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ON *PROTOCERATOPS*, A PRIMITIVE CERATOPSIAN DINOSAUR FROM THE LOWER CRETACEOUS OF MONGOLIA¹

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One of the most interesting of the many remarkable discoveries of the American Museum Third Asiatic Expedition is a small predentate dinosaur from the lower Cretaceous of Mongolia, which has been named *Protoceratops andrewsi* by Granger and Gregory. The type skull, which was received and worked out of the matrix some time before the rest of the seventy-odd specimens of the form arrived at the Museum, proves to be that of a young animal with an estimated extreme skull length of less than ten inches, while the largest skull of *Protoceratops* measures twenty-three inches in length.

Except for the absence of horns, the whole configuration of the skull conforms to the general ceratopsian type: the parietals and squamosals are produced into a perfectly formed, fenestrated occipital frill; the enlarged squamosal enters the side of the frill and is in contact below with the jugal; the mandible and the crowns of the teeth are much like those of later ceratopsians. On the other hand, many primitive features are retained which were lost or disguised in the typical ceratopsians. Thus, in half-grown specimens the "frill" is seen to be merely an enlarged scaffolding for the powerful jaw and neck muscles; there are no epoccipital bones, and the lateral and superior temporal fenestræ are instantly recognizable as such, whereas in later Ceratopsia, through the continued growth of the frill, their original character is largely concealed. The opposite prefrontals and "postfrontals" (postorbitals) remain in their primitive positions and do not form a secondary roof above the frontals as they do in the typical Ceratopsia; hence there is no median "pseudo-pineal" or postfrontal foramen. Freely articulating palpebral bones are attached to the anterosuperior corner of the orbits, as in *Psittacosaurus*. The premaxillæ each bear two fairly long, cylindrical teeth, instead of being edentulous as in the later Ceratopsia, and the very deep beak, in contrast to the anteroposteriorly elongate beak of *Triceratops*, also re-

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calls that of such relatively primitive predentates as *Psittacosaurus*. The anterior nares are simple ovals and the premaxillæ lack all the peculiar specializations of the later ceratopsians. The cheek teeth succeed each other in a closely appressed vertical series, including not more than two rows, in contrast with the numerous rows of the later Ceratopsia. The roots are single, not cleft buccolingually. The orbits are relatively much larger than in typical ceratopsians, especially in the young skulls. The preorbital fossæ are very large depressions, instead of being narrow slits, and the lachrymal bones are of considerable size. The well-developed parietal fontanelles are transversely oval, instead of being produced anteroposteriorly as in typical ceratopsians.

Many very primitive features are also retained in the postcranial skeleton. The first three cervical vertebræ, although appressed, are not coalesced, and the spine of the axis is not produced backward as it is in the typical Ceratopsia. The scapula is already elongate to aid in supporting the large head, but the fore limb as a whole is not nearly so large in proportion to the hind limb as it is in typical Ceratopsia; the small manus also is much smaller than the pes, the middle digit of the manus being much shorter than the middle digit of the pes, whereas in typical ceratopsians it is as large or larger.

The pelvis is in many respects remarkably primitive: the dorsal border of the ilium is vertical in position, whereas in later Ceratopsia (except *Leptoceratops*) it is more or less reflected outward and finally forms a wide shelf above the femur. The prepubic process of the pubis, instead of being a very large, vertically-extended process, as in later Ceratopsia, is relatively small and but little extended vertically; the postpubic process is relatively much less reduced than in the later types. The sacral complex includes seven to eight vertebræ, in contrast with the ten of *Triceratops*. The femur retains a large fourth trochanter and is slightly shorter than the tibia, while in typical Ceratopsia the fourth trochanter is reduced and the femur is longer than the tibia. The hind foot is remarkably long and slender for a ceratopsian, and is in fact more like that of *Psittacosaurus* than like that of *Triceratops* or *Monoclonius*. In short, the whole proportions and configuration of the skeleton indicate that *Protoceratops* was not far removed from the ancestral bipedal ornithischian, the former existence of which was long since inferred by Dollo (1905) after a brilliant analysis of the various types of dinosaurian pelvis. The tail vertebræ have very long neural spines, while in *Triceratops* the neural spines are much shortened. The feet and tail of *Protoceratops* possibly indicate partly aquatic habits.

