

JUVENILE SPECIMENS OF THE ORNITHISCHIAN DINOSAUR *PSITTACOSAURUS*

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ABSTRACT. Hitherto undescribed specimens of *Psittacosaurus mongoliensis* from the Oshih Fm., Mongolian Peoples' Republic, include two almost complete skulls and numerous postcranial elements. A rostral bone, present in these and other specimens of *Psittacosaurus*, is a cranial element otherwise known only in ceratopsians, and its presence indicates a sister group relationship for the Psittacosauridae and Ceratopsia. Each of the two new specimens of *Psittacosaurus* is a juvenile, and are among the smallest dinosaur specimens yet described. Parental attendance of nests was common, possibly universal among dinosaurs, but post-hatching parental care is uncertain. Juveniles of *Psittacosaurus*, as well as those of other dinosaurs, may have formed sibling groups.

Two skeletons of small bipedal ornithischians collected by the Third Asiatic Expedition (1922) of the American Museum of Natural History were described by Osborn (1923, 1924) as the types of *Psittacosaurus mongoliensis* (Oshih Fm.) and *Protiguanodon mongoliense* (Andai Sair Fm.), thought to be a primitive ankylosaur and a primitive iguanodontid, respectively. To the family Psittacosauridae, erected for reception of these two species (Osborn 1923), have been added several new species of *Psittacosaurus* and additional fragmentary remains from various localities in Mongolia and northern China (Young 1931, 1958; Bohlin 1953; Maleev 1954; Rozhdestvensky 1955; Chao 1962). Described below are two additional specimens of *Psittacosaurus* from the same locality as the type of *P. mongoliensis*.

MATERIAL

AMNH 6535 (= American Museum of Natural History, New York), partial skull and jaws.

AMNH 6536, almost complete skull and jaws with numerous distarticulated postcranial elements including: cervical, dorsal, and caudal vertebrae; ribs; scapulae; coracoid; partial ilium and ischium; humeri; femora; tibiae; fibulae; and an almost complete left pes. The postcranial material belongs to several individuals (there are fourteen distal ends of tibiae) of at least two different sizes (some femoral fragments are tiny and more compatible in size with the skull AMNH 6535). Rather than allot separate numbers to every element, all of the postcranial material is arbitrarily assigned to AMNH 6536.

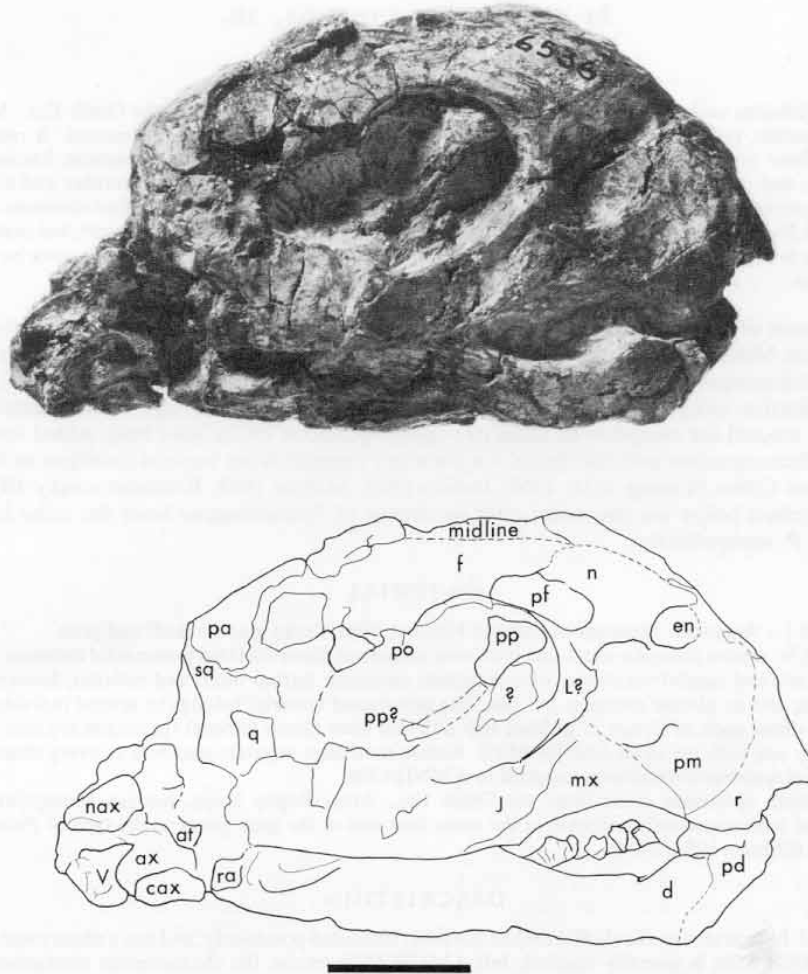
Locality. Both specimens come from the Oshih Fm., Artsa Bogdo basin, western Mongolian Peoples' Republic, and were apparently collected at the same time and in the same place as the type of *Psittacosaurus mongoliensis* (Osborn 1923, 1924).

DESCRIPTION

Skull, general. In lateral view the skull is arched dorsally, truncated posteriorly, and has a short snout (text-figs. 1, 3, 4). AMNH 6536 is laterally crushed, but AMNH 6535 retains the characteristic triangular shape of psittacosaur skulls, with the greatest breadth across the flaring jugals and a sharply pointed apex at the beak (Pl. 14). The apparent relatively large size of the brain in AMNH 6535 is a juvenile character (Pl. 14, figs. 1 and 2). The diameter of the orbit equals 33% of cranial length in AMNH 6536; 38% in AMNH 6535, the relatively large orbit also being a juvenile characteristic. The nostril is clearly delineated only on the right side of AMNH 6536, on which it is small, circular, and approximately at the level of the upper half of the orbit.

Cranial fenestrae. Both skulls are damaged posteriorly and borders of all temporal fenestrae are incomplete. The left supratemporal fenestra of AMNH 6536 is oval with its long axis paralleling the midline. The braincase is broad and devoid of a sagittal crest between the upper fenestrae (Pl. 14). Lateral temporal fenestrae are

evidently tall and narrow, and considerably smaller than the orbit, unlike the condition in adult *Psittacosaurus* in which the fenestrae are larger than the orbit (e.g. Osborn 1923, fig. 2). AMNH 6536 has a shallow depression, its depth somewhat exaggerated by crushing, between nostril and orbit in the region where an antorbital fenestra might be located, but there is no opening into the interior of the skull (text-fig. 1). AMNH 6535 is badly crushed in the immediate pre-orbital region, but it appears that a true antorbital fenestra was not present.



TEXT-FIG. 1. AMNH 6536, skull, lower jaws, and anterior cervical vertebrae; right side with key drawing. Abbreviations: at, atlas; ax, neural arch of axis; cax, centrum of axis; d, dentary; en, external naris; f, frontal; j, jugal; l, lacrimal; mx, maxilla; n, nasal; nax, neural spine of axis; pa, parietal; pd, predentary; pf, prefrontal; pm, premaxilla; po, postorbital; pp, palpebral; q, quadrate; r, rostral; ra, retroarticular process; sq, squamosal; and v, cervical vertebrae (post-atlas). Length of reference line = 1.0 cm (approximately twice natural size).

Rostral. Following Maryńska and Osmólska (1975, p. 172), the most anterior element of the snout is identified as a rostral, a bone diagnostic of ceratopsians, rather than as a premaxilla as suggested by Osborn (1923; see also Young 1958; Chao 1962). The rostral, best preserved on the smaller skull (text-fig. 4), is roughly triangular in lateral view with an ascending ramus that curves posteriorly to terminate near the ventral margin of the nostril. Most of the cutting margin of the beak is composed of the rostral, but it is unclear to what extent the rostral contributes to the anterior palatal shelf.

