SIWALIK MAMMALS IN THE AMERICAN MUSEUM OF NATURAL HISTORY

By Edwin H. Colbert

PART I. INTRODUCTION

Previous Publications Dealing with American Museum Siwalik Vertebrates

Several of the more interesting fossils in the American Museum Siwalik collection have been the subjects of papers by various authors. Most of these papers have been preliminary notices, issued as descriptions of new species or as detailed accounts of especially important forms. One, the Anthropological Paper by Gregory and Hellman is a thorough monograph, based in part on the primate remains discovered by Dr. Brown. Three other papers are general in their scope. One of these is a popular descriptive article by Dr. Brown giving an account of his expedition in India, and another is a popular article by Dr. Matthew dealing with Siwalik fossils and the general aspects of the Siwalik problem. The third is Dr. Matthew's "Critical Observations upon Siwalik Mammals," mentioned in the preface, a long report of extraordinary value.

The papers published by the American Museum, concerning Siwalik vertebrates are listed below. These publications, together with the present work and with Dr. Pilgrim's contribution on the Bovidae, bring to a completion the studies on the mammals in the collection, and with the exception of a few more shorter contributions which will come out on the remaining undescribed reptilian remains, they bring to a close the studies on the Siwalik collection. Thus, some ten years or so since it was made, the collection has been virtually completely studied, and it will now remain in the Museum as important reference material for future studies on vertebrate evolution. In the accompanying list all of the Siwalik contributions are included for the sake of completeness.

1. Matthew, W. D., 1924. Fossil Animals of India. Nat. Hist., XXIV, No. 4, pp. 208–214.
2. Brown, Barnum, Gregory, William K., and Hellman, Milo, 1924. On Three Incomplete Anthropoid Jaws from the Siwaliks, India. Amer. Mus. Novitates, No. 130.
3. Brown, Barnum, 1925. Glimpses of India. Nat. Hist., XXV, pp. 109–125.
4. Osborn, Henry Fairfield, 1926. Additional New Genera and Species of the Mastodontoid Proboscidea. Amer. Mus. Novitates, No. 238, pp. 4–6.
5. Gregory, William K., and Hellman, Milo, 1926. The Dentition of Dryopithecus and the Origin of Man. Amer. Mus. Anthropological Papers, XXVIII, Pt. 1.
6. Brown, Barnum, 1926. A New Deer from the Siwaliks. Amer. Mus. Novitates, No. 242.
7. Matthew, W. D., 1929. Critical Observations upon Siwalik Mammals. Bull. Amer. Mus. Nat. Hist., LVI, Art. VII, pp. 437–560.

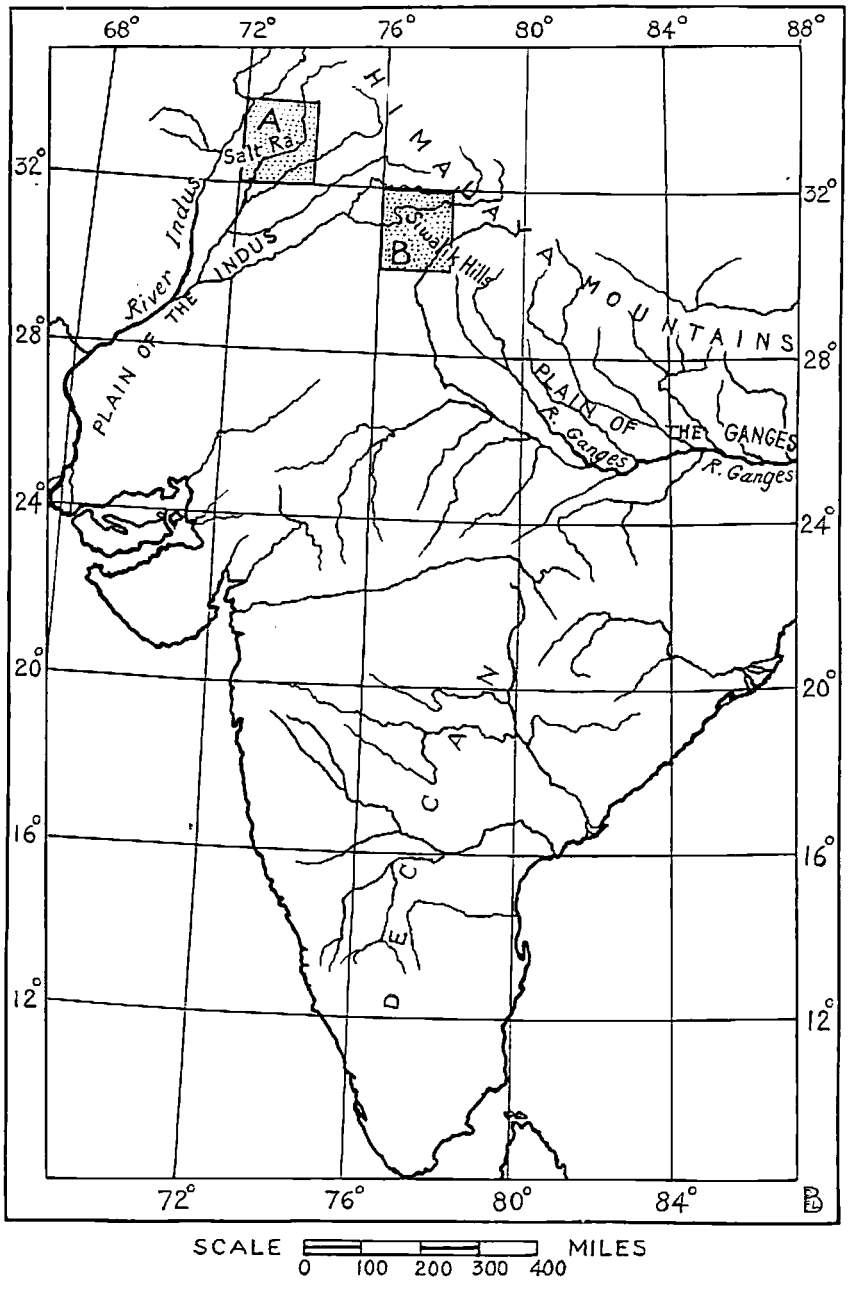

FIG. 15. Map of India, showing location of two key maps A and B, which include the localities whence the American Museum Siwalik collection was obtained.

RHINOCEROTOIDEA

General Considerations

The rhinoceroses from the Siwalik deposits have long been in a state of confusion, and in view of the prevalent difficulties standing in the way of a correct interpretation of our knowledge of any of the fossil rhinoceroses, it is doubtful whether we are in a position as yet to arrive at a clear picture of the history of this group in the Indian region.

Quite a number of species of fossil rhinoceroses have been described from the Siwaliks during the course of time since the first work of Falconer and Cautley. These species are listed below as they were originally described.

Rhinoceros sivalensis Falconer and Cautley, 1847.
Rhinoceros palaeindicus Falconer and Cautley, 1847.
Rhinoceros platyrhinus Falconer and Cautley, 1847.
Rhinoceros perimensis Falconer and Cautley, 1847.
Rhinoceros iravadicus Lydekker, 1876.
Rhinoceros planidens Lydekker, 1880.
Aceratherium blanfordi Lydekker, 1884.
Rhinoceros sivalensis intermedius Lydekker, 1884.
Aceratherium lydekkeri Pilgrim, 1910.
Teleoceras blanfordi mihi Pilgrim, 1910 (nomen nudum).
Gaindatherium browni Colbert, 1934.

Certain species from the Bugti beds are not included in this list, as they come from a series lower than the Siwaliks.

Pilgrim, in 1913, suggested that an acerathere close to *Aceratherium tetradactylum* of the Tortonian and Sarmatian of Europe is present in the Lower Siwaliks.

"In the Chinji beds a much smaller species is found, which is very nearly allied to *Aceratherium tetradactylum* of the Tortonian and Sarmatian of Europe, and which may be ancestral to both *A. perimense* and *A. lydekkeri.*" [55]

Dr. Matthew, in 1929, suggested that the so-called *Aceratherium tetradactylum* in the Lower Siwalik beds is more properly referable to the genus *Chilotherium*. Dr. Pilgrim, however, did not describe any *actual* material as being representative of the genus and species in question. Consequently *Aceratherium tetradactylum* can not be placed on a list of *described* rhinoceroses from the Siwalik Series.

The list of Siwalik rhinoceroses, presented above, may be revised in the following manner.

Rhinoceros sivalensis Falconer and Cautley ..... Upper Siwaliks
Synonym: *Rhinoceros palaeindicus* Falconer and Cautley
Gaindatherium browni Colbert ..... Lower Siwaliks
Coelodonta platyrhinus (Falconer and Cautley) ..... Upper Siwaliks
Aceratherium perimense (Falconer and Cautley) ..... Middle Siwaliks
Synonyms: *Rhinoceros planidens* Lydekker
Rhinoceros iravadicus Lydekker
Aceratherium lydekkeri Pilgrim ..... Middle Siwaliks

[55] Pilgrim, G. E., 1913B, p. 297.

Chilotherium blanfordi (Lydekker).....Lower Siwaliks
Synonym: *Teleoceras blanfordi mihi* Pilgrim
Chilotherium intermedium (Lydekker).....Middle Siwaliks

From the above list it may be seen that the rhinoceroses that lived during Siwalik times were representative of several distinct phylogenetic groups. Thus they show a gathering of various species that were evolving in different portions of Eurasia; a congregating of different forms in a single haven that afforded ample protection for their existence. One phylogenetic line, that of the *Rhinoceros*, would seem to have undergone its later evolutionary development in India. The others are, for the most part, immigrant forms, migrating in from outside regions.

RHINOCEROTIDAE

RHINOCERINAE

Coelodonta Bronn, 1831

Generic type, *Coelodonta boiei* Bronn

Coelodonta platyrhinus (Falconer and Cautley)

Rhinoceros platyrhinus, Falconer and Cautley, 1847, Fauna Antiqua Sivalensis, Pl. LXXII, figs. 1–7, Pl. LXXV, figs. 9–12.

Dicerorhinus platyrhinus, Pilgrim, 1910, Rec. Geol. Surv. India, XL, p. 201.

Coelodonta platyrhinus, Matthew, 1929, Bull. Amer. Mus. Nat. Hist., LVI, pp. 444, 534–535.

Additional References.—

Falconer, H., 1868A, pp. 157–169, Pl. XIV, figs. 3, 4.

Lydekker, R., 1876A, pp. 29–32, Pl. IV, fig. 4; 1880B, p. 31; 1883C, p. 83; 1884D, p. 132; 1884E, p. 82, Pl. III, fig. 2; 1885B, p. 65; 1886A, pp. 99–101.

Pilgrim, G. E., 1913B, pp. 305–306, 324.

Type.—(Lectotype.) Brit. Mus. No. 33662, a battered skull.

Cotypes.—Brit. Mus. Nos. M 2731, back portion of a skull, possibly associated with No. 33662; 39620, anterior portion of a mandible; 39640, right M^3; 39641, right upper molar; 39642, symphysis and right ramus of a mandible; 39643, right maxilla.

Neotype.—Brit. Mus. No. 36661, a nearly complete skull.

Horizon.—Upper Siwaliks.

Locality.—From the Siwalik Hills.

Specimens in the American Museum.—Amer. Mus. No. 19777, fragment of a right maxilla with P^4, M^{1-3}. From the Upper Siwaliks, one mile east of Mirzapur.

19822, fragment of a left maxilla with MM^{2-4}. From the Upper Siwaliks, three miles northeast of Siswan.

19875, fragment of left maxilla with M^{1-2}. Upper Siwaliks, three miles northeast of Mirzapur.

Diagnosis.—A large rhinoceros, showing many characters that would seem to ally it with *Coelodonta antiquitatus*. Skull without nasal septum. Premaxillaries heavy. Teeth hypsodont. Evidently two horns were present.

The species under consideration is closely related to the modern *Dicerorhius sumatrensis* and to the Pleistocene form, *Coelodonta antiquitatus*. As to which of these two genera it bears the closest resemblance is a question difficult to decide, due to the fact that *Dicerorhinus* and *Coelodonta* are very close to each other. In this regard the reader is referred to Breuning, Stephan, 1924, p. 27.

Breuning explains that although the genera *Coelodonta* and *Ceratorhinus* (*Dicerorhinus*) are separate, there are numerous characters in the various species that bridge the differences between the two genera. He then goes on to point out that certain characters generally considered as typical of *Coelodonta* and not of *Dicerorhinus*, such as the ossified nasal septum, the reduction of the incisors and the backward development of the occiput, are in reality quite variable and consequently of little phylogenetic or taxonomic importance. For instance, although *Dicerorhinus sumatrensis* is typically without a nasal septum, such a structure may occur in this species. Therefore it may be possible that *Coelodonta* has been derived directly from *Dicerorhinus*, and with this consideration in mind the two genera may be grouped together in the subfamily Ceratorhinae of Osborn.

The Siwalik form under discussion shows many approaches to the modern African Rhinoceros, *Diceros bicornis*, a fact pointed out first by Lydekker.

The several taxonomic possibilities concerning the relationships of "*Rhinoceros*" *platyrhinus* were fully recognized by Dr. Matthew, and at various times he referred this species successively to the genera *Dicerorhinus*, *Coelodonta*, and *Diceros*.[56]

The evidence may be summed up as follows:

1. The presence of incisors (Matthew, W. D., 1929, p. 535) would place *platyrhinus* with the genus *Dicerorhinus*. Moreover, in general skull form it is very similar to the Sumatran species. As a third point of resemblance there might be mentioned the separation of the postglenoid and the posttympanic, leaving the external auditory meatus open below. This latter is a primitive feature, characteristic of *D. sumatrensis* (a primitive form) and retained in *D. platyrhinus*.

2. As to the pattern and hypsodonty of the cheek teeth, the Siwalik species would seem to be close to *Diceros*, *Ceratotherium* and *Coelodonta*. Moreover it resembles these genera also in the separated postglenoid and posttympanic.

"The teeth are rather closely related to *Coelodonta* and *Ceratotherium*, not to *Dicerorhinus*." [57]

In view of the above evidence, it would seem that a safe course is to assign provisionally the species under consideration to the genus *Coelodonta*, recognizing however that it probably represents a separate phylogenetic side branch retaining certain primitive characters. *Coelodonta* (?) *platyrhinus* may well deserve a new generic designation, but it is not thought advisable to make such a distinction at this time.

