Fossil Mammals from Burma in The American Museum of Natural History

BY EDWIN H. COLBERT

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

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INTRODUCTION

The American Museum Palaeontological Expedition to Burma

During the early part of 1923, Dr. Barnum Brown, of The American Museum of Natural History, went to Burma for the purpose of collecting fossil vertebrates along the Irrawaddy River. Previous to this time Dr. Brown had spent about a year and a half in central and northern India, where he obtained a very large and complete collection of Siwalik vertebrates; consequently it was convenient for him to follow up the Indian work by a season of intensive collecting in the Tertiary beds of Burma.

Several months were spent in Burma, working along the Irrawaddy River between Yenangyaung and Mandalay and along certain tributaries of the Chindwin as far north as Kyawdaw. Fossil vertebrates were very rare in the Tertiary beds of Burma, so that in spite of these months of arduous and trying work, numerous discomforts and a long period of serious illness, Dr. Brown was able to bring back only a small collection of fossils. This collection is, however, very important, especially because of the completeness of many of the specimens contained in it, and it forms the subject of the present paper.

A general account of Dr. Brown's expedition to Burma has been published elsewhere.[1]

A recent addition to The American Museum Burma collection is a molar of *Elephas hysudricus*, collected by Mr. A. S. Vernay, in the upper Chindwin district and presented by him to the Museum.

Previous Publications on Fossil Mammals of Burma

The literature dealing with the fossil vertebrates of Burma is rather restricted. This is due to the fact that these fossils are very rare in the alternating Cenozoic estuarine and freshwater river deposits that are exposed along the Irrawaddy and the Chindwin rivers and their tributaries, and consequently only a few authors have described the scattered and fragmentary specimens that have from time to time been picked up in Burma.

It was a little over a hundred years ago that Mr. J. Crawfurd, a Fellow of the Royal Society, was sent on an embassy up the Irrawaddy River to Ava. Some two hundred and fifty miles south of Ava he stopped to explore the outcropping sediments along the river, and as a

[1] Brown, Barnum, 1925, 'Byways and Highways in Burma.' Natural History, XXV, pp. 294–308.

Fig. 1. Personnel and equipment of the expedition, near Monywa. Dr. Barnum Brown on horse. Madrasy servants in the foreground. The small bullock carts were used for carrying camp and collecting equipment. Photograph by Lilian Brown. (From Brown, 1925.)

result of his search he found a number of fossils. These were sent to the Rev. William Buckland, then professor of mineralogy and geology at Oxford University, who in turn submitted them for study to Mr. William Clift, conservator of the Museum of the Royal College of Surgeons. In 1828, Buckland and Clift each published a paper in the Transactions of the Geological Society of London, the former describing Mr. Crawfurd's journey up the Irrawaddy and giving an account of the geology of the region, the latter presenting a description of the fossils.

In 1847, Falconer and Cautley figured a hippopotamus, *Hexaprotodon iravaticus*, from Burma in their 'Fauna Antiqua Sivalensis.' After this, there were no descriptions of Burma fossils until the series of extensive monographs by Richard Lydekker on the fossil vertebrates of India. In the course of his work Lydekker made occasional references to or descriptions of Burma fossils.

Then at the turn of the century, Dr. Fritz Noetling published a few occasional notes on fossil vertebrates from the Pegu Series of Burma. This author was, however, primarily concerned with the invertebrate fossils of that region.

There should be mentioned, too, the description by Smith Woodward in 1915 of a giant panda skull from a cave at Mogok. This specimen is probably of late Pleistocene, or post-Irrawaddian age.

Finally, the last contributor to the literature on fossil vertebrates from Burma has been Dr. Guy E. Pilgrim, formerly Superintendent in the Geological Survey of India. In some of his earlier papers Dr. Pilgrim described new fossils from the well-known Irrawaddy beds, and in the course of his writings he often referred to the already established Burmese species.

All of these authors were concerned with the upper Tertiary and Quaternary fossils of Burma.

In 1915, however, Pilgrim and Cotter described an entirely new fauna of uppermost Eocene age from the Pondaung beds of Upper Burma, and since the discovery of the fossil-bearing Pondaung beds, Pilgrim has contributed a series of valuable papers on this new and exceptionally interesting fauna.

In conclusion it might be noted that the late Professor Osborn recently described a new stegodont from the Irrawaddy beds of Burma.

Studies on the American Museum Burma Collection

It had originally been intended that Dr. Brown would make a study of the Burmese fossil mammals in the American Museum. Certain events have, however, prevented the consummation of this plan, and Dr. Brown has kindly submitted the collection to the present author for study.

This study comes as a logical sequence to the recently completed studies on the American Museum Siwalik collection, published in various Novitates and Bulletins of the American Museum and in Volume twenty-six of the Transactions of the American Philosophical Society.[1] These earlier researches on Siwalik mammals carried on at the American Museum and at the British Museum in London, have furnished a background to the present author for his consequent studies of the Burma fauna.

It is the purpose of this paper to describe the various specimens that constitute the American Museum Burma collection, comparing them with the types and with similar forms from India, from other parts of Asia and from Europe and North America, and in addition to consider in detail the bearing of the new fossils on certain problems of phylogenetic development and geographic distribution. At the same time a complete revision of the fossil mammalian faunas from Burma will be presented, in order that the various genera and species that comprise these faunas may be brought together in a single publication, not only for the purpose of having them conveniently grouped, but also for discussing and determining if possible the status of doubtful forms.

ACKNOWLEDGMENTS

I wish to express my appreciation to Dr. Brown for his kindness in assigning the American Museum Burma collection to me for study. Further acknowledgments are due him for his help on matters of geographic and stratigraphic distribution.

To Miss Merlys Blakeslee I wish to express my deep appreciation for the valuable aid that she has given me in the preparation of this paper, particularly in the compilation of the systematic portions of the work and in the assembling of bibliographic material.

The illustrations of the fossils were made by John C. Germann and Louise Waller Germann. D. F. Levett Bradley traced the maps from originals furnished by the Geological Survey of India.

[1] See: Colbert, E. H., 1935, Transactions of the American Philosophical Society, (N.S.) XXVI, pp. 1–2.
Pilgrim, G. E., 1937, Bulletin of The American Museum of Natural History, LXXII, Art. 7, pp. 729–874.

THE CONTINENTAL TERTIARY AND QUATERNARY BEDS OF NORTHERN BURMA

General Observations

It is not the purpose here to discuss in great detail the Tertiary and Quaternary stratigraphy of Burma. This problem has been ably set forth by various authors having a first-hand knowledge of the subject, and to them the reader is referred. Perhaps one of the most lucid of recent expositions on the post-cretaceous stratigraphy of Burma is L. D. Stamp's article, 'An Outline of the Tertiary Geology of Burma,' published in the Geological Magazine for 1922. Many of the observations and diagrams on the accompanying pages are based on Stamp's work, and in several instances this author is quoted at some length.

It may be well to consider briefly the salient features of the physical geography of Burma, in order that a more complete understanding of the post-cretaceous deposits of that country may be had. Physiographically Burma may be divided into four regions as follows:

1.—The Shan Plateau, occupying the eastern half of the country. This is a rather high table-land composed of folded pre-Palaeozoic, Palaeozoic and Mesozoic rocks, bounded on the west by a line of dislocation, the Shan Boundary fault.

2.—The Central Tertiary Belt, bounded by the Shan Plateau on the east and by the folded Arakan Yoma on the west. This Central Tertiary Belt, with which we are now concerned, is a long, relatively narrow strip of lowlands, stretching about 600 miles from north to south and averaging about 130 miles in width.

3.—The Arakan Yoma, a long, narrow range of folded mountains, bounding the Central Tertiary Belt on the west.

4.—The narrow strip of Arakan coast land, bounding the Arakan Yoma on the west, and consisting of the Tertiary rocks belonging to the Assam Gulf of deposition.

In early Tertiary times a long arm of the sea, the Burmese Gulf, occupied the Central Lowlands of Burma, extending from the vicinity of Rangoon northwards to the upper reaches of the present Chindwin drainage, and bounded on the east and the west by the already existing Shan Plateau and the ancient Arakan Yoma, respectively. Into the upper end of this gulf flowed the ancestral Chindwin River, forming a delta there.

The Tertiary history of Burma is mainly a story of the gradual filling in of the Burmese Gulf by continental river and delta deposits, so that as time elapsed, the marine sediments retreated to the south and were progressively overlapped by continental deposits from the north. As Stamp has shown, this process of infilling of the Burmese Gulf was not a simple progressive advance of continental sediments and a consequent retreat of marine deposition, but rather it took the form of a series of cycles of marine and continental sedimentation. Due to epeirogenic and local disturbances there were many fluctuations in the retreat of the sea and the advance of land down the Burmese Gulf, so that after periods of continental infilling there would be periods when the marine sediments were swept northward by an advancing sea to cover partially the floodplain and delta deposits.

Thus it may readily be seen that the Tertiary stratigraphy of Burma is not a simple succession of broad, well-defined depositional units, but

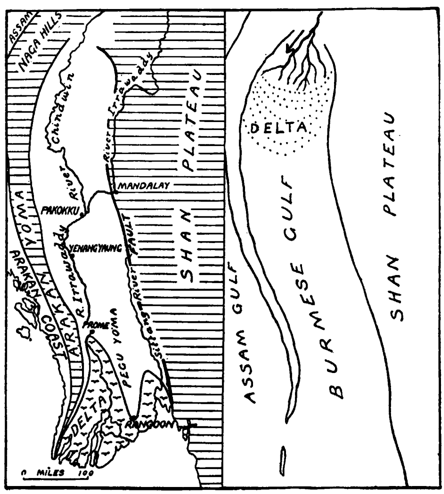

Fig. 2. Left; the natural regions of Burma. Right; the geography of Burma in early Tertiary times. (From Stamp, 1922.)

rather takes the form of complexly interfingered marine and continental beds, with numerous local differences causing many lateral variations in the lithology and the thickness of the several formations. Although this makes the stratigraphy very complicated, it does, on the other hand, cause an alternation of horizons containing marine and land faunas, thereby affording an opportunity for correlation between them.

The accompanying figure (Fig. 4) taken from Stamp, gives a graphic representation of the relationships between the various Tertiary formations of Burma.

Mammal-Bearing Beds of Northern Burma

Generally speaking, there are three well-defined fossil mammal faunas in Burma. These are, the Pondaung fauna of Upper Eocene age, the Lower Irrawaddy fauna of Pliocene age and the Upper Irrawaddy fauna of Lower Pleistocene age. As their names indicate, these faunas occur in the Pondaung sandstone, and in the Irrawaddy series of deposits. In addition to these well-defined and rather extensive faunas, the presence of a fourth fauna or rather a series of faunas is indicated by fragmentary remains in the Pegu beds. The fossils have been identified as being referable to the genera *Cadurcotherium*, *Telmatodon* and *Dorcatherium*, and they would seem to indicate several horizons ranging from the upper Oligocene into the Miocene. Descriptions of these deposits are presented below.

The Pondaung Sandstone

This formation occurs near the top of the Eocene sequence in middle and northern Burma. Being a continental deposit it thins out to the south and finally disappears, but in the more northerly sections of its exposure it is very thick, attaining a maximum thickness of more than 6000 feet. It rests on the Tabyin Clay, a marine deposit, except in the most northerly exposures, where it may rest on the Tilin sandstone. It is overlain by the Yaw stage, an interfingering marine deposit, in the southern portion of its extent, and in the north it is directly succeeded by the "Freshwater Pegu." The following description of the Pondaung sandstone is taken from Stamp, 1922.

PONDAUNG SANDSTONE.—A very interesting series of deposits. The lower part comprises beds of greenish sandstone (weathering yellow), with bands of conglomerate and greenish shale and passes down quite gradually into the Tabyin Clays below (1 in. map, sheet 84 K./5). Fossils here (latitude 21° 50′ to 22° 45′) are scarce, but include *Arca*, *Cardita*, and other marine forms. Going upwards in the series the Pondaung Sandstones exhibit a gradual change from marine to brackish and finally to freshwater and land conditions. Plant remains (wood) occur throughout; in the lower part the wood is carbonized, higher up partly carbonized and partly silicified, whilst in the highest part it is always silicified. It should be mentioned that silicified wood is highly characteristic of continental deposits in Burma. As one passes northward (as from latitude 21° 45′ to 23° 30′) the upper continental beds thicken at the expense of the lower marine. The most striking members of the continental facies are beds of clay—purplish, pale greenish, or mottled—with abundant vertebrate remains indicating their formation in freshwater lagoons. The remains include mammals (*Anthracotherium*, *Anthracohyus*, *Metamynodon* ? etc.), crocodiles (*Crocodilus*) and huge turtles. From about latitude 22° 0′ to 22° 30′ the highest bed is a "Red Bed" or layer of laterite denoting terrestrial conditions. To the south the whole of the Pondaung Sandstones become more marine, the mottled or purplish clays are not found much to the south of latitude 20° 30′, and oysters (*Alectryonia noetlingi*) are here abundant. Large nummulites are common from 20° 5′ southwards. The group is as thick as 6,500 feet in latitude 22° 5′. (Stamp, L. D., 1922, p. 490.)

