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A new species of *Psittacosaurus* (Dinosauria: Ceratopsia) from the Early Cretaceous Yixian Formation, Liaoning, China

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Abstract

Newly discovered, well-preserved skulls and mandibles from the lowest part of the Early Cretaceous Yixian Formation, western Liaoning Province, China, document the earliest known record of psittacosaurs and provide the basis for recognition of a new species, *Psittacosaurus lujiatunensis*. This discovery increases the taxonomic diversity of psittacosaurs to eight valid species and extends the stratigraphic range of the family Psittacosauridae from late Barremian-Albian to Hauterivian. Comparative study of the new species with other well-known psittacosaurs indicates that the new taxon is probably the most basal member of the psittacosaur clade now known. This interpretation is in agreement with the temporal distribution of the clade and supports the hypothesis that the Psittacosauridae originated from the basal ceratopsian stem no later than the earliest part of the Cretaceous.
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Keywords: Ceratopsian dinosaurs; Psittacosauridae; Early Cretaceous; Yixian Formation; Liaoning; China

1. Introduction

The Psittacosauridae (Osborn, 1923) are small, facultatively bipedal ceratopsian dinosaurs, characterized by a unique construction of the upper jaws to form a parrot-beak-like rostrum. Psittacosaurids are known only from the Early Cretaceous of eastern Asia, from beds of Aptian-Albian age (121–98.9 Ma; Remane, 2000). Most specimens have been recovered from China and Mongolia, but fragmentary psittacosaurid fossils have also been reported from southern Siberia, Japan, Korea and Thailand (e.g., Sereno, 1990; Dong, 1993), but some of these may not be valid (Sereno, 2000).

Recently, new ceratopsians have been discovered in the Lower Cretaceous of western Liaoning Province, northeastern China, as members of the renowned "Jehol Biota" (e.g., Chang, 2003). These species, *Psittacosaurus meileyingensis* Sereno, Chao, Cheng and Rao, 1988, *Chaoyangsaurus youngi* Zhao, Cheng and Xu, 1999, *Liaoceratops yanzigouensis* Xu, Makovicky, Wang, Norell and You, 2002 and *Hongshanosaurus houi* You, Xu and Wang, 2003, have added important new information concerning the early evolution of ceratopsians and their phylogenetic position among ornithischians. Herein we describe a new psittacosaur from this same region, from the lowest part of the Yixian Formation near Lujiatun Village, Beipiao City, Liaoning (Fig. 1). Although no radiometric dates are available for the beds exposed at Lujiatun, these strata have been placed directly below the Jianshangou beds of the

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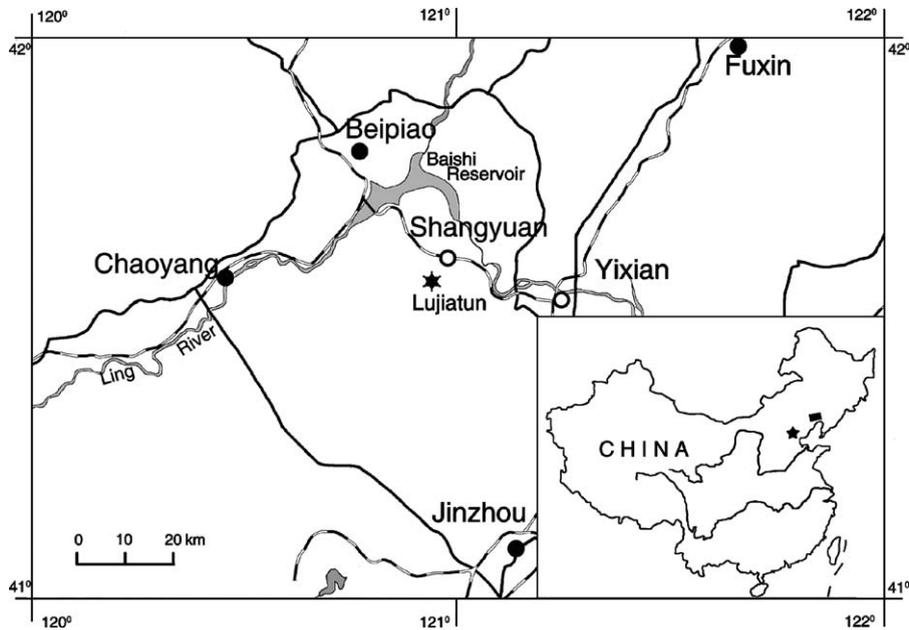*E-mail address:* kqgao@pku.edu.cn (K.-Q. Gao).

Fig. 1. Area map showing the type locality (*Lujiatun) of *Psittacosaurus lujiatunensis* n. sp. in western Liaoning Province, northeast China.

Yixian Formation at Sihetun (Wang et al., 2004). A basalt sample from the lower part of the Jianshangou sequence at Sihetun has yielded a ^{40}Ar/^{39}Ar date of 128.4 ± 0.2 Ma (Wang et al., 2001); in a recent study of mammalian fossils (Li et al., 2003), the age of the Lujiatun beds has been interpreted as Hauterivian (late Neocomian). Based on both stratigraphic correlation and radiometric determination, the new specimens reported here constitute the geologically earliest record of psittacosaurs. The new specimens not only represent a new species of *Psittacosaurus*, but also provide new information about the origin and early radiation of psittacosaurs and the relationships of psittacosaurids with neoceratopsians.

1.1. Institutional abbreviations

AMNH, American Museum of Natural History, New York, USA; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PKUP, Peking University Paleontological Collections, Beijing, China; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

1.2. Anatomical abbreviations

a, angular; ar, articular; bo, basioccipital; bs, basisphenoid; bt, basal tubera; c, coronoid; d, dentary; ec,

ectopterygoid; f, frontal; ic, opening for internal carotid artery; j, jugal; l, lacrimal; ls, laterosphenoid; m, maxilla; mf, meckelian foramen; n, nasal; oc, occipital condyle; p, parietal; pal, palatine; pm, premaxilla; po, postorbital; popr, paroccipital process; pr, prootic; pra, prearticular; prd, predentary; prf, prefrontal; ps, parasphenoid; pt, pterygoid; q, quadrate; qj, quadratojugal; r, rostral; sa, surangular; so, supraoccipital; sof, suborbital fenestra; spl, splenial; sq, squamosal; st, stapes; v, vomer; CN I-XII, foramina for cranial nerves I–XII.

2. Systematic paleontology

Order Ornithischia Seeley, 1888
Suborder Ceratopsia Marsh, 1890
Family Psittacosauridae Osborn, 1923
Genus *Psittacosaurus* Osborn, 1923
Psittacosaurus lujiatunensis n. sp. (Figs. 2–6)
Etymology: The specific epithet refers to the type locality.

Holotype: ZMNH M8137, a nearly complete skull with lower jaws (Figs. 2, 5A, B and 6A, B).

Type locality and horizon: Lujiatun, near Beipiao, Liaoning Province, China; lowest part of the Yixian Formation (Hauterivian, Early Cretaceous).