Some measurements and figures of the specimens in the American Museum collection are presented below.

[56] See Matthew, W. D., 1929, pp. 444, *Dicerorhinus;* 462, 534, *Coelodonta;* 1931, p. 7, *Diceros*.
[57] Matthew, W. D., 1929, p. 462.

MEASUREMENTS

Coelodonta platyrhinus

	Length	Width
Amer. Mus. No. 19777.		
Molar series	175 mm.	
M^1	51	78 mm.
M^2	61	74
M^3	66	63
Amer. Mus. No. 19822.		
MM^2	34	40
MM^3	49	49
MM^4	55	52

Rhinoceros Linnaeus, 1758

Generic type, *Rhinoceros unicornis* Linnaeus

Rhinoceros sivalensis Falconer and Cautley

Rhinoceros sivalensis, Falconer and Cautley, 1847, Fauna Antiqua Sivalensis, Pl. LXXIII, figs. 2, 3; Pl. LXXIV, figs. 5, 6; Pl. LXXV, figs. 5, 6.

Additional References.—

Falconer, H., 1868A, pp. 157–169, Pl. XIV, figs. 1, 2; pp. 514–516.

Lydekker, R., 1876A, pp. 26–29, Pl. V, figs. 2, 5; 1880B, p. 31; 1881A, pp. 28–42, Pls. V, VI, figs. 2, 3, Pl. VII, fig. 1, Pl. X, fig. 4; 1883C, p. 92; 1884D, p. 132; 1885B, pp. 61–64; 1886A, pp. 130–132.

Pilgrim, G. E., 1910B, p. 201; 1913B, p. 324.

Matthew, W. D., 1929, pp. 444, 531.

Type.—(Lectotype.) Brit. Mus. No. 39626, part of a skull.

Cotypes.—Brit. Mus. Nos. 39625, a skull; 39646, a mandibular symphysis; 39647, part of a skull.

Horizon.—Upper Siwaliks.

Locality.—Siwalik Hills.

Specimen in the American Museum.—Amer. Mus. No. 19793, a right first upper molar. From the Upper Siwaliks, six miles east of Chandigarh.

Diagnosis.—A large species of the genus. Molars with a parastyle buttress, distinct crochet which may unite with the protoloph to enclose a fossette, and without a crista.

The specimen in the American Museum collection need not be described. Reference should be made to the descriptions of Falconer and Cautley, Lydekker and Matthew. Measurements and a figure of the American Museum specimen are presented here.

Rhinoceros sivalensis, Amer. Mus. No. 19793.
Right M^1 Length... 61 mm. Width... 80 mm.

Rhinoceros palaeindicus Falconer and Cautley

Rhinoceros palaeindicus, Falconer and Cautley, 1847, Fauna Antiqua Sivalensis, Pl. LXXIII, fig. 1, Pl. LXXIV, figs. 1–4, Pl. LXXV, figs. 1–4.

Additional References.—

Falconer, H., 1868A, pp. 157, 514–516.

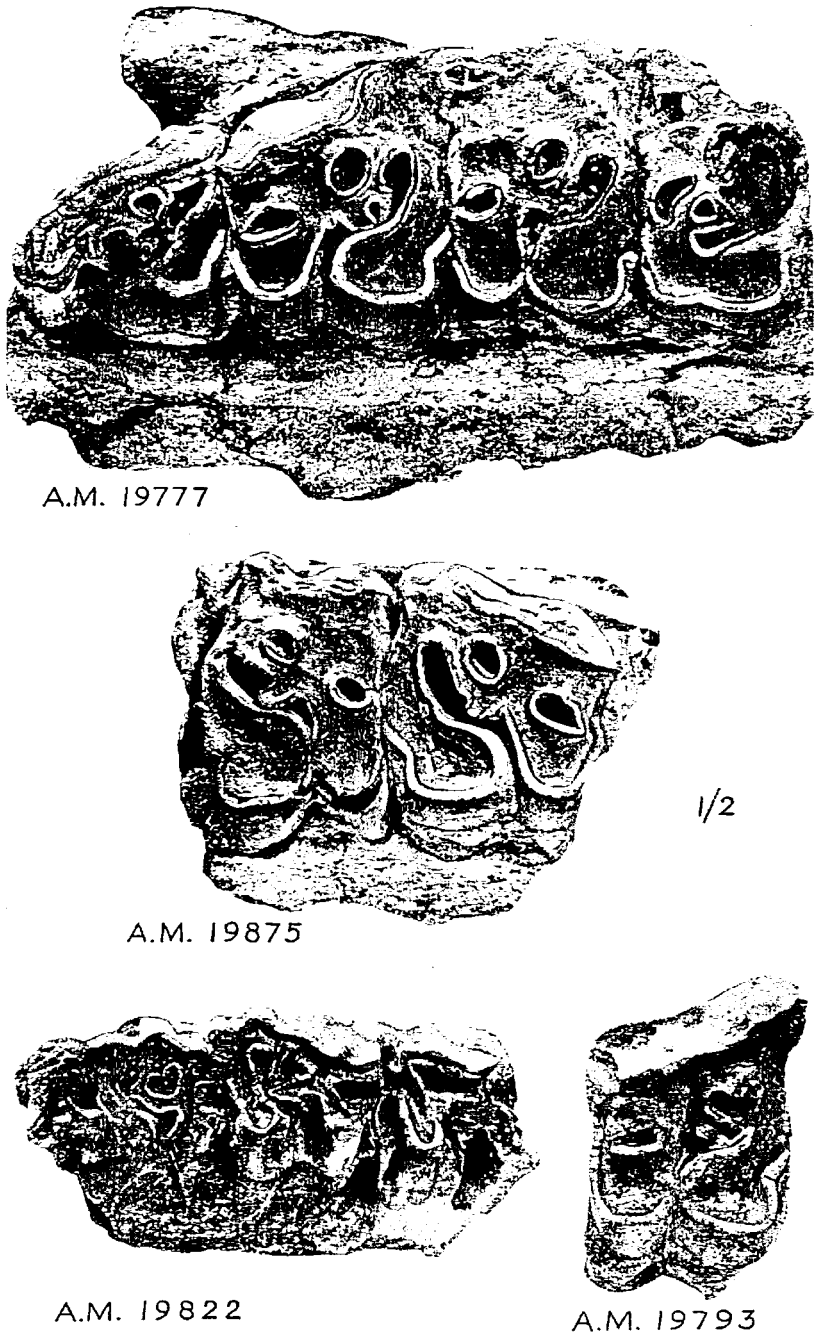

FIG. 78. *Coelodonta platyrhinus* (Falconer and Cautley). Amer. Mus. No. 19777, maxilla with right P^4, M^{1-3}; Amer. Mus. No. 19875, left M^{1-2}; Amer. Mus. No. 19822, maxilla with left MM^{2-4}. Crown views.
Rhinoceros sivalensis Falconer and Cautley. Amer. Mus. No. 19793, right M^1. Crown view.
All figures one half natural size.

Lydekker, R., 1876A, pp. 22–26, Pl. IV, figs. 3, 4; 1880B, p. 31; 1881A, pp. 42–48, Pl. VI, fig. 1, Pl. VII, figs. 2, 3, Pl. X, fig. 3; 1883C, p. 92; 1884D, p. 132; 1884E, pp. 82–83, Pl. III, fig. 1, 3; 1885B, p. 64; 1886A, pp. 132–135, fig. 15.

Pilgrim, G. E., 1910B, p. 201; 1913B, p. 324.

Matthew, W. D., 1929, pp. 444, 531–532.

Type.—(Lectotype.) Brit. Mus. No. 16444, a skull.

Cotypes.—Brit. Mus. Nos. M 2727, a skull; 36740, a skull; 39644, back portion of a left mandibular ramus; 39645, portion of a right mandibular ramus; 39646, mandibular symphysis; 39740, a skull. Also specimens figured in Pl. LXXV, figs. 1, 2, of the Fauna Antiqua Sivalensis.

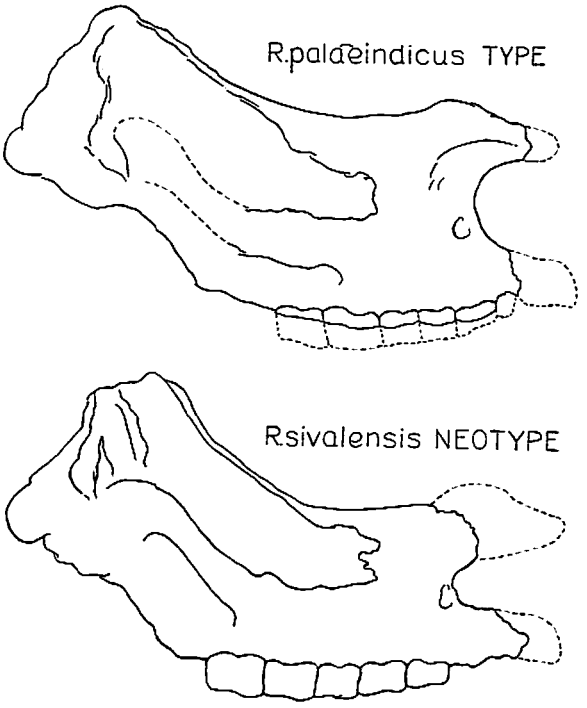

FIG. 79. Comparison of skulls of the type of *Rhinoceros palaeindicus* Falconer and Cautley (above), and the neotype of *Rhinoceros sivalensis* Falconer and Cautley (below). One eighth natural size. From Matthew, 1929.

Horizon.—Upper Siwaliks.

Locality.—Siwalik Hills.

Diagnosis.—Like *R. sivalensis*, but wider across the frontals, with a slightly different cranial profile and with a flat ectoloph to molars, without parastyle buttress.

Matthew (1929, pp. 531–532) has shown that this species is probably synonymous with *R. sivalensis*. He points out that the supposed differences in the dentition given above really do not exist, and that the skull differences may very well be within the bounds of individual variation. Consequently the two species are here considered as one, its designation being *Rhinoceros sivalensis*.

Gaindatherium Colbert, 1934

Generic type, *Gaindatherium browni* Colbert

Gaindatherium browni Colbert

Gaindatherium browni, Colbert, 1934, Amer. Mus. Novitates, No. 749.

Type.—Amer. Mus. No. 19409, an almost complete skull. From the Lower Siwaliks, Chinji zone, near Chinji Rest House, Punjab.

Paratypes.—Amer. Mus. No. 29838, associated right and left upper and lower dentitions. Lower Siwaliks, Chinji zone, near Chinji Rest House, Punjab. Amer. Mus. No. 19471, a mandibular symphysis. From the lower portion of the Middle Siwaliks, Nagri zone, one mile south of Nathot, Punjab. Amer. Mus. No. 29793, an upper incisor tooth Lower Siwaliks, Chinji zone, about 500 feet above the level of Chinji Rest House, one and one half miles west of Chinji Rest House, Punjab.

Horizon.—Lower Siwaliks, Chinji zone. The species may extend up into the lower portion of the Middle Siwaliks, into the Nagri zone.

Locality.—Vicinity of Chinji Rest House, south of Chinji village, Salt Range, Attock District, Punjab.

Specimens in the American Museum.—The type and paratypes, listed above.

Amer. Mus. No. 29837. Various teeth from the lower dentition. Lower Siwaliks, near Chinji Rest House, Punjab.

19422. A right M^2. Lower Siwaliks, Chinji zone, four miles west of Chinji Rest House, Punjab.

29792. A left P^4. Lower Siwaliks, Chinji zone, ten miles east of Chinji Rest House, Punjab.

Also miscellaneous teeth from the Lower Siwaliks, near Chinji Rest House.

Diagnosis.—An upper Tertiary rhinoceros of medium size, with a "saddle-shaped" skull having a single horn on the nasals, and with brachyodont, simple molar teeth. The orbit is located in an approximately central position above the first molar; the occiput is vertical; the postglenoid and posttympanic are fused, forming a closed tube for the external auditory meatus. There are two upper incisors, of which the lateral one is quite small; the upper molars are without an antecrochet or crista, and the crochet is but slightly developed.

This species has been described elsewhere (Colbert, E. H., 1934) in some detail. Consequently it need not be discussed at length here. The salient characters distinguishing *Gaindatherium* are listed below.

1. The skull is of medium size and of comparatively primitive structure. It is relatively long and narrow, with the orbit in an approximately central position. That is, the facial and the cranial portions of the skull are subequal in length.

2. There is a single nasal horn. The nasals are expanded laterally and vertically for the accommodation of this horn, thus giving the cranial profile a saddle shaped outline.

3. The occiput is vertical as is common among primitive rhinoceroses.

4. The postglenoid and posttympanic are fused, forming a closed tube for the external auditory meatus.

5. There are two upper incisors, of which the lateral one is small.

6. The cheek teeth are brachyodont and relatively simple, without antecrochet or crista, but with a crochet present in the last molar.

Fig. 80. *Gaindatherium browni* Colbert. Amer. Mus. No. 19409, type skull. Lateral view. One third natural size. From Colbert, 1934.