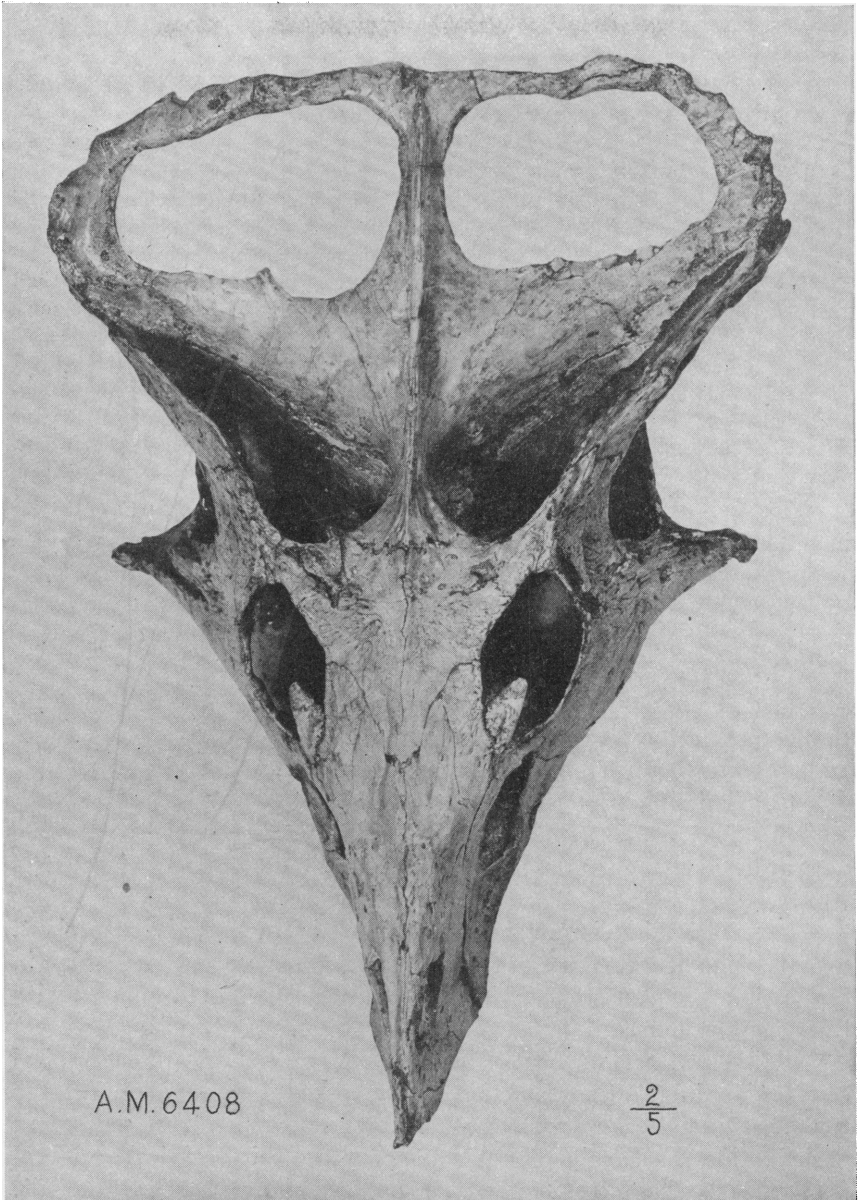


Fig. 1. *Protoceratops andrewsi*. Small, young adult skull, possibly a female. A. M. No. 6408. Viewed from above. Two-fifths natural size.