Paratypes: ZMNH M8138, a nearly complete, but somewhat compressed skull with lower jaws and the anteriormost three cervical vertebrae (Fig. 6C); PKUP
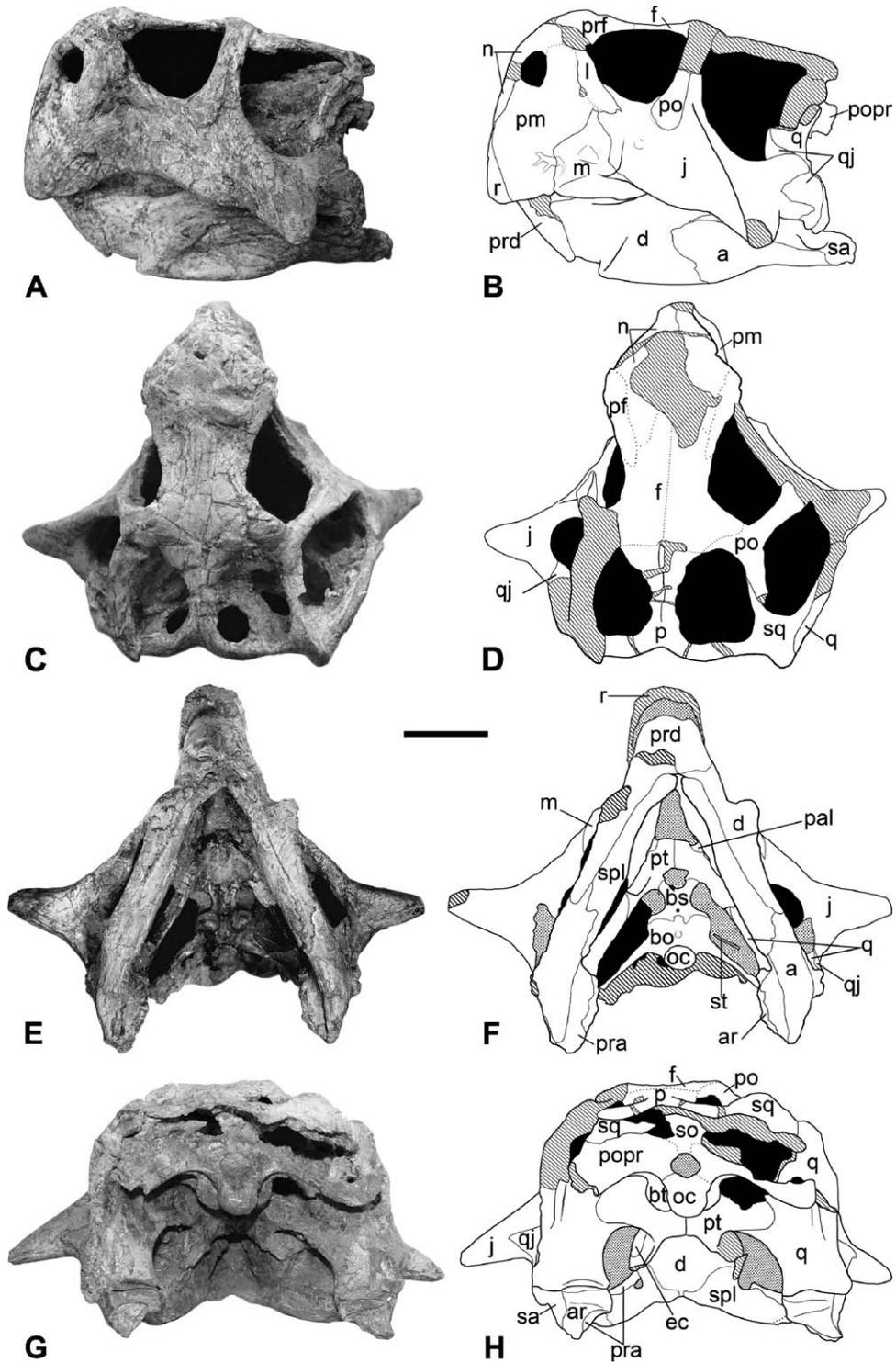
Fig. 2. *Psittacosaurus lujiatunensis* n. sp. (ZMNH M8137, holotype) from the lowest part of the Yixian Formation (Hauterivian, Early Cretaceous) of Lujiatun, near Beipiao, Liaoning Province, China; nearly complete skull in articulation with lower jaws in lateral (A and B), dorsal (C and D), ventral (E and F) and posterior (G and H) views. Scale bar = 50 mm; for explanation of abbreviations see Introduction.
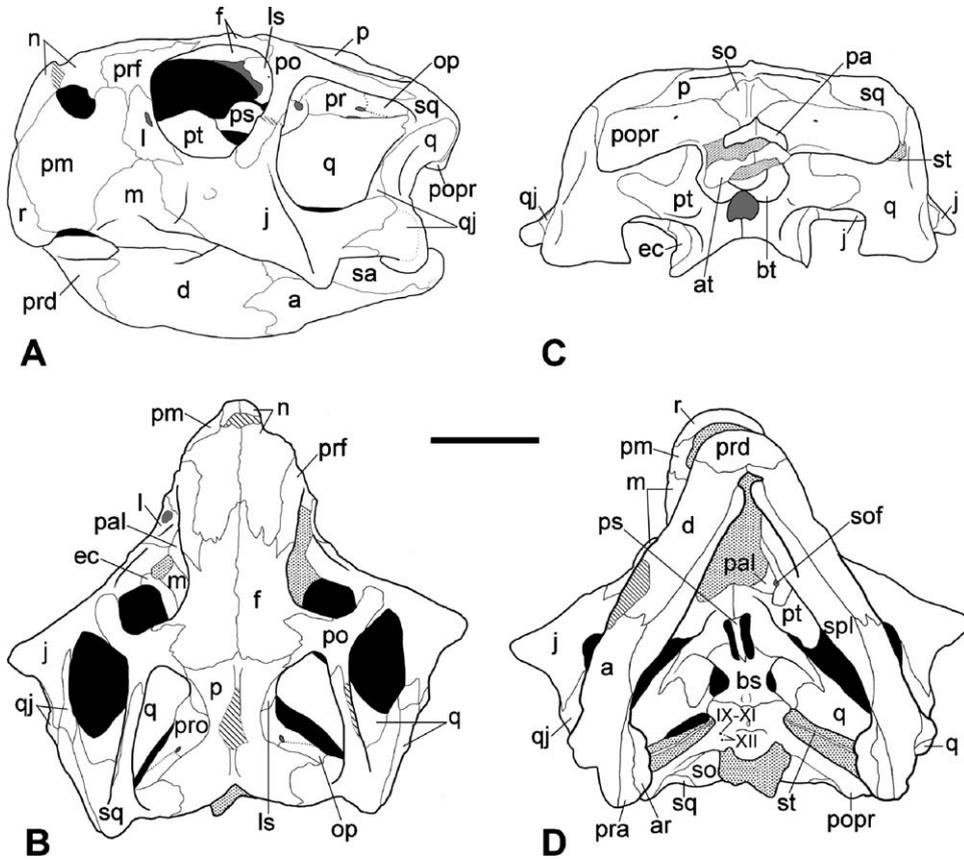
Fig. 3. *Psittacosaurus lujiatunensis* n. sp. (PKUP V1054, paratype) from the lowest part of the Yixian Formation (Hauterivian, Early Cretaceous) of Lujiatun, near Beipiao, Liaoning Province, China; complete skull with lower jaws in lateral (A), dorsal (B), posterior (C) and ventral (D) views. Scale bar = 50 mm; for explanation of abbreviations see Introduction.

V1053, a complete and slightly compressed skull and fragments of the lower jaws of a juvenile (Fig. 4); PKUP V1054, a complete and slightly compressed skull with lower jaws, and proatlas and atlas of a young adult individual (Figs. 3 and 5C, D). All paratypes from the type locality and type horizon.