Premaxilla. Exact limits of the premaxillae are unclear, but the bone probably intervenes between the rostral and the external nares and forms all the ventral border of the latter opening (text-fig. 3; Maryńska and Osmólska 1975). Because other authors have identified the rostral as the premaxilla, the true premaxilla has been identified as part of the maxilla. In consequence, *Psittacosaurus* has been reconstructed with a very large maxilla that separates the premaxilla from the lacrimals as well as from the margin of the nostril (Osborn 1923, fig. 2A; Young 1958, fig. 51; Chao 1962, fig. 1) a pattern atypical for ornithischians. The alternative interpretation presented here (text-fig. 3) indicates extensive contact of premaxilla and lacrimal with exclusion of the maxilla from the border of the nostril, a pattern common among ceratopsians and ornithischians in general (Lull 1933; Romer 1956). Ornithischians typically have a bony roof to the anterior part of the buccal cavity composed of premaxillae, maxillae, and sometimes the vomers. In the Ceratopsia the rostral bone forms much of the cutting edge of the beak, but forms only a small segment of the anterior palatal shelf (Lull 1933, figs. 5 and 30; Maryńska and Osmólska 1975, fig. 9). *Psittacosaurus* may have a similar arrangement, but sutures are unclear on the present specimens (Pl. 14, figs. 3 and 4).

Maxilla. Anteriorly the maxilla may contact the posterior limit of the rostral along the edge of the mouth in the present specimens, but contact is lost in adult *Psittacosaurus*. Maxillary teeth, numbering at least five in AMNH 6535 and at least six in AMNH 6536, are withdrawn medially, so that the maxilla forms a lateral shelf thus delineating the dorsal border of a 'cheek-pouch', a common feature among ornithischians (Galton 1973).

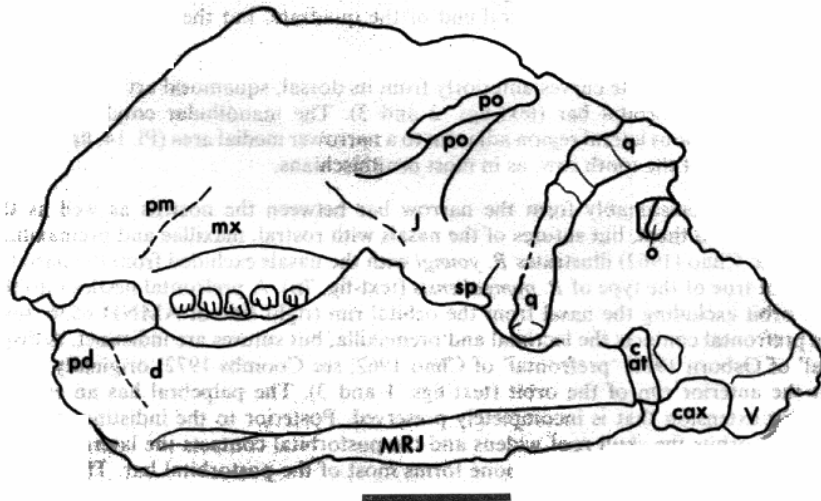
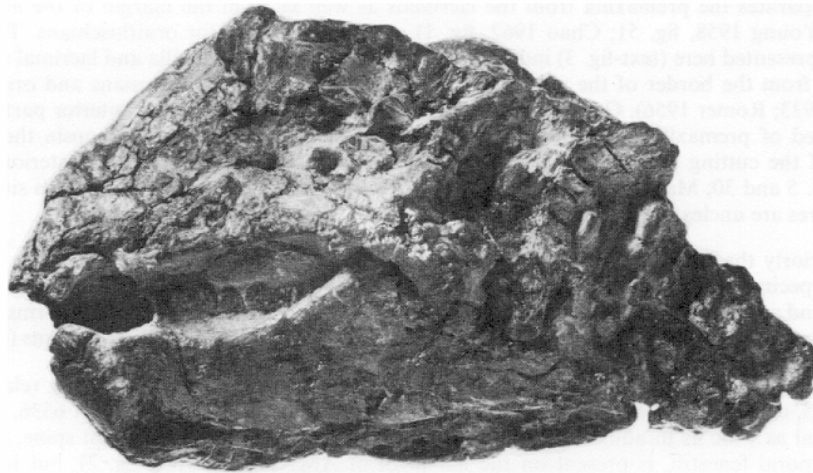
Jugal. All the ventral margin of the orbit is formed by the jugal, the suborbital bar being relatively slender in AMNH 6535, considerably wider and giving an impression of massiveness in AMNH 6536, but in neither skull is the jugal as wide as in adult *Psittacosaurus*. A ventro-laterally projecting jugal spine, located below the lateral temporal fenestra, is present on the left jugal of AMNH 6536 (text-fig. 2), but is considerably smaller than the prominent flange of adult *Psittacosaurus* skulls (Osborn 1923, 1924; Young 1958; Chao 1962). A slender ascending ramus of the jugal forms part of the postorbital bar. A quadratojugal presumably intervenes between the jugal and the ventral end of the quadrate, but the element cannot be distinguished on either of the present specimens.

Quadrate. The elongate quadrate curves anteriorly from its dorsal, squamosal articulation and is two to three times wider than the postorbital bar (text-figs. 2 and 3). The mandibular cotylus is compressed antero-posteriorly and has a bulbous lateral region adjacent to a narrower medial area (Pl. 14, figs. 3 and 4). The cotylus projects below the level of the tooth row, as in most ornithischians.

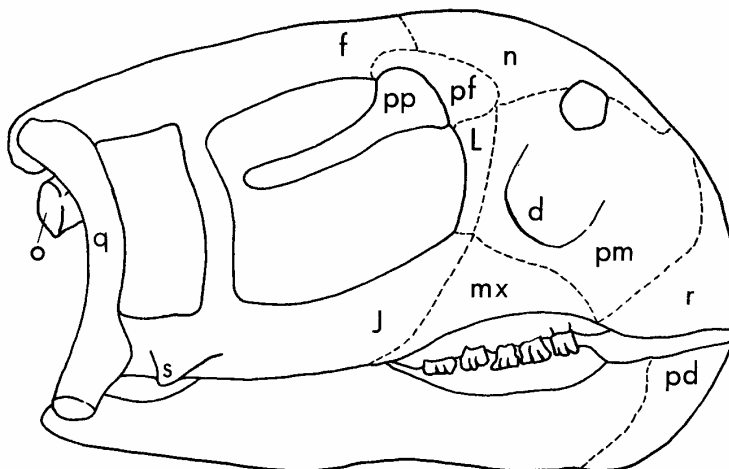
Skull roof. The nasals presumably form the narrow bar between the nostrils as well as the wider region immediately posterior to them, but sutures of the nasals with rostral, maxillae and premaxillae are not visible on either specimen. Chao (1962) illustrates *P. youngi* with the nasals excluded from the narial border (text-fig. 7C), but this is not true of the type of *P. mongoliensis* (text-fig. 7D). A prefrontal nestles into the antero-dorsal margin of the orbit excluding the nasal from the orbital rim (right side of AMNH 6536, text-figs. 1 and 3). Ventrally the prefrontal contacts the lacrimal and premaxilla, but sutures are indistinct. A displaced palpebral ('supraorbital' of Osborn 1923; 'prefrontal' of Chao 1962; see Coombs 1972) originally articulated with the prefrontal at the anterior rim of the orbit (text-figs. 1 and 3). The palpebral has an expanded base and a tapered posterior extension that is incompletely preserved. Posterior to the indistinct contact of nasals and frontals above the orbits the skull roof widens and the postorbital contacts the lateral edge of the frontal. A slender descending rod of the postorbital bone forms most of the postorbital bar. The relative contributions of the postorbitals, frontals, and parietals to the margins of the supratemporal fenestrae cannot be determined. Parietals form most of the arched posterior skull roof, without the sagittal crest present in adult skulls (see also skull of *Psittacosaurus osborni* Young, 1931, fig. 2). The parietals bend sharply downward at the posterior margin of the skull roof to form the most dorsal surface of the occipital region.

Occipital area. Very little of this region is exposed. The rugose distal tip of the left opisthotic of AMNH 6536 projects from matrix well below the level of the skull roof and the dorsal tip of the quadrate (text-fig. 2). The element is roughly triangular in section, not as flattened as is typical for Ornithischia.

