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PSITTACOSAURUS AND *PROTIGUANODON*: TWO LOWER CRETACEOUS IGUANODONTS FROM MONGOLIA¹

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The preliminary description of these iguanodonts² 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 SAIR 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 *Psittacosauridæ* has been applied.³ These short-skulled iguanodonts derive their family name *Psittacosauridæ* 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 *Protiguanodontinæ* 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)

¹Publications of the Asiatic Expeditions of The American Museum of Natural History. Contribution No. 25.

²Osborn, H. F. 1923. "Two Lower Cretaceous Dinosaurs of Mongolia." Amer. Mus. Novitates, No. 95, October 19, pp. 1-10.

³Idem, p. 6.

Fore limb, total length from humerus to extremity of phalanges, 250 mm. *Psittacosaurus*; 245 mm. *Protiguanodon*. (9) Pelvic girdle of characteristic iguanodont type, elongate ilium, pre- and postpubic extension, elongate ischium. (10) Hind limb, total length, 470 mm. *Psittacosaurus*; 435 mm. *Protiguanodon*. (11) Manus in both genera with 4 free carpalia, Digit I, 2 ph., D.II, 3 ph., D.III, 4 ph., D.IV, reduced, 1 vestigial ph. (12) Pes in both genera enlarged, elongate, 4+ free tarsalia in *Protiguan-*

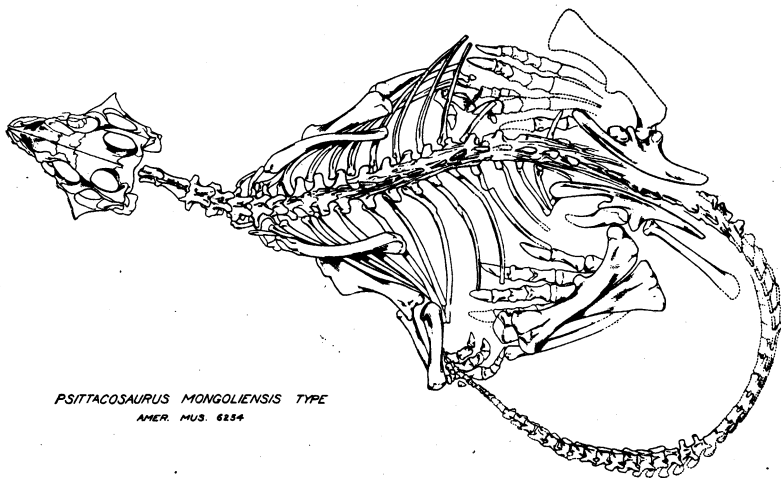


Fig. 1. Type skeleton of *Psittacosaurus mongoliensis* Osborn (Amer. Mus. 6254).

Since the original description the skeleton has been completely exposed and is very accurately represented in this figure as it lies in the matrix. The original pencil drawing is full size; the present figure is reproduced one-eighth natural size. The missing parts are represented in dotted lines.

odon, tibio-tarsus closely united but not coalesced. Digit I, 2 ph., D.II, 3 ph., D.III, 4 ph., D.IV, 5 ph., D.V, vestigial mts., 0 ph. (13) Osseous tendons extending from fourth or fifth thoracic through the sacral series to the anterior caudal.

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:

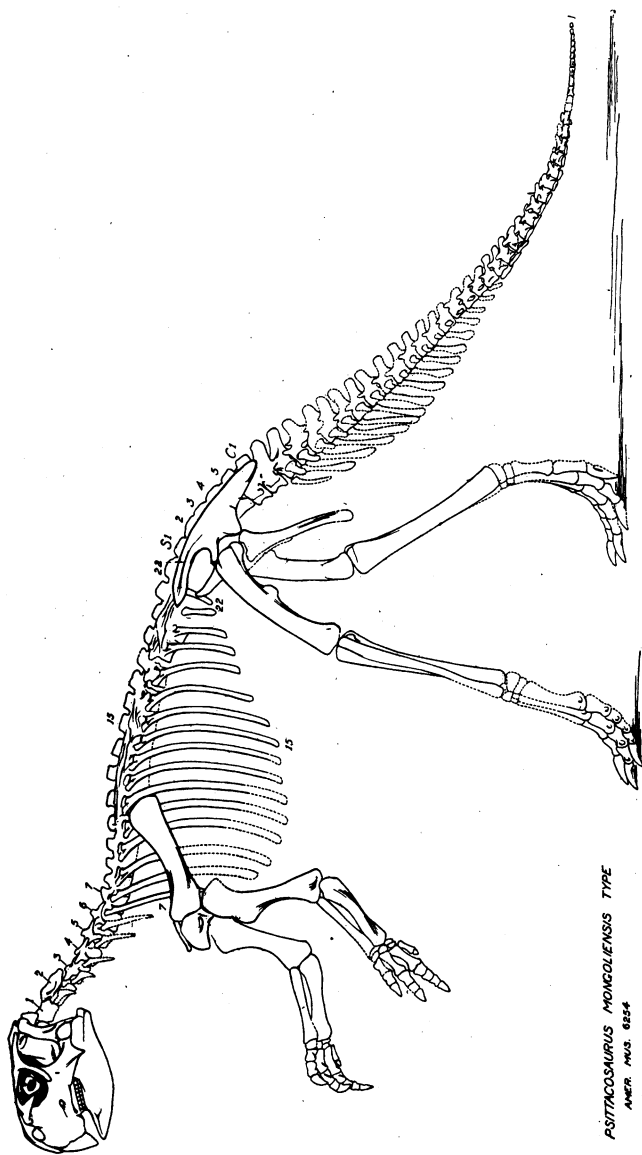


Fig. 2. Reconstruction of the *Psittacosaurus mongoliensis* type skeleton (Amer. Mus. 6254) in its lateral aspect. One-eighth natural size.

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.

	<i>Psittacosaurus</i>	<i>Protiguanodon</i>
Axial length from premaxillaries to 43d caudal	1310 mm.	1350 mm.
Length of fore limb extended	250	245
“ “ hind limb extended	470	435
“ “ humerus	119	123
“ “ ulno-radius	90	90
“ “ manus	85	92
“ “ femur	162	158
“ “ tibio-fibula	179	167
“ “ pes		158
“ “ “ Digit III	93	89
Ratio, femur to tibia, femoro-tibial	90%	89%
“ fore limb to hind limb, brachio-crural	53%	56%

COMPARISON.—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 vertebræ, while the ilio-sacral articulation of *Protiguanodon* includes six vertebræ. (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 “obturator processes” on the ischium, both in *Psittacosaurus* and *Protiguanodon*, a conspicuous difference from *Thecelosaurus*, *Camptosaurus*, *Trachodon*, *Iguanodon*, in which these

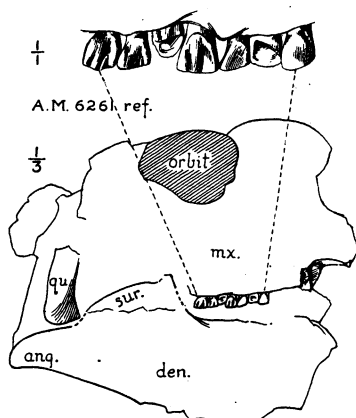


Fig. 3



Fig. 3A

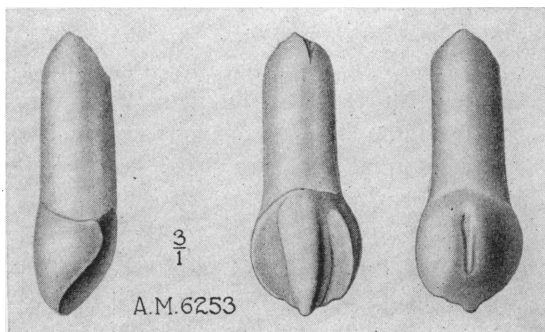


Fig. 3B

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*, *Troödon*. (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*, *Troödon*. (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

¹*Op. cit.*, pp. 2-6.

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 Psittacosauridæ, 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 Psittacosauridæ: Skull abbreviate; rostrum edentulous, prominent, parrot-like; jaws deep; teeth 7-9, trilobed, brachyodont 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 Protiguanodontinæ Osborn, 1923, p. 6: Type *Protiguanodon*. Cannot be further defined until it is known what the complete separation is between *Psittacosaurus* and *Protiguanodon*.

¹*Op. cit.*, p. 6.

