Article VI.—FOSSIL MAMMALS FROM BURMA IN THE AMERICAN MUSEUM OF NATURAL HISTORY

By Edwin H. Colbert

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and shape with the same bone in *Paramynodon*. As to size, its dimensions are about twice as great, linearally, in every direction as are those of the scaphoid of *Paramynodon*. It is furthermore distinguished by the flatness of its articular surfaces, the large dorsal one for the radius and the two ventral ones for the magnum and the trapezoid. These are distinct titanothere characters, to be seen in various American genera of upper Eocene titanotheres, and in decided contrast to the concave articulations in the scaphoid of *Paramynodon*. This bone is illustrated in the accompanying figure (Fig. 21).

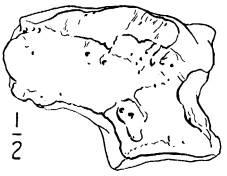

Fig. 21. Left scaphoid of a titanothere. Amer. Mus. No. 32540. Anterior view, one-half natural size.

Fig. 22. Left fifth metacarpal of a titanothere. Amer. Mus. No. 20009. Anterior view, one-fourth natural size.

The left fifth metacarpal (Amer. Mus. No. 20009) is short and quite heavy as contrasted with the same bone in *Paramynodon* (see Figs. 22 and 35). This bone, together with the scaphoid and magnum described in the preceding paragraph, would seem to be representative of an animal similar in size and weight to *Palaeosyops* or some of the advanced semi-graviportal upper Eocene titanotheres of North America.

The astragalus is a large and heavy bone as contrasted with the astragalus of *Paramynodon* (see Fig. 37). It is characterized particularly by its rather deep neck, by the strongly convex navicular facet, and by the relatively acute angle between this facet and the cuboid facet.

Rhinocerotoidea

Amynodontidae

The rhinocerotids in the Pondaung fauna are, to the best of our knowledge, restricted to a single genus, *Paramynodon*. In the descriptions by Pilgrim and Cotter (1916) and by Pilgrim (1925), *Paramynodon* was described, under the name of *Metamynodon*, from various upper and

lower teeth, jaw fragments and from an associated palate and mandible. Fortunately the material in the American Museum collection supplements the original specimens, for it includes the entire back portion of a skull, another broken skull, various teeth, jaw fragments, limb bones and feet (including an associated fore-limb) and other fragments too numerous to mention. Consequently *Paramynodon* assumes the position of being the most completely known of any of the Pondaung genera, with the possible exception of *Anthracokeryx*.

In the following pages a rather full description of the *Paramynodon* material in the American Museum collection will be presented, together with a discussion of these fossils, and a comparison of them with certain other amynodont genera and species. A monographic study of the Amynodontidae is now being prepared by Dr. Horace Elmer Wood, wherein a very full discussion of *Paramynodon* will be set forth. It is not the purpose of the present paper to anticipate Dr. Wood's conclusions; consequently in these pages emphasis will be given to the descriptions and discussions of the material, leaving a more complete survey of the genus to Dr. Wood.

PARAMYNODON MATTHEW, 1929

MATTHEW, W. D., 1929, Bull. Amer. Mus. Nat. Hist., LVI, p. 512.

GENERIC TYPE.—*Metamynodon birmanicus* Pilgrim and Cotter.[1]

AUTHOR'S DIAGNOSIS.—? More hypsodont than Amynodon.

Certainly more hypsodont than *Orthocynodon*.

Incisors appear to be reduced to $\frac{2}{1}$ in place of $\frac{3}{3}$ as in our forms, and are short, stubby, wider anteroposteriorly than transversely.

Canines wholly tagassuoid (peccary type).

Skull narrow and elongate, with long diastema.

Premolars considerably reduced, p_{3-4} longer than m_1 but less than m_2.

Lower molars narrow, but transverse crests are not so oblique as in *Metamynodon*, more perhaps than in *Amynodon*, certainly more than in *Orthocynodon*.

Appears to be nearer to *Amynodon* than to *Metamynodon*, but a partly intermediate, partly aberrant genus.

The *Cadurcotherium* from Gaj beds is also of intermediate type between *Metamynodon* and the large *Cadurcotherium*.

DIAGNOSIS (Revised).—An amynodont genus intermediate in size between *Amynodon* and *Metamynodon* but nearer to the former; closely comparable in size to *Amynodontopsis*. Dental formula 3/2(?), 1/1, 3/2, 3/3. Incisors regularly diminishing in size from median to lateral; cingula well developed. Canines large, upper canines rounded in cross section, lower canines more nearly triangular. Cheek teeth moderately hypsodont. Upper premolars progressively submolariform, with

[1] This species is chosen as the generic type because it is based on various definitive upper and lower cheek teeth. In *Paramynodon cotteri*, although an associated palate and mandible constitute the type, the teeth are worn to such a degree that they are of little use in the establishment of diagnostic characters.

the transverse crests permanently separated internally. Upper molars with moderately long ectoloph and with protoloph and metaloph more oblique than in *Amynodon* but less so than in *Metamynodon*. Lower premolars and molars transversely narrow. Third and fourth premolars submolariform. Transverse crests of lower cheek teeth more oblique than in *Amynodon* but less so than in *Metamynodon*. Premolars reduced so that they are relatively smaller than the lower premolars of *Amynodon* but perhaps a little larger than those of *Metamynodon;* therefore comparable to those of *Amynodontopsis* and considerably longer than those of *Cadurcotherium*.

Skull comparatively long, with a fairly long face and an elongated canine-premolar diastema. Zygomatic arches very broadly expanded, seemingly to a greater relative degree than is the case in any of the other amynodonts. Cranium expanded and sagittal crest relatively low. Orbit above the first molar; preorbital fossa of moderate size. Postglenoid and paroccipital processes widely separated, so that the opening of the external auditory meatus (auditory fossa) is not closed inferiorly.

Paramynodon birmanicus (Pilgrim and Cotter)

Metamynodon birmanicus, Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, pp. 65–71.

Metamynodon birmanicus, Pilgrim, 1925, Men. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 19–20, Pl. II, figs. 2, 3.

Paramynodon birmanicus, Matthew, 1929, Bull. Amer. Mus. Nat. Hist., LVI, p. 514.

Type.—G.S.I. No. C316, a right mandibular ramus. G.S.I. No. C317, a canine.

Paratypes.—G.S.I. Nos. C318, C319, fragments of three right upper molars; C320, an upper canine; "portions of four incisors including G.S.I. No. C322"; C323 an M^3; C324, maxilla; C325 upper premolar; C326 lower molars; C327, lower premolar, C328, upper molar; B321 incisor. The reference of C324, C328 to this species is questioned.

Referred Specimens.—G.S.I. No. C345, a left maxilla. (The right maxilla is in the British Museum.) G.S.I. No. C346, the right P^4, M^1 and M^2 and fragmentary M^3; and left fragmentary P^4 and the well-preserved M^2 and M^3; also a canine and some fragments of the front premolars.

Dr. Matthew made the following remarks about the type of *Paramynodon birmanicus*.

The type of this species is part of a lower jaw with five worn teeth; the paratypes are upper and lower teeth, mostly isolated; Nos. 345 and 346 were obtained later, and described by Pilgrim in a later memoir. No. 346 shows M^{2-3} of the left side and p^4–m^2 of the right side. The p^4 and m^1 are reversed in the drawing. It is a somewhat larger individual than No. 345, the teeth less worn; the premolar construction is the same in both but m^2 shows more apparent elongation; this may be due to greater size plus less wear. (Matthew, W. D., 1929, p. 514.)

Horizon.—Pondaung, Eocene.

Locality.—Myaing area, Burma.

Author's Diagnosis.—Molars.—These are of a roughly rectilinear outline. They are composed of two crescents, the sutures between which externally have

united to such a degree as to produce a practically continuous external wall to the tooth. This wall in m_1 and m_2 is regularly convex, but in m_3 forms a slight re-entrant curve. A very distinct cingulum is present on the external wall of m_3, but there does not appear to be any trace of this in m_1 or m_2. The surface of the molars is so worn that it is not possible to be certain that the anterior of the two crescents was the smaller of the two, although this was probably the case. At the antero-internal corner of m_3, a distinct cingulum is present, but this is absent from any other part of m_3, nor is such a cingulum visible in a corresponding position in m_1 or m_2.

PREMOLARS.—These are composed of double crescents of which the posterior one is the larger; moreover the front arm of the anterior crescent bends round but slightly, though more so in pm_4 than in pm_3. Consequently the outline of the latter tooth is triangular. The suture between the two crescents on the external wall is visible far more plainly in the premolars than in the molars, being shown as a very distinct furrow separating two convex surfaces.

LOWER CANINE.—This is a triangular tooth with an anterior ridge and two posterior ridges. The posterior surface of the tooth is slightly hollowed between the two hinder ridges, and laterally there is a faint groove visible both on the root as well as on the tooth. This is more marked on one side than on the other. On one side of the tooth the presence of a slight cingulum can be traced.

Specimens in the American Museum:

Amer. Mus. No. 20004, a fragment of a mandible with left M_{1-2}. One-half mile west of Mogaung. (Map, Fig. 8, locality A22.)

Amer. Mus. No. 20010, astragalus, navicular, lunars, phalanx, premolar teeth. One mile north of Koniwa. (Map, Fig. 8, locality A21.)

Amer. Mus. No. 20012, a badly broken skull, with the upper incisors and molars preserved. Three miles east of Gyat. (Map, Fig. 8, locality 13.)

Amer. Mus. No. 20013, associated humerus, radius-ulna, manus. One mile west of Bahin. (Map, Fig. 10, locality 11.)

Amer. Mus. No. 20018, two left lower molars. One mile east of Gyat. (Map, Fig. 8, locality A25.)

Amer. Mus. No. 20021, ulna and radius. One mile west of Myaing (?). (Map, Fig. 11, locality 12.)

Amer. Mus. No. 20025, fragment of left mandibular ramus with molar. Near Kyawdaw. (Map, Fig. 8, locality A26.)

Amer. Mus. No. 20026, right mandibular ramus with P_3–M_1. One-half mile northwest of Mogaung. (Map, Fig. 8, locality 17.)

Amer. Mus. No. 20030, left upper molar, right P_4 and fragment of molar. One mile northwest of Mogaung. (Map, Fig. 8, locality 15.)

Amer. Mus. No. 20032, radius and ulna. One-half mile northeast of Kyawdaw. (Map, Fig. 8, locality A27.)

Amer. Mus. No. 20033, tibia and fibula. Two miles east of Edgbaw. (Locality A34.)

Amer. Mus. No. 20034, left manus, almost complete. Two miles west of Mogaung. (Map, Fig. 8, locality 19.)

Amer. Mus. No. 20042, skull, lacking the portion in front of the first molar,

the right zygomatic arch and the occipital condyles. Near Than-u-daw. (Map, Fig. 11, locality 8.)

Amer. Mus. No. 32529, right mandibular ramus with molar fragments preserved. One-half mile northwest of Mogaung. (Map, Fig. 8, locality 17.)

Amer. Mus. No. 32530, phalanges. Near Legan. (Map, Fig. 8, locality A31.)

