	40
3	13	15	15	38
4	13	15	15	38
5	12	14	—	—
6	13	15	14	42
7	14	15	14	40
8	15	13	15	40
9	14	13	15	43
10	—	—	—	—
11	—	—	—	—
12	—	—	—	—
13	14	13	17	—
14	15	13	15	—
15	14	14	15	42
16	15	15	15	42
17	16	15	15	41
18	15	15	16	42
19	15	15	16	41
20	15	16	15	42
21	15	15	15	41
22	17	18	15	40
Sacrum				
1 (dorsosacral)	18	23	—	—
2	19	14	13	34
3	17	12	13	35
4	17	15	—	32
5	17	14	—	—
6	14	15	13	—
Caudals (not in sequence behind sacrum)				
"1"	15	14	14	39
"2"	16	14	12	37
"3"	16	14	13	37
"4"	17	13	15	44
"5"	17	13	14	40
"6"	17	12	15	43
"7"	17	11	15	42
"8"	17	12	15	43
"9"	17	12	14	41
"10"	17	11	14	39
A	17	11	13	37
B	16	10	12	35

Table 2 (*continued*).

Appendicular skeleton (lengths, except where noted; unguals are measured in a straight line from the centre of articular facet to the distal tip)

	Left	Right
Scapula	100	115
Scapula maximum width	38	36
Scapula minimum width	15	15
Scapula distal width	29	29
Coracoid width	39	39
Coracoid depth	35	38
Humerus	—	105
Humerus circumference	—	36.3
Radius	67	69
Ulna	—	72
Metacarpal I	16	15
Metacarpal II	—	25
Metacarpal III	—	25
Metacarpal IV	—	15
Phalanx I-1	10	10
Phalanx II-1	—	11
Phalanx II-2	—	8
Phalanx III-1	—	11
Phalanx III-2	—	8
Phalanx III-3	—	6
Ilium	156	—
Ilium, anterior end to middle of acetabulum	75	—
Ilium, middle of acetabulum to posterior end	80	—
Ilium, height above acetabulum	27	28
Pubis	112	105
Prepubis body	62	62
Prepubis body, anterior end to notch above posterior ramus	48	48
Prepubis body, notch above posterior ramus to posterior end	63	56
Ischium	140	144
Femur	129	130
Femur circumference	47.7	47.9
Femur, proximal end to fourth trochanter	65	64
Tibia–astragalus	146	146
Tibia	142	141
Tibia, combined width of calcaneum and astragalus	33	—
Fibula	—	136
Metatarsal I	47	48
Metatarsal II	65	64
Metatarsal III	—	66
Metatarsal IV	60	59
Phalanges		
Digit I	47	46
Digit II	—	55
Digit III	—	68
Digit IV	—	68
Phalanx I-1	26	26
Phalanx I-2	22	21

Table 2 (*concluded*).

Phalanx II-1	22	21
Phalanx II-2	17	16
Phalanx II-3	23	—
Phalanx III-1	20	20
Phalanx III-2	14	14
Phalanx III-3	13	13
Phalanx III-4	—	19
Phalanx IV-1	19	18
Phalanx IV-2	—	13
Phalanx IV-3	12	11
Phalanx IV-4	—	10
Phalanx IV-5	—	17

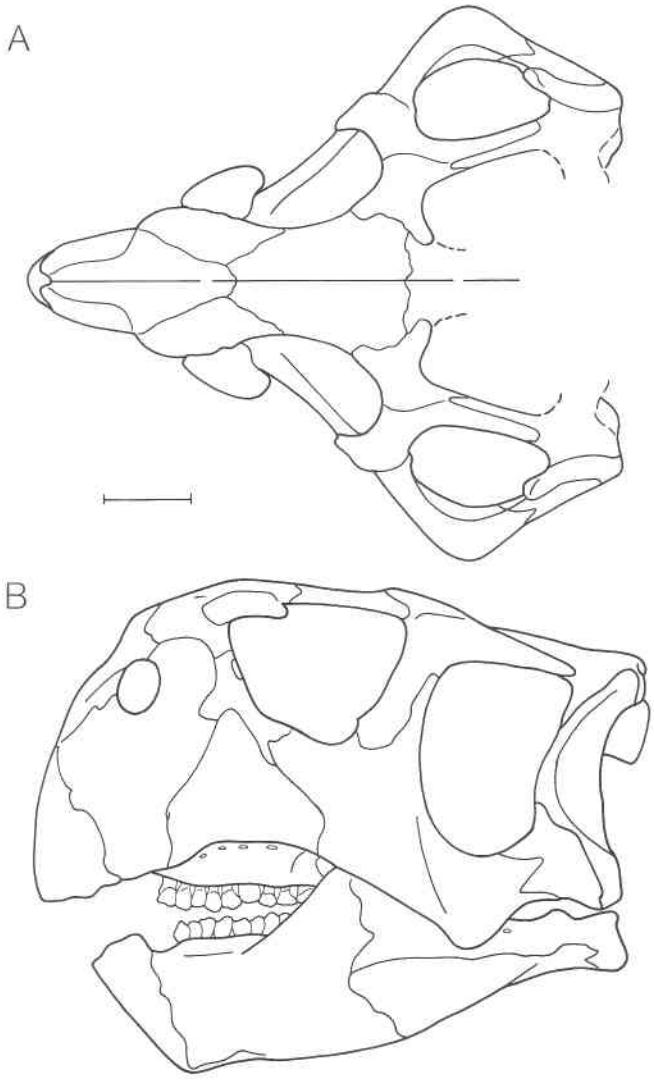
1987). The pterygoids are firmly sutured together on the cranial midline in front of the basipterygoid processes, and rise steeply toward the narial region of the skull (Fig. 2C). Behind the basipterygoid process, the pterygoidal ala of the quadrate bears a shallow sulcus ventrally, where it evidently contacted the lateral surface of the basioccipital. The left exoccipital–opisthotic articulates with the left quadrate, suggesting that the squamosal does not separate the elements. In lateral profile, the posterior margin of the quadrate is gently sulcate.