Diagnosis: Differing from all other species of *Psittacosaurus* in the following combination of character states: large size; prefrontal narrow, less than 50% of width of nasal; maxillary protuberance upturned; jugal depression shallow; jugal horn arising relatively posteriorly and strongly developed posterolaterally; ventral
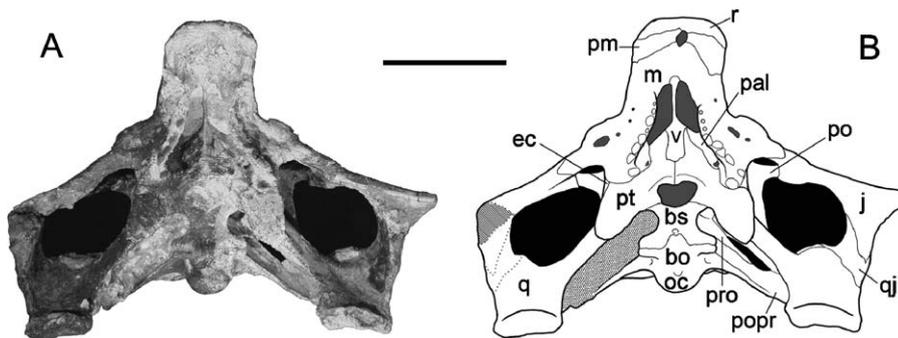

Fig. 4. *Psittacosaurus lujiatunensis* n. sp. (PKUP V1053, paratype) from the lowest part of the Yixian Formation (Hauterivian, Early Cretaceous) of Lujiatun, near Beipiao, Liaoning Province, China; photograph (A) and line drawing (B) of a nearly complete skull in ventral view. Scale bar = 50 mm; for explanation of abbreviations see Introduction.
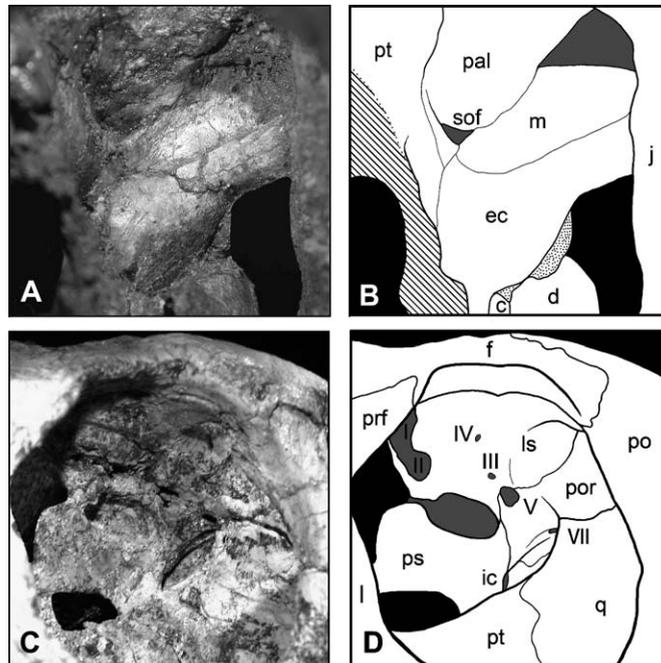
Fig. 5. Cranial elements in *Psittacosaurus lujiatunensis* n. sp. Posterolateral view of the right infratemporal fenestra of the skull (A and B) in ZMNH M8137 (holotype) from the lowest part of the Yixian Formation (Hauterivian, Early Cretaceous) of Lujiatun, near Beipiao, Liaoning Province, China). Anterolateral view of the left orbit of the skull (C and D) in PKUP V1054 (paratype; from the same locality and horizon). For explanation of abbreviations see Introduction.

ramus of squamosal contacting quadratojugal medial to quadrate; contact of jugal with quadrate narrow, overlapping quadratojugal; external mandibular foramen closed; angular large; maxillary tooth crowns trilobed, primary ridge enlarged into central lobe subequal to posterior lobe.

2.1. Description of the skull

The holotype (ZMNH M8137; Fig. 2) was three-dimensionally preserved in coarse purple-red sandstones, with the mandibles in articulation with the skull. The skull is large, having a length of 190 mm from the tip of the snout to the back of the quadrate, a maximum width of 250 mm across the jugal horns and a maximum height of 145 mm. A second skull (ZMNH M8138) is even larger, having a maximum length of 205 mm. The skull of *Psittacosaurus lujiatunensis* n. sp. is wider than long as in *Psittacosaurus sinensis* Young, 1958 but differing from other psittacosaur species, in which the skull is longer than wide.

2.1.1. Rostral

The rostral bone, a median element at the tip of the upper jaws in ceratopsians, is vertical and edentulous

(Fig. 2). In anterior view, it is subtriangular with a broad ventral margin and a narrow dorsal process. The outline of this bone in lateral view is also subtriangular, having an oblique sutural contact with the premaxilla, in contrast to the nearly vertical suture in *Psittacosaurus meileyingensis* Sereno, Chao, Cheng and Rao, 1988 (Sereno et al., 1988, fig. 2). The lateral surface is covered with short grooves and pits, suggesting that a horny sheath was present in life. The rostral meets the nasal dorsally and premaxilla posteriorly. The dorsal process projects between the rostral processes of the nasals along a V-shaped suture, with its apex directed dorsally.

2.1.2. Premaxilla

The premaxillae are well preserved on both sides of the holotype skull (Fig. 2A and B). The premaxilla makes up most of the lateral surface of the snout, contacting the rostral anteriorly, the nasal and prefrontal dorsally, and the lacrimal and maxilla posteriorly, as in other species except *P. sinensis*, in which the premaxilla also meets the jugal posteriorly. As a diagnostic character of the Psittacosauridae (Sereno, 1990), the premaxilla is strongly expanded posterolaterally to overlap the lacrimal, thereby precluding the maxilla from bordering the external naris. The lateral surface of the premax-
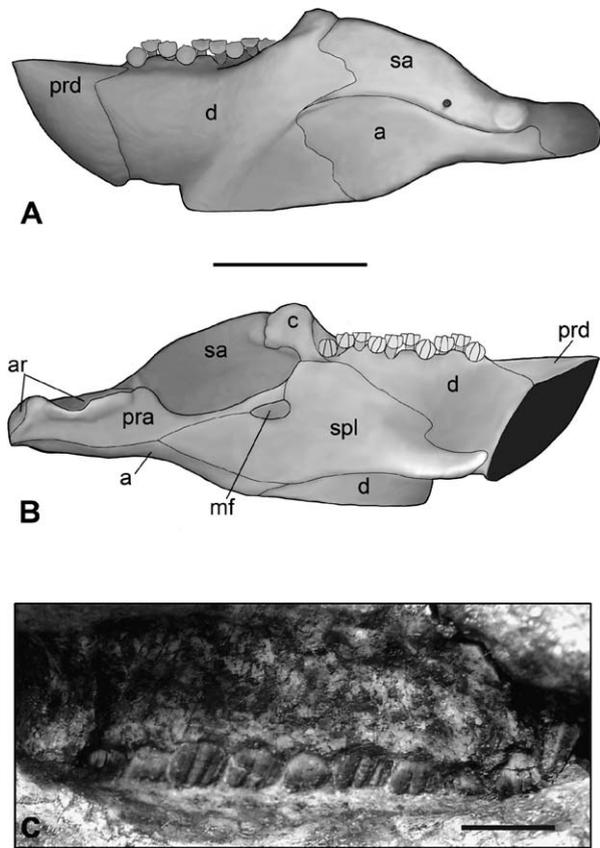
Fig. 6. Mandible and maxillary dentition of *Psittacosaurus lujiatunensis* n. sp. Reconstruction of the mandible (ZMNH M8137, holotype; from the lowest part of the Yixian Formation (Hauterivian, Early Cretaceous) of Lujiatun, near Beipiao, Liaoning Province, China) in lateral (A) and medial (B) views; scale bar = 50 mm. Right maxillary tooth row (C) in ZMNH M8138 (paratype; from the same locality and horizon); scale bar = 10 mm. For explanation of abbreviations see Introduction.

illa is smooth and slightly depressed below the external naris, but becomes roughened with grooves and pits near its buccal margin. Posteriorly, a low ridge arises on the surface of the premaxilla and as in *Psittacosaurus mongoliensis* Osborn, 1923 and *P. meileyingensis*, extends anteroventrally from the lacrimal to the central region of the premaxilla, where it disappears, level with the posterior margin of the external naris. In contrast, this surface is flat in *P. sinensis* and *Psittacosaurus neimongoliensis* Russel and Zhao, 1996. As in *P. mongoliensis* (Osborn, 1923, fig. 2; Sereno et al., 1988), a well-developed crest extends anterodorsally along the premaxillary-maxillary suture. A conspicuous groove (14 mm long and 6 mm wide) crosses this suture horizontally just below the distal end of the premaxillary-maxillary ridge and then connects with the other grooves on the lower portion of

the premaxilla. A similar feature is seen in *P. meileyingensis* and may have marked the posterior margin of the horny sheath in life.