Amer. Mus. No. 32531, lower molars. Two miles west of Myaing. (Map, Fig. 11, locality A33.)

Amer. Mus. No. 32532, astragalus, navicular, lunar, right fifth metacarpal, right phalanges. One and one-half miles northwest of Myaing. (Map, Fig. 11, locality 7.)

Amer. Mus. No. 32533, molar fragments and upper incisor. One mile northwest of Mogaung. (Map, Fig. 11, locality 14.)

Amer. Mus. No. 32534. Left fourth metacarpal. Locality unknown.

Amer. Mus. No. 32535, left second metacarpal. One mile north of Myaing. (Map, Fig. 11, locality A29.)

Amer. Mus. No. 32536, astragalus, phalanx. One mile north of Bahin. (Map, Fig. 10, locality 11.)

Amer. Mus. No. 32537, radius and ulna, carpals, phalanges. Two miles east of Edgbaw. (Locality A34.)

Amer. Mus. No. 32538, molar fragments, radius, right third metacarpal, phalanges. Two miles east of Edgbaw. (Locality A34.)

Amer. Mus. No. 32539, navicular, left second metacarpal. One mile west of Myaing. (Map, Fig. 11, locality A32.)

Amer. Mus. No. 32541, left second metacarpal. One mile north of Koniwa. (Map, Fig. 8, locality A21.)

See also Amer. Mus. Nos. 20006, broken teeth associated with *Anthracothema pangan* (p. 354); Amer. Mus. No. 20027, broken teeth and foot bones associated with *Anthracothema rubricae* (p. 357).

Two skulls of *Paramynodon* are preserved in the American Museum collection. One, No. 20042, is partially complete and shows all of the essential characters of the skull and dentition back of the last premolar; the other, No. 20012, is very badly shattered, but of the existing fragments there are some that supplement our knowledge as gained from the more perfectly preserved skull. These two specimens, together with the front portion of the skull and the mandible described by Pilgrim as the type of *Paramynodon cotteri* afford us the opportunity of making an accurate reconstruction of the complete skull and mandible in this genus, thereby providing a really adequate basis for comparisons with other genera, such as *Amynodon*, *Amynodontopsis*, *Metamynodon* and *Cadurcotherium*.

The skull of *Paramynodon* is somewhat intermediate in size between the skull of *Amynodon* and that of *Metamynodon*, but on the whole it is much nearer to the former than it is to the latter genus in size. Three characters are quite distinctive of the skull in *Paramynodon*, namely the

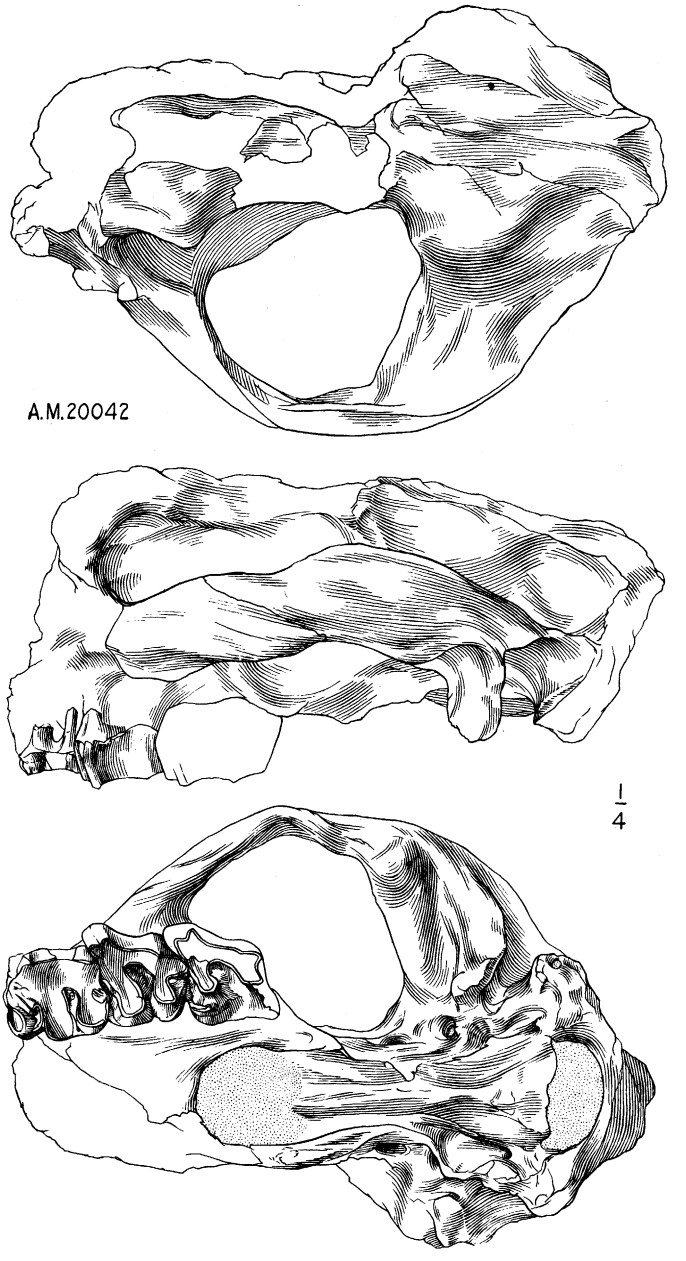

Fig. 23. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20042, skull. Dorsal view above, lateral view of left side in middle, palatal view below. One-fourth natural size.

comparatively long facial region, the great lateral expansion of the zygomatic arches and the expanded cranium. Matthew, in 1929, defined the skull of *Paramynodon* as being "narrow and elongate, with long diastema." Certainly the skull is elongate and the diastema is relatively long, as compared to the diastema in other genera of amynodonts, but it would seem likely that the narrowness of the skull cited by Matthew was more apparent than real. Undoubtedly the crushed skull of *Paramynodon cotteri*, described by Pilgrim, does look rather narrow, especially so since the zygomatic arches are missing. In the specimen at hand, however, (No. 20042) the skull cannot be called narrow, for the brain case is broad, the palate is broad, and the spread of the zygomatic arches is relatively greater than in the skull of *Metamynodon*.

The orbit is located above the first molar as in *Metamynodon*. In *Amynodon* the orbit is above the second molar, and in *Amynodontopsis* and *Cadurcotherium* the orbit is even farther back, being above the posterior edge of the second molar or the anterior edge of the last molar. Since the diastema is long the facial portion or the preorbital part of the skull in this genus is relatively longer than it is in *Metamynodon*, even though the orbits in both genera occupy approximately the same positions. In this respect *Paramynodon* resembles to some extent the more primitive *Amynodon* in which the preorbital part of the skull is relatively long. Part of the preorbital length in *Amynodon* is due, however, to the fact that the orbit is more posterior in its position than is the case with *Paramynodon*. In *Cadurcotherium* the preorbital region is relatively very short, even though the eye has been pushed back to a position more posterior than in any of the other amynodonts. It is probable that the preorbital fossa in *Paramynodon* was of moderate size as in *Metamynodon*—a distinct contrast to the fairly well-developed fossa of *Amynodon* and the extremely large fossa of *Amynodontopsis* and of *Cadurcotherium*.

As seen from the side, the skull of *Paramynodon* is distinguished by the upward sweep of the zygomatic arch; that is, the arch, instead of running back horizontally from the maxilla to the squamosal is strongly upbowed in its middle region. This character, together with the very broad lateral expansion of the two arches, and their considerable robustness, indicates that the masseter muscles of *Paramynodon* were exceptionally strong.

The postglenoid process is broad and flattened antero-posteriorly, and is widely separated from the massive paroccipital or posttympanic

process, so that the opening of the external auditory meatus is open below. In this respect *Paramynodon* resembles more the primitive *Amynodon* than it does the advanced *Metamynodon*, in which form the postglenoid and the posttympanic processes tend to be in contact with each other. This character is, however, variable within species of the rhinoceroses, and thus too much reliance cannot be placed on it as a diagnostic feature.

The glenoid articulation is shallow, or rather it is flat, and it merges imperceptibly into the under surface of the zygomatic arch. In the region of the glenoid the arch is very broadly expanded antero-posteriorly, so that it forms a wide shelf above the mandibular articulation and the ear. The posterior nasal choanae are very rounded and wide and extend to a point opposite the anterior border of the last molar. The pterygoids are strong.

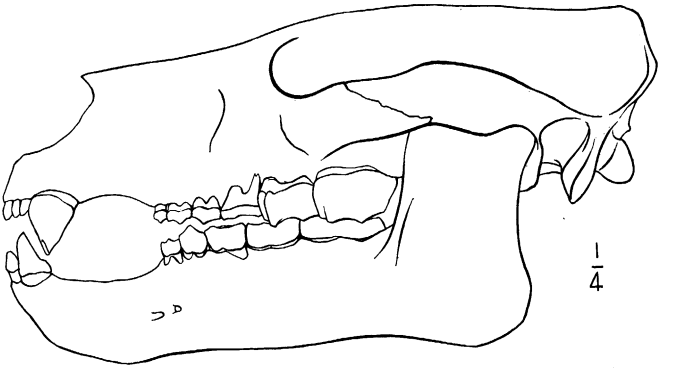

Fig. 24. *Paramynodon birmanicus* (Pilgrim and Cotter). Restoration of skull and mandible, based on Amer. Mus. Nos. 20042, 20010, 32530, 20026 and on G.S.I. No. C344 (type of *P. cotteri*). One-fourth natural size.

The basicranial foramina are not very plain but it would seem fairly evident that they are similar to the foramina in *Metamynodon*. Thus there is a well-developed alisphenoid canal, a separate foramen ovale opposite the internal border of the postglenoid process and seemingly a coalescence of the foramen lacerum medius and the foramen lacerum posterius around the small bulla (not preserved in the American Museum specimen). Presumably the foramen lacerum anterius and the foramen rotundum had a large opening anterior to the alisphenoid canal, while the ethmoid and optic foramina were very small, but these features are not preserved in the specimen now being discussed.

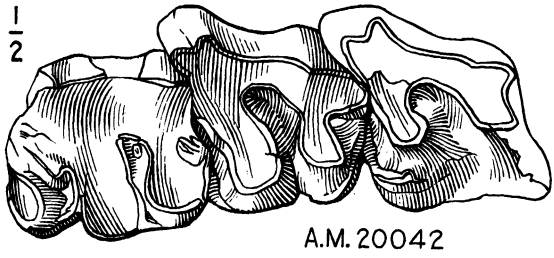

Fig. 25. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20042, left upper molars. Crown view, one-half natural size.

As seen from the top, the most striking features of the skull of *Paramynodon* are the widely expanded cranium and the transversely broad zygomatic arches. It would appear that the sagittal crest was low; evidently the temporal muscles were weak as compared to the extremely powerful masseter muscles. In front of the brain-case the skull becomes quite narrow, particularly in the region between the orbits. The postorbital processes are prominent and overhang the orbits.

