PSITTACOSAURUS AND PROTIGUANODON: TWO LOWER CRETACEOUS IGUANODONTS FROM MONGOLIA

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The preliminary description of these iguanodonts was, prior to the complete exposure and restoration of the two type skeletons, an extremely long, difficult and delicate process, followed by detailed drawings and restorations which give us an exceptionally complete knowledge of these animals. The types are:

Oshih (Ashile) Formation.—Psittacosaurus mongoliensis (Amer. Mus. 6254), an almost perfect skull and jaws with greater part of skeleton.

Ondai Saip Formation.—Protiguanodon mongoliense (Amer. Mus. 6253), an imperfect skull and left jaw with a practically perfect skeleton.

These two types resemble each other in so many characters that they obviously belong to a distinct family of iguanodonts to which the name Psittacosauridae has been applied. These short-skulled iguanodonts derive their family name Psittacosauridae from the very deep parrot-like beak, with small nostrils located at the top of the very deep maxilla. There is still some question as to the validity of the subfamily name Protiguanodontinae proposed at the same time.

The characters which Psittacosaurus and Protiguanodon exhibit in common are: (1) Cranium relatively short and broad, premaxillaries and anterior portion of dentaries edentulous; maxillary teeth of iguanid type. Functional teeth in a single row. Nine dentary teeth in Protiguanodon; 7+ maxillary teeth in Psittacosaurus. (2) Neck short; cervicals, 6 with 5 free ribs. (3) Thoracics: 16 in Psittacosaurus and 15 in Protiguanodon. (4) Sacrals: 5 in Psittacosaurus, 6 in Protiguanodon. (5) Caudals: 43 estimated in Psittacosaurus, 43 actual in Protiguanodon. (6) Cervicals, thoracics and sacrals: 27 in both Psittacosaurus and Protiguanodon. (7) Shoulder girdle with free clavicle, coracoid and coracoid foramen, and distally expanded, elongate scapula. This is the first record of the occurrence of a clavicle in ornithischian dinosaurs. (8)

The above practically common characters, which indicate a marked affinity between these two animals, are accompanied by certain differences in proportion of the fore and hind limbs as shown in the following table of measurements:

![Type skeleton of Psittacosaurus mongoliensis Osborn (Amer. Mus. 6254).](image)
Fig. 2. Reconstruction of the *Psittacosaurus mongoliensis* type skeleton (Amer. Mus. 6254) in its lateral aspect. One-eighth natural size.

The skull in this reconstruction combines sclerotic ring and dental characters observed in the type (Amer. Mus. 6254), also in the referred specimen (Amer. Mus. 6261) from the same geologic formation. Eight maxillary teeth are restored from the referred skull (Amer. Mus. 6261); the corresponding dentary teeth are conjectural. These restored parts are indicated by dotting.
Axial length from premaxillaries to 43d caudal 1310 mm. 1350 mm. 
Length of fore limb extended hind limb extended humerus ulno-radius manus femur tibio-fibula pes Digit III 250 470 119 90 162 179 93 470 435 123 90 158 167 89 90 92 90 85 92 158 158 89 158 89 89 
Ratio, femur to tibia, femoro-tibial fore limb to hind limb, brachio-crural 90% 53% 56% 56% 
Comparaison.—The above linear measurements as well as the femoro-tibial and brachio-crural ratios are very similar, demonstrating that both animals were: (1) Essentially bipedal in locomotion, with fore limbs well raised above the ground, a brachio-crural ratio of from 53% to 56%. (2) Manus functionally tridactyl, since D.IV is greatly reduced. (3) Pes also functionally tridactyl-subtetradactyl, because D.I is of considerable size although well raised off the ground, while D.V is vestigial. (4) Osseous tendons connecting the fourth thoracic with posterior sacral or first caudal vertebra, indicating adaptation to a bipedal gait. (5) The normal walking position was probably semi-erect, as indicated in figure 2 (Psittacosaurus), figure 5 (Protiguanodon). (6) The ilio-sacral articulation of Psittacosaurus includes five vertebrae, while the ilio-sacral articulation of Protiguanodon includes six vertebrae. (7) Limb and foot bones of Psittacosaurus are somewhat more massive, while the limb and foot bones of Protiguanodon are somewhat more slender. (8) Scapular arches, including clavicle, coracoid and scapula, are of about the same proportions in both species. (9) Pelvic girdle of Psittacosaurus, including the ilium, ischium and pubis, somewhat more massive than the pelvic girdle of Protiguanodon, in which the iliac crest is slender, the prepubic process much more slender and the ischium more slender and elongate than in Psittacosaurus. (10) There are 16 thoracic ribs in the Psittacosaurus thorax, which are slightly more robust than the 15 ribs in Protiguanodon. (11) From a comparison of the ten adaptations to a bipedal locomotion, we conclude that Protiguanodon was somewhat more cursorial in habit than Psittacosaurus.