2.1.3. Maxilla

In lateral view, above the buccal margin, the dorsal part of the maxilla is tall and trapeziform as in *P. meileyingensis* and *P. neimongoliensis*, differing from the lower, triangular maxilla in the other psittacosaur species. As in *P. mongoliensis*, a deep antorbital fossa is present on the lateral surface of the maxilla and a horizontal flange extends along its buccal margin. Posterior to the fossa, a protuberance arises adjacent to the maxilla-jugal suture as in several other psittacosaurs (although this feature is absent in *P. sinensis* and *P. neimongoliensis*) and *Chaoyangsaurus* Zhao, Cheng and Xu, 1999. Uniquely in *P. lujiatunensis*, however, a rounded ridge extends dorsally across the maxilla-jugal suture, ending midway along the orbital ramus of the jugal (Figs. 2A, B and 3A). In the holotype, three nutrient foramina of different sizes can be seen along the buccal margin of the maxilla; the posterior two are relatively large and open ventrolaterally. Immediately above the tooth row, the lateral surface of the maxilla is hollowed out, implying the development of cheek pouches external to the teeth, as in other ornithischians (Romer, 1956).

2.1.4. Lacrimal

The lacrimal is well preserved on the left side of the holotype. As in other psittacosaurs, the lacrimal forms the anterior margin of the orbit, but it is more restricted ventrally by the jugal than in other species, wedging into the jugal along a V-shaped suture (Figs. 2A, B and 3A). The lacrimal foramen opens on the orbital rim. As in *P. neimongoliensis*, a premaxilla-lacrimal foramen (Sereno, 1987) appears to be absent in *P. lujiatunensis*, although the surface of the lacrimal is broken at this position in the holotype.

2.1.5. Nasal

The nasal is somewhat damaged in the holotype (Fig. 2A–D), but is well preserved in PKUP V1054 (Fig. 3A and B). In dorsal view, the paired nasals contribute half of the preorbital portion of the skull roof, reaching their maximum width in front of the prefrontal. At its narrowest, the main body of the nasal is about twice as wide as the prefrontal. The nasal has an interdigital sutural contact with the frontal posteriorly, a longitudinal suture with the prefrontal laterally, and extensive articulation with the premaxilla anterolaterally. Anteriorly, the nasals are narrowed to form an internarial bar,

which bends downward to meet the rostral bone below the naris, roughly at the same level as the lower border of the orbit (Figs. 2A, B and 3A). As in other psittacosaurs, the external naris is bordered by the nasal and premaxilla, and is dorsal to the level of the ventral rim of the orbit.

2.1.6. Frontal and prefrontal

As shown in PKUP V1053 and V1054 (Fig. 3B), the paired frontals meet firmly along the midline. The frontal contacts the prefrontal laterally, postorbital posterolaterally and parietal caudally. A lateral extension of the frontal clearly separates the medial process of the postorbital from the orbital margin and is well exposed in dorsal view, as in *P. mongoliensis*.

The prefrontal is narrow and meets the premaxilla and lacrimal ventrally, forming the anterodorsal corner of the orbit (Fig. 3A and B). The prefrontal forms a flat lateral margin of the roof as in other species except *P. mongoliensis*, in which the lateral margin of the prefrontal is upturned. In dorsal view, the prefrontal contacts the nasal medially and frontal posteriorly. The maximum width of the prefrontal is less than 50% of that of the nasal. This ratio differs from that in other psittacosaurs, in which the prefrontal is as wide as or even wider than the nasal.

2.1.7. Parietal

The parietals (best preserved in PKUP V1053 and V1054; Fig. 3B) are fused along the midline to form a low sagittal crest as in other psittacosaurs. The parietal contacts the frontal and postorbital anteriorly, the laterosphenoid anteroventrally, the prootic, opisthotic and supraoccipital ventrally, and the squamosal laterally. Anterior to the supratemporal fenestrae, the sagittal crest diverges into two laterally curving crests, marking the anterior limit of the origin of the adductor muscles of the lower jaw. In dorsal view, the parietal frill has a distinctly incised margin at the midline, with its apex directed anteriorly as in other species except *P. meileyingensis*, in which the posterior margin of the frill is straight (Sereno et al., 1988, Fig. 3). The frill is a horizontal shelf over the occiput as in most other species, whereas its lateral parts slope posterodorsally in *P. meileyingensis* (Sereno et al., 1988).

2.1.8. Postorbital

The postorbital is incompletely preserved in the holotype, but is clearly shown in PKUP V1054 (Fig. 3) as a slender and triradiate element; the three rami diverge from one another at roughly right angles as in other psittacosaurs. The posterior ramus is the longest, forming

a large part of the upper temporal bar together with the anterior ramus of the squamosal. A horizontal ridge is well developed along the posterior ramus in adult skulls, but is absent in juvenile and young adult specimens (PKUP V1053 and V1054). The second ramus extends ventrally, separating the orbit from the infratemporal fenestra. The distal tip of this ramus is slightly expanded in the holotype (Fig. 2A and B) as in *P. meileyingensis*, differing from the narrow tip in other psittacosaurs. The ventral ramus bears a weakly developed prominence as in most other species, but in contrast to the well-developed prominence (postorbital-jugal horn core; Sereno, 1987) at the postorbital-jugal suture in *P. sinensis*. The medial ramus is the shortest and as in *P. mongoliensis*, it fails to contribute to the dorsal margin of the orbit (Fig. 3B). In *P. sinensis* and *P. meileyingensis*, however, the medial process of the postorbital excludes the frontal from the posterodorsal corner of the orbit (Sereno, 1987; Sereno et al., 1988).

2.1.9. Squamosal

The squamosals are partly preserved in the holotype, but are nearly complete in the paratypes (ZMNH M8138, PKUP V1053 and V1054). The squamosal is a tetraradiate bone as in other species (Fig. 3B). Previously, the short anterior ramus of the squamosal was considered as a diagnostic feature of *P. neimongoliensis* (Russell and Zhao, 1996), in which the ramus fails to reach the anterior border of the supratemporal fenestra. However, in *P. lujiatunensis*, the anterior ramus is short in adult specimens (Figs. 2C, D and 3B), but is long, approaching the anterior border of the fenestra, in the juvenile. These proportions in *P. lujiatunensis* suggest that the anterior ramus became proportionally shorter as the skull grew. The ventral ramus contacts the quadratojugal and forms the posterior margin of the infratemporal fenestra with the quadrate. This feature, previously unknown in psittacosaurs (although the region is not preserved in some specimens), is diagnostic of the new species *P. lujiatunensis*. The medial ramus juts medially to meet the parietal, with which it forms the posterior margin of the supratemporal fenestra. Further ventrally, the posterior process of the squamosal contacts the paroccipital process along a nearly horizontal suture. This process in the paratypes separates the quadrate completely from the paroccipital process (Fig. 3C), as in *P. mongoliensis* but differing from the other species.