Palate. Some palatal details are visible on the smaller skull (Pl. 14, figs. 3 and 4). An anterior palatal shelf is formed partly of the rostral and partly of the premaxillae, and is roughly semicircular in shape, being less pointed and less triangular than in adult *Psittacosaurus*. The vomers form a median vertical plate that dominates the interior palatal region. The ventral keel of this plate extends below the level of the tooth rows, a condition found in several ornithischians (e.g. the ankylosaur *Panoplosaurus*; Russell 1940). A narrow shelf from the maxillae appears to contact the vomer keel anteriorly, thus shifting the internal nares posteriorly. The internal nares are bounded laterally and anteriorly by maxillae, medially by the vomer keel, and are bounded posteriorly by a broad plate of bone that slants obliquely anteriorly and upward toward the skull



TEXT-FIG. 2. AMNH 6536, skull, lower jaws and anterior cervical vertebrae; left side with key drawing. Abbreviations: cat, centrum of atlas; cax, centrum of axis; d, dentary; J, jugal; MRJ, medial side of right lower jaw; mx, maxilla; o, opisthotic; pd, predentary; pm, premaxilla; po, postorbital; q, quadrate; sp, spine of jugal; v, cervical vertebra (post-atlas). Length of reference line = 1.0 cm (approximately twice natural size).



TEXT-FIG. 3. Restoration of a juvenile *Psittacosaurus* skull based primarily on AMNH 6536. Abbreviations: d, depression in premaxilla; f, frontal; j, jugal; L, lacrimal; mx, maxilla; n, nasal; o, opisthotic; pd, prementary; pf, prefrontal; pm, premaxilla; pp, palpebral; q, quadrate; r, rostral; and s, spine of jugal.

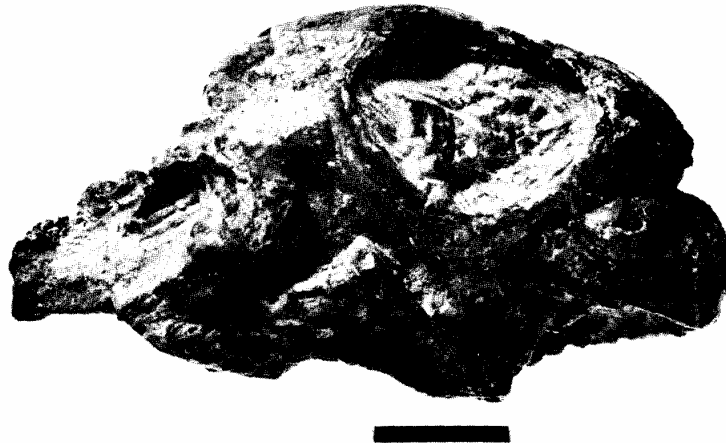
roof. The latter plate is composed of pterygoid, ectopterygoid, and palatine bones, but sutures are unclear. The palatal structure of *Psittacosaurus* is similar to that of many Ornithischia, especially the quadrupedal forms, and may be compared particularly to the palate of *Bagaceratops* (Maryańska and Osmólska 1975, fig. 9).

Basicranium. The partially exposed basicranium of AMNH 6535 (Pl. 14, figs. 3 and 4) is broad relative to other skull dimensions (a juvenile feature), and has a median longitudinal depression that is flanked by anteriorly converging ridges. A small, subspherical, posteriorly directed occipital condyle projects only slightly below the level of the basicranial floor.

Lower jaw. The deep, massive lower jaw has a straight ventral margin and medially displaced dentary teeth (text-fig. 1). A curved shelf marks the ventral border of the cheek pouch. The prementary and dentary bones are fused together. Posteriorly there is a pointed coronoid process projecting upward medial to the most anterior ventral corner of the lateral temporal fenestra. A short retroarticular process projects backward from the articular (text-fig. 1).

Teeth. Anterior maxillary teeth have three ridges on the lateral surface that upon wear produce the 'trilobate' cutting margin described by Osborn (1924; text-fig. 2). Posterior maxillary teeth may have four ridges and are generally larger but less worn than anterior teeth. All teeth that are adequately exposed on the two skulls are worn to some degree. There are no premaxillary teeth.

Vertebrae. Cervical vertebrae attached to the skull of AMNH 6536 include the axis, which has a low, laterally compressed, elongate neural spine as described in the type of *Protiguanodon mongoliense* (AMNH 6253; Osborn 1924). A small block of bones (part of AMNH 6536) contains several vertebrae, mostly dorsals (text-fig. 5). The centra are laterally compressed, with expanded, roughly heart-shaped articular ends. The neural arches are not fused to the centra, a juvenile characteristic. A particularly well-preserved neural arch of a dorsal(?) vertebra has about the same length as its centrum; the incomplete zygapophyses arch upward and there is an almost circular diapophysis high on the side of the neural arch. A sacral vertebra in the same block has a centrum similar in shape to dorsal centra, and has a low, broad neural arch with an elongate, laterally compressed neural spine most of which is broken off. The sacral rib articulated on anteroposteriorly compressed diapophyses positioned at the extreme anterior end of this sacral, which judged from the sacral



TEXT-FIG. 4. AMNH 6535, skull, partial lower jaw, and fragmentary anterior cervicals, right side. Length of reference line = 1.0 cm (approximately twice natural size).

series of *Protoceratops* (Brown and Schlaikjer 1940), is from the middle of the sacral series. Another sacral vertebra in the block also has an elongate, compressed diapophysis but it is oriented almost horizontally, suggesting that this vertebra belongs to the posterior end of the sacral series. A group of three caudal centra (text-fig. 6N), all lacking the neural arch, are smaller than either dorsals or sacrals but have similar shape and proportions. Transverse processes are not present on any of the caudals. The largest of these three caudal centra is about 4.5 mm in length.

Ribs. Rib fragments embedded in the block with other postcranial elements have cross sections that are either circular (proximal ends) or compressed (distal ends, text-fig. 5). One proximal end fragment has a large, almost circular head that matches in size and shape the articular surface on the dorsal vertebra described above, and a very small tubercle positioned a short distance from the head.

Pectoral girdle. Scapulae are represented by two almost complete elements (text-fig. 5), plus a partial scapular blade. The scapulae are elongate and narrow, with a much wider, slightly concave area adjacent to the glenoid and coracoid articulation. The upper end of the blade is broad but flattened. A low scapular spine arises from the extreme anterior edge of the scapula directly opposite the glenoid. The glenoid articulation is short, broad, slightly concave, and has a rather massive dorsal lip. The coracoid articulation is elongate and

EXPLANATION OF PLATE 14

Two views of AMNH 6535, a skull, partial lower jaw and fragments of anterior cervical vertebrae.

Fig. 1. Dorsal view, stereo pair.

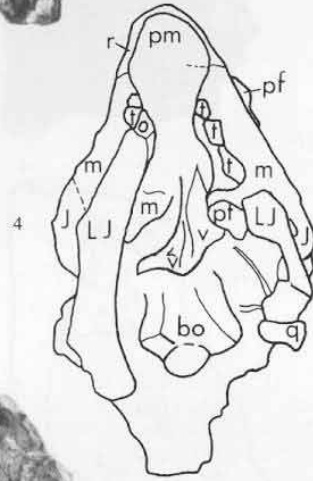
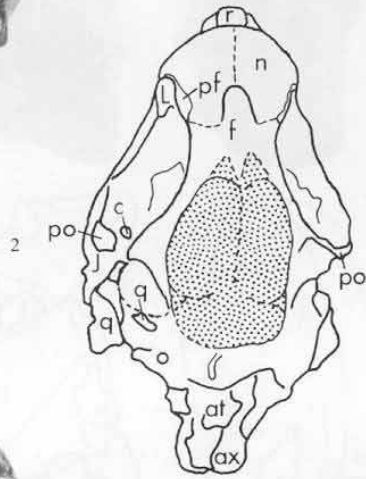
Fig. 2. Key to structures visible in the dorsal view. Stippling indicates the approximate extent of a natural endocranial cast that has been partially exposed through loss of some dorsal cranial bones. The anterior limit of the endocranial space was determined in part by examination of AMNH 6536 which has the anterior tip of a natural endocranial cast exposed through loss of some skull bones.