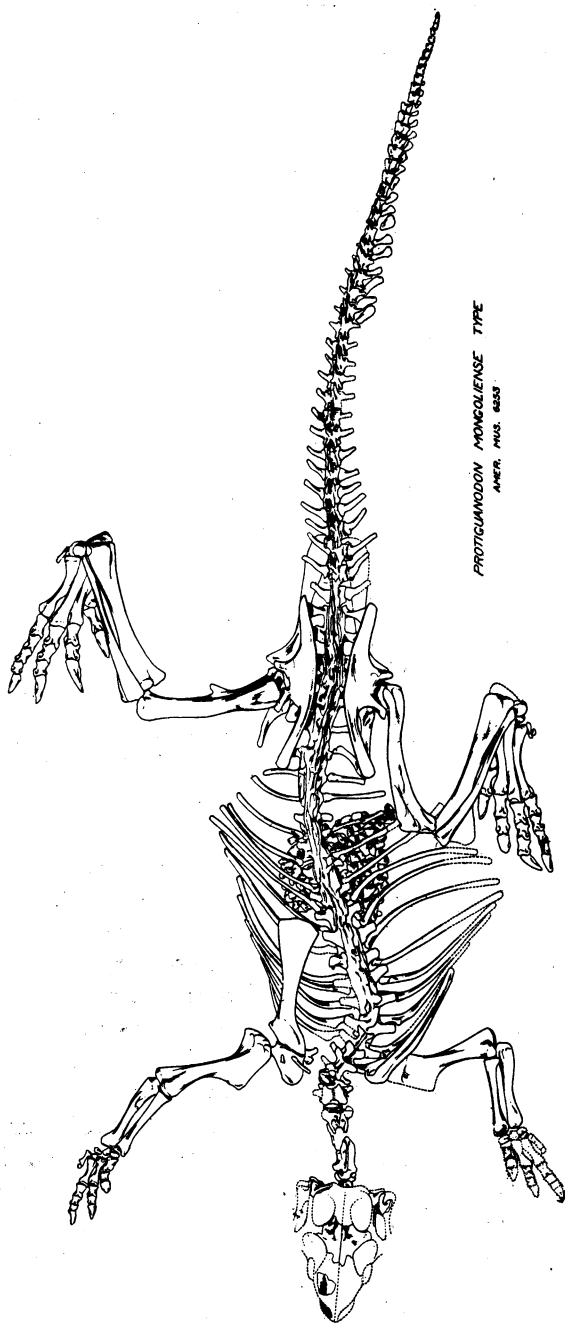


Fig. 4. Type skeleton of *Protiguanodon mongoliense* Osborn, 1923 (Amer. Mus. 6253). Ondai Sair formation, Mongolia. Since the publication of the original description, this type skeleton has been completely exposed and is very accurately represented in the present figure as it was found in the matrix, 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).

Maxillary teeth: 7+. Thoracic vertebrae: 16. Sacral vertebrae: 5. Pubis large, postpubis slender.

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).

Dentary teeth: 9. Thoracic vertebrae: 15. Sacral vertebrae: 6. Pubis and postpubis slender.

COMPARISON OF **PSITTACOSAURUS** AND **PROTIGUANODON**

DENTITION.—The striking difference in the external sculpture of the extremely short-crowned or brachyodont 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.