2.1.10. Jugal

The jugal is a large element, consisting of infraorbital, infratemporal and dorsal rami, and the jugal horn. A strong ridge runs posteroventrally from the tip of the dor-

sal ramus to the end of the jugal horn, dividing the lateral aspect of the jugal into anterior and posterior surfaces. As in *P. mongoliensis*, the anterior surface is much larger than the posterior, contrasting with the condition in *Psittacosaurus ordosensis* Russell and Zhao, 1996, in which these proportions are reversed (Xu and Zhao, 1999). The infraorbital ramus of the jugal is deeper dorsoventrally than the infratemporal ramus, leaving the ventral margin of the orbit higher than the ventral margin of the infratemporal fossa (Figs. 2A, B and 3A). The anterior surface of the jugal is smooth and shallowly depressed centrally. On the left jugal of the holotype, a depression is located in the center of the anterior surface, behind the dorsally directed ridge that extends from the maxillary protuberance (Fig. 2A and B). A similar depression is also present in the paratypes (ZMNH M8138, PKUP V1053 and V1054) (Fig. 3A). This depression of the jugal has not been reported in other species of the genus, and appears to be an autapomorphy of *P. lujiatunensis*. The dorsal ramus of the jugal is overlapped by the ventral ramus of the postorbital, forming the bar between the orbit and infratemporal fenestra. The infraorbital ramus contributes to the ventral margin of the orbit and anteriorly contacts the lacrimal and maxilla. The infratemporal ramus bifurcates posteriorly as in other psittacosaurs, but a strong posterodorsal process overlapping the quadratojugal to meet the quadrate is a unique feature of the new species. The posteroventral process is shorter, and does not extend far enough to contact the quadrate. Medially, the jugal, maxilla and ectopterygoid meet above the distal end of the tooth row. Dorsally, below the orbit, the jugal broadly contacts a lateral triangular process of the palatine medially.

The well-developed jugal horn projects posterolaterally, close to the level of the posterior margin of the infratemporal fenestra (Fig. 2A and B). The base of the horn arises from the posterior portion of the jugal, more posteriorly than in other species. The anterior surface of the horn is nearly vertical and its ventral surface horizontal. The jugal horn is grooved, indicating a keratinous covering sheath in life (Sereno and Chao, 1988).

2.1.11. Quadratojugal

In lateral view, the quadratojugal is divided into two parts by the contact between the jugal and quadrate (Fig. 2A and B). The dorsal part contributes to the posterior rim of the infratemporal fenestra, together with the ventral process of the squamosal (ZNHM M8138, PKUP V1053 and V1054). The ventral part supports a rugose prominence in the paratypes, as in *P. meileyingensis* and *P. sinensis* (ZCF, pers. obs. of IVPP V738), but in the holotype this surface is smooth (Fig. 2A). The ventral

part of the quadratojugal extends anteriorly to the level of the posterior margin of the infratemporal fenestra, as in *P. sinensis* and *P. neimongoliensis*. These proportions of the quadratojugal are also present in *P. mongoliensis*, and possibly in *P. meileyingensis* as well (Sereno et al., 1988, figs. 2 and 5). In lateral view, the posterior margin of the ventral part incompletely overlaps the quadrate. Medially, the quadratojugal is triangular in outline, wedging between the jugal and quadrate (Fig. 4).

2.1.12. Quadrate

The quadrate meets the jugal anteriorly, quadratojugal ventrally, squamosal dorsally, and pterygoid and prootic medially (PKUP V1053 and V1054; Fig. 3A). As in other psittacosaurs, the shaft is rotated anterolaterally and the condyle expanded transversely into a broad articular surface. The shaft is strongly concave along its posterior margin as in *P. sinensis* and *P. meileyingensis*, unlike the slightly arched condition in *P. mongoliensis* and *P. neimongoliensis*. Dorsal to the condyle, the quadrate is partly exposed in lateral view just posterior to the quadratojugal-quadrate suture, as in *P. meileyingensis*, *P. neimongoliensis* and *P. ordosensis* (Sereno et al., 1988, fig. 2; Russell and Zhao, 1996, figs. 1 and 5). Medially, the pterygoid ramus of the quadrate broadly overlaps the quadrate process of the pterygoid and with the latter forms a laterally convex shield, the pterygoquadrate wing (see Sereno, 1987). The pterygoquadrate wing is deep dorsoventrally, separating the orbital and laterotemporal cavities from the braincase wall, as in other species.

2.1.13. Palate

The palate is partly exposed in the holotype (Fig. 2E and F) and is well exposed in PKUP V1053 (Fig. 4). Anterior to the internal naris, a gentle vault is formed by the rostral, premaxilla and maxilla, and a medium-sized foramen at the midline is bordered by the same three elements. Between the internal nares, the vomers are fused along the midline, forming a long and narrow bar in the roof of the buccal cavity. The vomers arch dorsally, expanding anteriorly and posteriorly at their contacts with the maxilla, the pterygoid and possibly the palatine, respectively. The internal naris opens anterior to the maxillary tooth row, as in Protoceratopsidae Granger and Gregory, 1923 in contrast to that of Ceratopsidae Marsh, 1890 and *P. mongoliensis* (Xu et al., 2002). The proportions of the internal naris to the buccal cavity are intermediate between that in protoceratopsids (narial opening less than 50% of the diameter of the buccal cavity) and ceratopsids (naris and buccal cavity are subequal in diameter) (Dodson and Currie, 1990).

The palatine is well exposed in dorsal view as seen within the orbit of the holotype, and contacts the maxilla, jugal and lacrimal laterally, and pterygoid and ectopterygoid caudally. It is rhomboidal in outline, bordering the internal naris. The palatine strongly expands laterally and slopes anterodorsally at about a 60° angle in PKUP V1053 and V1054. Beneath the palatine, a short passage, connecting the orbit to the buccal cavity, is enclosed by the jugal laterally, maxilla ventrally, and palatine dorsally and medially (Fig. 5A and B), as in other species. In dorsal view, a foramen opens between the palatine and maxilla that is the remnant of the suborbital fenestra. In ventral view, the suborbital fenestra is exposed between the palatine, maxilla and possibly ectopterygoid (Fig. 3D).

The pterygoid is well developed and triradiate, with three principal rami: a posterolaterally directed quadrate ramus, a posteroventrally directed lateral ramus (mandibular ramus of Sereno, 1987) and an anterodorsally extending palatal ramus (Figs. 2–4). In ventral view, the left and right pterygoids meet at the midline, forming a basal plate (see Sereno, 1987) to enclose the interpterygoid vacuity as a common posterior opening (Figs. 2E, F, 3D and 4). Below the opening, the pterygoids form a small boss at the midline, without the distinct posterior process of the pterygoids in *P. mongoliensis*. The lateral ramus of the pterygoid is long and strap-like, joining with the ectopterygoid as in other species.

As seen through the orbit, the palatal ramus of the pterygoid forms the posterior palate at about the same level as the ventral orbital margin. It contacts the vomer anteriorly, palatine anterolaterally and parasphenoid posteriorly. The bifurcated quadrate ramus of the pterygoid extends posterolaterally to contact the quadrate, forming half of the medial side of the pterygoquadrate wing (Fig. 3D).