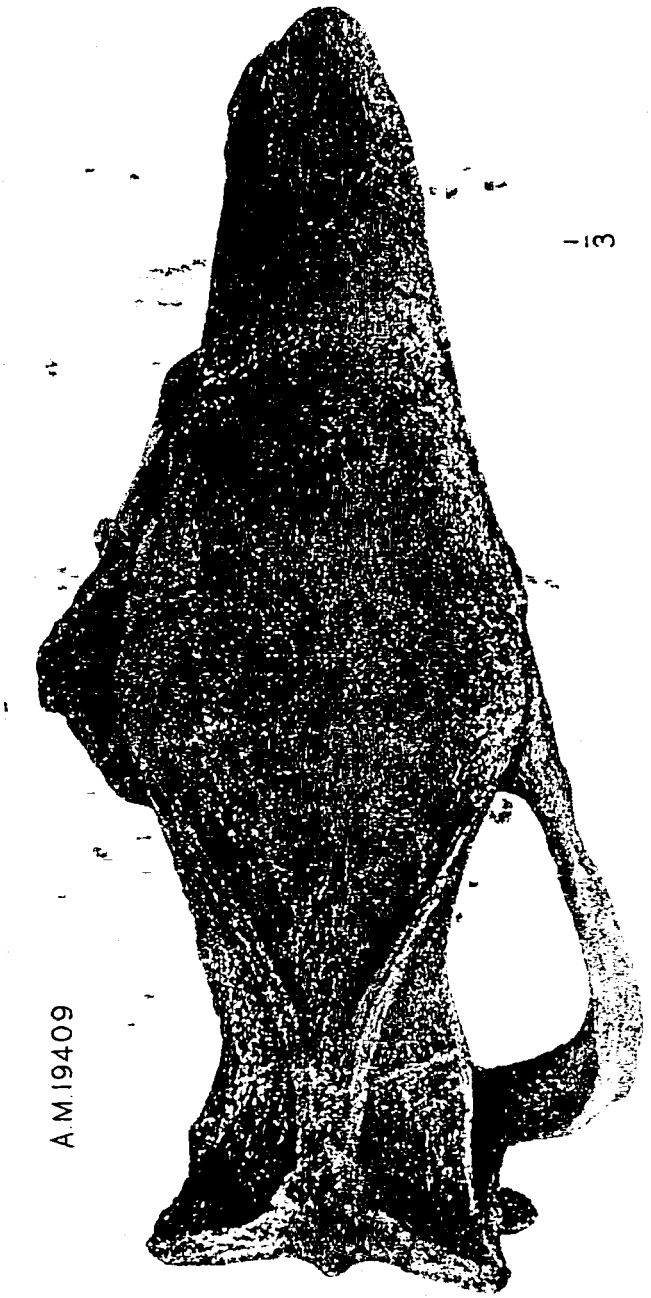

FIG. 81. *Gaindatherium browni* Colbert. Amer. Mus. No. 19409, type skull. Dorsal view. One third natural size. From Colbert, 1934.

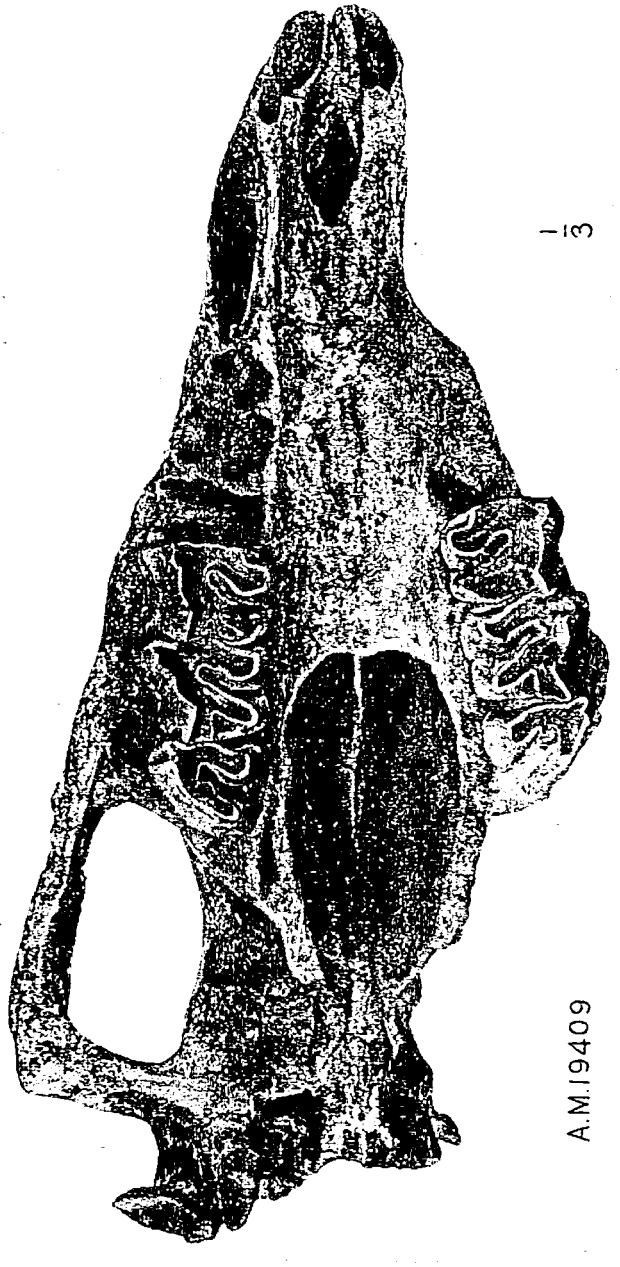

Fig. 82. *Gaindatherium browni* Colbert. Amer. Mus. No. 19409, type skull. Ventral view. One third natural size. From Colbert, 1934.

Measurements and figures are given below.

MEASUREMENTS

Gaindatherium browni, Amer. Mus. No. 19409, type

Skull.

Length, lamboidal crest to tip of nasals	496.0 mm.
Length, condyles to incisor alveolus (Estimated)	520.0
Length, anterior border of orbit to incisor alveolus	243.0
Length, anterior border of orbit to condyles	290.0
Width at glenoids	298.0
Width of parietals, narrowest portion	93.0
Width of frontals, supraorbital	168.0
Width of palate at M^1	68.0
M^1 length	40.0
width	51.0
M^2 length	42.0
width	52.0
M^3 length	37.0
width	48.0

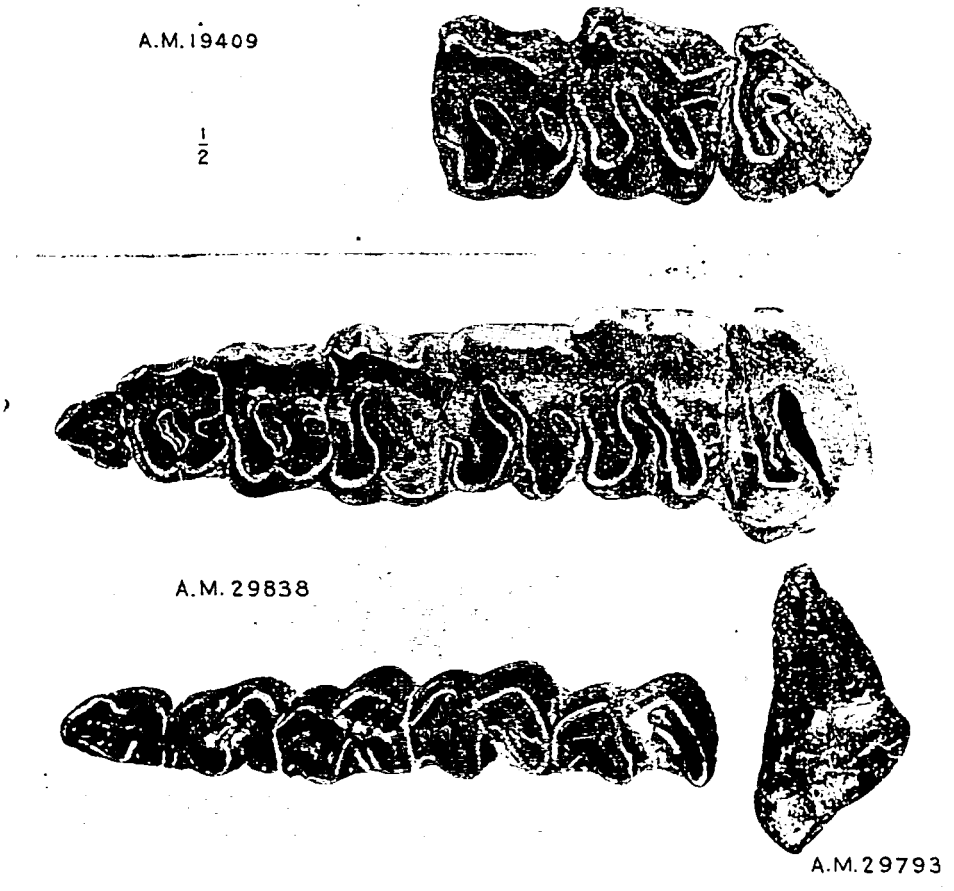

FIG. 83. *Gaindatherium browni* Colbert. Upper and lower dentitions. At top: type, Amer. Mus. No. 19409, left M^{1-3}, crown view. In middle: Amer. Mus. No. 29838, left P^{1}–M^{3}, crown view. At bottom: Amer. Mus. No. 29838, right P_2–M_2, crown view, and Amer. Mus. No. 29793, upper incisor, lateral view. All figures one half natural size. From Colbert, 1934.

Amer. Mus. No. 29838, paratype

	Length	Width
P^1	19.0 mm.	22.5 mm.
P^2	28.0	34.5
P^3	32.0	43.0
P^4	37.0	49.0
P_2	28.5	21.5
P_3	30.0	26.0
P_4	36.0	28.0
M_1	40.0	30.0
M_2	43.0	28.0

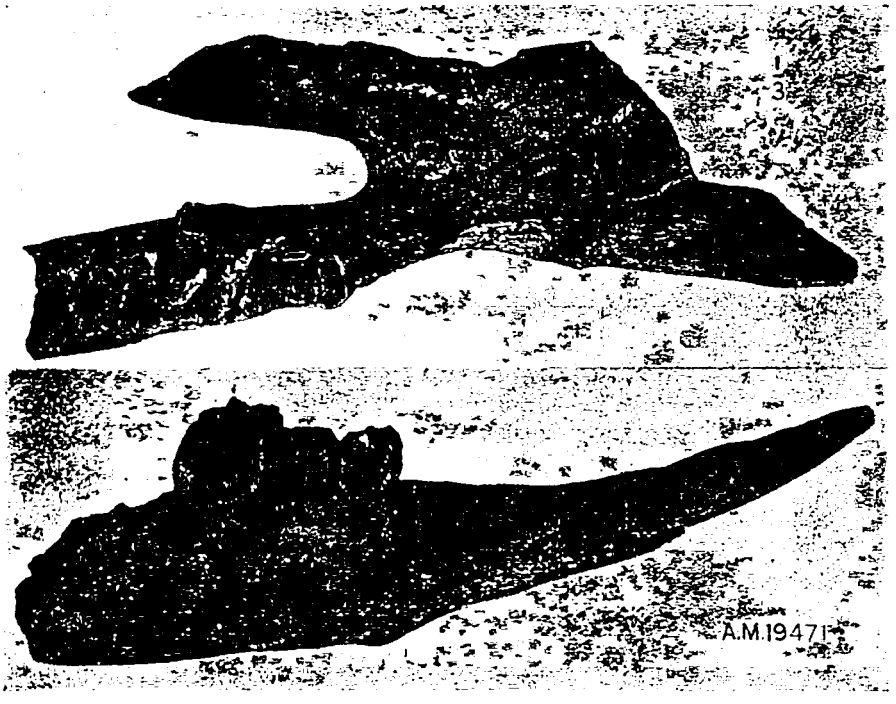

FIG. 84. *Gaindatherium browni* Colbert. Amer. Mus. No. 19471, symphysis of mandible. Superior view above, lateral view below. One third natural size. From Colbert, 1934.

Amer. Mus. No. 19471, paratype

Mandibular symphysis.

Depth of symphysis at P_2	66.0 mm.
Width of symphysis at narrowest part	79.0
Length of symphysis	135.0
Transverse diameter of incisor	39.0
Vertical diameter of incisor	27.0

In the original description of *Gaindatherium* it was shown that this genus, although in many ways primitive and thereby retaining heritage characters in common with other primitive Rhinocerinae, possessed certain habitus characters that definitely point in the direction of *Rhinoceros*. Therefore it was suggested that *Gaindatherium* is a form more or

less directly ancestral to the modern Asiatic rhinoceros and that it represents an intermediate link between the stem *Caenopus* type of true rhinocerine and the modern one horned rhinoceros. A list of heritage characters that demonstrate the derivation of *Gaindatherium* from a primitive *Caenopus*-like ancestor, and also a list of habitus characters that show the trend of the Siwalik genus towards *Rhinoceros*, are presented below.

A. Heritage Characters in *Gaindatherium*

1. The light, slenderly built skull is an heritage character derived from an ancestor of relatively small size and slender proportions.
2. The centrally placed orbit is a character derived from a primitive ancestor. In the primitive perissodactyls the preorbital portion of the skull is approximately equal in length to the postorbital region. In advanced forms the orbit tends to lose its central position.
3. The slight sagittal crest is a primitive character, due to the fact that the brain case has not expanded to any great degree.
4. The vertical occiput is a primitive heritage character.
5. The presence of the second upper incisor is primitive.
6. The brachyodont, simple molars show heritage characters of an ancestor similar to *Caenopus*.

B. Habitus Characters in *Gaindatherium*

1. The "saddle shaped" skull is a definite advance towards *Rhinoceros*.
2. The presence of one nasal horn is an habitus character in the direction of *Rhinoceros*.
3. The union of the postglenoid and the posttympanic is again an habitus character that is also found in *Rhinoceros*.
4. The presence of a crochet on the last molar in *Gaindatherium* is a character that would seem to point towards *Rhinoceros*. In the latter genus the crochet and crista are well developed, but the antecrochet is not distinct. In *Gaindatherium* the crochet is present on the last molar, and the antecrochet is not distinct.
5. The relatively narrow, shallow symphysis and the straight lower incisor would seem to be characters indicative of a relationship with *Rhinoceros*.

In order to demonstrate more clearly the gross anatomical characters of the skull of *Gaindatherium* that define it as a form intermediate between the *Caenopus* type and *Rhinoceros*, the accompanying chart (Fig. 85) has been prepared.