Fig. 3. Ventral view, stereo pair.

Fig. 4. Key to structures visible in ventral view. Abbreviations: at, atlas; ax, axis; bo, basioccipital; c, left coronoid process (protruding through matrix); f, frontal; j, jugal; L, lacrimal; LJ, lower jaw; m, maxilla; n, nasal; o, opisthotic; pm, premaxilla; po, postorbital; pt, pterygoid; q, quadrate; r, rostral; t, tooth. Length of reference line = 1.0 cm (approximately twice natural size).



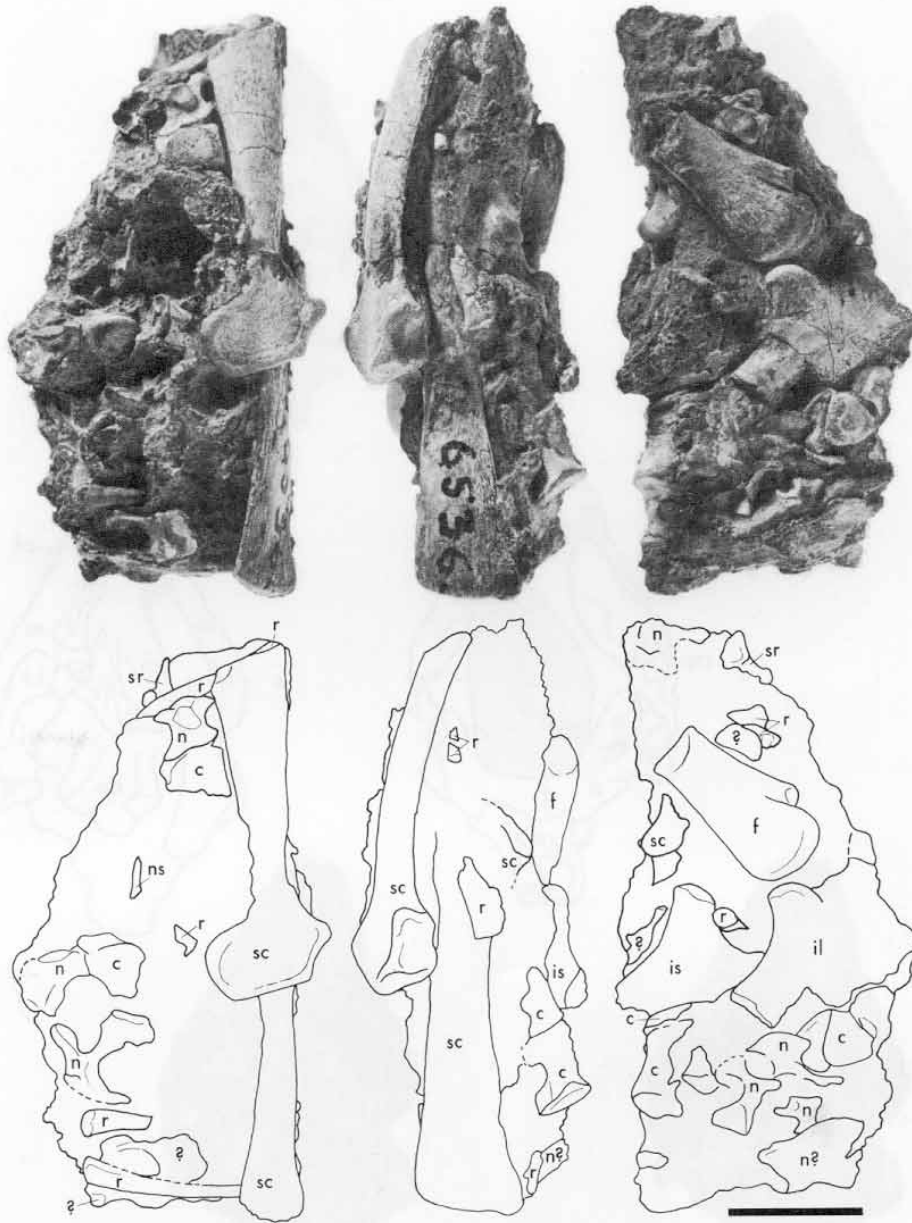
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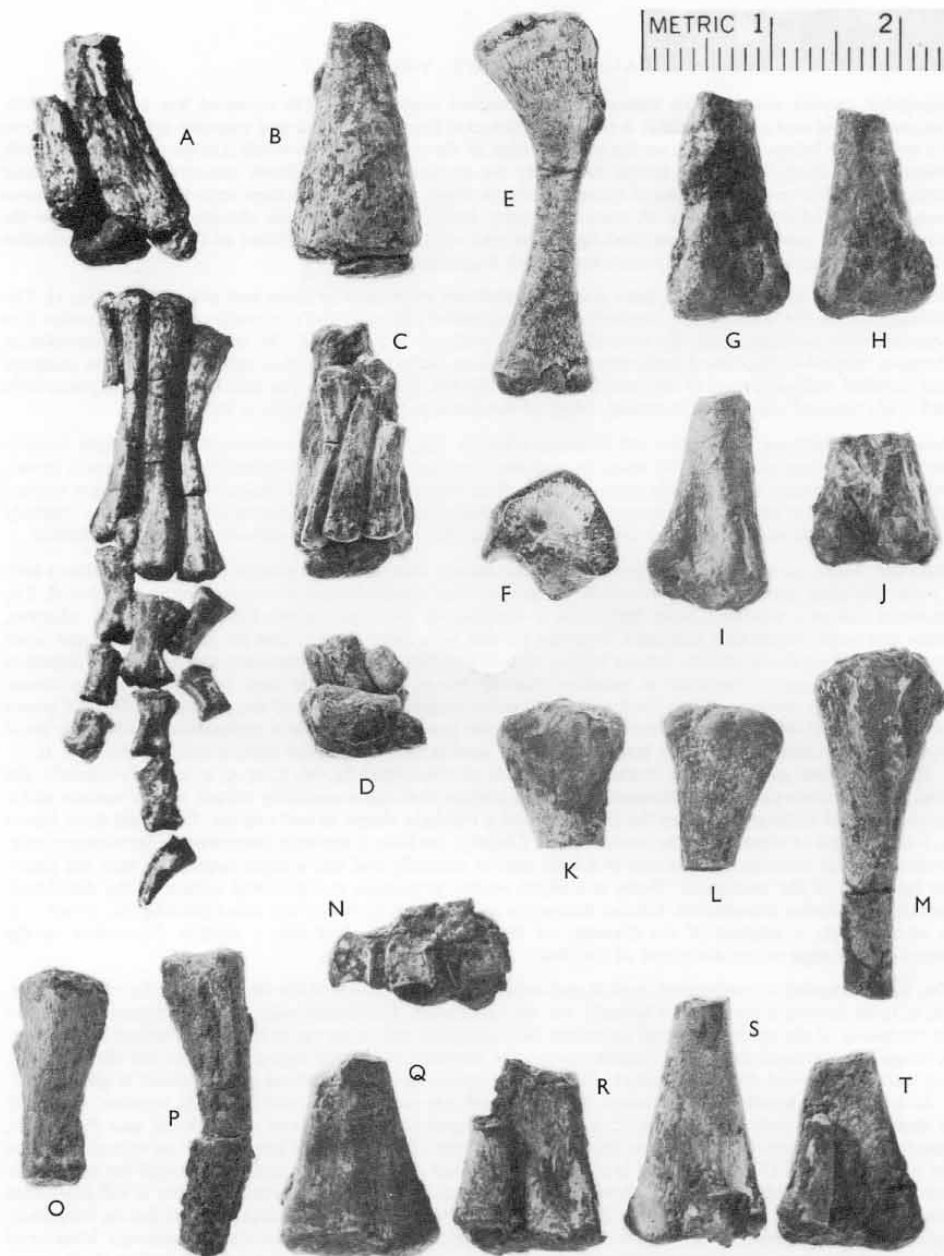
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COOMBS, *Psittacosaurus*



TEXT-FIG. 5. AMNH 6536, three views of a block containing various postcranial elements, with key drawings. Abbreviations: c, centrum; f, femur; il, ilium; is, ischium, n, neural arch, r, rib; sc, scapula; sr, sacral rib; and a question mark denoting an unidentified fragment. Length of reference line = 1.0 cm (approximately twice natural size).