The mandibular rami are straight, as in *P. mongoliensis*, not bowed laterally as in *P. sinensis* (Sereno 1987). There is no external mandibular foramen (IVPP 12-0888-2, 12-0888-3, 07-0888-11). The predentary measures 20.5 mm in width; its occlusal edge does not shear inside that of the rostrum, but lies in the same vertical plane. The dentary and angular lack the well-formed ventrolateral ridge (IVPP 12-0888-2, 12-0888-3) present in *P. mongoliensis* and *P. meileyingensis*. As in these species, the posterior end of the splenial tapers to a narrow tip; in *P. sinensis* (Sereno 1987, p. 136) the end is broadly rounded. The internal mandibular fenestra is at least as large (8 mm × 4 mm, long axis anterodorsally inclined) as in the former two species; it is reduced to a foramen in *P. sinensis*. There is no anterior surangular foramen, although two tiny foramina are present in front of, and dorsolateral to, the mandibular articular surface. No separate coronoid ossification was identified. On the ventral surface of the retroarticular process, an elongated spur of the angular separates the surangular from the prearticular, except at the extreme distal end.

Nine teeth are present in both the left maxilla and dentary. In lateral aspect, the maxillary crowns are vertically oval, and bear 8–11 denticles as in other psittacosaurs, except in *P. xinjiangensis*, where as many as 14 denticles are present (Sereno and Chao 1988). The posterior carina does not curve posteromedially as it does in *P. xinjiangensis*. Dentary crowns bear 9–15 denticles, as in other psittacosaurs.

Cervical vertebrae are here distinguished from dorsal vertebrae by a capitular facet that is either ventral to or centred upon the suture between the centrum and neural arch (Sereno 1987). By this criterion, there are eight cervicals, as in *P. mongoliensis*, not nine as in *P. sinensis* (Sereno 1987). Only the left neural arch of the atlas vertebra is preserved. The axis spine is broad, but the spine is acuminate back to the 8th cervical where it is flattened and subrectangular. The

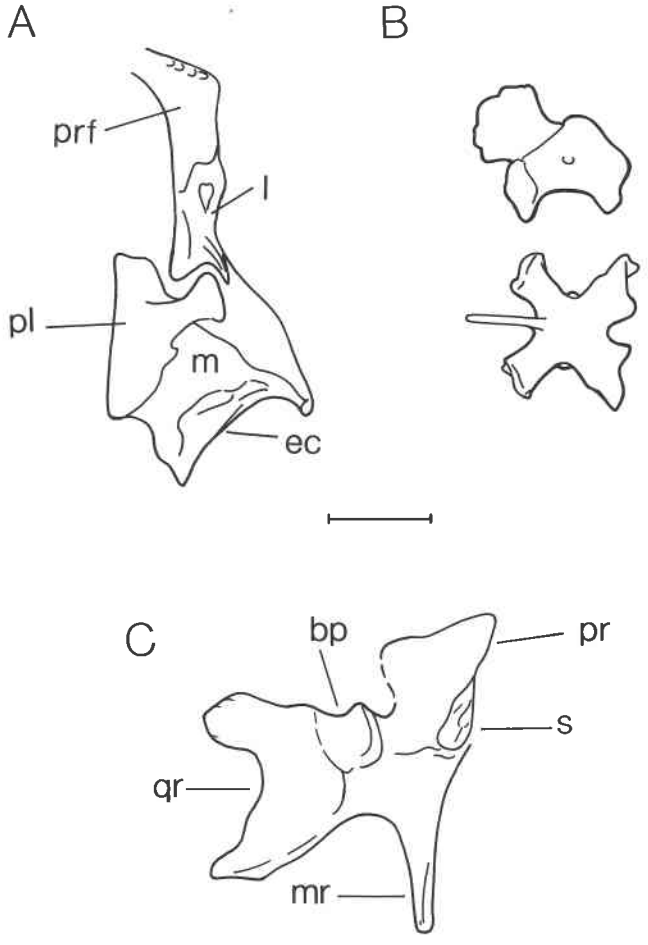
Fig. 1. *Psittacosaurus neimongoliensis*. Skull (IVPP 12-0888-2, partly reconstructed) in (A) dorsal and (B) left lateral views. Scale bar = 2 cm.