As the basis for this chart a skull of *Caenopus*, here considered as approximating in a general way the stem form of the Rhinocerinae, was drawn to scale. It was then overlain by a system of quadrants or squares of arbitrary size (*A* of figure). In the arrangement of these squares certain bases were established, namely the occlusal line of the upper molars for the horizontal components and the anterior border of the orbit for the vertical components. The horizontal lines were lettered *A*, *B*, *C*, etc., above the base or zero line, and *A'*, *B'*, *C'*, etc., below the base line. The vertical lines were numbered 1, 2, 3, etc., to the left of the base or zero line, and 1', 2', 3', etc., to the right of this datum. Then the skulls of *Gaindatherium* (*B* of figure), *Rhinoceros* (*C* of figure) and *Dicerorhinus* (*D* of figure) were drawn to the same scale as the first skull. The intersections of the various lines making up the various squares were plotted on the other skulls, retaining their special relationships to anatomical details as in the case of the *Caenopus* skull. Then when the numerous points

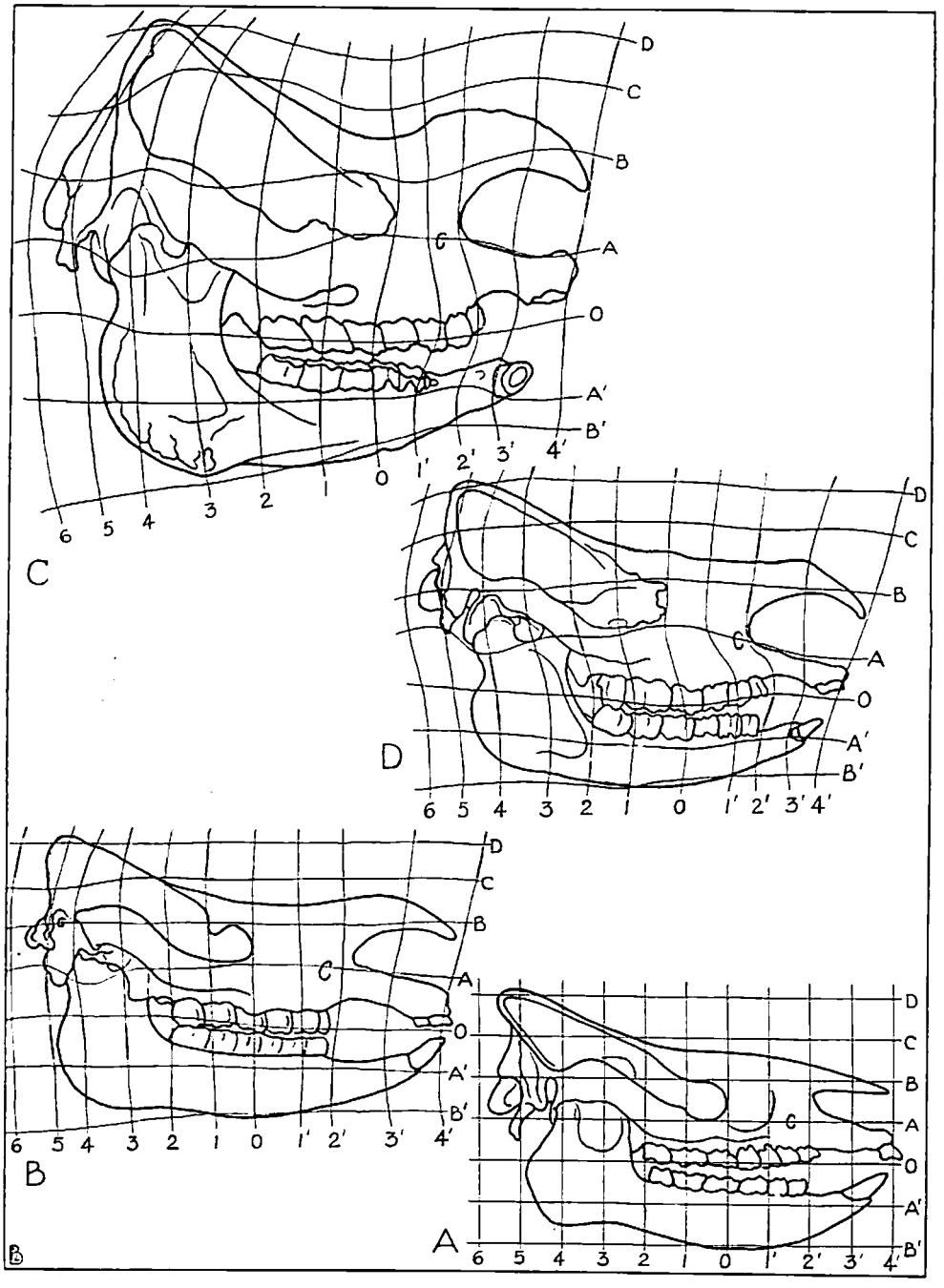

FIG. 85. Cartesian coordinate chart to illustrate the manner in which the skull of *Rhinoceros* might have evolved through *Gaindatherium* from a primitive form such as *Caenopus*.

A. Caenopus occidentalis Leidy = *Subhyracodon occidentalis* (Leidy).

B. Gaindatherium browni Colbert.

C. Rhinoceros unicornis Linnaeus.

D. Dicerorhinus sumatrensis (Cuvier).

The skull of *Dicerorhinus* is included in the chart for comparison with the skull of *Gaindatherium*. Both of these genera, being relatively primitive, have skulls that are somewhat similar to each other, although they belong to two different branches of rhinocerotid evolution.

so located were connected, figures of various shapes were obtained that show the proportional change of each portion of the skull in its relations to other portions of the skull.

This is essentially the method used so widely by d'Arcy Thompson, but here it is applied in a more detailed manner than was done by that author. Thus it may be seen that the skull of *Gaindatherium* is not greatly changed from the primitive *Caenopus* skull. Nor is the skull of *Dicerorhinus* greatly different from that of *Caenopus* or *Gaindatherium*. These are the skulls of relatively primitive animals, so that they show similarities indicating the community of their origin.

It may be noticed, however, that the *Dicerorhinus* skull, although primitive in a general way, does show characters that set it apart from *Gaindatherium* and *Rhinoceros*. It is marked by the forward position of the cheek teeth and the lack of a strong forward inclination of the occiput.

The *Rhinoceros* skull is, on the other hand, an exaggerated accentuation of the *Gaindatherium* skull, characterized by its great depth.

In making the accompanying chart, the skull of *Gaindatherium* was restored as nearly as possible to its original form.

Aceratherium Kaup, 1832

Generic type, *Rhinoceros incisivus* Cuvier

Aceratherium perimense (Falconer and Cautley)

Rhinoceros (*Acerotherium*?) *perimensis*, Falconer and Cautley, 1847, Fauna Antiqua Sivalensis, Pl. LXXV, figs. 13–16; Pl. LXXVI, figs. 14–16.

Aceratherium perimense, Lydekker, 1876, Pal. Indica (X), I, pp. 51–55, Pl. VI, figs. 2, 5.

Additional References.—

Falconer, H., 1868A, pp. 157, 171, 517–519.

Lydekker, R., 1880B, p. 31; 1880C, p. xiii, Pl. IV, figs. 7, 9; 1881A, pp. 9–28, Pls. I–IV; 1883C, p. 89; 1884D, p. 132; 1885B, pp. 66–68; 1886A, pp. 155–157, fig. 19.

Pilgrim, G. E., 1910B, p. 200; 1913B, p. 297.

Matthew, W. D., 1929, p. 507.

Cotypes.—The various specimens figured in Pls. LXXV, figs. 13–16, and LXXVI, figs. 14–17, of the Fauna Antiqua Sivalensis.

Matthew lists as the type of this species the two upper molars figured by Lydekker in the Palaeontologica Indica, Series X, Volume I, Pl. IV, figures 7 and 9. It is not quite clear why Matthew should have regarded these specimens as the type.

Aceratherium perimense was first published in the plates of the Fauna Antiqua Sivalensis, by Falconer and Cautley in 1847. No descriptions accompanied the figures, but nevertheless the figures alone constituted publication and thus the specimens so illustrated must be considered as the cotypes of the species.

Horizon.—Presumably from the Middle Siwaliks. Also from the Lower Siwaliks.

Locality.—Perim Island for the type specimens. The Punjab for referred specimens.

Specimens in the American Museum.—Amer. Mus. No. 19410. A right P^1, left P^3, right DM^3. Lower Siwaliks, 600 feet above the level of Chinji Rest House, 12 miles east of Chinji Rest House.

19418. A right M_{2-3}. Lower Siwaliks, locality uncertain.

19454. A right upper dentition and two mandibular rami. Lower Siwaliks, 1600 feet above the level of Chinji Rest House, one and one half miles northwest of Chinji Rest House.

19470. A skull, complete back of the premolars. Lower portion of the Middle Siwaliks, 1000 feet below the Bhandar bone bed, one mile south of Nathot.

19527. Teeth, vertebrae, foot bones, Middle Siwaliks, south of Nathot.

19528. Fragment of mandibular ramus with left P_1. Middle Siwaliks, one mile south of Kohala.

19531. A right P_3. Base of Middle Siwaliks, near Nathot.

19544. Miscellaneous teeth. At base of Middle Siwaliks, near Nathot.

19571. Second and third left upper deciduous molars. Lower Siwaliks, 600 feet above the level of Chinji Rest House, five miles west of Chinji Rest House.

19576. Right upper incisor. Lower Siwaliks, 1100 feet above the level of Chinji Rest House, one mile north of Chinji Rest House.

19585. Miscellaneous teeth. Lower Siwaliks, five miles east of Chinji Rest House.

19589. A right P_2 Lower Siwaliks, 1600 feet above the level of Chinji Rest House, one and one half miles west of Chinji Rest House.

19692. Palate with left P^4–M^2 and right M^2. Lower Siwaliks, six miles north of Dhok Pathan.

19743. A right P^4. Middle Siwaliks, two and one half miles northeast of Hasnot.

19921. A right P_2. Lower Siwaliks, near Rammagar.

19942. Miscellaneous teeth. Lower portion of the Middle Siwaliks four and one half miles west of Hasnot.

29790. A right DM^4. Lower Siwaliks, 1600 feet above the level of Chinji Rest House, twelve miles east of Chinji Rest House.

29794. Right M^3 and associated fragments. Lower Siwaliks, 500 feet above the level of Chinji Rest House, one and one half miles west of Chinji Rest House.

Diagnosis.—A rhinoceros of gigantic size with hypsodont teeth. Skull rather short and deep, with retracted nasals; zygomatic arch heavy; postglenoid separate from posttympanic. Upper incisor present and well developed. Molars with moderately developed crochet, weaker antecrochet and rudimentary crista. Protocone somewhat pinched off. Lower molars narrow and compressed. Mandibular symphysis narrow.

Aceratherium perimense is distinguished from the other Siwalik rhinoceroses by its great size, a fact pointed out by Lydekker in 1881, in his detailed description of the skull of the species. Number 19470 in the American Museum collection is quite indicative of the large proportions characteristic of this species. Perhaps it might be well to present at this juncture a short description of the skull just mentioned, to serve as a corollary to the original detailed description written by Lydekker in 1881.

The impression of gigantic size in *Aceratherium perimense* is due to the great mass of the skull, rather than to any preponderance over other large rhinoceroses in linear measurements. For instance, the length from the front of the orbit to the back of the occipital condyles is not much different in the specimen being considered than is the corresponding length in a modern *Rhinoceros unicornis*. But owing to the massiveness of the skull of *Aceratherium perimense* it gives the impression of being extraordinarily great in size.

The skull is short, as would be expected in a form belonging to the *Aceratherium* group, and the nasals are retracted. The back of the narial notch is above the last premolar, and it is but slightly separated from the front border of the orbit, which latter is above the anterior portion of the first molar. The position of the orbit above the first molar would seem to be a result of the shortening of the face in this species. A comparison between various genera and species of rhinoceroses would seem to show that as the face tends to become short, the orbit tends to move forward in its position relative to the cheek teeth. Conversely, when the face and skull elongate, the orbit tends to migrate backward in relation to the cheek teeth. These evolutionary trends are to be seen in other perisodactyls, notably the horses and the titanotheres. In the horses the face becomes long and the orbit moves back to a position above the posterior molars, while in the titanotheres the face becomes short and the orbit moves forward to a position above the premolars.

The zygomatic arch is heavy, especially below the orbit, so that its lower edge in the forward portion extends below the alveolus of the molars. The arches are not widely spread.

The glenoid is transverse and heavy, and from its inner side an extremely heavy postglenoid process extends down.

The top of the skull as seen in profile is bowed into a shallow saddle, or rather, the frontals are approximately flat, while the parietals rise sharply to the lambdoidal crest. In the skull under consideration the portions anterior to the first molar are missing, but evidently the nasals, the maxillaries and the premaxillaries were extremely short. The skull roof, consisting of the frontals and parietals, is quite narrow. The parietal crests, running from the blunt postorbital processes to the lambdoidal crest, approach each other very closely but they do not meet.

The occiput is vertical and the condyles, large but not of unduly great size, project back beyond it. The supraoccipital is indented for the attachment of powerful neck muscles, and since the lambdoidal crest follows the superior edge of this bone, it is strongly bowed forward, as seen from the top, forming a broad V. The junction of the squamosal and the exoccipital is flared out to form a crest projecting down from the lambdoidal crest, and this continues ventrally in the plate-like posttympanic. The paroccipital process is rather short and blunt.

As seen from behind the occiput is somewhat rectangular in shape, due to the great development of the lambdoidal crests, an adaptation for the attachment of strong neck muscles.

The postglenoid process is long and is quite separated from the posttympanic, thus leaving the external auditory meatus open below. The basioccipital is strongly keeled, and at its anterior termination is expanded into a large rugose tuberosity for the attachment of the rectus capitis ventralis major muscles. The pterygoids are extremely heavy, as might be expected in a large animal requiring heavy pterygoid muscles, and at their bases each is expanded and pierced by a large alisphenoid canal. The palate is narrow, and the posterior nares extend far forward to the anterior border of the second molars.

The basicranial foramina follow the usual rhinocerotid plan; that is the foramen lacerum anterius and the foramen rotundum open within a single common vestibule, there is a large alisphenoid canal, and the posterior foramina including the foramen ovale and the foramen lacerum medius are confluent.

Only the molars are present in the skull being discussed. The first two molars are fully erupted and but slightly worn, and the third molar is in the process of eruption. These teeth are remarkable for their large size and their hypsodonty. The antero-posterior length is relatively great, and the ectoloph is flat. At the antero-external corner of the tooth there is a well defined parastyle groove or fold, running vertically for the height of the tooth along its anterior edge. This fold in the parastyle is a characteristic *Aceratherium* feature. There are two oblique cross crests, the protoloph and the metaloph, and both the crochet and the antecrochet are strongly developed. There is a well developed anterior cingulum which runs around the internal side of the protocone. As in the other advanced rhinoceroses, the third molar is of triangular form, due to the bending back of the ectoloph and its fusion with the metaloph.