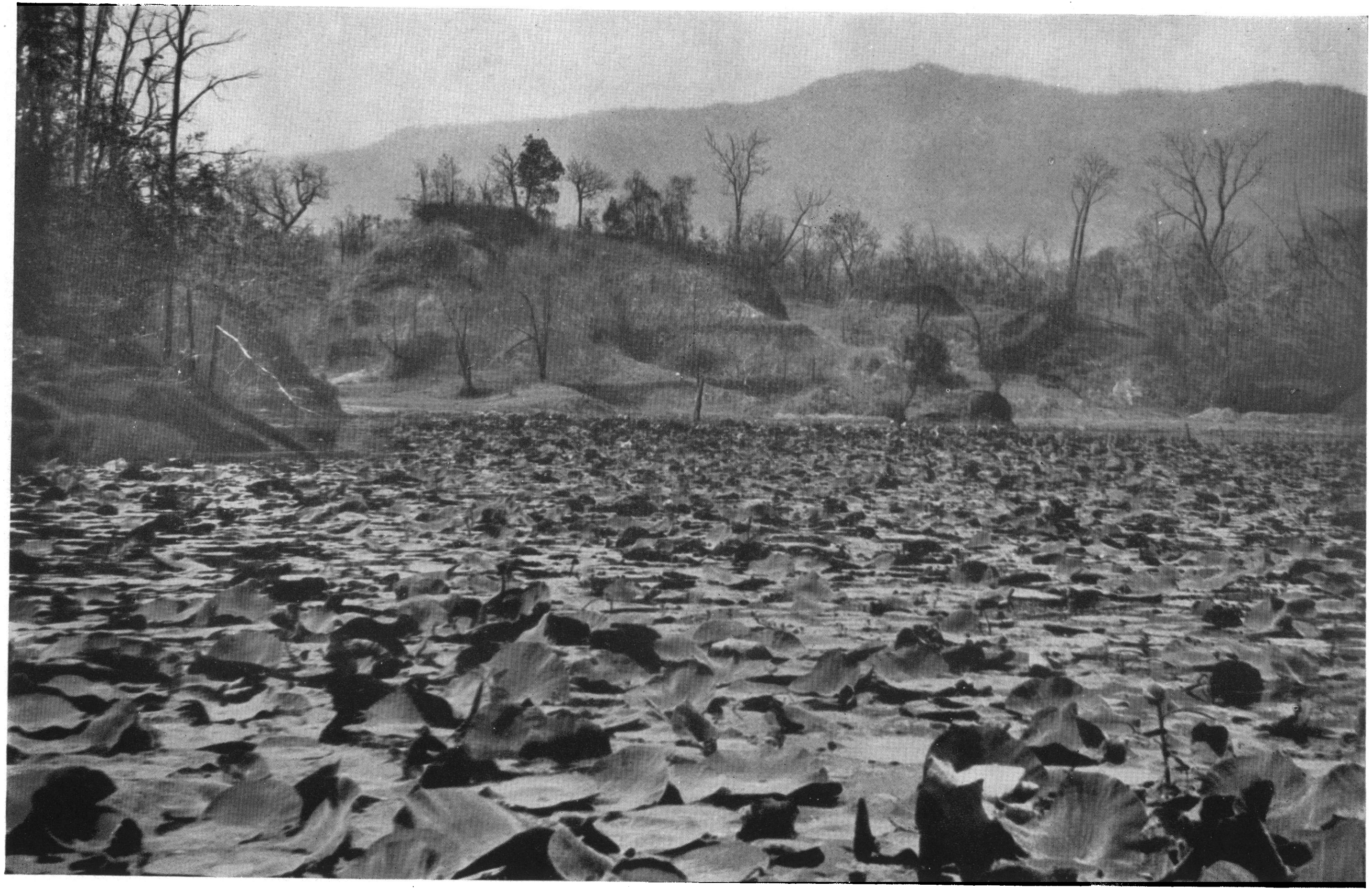

Fig. 3. Exposures of the fossiliferous Pondaung beds near Wetcha. A lotus pond in the foreground, in the background the Pondaung

The Freshwater Pegu Beds

The "Freshwater Pegu" is naturally restricted to the more northerly parts of Upper Burma. North of latitude 21° 30′ the Eocene Yaw Stage passes up gradually into a mass of somewhat coarse sandstone. At the base, logs of wood bored by molluscs and afterwards silicified are frequent, whilst in the higher part, and especially further north, silicified wood is abundant. North of latitude 22° 45′ the Freshwater Pegu rests directly on the Pondaung Sandstone, and bands of quartz-pebble conglomerate and lateritic "Red Beds" become frequent. Vertebrate remains—especially crocodilian—are occasionally found, and the occurrence of *Cadurcotherium* in the higher beds near Myaing has already been mentioned. . . . (Stamp, L. D., 1922, p. 497.)

As was mentioned above, and as will be considered in greater detail below, the time range of the Freshwater Pegu beds is considerable, extending from the Oligocene well into and perhaps far through the Miocene.

The Irrawaddy Series

Originally it was supposed that the "Freshwater Pegus" rested on the Eocene beds and were succeeded by the Irrawaddy beds. More recent work has shown, however, that the Lower Irrawaddy beds and the Freshwater Pegus merge, and are more or less correlative, so that the two series are continuous, representing the post-Eocene continental sediments of northern Burma.

Two distinct faunas come from the Irrawaddy sediments, a lower fauna of Pliocene age, from the base of the Irrawaddy beds at Yenangyaung, and an upper fauna of distinct lower Pleistocene affinities from a conglomeratic band some 4500 feet above the base of the Irrawaddies at Yenangyaung. It was this upper fauna that was first discovered by Crawfurd on his journey up the Irrawaddy in the early part of the last century.

Stamp makes the following remarks about the Irrawaddy beds:

The Irrawadian of Upper Burma comprises a thick series—certainly more than 5,000 feet in the neighbourhood of Yenangyaung—consisting mainly of coarse, current bedded sands. At the base there is usually a well-marked "Red Bed" or old lateritic land surface. Associated with this band either above it or below, there is frequently a bed of white sand rich in kaolin. Interbedded bands or even beds of some thickness of a clay, which approaches pipe-clay in general characters, are frequent in the lower beds and again in the higher part of the Irrawadian. The Irrawadian is famous for the enormous quantity of silicified fossil wood which it contains—hence the old name "Fossil Wood Group" (Theobald). The series has also yielded a number of interesting vertebrate remains, notably near Yenangyaung. . . . (Stamp, L. D., 1922, p. 497.)

In a subsequent paragraph Stamp says that:

The Irrawadian probably extended much further south than it does at present. It may occur under the alluvial deposits of the Irrawadi delta; indeed, a fossil bed containing Irrawadian vertebrates mingled with fish remains (*Lamna*), and probably in situ, has been recorded from below the alluvium near Rangoon. (Stamp, L. D., 1922, p. 498.)

(Stamp's remarks as to the correlation of the two fossiliferous horizons of the Irrawaddy are quoted in a subsequent section of this paper. See pp. 276, 277.)

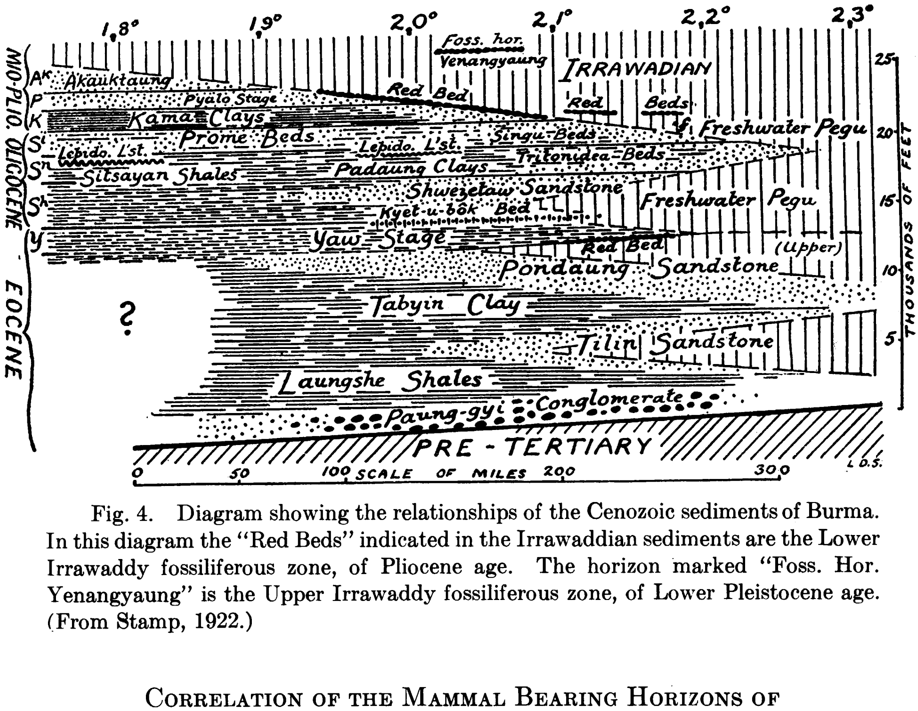

Fig. 4. Diagram showing the relationships of the Cenozoic sediments of Burma. In this diagram the "Red Beds" indicated in the Irrawaddian sediments are the Lower Irrawaddy fossiliferous zone, of Pliocene age. The horizon marked "Foss. Hor. Yenangyaung" is the Upper Irrawaddy fossiliferous zone, of Lower Pleistocene age. (From Stamp, 1922.)

Correlation of the Mammal Bearing Horizons of Northern Burma

Pondaung Fauna

It is pretty generally agreed that the beds containing the Pondaung fauna are of Middle to Upper Eocene age. This was the opinion of Pilgrim and Cotter in their original description of the Pondaung vertebrate fauna in 1916, and subsequent authors have for the most part accepted this correlation as the correct one. Pilgrim and Cotter made the following remarks in their original description of the Pondaung fauna.

. . . The Yaw stage and the bone-bearing beds of the Pondaungs come within the uppermost 5,000 ft. of the series; therefore it is probable in so rapidly deposited a series, that the Pondaungs are not very much older than the overlying Yaws, and that if the latter are Ludian in terms of European nomenclature, the former are not probably older than Bartonian, while if the latter are Bartonian, the former would be not older than Auversian. We are not at present prepared to say with what exact European sub-stage the Yaw clays correspond, but believe them to correspond with some part of the Upper Eocene, that is the Auversian, Bartonian and Ludian stages. (Pilgrim, G. E., and Cotter, G. de P., 1916, p. 47.)

In 1925, Pilgrim, in his discussion of the Eocene Perissodactyla of Burma, made the following remarks concerning the age of the Pondaung fauna.

The affinities of the species now described provide additional evidence of the Bartonian or Ludian age of the deposits, while the indications favour a correlation with the earlier rather than with the later portion of this period. At the same time, I would suggest that the older affinities of many of the species are explainable on the hypothesis that they represent an independent local, but parallel, evolution from the Middle or even Lower Eocene migrants from the Holarctic region. (Pilgrim, G. E., 1925, p. 1.)

And again, in 1928, in his discussion of the Eocene Artiodactyla of Burma, this same author made some additional observations as to the age of the Pondaung fauna.

The Pondaung Anthracotheroids now appear to be certainly more primitive than those of the Lower Oligocene beds of Egypt, while on the other hand they are more progressive than the *Helohyidae* of the Bridger Eocene of North America or of the Irdin Manha formation of Mongolia, which are regarded as Middle Eocene. [The Irdin Manha formation was placed by Matthew in the Middle or Upper Eocene as a correlative of the Pondaung beds. See Matthew, W. D., 1924, Amer. Mus. Novitates, No. 105, p. 7.—E. H. C.] This affords strong confirmatory evidence of the Upper Eocene age of the Pondaung fauna which Cotter maintained from stratigraphical considerations connected with his study of the invertebrate fauna of the overlying Yaw series. That they are at least as old as the Bartonian is rendered likely by the fact that the smaller forms referred to *Anthracokeryx* seem in some ways to be more primitive than the oldest European Anthracotheres of the type of *Haplobunodon* and *Lophiobunodon*, which have been regarded as Upper Lutetian. The question hinges largely on where the original centre of differentiation of the group lay, and its solution will probably be afforded by further discoveries in Central Asia. (Pilgrim, G. E., 1928, p. 1.)