A number of important additional characters in the pelvis should be noticed: (a) The absence of the "oburator processes" on the ischium, both in Psittacosaurus and Protiguanodon, a conspicuous difference from Thescelosaurus, Camptosaurus, Trachodon, Iguanodon, in which these
Fig. 3. Referred skull of *Psittacosaurus mongoliensis* (Amer. Mus. 6261).

Found in the same formation (Oshih) as the type. This skull contains seven maxillary teeth in situ. Skull, one-third natural size. Seven maxillary teeth, natural size. Two of the same teeth are shown in Fig. 3A enlarged three diameters.

Fig. 3A. Two superior teeth in referred skull of *Psittacosaurus mongoliensis* (Amer. Mus. 6261) enlarged three diameters.

For comparison with restored tooth of *Protiguanodon mongoliense* type (Amer. Mus. 6253) enlarged three diameters.

Fig. 3B. Type maxillary tooth of *Protiguanodon mongoliense* (Amer. Mus. 6253) enlarged three diameters; anterior, exterior and interior aspects. After Osborn, 1923, Fig. 5.

processes are present. (b) Superior border of ilium not reflected laterally,—an important character separating *Psittacosaurus* and *Protiguanodon* from *Iguanodon, Trachodon, Troodon*. (c) Prepubic process shorter than anterior process of ilium, differentiating *Psittacosaurus* and *Protiguanodon* markedly from *Iguanodon, Trachodon, Thescelosaurus, Camptosaurus*. (d) Ischia much flattened dorsoventrally. (e) Ischia not curved downward toward the posterior ends, distinct from *Iguanodon, Camptosaurus, Troodon*. (f) Postpubic processes short and slender,—probably a reduction character.

**THE PSITTACOSAURUS MONGOLIENSIS SKELETON**

**SKULL.**—The perfectly preserved skull was described and figured in great detail in the type description¹ in which the skull characters are

summarized as follows: "Psittacosaurus mongoliensis. Herbivorous diapsid reptile with predentary bone and horny beak. Maxillary teeth compressed, not fully known. Skull short and deep, narrow anteriorly, broad posteriorly. Rostrum prominent, parrot-like, edentulous. Nostrils small, orbits large. Infraorbital region and jaw heavy, with attachment for powerful muscles. Primitive dermal armature in head region; lateral osseous horns on jugals."

To the above description should be added the osseous sclerotic ring in the orbit represented in figure 2 and which is now exposed in the orbits of the skull. The osseous horns below the orbits and the impressions of the epidermal armature at the side of the jaw and throat led Osborn to the following conjecture:1 "Genotype of Psittacosauridae, new family. Skeleton and teeth only partly known; supposed primitive armored dinosaurs, possibly related to the fully armored Upper Cretaceous types."

Gregory remarks that Osborn’s term "osseous horns" on the jugal appears to be misleading; he believes that they correspond with a strong downwardly directed process on the jugal correlated with a development of the masseter muscle. Osborn is still disposed, however, to maintain that the osseous protuberances of the jugals are defensive bony spines (compare Ankylosaurus) and not muscular adaptations, and that the dermal impressions of the throat in Psittacosaurus are part of a dermal defensive system.