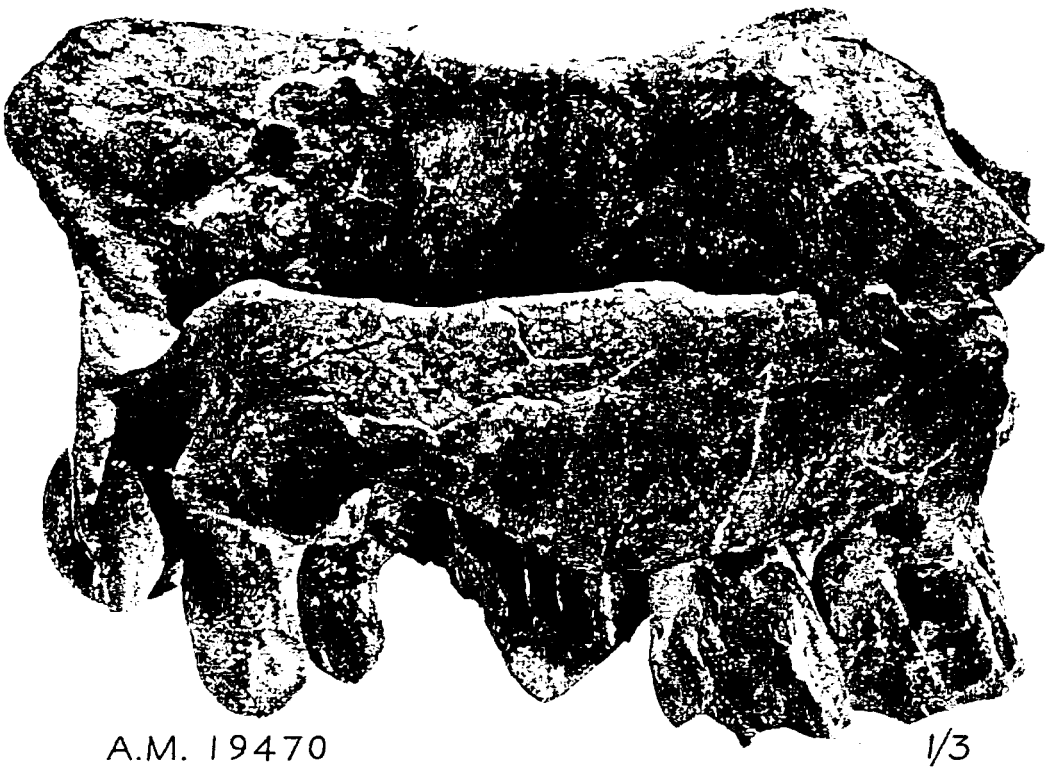

FIG. 86. *Aceratherium perimense* (Falconer and Cautley). Amer. Mus. No. 19470, a skull. Lateral view. One third natural size.

A second specimen, Amer. Mus. No. 19692, shows the anterior premolars and the premaxillaries. It conclusively shows that in this form the upper incisor was present. The incisor premolar diastema was relatively shorter than in *Aceratherium incisivum*.

A third specimen, Amer. Mus. No. 19454, an associated palate and mandible, shows the characters of the premolars. The upper premolars are, with the exception of the first one, completely molariform. The premolar incisor diastema is short. In the mandible the last two premolars are molariform, the second one is compressed and the first is absent.

The diastema is relatively short. The mandibular symphysis is not expanded, and the lower incisors point forward and upward.

Measurements and figures of the several specimens considered in the above discussion, are given below.

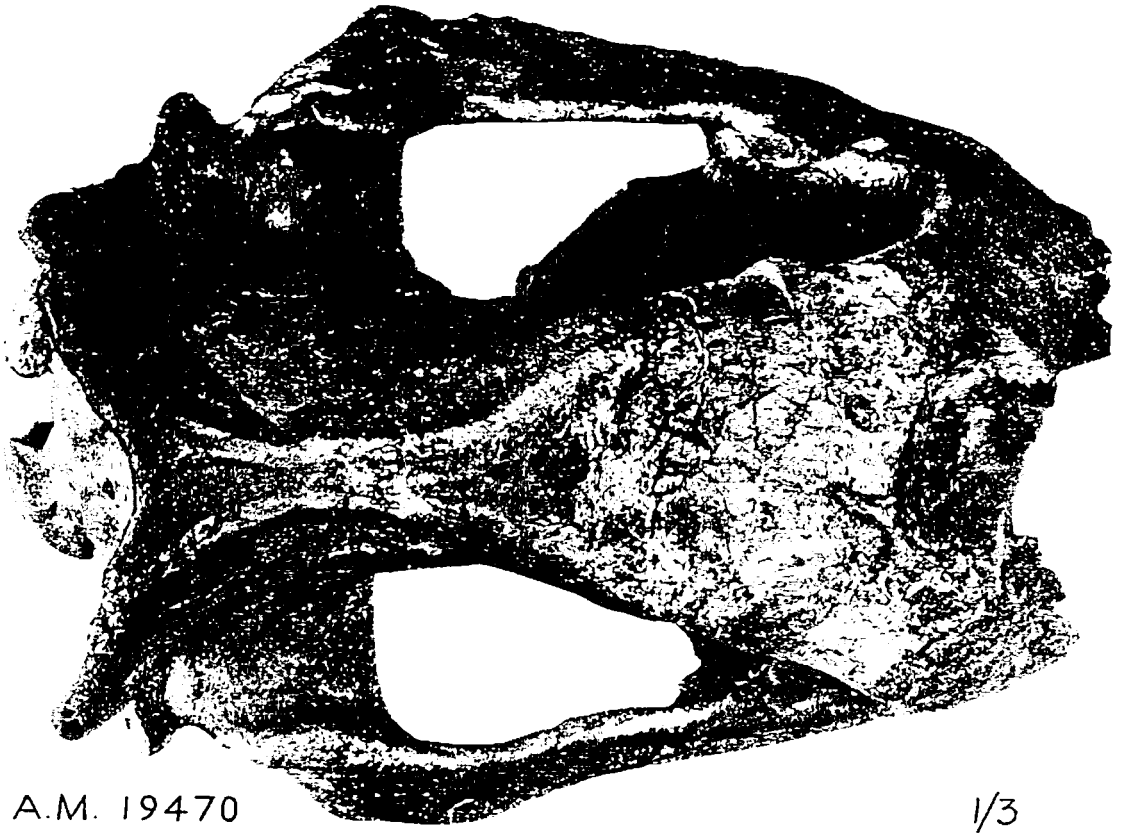

FIG. 87. *Aceratherium perimense* (Falconer and Cautley). Amer. Mus. No. 19470, skull. Dorsal view. One third natural size.

MEASUREMENTS OF *Aceratherium perimense*

A.M. 19470. Skull.

Length, lambdoidal crest to posterior boundary of narial notch	400 mm.
Length from anterior border of orbit to condyles	395
Width at glenoids	363
Width at parietals, narrowest portion	108
Width of frontals, at postorbital process	188
Width of palate at M^1	85
Height of skull at M^1	230
Diameter of orbit	83
Greatest depth of zygomatic arch	124
Greatest width of occiput	290
Height of occiput above foramen magnum	195
Transverse diameter of condyles	134

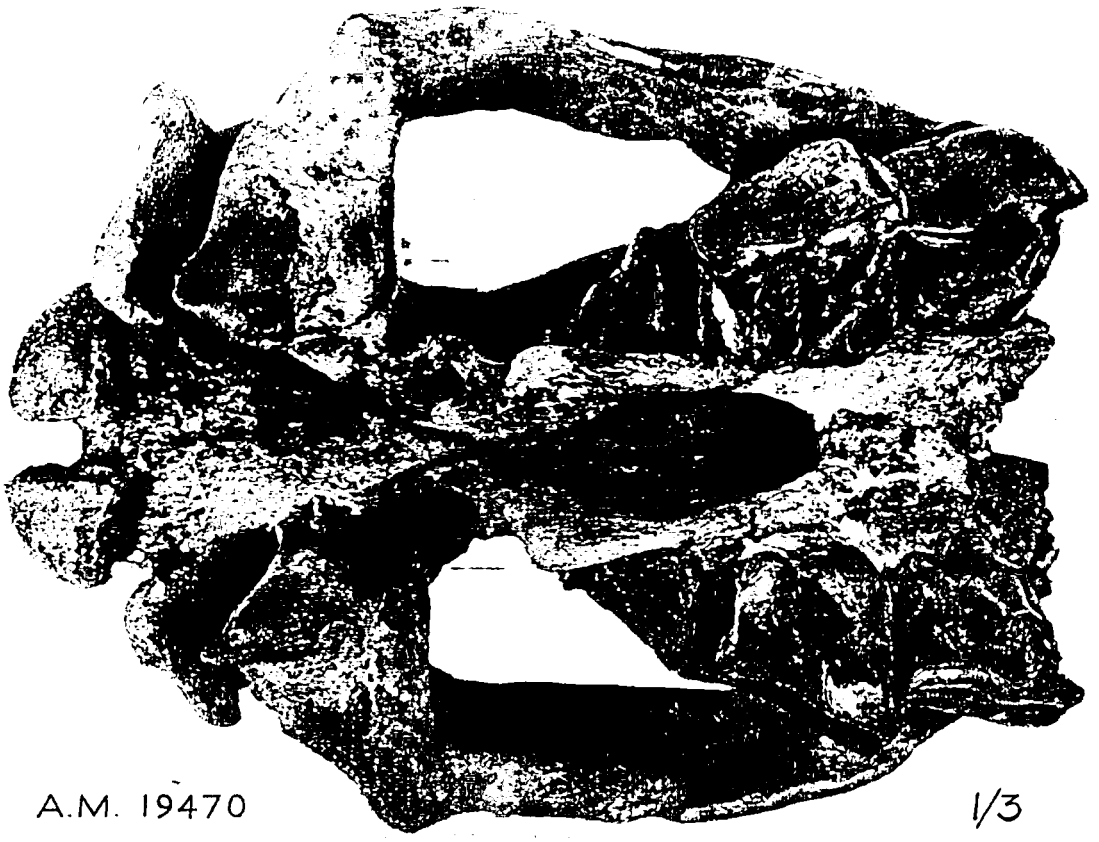

FIG. 88. *Aceratherium perimense* (Falconer and Cautley). Amer. Mus. No. 19470, skull. Ventral view. One third natural size.

Dentition

M^1....length..... 81 mm.	width..... 88 mm.	height..... 91 mm.
M^2....length..... 87	width..... 94	height..... 95
M^3....(in alveolus)		

COMPARATIVE MEASUREMENTS OF *Aceratherium perimense*

	A.M. 19470	After Lydekker
Height of occiput from base of foramen magnum to crest	259 mm.	254 mm.
Greatest width of occiput	290	305
Width of frontals at postorbital process	188	266
Interval between anterior angle of orbit and auditory fissure	285	335
Vertical diameter of orbit	83	95
Breadth of base of nasals	85*	101
Width of palate at M^1	85	76
Width of palate at M^3	84	112
Long diameter of occipital condyles	87	82

* Estimated.

FIG. 89. *Acerathrium perimense* (Falconer and Cautley). Amer. Mus. No. 19454, right maxilla and mandible. Crown view of upper dentition above, lateral view of mandible below. One fourth natural size.

A.M. 19454. *Aceratherium perimense.* Maxilla.

	Length	Width
P^1	37 mm.	25 mm.
P^2	38	46
P^3	46	62
P^4	51	74*
M^1	60	80*
M^2	69	78
M^3	63	63
Length premolar series	161	
Length molar series	183	
Length premolar-incisor diastema	90	
Incisor	71	31

* Estimated

A.M. 19454. *Aceratherium perimense.* Mandible.

	Length	Width
P_2	32 mm.	23 mm.
P_3	40	26
P_4	49	37
M_1	53	36
M_2	64	40
M_3	72	35
Length premolar series	123	
Length molar series	187	
Incisor	58	45
Length from symphysis to condyle	625	
Length premolar-incisor diastema	48	
Depth of ramus at M_1	106	
Height of condyle above lower border of ramus	305	

The question of the generic and specific identity of the American Museum skull, No. 19470, has indeed been a perplexing one. At first sight it would seem to be considerably different from the large skull of *A. perimensis*, figured by Lydekker. On the other hand, a more careful comparison would seem to indicate that the apparent differences between the two specimens may not be as great as first they appeared to be. Supposing the two specimens to belong to one species, how should they be generically classified?

In speaking of the characters and affinities of the Middle Siwalik rhinoceroses Dr. Matthew pointed out the inappropriateness of some of the previous identifications applied to certain genera. "The so-called Aceratheria from India were referred to *Aceratherium* by Lydekker on the quite arbitrary ground that they were hornless. They appear to me to be gigantic species of *Chilotherium*, and whether or not they are placed within that genus (the skull differences are considerable) they have nothing to do with the true *Aceratherium*, but belong in the Oriental rhinoceros group." [58]

Certain anatomical characters of the American Museum material would seem to ally it, if not with the skull described by Lydekker, at least with the genus *Aceratherium*. Such for instance is the presence of an upper incisor, which is definitely established by the American Museum specimens. The retracted narial notch, the close approach to each

[58] Matthew, W. D., 1929, p. 451.

other of the parietal crests, the proportions of the upper teeth, especially as regards length and breadth, and the seeming lack of any expansion in the mandibular symphysis, are all characters that would seem to link this form with *Aceratherium* rather than with *Chilotherium*.

At this point a table is presented to show the comparative features of *Chilotherium*, *Aceratherium* and *Aceratherium perimense*. This table was prepared by the writer. Since its preparation, a very similar table has been published by Forster Cooper (1934) in his excellent paper on the rhinoceroses of Baluchistan, and some of the facts brought out by Forster Cooper appear on the present table. They were, however, deduced quite independently of Forster Cooper's work.