capitular facet becomes much larger on the 6th cervical, and the transverse processes lengthen on cervical 7 to resemble those in the dorsal series. The axis intercentrum is not fused to the axis. Cervical centra decrease in length through the mid-cervical region as in *P. mongoliensis* (Sereno 1987), and the hypapophyses are largest on cervicals 4–6. IVPP 12-0888-3 differs from the type specimen in that the capitular facet was still located entirely below the centrum – neural arch suture on the 8th cervical. Other differences include a subrectangular spine on cervical 7 (in *Leptoceratops* the spine becomes subrectangular on the 9th postcranial vertebra; Russell 1970, Fig. 1), and the hypapophyses are largest on cervicals 5–7.

The 1st dorsal vertebra is complete, and the posterior 10 are preserved in articulation. Parts of two intervening vertebrae are clearly represented: two left transverse processes bear a broad capitular facet, but one on the right bears a narrow capitular facet similar to that of the 1st dorsal. The presacral count is thus at least 21; if the narrow capitular

Fig. 2. *Psittacosaurus neimongoliensis*. Cranial elements (IVPP 12-0888-2). (A) Posterolateral view of right orbit. ec, ectopterygoid; l, lacrimal; m, maxilla; pl, palatine; prf, prefrontal. (B) Basiphenoid in left lateral (upper figure) and ventral (lower figure) views. (C) Left pterygoid in medial view. bp, facet for basipterygoid process of basiphenoid; mr, mandibular ramus; qr, quadratic ramus; pr, palatine ramus; s, sutural surface for right pterygoid. Scale bar = 2 cm.



facet represents an additional vertebral segment, the minimal count is 22 (the latter alternative is shown in Fig. 3). There are 21 or 22 presacrals in *P. mongoliensis* (Sereno 1987) and other ceratopsians (Russell 1970). The neural spines of the dorsal vertebrae are relatively short, as in *P. mongoliensis*, but, unlike in the latter species (Osborn 1924, Fig. 5), they diminish in breadth posteriorly. On the posteriormost two dorsals, the parapophysis merges with the diapophysis on a shortened transverse process, as in *P. mongoliensis* and *P. xinjiangensis*. The centrum of the last dorsal contacts that of the 1st sacral in an irregular suture-like surface, and a cartilaginous intervertebral disc was evidently absent.

The general morphology of the ribs is shown in the restoration (Fig. 3). An atlas rib, if preserved, was not identified. Two small, short-shafted cervical ribs articulate best with the 3rd and 5th cervical vertebrae. In IVPP 12-0888-3 the anteriormost large rib articulates with the 7th cervical. Distal to the tuberculum its shaft is at least 75 mm long, and the rib

Table 3. Relative bodily proportions of *Psittacosaurus neimongoliensis*.

(A) Proportions of the axial skeleton of IVPP 12-0888-2 relative to those in *P. mongoliensis* (Osborn 1924, Fig. 5; Sereno 1987)

	A	B	C	D	E
Head	152	10.9	0.90	136.8	11.5
Neck	156	11.2	0.72	112.3	9.4
Back	320	23.1	0.72	230.4	19.4
Sacrum	152	10.9	0.84	127.7	10.7
Tail	608	43.8	0.96	583.7	49.0

(B) Proportions of the skeletal elements in *Psittacosaurus neimongoliensis* relative to those in *P. mongoliensis* and *P. sinensis* (the ratios were obtained from dividing the length of the segment in IVPP 12-0888-2 by that in specimens referrable to the other two species (Sereno 1987, Appendix B)).

	P. mongoliensis		*P. sinensis*
	AMNH 6253	AMNH 6254	IVPP V738
Skull	—	0.90	1.14
Cervical vertebrae (2–8)	0.72 (2, 4)	0.79	
Dorsal vertebrae (9, 16–18)	0.72		
Sacral vertebrae			
Caudal vertebrae (?3–12)	0.96		
Humerus	0.85		1.27
Radius	0.84		
Ulna	0.82	0.80	
Metacarpal III	0.81		
Femur	0.83	0.81	1.31
Tibia	0.84	0.78	1.42
Metatarsal III	0.84		1.25

Notes: A, *Psittacosaurus mongoliensis*, length (in mm) of axial segments (as illustrated in Osborn 1924, Fig. 4; total length estimated to be 1338 mm); B, *Psittacosaurus mongoliensis*, length of segments expressed as a percentage of total length of skeleton (compare with E); C, *Psittacosaurus neimongoliensis*, length of segment in IVPP 12-0888-2 divided by length of segment in A; D, *Psittacosaurus neimongoliensis*, calculated length (in mm) of axial segments (A × C; total skeletal length estimated to be 1191 mm). E, *Psittacosaurus neimongoliensis*, length of segments expressed as a percentage of total length of skeleton (compare with B).

is essentially thoracic in form. The anteriormost large (''thoracic'') rib also articulates with the 7th cervical vertebra in *Centrosaurus* (Brown 1917) and *Leptoceratops* (Russell 1970).