TEETH.—The teeth in the type skull (Amer. Mus. 6254) are still deeply buried in the matrix. Fortunate, therefore, is the discovery in the same Oshih formation of a second specimen of skull and skeletal parts (Amer. Mus. 6261) apparently referable to the species Psittacosaurus mongoliensis, in which seven of the maxillary teeth are preserved. These referred teeth are shown natural size in figure 3 and enlarged three diameters in figure 3A; the sculpturing of these teeth is apparently different from that of the type tooth of Protiguanodon mongoliense (Fig. 3B).

Family Psittacosauridae: Skull abbreviate; rostrum edentulous, prominent, parrot-like; jaws deep; teeth 7–9, trilobed, brachydont in dentaries and maxillaries; nostrils small; orbits large; cervicals 6; thoracics 16–15; sacrals 5–6; caudals 43+; clavicles reduced; brachio-crural ratio 53–56%; bipedal locomotion; manus and pes tridactyl-sub-tetradactyl; gait cursorial; ischia flattened, a broad ischiac symphysis.

Subfamily Protiguanodontinae Osborn, 1923, p. 6: Type Protiguanodon. Cannot be further defined until it is known what the complete separation is between Psittacosaurus and Protiguanodon.

Fig. 4. Type skeleton of *Protiguanodon mongoliense* Osborn, 1923 (Amer. Mus. 6253). Ondai Sair formation, Mongolia.

Since the publication of the original description, this type skeleton has been completely exposed and is very accurately represented in the present figure as it was found in the matrix, the only restored portion being the skull. The original pencil drawing is full size; the present figure is reproduced one-eighth natural size. The missing parts are represented in dotted lines. The skull is largely restored (dotted lines), in comparison with *Psittacosaurus*; see also Fig. 6.
GENERIC DISTINCTIONS.—These two animals prove to be so similar in general size, proportions, gait, skeleton and limb segments, that while specific distinctions are very obvious indeed, and generic distinctions are more difficult than was at first supposed by Osborn (op. cit., pp. 9, 10), yet the genera may be distinguished as follows:

Psittacosaurus
Cranium solid, with suborbital horns, large occipital condyles, epidermal tubercular armature on throat and side of face. (See remarks, Gregory, Granger.)
Neural arch of atlas vertebra elongate.
Superior maxillary teeth flattened, with asymmetrical trilobate sculpturing (Figs. 3, 3A).

Protiguanodon
Cranium slender, bones light, small occipital condyles (suborbital region and epidermal armature unknown at present).
Atlas vertebral elements apparently abbreviate.
Superior maxillary teeth convex, with symmetrical trilobate sculpturing (Fig. 3B).

COMPARISON OF Psittacosaurus AND Protiguanodon

DENTITION.—The striking difference in the external sculpture of the extremely short-crowned or brachydont teeth is well displayed in Psittacosaurus (Figs. 3, 3A), and in Protiguanodon (Fig. 3B); see also Fig. 4 of Osborn, op. cit., p. 8. The Psittacosaurus teeth, viewed externally, are relatively broad, flat, and the median ridge is on the posterior half of the tooth, whereas in Protiguanodon (Fig. 3B) the contour is a deep oval, the median ridge very prominent and directly in the center of the tooth. On wear these teeth become trilobate.

SKULL.—The fully preserved skull of Psittacosaurus, described and figured in detail in the type description (Osborn, op. cit., Figs. 2A, 2B, 2C), differs from that of all iguanodonts previously described in its solid, massive characters, the sutures being partly closed, excepting the pre-maxillo-maxillary; this skull certainly had a powerful horny beak like that of a chelonian and was adapted to feeding upon very resistant plants. In the referred skull (Amer. Mus. 6261) the sclerotic ring and the same characters are observed; the dentaries are relatively short and massive. The sclerotic ring is observed in the type skull of Psittacosaurus. Granger believes that the supposed “epidermal tubercles” on the side of the skull of Psittacosaurus, regarded as epidermal impressions by Osborn, more strongly resemble concretions such as may be seen where no organic remains are present.
Fig. 5. Reconstruction of the *Protiguanodon mongoliense* type skeleton (Amer. Mus. 6253) in its lateral aspect. One-eighth natural size.