TEXT-FIG. 6. AMNH 6536, various postcranial elements. A, partial left pes with distal ends of tibia and fibula; B, posterior view of a partial left tibia with astragalus and metatarsals II, III, and IV; C, same as B in anterior view; D, same as B in distal view; E, left humerus, flexor surface; F, right coracoid, lateral view; G, H, I, and J, distal ends of four femora, posterior views; K, L, and M, proximal ends of three tibiae, anterior views; N, block containing three caudal centra; O and P, proximal ends of two small femora, anterior views; Q, R, S, and T, distal ends of four tibiae, anterior views, with distal ends of fibulae on R and T. Scale divisions in mm (approximately twice natural size).

triangular, exactly matching an associated left coracoid (text-fig. 6F). The coracoid has a broad, slightly concave glenoid and a foramen that is roughly equidistant from the glenoid and scapular articulations. There is a prominent biceps tuberosity on the anterior edge of the coracoid, from which a ridge extends posteriorly toward the glenoid. Below the biceps tuberosity the coracoid has a shallowly concave, medially inclined surface that is the probable region of coracobrachialis origin. Clavicles have been reported for *Psittacosaurus mongoliensis* (Osborn 1924) and *P. sinensis* (Young 1958), but there are no clavicles associated with the scapulae of the present specimens (text-fig. 5). In view of the jumbled condition of the bones, the clavicles could well be displaced and easily mistaken for rib fragments.

Pelvic girdle. Of the pelvic girdle there is one fragmentary piece each of ilium and ischium (text-fig. 5). The ilial fragment is flat with a blunt, ventrally projecting ischial peduncle and a laterally compressed, rather thin postacetabular segment. Only the base of the pubic peduncle is preserved. The ischial fragment includes an elongate, laterally compressed pubic articulation, and an ilial articulation that appears to be more compact and rounded, although most of the latter is hidden below the ilial fragment. The ischial blade slants posteriorly and is narrow and laterally compressed. Most of the distal part of the ischium is missing.

Forelimb. In addition to a perfect left humerus (text-fig. 6E), there are two proximal ends of right humeri, one about the same size as the left humerus and one considerably smaller. Proximally, the humerus is broad, but it tapers quickly to a roughly circular shaft, then widens at the distal articulations which are rotated relative to the head such that the extensor surface is twisted medially. A deltopectoral crest projects ventrally and is rather close to the proximal end of the humerus. No other forelimb elements have been identified.

Hindlimb. There are numerous fragments, but unfortunately there is no association of a particular femur with a particular tibia, nor with the pes described below, so that hindlimb proportions cannot be established. The proximal end of a relatively large femur has a compressed, crest-like greater trochanter with an adjacent, finger-like lesser trochanter separated from the former by a deep furrow, and an irregularly circular shaft (text-fig. 5). Two much-smaller femora have a virtually identical set of trochanters and a medially displaced head that is as much cylindrical as spherical (text-fig. 6O, P). The femoral shaft is curved with the convex surface lateral, a common shape for femora of bipedal Ornithischia. None of the eight distal femoral pieces included in AMNH 6536 can be fitted on to any of the proximal ends. Distal articulations follow the usual bipedal ornithischian pattern of a larger lateral and smaller medial articular surface (text-fig. 6G, H, I, J).

There are seven proximal and fourteen distal ends of tibiae (text-fig. 6K, L, M, Q, R, S, T). Proximally, the tibia has an antero-posteriorly elongated articular surface that has a smoothly curved medial surface and a notched lateral surface that gives the proximal end a trilobate shape viewed end-on. The tibial shaft tapers to a slender rod of almost circular cross-section. Distally, the tibia is strongly compressed antero-posteriorly, creating a wide articular surface that is a little thicker medially and has a slight depression near the centre for reception of the astragalus. There is a slight ventral projection at the lateral corner of the distal end, marking the fibular articulation. Fibular fragments still attached to two of the tibiae (text-fig. 6R, T) are oval in section, only a fraction of the diameter of the tibial shaft, and fit into a shallow depression on the antero-lateral edge of the distal end of the tibia.

Pes. The astragalus is compressed against and covers about two-thirds of the distal end of the tibia (text-fig. 6A, B, C, D) leaving a small space laterally for the calcaneum. The lateral edge of the astragalus is notched for reception of the calcaneum, and anteriorly the astragalus curves up on to the flexor surface of the tibia. A roughly cup-shaped calcaneum nestles against the ventrally projecting lateral corner of the tibia (text-fig. 6A), and as preserved does not contact either the astragalus or fibula. A distal row of tarsals is not present.

As is typical of bipedal ornithischians, the metatarsals are long, slender, and fit tightly together, especially at their proximal ends (text-fig. 6A, C, D). As in the types of *Psittacosaurus mongoliensis* and *P. sinensis*, metatarsals I through IV are present, but there is no trace of metatarsal V nor is there an articular surface for it on metatarsal IV. Metatarsal I is strongly compressed at the proximal end and through the upper two-thirds of the shaft. Metatarsal II is about double the width of metatarsal I proximally, but is still somewhat compressed. Metatarsal II has a wider shaft and is longer than metatarsal I. Metatarsal III has an irregularly square proximal articular surface and is the longest, straightest, and most massive of the metatarsals. Metatarsal IV is about the same length as metatarsal II, but is more compressed at the proximal end, and its shaft curves slightly away from the axis of the pes running through metatarsal III. Phalanges have the typical form found in small bipedal ornithischians (text-fig. 6A). All are relatively long (length greater than diameter) and are circular to subrectangular in cross-section, not dorsoventrally compressed. One almost complete ungual of digit III is slightly longer than the adjacent phalanx and has a narrow, semi-claw shape as in *Leptoceratops* (Brown 1914; Brown and Schlaikjer 1942) rather than the broad, hoof-like unguals of *Protoceratops* (Brown

and Schlaikjer 1940). The pes is narrow, long, and gracile (text-fig. 6A), suggesting a relatively fleet animal. Of interest is the manner in which the pes is folded against the anterior surface of the tibia in one specimen (text-fig. 6B, C, D), a post-mortem posture also found in the types of *Psittacosaurus mongoliensis*, *Protiguanodon mongoliense*, and *Stenopelix valdensis* (Osborn 1923, 1924; Meyer 1857; Koken 1887). When these animals died, they settled on to their belly with the hindlimbs folded into a sharp 'Z', the knee projecting forward, ankle backward, femur atop the tibia, and pes pressed against the anterior surface of the tibia and apparently set flat against the ground (this posture is imperfectly preserved also in specimens of *Psittacosaurus sinensis*: Young 1958, figs. 52, 53, and 54). The imprint of the pes would conform to the sitting dinosaur trackways from the Connecticut Valley (e.g. *Sauropus barrattii* and *Anomoepus scambus* specimens described by Lull 1953). The belly-down position is not common among bipedal ornithischians. The skeletons of *Iguanodon* and most hadrosaurids are typically found lying on their side with the knee and ankle both flexed rearward, or with the pes almost aligned with the tibia. Psittacosaurids apparently had great mobility of the knee and mesotarsal joint, with hyperextensibility of the ankle permitting the entire length of the pes to be laid flat on the ground. The difference in joint mobility in psittacosaurids and large bipeds may be related to total body size, the larger ornithischians sacrificing some ankle extensibility for the sake of rigidity necessary for weight-bearing.