The occipital frill is composed exclusively of the expanded parietals. There is no good evidence of a separate interparietal or fused dermosupraoccipitals. The squamosals are limited to the anteroexternal border of the frill. There being no horns on the postorbitals, there is no secondary skull roof above the frontals and consequently no "pseudopineal" opening.

The definition of the family Protoceratopsidæ, proposed by Granger and Gregory, may now be extended as follows:

Primitive small ceratopsians, with a hornless skull, without either secondary skull roof or pseudopineal foramen above the frontals, no epoccipital bones; with simple oval anterior nares and unspecialized premaxillæ. A well-developed occipital frill, with large transversely oval parietal fontanelles. Freely articulating palpebral bones (supraorbitals) attached to the anterosuperior corner of the orbits. Pre-maxillaries with teeth. Cheek teeth arranged in a vertical series of not more than two developed at one time; roots simple (not bifid). Fore limb slender, manus much smaller and shorter than pes, the latter elongate, compressed. Sacral complex of seven or eight vertebræ. Ilium with blade but slightly inclined outward to the sagittal plane, not reflected or produced laterally above the femur. Prepubic process relatively small, not expanded vertically; postpubic process but little reduced. Femur with large fourth trochanter, femur shorter than tibia. Midcaudal vertebræ with very long spines.

The genus *Leptoceratops* of Brown (1914) is a little-modified survivor in the Edmonton formation in North America, of the Protoceratopsidæ. It agrees with *Protoceratops* in the following characters.

- (1.) The roots of the cheek teeth are simple, not bifid.
- (2.) The nasals are hornless.
- (3.) The parietal frill has a long, high, sagittal crest.
- (4.) The mandible is short and deep, in contrast with the elongate proportions of the mandible in *Triceratops*.
- (5.) The femur has a large fourth trochanter.
- (6.) The tibia is longer than the femur.
- (7.) The medial surface of the ilium is not reflected or produced outwardly over the femur, the whole ilium being extremely like that of *Protoceratops*.
- (8.) The ischium is long, not shortened as in the typical ceratopsians.
- (9.) The neural spines of the caudal vertebræ are extremely high in proportion to the anteroposterior extent of the centrum, in contrast with the very low spines of *Triceratops*.

On the other hand, *Leptoceratops* has progressed toward the typical ceratopsian in (1) the reduction of the parietal fontanelles, (2) the coalescence of the anterior three cervical vertebræ, (3) the backward prolongation of the spine of the axis above the third cervical vertebra, (4) the shortening of the metacarpals and especially of the metatarsals.

The genus *Brachyceratops* Gilmore, from the Belly River formation of the upper Cretaceous, clearly belongs with the Ceratopsidæ, of which it represents a young individual and a very primitive stage. Thus it shows: (1) an early stage in the development of the horns, (2) the beginning of the lateral reflection of the iliac blade, (3) the incipient shortening

of the tibia as compared with the femur, (4) the lack of coalescence of the two halves of the secondary skull roof above the frontals.

Of the typical Ceratopsidæ, the genus *Ceratops* (*Chasmosaurus*) represents a stage in which the frill has become produced backwardly,