The ectopterygoid meets the jugal laterally, maxilla anteriorly, and pterygoid and palatine medially (Fig. 5A and B). It contacts the palatine as in *P. mongoliensis*, whereas the ectopterygoid is evidently separated from the palatine by the maxilla in *P. sinensis* and *P. neimongoliensis* (Sereno, 1987; Russell and Zhao, 1996). The ectopterygoid reaches the jugal above the posterior end of the maxillary tooth row. Behind the contact with the jugal, the ectopterygoid turns medially along the maxilla to the pterygoid and then extends caudally, forming a crest dorsolaterally on the lateral ramus of the pterygoid.

2.1.14. Braincase

The occiput is incompletely preserved in the holotype (Fig. 2G and H), but is well exposed in the paratypes (ZMNH M8138; PKUP V1053 and V1054; Fig. 3C). A narrow, vertical occipital crest extends dorsally at the midline from the dorsal margin of the foramen magnum and across the supraoccipital to the parietal shelf. This crest consolidates the occiput, supporting the overhanging shelf and providing attachment for the ligamentum nuchae (Sereno, 1987). A pair of ridges arises along the sutures between the supraoccipital and exoccipitals above the foramen magnum. The foramen magnum is about 25 mm in diameter (ZMNH M8137), bounded by the supraoccipital dorsally, basioccipital ventrally and exoccipitals laterally. The occipital condyle, formed by the basioccipital, is subequal to the foramen magnum in diameter.

The exoccipital and opisthotic are fused to form the paroccipital process, extending posterolaterally (Fig. 2G and H). The height of the paroccipital process is less than half of its length, contrasting to the condition in *P. sinensis*, in which the height is more than half of its length (Xu et al., 2002). Dorsally, the paroccipital process meets the parietal and squamosal along a horizontal contact. The foramen for the posterior cerebral vein opens more laterally in the paratypes (Fig. 3C). On the underside of the paroccipital process at its base, two ridges arise from the condyle and basal tubera, respectively, and join on the ventral margin of the paroccipital process. Proximally, the ridges surround a concavity that contains three nerve foramina, as in *P. mongoliensis* (Sereno, 1987), one anterior and two posterior, which are presumably for CN IX-XI and XII, respectively (Fig. 3D).

The basioccipital, as a major element of the braincase floor, contacts the basisphenoid anteriorly, at a median cleft across the basal tubera. The basal tubera have a subcircular and subvertical posterior surface, with a round, rough ventral margin that is at the same level or slightly ventral to the occipital condyle. Between the condyle and the tubera, a small, oval fossa opens at the midline of the basioccipital (Figs. 2E, F and 3D), as in *P. mongoliensis* (Sereno, 1987).

The basisphenoid contacts the pterygoids anteriorly via the stout, ventrolaterally directed and divergent basipterygoid processes. More posteriorly, the basipterygoid processes are continuous with parasagittal prominences, which cross the basisphenoid to the basal tubera and surround a deep, smoothly contoured basisphenoid recess.

In the holotype and paratypes of *P. lujiatunensis*, the limits of the otic region are mostly obscure and the sutures are difficult to identify. A major element of the braincase, the laterosphenoid, forms most of the anterolateral walls of the braincase; however, the laterosphenoid is not completely ossified and does not enclose

the forebrain anteriorly, leaving an opening just beneath the olfactory tracts (PKUP V1054; Fig. 3A). The juvenile specimen (PKUP V1053) is also poorly ossified here. The laterosphenoid, as in other species (Sereno, 1987), meets the frontal, parietal and postorbital dorsally, and prootic posteriorly. Ventrally, the laterosphenoid expands and approaches the parasphenoid, leaving but a narrow space between them that in life may have been filled with soft connective tissue.

Foramina for several cranial nerves are visible in PKUP V1054 (Fig. 5C and D). The opening for the olfactory tracts (CN I) is in the upper part of the unossified portions of the laterosphenoids. The optic nerve (CN II) may have exited from the lower part below the olfactory tracts. Posteroventrally, a large unossified region is between the laterosphenoids and parasphenoid, which may be the unossified wall for the hypophysial fossa. An anterodorsally directed groove is present in PKUP V1054 dorsal to the optic foramen; a similar groove has been reported in *P. sinensis* (IVPP V 738), extending from the probable opening for the oculomotor nerve (CN III) (Sereno, 1987). The small trochlear foramen (CN IV) is positioned dorsally above the oculomotor foramen. The opening for the trigeminal nerve (CN V) is a large foramen bordered by the laterosphenoid anteriorly and prootic posteriorly, although the sutures here are unclear; several grooves around the rim of the foramen may be traces indicating the paths of the ophthalmic, maxillary, and mandibular branches of the nerve.

The posterior sidewall of the braincase is formed by the prootic, which meets the basisphenoid ventrally, parietal dorsally, and opisthotic and squamosal posteriorly (best shown in PKUP V1053 and V1054). The prootic is divided into dorsal and ventral parts by an elongate horizontal ridge (crista prootica), which extends posterolaterally to contact the opisthotic, as in other species (Sereno, 1987). Laterally, the prootic has a short contact with the pterygoquadrate wing in its anterior portion. Behind the contact, there is a long and narrow cranioquadrate passage (Sereno, 1987); accordingly, the ventral part of the prootic is not exposed in lateral view. Besides bordering the trigeminal foramen, the prootic also borders the small facial foramen (CN VII) on the ventrolateral margin of the bone; a long, deep groove extends anteroventrally from the foramen (best observed in PKUP V1054, left side; Fig. 5C and D). The foramen for the lateral head vein exiting from the braincase (Sereno, 1987) is present, but its position in relation to the prootic-opisthotic suture cannot be determined in the holotype or paratypes of *P. lujiatunensis*.

As in other species, the opening for the internal carotid artery is at the base of the basipterygoid processes of the basisphenoid. The opening passes into the pituitary fossa. Normally, the foramen for CN VI is located at the base of the basipterygoid processes of the basisphenoid in ornithischians (Romer, 1956), but such a foramen has not been identified in *P. lujiatunensis*. Therefore, the exit of CN VI may be confluent with the opening of the internal carotid artery. The fenestra ovalis appears large, as in *P. mazongshanensis* Xu, 1997, but this character is unknown in other species.

2.1.15. Stapes

Until this study, the stapes of psittacosaurs, including the footplate and columella, has only been known from two individuals of *P. mongoliensis* (Sereno, 1987). Fortunately, in the holotype of *P. lujiatunensis* (ZMNH M8137) the left stapes is well preserved, with the footplate and proximal part of the columella still embedded in matrix. The exposed columella is rod-like and lies subparallel to the paroccipital process, as in *P. mongoliensis* (Sereno, 1987). It is about 20 mm long and 1.5 mm in diameter, extending posterolaterally from the fenestra ovalis toward the presumed site of the tympanum (eardrum) (Fig. 2E and F), but is broken off at about half the distance to the probable position of the membrane. In addition, the stapes is even better preserved in PKUP V1054 (Fig. 3C and D), with its columella completely ossified, from the fenestra ovalis to the quadrate. The columella in this specimen is approximately 46 mm long and 1 mm in diameter; its lateral tip is near the posterolateral margin of the quadrate, which presumably supported the tympanic membrane in life. The tympanic cavity is partly enclosed by the quadrate shaft rostrally and by the paroccipital process and posterior process of the squamosal caudally.

2.1.16. Mandible

As in other species of *Psittacosaurus*, the lower jaw of *P. lujiatunensis* is composed of eight elements: predentary, dentary, surangular, angular, splenial, coronoid, prearticular and articular. In lateral view, the ventral border of the mandible is moderately bowed dorsally along its length, with the predentary and angular forming the anterior and posterior ends of the arc, respectively. The mandible is relatively shallow (Fig. 6A and B), in contrast to the deeper mandible in *P. sinensis*. As in *P. sinensis* and *P. neimongoliensis*, the external mandibular foramen is closed in *P. lujiatunensis*, suggesting that this is not an ontogenetic variant but a taxonomic feature or a taphonomic artifact. In ventral view, the mandibular rami are nearly straight as in all other species except *P. sinensis*, in which the mandible is laterally bowed. The ventral border of the ramus is formed

by the dentary, with a narrower contribution from the splenial.