DISCUSSION

Taxonomy. Rozhdestvensky (1955) regarded *Psittacosaurus mongoliensis* Osborn (1923) as the senior synonym of the following: *Protiguanodon mongoliense* Osborn (1923 = *Psittacosaurus protiguanodonensis* of Young 1958); *Psittacosaurus osborni* Young (1931); *?Psittacosaurus tingi* Young (1931); and *Protiguanodon cf. mongoliense* (of Young 1931). Trivial differences among these species are reasonably regarded as stemming from ontogenetic state and individual variation. *Psittacosaurus sinensis* Young (1958) and *P. youngi* Chao (1962) may also be junior synonyms of *P. mongoliensis* although, without having all the specimens in hand for detailed comparison of measurements and proportions not available in extant descriptions, formal suppression of all but one species is premature. *Stenopelix valdensis* Meyer (1857; see also Koken 1887; Huene 1908) from Wealden deposits (Swinton 1936) of northern Germany was originally classified in the Hypsilophodontidae (Huxley 1870), but has also been suggested as a ceratopsian (Huene 1909; Lull 1910) and a psittacosaur (Romer 1956). The reported absence of a postpubic process and the exclusion of the pubis from the acetabulum in *Stenopelix* are features unknown in psittacosaurids, but have been reported for the pachycephalosaur *Homalocephale* (Maryńska and Osmólska 1974), and *Stenopelix* has been classified in the Pachycephalosauridae (Galton 1976; Olshevsky 1978). Contact of the ischium with the pubic peduncle with resultant exclusion of the pubis from the acetabulum may also be common among ankylosaurs, although obscured in most specimens by fusion of the pelvic elements, and ankylosaurs have a very short postpubic process. In any case, assignment of *Stenopelix* to the Psittacosauridae cannot be defended on the basis of common derived characters, and the genus is here considered as Ornithischia, *incertae sedis*. The family Psittacosauridae is therefore regarded as having a single genus, *Psittacosaurus*, with the type species *P. mongoliensis*, and other species being of questionable validity.

AMNH 6535 and 6536 come from the same stratigraphic and geographic locality as the type of *Psittacosaurus mongoliensis*. While the two new skulls differ in detail from the type of *P. mongoliensis*, the differences are of a kind and magnitude that are reasonably expected in such juvenile specimens, as may be appreciated by studying the hypothesized growth series (text-fig. 7). AMNH 6535 and 6536 are therefore assigned to the species *Psittacosaurus mongoliensis*.

Phylogenetic position of the Psittacosauridae. Bipedality has long been the justification for inclusion of several families, including the Psittacosauridae, within the suborder Ornithopoda, despite recognized peculiarities and the absence of critical features. Maryńska and Osmólska (1974) argued that bipedality alone was insufficient evidence for such a grouping, and removed pachycephalosaurs from the Ornithopoda (see also Olshevsky 1978). If the general dogma that bipedality is primitive (plesiomorphic) for the order Ornithischia is true (e.g. Galton 1978), then it is unsuitable as a

unifying character for the suborder Ornithopoda. Moreover, psittacosaur, like pachycephalosaurs, have no obturator process on the ischium, a feature apparently synapomorphic for the Ornithopoda *sensu stricto*. Psittacosaur has been recognized as ceratopsian-like by several authors (Rozhdestvensky 1955, 1960; Romer 1956; Gregory 1957; Young 1958; Colbert 1965; Maryńska and Osmólska 1975) but Steel (1969) noted that the absence of premaxillary teeth removed *Psittacosaurus* from the immediate ancestry of *Protoceratops*, and the peculiar structure of the *Psittacosaurus* manus (Osborn 1924) is a further barrier to placing the genus in a position ancestral to any known ceratopsian.

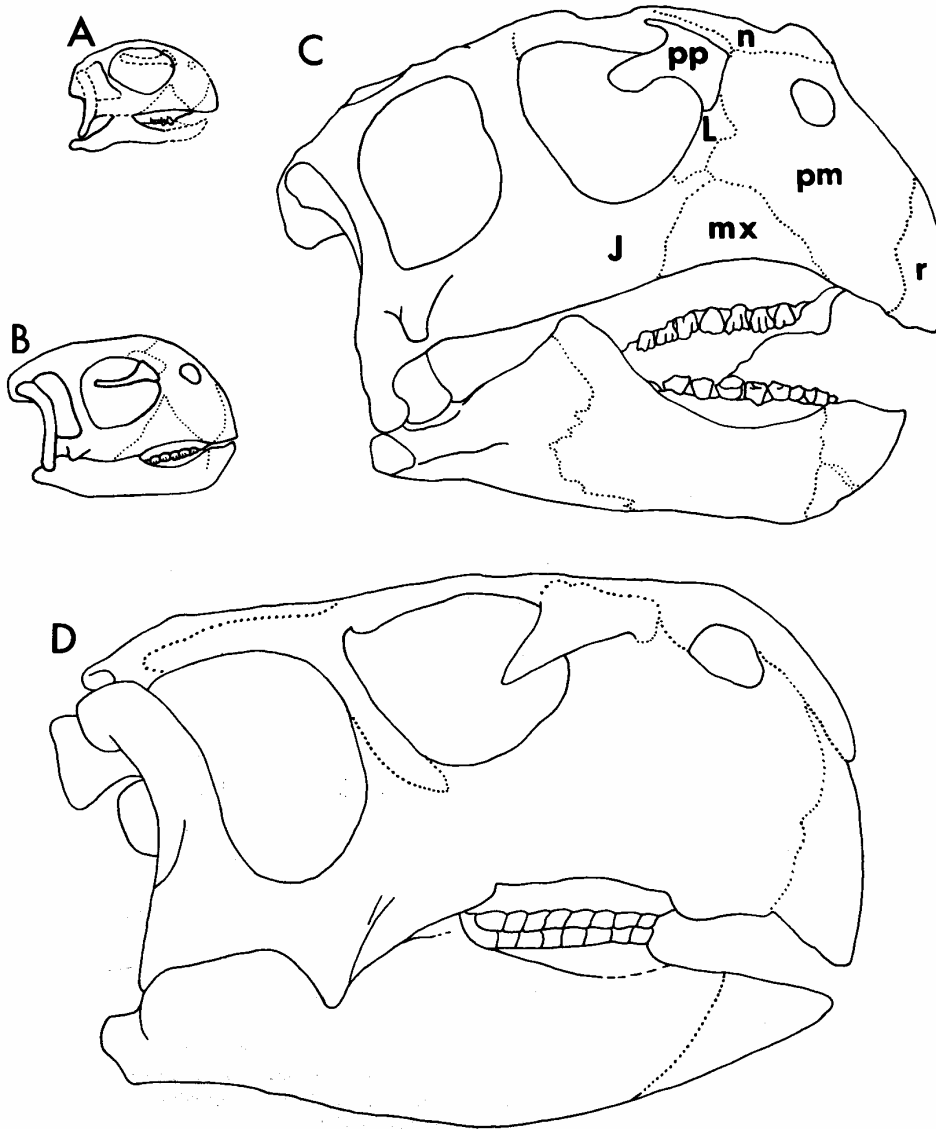
Maryńska and Osmólska (1975) recognized that the substantial similarity in general cranial morphology shared by psittacosaur and ceratopsians outweighed any arguments on the unsuitability of the former as 'ancestors' for the latter. They also realized that failure to identify a rostral bone in *Psittacosaurus* was the single major objection to transferring the Psittacosauridae to the suborder Ceratopsia, and they boldly suggested that the snout of *Psittacosaurus* had been incorrectly interpreted by Osborn (1923, 1924) and others (Young 1958; Chao 1962). Maryńska and Osmólska (1975) contended that a rostral bone is in fact present in *Psittacosaurus*, an opinion with which I fully concur (see also Olshevsky 1978).

The rostral of ceratopsians probably originated as an epidermally induced ossification, with the large, overlying epidermal scale eventually becoming a thick, heavily keratinized upper beak. The rostral and upper beak thus correspond to the prementary and associated beak of the lower jaw in origin and function. In *Psittacosaurus* the rostral is ill defined and in large part fused to the premaxillae, similar to the way in which epidermal ossifications overlie and are fused to the skull roof of ankylosaurs (e.g. Maryńska 1971, 1977). The *Psittacosaurus* rostral is not, therefore, a completely separate cranial element as it is in advanced ceratopsians, but it is nevertheless present. Revised identifications of psittacosaur skull bones (text-figs. 3 and 7c) may be compared with identifications in original descriptions.