L. Dudley Stamp, in 1922, placed the Pondaung sandstone as definitely older than the Bartonian of Europe (with which stage he correlated the Yaw) but younger than the Lutetian. It might be inferred that he correlated the Pondaung more or less approximately with the Auversian of Europe. His correlations were made in tabular form, and the manner in which he expressed the position of the Pondaung sandstone is shown below.

Burmese Gulf	N. W. Europe	N. W. India
	Bartonian	
Yaw Stage	Ledian	
Pondaung Sandstone		Kirthar
	Lutetian	
Tabyin Clays		

To facilitate this discussion of the correlation of the Pondaung formation, a list of the Pondaung mammalian genera is presented at this point. Complete faunal lists are given on a subsequent page (page 280).

The Pondaung genera will be compared with various mammalian faunas from Mongolia, Africa, Europe and North America, in an attempt to determine their probable age relationships.

Genera of Pondaung Mammals

Primates	Perissodactyla	Artiodactyla
Incertae Sedis	Titanotherioidea	Anthracotherioidea
Pondaungia	*Sivatitanops*	*Anthracohyus*
Anthropoidea	*Metatelmatherium*	*Anthracothema*
Amphipithecus	Rhinocerotoidea	*Anthracokeryx*
	Paramynodon	Traguloidea
	Tapiroidea	*Indomeryx*
	Indolophus	
	Deperetella	

Three Eocene horizons are recognizable in Mongolia, namely the Arshanto of approximately middle Eocene age, the Irdin Manha (of which the Ulan Shireh, the Tukhum and the Kholobolchi are equivalents) above it and the Shara Murun at the top of the series. Above the Shara Murun formation is the Ardyn Obo formation of lower Oligocene age.

Comparing the Pondaung fauna with the faunas of the above named formations, it is to be noted, first of all, that the Burma horizon is distinguished by the presence of Primates, of which there are none in Mongolia. Conversely, there are no creodonts known from the Pondaung horizon, while these forms are well developed along various lines of adaptive radiation in Mongolia. These differences between the two regions cannot be taken too seriously, for it is very probable that they are due to the accidents of collecting. It is possible, however, that the absence of the Primates in Mongolia is real—that these animals originated in more southerly regions and that in Eocene times they had not extended their range sufficiently to reach central Asia.

The titanotheres of the Pondaung beds are closely comparable to those of the Irdin Manha formation. Thus *Sivatitanops* is in many ways comparable to one of the titanotheres from the Ulan Shireh beds, while there would seem to be a true genetic identity between the supposed *Metatelmatherium* of the Pondaung horizon and *Metatelmatherium* of the Irdin Manha.

On the other hand, the amynodont rhinoceros *Paramynodon* of the Pondaung beds is considerably more advanced than *Amynodon mongoliensis* of the upper Eocene Shara Murun formation. In fact, the Burma genus approaches closely the Oligocene forms, such as *Metamynodon.*

Coming to the tapirs it is interesting to see that one of the two Pondaung genera shows close affinities to certain Irdin Manha and Shara Murun forms. Thus *Chasmotherium* (?) *birmanicum* is comparable in its stage of development to *Deperetella* of the Shara Murun, and to a lesser degree to *Teleolophus* of the Irdin Manha. This Burma tapir would seem to be somewhat later than the Irdin Manha form and about equivalent to or perhaps slightly earlier than the Shara Murun genus.

Considering now the artiodactyls, it is to be seen that the Pondaung anthracotheres are more advanced than any comparable forms, such as *Gobiohyus* in the Eocene Irdin Manha of Mongolia. It might be added parenthetically at this point that the Pondaung anthracotheres are nevertheless not as highly developed as the lower Oligocene forms of the Fayûm region in Egypt, so that they would therefore seem to be of definite Eocene affinities.

Indomeryx, the little traguloid from the Pondaung beds is seemingly more advanced than the primitive pecoran, *Archaeomeryx* of the Irdin Manha and the Shara Murun, but it is perhaps not so highly developed as *Lophiomeryx,* from the Ardyn Obo formation.

Analyzing these foregoing statements, it may be said that the mammals of the Pondaung formation are for the most part indicative of an uppermost Eocene age for these beds. *Paramynodon, Deperetella* (?) *birmanicum,* the anthracotheres[1] and *Indomeryx* are progressive forms that tend to place the Pondaung at least as high in the Eocene as the Shara Murun formation. (In fact, *Paramynodon* might be considered as an exceptionally highly developed genus, more advanced than the comparable *Amynodon mongoliensis* of the Shara Murun, and therefore indicative of the fact that the Pondaung beds are even later in age than the Shara Murun formation.) *Indolophus, Sivatitanops* and *Metatelmatherium* are the more conservative elements of the Pondaung fauna, and their affinities would seem to be, generally considered, with the com-

[1] Progressive as compared with other Eocene artiodactyls. But these are primitive anthracotheres.

parable genera of the Irdin Manha formation. But conservative elements in a fauna have a way of persisting to periods beyond the time of their typical expression, and for this reason the more progressive forms, particularly migrants into the region from an outside source, are usually the most accurate guides to the correct age of a fauna.

Therefore it would seem plausible to think that the Pondaung fauna is approximately equivalent to the Shara Murun fauna, and slightly more advanced in certain respects than is the Irdin Manha fauna. Consequently the age of the Pondaung beds would be uppermost Eocene, just preceding the transition from Eocene to Oligocene times.

The age relationships of the Pondaung formations in comparison with the several Mongolian horizons is represented in the following graphic manner.

	Burma		Mongolia
Oligocene			Ardyn Obo
Eocene		Yaw	
	Pondaung		Shara Murun
			Irdin Manha—Ulan Shireh—Tukhum—Kholobolchi
			Arshanto

[The marine Yaw beds, overlying the Pondaung formation, are also of upper Eocene age. As Pilgrim has shown, these various horizons in Burma were probably deposited at a relatively rapid rate, so it is probable that the Yaw beds are not much later than are the Pondaungs.]

A direct general comparison of the Pondaung fauna with the fauna of the fluvio-marine series of Fayûm is difficult, because there are so few mammalian orders common to both assemblages. Consequently it is necessary to base the comparison between these faunas on two groups of mammals, namely the primates and the anthracotheres.

The Fayûm primates show various stages of development and specialization, so that each genus must be considered more or less by itself. Thus it may be said that *Propliopithecus* is perhaps somewhat more advanced on the anthropoid line of development than is the Burmese *Amphipithecus,* while *Parapithecus* of the Fayûm is perhaps less advanced, at least in some particulars, than is the form from the Pondaung beds. On the other hand, both *Parapithecus* and *Amphipithecus* show definite specializations along certain lines of their own, and this is particularly true of the latter genus. *Moeripithecus* of the Fayûm is perhaps more or less comparable to the Pondaung form, *Pondaungia,* although this is a point that must of necessity be rather obscure, because of the fragmentary nature of the specimens comprising the Burmese form.

As for the anthracotheres, the situation is reversed, for it is in the Pondaung fauna that there is a great variety of genera and species in different stages of development. On the whole, it might be said that the Fayûm anthracotheres are perhaps slightly more advanced than are the Pondaung genera, particularly in the somewhat higher specializations of their premolar teeth.

Therefore it would seem to be evident that the fluvio-marine beds of the Fayûm series are perhaps a little later in age than are the Pondaung beds. This conclusion is probably borne out in an indirect way by an evaluation of various other advanced types in the Fayûm beds, such as the creodonts (*Pterodon*), the proboscideans (*Palaeomastodon* and *Phiomia*) and the embrithopods (*Arsinoitherium*), which would seem to point to a stage of development of the Fayûm fauna beyond that of the Pondaung fauna, in which the advanced types are *Paramynodon* and *Indomeryx*.

Continuing this comparison of the Pondaung fauna for the sake of broad, interregional correlation, we may consider briefly its affinities to related elements in the early faunas of Europe. A comparison of the primates is difficult, because the early European forms are lemuroids, not directly comparable with the primitive anthropoids of the Pondaung beds. As it has been shown above, the closest correlations in this case are to be found with the early anthropoids of the Fayûm deposits of Egypt.

Paramynodon is certainly a more primitive form than the European *Cadurcotherium*, which is an Oligocene genus.

Pilgrim has provisionally referred the tapiroid mandible from the Pondaung beds to the European genus *Chasmotherium*. Whether the Pondaung form should be placed in this genus is a question open to debate, but at least its affinities would seem to lie in this direction. *Chasmotherium* (in the strict sense) occurs as low as the middle Eocene in Europe. The other Pondaung tapir, *Indolophus*, is more nearly related to certain North American forms and therefore will be considered subsequently.

The Pondaung anthracotheres are more primitive in most respects than the upper Eocene genera of Europe, particularly such forms as *Haplobunodon*, *Rhagatherium* and the like, a point that has been stressed by Pilgrim. And they are certainly much more primitive than the European Oligocene genera, *Anthracotherium*, *Brachyodus* and *Ancodus*. Here again the argument is in favor of an upper Eocene age for the Pondaung beds. It should be noted, however, that although the Pondaung anthracotheres are structurally more primitive than certain of the European Eocene forms, noted above, they are probably later in age than these European genera. This interpretation is borne out by the stage of development of other forms such as *Paramynodon*, *Indomeryx* and the primates. Evidently, therefore, the Pondaung anthracotheres are persistently conservative genera.

Comparing *Indomeryx* with related genera of Europe, we see that it is perhaps most closely comparable to *Gelocus*, a genus of upper Eocene and Oligocene age. As was mentioned in a preceding paragraph, *Indomeryx*, since it is one of the progressive elements in the Pondaung fauna, is probably a fairly accurate indicator of the age of the beds. And the evidence of this genus, taken in conjunction with that of other progressive forms in the Pondaung assemblage, would seem to indicate an uppermost Eocene age for the Pondaung mammal bearing beds.

Finally, we may consider the relationships of the Pondaung mammals to comparable forms in North America, to see how such a comparison affects the foregoing conclusions regarding the age of the Pondaung fauna. No comparison of the Pondaung primates is possible, since the primates of North America are of an earlier age and of lemuroid and tarsioid, rather than of anthropoid affinities.

The Pondaung titanotheres are closely comparable to the titanotheres of the Uinta beds. Thus *Sivatitanops* may be compared with *Dolichorhinus* of the Uinta, while the supposed *Metatelmatherium* of the Pondaung is seemingly closely allied to but somewhat more progressive than the same genus in the Utah beds. On this score the Pondaung horizon is comparable in age to the uppermost Uinta of North America.

It is an interesting fact that *Paramynodon* is distinctly more advanced than any of the several species of Uinta amynodonts, but decidedly less progressive than the Oligocene *Metamynodon* of North America. Therefore this evidence might indicate that the Pondaung beds are slightly later in age than are the uppermost Uinta, but somewhat earlier than the lower Oligocene of North America.

Indolophus is closely comparable to some of the Eocene tapiroids of North America, particularly to *Parisectolophus* of the Bridger beds and to *Isectolophus* of the Uinta formation.

It is only necessary to state that the Pondaung anthracotheres, as might be expected, are more primitive than any of the American forms, which latter are of Oligocene age.

Indomeryx is comparable in many ways to the Oligocene hypertragulids of North America, as exemplified by such genera as *Hypertragulus* and *Leptomeryx*, and also to the Uinta genus, *Leptotragulus*. Thus on the basis of *Indomeryx*, the age of the Pondaung fauna would seem to be uppermost Eocene, more or less correlative with the Uinta fauna, or possibly a little later than this North American assemblage.

To sum up the foregoing comparisons, it may be said that the Pondaung fauna contains a mixture of conservative and progressive forms, the former quite definitely of middle to upper Eocene relationships, the latter very much advanced toward Oligocene types. The conservative elements must be considered as persistent members of the fauna, and thus it is necessary to turn to the progressive species for a true evaluation of the age of the fauna. On this basis the Pondaung fauna may be considered as of uppermost Eocene age, approximately equivalent to the Shara Murun fauna of Mongolia and decidedly later than the Irdin Manha assemblage of that same region, somewhat more primitive than the fauna of the fluvio-marine beds of the Fayûm, more or less contemporaneous with the uppermost Eocene (Ludian) of Europe and equal to or possibly slightly later than the upper Uinta of North America.

Pegu Series

The Freshwater Pegu beds are very thick, and all evidence would seem to point to the fact that in their entirety they cover a considerable extent of geologic time. This is borne out by the few very fragmentary mammalian fossils that have been discovered in these beds. The two fragmentary molars of *Cadurcotherium*, which were discovered by Mr. Lister James, came from that part of the Pegu series immediately above the *Tritonoidea* beds. (See Stamp, L. D., 1922, Geol. Mag., LIX, p. 497, Fig. 3.) In 1910, Pilgrim regarded this discovery as indicating an Aquitanian age for the above named portion of the Pegu series, while this same conclusion was presented by Pilgrim and Cotter again in 1916. Certainly *Cadurcotherium* would seem to indicate a probable upper Oligocene age for the beds in which it was found.