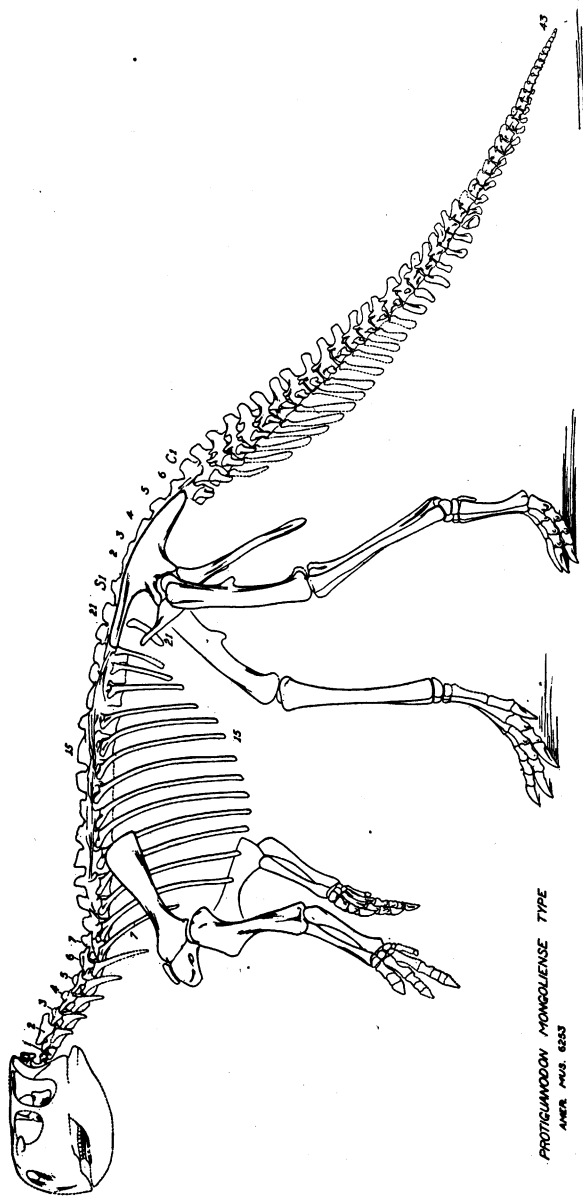


Fig. 5. Reconstruction of the *Protiguanodon mongoliense* type skeleton (Amer. Mus. 6253) in its lateral aspect. One-eighth natural size.

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) *Troödon* 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."

VERTEBRÆ.—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

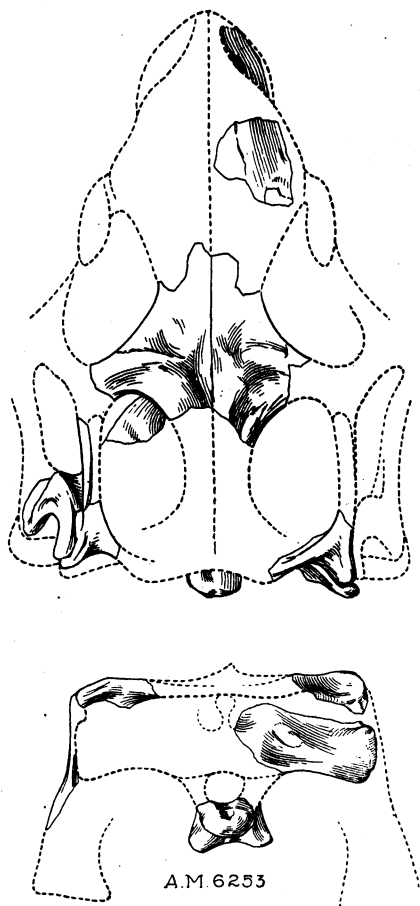


Fig. 6. Type skull, largely restored, of *Protiguanodon mongoliense* (Amer. Mus. 6253).

The type jaw of the same skull is shown in Osborn, 1923, p. 8, Fig. 4.

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 bernisartensis*. 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) Ilii 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

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.
- Montana, Upper Cretaceous. *Thescelosaurus neglectus* (Amer. Mus. 5889). After Brown.
- Belgium, Lower Cretaceous. *Iguanodon bernissartensis*. After Dollo, 1883, slightly modified.
- Wyoming, Upper Jurassic. *Camptosaurus medius*. After Gilmore, 1909.
- Mongolia, Oshih Formation. *Psittacosaurus mongoliensis* (Amer. Mus. 6254). After Osborn, 1923.
- Mongolia, Ondai Sair Formation. *Protiguanodon mongoliense* (Amer. Mus. 6253). After Osborn, 1923.
- England, Lower Cretaceous, Wealden. *Hypsilophodon foxii*. After Hulke, 1882.