Chilotherium	*Aceratherium*	*Aceratherium perimense* (A.M. 19470, 19454)
1. Skull of moderately large size, brachycephalic.	1. Skull of moderately large size, dolichocephalic.	1. Skull extremely large, brachycephalic.
2. Horns absent.	2. Horns absent.	2. Horns absent.
3. Nasals straight and pointed.	3. Nasals straight and pointed.	3. Nasals straight and pointed.
4. Parietal cristae widely separated.	4. Parietal cristae close together.	4. Parietal cristae close together.
5. Narial notch moderately retracted.	5. Narial notch greatly retracted.	5. Narial notch greatly retracted.
6. Occiput vertical.	6. Occiput vertical.	6. Occiput vertical.
7. Lambdoidal crest transversely expanded.	7. Lambdoidal crest not expanded.	7. Lambdoidal crest expanded.
8. Zygomatic arch of average size.	8. Zygomatic arch slightly expanded.	8. Zygomatic arch greatly expanded.
9. Postglenoid and posttympanic separated, or in some cases touching.	9. Postglenoid and posttympanic separated, or in some cases touching.	9. Postglenoid and posttympanic separated.
10. Premaxillaries short and attenuated.	10. Premaxillaries long and heavy.	10. Premaxillaries of moderate length, and heavy.
11. Upper incisor absent.	11. Upper incisor present.	11. Upper incisor present.
12. Cheek teeth hypsodont.	12. Cheek teeth sub-hypsodont.	12. Cheek teeth hypsodont.
13. Parastyle fold indistinct or lacking	13. Parastyle fold stong.	13. Parastyle fold strong.
14. Protocone constricted.	14. Protocone constricted.	14. Protocone constricted.
15. Ectoloph greatly elongated.	15. Ectoloph not elongated.	15. Ectoloph moderately elongated.
16. Mandibular symphysis transversely expanded.	16. Mandibular symphysis not expanded.	16. Mandibular symphysis not expanded.
17. Lower incisors directed up and outwardly.	17. Lower incisors not directed outwardly.	17. Lower incisors not directed outwardly.

From the above table it may be seen that the definitive characters of the American Museum material referable to *Aceratherium perimense* would seem to ally this material with the genus *Aceratherium* rather than with *Chilotherium*.

The presence of an upper incisor in the American Museum material is especially significant. That an incisor was present is definitely shown by Amer. Mus. No. 19692, in which specimen the molar teeth are certainly like the molars of the large skull, Amer. Mus. No. 19470. An associated palate and mandible, Amer. Mus. No. 19454 also show the

upper incisor as a well developed tooth. Although this latter specimen is somewhat smaller than Amer. Mus. No. 19470, there seems to be no valid reason for separating it specifically from the large skull.

All of the large Middle Siwalik and Lower Siwalik rhinoceros material in the American Museum collection is hereby referred to *Aceratherium perimense*. The fact is recognized, however, that this material does show certain important diagnostic characters, such as the hypsodont cheek teeth, the great development of the lambdoidal crest, etc., that set it apart from the typical *Aceratherium*. Consequently it is referred to the genus *Aceratherium* with a full realization that when more material makes the species under consideration better known, it may be transferred to a separate and a new genus. It may be, too, that more complete studies will prove that the Perim Island material, the true *Aceratherium perimense*, is separate from the gigantic rhinocerotid from the Punjab.

Aceratherium lydekkeri Pilgrim

Aceratherium lydekkeri, Pilgrim, 1910, Rec. Geol. Surv. India, XL, pp. 65–66.

Additional References.—

Pilgrim, G. E., 1910B, p. 200; 1913B, pp. 284, 297.

Matthew, W. D., 1929, pp. 449, 507.

Type.—Not definitely designated. "It is therefore necessary to refer the Dhariala skull to Falconer's species *A. perimense* and to establish a fresh specific name for the Middle Siwalik skull and teeth described by Lydekker." According to this it would be inferred that Pilgrim meant to include G.S.I. Nos. C 1, C 2, C 3, C 4, C 7, C 14, C 18, C 238 in the new species.

Cotypes.—See remarks under type.

Horizon.—Middle Siwaliks.

Locality.—From the Punjab, particularly around Hasnot.

Diagnosis.—Like *Aceratherium perimense* but smaller and more dolichocephalic.

This species is probably synonymous with *Aceratherium perimense*. The reader is referred to Matthew, W. D., 1929, p. 507.

Aceratherium planidens (Lydekker)

Rhinoceros planidens, Lydekker, 1876, Pal. Indica (X), I, pp. 41–43, Pl. IV, figs. 7, 9.
Aceratherium perimense, Lydekker, 1880, Pal. Indica (X), I, p. xiii.

Type.—G.S.I. No. C 13, two imperfect upper molars.

Horizon.—Middle Siwaliks.

Locality.—Padri, Punjab.

Diagnosis.—(After Lydekker, R., 1876A, p. 41.) Median valley of upper molars wide at entrance; crochet blunt and simple; antecrochet large; anterior cingulum well developed.

Synonymous with *Aceratherium perimense*.

Aceratherium iravadicus (Lydekker)

Rhinoceros iravadicus, Lydekker, 1876, Pal. Indica (X), I, pp. 36–41, Pl. V, figs. 1–4.
Aceratherium perimense, Lydekker, 1881, Pal. Indica (X), II, p. 10.

Cotypes.—G.S.I. Nos. C 74, a left M^2; C 73, portion of a skull; C 75, a right M^2; C 76, a fragmentary maxilla.

Horizon.—Irrawaddy beds, probably an equivalent of the Middle Siwaliks.

Locality.—Burma, Irrawaddy River.

Diagnosis.—(After Lydekker, R., 1876A, p. 36.) Entrance to median valley in upper molars blocked by a large tubercle; prominent parastyle groove; crochet simple; well developed antecrochet and anterior cingulum.

A synonym of *Aceratherium perimense*, as was recognized by Lydekker in 1881. "In consequence of the above re-determinations the species *R. planidens* and *R. iravadicus* must be removed from the list of Siwalik mammals." [59]

Chilotherium Ringström, 1924

Generic type, *Chilotherium anderssoni* Ringström

Chilotherium intermedium (Lydekker)

Rhinoceros sivalensis intermedius, Lydekker, 1884, Pal. Indica (X), III, p. 5, Pl. I, fig. 3.
Aceratherium gajense intermedium, Pilgrim, 1910, Rec. Geol. Surv. India, XL, p. 200.
Chilotherium intermedium, Matthew, 1929, Bull. Amer. Mus. Nat. Hist., LVI, p. 508, fig. 32.

Additional References.—

Lydekker, R., 1885B, p. 64.

Type.—G.S.I. No. C 34, a second right upper molar.

Paratypes.—None.

Horizon.—Lower Siwaliks, for the type. Lower and Middle Siwaliks for referred specimens.

Locality.—Sind, for the type. Punjab for referred specimens.

Specimens in the American Museum.—Amer. Mus. No. 19477. Anterior portion of a mandible with right and left P_{2-3}. From the Middle Siwaliks, near Dhok Pathan.

19483. A left P_3. Middle Siwaliks, two miles east of Dhok Pathan.

19563. Left M^3. Lower Siwaliks, 200 feet above the level of Chinji Rest House, one half mile north of Chinji Rest House.

19580. Portions of the right upper dentition. Lower Siwaliks, 100 feet above the level of Chinji Rest House, two miles west of Chinji Rest House.

19680. Right lower molar. Middle Siwaliks, four miles west of Dhok Pathan.

19681. Fragment of a left ramus with M_{1-2}. Middle Siwaliks, one mile west of Dhok Pathan.

19689–19690. A complete skull and mandible of a juvenile animal. Milk dentition. Middle Siwaliks, one half mile southwest of Dhok Pathan.

19722. Fragment of right ramus with broken cheek teeth. Middle Siwaliks, three miles east of Dhok Pathan.

19898. Right lower molar. Middle Siwaliks, two miles north of Hasnot.

29795. Left M^3. Middle Siwaliks, one mile west of Hasnot.

29797. Left M^3. Lower Siwaliks, 1600 feet above the level of Chinji Rest House, one mile west of Chinji Rest House.

29799. Various associated cheek teeth. Lower Siwaliks, near Chinji Rest House.

Diagnosis.—A *Chilotherium* of medium size, very close to *C. blanfordi*. Distinguished by its rather prominent parastyle fold, and the slight constriction of the protocone.

[59] Lydekker, R., 1881, Pal. Indica (X), II, p. 10.

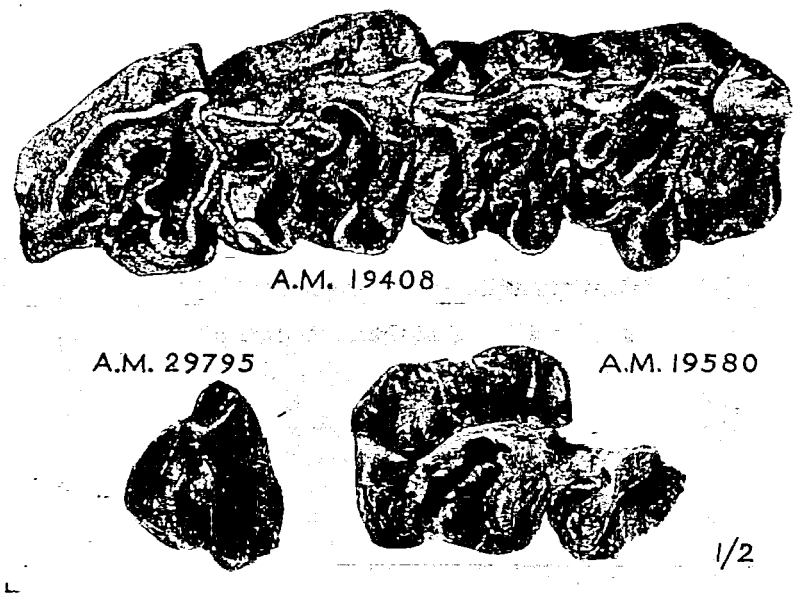

FIG. 90. *Chilotherium blanfordi* (Lydekker). Amer. Mus. No. 19408, right P^2–M^3. Crown view.
Chilotherium intermedium (Lydekker). Amer. Mus. No. 29795, left M^3, crown view; Amer. Mus. No. 19580, right upper molars, crown view.
Figures one half natural size.

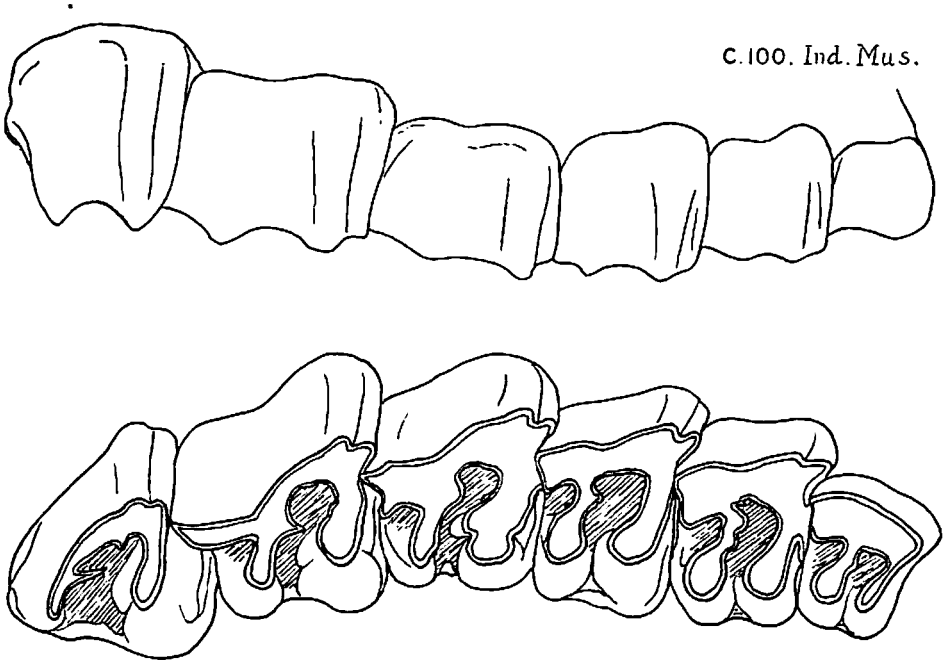

FIG. 91. *Chilotherium intermedium* (Lydekker). Geol. Surv. India, No. C 100, right upper dentition. External view above, crown view below. One half natural size. From Matthew, 1929.

Matthew first suggested that this species, assigned by Lydekker to the genus *Rhinoceros*, and by Pilgrim to the genus *Aceratherium*, should be properly classified in the genus *Chilotherium*. Matthew's opinion is followed in this present work. Although *Chilotherium intermedium* is typically of Lower Siwalik age, there are several specimens from the Middle Siwaliks in the American Museum collection that would seem to be referable to this species. The differences between these specimens and the typical *C. intermedium* do not seem to be enough to warrant their separation as a distinct form, so they are included within the species under discussion, and this species is thereby considered as ranging through the Chinji and the Middle Siwalik beds.

A Juvenile Skull and Mandible, Referred to *Chilotherium intermedium*

The associated skull and mandible (Amer. Mus. Nos. 19690, 19689) would seem to be referable to *Chilotherium intermedium*. The skull is slightly crushed and it lacks the floor of the brain case. The mandible lacks only the tip of the coronoid processes and the borders of the angles. The full milk dentition is preserved above and below.

This skull bears out Ringström's interpretation of the dental formula for the milk dentition of *Chilotherium*, in that it shows DI 0/2, DC 0/0, DM 4/4. The skull is rather small, being about 300 millimeters in length, which is slightly smaller than a skull of *Chilotherium anderssoni* of comparable ontogenetic development, figured by Ringström.

The skull and mandible under consideration are quite similar to the skull and mandible of *Chilotherium anderssoni;* the nasals are straight and hornless and the premaxillaries are very much reduced, an indication of the complete reduction of the incisors in this genus. An interesting character of this skull is the division of the infraorbital foramen, so that there are two separate exits near the narial notch. This division of the infraorbital foramen is a *Chilotherium* character, as has been pointed out by Ringström in his original description of the genus. The postglenoid process is long and is separated from the posttympanic. The frontal region has begun to show a concavity between the orbits, a feature typical of the adult *Chilotherium*. The mandible shows the beginning of the increase in symphyseal width which is characteristic of the adult animal. The symphysis, however, is not broadened to the same degree as is the symphysis in the juvenile *C. anderssoni*, so it would seem likely that *C. intermedium* showed a lesser degree of specialization in this particular feature than did the species from North China.

The first upper milk molar of the specimen under consideration, a tooth just erupting, is small and of triangular outline. It consists essentially of an outer ectoloph and of a posterior transverse cross crest. The second upper milk molar is quadrate with a convex ectoloph and a fairly strong parastyle. There is a large anterior cingulum in this tooth, separated by a valley from the protoloph, and it continues around to the lingual side of the tooth to close the median valley. An antecrochet and a crochet are present.