As seen in its posterior aspect the skull is very low and broad, an appearance that is emphasized by the great spread of the zygomatic arches. The occiput is triangular in shape, wide at the bottom between the paroccipital processes, and narrowing at the top to meet the sagittal crest. In other words, the lambdoidal crest is not transversely expanded as it is in many of the advanced rhinoceroses, such as *Metamynodon* among the Amynodontidae.

The dental formula of *Paramynodon* has been a subject of considerable speculation. Pilgrim thought that he had evidence for three upper incisors and probably three lower incisors in this form. Dr. Matthew, on the other hand, in his generic diagnosis of *Paramynodon* stated that:

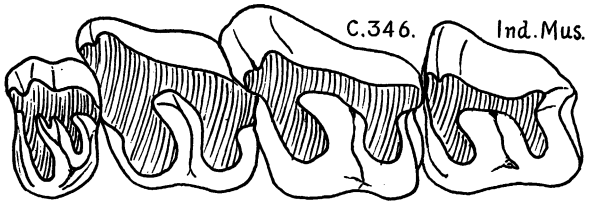

Fig. 26. *Paramynodon birmanicus* (Pilgrim and Cotter). G.S.I. No. C346, right P^4–M^2 and left M^{2-3}. P^4–M^1 reversed in drawing. (From Matthew, 1929.)

"Incisors appear to be reduced to 2/1 in place of 3/3 as in our forms. . . ." But in a caption for a figure of *Paramynodon cotteri* he wrote: "There are pretty surely three upper incisors, of which i^3 is quite small. . . ." (Matthew, W. D., 1929, p. 512.)

In the fragmental skull, Amer. Mus. No. 20012, there are three well preserved incisor teeth, all of different sizes. Thus it becomes certain that *Paramynodon* has a full incisor formula above, as Pilgrim suggested, and that the incisors are progressively smaller from the central to the lateral member of the series. Dr. Pilgrim has given good evidence in favor of three lower incisors in this genus.

As for the upper premolars, there are certainly three, all very much reduced in size. Dr. Pilgrim supposed that he had evidence for a fourth, namely the first of the series, but his contention was disputed by Matthew. The evidence would seem to favor Matthew's view. In the first place, the supposed first premolar, figured by Pilgrim and Cotter in 1916, is in reality an incisor, as Pilgrim admitted in 1925. Then Pilgrim's supposition, based on a published figure, that there are four upper premolars in *Metamynodon*, (and therefore by analogy four in *Paramynodon*) is erroneous. An examination of several *Metamynodon* skulls proves conclusively that there are only three upper premolars in this genus. Then again the jaws of *Paramynodon* indicate that only two lower premolars were present, and this would favor the presence of three upper premolars to oppose them.

A fragmentary mandible, Amer. Mus. No. 20026, gives further evidence that there were but two lower premolars in *Paramynodon*.

The upper incisors of *Paramynodon*, as preserved in Amer. Mus. No. 20012, are long anteroposteriorly (except the very small third incisor, which has a round cross section) and all of them have well-developed internal cingula.

The canines, as shown by certain isolated specimens, are of two kinds; one with a roughly elliptical cross section, the other with a triangular cross section. There can be no doubt but that these are upper and lower canines, respectively, as is shown by the anterior and posterior wear surfaces developed on them. Thus it would seem probable that the upper canines in *Paramynodon* are large and robust, with elliptical cross sections, whereas the lower canines are somewhat smaller with triangular cross sections. This contention is borne out by a comparison of *Paramynodon* with *Metamynodon*, in which latter genus the upper canines are elliptical and the lower ones are triangular. (See Fig. 28.)

Pilgrim's distinction of *Paramynodon cotteri* from *Paramynodon*

birmanicus on the basis of elliptical lower canines in the former and triangular canines in the latter may not be valid. In the triangular canines in the American Musum collection, the roots are more or less elliptical in cross section, as might be expected. And at points on the roots progressively more distant from the crown, the cross section becomes more and more elliptical and less and less triangular. Thus it is quite possible that this supposed specific differentiation is due in reality

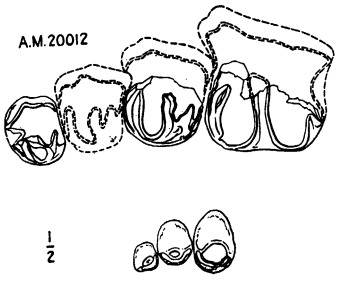

Fig. 27

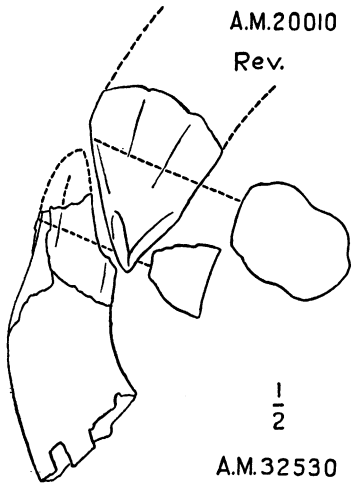

Fig. 28

Fig. 27. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20012, incisors and cheek teeth from a broken skull. Left P^2–M^1 above, right I^{1-3} below. Crown views, one-half natural size.

Fig. 28. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. Nos. 20010, upper canine, and 32530, lower canine. No. 20010 has been reversed in the drawing. Lateral views and cross sections. One-half natural size.

to a comparison between roots and crowns of different canine teeth, or between points on the root near to and far from the crowns.

The wear surfaces of the canines show that the upper canines were directed both forward and down, while the lower canines were approximately vertical in their position.

The upper premolars of *Paramynodon* are similar to those of *Metamynodon* in that the transverse crests are not joined internally by a crescent, as is the case with *Cadurcotherium;* that is, the valley between the protoloph and what might be termed the incipient metaloph is open internally and not enclosed. There is, however, a strong cingulum en-

circling the internal and the anterior edges of the tooth. The second premolar has one cross crest, bounded fore and aft by cingula, while the third and fourth premolars are doubly cross crested, but with the posterior crest relatively small. There is a strong vertical rib in the middle of the ectoloph of these teeth. In all of these premolar characters the closest resemblance to *Paramynodon* is to be found in *Metamynodon*, and to a lesser extent in *Amynodon*.

The upper molars are truly intermediate in construction between the upper molars of *Amynodon* and those of *Amynodontopsis* and *Meta-*

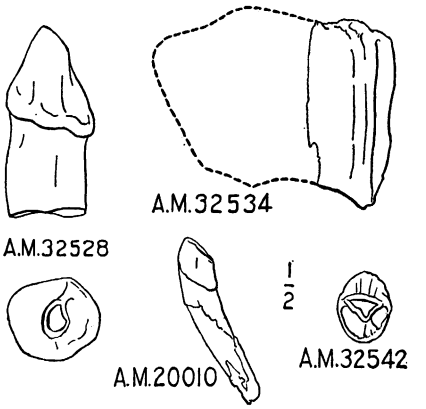

Fig. 29. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 32534, portion of unworn ectoloph of upper molar, showing height of crown. Lateral view. Amer. Mus. No. 20010, incisor tooth, lateral view.

Titanothere. Amer. Mus. No. 32528, incisor tooth. Lateral view above, crown view below. Compare the difference in size between this tooth and the incisor tooth of *Paramynodon*. Amer. Mus. No. 32542, incisor tooth, crown view. All figures one-half natural size.

mynodon. That is, they are more or less quadrate in their outlines, the ectoloph is long, there is a distinct paracone groove, the obliquity of the protoloph and the metaloph to the ectoloph is closely comparable to the condition typical of the two American genera mentioned above, the anterior cingulum is well developed, and the teeth are open internally. In all of these characters the molars of *Paramynodon* are in distinct contrast to the teeth of *Cadurcotherium*. It might be mentioned, too that the hypsodonty of the molars of *Paramynodon* is intermediate between *Amynodon* and *Metamynodon*.

The lower premolars of *Paramynodon* are reduced in size and are pro-

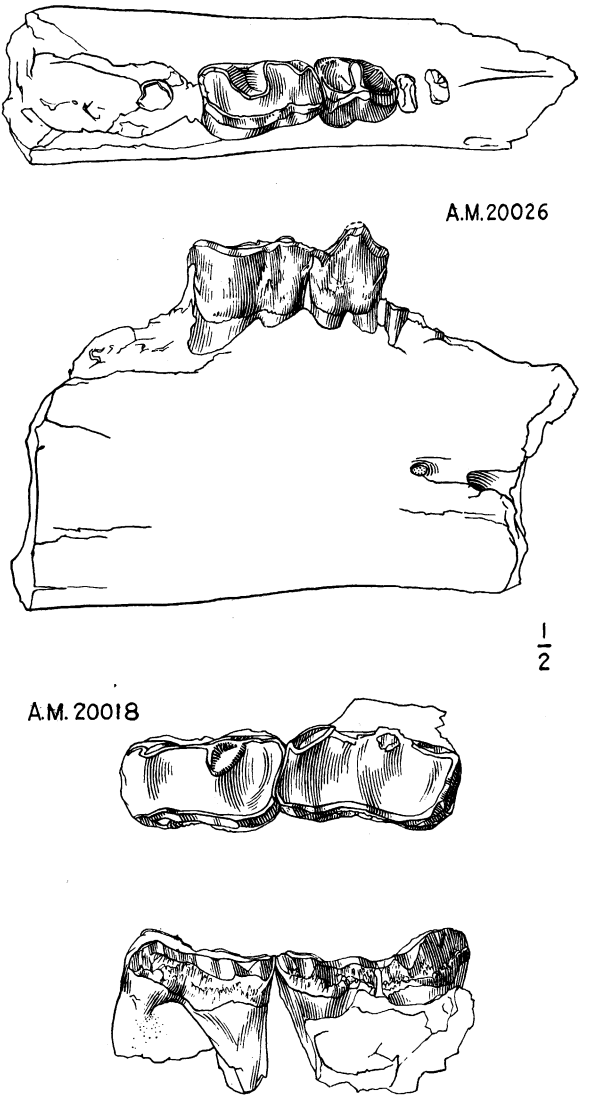

Fig. 30. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20026, portion of right mandibular ramus with P_3–M_1. Crown view above, lateral view below. Amer. Mus. No. 20018, left lower molars. Crown view above, lateral view below. All figures one-half natural size.

gressively more molariform from front to back. The molars are closely comparable to those of *Amynodon* and *Metamynodon*, both in their relative transverse compression and in the obliquity of the cross crests.

The upper and lower cheek teeth of *Paramynodon* furthermore are similar to those of *Amynodon* and *Metamynodon* by reason of the fact that they are not transversely compressed, as is the case in *Cadurcotherium*.

Comparing *Paramynodon* with those Asiatic amynodonts that are geographically fairly close to it, the following observations may be made.

Cadurcotherium indicum Pilgrim, from the Gaj series of the Bugti Hills is a large and specialized form of lower Miocene age. As Pilgrim has shown, this species is a true *Cadurcotherium*, comparable in size to the European form, *Cadurcotherium nouleti*, and characterized by its very large, transversely compressed molars with flat ectoloph surfaces. It is much larger and more advanced than *Paramynodon*.