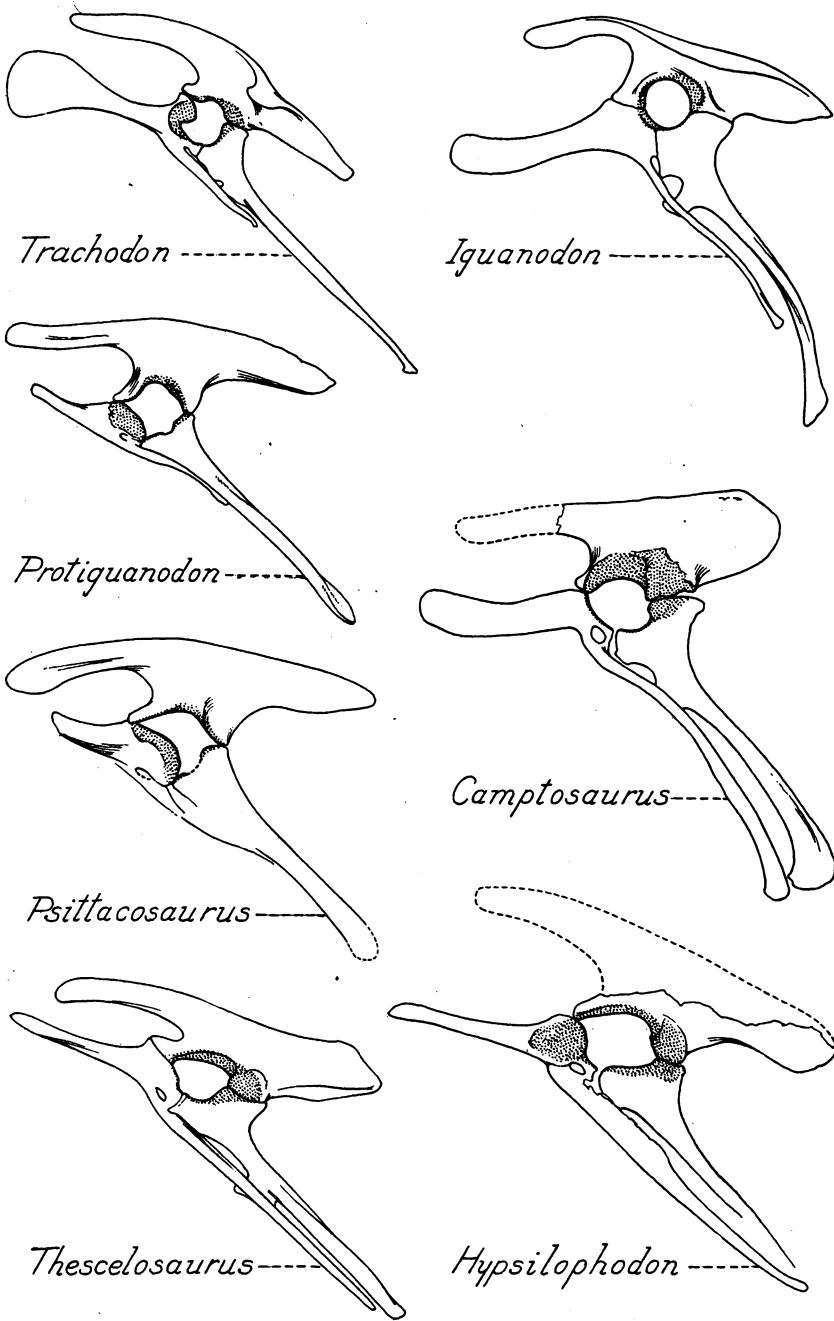


Fig. 7. See legend on opposite page.