The third and fourth upper milk molars are essentially similar to the permanent molars. They have a broad and flat ectoloph with a strong parastyle well developed, a somewhat oblique protoloph and metaloph, and strong crochet. There is no internal cingulum. It might be well to point out the fact that in the specimen at hand the protocone is not divided by a posterior vertical fissure, as in the juvenile specimen of *C. anderssoni*. This is as it should be, for we find that in the adult *C. intermedium* the protocone is not strongly divided as in the adult *C. anderssoni*.

The first lower milk incisor was seemingly very small and rudimentary, as may be judged from the alveolus, which is located medially to the erupting second milk incisor. A very small alveolus in front of DM_2 would indicate that a rudimentary DM_1 was present, but was soon lost. The remaining milk molars show the typical rhinocerotid pattern, each tooth being composed of two crescents. Measurements of the specimen are given in the accompanying tables.

FIG. 92. *Chilotherium intermedium* (Lydekker). Amer. Mus. No. 19690, juvenile skull. Dorsal view above, ventral view below. One third natural size.

The question arises as to whether the skull and mandible considered above really do belong to the species *C. intermedium*, or whether they represent a distinct new species of *Chilotherium*. As compared to the adult teeth of *C. intermedium* in the American Museum collection, the milk molars of the specimen under consideration seem rather small. The proportions between milk and permanent teeth in *C. anderssoni*, as taken from measurements given by Ringström, are as follows:

DM^4....length.... 56 mm. M^2....length.... 65 mm. Ratio.... 86

A comparison between juvenile and adult of *C. intermedium*, as demonstrated by the American Museum material, shows the following ratio.

DM^4....length.... 40 mm. M^2....length.... 58 mm. Ratio.... 69

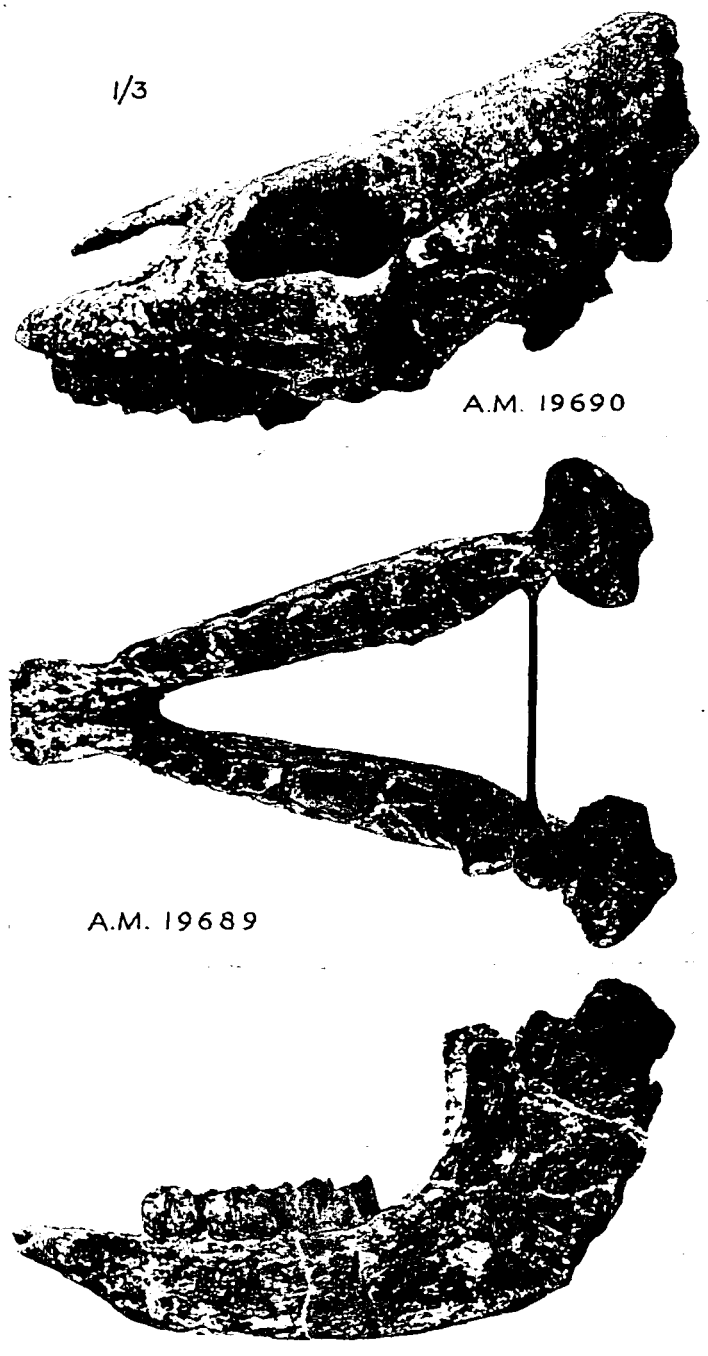

FIG. 93. *Chilotherium intermedium* (Lydekker). Amer. Mus. Nos. 19690, 19689, juvenile skull and mandible. Lateral view of skull at top, dorsal view of mandible in middle, lateral view of mandible at bottom. One third natural size.

Thus there is a greater discrepancy between the supposed juvenile of *C. intermedium* and the adult in the American Museum collection, than exists in *C. anderssoni*. In view, however, of the inadequacy of material for measurements the above figures can not be taken too seriously. Consequently it seems best for the time being to consider the juvenile skull and mandible, discussed above, as belonging to the species *C. intermedium*, rather than to a new species.

MEASUREMENTS (IN MM.) OF *Chilotherium*

	A.M. 19690 *C. intermedium*	A.M. 26340 *C. anderssoni*
Length of skull (premaxilla-lambdoidal crest)	298 mm.	
Width across glenoids	165	
Width at frontals (postorbital process)	106	113 mm.
DM^2 Length	34	38
Width	27	33
Height	25	28
DM^3 Length	35	43
Width	31	39
Height	28	34
DM^4 Length	40	52
Width	33	44
Height	31	43

	A.M. 19689 *C. intermedium*	A.M. 26341 *C. anderssoni*
Length of mandible (condyle-symphysis)	273 mm.	285 mm.
Width across condyles	175	
Width of symphysis	39	48
DM_2 Length	27	30*
Width	14	16*
Height	18	
DM_3 Length	31	38*
Width	16	20*
Height	20	
DM_4 Length	36	45*
Width	18	22*
Height	23	

* Ringström, T., 1924, Pal. Sinica, Ser. C, I, Fas. 4, p. 37.

A.M. 19477. *Chilotherium intermedium*. Mandible.

Transverse diameter between outside surfaces of rami at P_3	105 mm.
Transverse diameter of symphysis at narrowest part	83
Transverse diameter of symphysis at incisors	78
Depth of ramus at P_2	56

A.M. 29798. *Chilotherium blanfordi*.

DM^4 Length..... 50 mm. Width..... 45 mm.

Chilotherium blanfordi (Lydekker)

Aceratherium blanfordi, Lydekker, 1884, Pal. Indica (X), III, pp. 2–11, figs. 1–3, Pl. I, figs. 1, 2, 6, Pl. II, figs. 1, 2, 3.

Teleoceras blanfordi, Pilgrim, 1910, Rec. Geol. Surv. India, XL, p. 200.

Chilotherium blanfordi, Ringström, 1924, Pal. Sinica, Ser. C, I, Fas. 4, pp. 75–76.

Aceratherium blanfordi, Forster Cooper, 1934, Phil. Trans. Royal Soc., London, Ser. B, CCXXIII, pp. 589–594, fig. 9.

Additional References.—

Lydekker, R., 1885B, pp. 68–69; 1886A, pp. 154–155, fig. 18.

Pilgrim, G. E., 1912, pp. 30–32, Pl. VII, figs. 4–7; 1913B, p. 312.

Matthew, W. D., 1929, p. 508.

Type.—(Lectotype.)—G.S.I. No. C 268, a left maxilla with M^{1-3}.

Cotypes.—G.S.I. Nos. C 50, left maxilla; C 258, milk molar; C 260, right MM^{1-2}; C 262, molar; C 267, right ramus; C 271, right ramus; C 269 a left maxilla; C 270, left mandibular ramus. The last two specimens were figured as *A. blanfordi minus*.

Horizon.—Bugti beds for the type. Kamlial and Chinji zones, Lower Siwaliks, for the referred specimens. Also Middle Siwaliks.

Locality.—Dera Bugti and Gandoi in Baluchistan for the type and cotypes. Northern Punjab for referred specimens.

Specimens in the American Museum.—Amer. Mus. No. 19408. A portion of the palate and the basicranium, with right P^3–M^3. Lower Siwaliks, 100 feet below the level of Chinji Rest House, near the contact between the Chinji and the Kamlial formations, near Chinji Rest House.

19469. Right mandibular ramus with P_2–M_3. Lower portion of Middle Siwaliks, 1000 feet below the Bhandar bone bed, one mile south of Nathot.

19532. Fragments of teeth and a mandible. Lower portion of the Middle Siwaliks 1000 feet below the Bhandar bone bed, five miles west of Hasnot.

19538. Fragments of mandibular ramus and teeth. Middle Siwaliks, one mile south of Nathot.

19539. Right M^2, and miscellaneous fragments. Middle Siwaliks, one mile south of Nathot.

29788. A left DM^3. Lower Siwaliks, at the level of Chinji Rest House, two miles west of that place.

29789. A right P^2. Middle Siwaliks, one half mile north of Hasnot.

29791. A left P^3. Middle Siwaliks, one mile northeast of Hasnot.

29798. A left DM^4. Middle Siwaliks, four and one half miles west of Hasnot.

Diagnosis.—A rather large species of *Chilotherium*. Molars with flat ectoloph, and with rather sharply constricted protocone.

Ringström first placed this species in the genus *Chilotherium* and in this he was followed by Matthew, in 1929. Later, however, Matthew referred this species to *Rhinoceros*, and subsequently it was classified by Forster Cooper as *Aceratherium* and as "Rhinoceros" *sensu lato*.

It is thought most expedient for the present to consider it as belonging to the genus *Chilotherium*. This designation is provisional at best.

It will be noticed that a considerable number of teeth referred to this species in the American Museum collection range up into the Middle Siwaliks. Although this extends the range of the species beyond its hitherto known limits, there seems to be no other very logical solution as to the identification of the teeth in question. The discovery of additional skulls and skeletal material will aid materially in the interpretation of the confusion of Siwalik rhinoceros remains. Until these skulls can be found, the isolated teeth must needs be assigned in the best way possible to the genera and species that they would seem to represent. Naturally, on the basis of teeth alone, a great many errors will appear in the identification of the American Museum specimens, when at some time they can be studied in the light of supplementary and more detailed knowledge.

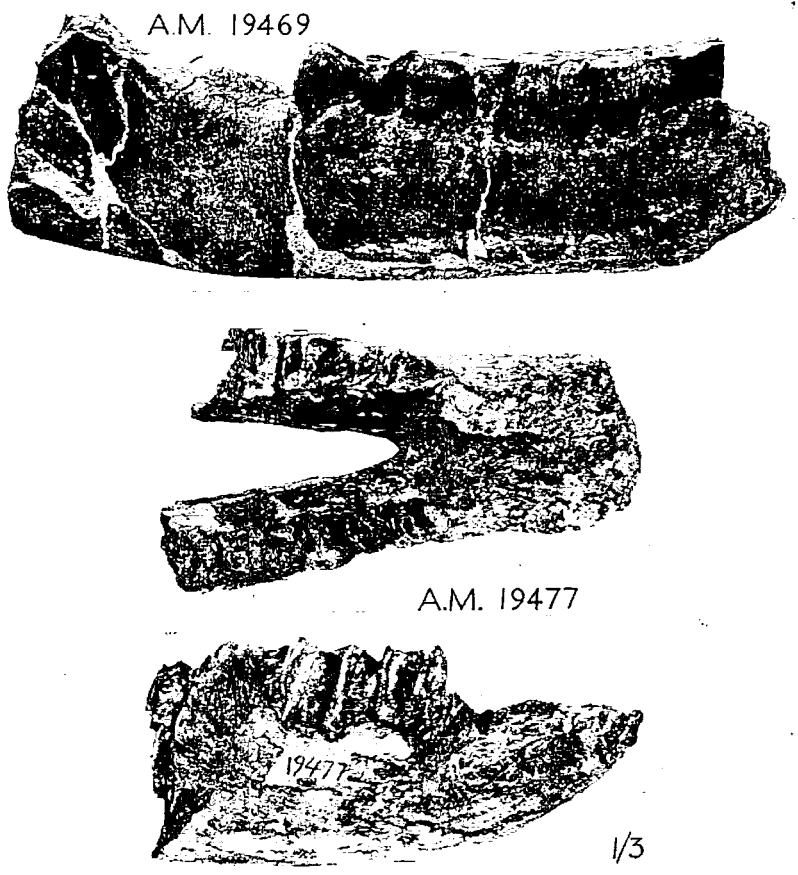

FIG. 94. *Chilotherium blanfordi* (Lydekker). Amer. Mus. No. 19469, mandibular ramus. Lateral view.
Chilotherium intermëdium (Lydekker). Amer. Mus. No. 19477, symphysis of mandible. Dorsal view above in middle, lateral view below.
Figures one third natural size.

The two species supposedly representing the genus *Chilotherium* in the Siwalik deposits are very similar to each other, a fact recognized by Dr. Matthew in 1929.

"This [i.e., *Chilotherium intermedium*] is close to *C. blanfordi* Lydekker of the Bugti Hills, differs chiefly in more prominent antero-external pillar and protocone less constricted off. Doubtful if really separable." [60]

A review of the literature and of the material in the American Museum would seem to point to the following facts.

1. *C. blanfordi* and *C. intermedium* are probably distinct species.

2. Both species were geologically of long range, and persistent. The former appeared in the Bugti beds and lasted through the Kamlial, Chinji and into the Middle Siwaliks, while the latter appeared in the Chinji and was well developed in the Middle Siwaliks.