Metamynodon bugtiensis, described by Forster Cooper from the Bugti beds of Baluchistan, is also a form much larger and more advanced than *Paramynodon*. This species resembles *Metamynodon planifrons* by reason of its large size, relatively straight ectoloph, development of parastyle fold (long but not as deep as in *Paramynodon*), crochet on the second upper molar and internal cingulum on the third lower premolar. In the American form there is a crochet on the third upper molar and an internal cingulum on all of the premolars. Thus, *Metamynodon bugtiensis* is close to *Metamynodon planifrons* and shows many evolutionary advances over *Paramynodon*.

Amynodon sinensis Zdansky and *Amynodon mongoliensis* Osborn show more resemblances in their dental characters to *Paramynodon* than do the Asiatic species of *Metamynodon* and *Cadurcotherium*, discussed above. *Amynodon sinensis* is a small form, much smaller than *Paramynodon*, whereas *Amynodon mongoliensis* is closely comparable in size to the Burmese genus. Both of these species resemble *Paramynodon* in the prominent parastyle groove and ridges, the rather curved ectoloph, the lack of a crochet on the molars, the internal cingulum of the premolars and the relative hypsodonty. Thus, as has been shown in the description of the dentition of *Paramynodon*, this genus is similar to but more advanced than *Amynodon*, and it is perhaps closer to the Asiatic than to the American species because of the greater progressiveness of the oriental forms. Detailed comparisons between the skulls of *Paramynodon* and *Amynodon* (including *Amynodon mongoliensis*) have been set forth in preceding paragraphs.

Considering now the general phylogenetic position of *Paramynodon* (as based on the preceding detailed comparisons of skulls and dentitions and on the following studies of the limbs and feet) it may be said that this genus is more or less intermediate in size and structure between *Amynodon* and *Metamynodon*, but it has followed an evolutionary trend of its own. That is, *Paramynodon* must not be considered as a direct, intermediate form between *Amynodon* and *Metamynodon*, but rather it and *Metamynodon* are to be viewed as having a common descent from *Amynodon*. Naturally, since these lines of descent were at first contiguous, and drew apart only gradually during the long succession of geologic time, it is to be expected that similarities in size and structure will be found in *Paramynodon* and *Metamynodon*. *Metamynodon*, developing through a much longer period of time than *Paramynodon*, became much larger and in most of its characters more specialized than the Burmese form. *Paramynodon*, being somewhat isolated from the other Asiatic amynodonts, and particularly from the American forms, evolved along lines of its own, and thus developed certain structures quite different than what might be expected in any form directly intermediate between *Amynodon* and *Metamynodon*.

The subject of the relationships of *Paramynodon* will be fully expounded by Dr. H. E. Wood, in his forthcoming monograph on the amynodonts. Consequently further remarks here are not necessary.

MEASUREMENTS

	A. M. 20042	G.S.I.[1] *P. birmanicus*	G.S.I.[1] *P. cotteri*
Length of skull, occ. cond.-ant. border of orbit	290 mm.		
Diameter of orbit	52		
Greatest width of zygomatic arches	350		
Greatest width of parietals	135		
Narrowest width of frontals	70		
Height of occiput (base of for. mag.)	112		
M^1 length	41	32 mm.	38 mm.
width	47	43	50
M^2 length	52	44	46
width	55	51	56
M^3 length	60	45	50
width		46	49

[1] Measurements from Pilgrim, 1925. Numbers of specimens not specified.

Paramynodon cotteri (Pilgrim)

Metamynodon cotteri, PILGRIM, 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 15–19, Pl. II, fig. 1, a–e.

Paramynodon cotteri, MATTHEW, 1929, Bull. Amer. Mus. Nat. Hist., LVI, p. 513.

TYPE.—G.S.I. No. C344, an almost complete mandible and the front portion of a skull.

PARATYPES.—None.

HORIZON.—Pondaung, Eocene.

LOCALITY.—1 1/4 miles west of Mindezu village, Burma.

DIAGNOSIS (Revised).—The skull is elongated and rather narrow, with a large preorbital cavity; the premolar-canine diastema is much longer than in the other

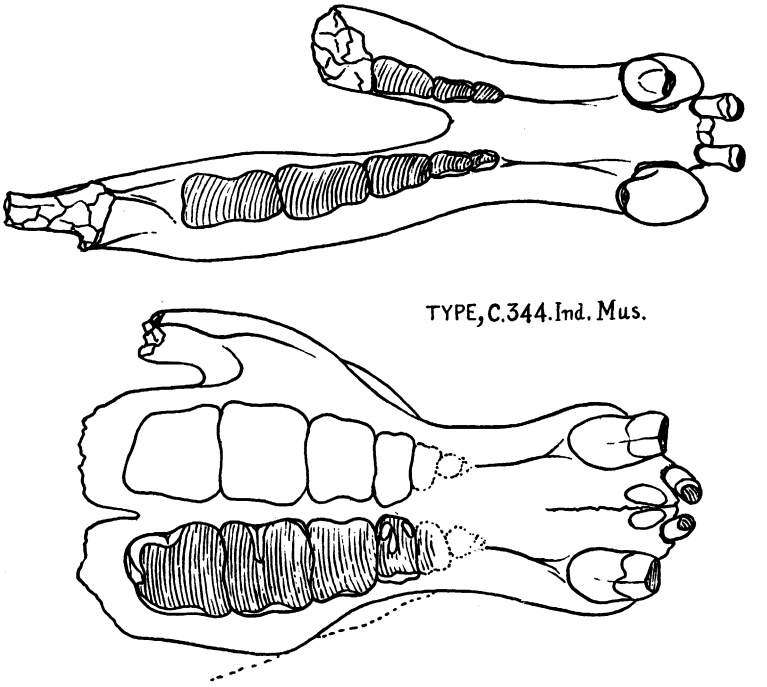

Fig. 31. *Paramynodon cotteri* Pilgrim. G.S.I. No. C344, type skull and mandible. Crown views. (From Matthew, 1929.)

amynodonts. A full set of upper incisors is present; the second incisor is the largest of the series. The upper canine is large, transversely flattened, so that it has an oval cross section. It projects strongly forward. There were probably four upper premolars. The molars are amynodont, M^3 with a well-developed metaloph, as in *Amynodon* and *Metamynodon*, in distinct contrast to *Cadurcotherium*. The lower second incisors are well developed, whereas the first and third incisors would seem to be quite small. The lower canine is relatively large, transversely flattened. Only two lower premolars are present. The ectoloph of the lower molars is continuous.

Dr. Matthew made the following remarks about the type specimen of *Paramynodon cotteri* in 1929.

The teeth of this specimen are greatly worn, so that the pattern is almost wholly obliterated on the molars and nearly gone on the premolars. The molars of the left side are clear, but on the right side the crowns of the lower molars are fast to the crowns of the upper teeth and have not been disengaged, so that neither is visible completely. Tips of canines have been considerably damaged and restored with plaster and the muzzle has been roughly cemented with plaster to the rest of the skull, covering up some of the construction. Skull is considerably crushed laterally and was broader than appears in the drawing, but is not so broad as *Metamynodon*, arch not so deep, muzzle longer, teeth more vertical (cf. *Orthocynodon*). Proportions and patterns of teeth appear to be intermediate in most particulars between *Amynodon* and *Metamynodon*, but premolars less pocketed than *Metamynodon*, much less than *Cadurcotherium*. (Matthew, W. D., 1929, p. 513.)

Dr. Pilgrim separated *Paramynodon cotteri* from his original species, *Paramynodon birmanicus* on the basis of:

a.—Its larger size;

b.—The elliptical cross section of the lower canine, as contrasted with a trihedral cross section in *Paramynodon birmanicus*.

Due to the badly worn teeth in the type of *Paramynodon cotteri*, and the lack of any skull fragments of value in the type of *Paramynodon birmanicus*, direct comparisons between the types of these two species unfortunately are impossible. Consequently truly valid distinctions between these species, as based on their respective types, cannot be made.

Looking at Pilgrim's differentiation of the two species of *Paramynodon* the following facts may be brought out.

Size Differences

Expressing certain linear measurements of *Paramynodon cotteri* as 100, the corresponding measurements of *Paramynodon birmanicus* are as follows:

	Paramynodon birmanicus	*Paramynodon cotteri*
P^3	94	100
P^4	90	100
M^1	84	100
M^2	96	100
M^3	90	100
Upper molar series	86	100
Lower premolar series	92	100
Lower molar series	83	100
Lower canine	49	100

Now it may easily be seen that most of the size differences are relatively small, while practically all of them are less than fifteen per cent.

Thus there is no difficulty in supposing the size differences between the two species of *Paramynodon* to come within the bounds of individual variation. As to the great difference in size between the canines in the two forms, it is very likely that this may be attributed to sexual dimorphism. Therefore, on the basis of size alone, it would seem probable that *Paramynodon cotteri* is a large male, whereas *Paramynodon birmanicus*, being smaller and having much smaller canines, is a female.

The measurements on which the above ratios are based, were seemingly taken from a referred specimen of *Paramynodon birmanicus* (G.S.I. No. C345) and from the type of *Paramynodon cotteri* (G.S.I. No. C344). The teeth of G.S.I. No. C346, identified by Pilgrim as *Paramynodon birmanicus* and figured by Matthew in 1929, are seemingly even larger than the teeth of No. C345, so that they serve to break down the size differences between the supposedly different species.

The Shape of the Lower Canines

Pilgrim placed a great deal of emphasis on the elliptical (lower) canine of *Paramynodon cotteri* as compared with the trihedral (lower) canine of *Paramynodon birmanicus*. Whether the difference here is as real as Pilgrim maintains it to be, is a debatable question. The cross section of the lower canine in any of the amynodonts is certainly dependent to a great extent on the manner in which it is observed. Below the crown of the tooth it is invariably more or less elliptical in form while at the base of the crown, just at or slightly below the posterior facet of a fully erupted tooth, the cross section tends toward a trihedral shape. Farther up on the crown the cross section is naturally strongly trihedral, due particularly to the development of the posterior facet by occlusion with the upper canine. This is illustrated by the lower canine of *Metamynodon planifrons*, which Pilgrim cites as a form in which this tooth has an elliptical cross section. Below the crown the cross section is undeniably elliptical in shape, but toward the crown the cross section becomes more and more strongly trihedral, becoming markedly so at and above the base of the posterior facet.

One difference between the two supposed species of *Paramynodon* that was not brought out by Dr. Pilgrim, is the difference in the lower third premolar. In *Paramynodon birmanicus* this is a well-developed, fully premolariform tooth, while in *Paramynodon cotteri* it is reduced to a small, oval peg. This may constitute a truly valid distinction between the two species, indicating the further progression of *Paramynodon cotteri* toward the premolar reduction so characteristic of this genus.

I wish to acknowledge the kindness of Dr. H. E. Wood for calling my attention to this point of difference between the two species of *Paramynodon.* In his forthcoming study of the amynodont rhinoceroses, he will deal fully with the taxonomic and phylogenetic position of *Paramynodon* and of its species, questions that have only been touched upon in the foregoing paragraphs.