In 1910, Pilgrim announced the discovery of an anthracothere from the Pegu series, which he designated as *Telmatodon* on the basis of its similarities to *Telmatodon bugtiensis* from the Gaj series of the Bugti Hills. The evidence would seem to be in favor of a probable Burdigalian or lower Miocene age for the beds in which this specimen was discovered, a point that has already been stressed by Pilgrim.

Finally we may consider the few fragments of *Dorcatherium birmanicum* described by Noetling as "*Anoplotherium*" and coming from a level about 1200 feet below the top of the Pegu series. This species is certainly of Miocene affinities and it is probable that it is indicative of a middle or an upper Miocene age for the uppermost portion of the Pegu series.

Thus on the basis of the few scattered mammalian fossils that have been discovered to date in the Pegu series, these beds are shown to range from the Oligocene through the upper Miocene.

Lower Irrawaddy Fauna

Unlike the Pondaung fauna, the fossils from the Irrawaddy series have been intermittently discovered and described over a period of more than a hundred years. Consequently they have been subjected to the critical examinations of various authors, who have differed from each other as to the age of these fossils. The first specimens discovered in Burma by Crawfurd came from the banks of the Irrawaddy River and undoubtedly were high in the series. It was not until many years later that fossils from the lower portion of the Irrawaddy beds were found. Even then the relationships of the specimens from the two faunal levels of the Irrawaddy series were not always clear, and as late as 1910 Dr. Pilgrim included certain Upper Irrawaddy species in his list of the Lower Irrawaddy fauna.[1]

A very clear statement as to the relationships of the Irrawaddy faunas was presented by Stamp in 1922. Some of his remarks are quoted below.

> . . . The series has also yielded a number of interesting vertebrate remains, notably near Yenangyaung. Specimens from this locality come from two distinct horizons:
>
> (*a*) Lowest beds containing *Hipparion punjabiense* Lyd. (*Hippotherium antelopinum* of Noetling and earlier writers), *Aceratherium lydekkeri* Pilg. (*A. perimense* of Noetling), crocodilian and chelonian remains. At this lower horizon *Mastodon* and *Hippopotamus* seem to be rare or absent, no undoubted occurrence being known to the writer.
>
> (*b*) A conglomeratic band some 4500 feet higher in the series and exposed along the banks of the Irrawaddy between Yenangyaung and Nyaunghla yielding numerous *Mastodon latidens*, *Stegodon clifti*, and *Hippopotamus iravaticus*.

Continuing, Stamp says that:

> The lower horizon, that is the base of the Irrawadian at Yenangyaung, may be correlated with the Dhok Pathan horizon (Upper Pontian), or, since *Mastodon* and *Hippopotamus* both seem to be absent, possibly with the Nagri horizon (Lower Pontian) of North-Western India. In any case, *Aceratherium* indicates a pre-Pliocene age. (Stamp, L. D., 1922, pp. 497–498.)

[1] Pilgrim, G. E., 1910*b*, Rec. Geol. Surv. India, XL, p. 196.

In a recent publication the present author, following the lead of Matthew (1929), has attempted to show that the Dhok Pathan fauna of the Siwaliks is probably of post-Pontian age.[1] The evidence of this conclusion need not be presented here since it has been fully outlined in the publications cited. Suffice it to say that the presence of *Hipparion* in the Chinji zone of the Lower Siwaliks, in conjunction with other evidence, would seem to point to the fact that this horizon may be correlated with the Pontian or at the earliest with the Sarmatian of Eurasia. Consequently, the Dhok Pathan must be of post-Pontian age, and there is much reason to believe that it comes well up toward the middle portion of the Pliocene.

Therefore, the Lower Irrawaddy beds, being closely correlative with the Dhok Pathan zone of India, may be regarded as probably of post-Pontian age. Of course there is the possibility that the Lower Irrawaddies may be older than the Dhok Pathan beds, and therefore conceivably of Pontian age, but the evidence is strongly against this conclusion. The very close correspondence between the faunas of the Lower Irrawaddy beds and the Dhok Pathan (particularly as regards *Hipparion*, *Aceratherium* and *Hydaspitherium*) together with the probable geographic connection of India with Burma during Pliocene times, makes it very likely that the Lower Irrawaddy fauna is strictly correlative with the Dhok Pathan fauna, and therefore of post-Pontian, Pliocene age.

Upper Irrawaddy Fauna

Stamp's definition of the zone in which this fauna occurs has been given in a preceding paragraph. In discussing the age of the fauna he says that:

> . . . The higher horizon agrees faunally with the Tantrot [*sic.*] horizon (Lower Pliocene) of North-Western India. The presence of later Pliocene deposits amongst the Irrawaddian is indicated by the presence of *Boselaphus* and *Bos* further north in latitude 22° 3′. (Stamp, L. D., 1922, p. 498.)

As to the Upper Irrawaddy fauna, there seem to be many reasons for considering it as of lower Pleistocene affinities, not of lower Pliocene age as stated by Stamp. In the publications of the present author, cited above, it has been shown that the Pinjor zone of the Upper Siwalik beds of India is quite definitely of lower Pleistocene age, while it is indicated that the Tatrot zone may be more or less transitional between the Pinjor and the Pliocene Dhok Pathan beds. In a recent publication de Terra

[1] Colbert, E. H., 1935, Trans. Amer. Phil. Soc., XXVI, pp. 21–26. See also: Colbert, E. H., 1935, Amer. Mus. Novitates, No. 797.

and Teilhard de Chardin[1] have come to the conclusion that the Tatrot and Pinjor zones are essentially an individual unit, distinctly separated by an erosion interval from the underlying Dhok Pathan formation. More recently Lewis[2] has come to the conclusion that the Tatrot and Pinjor are even more closely related to each other than was indicated by de Terra and Teilhard. In both of these papers the Tatrot, on the basis of new field evidence, is placed definitely in the lower Pleistocene.

Whether the Tatrot and Pinjor zones are separate or correlative, the evidence would seem to favor the inclusion of both of them in the lower Pleistocene. And the entire complexion of the Upper Irrawaddy fauna would make it undoubtedly of lower Pleistocene age, closely comparable to these Indian horizons. *Rhinoceros*, *Tetraconodon*, *Hexaprotodon*, *Stegodon* and *Stegolophodon* are all definite lower Pleistocene forms in the Upper Irrawaddy fauna. In the present work the Upper Irrawaddy fauna is therefore considered as of lower Pleistocene age.

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[1] de Terra, H., and Teilhard de Chardin, P., 1936, Proc. Amer. Philos. Soc., LXXVI, No. 6, pp. 791–822.

[2] Lewis, G. E., 1937, Amer. Jour. Sci., XXXIII, pp. 191–204.

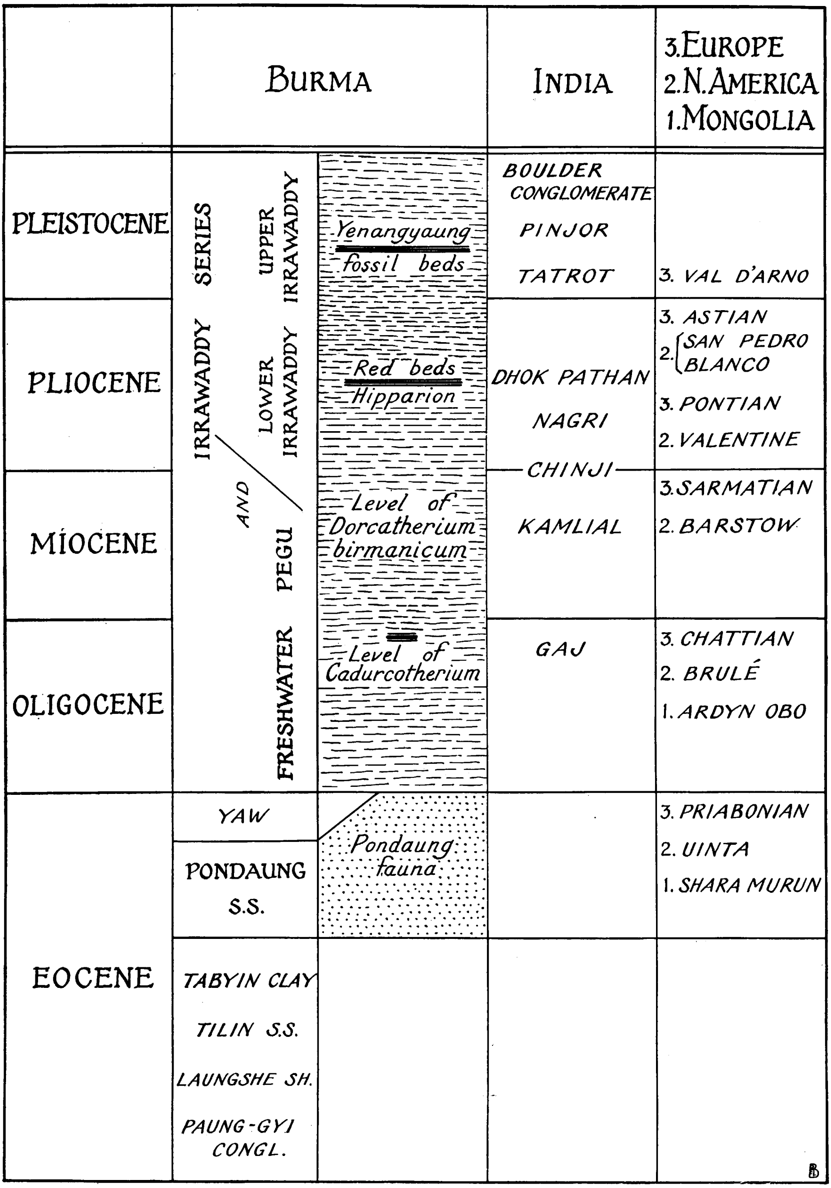


Fig. 5. Correlation of the Cenozoic mammal bearing horizons of Burma.

THE FOSSIL MAMMAL FAUNAS OF BURMA

Pondaung Fauna

Primates
- Pongidae (?)
  - *Pondaungia cotteri* Pilgrim, 1927
  - *Amphipithecus mogaungensis* Colbert, 1937

Perissodactyla
- Titanotheriidae
  - *Sivatitanops cotteri* Pilgrim, 1925
  - *Sivatitanops birmanicum* (Pilgrim and Cotter, 1916)
  - *Sivatitanops* (?) *rugosidens* Pilgrim, 1925
  - *Metatelmatherium* (?) *browni*, new species
  - *Metatelmatherium* (?) *lahirii* (Pilgrim, 1925)
- Amynodontidae
  - *Paramynodon birmanicus* (Pilgrim and Cotter, 1916)
  - *Paramynodon cotteri* (Pilgrim, 1925)
- Tapiridae
  - *Indolophus guptai* Pilgrim, 1925
  - *Deperetella* (?) *birmanicum* (Pilgrim, 1925)

Artiodactyla
- Anthracotheriidae
  - *Anthracohyus choeroides* Pilgrim and Cotter, 1916
  - *Anthracothema pangan* (Pilgrim and Cotter, 1916)
  - *Anthracothema crassum* (Pilgrim and Cotter, 1916)
  - *Anthracothema palustre* (Pilgrim and Cotter, 1916)
  - *Anthracothema rubricae* (Pilgrim and Cotter, 1916)
  - *Anthracokeryx birmanicus* Pilgrim and Cotter, 1916
  - *Anthracokeryx ulnifer* Pilgrim, 1928
  - *Anthracokeryx tenuis* Pilgrim and Cotter, 1916
  - *Anthracokeryx hospes* Pilgrim, 1928
  - *Anthracokeryx myaingensis* Pilgrim, 1928
  - *Anthracokeryx bambusae* Pilgrim, 1928
  - *Anthracokeryx moriturus* Pilgrim, 1928
  - *Anthracokeryx* (?) *lahirii* Pilgrim, 1928
- Tragulidae (?)
  - *Indomeryx cotteri* Pilgrim, 1928
  - *Indomeryx arenae* Pilgrim, 1928

Mammals from the Pegu Series

Perissodactyla
- Amynodontidae
  - *Cadurcotherium* sp.