Outline of the skull drawn in dotted lines from *Psittacosaurus.*
In the type skull of *Protiguanodon* (Amer. Mus. 6253), as shown in figure 6, there is a marked contrast in the relatively slender character of the bones, the apparent sutural separation, the relatively small and broad occipital condyles, the very deep depression of the dentary below the nine dentary teeth. The inference is that this skull was adapted to less resistant food.

Gregory further observes: “All the fragments of the *Protiguanodon* skull, when compared with *Psittacosaurus, Camptosaurus, Iguanodon*, etc., show that it is unmistakably much closer to *Psittacosaurus*. The small nostril, located at the top of the deep maxilla, the form of the frontoparietal, of the quadrate, squamosal, etc., differ from *Psittacosaurus* chiefly in greater slenderness.” That *Protiguanodon* is on the whole far more primitive than *Iguanodon* one can hardly doubt, but that it is geologically older, he would question for the following reasons: “(a) *Hypsilophodon* is certainly far more primitive than *Iguanodon*, but both occur in the Wealden. (b) *Troodon* of the Lance (Upper Cretaceous) is far more primitive than the ankylosaurs of older formations. (c) *Thescelosaurus* is a survivor in the Lance, retaining many primitive features recalling *Hypsilophodon* of the Wealden.”

**Vertebrae.**—Correlated with the massive skull of the *Psittacosaurus* type is the unusual elongate neural arch of the atlas (C 1) that may be seen in figures 1 and 2. The axis (C 2) and remaining cervicals (C 3–7) appear to be of the same length in the two genera. The thoracics, including neuropophyses, pre- and postzygopophyses and parapophyses, exhibit the same general characters in both genera. Ten bicipital ribs are observed in *Psittacosaurus*; 9+ bicipital ribs in *Protiguanodon*. Five sacrals unite with the iliac crest in *Psittacosaurus*; 6 sacrals unite with the iliac crest in *Protiguanodon*. Eight free caudal ribs are observed in *Protiguanodon*; the anterior caudals of *Psittacosaurus* are imperfectly preserved; the 9th to the 20th caudals in *Protiguanodon* have consolidated ribs or pleurapophyses; the 15th to the 34th caudals in *Protiguanodon* bear chevrons.

**Limb Characters.**—The limb characters in *Psittacosaurus* and *Protiguanodon* are clearly displayed in figures 1, 2, 4 and 5; resemblances and contrasts are as enumerated above. The ulna, radius and manus resemble in proportions the manus of *Hypsilophodon foxii*; Digit IV is somewhat more reduced than that in *Hypsilophodon*, and there is no trace of D.V; large D.I is closely applied to D.II and shows no sign of the abduction characteristic of *Iguanodon*. The manus is still of locomotor type and shows little if any prehensile adaptation. The
pes of Protiguanodon (Fig. 4) is double the size of the manus, from which we may infer that the pes performed twice as much work as the manus.

LOCOMOTION.—The proportions of the organs of the axial and appendicular skeletons are approximately similar to those of Iguanodon bernis-sartensis. In Iguanodon the vertebral column on the whole is relatively more massive. The ossified tendons of Iguanodon extend down along the sides of the elongated spines of sixteen to twenty of the anterior caudals,
whereas in Protiguanodon the ossified tendons stop at the first or second caudal. The neural spines of the anterior caudals are not elongate.

Consequently, we infer that adaptation to bipedal locomotion, to a suberect position, to arboreal feeding habits, was much further advanced in Iguanodon than in Protiguanodon. This comparison supports the idea that Protiguanodon of Mongolia is far more primitive in structure and may belong to a much older geologic stage than Iguanodon of the Wealden of England and Belgium.

**PELVES OF **Psittacosaurus** AND Protiguanodon**

Comparison of the pelves of these Mongolian species with the pelves of five other iguanodonts seen in the diagrammatic drawing (Fig. 7) shows the dominant ornithischian type. We observe that the prepubis of Psittacosaurus and of Protiguanodon is more abbreviate than in any of the other genera, while the postpubis has the same proportions as in Trachodon, somewhat less developed than in Iguanodon, far less developed than in Camptosaurus, Thescelosaurus or Hypsilophodon. The ischia of Protiguanodon and Psittacosaurus are relatively well developed; a very distinctive feature of the ischium is the ischiac symphysis, namely, the broad plate-like union of the ischia posteriorly, as observed in Thescelosaurus. The ilia are relatively longer than in any of the other iguanodonts figured.