All in all the evidence would seem to be against the validity of *Paramynodon cotteri* as a species separate from *Paramynodon birmanicus.* But due to the inconclusive nature of the evidence, and the impossibility of interpreting it definitely either in one direction or in the other, it would seem best, on the basis of the known material of this genus, to let the second species stand as tentatively valid. In the opinion of the present author, future discoveries will tend to prove that *Paramynodon cotteri* is synonymous with *Paramynodon birmanicus.*

Limbs and Feet of *Paramynodon*

The American Museum Burma collection is noteworthy because of the amount of perissodactyl limb and foot material that it contains, some of which is extraordinarily complete, such as the associated fore-limb (Amer. Mus. No. 20013) and the manus (Amer. Mus. No. 20034). Certain specimens have been identified as belonging to titanotheres, and consequently have been discussed in preceding pages of this paper, but by far the major portion of them are identifiable as *Paramynodon.*

The Fore-Limb

Considered in its entirety the fore-limb of *Paramynodon* is more or less intermediate in size and structure between the fore-limb of *Amynodon* and that of *Metamynodon.* It is somewhat heavier, but no longer than the limb in the former of these two genera, and naturally considerably smaller, both as to length and breadth than the limb of the latter.

The humerus is a rather heavy bone with a long and prominent deltoid crest. The head of the humerus is strongly convex antero-posteriorly and has a very low transverse convexity. The articular surface is roughly triangular as seen from above, with one base of the triangle facing anteriorly toward the bicipital groove. This latter structure is double, seemingly a characteristic feature of the amynodonts, and it is located between the very prominent external tuberosity and the much smaller internal tuberosity. The external tuberosity consists of two rather separate processes (again a character that would seem to be fairly

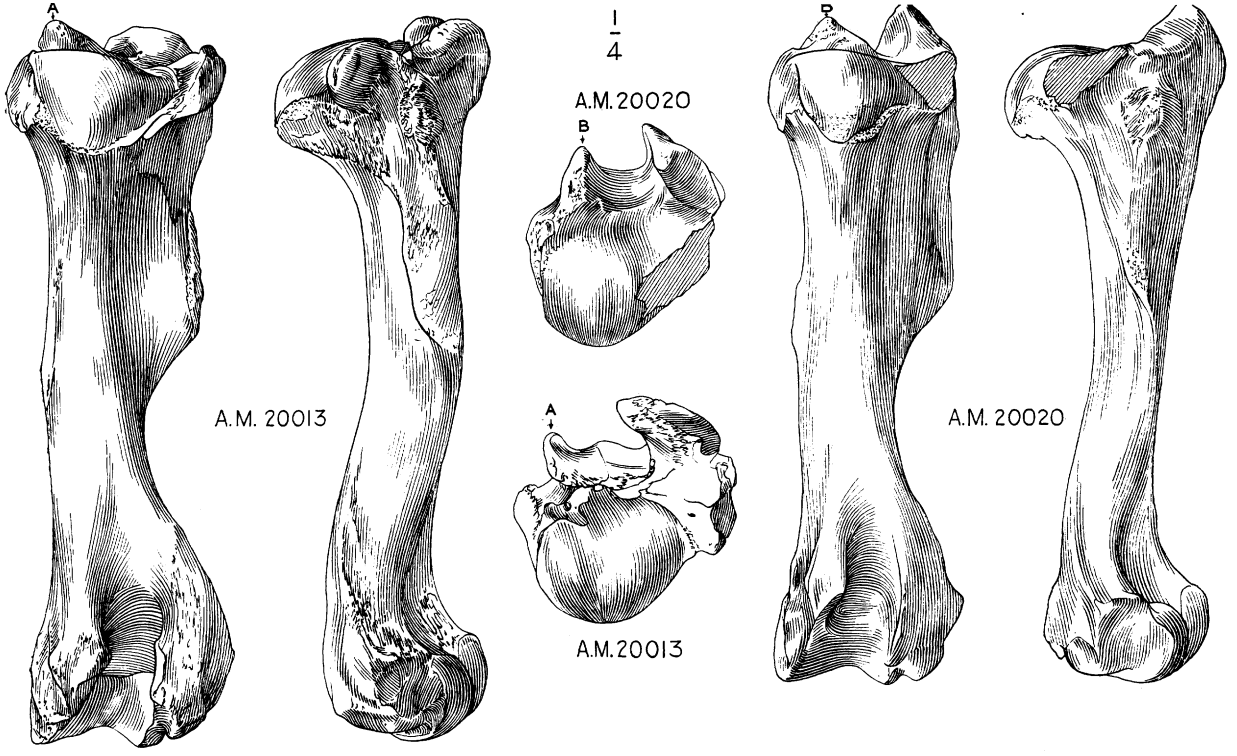

Fig. 32. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20013, right humerus. Dorsal, lateral external and proximal views.

Titanothere. Amer. Mus. No. 20020, right humerus. Dorsal, lateral external and proximal views.

A and B indicate the lesser or internal tuberosity in Amer. Mus. No. 20013 and 20020, respectively. Notice the double bicipital groove in Amer. Mus. No. 20013; the single groove in 20020.

All figures one-fourth natural size.

typical of the amynodonts): namely, an anterior one that is very large and strong, and curves in an antero-internal direction to form a sort of a hook in front of the external rotula of the bicipital groove, and a posterior one that lies directly external to the head of the humerus. A strong ridge extends from this posterior process of the greater tuberosity so that it runs distally along the upper portion of the deltoid crest, and served perhaps as a surface for the insertion of a part of the infraspinatus muscle. There is a prominent swelling at the antero-internal corner of the head and directly internal to the lesser tuberosity, that probably served in part as an attachment for the subscapularis muscle.

The distal end of the humerus is characterized by its rather large and prominent supinator crest, and particularly by the articular surfaces on the sides of the olecranon fossa for the anconeal process of the olecranon The trochlea is much wider anteroposteriorly than is the capitellum, but the disparity, although quite marked, is not so great as in the titanotheres.

Of these characters described above, the double bicipital groove, the division of the greater tuberosity into an anterior and a posterior process and the asymmetry between the trochlea and capitellum of the distal articular surface are features that ally *Paramynodon* on the one hand with *Amynodon* and on the other with *Metamynodon*. That is, these characters are developed to the least extent in *Amynodon*, to the greatest extent in *Metamynodon* and to an intermediate degree in *Paramynodon*. They are characters that separate the humerus of *Paramynodon* from the same bone in the titanotheres, of which specimens are found in the Pondaung deposits.

The radius is a comparatively slender bone. It is about four-fifths as long as the articular length of the humerus, in which respect it offers a contrast to the radius of *Amynodon*, which is either equal to or longer than the humerus, but resembles that of *Metamynodon*, which is considerably shorter than the humerus. Its distal portion is characterized by the strongly concave, raised outer articular surface, and the rather depressed and flattened inner surface for the capitellum and the trochlea, respectively, of the humerus. Other noteworthy features are the very prominent external process, the very deep pit on the front of the bone, just below the head (which served in part for the insertion of the biceps brachialis), and the strongly rugose area on the back of the bone to serve as an articulation with the proximal end of the ulna. On the back of the radius, at the middle of the shaft, there is a long groove, bounded externally by the ridge for the interosseous membrane, ending in a shal-

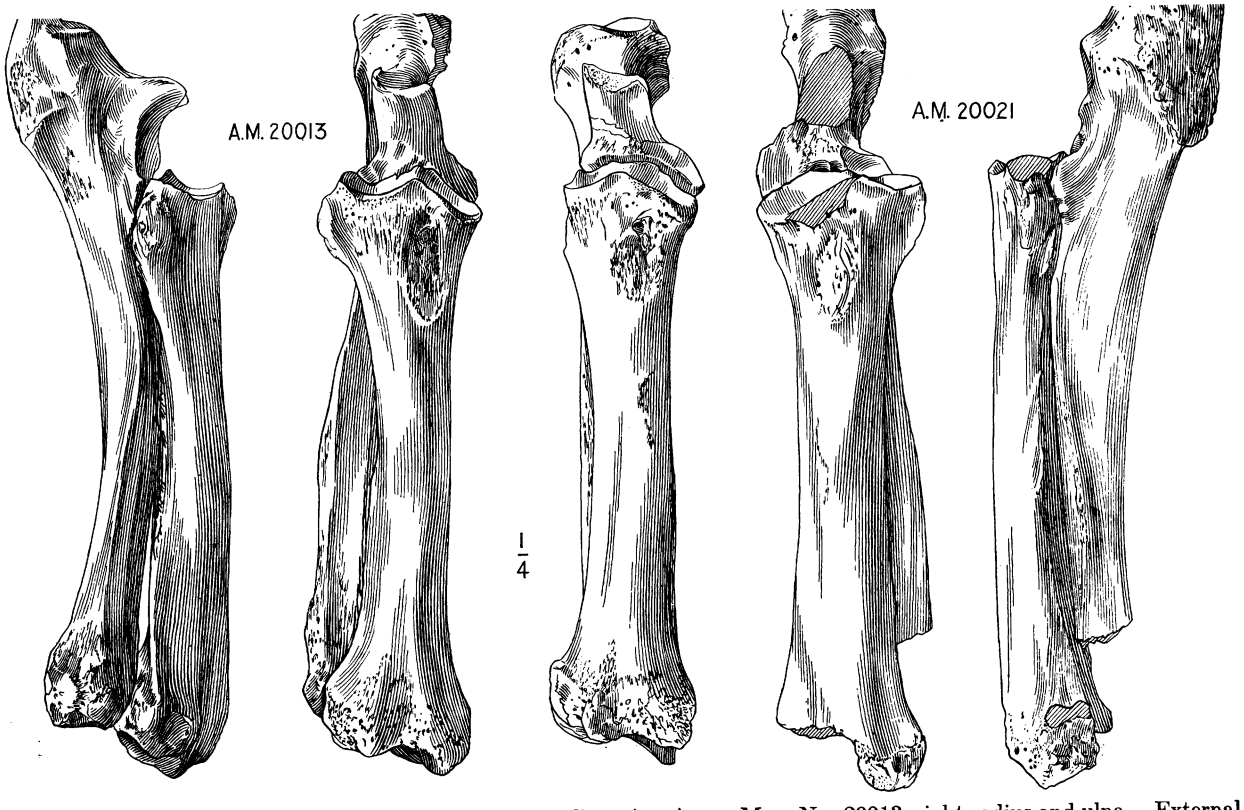

Fig. 33. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20013, right radius and ulna. External lateral and anterior views. Amer. Mus. No. 20032, right radius and ulna. Anterior view. Amer. Mus. No. 20021, left radius and ulna. Anterior and external lateral views. All figures one-fourth natural size.

low pit. Into this groove and pit fitted a corresponding ridge on the internal edge of the ulna, thereby forming an extraordinarily close and strong connection between these two bones. Because of this structural connection between the radius and ulna, it is quite evident that there was practically no pronation or supination in the fore-arm of *Paramynodon.*

The distal end of the radius of *Paramynodon* is strongly expanded, both transversely and anteroposteriorly, and it has a convex and a concave articulation for the scaphoid and the lunar bones, respectively.