Artiodactyla
- Anthracotheriidae

Telmatodon sp.
Tragulidae
Dorcatherium birmanicum (Noetling, 1901)

Lower Irrawaddy Fauna

Perissodactyla
Equidae
Hipparion antelopinum (Falconer and Cautley, 1849)
Rhinocerotidae
Aceratherium lydekkeri Pilgrim, 1910
Artiodactyla
Suidae
Tetraconodon minor Pilgrim, 1910
Giraffidae
Hydaspitherium birmanicum Pilgrim, 1910
Vishnutherium iravaticum Lydekker, 1876
Bovidae
Pachyportax latidens (Lydekker, 1876)
Proleptobos birmanicus Pilgrim, 1910 [*nomen nudum*]

Upper Irrawaddy Fauna

Proboscidea
Stegodontidae
Stegolophodon latidens (Clift, 1828)
Stegodon elephantoides (Clift, 1828)
Stegodon insignis birmanicus Osborn, 1929
Elephantidae
Hypselephas hysudricus (Falconer and Cautley, 1846)

Perissodactyla
Rhinocerotidae
Rhinoceros sivalensis Falconer and Cautley, 1847

Artiodactyla
Anthracotheriidae
Merycopotamus dissimilis (Falconer and Cautley, 1836)
Hippopotamidae
Hexaprotodon iravaticus Falconer and Cautley, 1847
Hexaprotodon cf. *sivalensis* Falconer and Cautley, 1847
Bovidae
Bovids

Post-Irrawaddy Fossils

Carnivora
Procyonidae
Aelureidopus baconi Woodward, 1915

Explanation of Maps and Locality Lists

On the following pages are given a series of maps, showing the various localities at which the Burma fossil mammals in the American Museum collection were collected. The general map showing the area between Yenangyaung and Mandalay and adjacent regions to the west (Fig. 6) has indicated on it several rectangles which show the locations of the detailed maps (Figs. 8 to 12), and a very large rectangle showing the posi-

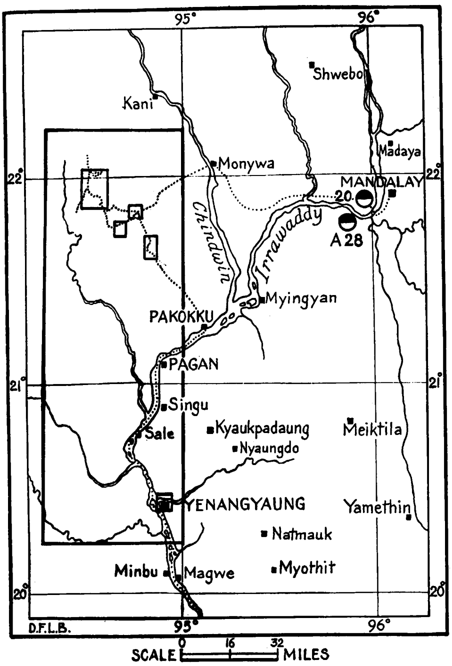


Fig. 6. Map of Burma in the region of Yenangyaung and Mandalay, showing the location of the area included in the key map (Fig. 7) and the locations of the five detailed maps (Figs. 8 to 12). Collecting localities 20 and A28, near Mandalay, are also shown. Route of the expedition indicated by dotted lines. Scale, one inch equals sixty-four miles.

tion of the detailed key map (Fig. 7). On this general map are shown also collecting localities 20 and A28, near Mandalay, since there are no detailed maps to include these localities.

The detailed key map (Fig. 7) gives additional information as to the location of the detailed maps, numbered I to V (Figs. 8 to 12). These

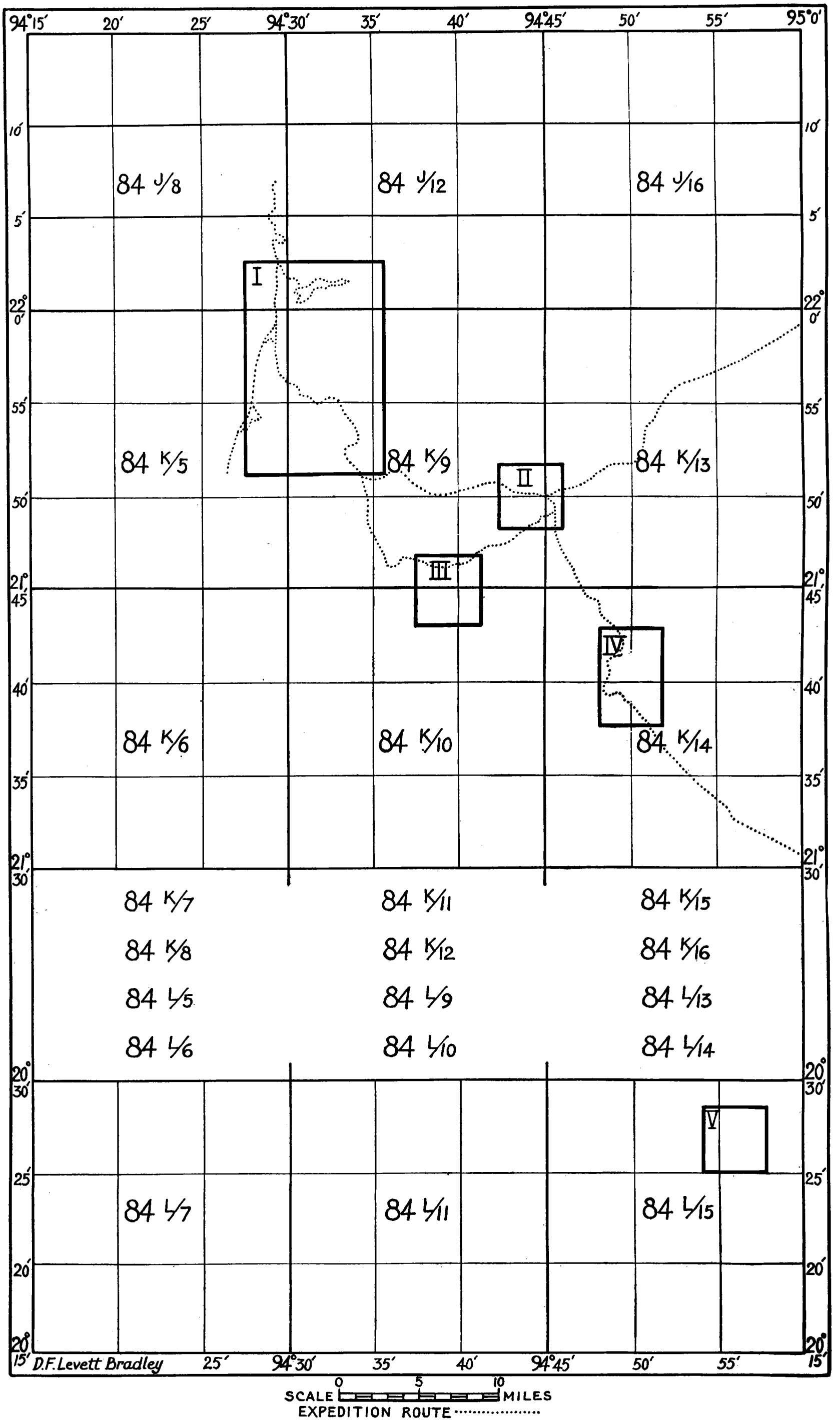


Fig. 7. Key map, showing the locations of the five detailed maps (Figs. 8 to 12) in relation to the published sheets of the Indian Geological Survey. Expedition route indicated by dotted lines. Scale, one inch equals twelve miles.

detailed maps need no explanation beyond the fact that they show the collecting localities, indicated by circles and numbers. Circles enclosing crosses designate localities at which Pondaung fossils were found. Circles of which the lower half is colored black designate Lower Irrawaddy localities, while circles with the upper half colored black indicate Upper Irrawaddy localities. Crosses without circles or numbers accompanying them indicate localities where fragmentary fossils, too poorly preserved to warrant their saving or numbering, were found.

The locality lists preceding the maps give the field localities in order, their horizons and the numbers and identifications of the fossils found at each of them. Thus these lists present a résumé of the collection according to its field relationships.

List of American Museum Burma Fossil Localities

Field Number	Level	Locality	Map	Museum Number	Identification
1	Upper Irrawaddy 4000 ft. a.b. (above base)	River below B.B.P. Post-office, Yenangyaung	V	20037	*Hexaprotodon iravaticus*
2	Upper Irrawaddy 4000 ft. a.b.	River below B.B.P. Post-office, Yenangyaung	V	20040	*Rhinoceros sivalensis*
3	Upper Irrawaddy 4000 ft. a.b.	River below B.B.P. Post-office, Yenangyaung	V	20038	*Hexaprotodon iravaticus*
4	Upper Irrawaddy 4500 ft. a.b.	River below B.B.P. Post-office, Yenangyaung	V	20036	Bovid
5	Upper Irrawaddy 4500 ft. a.b.	River below B.B.P. Post-office, Yenangyaung	V	20039	*Stegodon elephantoides*
6	Lower Irrawaddy	Beme Dome, 1/2 mi. S.E. Yenangyaung	V	20035	*Hipparion*
7	Pondaung	1 1/2 mi. N.W. Myaing	IV	20020	Titanothere
				32524	*Anthracothema pangan*
				32532	*Paramynodon birmanicus*
8	Pondaung	Near Than-u-daw	IV	20042	*Paramynodon birmanicus*
	Upper Irrawaddy			20005	*Hypselephas hysudricus*

9	Upper Irrawaddy	3 mi. W. Chaungsongyi	II	20001	*Stegodon insignis birmanicus*
10	Pondaung	1 mi. W. Bahin	III	20017	*Anthracokeryx ulnifer*
11	Pondaung	1 mi. W. Bahin	III	20013	*Paramynodon birmanicus*
				20015	*Anthracokeryx birmanicus*
				32536	*Paramynodon birmanicus*
12	Pondaung	1 mi. W. (Myaing?)	IV	20021	*Paramynodon birmanicus*
13	Pondaung	3 mi. E. Gyat	I	20012	*Paramynodon birmanicus*
14	Pondaung	1 mi. N.W. Mogaung	I	20014	*Sivatitanops cotteri*
				20028	*Anthracothema* sp.
				32533	*Paramynodon birmanicus*
15	Pondaung	1 mi. N.W. Mogaung		20029	*Anthracothema rubricae*
				20030	*Paramynodon birmanicus*
16	Pondaung	2 mi. N.W. Mogaung	I	20011	*Anthracokeryx moriturus*
17	Pondaung	1/2 mi. N.W. Mogaung	I	20023	*Indomeryx cotteri*
				20026	*Paramynodon birmanicus*
				32520	*Amphipithecus mogaungensis*
				32529	*Paramynodon birmanicus*
	Upper Irrawaddy			20007	Bovid
18	Pondaung	1 mi. N.W. Mogaung	I	20022	*Metatelmatherium* (?) *browni*
19	Pondaung	2 mi. N.W. Mogaung	II	20034	*Paramynodon birmanicus*
20	Upper Irrawaddy	Mingun, opp. Mandalay		20002	*Stegodon insignis birmanicus*
				20003	Bovids
A21	Pondaung	1 mi. N. Koniwa	I	20009	Titanothere
				20010	*Paramynodon birmanicus*
				32521	*Indomeryx cotteri*
				32522	*Anthracothema* sp.
				32523	*Anthracothema pangan*(?)
				32525	*Anthracothema rubricae*
				32541	*Paramynodon birmanicus*
				32542	Titanothere
A22	Pondaung	1/2 mi. W. Mogaung	I	20004	*Paramynodon birmanicus*
A23	Pondaung	1 mi. N.E. Gyat	I	20006	*Anthracothema pangan*

				20016	*Metatelmatherium* (?) *browni*
				32528	Titanothere
A24	Pondaung	2 mi. N.E. Gyat	I	20008	*Metatelmatherium* (?) *browni*
A25	Pondaung	1 mi. W. Gyat	I	20018	*Paramynodon birmanicus*
A26	Pondaung	Near Kyawdaw	I	20024	*Anthracothema* sp.
				20025	*Paramynodon birmanicus*
A27	Pondaung	1/2 mi. N.E. Kyawdaw	I	20027	*Anthracothema rubricae*
				20031	*Anthracokeryx* sp.
				20032	*Paramynodon birmanicus*
				32540	Titanothere
A28	Upper Irrawaddy	16 mi. below Mandalay		20041	*Hexaprotodon* sp.
A29	Pondaung	1 mi. N. Myaing	IV	32535	*Paramynodon birmanicus*
A30	Pondaung	1 mi. W. Zeit-taung	I	32527	Titanothere
A31	Pondaung	Near Legan	I	32530	*Paramynodon birmanicus*
A32	Pondaung	1 mi. W. Myaing	IV	32539	*Paramynodon birmanicus*
A33	Pondaung	2 mi. W. Myaing	IV	32531	*Paramynodon birmanicus*
A34	Pondaung	2 mi. E. Edgbaw		20033	*Paramynodon birmanicus*
				32537	*Paramynodon birmanicus*
				32538	*Paramynodon birmanicus*
A35	Upper Irrawaddy	1 mi. S. Yegyaw	I	20019	*Stegolophodon latidens*