In the type specimen, 12 complete or nearly complete thoracic ribs are preserved along the right side. The three anteriormost ribs bear an enlarged distal end for articulation with a sternal rib. The maximum widths across the capitular–tubercular facet for ribs 7(?)–9 are 24, 18, and 18 mm, respectively. The lengths of the three ribs posterior to the 7th, measured in a straight line from the tuberculum to the distal end, are 118, 131, and 129 mm. In the six ribs posterior to the three with sternal articulations, the tubercu-

lum no longer diverges from the rib shaft. The tuberculum – distal end length diminishes from about 124 to 58 mm, and the shaft becomes straighter. The capitular and tubercular facets approach each other on the proximal end of the rib. These facets merge on the last three dorsal ribs. The rib length continues to diminish from about 41 to 31 mm, and the shafts are only slightly bowed. The width of the shafts does not diminish, giving the last ribs a more robust appearance. The ribs of the left side are incomplete in all but the posteriormost elements. The form of the transverse processes and ribs indicates that the chest was about 16 cm wide and 19 cm deep.

Six sacral vertebrae are present in the type specimen. Zygapophyseal articulations are unfused and apparently functional on all of them. The transverse processes of the 1st sacral resemble those of the preceding dorsal, although two isolated, delicate, and broadly alate structures evidently represent the 1st sacral ribs (see also Sereno 1990*a*, p. 584). The 2nd sacral ribs are the largest. The ventral process is broadly expanded distally and buttresses the pubic peduncle of the ilium (Sereno and Chao 1988). The more slender dorsal process is separated distally from the ventral process by a deep sulcus, and contacts the dorsal edge of the ilium. The succeeding four sacral ribs resemble caudal transverse processes in their high, centrally placed position on the lateral surface of the vertebrae, but swell distally to support the medial surface of the ilium. There is no transverse suture crossing them at midlength, such as separates the dorsal surface of the transverse process and the rib of the 2nd sacral.

Ten proximal caudal vertebrae are preserved in articulation, and two isolated vertebrae are assumed to continue the series (see Fig. 3). Each proximal caudal has transverse processes (caudal ribs); the two isolated caudals bear short, nubbin-like processes (in *P. mongoliensis* the anterior 21 caudals bear transverse processes, Sereno 1987). There are chevron facets on the posteroventral edge of the 3rd caudal centrum, to which the single chevron preserved has arbitrarily been articulated in Fig. 3. Chevron facets occur on the 2nd caudal in *P. mongoliensis* and *P. meileyingensis* (Sereno 1987).

As in *P. sinensis* and possibly *P. meileyingensis*, no ossified epaxial tendons span the sacral region. These structures extend from the 10th presacral to the 15th caudal in *P. mongoliensis*, and from the 10th presacral to the mid-caudals in *P. xinjiangensis* (Sereno 1987).

No sternals were preserved. The scapula and coracoid resemble those of *P. mongoliensis*, and are not as narrow as in *P. sinensis* (Young 1958, Fig. 53; Sereno 1987, Table 8). The humerus-to-femur length ratio (0.80) is similar to that in *P. mongoliensis* and *P. xinjiangensis*, but less than that in *P. sinensis* (0.84). No carpals have been identified. Four metacarpals and three phalanges, probably from digits I and II, are the only elements remaining of the manus (Fig. 4A).

The postacetabular process of the ilium resembles that in *P. mongoliensis*, but is slightly more slender. It is not as narrow as in *P. xinjiangensis*. The anterior process of the pubis terminates parallel to the anterior end of the ilium (Fig. 3), as in *P. sinensis* but unlike in *P. mongoliensis* and *P. xinjiangensis*. However, the end of the process is expanded in a dorsomedial–ventrolateral plane as in the latter two species and unlike in *P. sinensis* where it is