The ulna of *Paramynodon* is distinguished by its rather slender shaft and expanded olecranon, which makes it rather closely comparable to

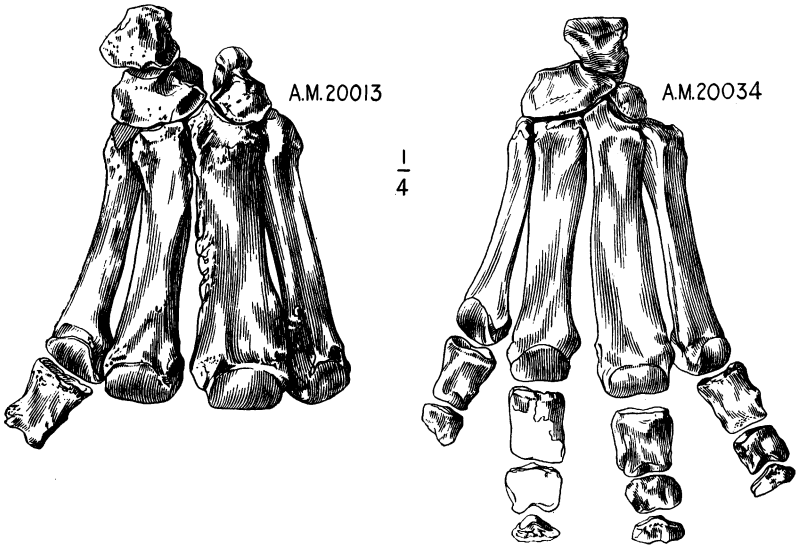

Fig. 34. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20013, right manus, dorsal view. Amer. Mus. No. 20034, right manus, dorsal view. Both figures one-fourth natural size.

the ulna of *Amynodon,* rather than to the ulna of *Metamynodon,* in which form the shaft is quite robust. This bone is, however, relatively shorter than the comparable bone in *Amynodon.* The shaft is broadly triangular in cross section, and on its front side is a rugose proximal area and a medial, internal ridge, both for articulation with the radius, as described above. The end of the olecranon is greatly expanded, to serve as a strong attachment for the various heads of the triceps muscle. There is a distal articular surface for the cuneiform bone of the manus.

The manus has four digits, of which the outer one, or the fifth in the series, is large and fully functional. The metacarpals are transversely broad, but antero-posteriorly (or dorso-ventrally) rather thin, thereby giving to them a rather flat appearance. This is a rhinoceros character that is particularly well-marked in the genus under discussion, and even more prominent in the Oligocene form, *Metamynodon*. In *Amynodon*, as might be expected, the metacarpals are less flattened, due to their lesser amount of transverse growth. Curiously enough, the metacarpals (and the entire manus for that matter) of *Paramynodon* are not only proportionately but in some cases *actually* shorter than the same bones in *Amynodon*. This is in accord with the fact that elongation in the evolution of a structure usually precedes transverse growth. The limbs and feet of *Amynodon* were elongated from a more primitive ancestral form. Then, having attained a suitable linear dimension, these structures began to broaden in the descendents of *Amynodon*, so that they became moderately broad in the moderately specialized *Paramynodon*, and very broad in the more highly specialized *Metamynodon*. The medial and ungual phalanges (as shown in 20034) are very short, a rhinoceros character. The carpals need no special description—their form and arrangement are shown in the accompanying figures.

Comparing particularly the limbs of *Paramynodon* and *Amynodon mongoliensis* it becomes evident that the latter form is characterized by the elongation of the lower portions of the legs. Whereas *Paramynodon* is larger in every way than *Amynodon intermedius*, its lower limb and foot elements are shorter, not only proportionately but also actually, than the same bones of the Mongolian amynodont. Thus it would seem that *Paramynodon* followed the usual amynodont trend toward a graviportal, and probable aquatic habitus, whereas *Amynodon mongoliensis*, on the other hand, specialized to some degree in the direction of a sub-cursorial habitus. These phylogenetic trends are shown graphically in the accompanying tables of measurements and charts.

The proportions of the manus in *Paramynodon* and other amynodonts are given in the following table. It is to be noticed that *Paramynodon* is intermediate between *Amynodon* and *Metamynodon*, but somewhat closer to the former.

	$\frac{\text{Width of manus, across carpals} \times 100}{\text{Extended length of manus}}$
Amynodon mongoliensis	31
Amynodon intermedius	34
Paramynodon birmanicus or *cotteri*	37
Metamynodon planifrons	45

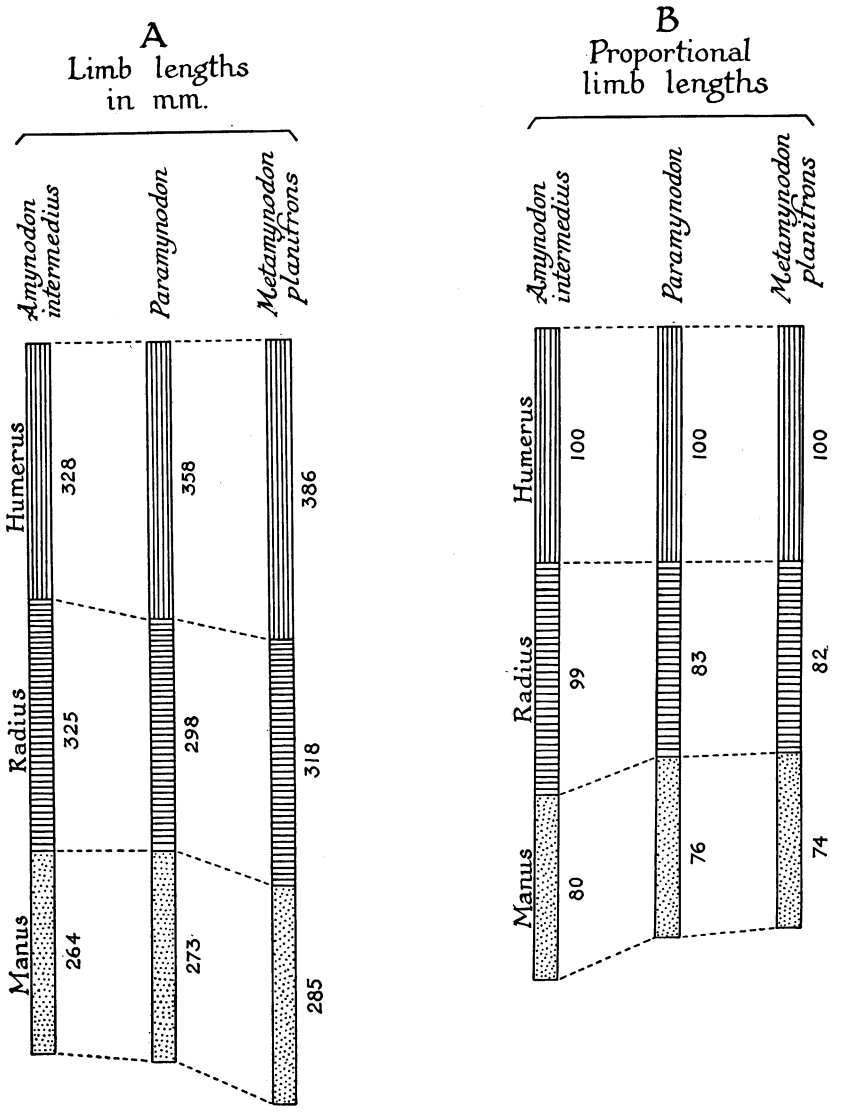

Fig. 35. Diagram to show the comparative lengths of the fore-limbs and their components in three genera of amynodont rhinoceroses.

MEASUREMENTS

	Amynodon intermedius A. M. 1933	*Paramynodon birmanicus* A. M. 20013	*Metamynodon planifrons* A. M. 546
Humerus, articular length	328 mm.	358 mm.	386 mm.
greatest length	355	380	430
proximal breadth		116	150
distal breadth	75	105	131
Radius, articular length	325	298	318
median breadth	25	36	61
Ulna, greatest length	397	378	430
proximal breadth	51	66	83
distal breadth	40	40	62
Manus, extended length	264	273e	285
Metacarpal III, length	163	161	166
breadth	33	38	46
Carpus, breadth	91	100e	127
height	67	54e	71
Digit III, prox. phalanx, length	28	35	26
breadth	20	29	41
med. phalanx, length	16		15
breadth	28		35
ung. phalanx, length	12		25
breadth	27		47

RATIOS AND INDICES

	Amynodon intermedius A. M. 1933	*Paramynodon birmanicus* A. M. 20013	*Metamynodon planifrons* A. M. 546
Length of humerus	100	100	100
radius	99	83	82
manus	80	76	74
metacarpal III	50	45	43
Length of fore-limb, extended	100	100	100
humerus	36	39	39
radius	35	32	32
manus	29	29	29
metacarpal III	18	17	17
Humerus, breadth × 100/art. length		32	39
Radius, breadth × 100/art. length	7.7	12	19
Manus, breadth × 100/ext. length	34	37	45
Metacarpal III, breadth × 100/length	20	24	28

	A. M. 20034
Index: Manus, breadth × 100/ext. length	33
Metacarpal III, breadth III × 100/length	22

MEASUREMENTS

	Paramynodon manus	
	A. M. 20013	A. M. 20034
Extended length of manus	273e mm.	261 mm.
Carpal breadth	100e	85e
Carpal height	54e	56
Metacarpal II, greatest length	153	136
breadth	27	26
Metacarpal III, greatest length	161	152
breadth	38	33
Metacarpal IV, greatest length	148	135
breadth	26	26
Metacarpal V, greatest length	132	123
breadth	19	18
Proximal phalanx, digit II, length × width		29 × 24
III	35 × 29	31 × 31
IV		
V		30 × 25
Median phalanx II		20 × 23
III		20 × 28
IV		
V		15 × 21
Ungual phalanx II		10 × 24
III		13 × 27
IV		12 × 25
V		

The Hind-Limb

Curiously enough, there is comparatively little material from the hind-limb of *Paramynodon* in the American Museum collection. A tibia and fibula, which can be only provisionally assigned to the genus, a number of astragali, a few scattered bones of the tarsus, particularly a navicular and an ectocuneiform, and a left third metatarsal (probably associated with the fore-limb, Amer. Mus. No. 20013, comprise practically all of the hind-limb bones that may be referred to *Paramynodon.*

The tibia and fibula, Amer. Mus. No. 20033, are tentatively identified as belonging to *Paramynodon,* with a full realization that they may eventually prove to be of titanotheroid, rather than of rhinocerotid relationships. They are of a size, however, that would correspond closely with the fore-limb bones of *Paramynodon,* and moreover the distal articulations fit very well some of the *Paramynodon* astragali. It is interesting to note, too, that the supposed titanothere astragalus, Amer. Mus. No. 32527 (p. 342, Fig. 37) does *not* articulate with the tibia now under consideration. Therefore, the evidence in favor of this tibia

and fibula being referable to the genus *Paramynodon* is seemingly very good.