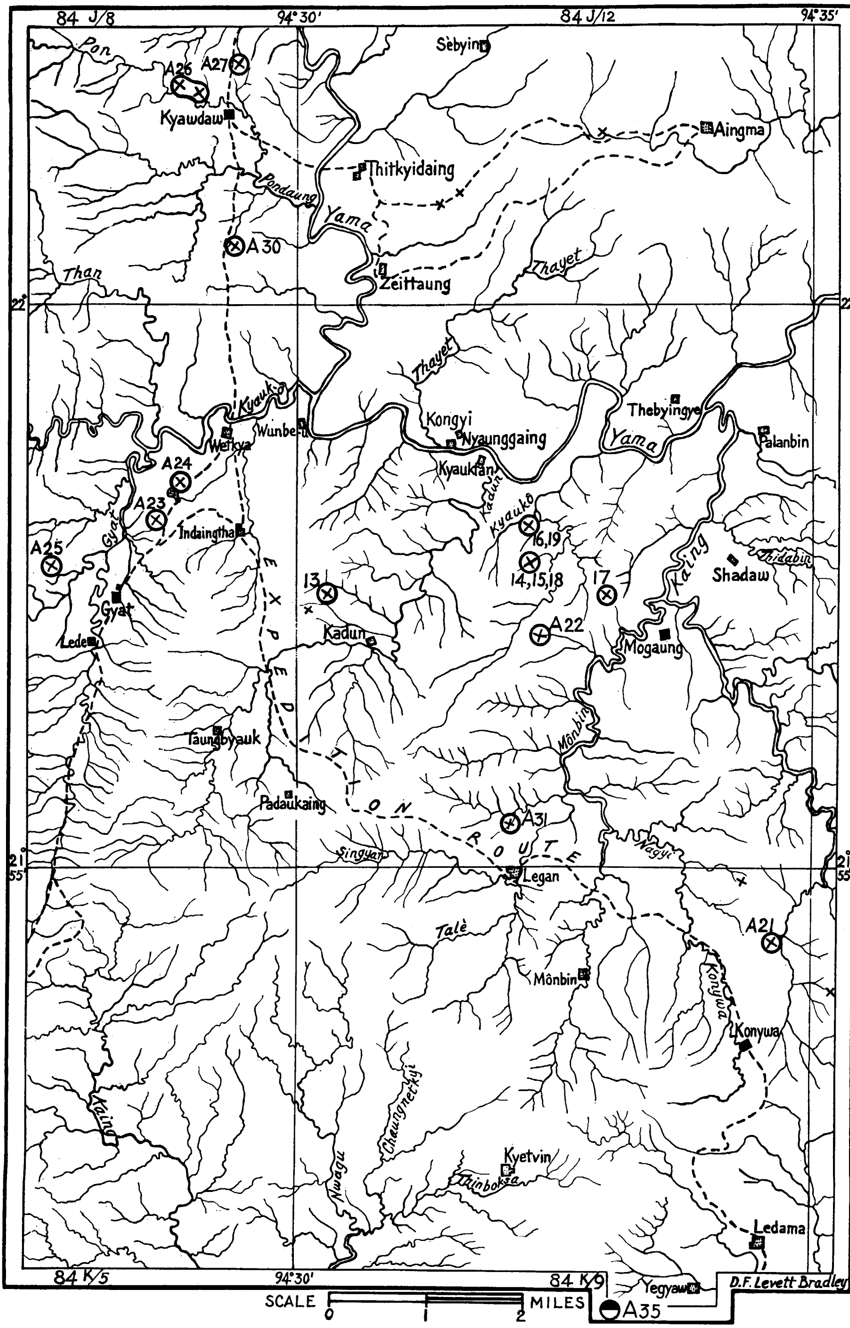


Fig. 8. Map I showing the collecting localities in the Pondaung beds near Gyat, Kyawdaw, Mogaung and Konywa. Scale, one inch equals two miles.

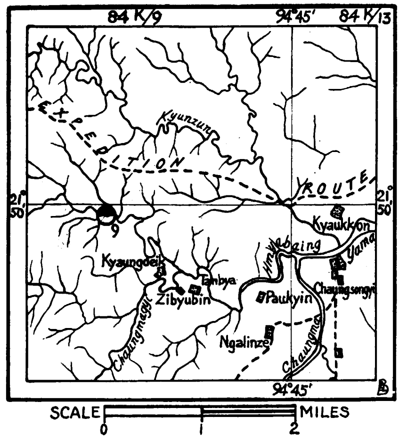


Fig. 9

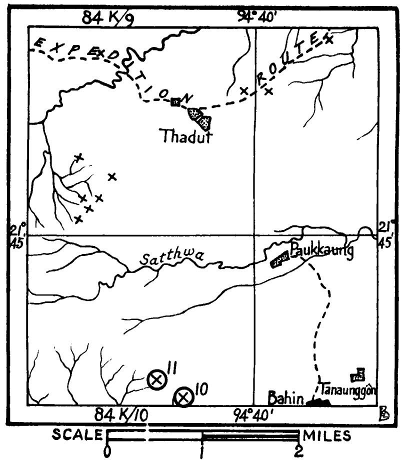


Fig. 10

Fig. 9. Map II showing the collecting locality in the Upper Irrawaddy beds west of Chaungsongyi. Scale, one inch equals two miles.

Fig. 10. Map III showing the collecting localities in the Pondaung beds near Bahin. Scale, one inch equals two miles.

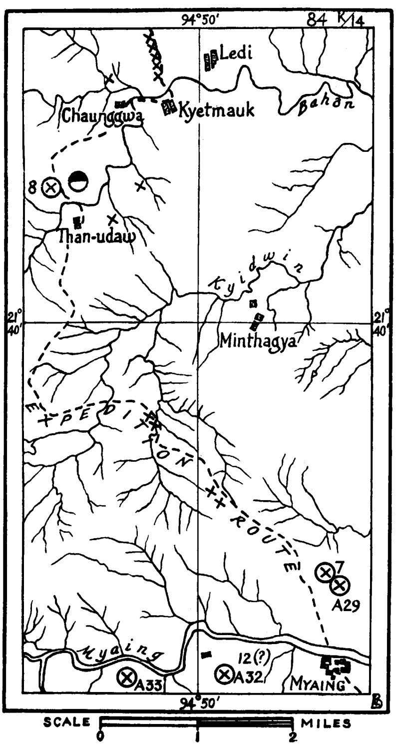


Fig. 11

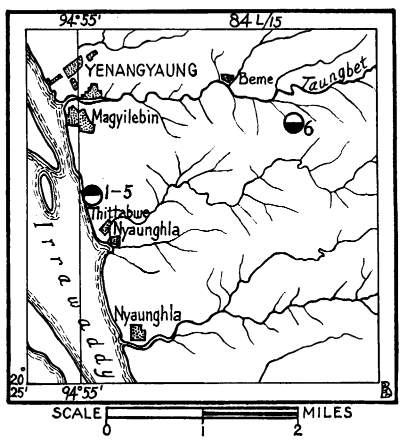


Fig. 12

Fig. 11. Map IV showing the collecting localities in the Pondaung beds near Than-udaw. Scale, one inch equals two miles.

Fig. 12. Map V showing the collecting localities in the Upper Irrawaddy beds near Yenangyaung and in the Lower Irrawaddy beds near Beme. Scale, one inch equals two miles.

SYSTEMATIC DESCRIPTIONS AND DISCUSSIONS

A.—THE PONDAUNG FAUNA

PRIMATES

Our knowledge of the fossil primates of Burma is at the present time based on some very fragmentary remains from the Pondaung beds. In 1927, Pilgrim described some teeth under the name of *Pondaungia*, indicating that they were probably of Primate affinities but that on the basis of the material in hand their relationships could not be definitely determined. At the present time the status of *Pondaungia* is essentially the same as it was when Pilgrim described it. The animal is very probably a Primate, and it may be of tarsioid or of anthropoid affinities. On the other hand, it may belong to one of two or three other orders of Eocene mammals.

In a somewhat different category is the new genus *Amphipithecus*, described by the present author in 1937. This form is undoubtedly a Primate, and the evidence would seem to be conclusive for regarding it as a primitive anthropoid. Thus it assumes a very important position in any discussion of the evolution of the Anthropoidea, and for this reason it will receive full consideration in the discussion that follows its systematic treatment.

ANTHROPOIDEA

Simiidae(?)

PONDAUNGIA PILGRIM 1927

PILGRIM, G. E., 1927, Mem. Geol. Surv. India, (N. S.) XIV, pp. 12–15, Pl., figs. 8–10.

GENERIC TYPE.—*Pondaungia cotteri* Pilgrim.

DIAGNOSIS.—The generic and specific diagnoses are the same, since this is a monotypical genus. See the specific diagnosis below.

Pondaungia cotteri Pilgrim

Pondaungia cotteri, PILGRIM, 1927, Mem. Geol. Surv. India, (N. S.) XIV, pp. 12–15, Pl., figs. 8–10.

TYPE.—G.S.I. No. D201–203, a fragment of the left maxilla containing two molars probably M^1 and M^2, a fragment of the left mandibular ramus containing M_2 and M_3 and a fragment of the right mandibular ramus containing M_3 only. (All belonging to the same individual.)

PARATYPES.—None.

HORIZON.—Pondaung, Upper Eocene.

LOCALITY.—$^1/_4$ mile W. of Pangan, Myaing township, Pakokku district, Burma.

DIAGNOSIS (Revised).—The upper molars are broader than they are long, quinquetubercular and quadrangular, with three roots. Paracone and metacone are separated from each other, the protocone and hypocone are connected; small hypoconule and internal cingulum present. The lower molars are quadrangular, except M_3, which has a rather long, narrow heel. The cusps are distinct from each other, and cingula are absent. Paraconid present on M_3, the trigonid slightly higher than the talonid.

If my interpretation of the structure of the teeth in *Pondaungia* is correct, and if it is really a Primate, then it must represent an earlier Anthropoid stage than *Propliopithecus*. If Gregory is right in regarding *Apidium* as an early Cercopithecoid, it is likely that these two phyla were distinct in the Upper Eocene, and their common ancestor must be sought in the Middle Eocene at any rate. . . . It seems, however, worthy of consideration whether *Pondaungia* does not partially fill the gap between the definitely Anthropoid *Propliopithecus* and some Lower or Middle Eocene Tarsioid. In any case *Pondaungia* by its size is recognizable as a terminal or almost terminal branch, not directly ancestral to *Propliopithecus*. This is the extent to which we are justified in going on the evidence of these interesting but fragmentary specimens, and confirmation of my views must await more perfect material of the genus. (Pilgrim, G. E., 1927, p. 15.)

AMPHIPITHECUS COLBERT, 1937

COLBERT, EDWIN H., 1937, American Museum Novitates, No. 951.

GENERIC TYPE.—*Amphipithecus mogaungensis* Colbert.

AUTHOR'S DIAGNOSIS.—Since the generic and specific diagnoses are the same, this being at present a monotypical genus, the author's diagnosis is presented below as the specific diagnosis.

Amphipithecus mogaungensis Colbert

Amphipithecus mogaungensis, COLBERT, 1937, Amer. Mus. Novitates, No. 951.

TYPE.—Amer. Mus. No. 32520, a left mandibular ramus with the roots of the canine and P_2, and P_{3-4}, M_1.

PARATYPES.—None.

HORIZON.—Pondaung, Eocene.

LOCALITY.—$^1/_2$ mile northwest of Mogaung, Burma. (Map, Fig. 8, locality 17.)

AUTHOR'S DIAGNOSIS.—A relatively small primate. Mandible very deep and heavy in comparison with the size of the cheek teeth, with a very short, vertical symphysis and a heavy lingual torus. There is a pronounced pit on the posterior surface of the symphysis for the genioglossus muscle. Mental foramen beneath the fourth premolar, and placed about midway between the alveolar and the ventral borders of the jaw.

Dental formula seemingly $\overline{?\text{–}1\text{–}3\text{–}3}$ Premolars very much compressed anteroposteriorly and transversely broad, due to the lingual extension of the postero-internal corner of each tooth. Crowns of premolars almost as high anteriorly and posteriorly as in the region of the central cone. Crown patterns very peculiar, consisting essentially of a central cone, from which run ridges anteriorly, posteriorly and internally, this last ridge joining at the postero-internal corner of the tooth with a posterior transverse ridge, to enclose a postero-internal fossa.

Molars brachyodont, with trigonid and talonid of subequal heights, narrower anteriorly than posteriorly. Protoconid and metaconid rather close together, hypoconid and entoconid farther apart and forming a part of a continuous rim around the well-developed talonid basin. Paraconid seemingly present but very small, hypoconulid incipient.