The predentary is short and deep with a rounded buccal margin anteriorly, as in other psittacosaurs. This feature distinguishes psittacosaurids from Neoceratopsia (Sereno, 1986), in which the predentary narrows to a sharp tip (e.g., Sereno, 1990, 1999, 2000; Xu et al., 2002). As shown in the holotype, the subtriangular predentary is divided into dorsal and ventral rami: the dorsal ramus extends a short distance along the buccal margin, whereas the much deeper ventral ramus extends further posteroventrally and with the dorsal ramus embraces the dentary in an immoveable joint. In anterior view, the predentary gradually expands transversely from the tip to its posterior end and is subtriangular in anterior and ventral views.

Posterior to the predentary, the dentary occupies the lateral surface of the mandibular corpus anteriorly, being supplanted by the angular and surangular more posteriorly. Anteriorly, it is overlapped by the predentary but meets its opposite element at the midline just posterior to the predentary. In medial view, the dentary is exposed posterior to the predentary and is ventrally overlapped by the splenial. In lateral view, the dentary, as in other psittacosaurs, is subequal to half of the total length of the mandibular body. This morphology distinguishes Psittacosauridae from Neoceratopsia, in which the dentary is more than 50% of the length of the mandible (P. Makovicky, Personal Communication, April 2005). As in *P. meileyingensis*, a long, prominent ridge crosses the lateral surface of the dentary, from the coronoid process to the prominent anterior corner of the dentary flange ventrally. The dentary flange is well developed ventrolaterally, as in *P. meileyingensis*. The flange is robustly developed in adult specimens (ZMNH M8137, M8138), but is only incipient in PKUP V1054 (Fig. 3) and unknown in PKUP V1053. The coronoid process of the dentary covers the lateral aspect of the coronoid bone and meets the surangular posteriorly, rising to a level slightly dorsal to the latter and forming the highest point on the lower jaw. A notch is developed in the posterior border of the dentary that is occupied mainly by the angular but also by the surangular; in *P. mongoliensis*, *P. meileyingensis* and *P. ordosensis*, the external mandibular foramen opens in the position of this notch. However, the presence of the external mandibular foramen is questionable in *P. mongoliensis* (P. Makovicky, Personal Communication, April 2005).

The angular in the holotype mandible is larger than the surangular (Fig. 6A), a condition also possibly present in *P. meileyingensis*, but differing from other species of *Psittacosaurus*, in which the surangular is the larger of the two bones. The angular forms the posteroventral margin of the mandible and sheaths the retroarticular process ventrally. Anteriorly, the ventral margin of the angular curves dorsally towards the surangular, but further posteriorly, it is nearly straight and parallels the surangular to the base of the retroarticular process. The ventral margin of the angular shows a slight lateral flange continuing posteriorly from the dentary flange. A long groove for a blood vessel crosses the lateral surface of the angular, just above and parallel to its ventral margin. In ventral view, the angular is covered by the splenial anteriorly and medially meets the prearticular along a straight suture.

Posterior to the apex of the coronoid process, the surangular forms the dorsal margin of the mandible, contacting the angular ventrally, coronoid and prearticular medially, and articular caudally. Posterior to the suture with the dentary, the surangular drops to the articular surface along a gently curved margin. The surangular is swollen laterally at the outer side of the articular, joining it in a continuous glenoid surface to receive the quadrate condyle. More anteriorly, a small nutrient foramen opens above the surangular-angular suture. Posterior to the jaw joint, the surangular turns medially to end at the base of the retroarticular process of the articular. In medial view, the surangular forms the lateral wall of the adductor fossa, which is the entry into the mandible for the jaw-closing musculature and for the mandibular branch of the trigeminal nerve (CN V_3), arteries and veins (Romer, 1956). The fossa is also bordered by the dentary and coronoid anteriorly, prearticular and splenial medially, and articular and angular posteroventrally (Fig. 6B).

The jaw articulation is slightly below the level of the tooth row. The articular is restricted to the medial surface of the jaw joint by the lateral process of the surangular; it contacts the surangular laterally, angular ventrally and prearticular medially. The dorsal surface of the articular is only partly exposed; as in other psittacosaurs, it is divided by a straight transverse crest into articular and retroarticular surfaces (Sereno, 1987). The surface of articulation for the quadrate condyle is a smooth plane in psittacosaurs. A deeply cupped articular surface was reported as a diagnostic character of *P. mazongshanensis* (Xu, 1997), but Xu and Zhao (1999) later showed that the articular surface of the species is actually flat as in other species. Posterior to the transverse crest, the retroarticular surface forms a deep depression. Immediately posterior to the depression, the convex portion of the retroarticular process tapers to the distal tip of the mandibular corpus; the depressed process provides the insertion for the depressor mandibulae muscle that opened the lower jaws (Romer, 1956).

The prearticular covers the medial surface of the caudal portion of the mandibular corpus (Fig. 6B), and anteriorly forms the inner margin of the adductor fossa posteroventrally. A Meckelian foramen (internal mandibular fenestra of Sereno, 1987), bordered by the prearticular dorsally and splenial ventrally, opens on the medial wall of the mandible. This foramen is large, about 11 mm long and 5 mm wide in the holotype. The Meckelian foramen mainly transmits the mandibular branch of CN VII, which descends from the middle ear region to enter the adductor fossa and join the main mandibular nerve (CN V_3) (Romer, 1956). Posteriorly, the prearticular forms the distal end of the lower jaw with the retroarticular process dorsally, surangular laterally and angular ventrally.

As in other species of *Psittacosaurus*, the splenial covers most of the medial surface of the mandibular corpus, but does not join its counterpart anteriorly. Posteriorly, the splenial is located beneath the prearticular and with the latter covers the Meckelian canal, bordering the Meckelian foramen ventrally. Posteriorly, it partly overlaps the prearticular and the medial surface of the angular with a rounded ventral margin. Its posterior apex, however, tapers to a narrow tip as in most other species, but differing from the rounded apex in *P. sinensis*. The splenial only contributes to the medial and ventral surfaces of the lower jaw and is not exposed laterally.

Until the present study, the coronoid bone in psittacosaurs was known only from a single specimen of *P. mongoliensis* (see Sereno, 1987), but it is well preserved in *P. lujiatunensis* (Fig. 6B); psittacosaurids lack the intercoronoid of other ceratopsians (Sereno, 1987). Dorsally, the coronoid is broad and rugose, and it articulates laterally with the surangular and coronoid process of the dentary. It extends anteroventrally to the tooth row and continues further anteriorly as a short, slender process lingual to the posteriormost teeth. The coronoid meets the prearticular and splenial medially, as in *P. mongoliensis*. In *P. mongoliensis*, the anterior process of the coronoid overlaps the latter two bones and is well exposed on the medial side of the mandibular ramus. In *P. lujiatunensis*, however, the anterior process of the coronoid overlaps the prearticular, but this overlap is in turn covered by the splenial medially and is not evident in medial view (Fig. 6B).