The tibia is a rather stout bone, expanded proximally in a transverse direction, to accommodate the broad articular surfaces for the femur. The cnemial crest is low, with a proximal roughened depression for the ligamentum patellae. The internal surface of the bone is rounded, with a certain amount of distal rugosity, presumably an attachment in part for the flexor longus digitorum, while on the outer surface of the bone

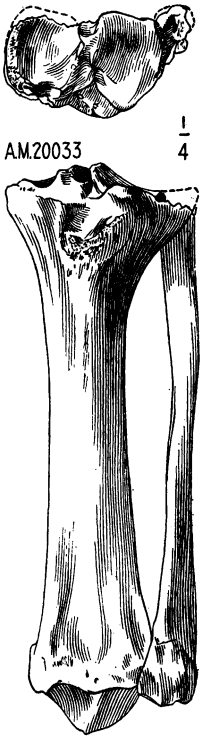

Fig. 36. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20033, left tibia and fibula. Proximal view above, anterior view below; one-fourth natural size.

there is a long sharp crest for the interosseous ligament. The distal articulation is directed somewhat obliquely to the fore and aft axis of the shaft, and this fits very well the oblique astragalar pulley of *Paramynodon*. The fibula is slender but complete. Distally it articulates with the astragalus. Both of these bones have been crushed to a considerable degree.

The astragalus in this genus is rather light, considering the breadth of the metatarsals, and the trochlea is moderately deep. There is a

broad, concavo-convex articular surface for the navicular and a small cuboid facet. A separate articular facet on the posterior surface of the bone indicates that the sustentaculum of the calcaneum extended to a point beneath the internal crest of the astragalus.

The navicular is broad, with a prominent process extended up on its postero-internal surface, thereby carrying the astragalar articulation up posteriorly in a strongly concave curve. Distally there are two facets, each for a cuneiform bone. The single cuneiform bone preserved, number three of the series, is characterized by its concave dorsal surface for articulation with the navicular. The distal articulation for the metatarsal is also somewhat concave.

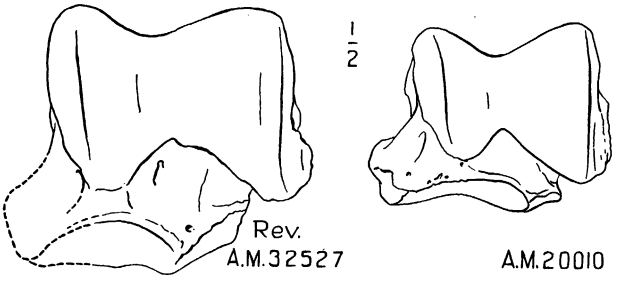

Fig. 37. Astragalus of *Paramynodon* (Amer. Mus. No. 20010) compared with the astragalus of a Pondaung titanothere (Amer. Mus. No. 32527). Figures one-half natural size.

The single metatarsal is a relatively broad bone, considerably shorter than the similar bone of the manus. Its form is shown in the accompanying figure.

MEASUREMENTS

	A. M. 20023
Tibia, greatest length	293 mm.
breadth, mid-shaft	40
Fibula, greatest length	267
breadth, mid-shaft	17
Left metatarsal III, greatest length	139
breadth	37

VARIATIONS IN THE METACARPALS OF *Paramynodon*

In addition to the complete fore feet of *Paramynodon*, Amer. Mus. Nos. 20013 and 20034, there are a number of separated metacarpals that afford supplementary evidence about the degree of variability in certain individual foot elements of this genus. These are Amer. Mus. Nos.

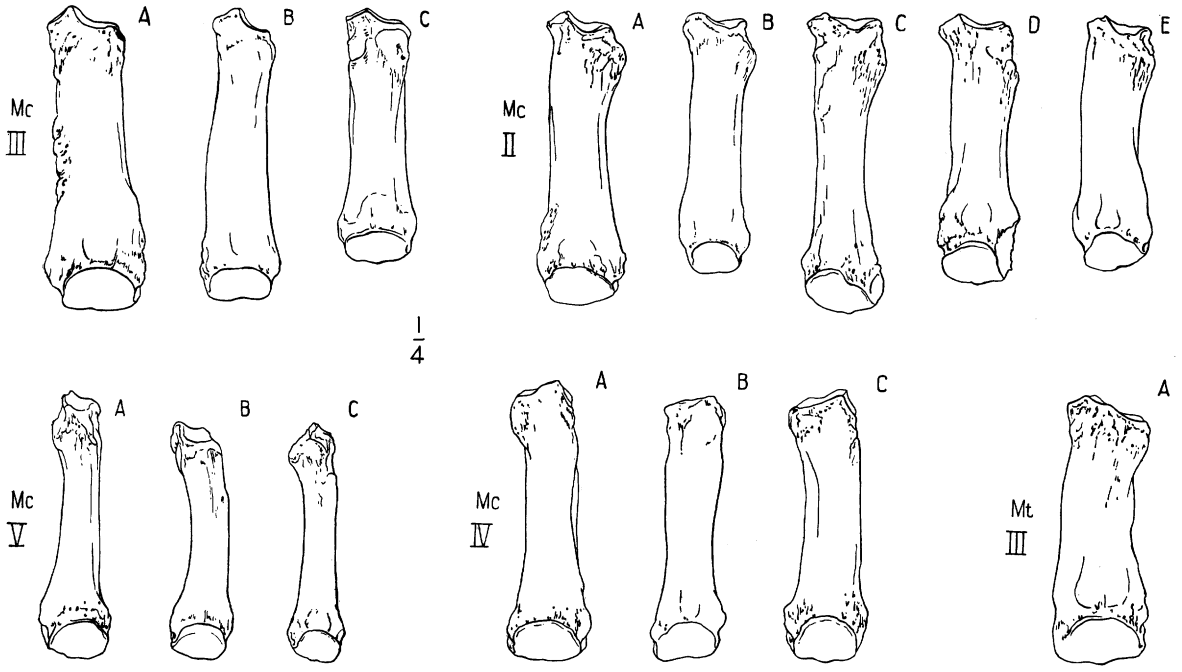

Fig. 38. Variability in the metacarpals of *Paramynodon*. A: 20013. B: 20034. C: (Mc. II) 32539; (Mc. III) 32538; (Mc. IV) 32534; (Mc .V) 32532. D: 32541. E: 32535. A: (Mt. III) probably associated with 20013. All figures one-fourth natural size.

32532, a right fifth metacarpal; 32534, a left fourth metacarpal; 32535, a left second metacarpal; 32538, a right second metacarpal; and 32539, a left second metacarpal. Amer. Mus. No. 32541, a left second metacarpal is also considered here, although it is only questionably referred to the genus *Paramynodon*. It may belong to a titanothere.

Considerable variation is shown in comparable bones from different individuals, as might be expected. There is some variation in the length of the bones, and a more pronounced variation in their width, this latter factor being attributable particularly to the greater weight or massiveness of some individuals over others, thereby resulting in a broader, stronger foot. Perhaps these differences are due in part to sexual dimorphism, the larger, heavier males being characterized by broader feet than the more slender females. Even so, the indices of breadth to length in the metacarpals of *Paramynodon* are surprisingly uniform, thereby indicating that in spite of size differences we are dealing here with a single form, probably a single species.

Perhaps the most noticeable variable on any particular metacarpal is the pair of facets on the fourth metacarpal for articulation with the third member of the series. These surfaces vary considerably as to size and shape.

The variability of the metacarpals in *Paramynodon* is shown in the accompanying table and the comparative figures.

It might be interesting in this connection to compare the degree of variability in the foot of the *Paramynodon* from Burma with that in some other type of rhinoceros. The recent study by Granger and Gregory (1936) of the genus *Baluchitherium* from the Oligocene Houldjin gravels ofMongolia bears on this problem in a particularly apt manner, since it has to do with an extraordinarily variable species. Therefore the degree of variability in the third metacarpal of *Baluchitherium*, as figured by Granger and Gregory (Figs. 44 and 45), is compared with the variability of this same bone in *Paramynodon* from Burma. The following interesting results are obtained.

RATIOS OF LENGTHS, RIGHT METACARPAL III

Baluchitherium grangeri	
Amer. Mus. 26175 (largest individual)	100
Amer. Mus. 26389 (smallest individual)	65
Amer. Mus. 26166 (intermediate size)	100
Amer. Mus. 26389	79
Paramynodon birmanicus	
Amer. Mus. 20013 (largest individual)	100
Amer. Mus. 32538 (smallest individual)	83

Thus it may be seen that the difference between the smallest and largest individuals of *Paramynodon* is approximately equivalent to that between the smallest and an intermediate-sized individual of *Baluchitherium*, and is much less than the difference between the smallest and largest individuals of this latter genus. In other words, the degree of variability in *Paramynodon* (as measured by metacarpal dimensions) does not exceed twenty per cent, while in *Baluchitherium* it may be as much as thirty-five per cent. Of course the greater variability would be expected in the Mongolian genus because of its excessive giantism. On the other hand, this comparison will show that the variability in the foot of *Paramynodon*, though considerable, is not excessive, and it falls well within the range of expected specific differences.

MEASUREMENTS AND INDICES

	Greatest Length	Width, Mid-Shaft	Index
Metacarpal II			
A. M. 20013	153 mm.	27 mm.	17.7
A. M. 20034	136	26	19.1
A. M. 32539	155	23	14.8
A. M. 32535	133	28	21
A. M. 32541	139	27	19.4
Metacarpal III			
A. M. 20013	161	38	23.5
A. M. 20034	152	33	21.7
A. M. 32538	133	29	21.8
Metacarpal IV			
A. M. 20013	148	26	17.5
A. M. 20034	135	26	19.3
A. M. 32534	139	27	19.4
Metacarpal V			
A. M. 20013	132	19	13.7
A. M. 20034	123	18	14.6
A. M. 32532	124	16	12.9

TAPIROIDEA

Our knowledge of the Pondaung tapirs rests on the very limited evidence of two fragmentary specimens that have been referred to two genera and species. And although much more complete material is needed, still the specimens now known are sufficiently well preserved to afford some clues as to the relationships of the Eocene tapirs of Burma.

Thus it would seem that in this one horizon there are two types of tapiroids belonging to distinct families and showing very different stages in their evolutionary development. *Indolophus*, known from

the upper teeth is seemingly a primitive type, related to such generalized forms as *Systemodon* (*Homogalax*), *Parisectolophus* and *Isectolophus*, and may be referred to the family Isectolophidae as defined by Peterson. The lower jaw, described by Pilgrim as *Chasmotherium* (?) *birmanicum* and here questionably referred to the genus *Deperetella* is a much more advanced type of tapiroid, and it may be referred to the family Helaletidae.

Isectolophidae

INDOLOPHUS PILGRIM, 1925

PILGRIM, G. E., 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 22–25.

GENERIC TYPE.—*Indolophus guptai* Pilgrim.

DIAGNOSIS (Revised).—A small tapiroid perissodactyl in which the teeth resemble to some extent those of *Homogalax* and *Isectolophus*. The premolars are not molariform, consisting of subconical deuterocone and tritocone, the former joined by a transverse crest to the internal median protocone. Molars with well-developed protoloph and metaloph. It differs from *Homogalax* in that there is no protoconule; instead, it has a conical protocone and hypocone, and a weaker internal cingulum; it differs from *Isectolophus* and *Homogalax* by the fact that the posterior cingulum joins the hypocone.