The family Psittacosauridae is here regarded as belonging in the suborder Ceratopsia rather than in the Ornithopoda, but further refining of its position among ceratopsians is difficult. Many taxa included in the Protoceratopsidae share synapomorphies with the Ceratopsidae, for example the development of a posterior parietal-squamosal frill and at least incipient development of horns, features not present in psittacosaur. On the other hand, absence of premaxillary teeth in *Psittacosaurus* is possibly a derived character shared with the Ceratopsidae, but not with the Protoceratopsidae some of which have premaxillary teeth. The peculiar manus of *Psittacosaurus*, and the related bipedal stance, are unique developments among ceratopsians, but whether these are derived characters defining the basal sister group split of the suborder, or merely retention of primitive features by *Psittacosaurus*, is unclear. Potentially, at least, the Psittacosauridae could be the sister group of all other Ceratopsia, such a position leaving uncertain the question as to whether bipedal or quadrupedal posture was the primitive condition for the suborder.

Juvenile features. Differences between adult and juvenile ceratopsian skulls (Brown and Schlaikjer 1940; Maryńska and Osmólska 1975; Dodson 1976) provide a basis for recognition of juvenile features in the two *Psittacosaurus* skulls under consideration. Among these features are the following: orbit very large; braincase relatively large; skull roof more curved than in adult; snout short; rostral approaches and may contact maxilla, thus excluding premaxilla from border of mouth; small, narrow lateral temporal fenestrae; no sagittal crest; suborbital bar slender; and jugal flange small or absent. General changes in cranial proportions can be seen in the hypothetical ontogenetic series (text-fig. 7). Quantification of allometric relationships is not justified in view of the small sample for each age category. Consideration of juvenile features in AMNH 6535 and 6536 serves less for establishment of growth trends than for confirmation of these specimens as young *Psittacosaurus mongoliensis* and not a new taxon of small dinosaur.

Smallest dinosaur. AMNH 6535 and 6536 are each smaller than any previously reported dinosaur specimen. A listing of the smallest dinosaurs based on basal skull length yields the following



TEXT-FIG. 7. A hypothetical ontogenetic series of *Psittacosaurus* skulls based upon A, AMNH 6535; B, AMNH 6536; C, the type of *P. youngi* (after Chao 1962); and D, AMNH 6254, the type of *P. mongoliensis* (after Osborn 1923). Readily observed are a decrease in relative size of the orbit, a lengthening of the snout (pre-orbital region of skull), and a shift from a rounded to a flat-topped cranial contour. Revised identifications of some cranial elements are given in C. Abbreviations: J, jugal; L, lacrimal; mx, maxilla; n, nasal; pm, premaxilla; pp, palpebral; and r, rostral.

sequence: *Lesothosaurus diagnosticus*, 94 mm (Galton 1978; = *Fabrosaurus australis* of Thulborn 1970); *Protoceratops andrewsi*, 76 mm and 62 mm (respectively AMNH 6419 and ZPAL MgD II/7; Brown and Schlaikjer 1940; Dodson 1976; Maryńska and Osmólska 1975); *Compsognathus longipes*, 70 to 75 mm (Huene 1925; Ostrom 1978); *Bagaceratops rozhdestvenskyi*, 47 mm (ZPAL MgD I/123; Maryńska and Osmólska 1975); juvenile prosauropod(?), 32 mm (Charig 1979); *Psittacosaurus mongoliensis* 42 mm and 28 mm (respectively AMNH 6536 and 6535). An estimate of total body length for the two *Psittacosaurus* juveniles can be obtained by scaling down the dimensions of the two large, almost complete skeletons described by Osborn (1923, 1924), using comparisons of median skull length. The calculated snout to tail tip length for AMNH 6536 is about 390 mm, and that for AMNH 6535 is about 265 mm. Possible allometric changes in skull size relative to body length were not considered in these estimates but, since the skull is proportionately larger in juveniles, the calculated total body lengths probably err on the high side. Scaling the complete *Psittacosaurus* skeleton based on a comparison of humeral length (using the humerus shown in fig. 5) gives an estimated total length for AMNH 6536 of 340 mm. Allowing for some allometric changes in skull size, I would estimate the total body length of AMNH 6535 at about 230 mm. For comparison with the size of these two juvenile psittacosaurus, the famous skeleton of *Compsognathus longipes*, also probably a juvenile, has a length of between 750 and 810 mm (based on restorations by von Huene 1925, 1926; Ostrom 1978). The smaller *Psittacosaurus* specimen described herein (AMNH 6535) belonged to a dinosaur slightly smaller than a common pigeon (*Columba livia*).

Parental care. Recently it has become fashionable to ascribe mammalian or avian behaviour patterns to dinosaurs despite the reptilian aspect of the brains of all dinosaurs except small theropods (Hopson 1977) and the acknowledged difficulty of deducing habits from osteology even for living animals. Among behavioural patterns considered for dinosaurs is parental care of young (e.g. Horner and Makela 1979). In attempting an objective analysis of parental care in dinosaurs, three points must be kept in mind. First, there is no such thing as an 'accepted interpretation'. The suggestion that dinosaurs abandoned their eggs as do modern chelonians is a hypothesis that requires proof as rigorous as that required to prove that dinosaurs cared for their young in the manner of modern ducks or ungulates. Casting aspersions on arguments favouring parental care does not constitute proof of the alternate hypothesis. Second, the morphologic diversity and long evolutionary history of dinosaurs makes it exceedingly unlikely that every species practiced a similar amount of parental care. Indeed, the egg-laying pattern of the hadrosaur *Rhabdodon* has been interpreted as precluding parental care (Ginsburg 1980) while nests of the hadrosaur *Maiasaurus* have been interpreted as requiring parental care (Horner and Makela 1979). Dinosaur parental behaviour should be approached on a case-by-case basis, and generalities applicable to all dinosaurs will necessarily be few. Finally, the selection of modern analogues to interpret dinosaur behaviour is a subtle trap that encourages interpretations far beyond what can reasonably be concluded from actual data. This problem has been discussed elsewhere (Coombs 1975), but the warning merits repetition. The mental image of the relationship between adult and juvenile dinosaur is greatly altered if described as being: (1) like elephants; (2) like opossums; (3) like ducks; (4) like crocodiles; or (5) like mouth-breeding fishes. Use of modern analogues must be approached with great caution.

In the absence of contrary evidence it is assumed that most dinosaurs laid eggs (Hopson 1977). *Coelophysis* specimens from Ghost Ranch, New Mexico (Colbert 1961), are sometimes cited as demonstrating dinosaurian viviparity, but are more likely a case of cannibalism in so far as jumbled, disarticulated juvenile skeletons are enclosed in almost perfectly articulated adult skeletons (making parental care unlikely for *Coelophysis*). The supposed juvenile within the type of *Compsognathus longipes* is in fact a skeleton of the lacertilian *Bavarisaurus* (Ostrom 1978). Dinosaur egg morphology indicates nests buried in leaf litter or sand (Seymour 1979; Seymour and Ackerman 1980), a construction pattern similar to that of both crocodylians and megapode birds (Frith 1956, 1962; Seymour and Ackerman 1980). Megapode nesting habits are regarded as primitive among birds

(Welty 1963) and are thus an appropriate analogue for at least the primitive pattern of dinosaur nest-building behaviour. Parental attendance of buried nests, involving protection (crocodilians), temperature regulation (megapodes), and assistance to young at hatching (both crocodilians and megapodes) may be a primitive archosaurian behaviour pattern that is reasonably inferred for dinosaurs. Hatchlings of crocodilians, megapodes, and ground-nesting birds in general (excluding those relatively free of terrestrial predator threat, e.g. most insular, Arctic, and Antarctic marine birds) are generally precocial (mobile, self-feeding, and fast maturing). Megapode hatchlings are notoriously precocial, at least one species being capable of flight within 24 hours of hatching (Frith 1962). The *Psittacosaurus* juveniles had been feeding on abrasive material, probably vegetation, for some time prior to death, as evidenced by wear on teeth of both skulls (similar conclusion for juvenile *Maiasaurus*: Horner and Makela 1979). It is therefore probable that the juveniles of *Psittacosaurus* were precocial; parental offering of transported, pre-masticated, or regurgitated food is unlikely, implying that parental care was unnecessary at least for feeding.