Roots of cheek teeth very long and vertical. P_4 with four roots, of which the antero-internal one is small. P_3 with three roots, there being no antero-internal root. P_2 with two roots, one internal and one external, but so fused as to form a single transverse root.

Canine root vertical, flattened, the internal surface being very flat and the external surface being rather convex. No appreciable diastema between canine and second premolar.

The generic and specific diagnoses are the same.

AUTHOR'S DESCRIPTION.—To reiterate in a detailed manner the information set forth in the foregoing diagnosis, the following description is presented.

As to size (on the basis of tooth dimensions), this new form is slightly larger than the Fayûm genus, *Propliopithecus*, and the American form, *Pelycodus*, and is more or less comparable to the bunodont artiodactyl, *Wasatchia*. It is at once distinguished, however, by its very heavy mandibular ramus and its short symphyseal region. The relationship between the depth of the ramus and the length of the first molar may be expressed in the following terms.

Length of M_1 = 6.3 mm. Depth of ramus = 19.5 mm.
Length of M_1/depth of ramus = 6.3/19.5 = 31/100

In other words, the depth of the mandibular ramus is about three times as great as the length of the first lower molar. The mandibular symphysis is heavy and vertical, and its posterior border is opposite the second premolar. The ramus is thick, due to the well-developed lingual torus. The mental foramen is surprisingly high and in a posterior position, being beneath the fourth premolar.

Unfortunately the anterior portion of the mandible is broken away, so that no information is to be had about the incisor teeth. However, the vertical position of the canine root renders impossible a very marked alveolar prognathism of the incisors, and as this jaw is possibly that of a higher primate (as will be shown below) it probably had not more nor less than two incisors on each side. It would seem certain that there was a well-developed canine, three premolars (following the canine without any appreciable diastema) and probably three molars. The jaw is broken behind the first molar, so that the last two teeth are missing.

Of the canine, only a basal portion, deep in the mandibular ramus is preserved. This fragment serves to give some information as to the position and the cross section of the root of this tooth. Evidently the canine root was flattened, with a very flat inner surface and a convex outer surface, and its long axis was placed obliquely to the dental arcade. The position of the canine root and the preserved portion of the alveolus shows that this tooth was vertical.

The premolars of this specimen are quite distinctive. They are characterized particularly by their rather high crowns and long roots, and by the peculiarity of their coronal surface patterns. Each premolar is very broad posteriorly and narrow

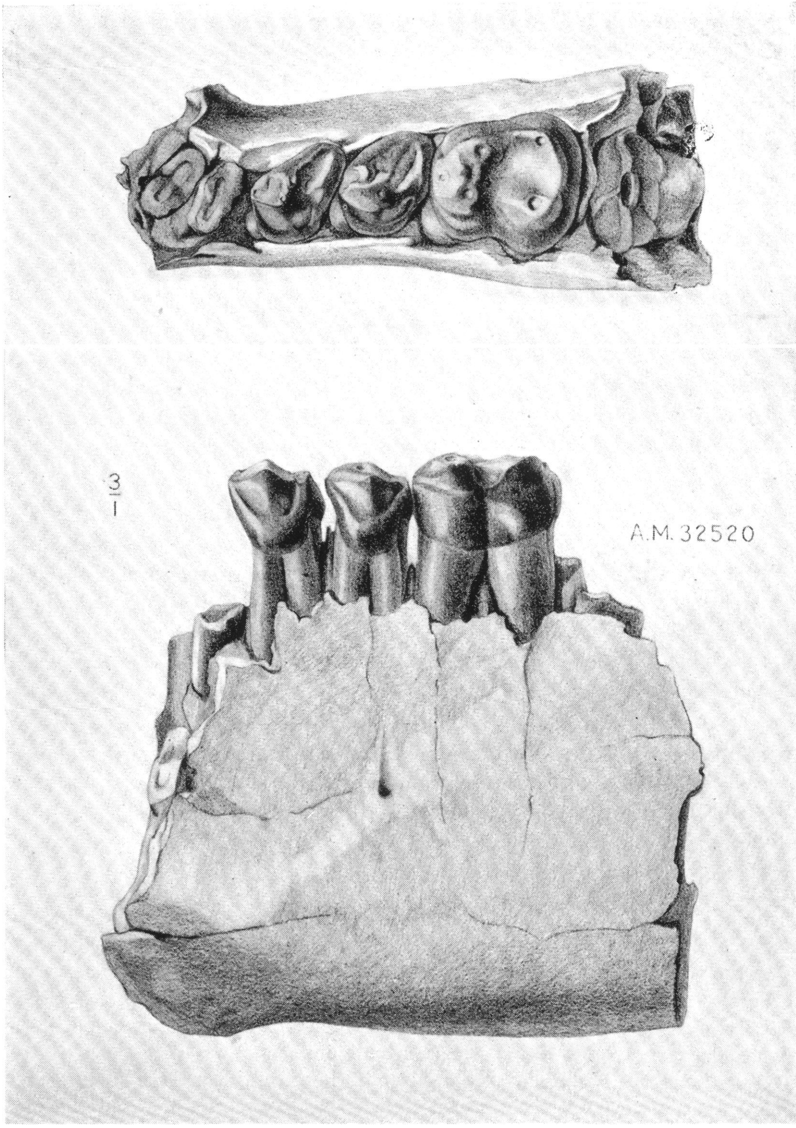


Fig. 13. *Amphipithecus mogaungensis* Colbert. Type, Amer. Mus. No. 32520, fragment of left mandibular ramus with roots of canine and P_2, and P_3–M_1. Crown view above, external lateral view below. Three times natural size.

anteriorly, and because of the short antero-posterior diameters of these teeth, this causes the postero-internal portion of each tooth to be extended lingually to a very considerable degree. Each tooth has a central cone, from which ridges extend anteriorly, posteriorly and internally. It is an interesting fact that the anterior and posterior ridges do not slope downward toward the base of the tooth to any appreciable degree, but instead they are almost as high as the central cusp. On the internal side of the tooth there is a very small anterior fossa or pocket, lying between the median transverse ridge and the anterior corner of the tooth, and a posterior

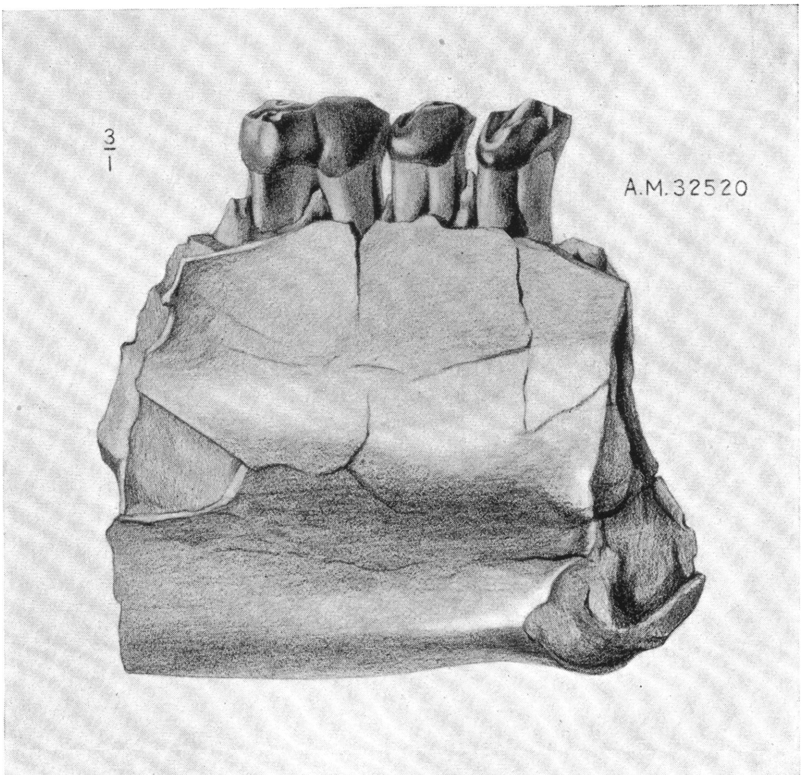


Fig. 14. *Amphipithecus mogaungensis* Colbert. Type, Amer. Mus. No. 32520. Internal lateral view. Three times natural size.

fossa, lying between the median ridge and a posterior transverse ridge. These transverse ridges are not horizontal, but slope very strongly from the median to the lingual borders of the tooth, so that the fossae or pockets face obliquely upward and inward. The external or buccal side of each tooth is sculptured by a cingulum that runs in a semicircle from the base up to the anterior and posterior portions of the tooth, and by a central vertical ridge, extending up to the main cusp. All in all, the crowns of these teeth, though peculiar in their configuration and difficult to describe, are essentially similar to the bicuspids of some of the higher primates. The figure clearly shows their form.

The last premolar has four roots, two internal and two external, of which the anterior internal one is very small. There are only three roots in the third premolar, for there is no antero-internal root. The second premolar, of which the crown is missing, would seem to have a single internal and a single external root, probably corresponding to the posterior roots of the fourth premolar, strongly fused to form one large transverse root. The roots of the cheek teeth are all extraordinarily long and vertical—a character typical of many of the higher primates.

The first molar is a somewhat elongated tooth, with a brachyodont crown and long roots. The trigonid is relatively low, so that it is not appreciably elevated above the talonid. The front portion of the tooth is somewhat narrower than the posterior portion, so that the protoconid and the metaconid lie closer to each other than do the hypoconid and the entoconid. These cusps are essentially conical, but a low transverse ridge connects the anterior ones, while anterior and postero-transverse ridges from the posterior cusps form a rim around the basined talonid. In front of the metaconid is a flat facet, the center of which shows a small pit, evidently indicating the presence of a very small paraconid. There are well-developed cingula on the anterior portion of the tooth, both externally and internally, while at the back of the molar there is a very slight cingulum. At the external junction of this posterior cingulum with the talonid rim there is evidence of an incipient hypoconulid, but the indications of this cusp are so slight that it may be considered as non-existent. It would seem that we see here the initial stage in the formation of a hypoconulid. (Colbert, E. H., 1937, pp. 1–6.)

A detailed discussion of this genus is presented in the paper cited above, so that a complete review of its probable affinities need not be presented here. In the following paragraphs an abridged discussion of the genus and its probable relationships will, however, be presented.

Considering *Amphipithecus* in light of its broadest possible relationships, its affinities would surely seem to lie within four groups of Upper Eocene mammals, namely (*a*) the Primates, (*b*) the condylarths (considering *Hyopsodus* as a condylarth), (*c*) the rodents and (*d*) the artiodactyls. In all of these mammalian Orders the molars are more or less comparable to the molar of *Amphipithecus*, but only in the Primates is a direct comparison of the premolars possible. Therefore the last three of the above listed groups may be eliminated from further consideration.

Following this line of study by progressive elimination it soon becomes evident that the lemuroid and tarsioid primates may be excluded from this search for forms related to the genus under consideration. In both of these primate groups the mandible is shallow and elongated, as compared with the very short and excessively heavy and deep mandible of *Amphipithecus*. In both the premolars are simple by reason of their conical form while the molars are cross-crested or otherwise sectorially developed. Perhaps some attention might be called to the fact that there is a certain amount of resemblance between *Amphipithecus* and the Eocene lemuroid, *Pelycodus*, particularly in the form of the last premolar and the molars. But this resemblance is at best slight, indicating that *Amphipithecus* has advanced far beyond the primitive lemuroid condition and is more closely related to the higher forms, discussed below. (The comparison between the cheek teeth of *Amphipithecus* and *Pelycodus* is shown in the accompanying illustration, Fig. 15.)

The presence of three premolars in *Amphipithecus* suggests the possibility of its relationship with the platyrrhine primates. A detailed comparison will show, however, that this similarity does not constitute a true link between the Burmese and the South American primates, for in the former the second premolar is very small—evidently a structure that was being gradually eliminated—while in the latter this tooth is large and well developed. Thus the presence of the second premolar in *Amphipithecus* is obviously the retention of a primitive character, once possessed by all of the primates, whereas the second premolar in the platyrrhines is a highly specialized structure which has been emphasized during the course of the group's evolutionary development. Furthermore the premolars, the molars and the mandibular ramus of the platyrrhines show so many differences from these features in *Amphipithecus* that the wide gap between the Burma genus and the New World monkeys is quite evident. (See Fig. 15.)

Naturally the possibilities of a relationship between *Amphipithecus* and *Pondaungia* must be considered in this discussion. It might be wished that the material and the figures of *Pondaungia* were more adequate; the genus in its present state is of puzzling and uncertain relationships. It would seem, however, that there are not many characters in common between *Amphipithecus* and *Pondaungia* and there are certainly many differences. In *Pondaungia* the molars are rather quadrate and have four cusps, in *Amphipithecus* they are more elongated and quinquetubercular. In *Pondaungia* the mandibular ramus is relatively shallow, whereas in *Amphipithecus* it is very deep and heavy. (See Fig. 13.)