2.1.17. Dentition

The upper dentition is well preserved in ZMNH M8138, with 10 teeth in the maxillary tooth row (Fig. 6C). The upper teeth are also preserved in the juvenile specimen (PKUP V1053), but with only nine positions (Fig. 4). The maxillary tooth row is gently convex medially along its length. As in other psittacosaurs, but in contrast to ceratopsids (see Sereno, 1987), no more than one replacement tooth is present at each tooth position. The tooth crowns are closely spaced and the posterior edge of each overlaps the anterior edge of the next successive crown, following the primitive ornithischian pattern (Sereno and Chao, 1988). Morphologically, the crowns are similar to those in *P. mazongshanensis* (Xu, 1997), with three lobes, anterior, central and posterior, in contrast to the two-lobed condition in other species. The anterior lobe is broad and flat, the posterior lobe narrow and swollen, and the primary ridge is enlarged to form the central lobe, which is subequal to the posterior lobe in its dimensions (Fig. 6C). The primary ridge is high and straight from the base to the apex of the crown, as in *P. sinensis*, *P. ordosensis* and *P. mazongshanensis* (Sereno, 1987; Russell and Zhao, 1996; Xu, 1997).

The dentary teeth are partly preserved in the holotype and PKUP V1053. As in other species, the crowns are subcircular in lateral aspect and subdivided into three lobes; the secondary ridges are weakly developed. Although in the lower dentition of the holotype many of the denticles are damaged, 15 appears to be the common number on well-preserved teeth. In other species, the number of denticles varies from 9 to 15 (Russell and Zhao, 1996), except for more than 21 in *P. xinjiangensis* Sereno and Chao, 1988 and *P. mazongshanensis* (Brinkman et al., 2001).

2.2. Remarks

The referral of the new species *Psittacosaurus lujiatunensis* to the genus *Psittacosaurus* is based on several shared derived characters listed as follows: the preorbital region is less than 40% of the length of the skull; the external naris is dorsally positioned on the side of the snout; the nasal meets the rostral bone well below the external naris; the premaxilla intervenes between the maxilla and external naris; the premaxilla, maxilla, lacrimal and jugal nearly meet at a point on the side of the snout; the dentary teeth have a bulbous primary ridge; and the tip of predentary is rounded (see Sereno, 1990). Within the genus, *P. lujiatunensis* is clearly distinguished from other species by its diagnostic characters (see above).

Until now, the valid species of *Psittacosaurus* have been limited to no more than seven (Xu and Zhao, 1999): *Psittacosaurus mongoliensis*, *P. sinensis*, *P. xinjiangensis*, *P. meileyingensis*, *P. neimongoliensis*, *P. ordosensis* and *P. mazongshanensis*. Of these, the validity of *P. mazongshanensis* (Xu, 1997) has been recently ques-

tioned and the species name regarded as a nomen dubium (Sereno, 2000). Our examination of the fossil material, however, indicates that this species is valid based on a peculiar character, the strong ventral expansion of the maxillary protuberance, differing from the laterally expanded condition in other species. Unfortunately, the holotype of *P. mazongshanensis* (IVPP V12165) was broken and some fragments of the skull and jaws were lost after the specimen was accessioned in the IVPP collections. All of the teeth have been lost, so that the diagnostic characters of the tooth crowns cannot be observed. The skull is compressed dorsoventrally, with the roof having been flattened on to the palate. Some "diagnostic" characters – the Y-shaped lower jaw, and three planes of the maxillary lateral surface, for example – are apparently artifacts caused by this compression.

The temporal distribution of psittacosaurids has been limited to the late Early Cretaceous (Aptian-Albian) (Sereno, 1990; Dong, 1993; Xu and Zhao, 1999). Based on more recent and detailed stratigraphic studies of psittacosaur-bearing sediments in northern China, the geological range of psittacosaurs has been narrowed to mostly late Barremian–early Albian (e.g., Eberth et al., 1993; Tang et al., 2001). Because the upper parts of the Lujiatun beds of the Yixian Formation in western Liaoning have been dated as 128.4 ± 0.2 Ma by ^{40}Ar/^{39}Ar radiometric techniques (Wang et al., 2001), the age of these beds appears to be Hauterivian (132.0–127.0 Ma) (Li et al., 2003; Zhou et al., 2003). Therefore, the psittacosaur fossils from this horizon in the Jehol Group comprise the oldest record of the family Psittacosauridae.

Previous studies of psittacosaur phylogeny have shown some serious ambiguities: One paper (Russell and Zhao, 1996) presented a data matrix, but no phylogenetic hypothesis (cladogram), and another paper (Xu, 1997) presented a data matrix that is inconsistent with the character description and codings as given in the text. In view of the resulting uncertainties, the interrelationships of the *Psittacosaurus* species remain unresolved. From previous studies, however, four characters are worth considering in comparing *P. lujiatunensis* with other psittacosaur species. First, the posterior process of the pterygoid has different states in *P. mongoliensis* and *P. lujiatunensis* (although this feature is unknown in other psittacosaurs). The posterior process is prominent in *P. mongoliensis* and most neoceratopsians (Xu et al., 2002), but it is absent in *P. lujiatunensis*. The process is also absent in the more basal groups, *Chaoyangsaurus* and *Hypsilophodon* (Huxley, 1869), whereas it is present, probably independently, in the pachycephalosaur *Stegoceras* (Lambe, 1902; Xu et al., 2002); therefore, its occurrence

in *P. mongoliensis* and neoceratopsians appears to be derived. Second, the internal naris in *P. lujiatunensis* is anterior to the maxillary tooth row, a primitive character state, differing from that in *P. mongoliensis*, in which it occurs at the level of the maxillary tooth row (this feature is unknown in other psittacosaur species). The primitive state is also present in the more basal groups (*Hypsilophodon* and *Stegoceras*), although unknown in *Chaoyangsaurus*. Third, the reduced antorbital fossa is present in *P. mongoliensis* and *P. lujiatunensis*, absent in *P. sinensis* and *P. neimongoliensis*, and only weakly developed in other species. A large antorbital fossa is always present in the basal groups and neoceratopsians. Therefore, the reduced antorbital fossa in *P. mongoliensis* and *P. lujiatunensis* possibly represents a primitive character state within the Psittacosauridae. Last, the ectopterygoid is exposed in the palate, a primitive character present in *P. lujiatunensis*, *P. sinensis* and the more basal groups. However, the ectopterygoid is not exposed in the palate in *P. mongoliensis* (it is unknown in other psittacosaur species). In sum, these characters suggest that *P. lujiatunensis* is more basal than *P. mongoliensis*, *P. sinensis* or the other known psittacosaur species, although most characters are undiscovered in these other species. The result of this comparison is consistent with the temporal distribution of the new specimens, which represent the oldest record of the genus.

As the oldest known psittacosaurs, *P. lujiatunensis* is morphologically distinct from *Liaoceratops* Xu, Makovicky, Wang, Norell and You, 2002, the most closely related group of neoceratopsians (Xu et al., 2002). Hence, the discovery of *P. lujiatunensis* further supports the hypothesis that the divergence of psittacosaurids and neoceratopsians from the ceratopsian stem took place no later than the earliest part of the Cretaceous (Xu et al., 2002).

3. Conclusions

This study comes to the following conclusions:

1. A new taxon, *Psittacosaurus lujiatunensis*, is erected based on well-preserved specimens recently found from the Lujiatun beds, the lowest part of the Yixian Formation in western Liaoning Province, China. This discovery increases the taxonomic diversity of *Psittacosaurus* to eight valid species, and provides new information for understanding character evolution among psittacosaurs.

2. The new taxon *Psittacosaurus lujiatunensis* represents the oldest known psittacosaur so far, extending

the stratigraphic range of psittacosaurs in the Early Cretaceous from late Barremian-Albian to Hauterivian.

3. Comparative study of the new species with other well-known psittacosaurs indicates that the new taxon is probably a basal member of the psittacosaur clade. This interpretation, in agreement with temporal distribution of the clade, supports further the hypothesis that the Psittacosauridae split from basal ceratopsians no later than the earliest part of the Cretaceous.

Acknowledgments

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