Consequently, we may sum up the comparative characters of the pelvis in Psittacosaurus and in Protiguanodon as follows: (1) Prepubis slender; small pubic foramen. (2) Postpubis very slender, closely apposed to ischium. (3) Ischia relatively elongate, flattened, produced into a very broad ischiac symphysis. (4) Ilia relatively elongate and depressed, extending anteriorly beyond the extremity of the prepubis.

**Comparison of Pelves.—**In figures 8 and 9 we are afforded a detailed study of the pelvis in Psittacosaurus and in Protiguanodon made after complete removal from the matrix, that of Protiguanodon being especially perfect in preservation. It is shown that: (1) The postpubis

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*Fig. 7. Pelvic characters of the Iguanodontia. Diagrammatic.*

The seven pelves here figured are reduced for purposes of comparison to the same absolute size, regardless of actual wide differences in scale. The pelves should be examined in descending geologic order as follows:

- **Montana, Upper Cretaceous.** Trachodon mirabilis. After Brown, 1913.
- **Belgium, Lower Cretaceous.** Iguanodon bernissartensis. After Dollo, 1883, slightly modified.
- **Wyoming, Upper Jurassic.** Camptosaurus medius. After Gilmore, 1909.
- **Mongolia, Ondai Sair Formation.** Protiguanodon mongoliensis (Amer. Mus. 6253). After Osborn, 1923.
Fig. 7. See legend on opposite page.
Protiguanodon
Amer. Mus. 6253

Psittacosaurus
Amer. Mus. 6254

Fig. 8. Pelves of Psittacosaurus and Protiguanodon.
Lower. *Psittacosaurus mongoliensis*, type skeleton (Amer. Mus. 6254), drawn from both sides.
Upper. *Protiguanodon mongoliense*, type skeleton (Amer. Mus. 6253), right lateral aspect partly reconstructed from left side.
Both figures one-half natural size.
Fig. 9. Pelvis and sacrum of *Protiguanodon mongoliense*, type skeleton (Amer. Mus. 6253).

Upper. Internal aspect of right os innominatum showing attachment of 6 sacral vertebrae.

Lower. Superior aspect of pelvis showing 6 sacral vertebrae, also coalescence of ischia at the ischiac symphysis.
is elongate, slender and closely appressed to the flattened under surface of the ischium; (2) the prepubis (Fig. 8) is much more robust in Psittacosaurus than in Protiguanodon; the pubic foramen is apparently an enclosure between the postpubis and the peduncle or acetabular border of the pubis. As these pelves are primitive, the postpubis appears as of secondary origin, or part of the extension of the primitive pubis. In figure 9 there is clearly shown the internal and superior aspects of the Protiguanodon innominate bone, namely: (1) Ilium with rugose attachment of six sacral vertebrae; slender anterior or pubic peduncle. (2) Short ischiac peduncle. (3) Slender prepubis when seen from above. (4) Flattened ischia, when seen from above, conjoined posteriorly into the ischiac symphysis.

Comparison (Fig. 7) of the pubic components in these iguanodonts would support the view that the prepubis is the primary element (= pubis), the postpubis a secondary element.

PREPUBIS.—Gregory remarks that the Protiguanodon skeleton affords convincing evidence for his view that the prepubic processes of Ornithischia diverge widely on each side toward the last rib. He doubts whether the pelves of Psittacosaurus and Protiguanodon afford any support of the view (see Osborn above) that the postpubis is a new process. These animals are very far removed in skull and other structures from the primitive Triassic Pseudosuchia which appear to be their nearest relatives. The postpubic process lies immediately below the pubic foramen in the position of the true pubis of embryo birds and adult Triassic Erythrosuchus; consequently the postpubis = pubis.

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