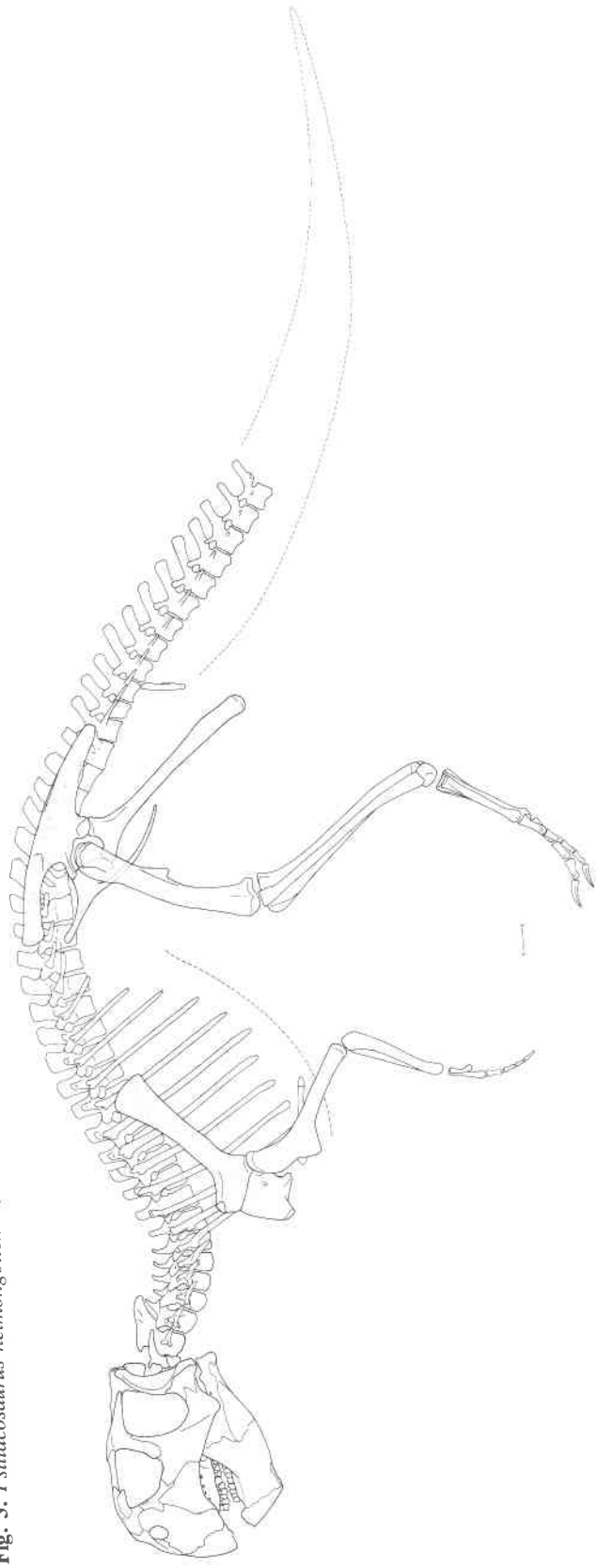
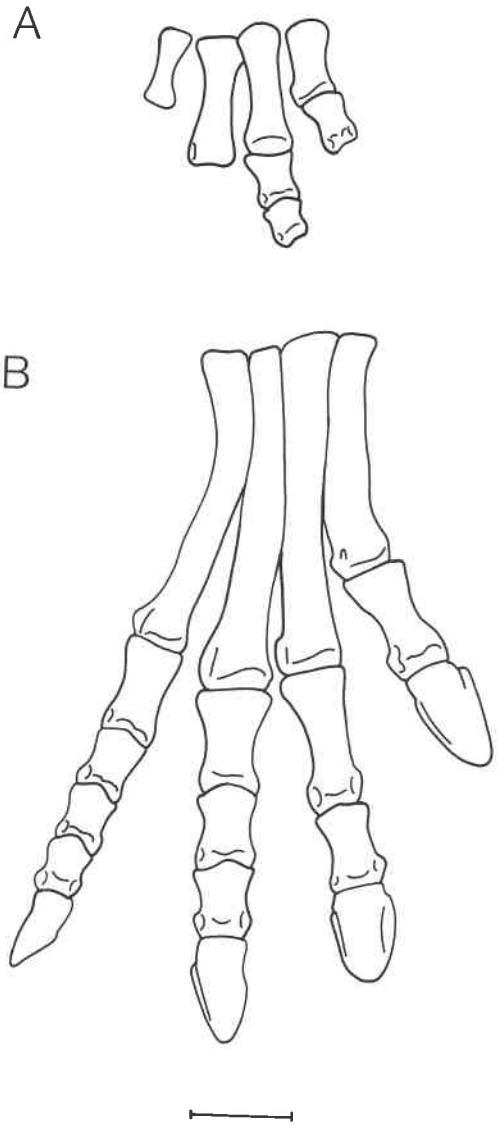


Fig. 3. *Psittacosaurus neimongoliensis*. Reconstruction of skeleton (IVPP 12-0888-2). For further explanation see text. Scale bar = 2 cm.

Fig. 4. *Psittacosaurus neimongoliensis*. Metapodials and phalanges (IVPP 12-0888-2) of (A) manus and (B) pes in extensor aspect. Scale bar = 2 cm.



expanded in a horizontal direction (Sereno 1987). The postpubic ramus is long as in *P. mongoliensis*, not short as in *P. sinensis* (Sereno 1987). It is rodlike throughout its entire length, unlike in the other two species. The ischium differs from that in *P. mongoliensis* in being very long and unexpanded distally. There is no distal facet indicating the presence of a symphysis. A short symphysis is present in *P. mongoliensis*, but the distal end of the ischium is unknown in other species (Sereno 1987). The bones of the hind limb and pes (Figs. 3, 4B) lack unique features. The ratio between the lengths of metatarsals I and III is 0.70 as in *P. mongoliensis*; it is about 0.6 in *P. sinensis*.