Indolophus guptai Pilgrim

Indolophus guptai, PILGRIM, 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 22–25, Pl. II, figs. 8 a–d.

ADDITIONAL REFERENCE.—Matthew, W. D., 1929, Bull. Amer. Mus. Nat. Hist., LVI, p. 515.

TYPE.—G.S.I. No. C347, a left maxilla of a young individual in which two of the molars have erupted.

PARATYPES.—None.

HORIZON.—Pondaung, Eocene.

LOCALITY.—$1^1/_4$ miles N. of Konywa, Burma.

DIAGNOSIS (Revised).—Upper premolars with sub-conical deuterocone and tritocone, the former connected to the centrally placed protocone by a transverse crest. Anterior and posterior cingula well developed. P^2 with prolonged antero-external angle. Upper molar with conical paracone and metacone, connected to the protocone and hypocone by well-developed protoloph and metaloph. Anterior and posterior cingula well developed.

Indolophus is seemingly a very primitive tapiroid, particularly with regard to the structure of the premolars—a fact that was recognized by Pilgrim in his original description of the genus. Generally speaking, it shows resemblances to *Systemodon* (*Homogalax*), *Parisectolophus* and *Isectolophus*, but in certain features, namely the rounded, conical deuterocone and tritocone of the premolars and paracone and metacone of the molars, the undivided premolar protocone and the lack of a second

transverse crest in the premolars, this genus may be considered as being more primitive than any of the other known tapiroids of the middle or upper Eocene. This conclusion was expressed by Pilgrim in his original description, as follows.

In conclusion *Indolophus* seems to be in some ways intermediate between *Systemodon* and *Isectolophus*, but certainly shows features which are distinct from both of them. The primitive condition of the upper premolars undoubtedly shows that it represents an early stage of development, which cannot belong, we should say, to a later period than the upper Eocene, and may even be earlier. I am inclined to regard it as a descendant of an early emigrant of the Lower Eocene, even more primitive than *Systemodon*, in which the posterior crest of the premolars had not as yet made its appearance. (Pilgrim, G. E., 1925, p. 25.)

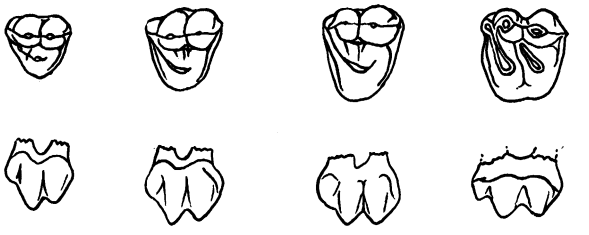

Fig. 39. *Indolophus guptai* Pilgrim. G.S.I. No. C347, type upper premolars and first molar. Crown views above, external views below. Natural size. (From Matthew, 1929.)

In 1929, Dr. Matthew made the following observations with regard to the type specimen of *Indolophus guptai.*

Founded on upper teeth, the only specimen. The teeth p^2-m^1 are almost unworn and compare best with *Parisectolophus* and *Isectolophus*. The pattern has some very primitive features, reminiscent of *Eohippus;* nothing like it in the Mongolian Eocene. I should place it among the Tapiroidea, probably in the family *Parisectolophidae* but not nearly related to any genus that I recall. (Matthew, W. D., 1929, p. 515.)

Recently (1937) Schlaikjer has discussed *Indolophus* briefly, comparing it with *Helaletes* on the basis of the general premolar construction, rather than with *Parisectolophus* and *Isectolophus*. It is true, of course, that the single, undivided protocone of the third premolar in *Indolophus* resembles the single, or but slightly divided internal cusp in the third premolar of *Helaletes*. On the other hand, the general construction of the molar and the premolars would seem to link the Burma form perhaps more closely with *Parisectolophus*, as Matthew maintained, than with *Helaletes*. Schlaiker concludes that:

I am inclined to agree with Mr. Peterson that *Isectolophus*, *Parisectolophus* and *Helaletes* are already too specialized in the dentition, particularly in the superior premolars, to be regarded as ancestral to the later true tapirs. *Indolophus*, although very imperfectly known, seems to show those same specializations, especially in the slight division of the internal cusp of P^4, and on the basis of this should, for the present be eliminated from the true tapir ancestry. (Schlaikjer, E. M., 1937, p. 244.)

As has been shown above, however, *Indolophus* is even more primitive than *Parisectolophus*, *Isectolophus* and *Helaletes* in the premolar specializations typical of these latter genera. Thus *Indolophus* may be regarded as a tapiroid approaching in structure the generalized perissodactyl ancestral type.

Helaletidae

DEPERETELLA MATTHEW AND GRANGER, 1925

MATTHEW, W. D., AND GRANGER, WALTER, 1925, Amer. Mus. Novitates, No. 196, pp. 4–6.

GENERIC TYPE.—*Deperetella cristata* Matthew and Granger.

AUTHORS' DIAGNOSIS (in part).—Molar pattern related to that of *Desmatotherium* and *Colodon* but more specialized in the direction of sharp transverse crests; the premolars more molariform. . . . Lower molars with wide, sharp transverse crests, no connecting ridge, a low, transverse, crested cingulum behind the posterior crests of all three, but no heel on m_3. External and anterior basal cingula, inner cingulum imperfect to absent. Fourth lower premolar fully molariform, third partly so, with strong connecting crest between the transverse crests and well-developed paraconid First and second premolars compressed, two-rooted, the second submolariform and longer than the posterior premolars. Diastema short, canine of moderate size, incisors smaller.

Deperetella (?) birmanicum (Pilgrim)

Chasmotherium (?) *birmanicum*, PILGRIM, 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 25–28, Pl. II, fig. 9.

ADDITIONAL REFERENCE.—Matthew, W. D., 1929, Bull. Amer. Mus. Nat. Hist., LVI, p. 515.

TYPE.—G.S.I. No. C348, two mandibular rami belonging to the same individual.

PARATYPES.—None.

HORIZON.—Pondaung, Eocene.

LOCALITY.—About $1\frac{1}{2}$ miles S.W. of Thadut Village, Myaing township, Burma.

DIAGNOSIS (Revised).—Lower fourth premolar almost completely molariform with two transverse crests; joined on the external side of the tooth by anteriorly and posteriorly directed processes. Lower molars doubly crested, the crests being slightly concave anteriorly and slightly convex posteriorly, and the valley between the crests being entirely open. M_3 without a hypoconulid.

Although Pilgrim suggested the possibility that the upper dentition of *Indolophus guptai* and the lower dentition of *Chasmotherium birmanicum* might be generically identical, he considered it more likely

that they are quite distinct. His conclusions in this matter would seem to be amply justified.

At the time he described the Pondaung tapiroids, he was of course unacquainted with the new tapiroids from Mongolia, which were then being studied by Dr. Matthew. Naturally, Pilgrim found that the closest resemblances to the new specimen from Burma was to be seen in the European genus *Chasmotherium*, and so he accordingly referred the Burma species to this genus. However, he made this reference a provisional one, realizing that the Burma species is more advanced than the typical European *Chasmotherium* by virtue of (*a*) its more completely lophodont molars and (*b*) its more molariform premolar.

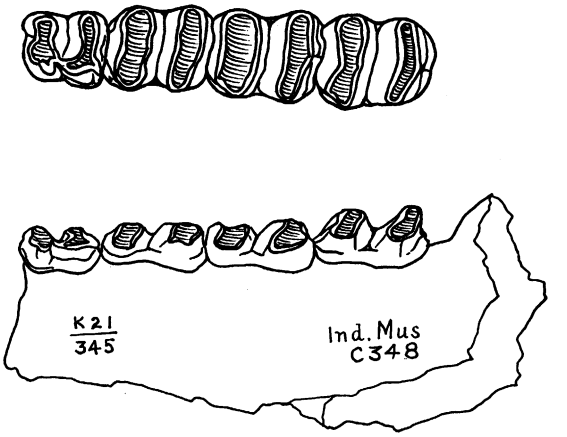

Fig. 40. *Deperetella* (?) *birmanicum* (Pilgrim). G.S.I. No. C348, type left mandibular ramus. Crown view above, lateral view below. Natural size. (From Matthew, 1929.)

In 1929, Dr. Matthew compared *Chasmotherium birmanicum* with the two new genera from the upper Eocene of Mongolia, namely *Deperetella* and *Teleolophus*, and came to the conclusion that the Burma form was more closely related to these Mongolian genera than to the European *Chasmotherium*.

[*Chasmotherium birmanicum* is] founded on a lower jaw, the only specimen. Appears to be related to *Teleolophus* and *Deperetella* of the Mongolian Eocene. Smaller than *Deperetella* and lower crowned molars, premolar less fully molariform, and broader and shorter anteroposteriorly. The premolar is more advanced than in *Teleolophus*, the molars of about the same size, but the size of the teeth from p_4–m_3 is more uniform, less increase in size than in *Teleolophus*.

Probably this is not *Chasmotherium*, but careful comparison with Depéret's and

Stehlin's material would be advisable. It is certainly distinct from *Indolophus*. (Matthew, W. D., 1929, p. 514.)

A careful comparison of the Burma species with *Chasmotherium* as described and figured by Stehlin and by Depéret would seem to show that the Pondaung form is certainly less closely related to the European genus than it is to the Mongolian genera cited above. Therefore Dr. Matthew's conclusions as to the relationships of *Chasmotherium birmanicum* would seem, on the basis of our present knowledge of the species, to constitute the most accurate statement as to its position.

All in all, *Deperetella* is more closely comparable to the species under consideration than is any other genus of tapiroids. In size the Mongolian form is about half again as large as the Burma jaw. On the other hand, close resemblances between them are to be seen in the structure of the lower molars, consisting of two slightly bowed cross-crests without antero-posterior connecting ridges, in the lack of a heel on the third molar, and in the molariform structure of the last premolar. In *Deperetella* the fourth lower premolar is slightly more molariform than is this same tooth in the specimen from Burma, and there are certain other minor differences in the structure of this tooth in the two forms.

Teleolophus, on the other hand, would seem to be more primitive in certain respects than *Chasmotherium birmanicum*. This is particularly apparent in the development of the fourth lower premolar, which in *Teleolophus* is not molariform. Also in the lesser degree of uniformity in the size of the molars, a point that was stressed by Matthew. On the other hand, however, *Teleolophus* resembles *Chasmotherium birmanicum* by reason of its similarity of size and also by the lack of surrounding cingula, which are so prominent on the teeth of *Deperetella*.

On the basis of our present evidence it would therefore seem probable that the tapiroid described by Pilgrim as *Chasmotherium* (?) *birmanicum* is in reality a distinct and a new genus, closely related to *Deperetella* and perhaps less closely related to *Teleolophus* of the upper Eocene beds of Mongolia. It does not seem advisable at this time to create a new genus for the Burma form, particularly in view of the fragmentary nature of the specimen on which the species is founded. Therefore the species hitherto known as *Chasmotherium* (?) *birmanicum* is here designated as *Deperetella* (?) *birmanicum* in the belief that this name more accurately expresses its relationships. It is realized, however, that the discovery of additional material will probably prove the necessity of creating a new genus for this Burmese species.