Several characters serve to separate *C. blanfordi* from *C. intermedium.*

1. *C. intermedium* is typically somewhat smaller than *C. blanfordi.*

2. In *C. intermedium* the antero-external pillar is prominent while in *C. blanfordi* the ectoloph is relatively flat.

3. In *C. intermedium* the protocone is much less constricted off from the protoloph than is the case in *C. blanfordi.*

4. In *C. intermedium* the metaloph of the third upper molar is longer than the protoloph, while in *C. blanfordi* the two crests are more nearly equal in length.

Forster Cooper (1934) has made the following helpful remarks about these two species.

"The animal here under discussion [*A. blanfordi*] has been placed in the genus *Chilotherium* by Ringström (1924) and by Matthew (1929), presumably on the evidence of the structure of the molars. This structure, however, the constricted protocone, the large crochet, the heavy cingulum, etc., is found in so many genera that it has little value as evidence of affinity. There is, moreover, no evidence that the lower jaw, to which a symphysis is here referred, fig. 10, A, had that exceptionally wide symphysis which is such a leading characteristic of *Chilotherium.* The structure of the feet and skeleton, from which much information might be obtained, is entirely unknown. Matthew (1929) states that '*Chilotherium*' *intermedium* (Lydekker) is close to '*C.*' *blanfordi* (Lydekker). The type of the first-named is no more than a second upper molar, but Matthew (1929, fig. 32, p. 508) refers to this species a specimen in the Indian Museum. According to him it is doubtful if the two species are really separable. They differ only in that the first-named has a more prominent antero-external pillar and a less constricted protocone. In the light of the specimens here described it can be seen that *C. intermedium* is much more advanced in the evolution of the premolars, in the lesser development of the cingulum and in the development of a much larger crochet on the molars, and appears therefore to be a separate species. All that can be said, therefore, about the generic position of *R. blanfordi* is that it appears to have been derived from some *Caenopus* stock and that, as far as the evidence goes, there is nothing to prevent it from being regarded as having some affinity with *Aphelops.*" [61]

[60] Matthew, W. D., 1929, p. 508.

[61] Forster Cooper, C., 1934, p. 594.

Fig. 95. *Chilotherium blanfordi* (Lydekker). Amer. Mus. No. 19408, lower portion of skull. Ventral view. One third natural size. (See Fig. 90 for detail of teeth.)

MEASUREMENTS

Chilotherium blanfordi

Amer. Mus. No. 19408.

	Length	Width
Right M^1	52 mm.	64 mm.
M^2	64	66
M^3	56	61
Transverse diameter, occipital condyles		122
Width of skull at glenoids		352

Amer. Mus. No. 19469, mandible.

Length of premolar series	83
Length of molar series	143
Depth of ramus at M_1	77
Thickness of ramus at M_1	49

Amer. Mus. No. 29798.

DM^4 . . . Length 50 mm. Width . . . 45 mm.

Limb and Foot bones Referable to Chilotherium.

Amer. Mus. No. 19435. Various foot bones from the Lower Siwaliks.

29818. Phalanges and proximal end of a metacarpal. Middle Siwaliks, fifteen miles northwest of Bilaspur.

29832. Right femur, tibia, tarsus, pes; left radius and ulna. Middle Siwaliks, one half mile southwest of Dhok Pathan.

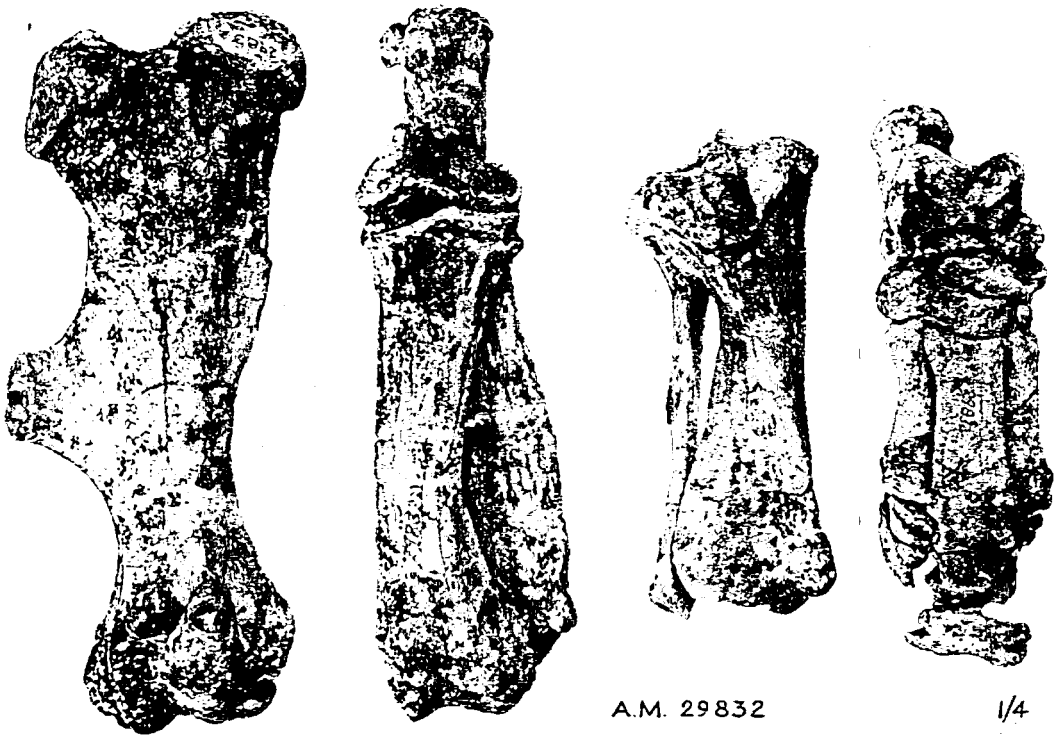

FIG. 96. Associated limb and foot bones referable to *Chilotherium*. Amer. Mus. No. 29832. From left to right: right femur, left radius-ulna, right tibia-fibula, right pes. Anterior views. Figures one fourth natural size.

Of the skeletal elements in the American Museum collection, referable to *Chilotherium*, the associated hindlimb and foot show particularly well the characters of the genus. The limb bones and the pes are very short. The median metatarsal is much wider than the lateral ones, a character shown by Ringström to be especially characteristic of the genus under discussion.

MEASUREMENTS

Amer. Mus. No. 29832.

Radius, articular length	249 mm.
Ulna, greatest length	325
Femur, greatest length	360
Femur, breadth at mid-shaft, below trochanter	64
Tibia, greatest length	245
Tibia, breadth at mid-shaft	43
Calcaneum, length	65
Calcaneum, breadth	65
Astragalus, breadth	77
Metatarsal II, length	92
Metatarsal II, breadth at middle of bone	25
Metatarsal III, length	103
Metatarsal III, breadth in middle of bone	33
Metatarsal IV, length	90
Metatarsal IV, breadth in middle of bone	24

A comparison of the Siwalik *Chilotherium* hindlimb with that of the *Chilotherium* figured by Ringström (1924, Pl. IX, figs. 3, 4, 5) shows that a great similarity exists between the Indian form and the species from North China. This comparison is shown graphically in the accompanying figure, in which the femur in both species is reduced to unity.

It will be seen that the third trochanter is well down towards the distal end of the femur in both of these species, but in the Siwalik one it is lower than in the North China form. The portion of the femur below the trochanter is correspondingly short. It would seem that in the shortening of the limbs in this brachypodine rhinoceros there has been a differential shortening in the femur. That is, the upper end of the bone has retained to a large extent the proportions that would be found in a rhinoceros having limbs of normal length, whereas the lower end of the femur, the tibia and the foot have become greatly abbreviated. This offers an interesting example of the differential growth in one working unit, whereby an evolutionary trend is accomplished differently by separate portions of the same unit.

In both species the tibia and fibula are short, but in the Siwalik form the tibia is proportionately wider than in the Chinese species. The pes is similar in both species, but it would seem to be proportionately somewhat longer in the Siwalik than in the Chinese form.

RHINOCEROTIDAE IN THE AMERICAN MUSEUM, NOT SPECIFICALLY IDENTIFIABLE

Amer. Mus. No. 19427. Mandibular fragments. Lower Siwaliks, 1600 feet above the level of Chinji Rest House, twelve miles east of Chinji Rest House.

19473. *Chilotherium* carpals. Lower portion of Middle Siwaliks, one mile south of Nathot.

19532. Miscellaneous teeth. Middle Siwaliks, 1000 feet below the level of the Bhandar bone bed, five miles west of Hasnot.

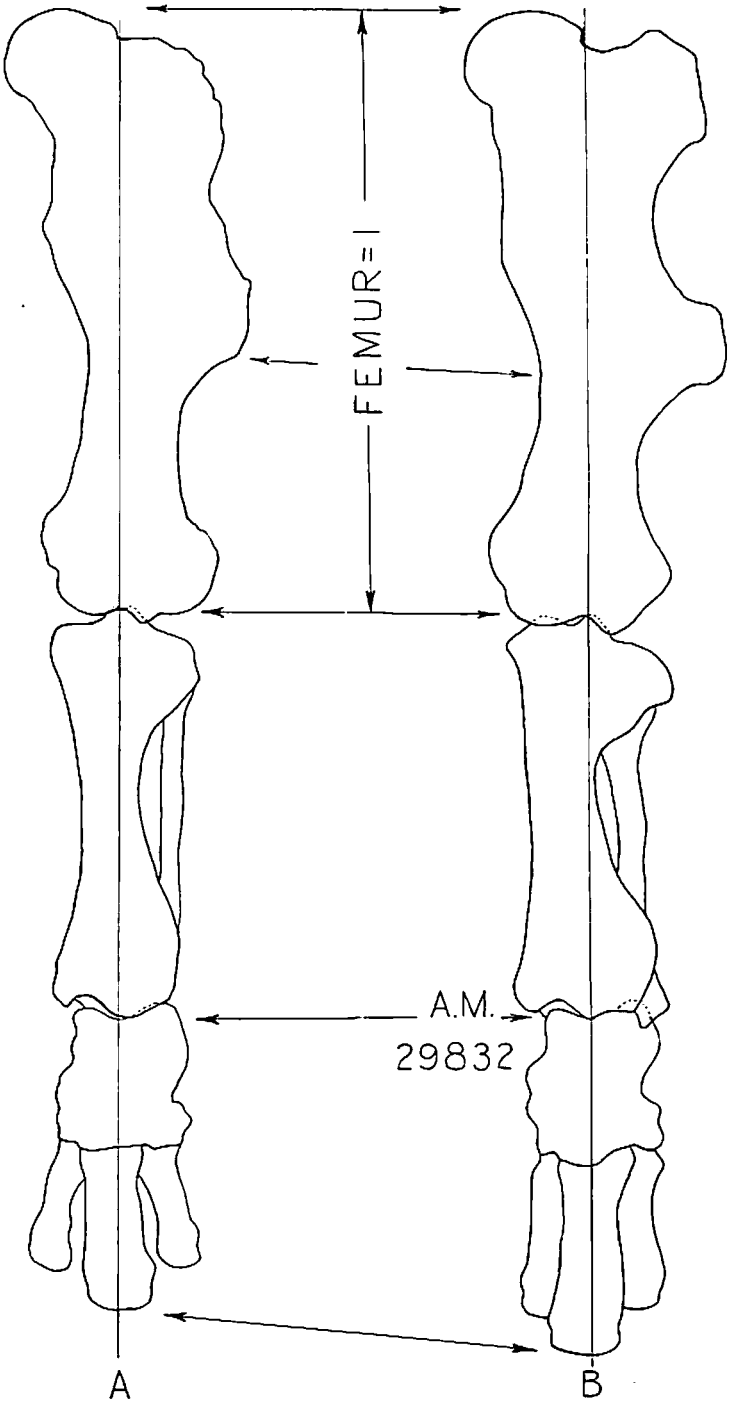

FIG. 97. Comparison of the hind limb in *Chilotherium* from North China (left) with *Chilotherium* from the Siwaliks, Amer. Mus. No. 29832 (right). Femur reduced to unity. North China form (*A*) taken from Ringström, 1924, Pl. IX, figs. 3, 4, 5.

19547. Carpal bones. Middle Siwaliks, near Hasnot.
19619. *Chilotherium*, mandibular ramus. Lower Siwaliks, 1600 feet above the level of Chinji Rest House, one mile west of Chinji Rest House.
19684. Fragmentary mandibular ramus. Middle Siwaliks, one half mile southwest of Dhok Pathan.
19696. Broken teeth. Middle Siwaliks, three miles east of Dhok Pathan.
19718. Miscellaneous teeth. Middle Siwaliks, one mile east of Dhok Pathan.
19903. Teeth. Middle Siwaliks, 1000 feet below the level of the Bhandar bone bed, four and one half miles west of Hasnot.
19941. Teeth. Middle Siwaliks, 1000 feet below the level of the Bhandar bone bed, four and one half miles west of Hasnot.
19290. Tooth. Middle Siwaliks, four miles east of Dhok Pathan.
29812. *Chilotherium*, symphysis of mandible. Lower Siwaliks, locality not known.

ARTIODACTYLA

BUNODONTA

SUOIDEA

TAYASSUIDAE (?)

Pecarichoerus Colbert, 1933

Generic type, *Pecarichoerus orientalis* Colbert

Pecarichoerus orientalis Colbert

Pecarichoerus orientalis, Colbert, 1933, Amer. Mus. Novitates, No. 635.

Type.—Amer. Mus. No. 29955, various isolated cheek teeth from a single individual.

Paratypes.—None.

Horizon.—Lower Siwaliks, Chinji zone, about 1600 feet above the level of Chinji Rest House.

Locality.—Three miles west of Chinji Rest House, Salt Range, Attock District, Punjab.

Specimens in the American Museum.—The type, listed above.

Diagnosis.—(Colbert, E. H., 1933G, p. 2.) "Molar teeth short, brachyodont and quadricuspid. Cusps conical and separated from each other. Median valley of the third molar occupied by sharp, oblique ridges, which run between the anterior and the posterior pairs of cusps. Enamel smooth."

This genus and species would seem to be indicative of a true peccary in India in Lower Siwalik times. The paper quoted above, gives a full description, as well as the evidence for considering *Pecarichoerus* a member of the Tayassuidae.

The type figures and the measurements are reproduced below.

MEASUREMENTS

Pecarichoerus orientalis, Amer. Mus. No. 29955

M^1....	Length...	13.5 mm.	Width...	12.5 mm.	Index... 93
M^3....	Length...	14.0	Width...	12.0	Index... 86