According to its general skeletal proportions (see Fig. 3; Table 3), *P. neimongoliensis* was a smaller animal than *P. mongoliensis*, and differed in possessing a larger head, shorter neck and back, and longer tail. It was larger than both *P. sinensis* and *P. xinjiangensis*, and the skull was smaller relative to the body than in the latter species. With a large head and nipping beak, a body a little over a metre in length, and a weight of approximately 14 kg (according to the midshaft circumferences of the humerus and femur, Anderson et al. 1985), *P. neimongoliensis* was similar in general appearance, length, and mass to a large rodent. Less immediately obvious, but even more striking, is the sulcus on the undersurface of the right frontal, which covered a cerebral hemisphere. It is no more than 8.7 mm wide; the same cavity measures 21 mm in width in a beaver skull of about the same size, indicating a volumetric difference of a factor of nearly 15. The comparison dramatically reflects the increase in encephalization that has occurred in terrestrial vertebrates since Cretaceous time (Russell 1994).

Table 4. Measurements of IVPP 07-0888-1, the type specimen of *Psittacosaurus ordosensis* (lengths in mm, unless otherwise noted).

Skull	
Skull, from premaxilla to quadratomandibular articulation	95
Height coronoid	35
Left hind limb	
Tibia–astragalus	109
Tibia	105
Tibia, combined width of calcaneum and astragalus	26
Fibula	101
Metatarsal I	38
Metatarsal II	49
Metatarsal III	55
Metatarsal IV	52
Phalanges	
Digit I	37
Digit II	46
Digit III	—
Digit IV	—
Phalanx I-1	21
Phalanx I-2	18
Phalanx II-1	17
Phalanx II-2	13
Phalanx II-3	19
Phalanx III-1	17
Phalanx III-2	13
Phalanx III-3	—
Phalanx III-4	—
Phalanx IV-1	14
Phalanx IV-2	12
Phalanx IV-3	10
Phalanx IV-4	8
Phalanx IV-5	—

Psittacosaurus ordosensis, new species

Type

IVPP 07-0888-1, ventral half of a skull, lower jaws, and left crus and foot (for measurements see Table 4).

Etymology

The species name refers to the Ordos region of Inner Mongolia, in which the type locality occurs.

Referred specimens
IVPP 07-0888-5, left jugal and quadrate, two cervical vertebrae, several vertebral and rib fragments, and left scapula. Two unprepared specimens.

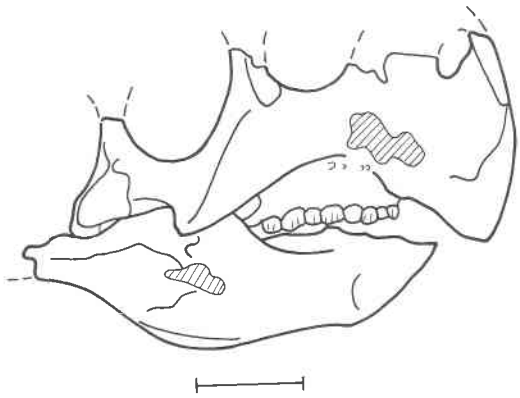
Occurrence
The type skeleton was nearly complete when discovered, but only part of it has been prepared. Available elements are about 0.82 times the length of those in the type of *P. neimongoliensis*. Another, still smaller specimen is referred to this species because it was found near the type specimen and had an enlarged horn on the jugal. The specimens were recovered from alternating red aeolian sandstones (T. Jerzykiewicz in Russell and Dong 1993*b*, p. 2170) and greyish mudstones of the Ejinhoro Formation exposed near the villages of Huamuxiao and Amulonggui. Near the latter village, 1 km to the south of the former, a 41.5 m sequence of red sandstones with large-scale cross-bedding contains no intercalations of greyish mudstone. Huamuxiao village is located 4.1 km west of Duguijiahan, which in turn is 29 km south of Hangginqi, in the Ordos region of Inner Mongolia. The locality is mapped as occurring within the Zhidan Group, although the sequence appears to conform better to "brick red with greyish green clastics" referred to the Ejinhoro Formation (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region 1991, map 1).

Associated fauna
Vertebrate fossils include three *Psittacosaurus* specimens in addition to the four cited above, a troodontid skeleton (*Sinornithoides youngi*), fragments of turtle and pterosaur bone, a stegosaur tooth, and a weathered femoral shaft from a moderately large saurischian (Russell and Dong 1993*b*).

Diagnosis (differentia)
A small psittacosaur with prominent jugal horns, distinguishable from: (*i*) *P. sinensis* (see Sereno 1987) in that maxillary dentition arranged in straight line (not medially bowed), jugal horn relatively short, quadrate not strongly emarginate posteriorly, ventrolateral ridge present medially on mandible, lateral mandibular fenestra apparently present, tibia longer (not shorter) than skull, and ratio of lengths of metatarsal I to III approximately 0.7 (not 0.6); and (*ii*) *P. xinjiangensis* (Sereno and Chao 1988) in that unworn maxillary crowns vertically oval (not subcircular) in outline, maxillary teeth bear 8–11 relatively large rather than 14 relatively small denticles, shallow sulcus between primary ridge and anterior margin of tooth rather than flat surface.