A great difference in physical size between juvenile and adult increases liability of injury to young in species having large adults and parental care after hatching. Habits and posture also play a part. Some crocodilians practice extended parental care after the young hatch, but crocodilians are semi-aquatic, with young more aquatic than adults, and the posture is sprawling to semi-erect quadrupedal with long, slender, flexible toes. The danger of injury to a juvenile crocodilian is thus far less than to juveniles of terrestrial, bipedal dinosaurs that have a compact foot and digitigrade stance. Among both mammals and birds that are ground dwellers and that have precocial young, the minimum relative newborn size (= newborn body mass expressed as a percent of adult body mass, and hereafter abbreviated RNS) is about 0.9% (in *Struthio*; Welty 1963). RNS values for mammals with precocial young range from about 1 to 12% (calculated from data in Walker 1968) with typical values of about 3-5% (e.g. *Odocoileus*, *Giraffa*, *Rhinoceros*, *Antilocapra*, *Rangifer*, *Taurotragus*, and *Loxodonta*: Walker 1968; Case 1978). Adult body size has little influence on RNS for mammals with precocial young. Relatively immobile, altricial young whose position and movements are either limited or controlled by the parent have much lower RNS values (e.g. 0.33% in *Euarctos*: Walker 1968; Case 1978). The recent death of a zoo-born *Ailuropoda*, apparently by smothering under a careless (inexperienced) adult female, points up the potential dangers to young of very low RNS and terrestrial habits. RNS values of modern reptiles follow a different pattern: values decline as adult body mass increases (Table 1). The RNS of *Psittacosaurus* is 0.7 to 0.8% (calculated by cubing equivalent linear dimensions of adult and juvenile) which is low compared to precocial young of mammals or birds, but is high compared to that of modern reptiles of similar adult body mass (10 to 100 kg category, Table 1). RNS values for other dinosaurs include 0.24% for *Protoceratops* and 0.06% for *Hypselosaurus* (Case 1978). Thus dinosaurs appear to follow the reptilian pattern of declining RNS at high adult body mass. The combination of low RNS and mobile, self-feeding habits of *Psittacosaurus* contrasts with the pattern for mammals and birds that practice parental care after birth or hatching and that have active, mobile young. On the basis of RNS values, parental care is marginally possible, but not probable for *Psittacosaurus*, and is very unlikely for dinosaurs of high adult body mass.

TABLE 1. Data from Case (1978) showing the decline in relative newborn size (RNS) at higher adult body masses among modern reptiles.

| Adult mass | Number of species averaged | Average RNS |
|----------------|----------------------------|-------------|
| Less than 1 kg | 6 | 3.8% |
| 1-10 kg | 7 | 1.9% |
| 10-100 kg | 5 | 0.42% |
| Over 100 kg | 7 | 0.04% |

Indirect support for the hypothesis that some dinosaurs did not care for their young after hatching comes from Triassic–Jurassic trackways known as *Selenichnus* (text-fig. 8). The footprint maker was a tridactyl biped with a tail sufficiently long to occasionally imprint, and the animal was probably a juvenile of one of the many large bipedal dinosaurs that are so ubiquitous in the Connecticut Valley (e.g. *Eubrontes*, *Gigandipus*, *Anomoepus*, *Anchisauripus*, or *Sauropus*; Lull 1953). The *Selenichnus* trackmaker was intermediate in size between the two juvenile *Psittacosaurus* described herein, although in view of the disparity in geologic age, *Selenichnus* trackways could not belong to *Psittacosaurus*. The five slabs at the Pratt Museum (Amherst College, Amherst, Massachusetts, U.S.A.) that contain *Selenichnus* tracks have the following characteristics in common: (1) there are no instances of ‘adult’ footprints in company with *Selenichnus*; and (2) there are no instances of two or more *Selenichnus* tracks on a single bedding plane, headed in roughly the same direction. Insufficient numbers of *Selenichnus* tracks are known to draw unequivocal conclusions, but the evidence indicates that tiny dinosaurs, the size of small juvenile *Psittacosaurus*, travelled alone, unaccompanied by either adults or fellow hatchlings, at least sometimes. This evidence suggests that at least some dinosaurs did not practice post-hatching parental care.



TEXT-FIG. 8. *Selenichnus brevisculus*, trackway made by a small tridactyl, bipedal dinosaur that at least sometimes left a sinuous tail trace (pseudo-tail traces are sometimes made by dragging the tip of one toe through soft sediment, but that does not appear to be the case with this specimen). This particular trackway was made on a raindrop splattered surface. According to Lull (1953) the average print length for this species is 46 mm and the average step length is 58 mm. I estimate the size of the trackmaker to be a little smaller than AMNH 6536, the larger *Psittacosaurus* specimen described herein. Lull (1953) regarded these tracks as pertaining to a theropod. Specimen in the collection of the Pratt Museum, Amherst College (Amherst, Massachusetts, U.S.A.).

Association of adult and juvenile skeletons might be taken as an indication of parental care. The remarkable assemblage of *Protoceratops andrewsi* at Djadochta includes numerous individuals of every age category, unhatched eggs to old adults (Brown and Schlaikjer 1940; Dodson 1976) and association of adults and juveniles in life is thus indisputable. Horner and Makela (1979) interpreted a group of juvenile hadrosaurs (*Maiasaurus*) as requiring parental guidance to remain a coherent group, and an adult specimen was unearthed reasonably nearby. As noted above, the juvenile *Psittacosaurus* described herein were excavated in the vicinity of the type of *P. mongoliensis*, although exactly how close is difficult to ascertain from available records. Association of adults and juveniles in fossil assemblages has little bearing on the question of parental care in so far as such an association would sometimes occur even if the adults abandoned their eggs immediately after laying. Only if nests were constructed far from the normal range of the adult (note arguments of Horner and Makela 1979), and if the juveniles lived entirely outside of adult habitats would the incidence of adult–juvenile association in fossil assemblages be reduced to nil. While such a set of conditions may have existed for some dinosaurs, it is unlikely it was a universal situation.

Thus the association of adult and juvenile skeletons even in a single quarry is not sufficient proof of extended post-hatching care.

Parental care, summary. Available evidence for parental care by dinosaurs is scant and equivocal. Moreover, there is no clear indication of what constitutes necessary and sufficient proof of either competing theory (i.e. that dinosaurs did, or that dinosaurs did not, care for their young). On the basis of the data and arguments developed above, the following conclusion might be drawn: (1) guarding of nests may be a general archosaurian pattern inherited as the primitive behaviour of dinosaurs; (2) nests of some dinosaurs were buried and may have required parental attendance for temperature regulation and perhaps for assisting the young at hatching; (3) egg distribution of other dinosaurs seems to preclude parental care after laying; (4) adult-juvenile size disparity makes parental care unlikely for very large dinosaurs, but for smaller genera the size disparity may not have been a problem; (5) footprints indicate that at least some tiny dinosaurs, probably juveniles, were independent of adults; and (6) for *Psittacosaurus*, available evidence is inconclusive.

Sibling groups. One of the two juvenile *Psittacosaurus* specimens is a composite of several skeletons, with fourteen distal ends of tibiae indicating a minimum of seven individuals represented. The jumbled, broken, incomplete condition of the skeletons suggests a post-mortem assemblage, yet the majority of bones are from juveniles of similar, indeed almost identical, size (text-fig. 6). Such an assemblage could result from mechanical sorting processes, or from the simultaneous deaths of several individuals of a sibling group. Horner and Makela (1979) described an assemblage of juvenile hadrosaurs probably derived from a single clutch, and footprints possibly belonging to juvenile dinosaurs travelling in unison have been reported (Currie and Sargeant 1979; contra *Selenichnus* evidence described above). Therefore juveniles, possibly clutch mates of some dinosaurs, may have formed cohesive aggregates, for which the term 'sibling group' is proposed in preference to 'herd' or 'flock' or 'school' all of which imply behavioural interactions not yet proven for dinosaurs. A behavioural complexity similar to that of modern gregarious reptiles (e.g. *Amblyrhynchus*) is sufficient to explain sibling groups among dinosaurs. Aggregates of adult dinosaurs might have resulted from persistence of bonds formed in juvenile sibling groups.

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