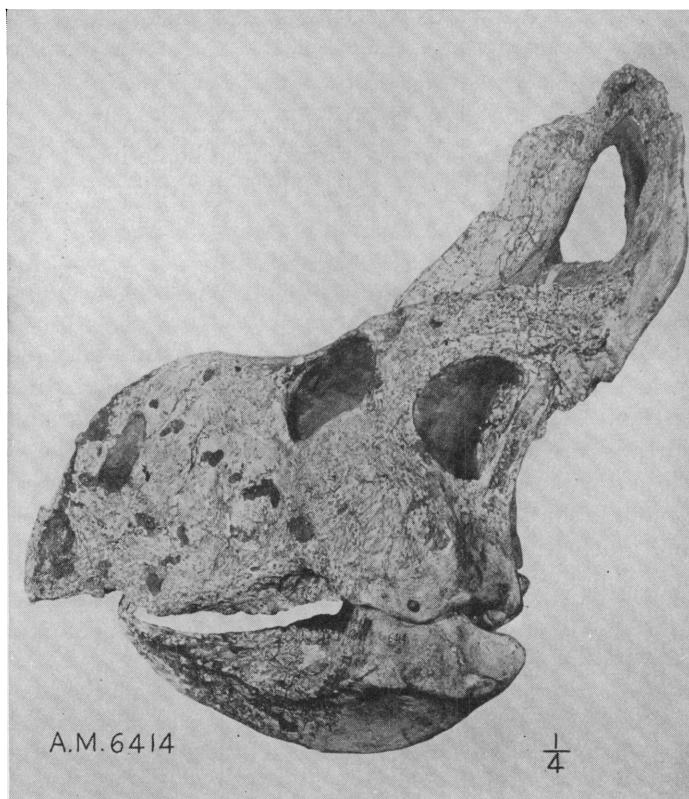


Fig. 2. *Protoceratops andrewsi*. Side view of supposed old male skull. A. M. No. 6414. One-fourth natural size.

Although considerably distorted by the lens, this view shows well the great depth of the beak, which recalls that of *Psittacosaurus*, the shortness and depth of the lower jaw, the height and prominence of the sagittal crest of the parietal, the relatively small size of the orbit as compared with that of the younger skull, etc. The great development of the occipital frill and of the jugal is obviously not primarily for the protection of the neck but for the support of the robust muscles necessary to operate the great beak and grinding apparatus. The cheek teeth are not shown in this specimen. One-fourth natural size.

elongating the parietal fontanelles so that their longitudinal much exceeds their transverse diameter. The nasal and supraorbital horns are still small. *Torosaurus*, with its highly fenestrated frill, would be the logical outcome of this line of development.

Styracosaurus would seem to be an aberrant offshoot of a primitive *Ceratops*. In all these the parietal crest is produced far behind the squamosals.

Monoclonius may well be a direct descendant of *Protoceratops*, in which the nasal convexity has grown up into a long horn, and the frill, acquiring epoccipital bones, has been produced at the upper end into the erratic processes of *Centrosaurus*.

Anchiceratops may be regarded as one of the *Monoclonius* group, with a secondary tendency for the closure of the fontanelles.

The *Triceratops-Diceratops* group may also be derived from *Protoceratops*, perhaps by way of a form related to *Leptoceratops*, which already shows a strong tendency toward the secondary closure of the parietal fontanelles and a transverse widening of the crest.

Although most of the *Protoceratops* material has still to be cleaned up, a series of skulls has been worked out, starting with an extremely young stage not long out of the egg, and ending with a very old stage with a wide frill 511 mm. wide. In one of the younger stages, with a total skull length of 283 mm., the frill is not much wider than the skull itself, but is already produced behind the occipital condyle. The parietal fontanelles are large, broad ovals. The orbits are relatively very large and the snout is short. As growth proceeds the crest becomes relatively larger and much wider, and the orbits become relatively smaller, the snout more compressed and the lateral temporal fenestræ smaller. There seem to be two kinds of skulls, a long and a very broad kind, possibly representing females and males. Specific differences have not yet been worked out.

In conclusion, *Protoceratops* affords decisive evidence for Dollo's inference that the gigantic quadrupedal Ceratopsia have been derived from some small bipedal predentates. In skull characters it is already in a primitive ceratopsian stage, but its postcranial skeleton retains much of the bipedal heritage, especially in the pelvis and hind limbs, which was lost by its gigantic graviportal descendants.