Comments
The type specimen pertains to a small but adult psittacosaur in which the sutures between the dermal cranial elements are partly obliterated (Fig. 5). The jugal horn resembles that of *P. xinjiangensis*, not being as prominent as that in *P. sinensis*. However, the combination of characters renders it referrable to neither of the two known species with well-developed jugal horns. A fontanel appears to be present in the dorsal ala of the maxilla, anterior to its internal contact with the lateral process of the palatine. The area was either unossified or thin bone was broken prior to fossilization. The external surfaces

Fig. 5. *Psittacosaurus ordosensis*. Skull (IVPP 07-0888-1) in right lateral view. Scale bar = 2 cm.



of eight crowns are exposed in the right maxilla. As in the case of the maxillary fontanel, an unossified area may be present on the lateral surface of the mandible between the dentary, angular and surangular.

Psittacosaurus, species undetermined

Psittacosaur materials collected from five additional localities are too incomplete and exhibit too little morphologic detail to establish their specific affinities.

(1) Alouchaideng
Yellowish sandstones and greenish-buff siltstones mapped as belonging to the Ejinhoro Formation (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region 1991, map 1) are exposed a few hundred metres south of the main east–west highway, 90 km west of Dongsheng, and 10 km east of Alouchaideng truck stop, in the Ordos region of Inner Mongolia. The sediments are more sombre and more horizontally bedded than those exposed near Yangpo village, the type locality of *P. neimongoliensis* 14 km to the northeast (see above), and appear to underlie them stratigraphically. Fourteen fragmentary psittacosaur specimens were recovered, all of which pertain to small (immature?) individuals between 65 and 77% of the linear dimensions of the type of *P. neimongoliensis*. They differ from this species in having a metatarsal I to III length ratio of about 0.5 instead of 0.7, although the difference could be due to immaturity. As in *P. neimongoliensis*, however, no depression is present on the lateral surface of the maxilla.

(2) Ulan Obo
Rusty-red strata are exposed 1 km north of the main east–west highway about 35 km west of Hangginqi, 2 km east of the village of Ahlingbola, in the Ordos region of Inner Mongolia. The 12 m sequence yielded remains of three specifically undetermined *Psittacosaurus* specimens, a fragment of a turtle plastron, and a champsosaur vertebra. The red beds are overlain by at least 30 m of highly cross-bedded micaceous green sandstones containing little fossil material except a few scraps of aquatic turtles. The locality is mapped within the Zhidan Group, although lithologically it more closely resembles "brick red with greyish green clastics"

Table 5. Characters variably expressed among species of *Psittacosaurus*.

(A) Description of characters.

Character No.	Description
1*	Skull profile rectangular with long preorbital region (0), intermediate (1), rounded with short preorbital region (2)
2*	Antorbital fossa present on maxilla (0), very shallow or absent (1)
3	More than 10 teeth present in the maxilla and dentary (0), 10 or less than 10 teeth present (1)
4	Lateral margin of prefrontal not upturned or slightly upturned (0), strongly upturned (1)
5*	Postorbital region narrow (0), broad (1)
6	Horizontal ridge weakly developed on postorbital (0), strongly developed (1)
7	Anterior ramus from squamosal does not extend as far as anterior wall of supratemporal fenestra (0), ramus extends to anterior wall (1)
8*	Pyramidal, laterally projecting jugal horn absent (0), present (1)
9	Posterior margin of quadrate gently sulcate in lateral profile (0), deeply sulcate (1)
10	External mandibular foramen present (0), absent (1)
11*	Ventrolateral ridge on dentary absent (0), present and well formed (1)
12	Primary ridge of maxillary teeth not posteroventrally angled (0), posteroventrally angled (1)
13	Length of metatarsal one about 60% that of metatarsal three (0), about 70% (1)

(B) Distribution of characters among seven ornithischian taxa.

	Ld	Pmo	Psn	Pml	Pxj	Pnm	Por
1	0	0	1	2	?	1	1
2	0	1	0	1	1	0	0
3	0	0	1	1	1	1	1
4	0	1	0	0	?	0	?
5	0	0	1	0	?	1	1
6	0	0	1	1	0	1	?
7	0	1	1	1	1	0	?
8	0	0	1	0	1	0	1
9	0	0	1	1	0	0	0
10	0	0	1	0	?	1	0
11	0	1	0	1	?	0	1
12	0	1	0	1	1	1	0
13	0	1	0	?	?	1	1

Notes: Numbers refer to the character as listed in Table 5. Ld, *Lesothosaurus diagnosticus*; Pmo, *Psittacosaurus mongoliensis*; Psn, *P. sinensis*; Pml, *P. meileyingensis*; Pxj, *P. xinjiangensis*; Pnm, *P. neimongoliensis*; Por, *P. ordosensis*. Character states coded 0 indicate ancestral conditions, those coded 1 and 2 indicate successively more derived conditions, and those coded ? indicate that the state is unknown.