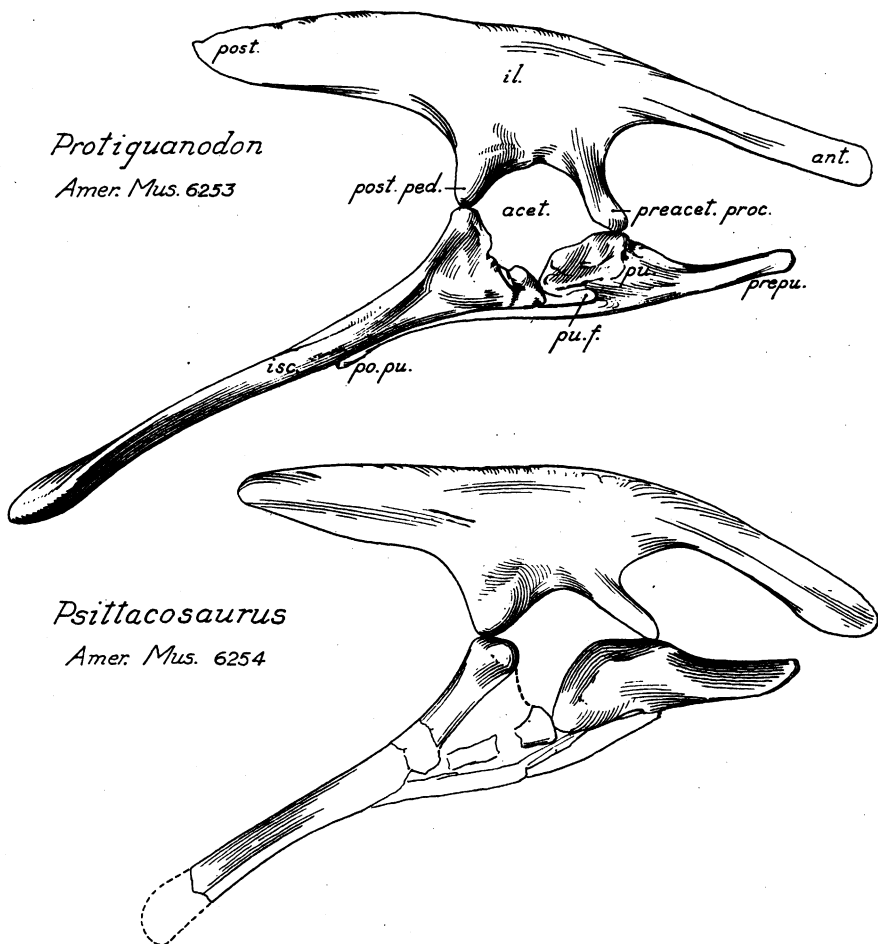


Fig. 8. Pelves of *Psittacosaurus* and *Protiguanodon*.

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.

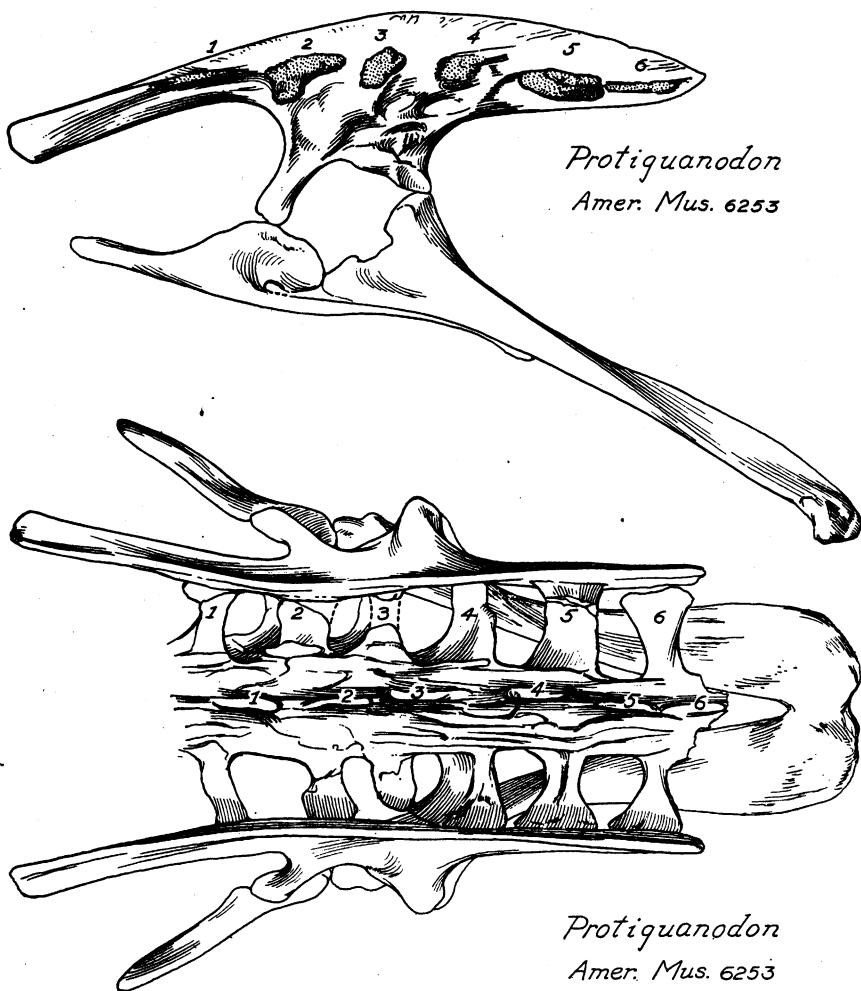


Fig. 9. Pelvis and sacrum of *Protiguanodon mongoliense*, type skeleton (Amer. Mus. 6253).

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 vertebræ; 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.

ACKNOWLEDGMENTS

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