When compared with the small bipedal predentates *Psittacosaurus* and *Protiguanodon*, also of the Cretaceous of Mongolia, *Protoceratops* exhibits such a great number of significant agreements in the skull, dentition, vertebræ, and limbs, that the existence of an earlier common ancestral stock is virtually demonstrated, *Psittacosaurus* retaining much the greater number of primitive characters. More precisely, some pre-Wealden bipedal predentate closely allied to *Hypsilophodon* appears to be indicated as the common ancestral stock, not only for the camptosaurus,

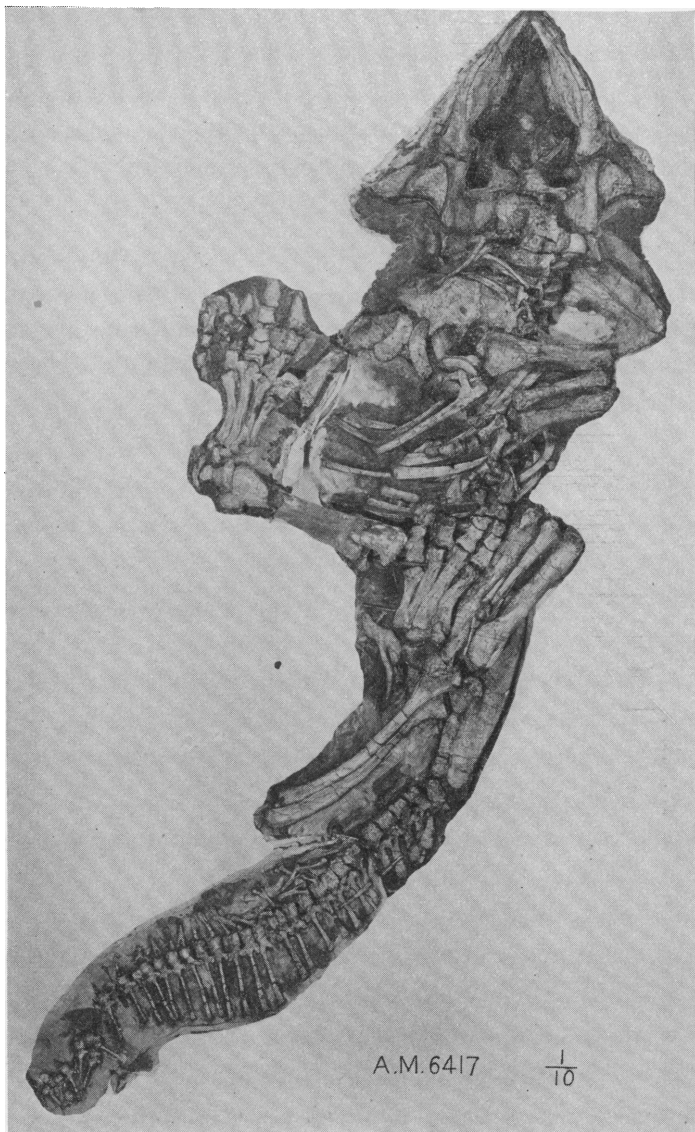


Fig. 3. *Protoceratops andrewsi*. Under side of a nearly complete skeleton. A. M. No. 6417. One-tenth natural size.

Note the large size of the hind limb and foot, as compared with the forearm and hand; the elongation of the metatarsus as in bipedal Ornithischia. The dorsal border of the ilium is not reflected outward above the acetabulum. The prepubic process of the pubis, while stout, is not nearly as long or as much expanded vertically as it is in later Ceratopsia, and the postpubic process is not so much reduced. The long ischia are concave on the lower border but lack an obturator process. The spines of the caudal vertebrae are very long and slender.

iguanodons, trachodons, and corythosaurs, but also for the variously specialized psittacosaur, troödon, acanthopholid, nodosaur or ankylosaur, and ceratopsians. The stegosaurs of the Comanchean, retaining a relatively unspecialized skull and pelvis, are on the whole an older branch usually recognized as derived from the Liassic *Scelidosaurus*.

The *Protoceratops* material is also of interest as affording strong evidence for the older view that the middle part of the ceratopsian frill is formed from the parietals, as maintained by Marsh, Hatcher, Lull, and Lambe, in opposition to the newer view of Hay, von Huene, and Gilmore that it is formed from the enlarged dermosupraoccipitals. These originally paired elements are unknown in any other group of dinosaurs and, aside from doubtful vestiges in Crocodilia, appear to be limited to the Permian orders of reptiles.

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