*Also identified by Sereno (1987); for further explanation see text.

referred to the Ejinhoro Formation (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region 1991, map 1).

(3) Hangginqi

The main highway south from Hangginqi descends a gentle escarpment about 16 km south of the city. Exposures of a 35 m sequence of rusty-red, southward-dipping cross-bedded sandstones extend from the highway along the escarpment toward the west, near the villages of Wulahattatu, Argaiwusu, and Gutanwusu. The sandstones are coarser and "rustier" than those exposed near Huamuxiao, the type locality of *P. ordosensis*, about 13 km to the south, but nevertheless appear to generally resemble "brick red clastics" of the Ejinhoro Formation. Associated remains of at least seven specifically undetermined small *Psittacosaurus* specimens were collected. No other fossil vertebrate materials were seen.

(4) Laolonghuozi

Approximately 100 m of coarse, cross-bedded, greenish, micaceous sandstones of the Luohandong Formation (Zhidan Group) are exposed in buttes along both sides of the main east–west highway approximately 55 km west of Hangginqi and 120 km east of Deng Kou (Brinkman and Peng 1993*a*, Fig. 1; Brinkman and Peng 1993*b*, p. 2151). They resemble the "greyish green clastic" facies of the Ejinhoro Formation more closely than the "rhythmic clastics with marl" of the Zhidan Group (Bureau of Geology and Mineral Resources of Nei Mongol Autonomous Region 1991, map 1). A 75 m high butte immediately south of the highway is capped by 2–3 m of rusty-red strata. Fossils recovered include the remains of fishes, aquatic turtles, champsosaurs, and crocodiles, and a few isolated bones and teeth of dinosaurs. Only two specifically undetermined limb elements and a few fragments from this locality are referrable to *Psittacosaurus*.

(5) Elesitai

A sequence of over 400 m of shallow lacustrine strata of the Bayin Gobi Formation is exposed near the abandoned village of Elesitai, 23 km west of Tukemu village in the Alashan Desert of Inner Mongolia. Recovered fossils include those of trionychid and larger turtles, champsosaurs, primitive therizinosaurian dinosaurs, and mammals (Russell and Dong 1993*a*), as well as two incomplete *Psittacosaurus* specimens of uncertain specific affinity.

Evolution of *Psittacosaurus*

The age of most of these new psittacosaur occurrences is uncertain. In the case of the undetermined species of *Psittacosaurus* at Elesitai, however, the co-occurrence of angiosperm palynomorphs is suggestive of an Albian age (Russell and Dong 1993*a*). Records of *Psittacosaurus* in China, Mongolia and Siberia appear to be Barremian to Albian in age (Table 1; Sereno 1987; Jerzykiewicz and Russell 1991; Eberth et al. 1993). Recently obtained radiometric dates from the base of the Jehol Group in Liaoning suggest that the beginning of Jehol deposition did not antedate this interval (P.E. Smith, personal communication, 1994). Thus, *Psittacosaurus* may have survived from Valanginian through Albian time, or approximately 40 Ma (Harland et al. 1990).

The character matrix of Sereno (1987, pp. 267–271) has been extended in an attempt to reassess species-level relationships (Table 5). In the absence of a closely related sister group for the Ceratopsia, the primitive Early Jurassic ornithischian *Lesothosaurus* (Weishampel and Witmer 1990;

Sereno 1991) and protoceratopsids (Brown and Schlaikjer 1940; Sternberg 1951; Maryanska and Osmolska 1975; Ostrom 1978) were used to establish character polarity. Using PAUP/Mac 3.1.1, a consensus tree was obtained from three equally parsimonious trees with *Lesothosaurus* as the outgroup and character 1 ordered. Each tree contained 23 steps, and yielded a consistency index of 0.609 and homoplasy index of 0.409. The consensus tree suggests that *P. sinensis*, *P. ordosensis*, and *P. neimongoliensis* form a cluster of related species that is more closely related to *P. meileyingensis* and *P. xinjiangensis* than to *P. mongoliensis*. A larger matrix will be required to resolve the phylogenetic relationships of species of *Psittacosaurus*.

Conclusions

A total of six species of *Psittacosaurus* are recognized in strata of Valanginian through Albian age within China and Mongolia. The genus, one of the most abundantly preserved of all dinosaurian genera, may have experienced an extensive species-level diversification, which cannot yet be resolved in an unambiguous manner.

Psittacosaurs were small dinosaurs that preferred semiarid environments in proximity to sources of aeolian sand (Jerzykiewicz and Russell 1991) that provided opportunities for rapid burial with minimal disturbance to their delicate skeletons. In fluvial environments in North America, dinosaurs of this size are rarely preserved in articulation (Béland and Russell 1978). The small brain size of psittacosaurs implies a very restricted behavioral repertoire relative to that of modern mammals of similar body size.

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