In some ways *Amphipithecus* may be compared with the cercopithecoids, particularly the more advanced forms. Thus there is some resemblance between the premolars, the heavy mandible and the short symphysis of *Amphipithecus* and those of *Mesopithecus*, a Pliocene monkey from Eurasia. But the comparison is not as close as in the case of the anthropoids (to be discussed next) and it breaks down when the highly specialized, cross-crested molars of the cercopithecoids are considered. Naturally resemblances would be expected here, because the

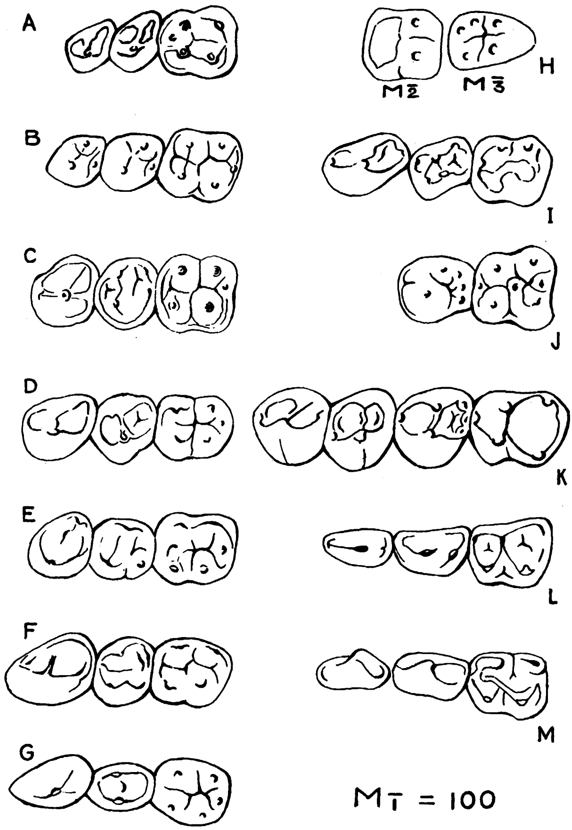


Fig. 15. Left P_{3-4}, M_1 of various primates and an artiodactyl. (H, M_{2-3}; K, P_{2-4}, M_1) M_1 reduced to a unit length in each case.

SIMIIDAE: A.—*Amphipithecus*—Eocene, Burma; B.—*Parapithecus*—Oligocene, Egypt; C.—*Propliopithecus*—Oligocene, Egypt; D.—*Dryopithecus*—Miocene, Europe; E.—*Pan*—Recent, Africa; F.—*Gorilla*—Recent, Africa; G.—*Hylobates*—Recent, Orient; H.—*Pondaungia* (this family?)—Eocene, Burma.

CERCOPITHECIDAE: I.—*Mesopithecus*—Pliocene, Greece; J.—*Apidium*—Oligocene, Egypt.

CEBIDAE: K.—*Alouatta*—Recent, Central America.

LEMURIDAE: L.—*Pelycodus*—Eocene, North America.

ARTIODACTYLA: M.—*Wasatchia*—Eocene, North America.

cercopithecoids and the anthropoids are closely related. When *Apidium*, supposedly an ancestral cercopithecoid, is compared with *Amphipithecus* very few resemblances are to be seen. (See Fig. 15 for *Apidium* and *Mesopithecus*.)

Thus the comparison narrows down to that between *Amphipithecus* and the true anthropoids, and here the points of resemblance would seem to be many. In the construction of the mandibular ramus, its great depth, the strong lingual torus, the abbreviated symphysis that is heavy, broad and vertical, and the presence of a deep genioglossus pit, *Amphipithecus* shows striking resemblances to many of the most advanced primates, such as *Dryopithecus*, *Proconsul*, *Simia* and *Gorilla*. This resemblance is strengthened by the probable parallelism of the two rami in *Amphipithecus*, resulting in a dental arcade similar to that of the above named forms and like that of *Propliopithecus* of the Fayûm, rather than like the more primitive, divergent rami and arcade of *Parapithecus*.

The canine of *Amphipithecus*, though broken, would seem to have been upright as in the anthropoids and not procumbent as in the more primitive forms. All in all, the premolars and molars of the genus under consideration resemble these teeth in *Propliopithecus* and in the higher anthropoids. The premolars, especially, are quite highly developed, and may be compared with those of *Dryopithecus*, *Pan* and *Gorilla*. This resemblance is brought out by the lingual extension of their postero-internal corners, and by the development in each of a transverse ridge from its main cusp. The molar of *Amphipithecus*, on the other hand, shows certain primitive characters that make it appear to be less advanced than the same tooth in *Parapithecus* or *Propliopithecus*, and much less advanced than the same tooth in the higher forms. Thus it has retained a paracone but has not developed an hypoconulid, it is elongated and the anterior portion of the tooth is appreciably narrower than its posterior portion. (The points emphasized in the foregoing remarks are illustrated in Fig. 13.)

In the original paper on *Amphipithecus* the following remarks were made at the conclusion of the discussion:

> As to the family relationships of *Amphipithecus*, two possibilities are evident. In the first place, this new genus might be placed in the family Simiidae because of its obvious affinities to *Parapithecus*, *Propliopithecus*, *Dryopithecus* and the other higher anthropoids. If this were to be done, however, the long established distinction of the anthropoids as primates having only two premolars would be broken down. For this reason the desirability of including *Amphipithecus* in the family Simiidae is questionable, even though the morphological details that characterize this genus make such a step a logical one.

In the second place, a new family or subfamily might be created to contain this single genus and species. But this would involve the founding of a new group of major taxonomic importance on very fragmentary evidence.

Amphipithecus A.M. No. 32520

P_3 length	3.8	M_1 length	6.3
width	4.2	width (ant.)	5.2
height (crown)	4.0	width (post.)	5.9
P_4 length	3.6	height (crown)	3.6+
width	4.6	Depth of mandible-M_1	19.5
height (crown)	4.0+	Thickness of mandible-M_1	9.0

PERISSODACTYLA

Brontotherioidea

Brontotheriidae

In 1925, Dr. Pilgrim described two genera and four species of titanotheres from the Pondaung deposits. Of these, one genus, *Sivatitanops*, was new, and it contained three species, one of which had been described in 1916 under the generic name of *Telmatherium*. These three species were based on a badly battered palate, various fragments of teeth and several complete premolars and molars, and while it is to be doubted that this material should be divided between three species, it is sufficiently complete to establish at least one good species, thereby putting the genus on a firm foundation. Thus, in spite of certain doubts expressed in Dr. Matthew's statement of 1929,[1] there would seem to be good grounds for regarding the genus *Sivatitanops* as valid.

Sivatitanops and *Eotitanotherium*. These are too fragmentary for generic determination. The best specimens are two or three complete teeth, three premolars and one true molar (upper). They are titanotheres, however, safely enough.[1]

As to the remaining form, *Eotitanotherium* (?) *lahirii*, the type material is so very fragmentary as to make the species practically invalid.

Sivatitanops Pilgrim, 1925

Pilgrim, G. E., 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 3–5.

Generic Type.—*Sivatitanops cotteri* Pilgrim.[2]

Author's Diagnosis.—*Sivatitanops* is a Titanothere possessing a short, broad facial region, with widely expanded zygomata and a stoutly built jugal process. The presence or absence of horns is unknown, but if present, they must have been merely in an incipient condition. The infra-orbital foramen is large and situated directly over p^4. The posterior nasal foramina open opposite m^3. The molar series

[1] Matthew, W. D., 1929, Bull. Amer. Mus. Nat. Hist., LVI, p. 462.
[2] This species is selected as the generic type since it is based on a definitive molar and several well-preserved premolar teeth.

greatly exceeds in length the premolar series. The latter is much reduced: in the species *S. birmanicum* p^1 is absent, and there is no diastema between the canine and p^2. M^3 is as large as m^2 and possesses a well-marked hypocone. All the molars are rectangular in outline; in front of the protocone is a broad cingular shelf, elevated into a cusp which is much more prominent than in the genus *Titanotherium*. Running backward from the cusp along the median valley, is a rugose ridge, which may represent a rudimentary protoconule. Internal cingulum absent. Premolars in a merely incipient stage of molarization; tetartocone scarcely differentiated from the cingulum, and without marked ridges connecting the deuterocone to the ectoloph; p^2 with a broad posterior cingular shelf; p^1, if present, a small elongate tooth, without an internal lobe.

Canine large, with antero-posterior ridges passing down into a strong basal cingulum.

Incisor series complete. Incisors large; i^2 the smallest of the three; elongate transversely, with a convex external surface and an internal ridge, without a distinct cingulum.

Sivatitanops cotteri Pilgrim

Sivatitanops cotteri, Pilgrim, 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 5–9, Pl. i, figs. 3–6, 9; Pl. ii, figs. 4, 5.

Type.—G.S.I. No. C330–333, a second upper molar, second and third premolars and an upper canine.

Paratypes.—G.S.I. No. C334–336, a last upper premolar, an incisor and a small low-rooted tooth. G.S.I. No. C337, an incisor.

Horizon.—Pondaung, Eocene.

Locality.—Myaing township of Pakokku district, 6 1/2 furlongs distant from Hill 1258 and in a direction 9° W. of S. from it.

Diagnosis (Revised).—The upper incisors are elongated antero-posteriorly, with lateral cutting ridges running to the base in each tooth; there is a median lingual ridge, but no basal cingulum. The upper canine is approximately circular in cross section, with a basal cingulum and anterior and posterior ridges. The upper premolars are of primitive form in that they are not molarized to any appreciable degree; in the posterior ones the protocone has an external concavity, deuterocone sub-conical and tritocone flat externally; tetartocone present as a low, ridge-like tubercle; an anterior cingulum with a turbercle more or less in the position of a protoconule. The anterior premolars are even more primitive than the posterior ones; all of the premolars are small as compared to the molars. The upper molars are elongated antero-posteriorly, with moderately high crowns; the protocone and hypocone are sub-equal in size and are sub-conical; the protocone is situated about in the middle of the tooth, much behind the paracone; a small ridge is present which may be a rudimentary protoconule; ectoloph with strong parastyle and mesostyle, and with pronounced buttresses on the paracone and metacone.

The lower canine is smaller than the upper canine, but like it, has the antero-posterior cutting ridges and the basal cingulum. The lower cheek teeth are doubly crescentic as in the other forms of titanotheres.

Specimen in the American Museum.

Amer. Mus. No. 20014, a crushed mandible with both horizontal rami and the cheek teeth preserved, and with a canine present on one side. From the Pondaung beds, one mile northwest of Mogaung. (Map, Fig. 8, locality 14.)

This jaw, Amer. Mus. No. 20014, is only provisionally referred to the genus *Sivatitanops* and to the species *Sivatitanops cotteri.* Full recognition is given to the fact that subsequent discoveries may prove the specimen under consideration to belong to another species of *Sivatitanops,* or even to some other genus of titanotheres. At the present time, however, in order to avoid the further multiplication of names in the Eocene Burma fauna, the specimen is tentatively referred to an already established genus and species.

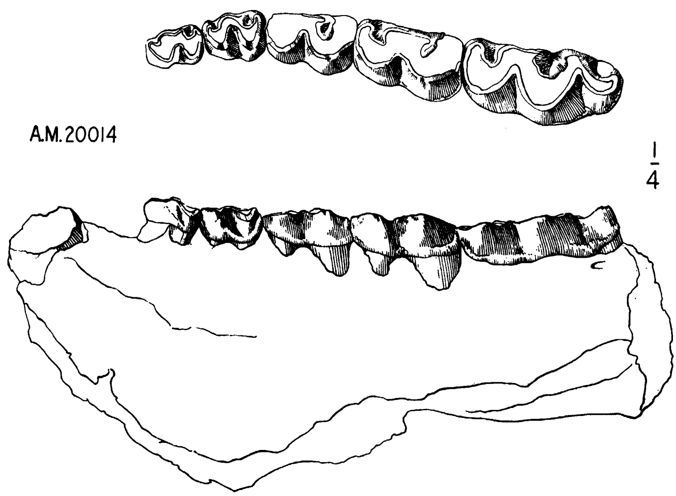


Fig. 16. *Sivatitanops cotteri* Pilgrim. Amer. Mus. No. 20014, mandible. Crown view above, lateral view of the left side below. One-fourth natural size.

The upper molar of *Sivatitanops cotteri,* described by Pilgrim, is a rather elongated tooth. Measurements show that the protocone and the hypocone of this tooth (presumably a second molar) would fit very nicely inside of the hypoconid of M_2 and the protoconid of M_3 of 20014. Thus because of this possible occlusal relationship and the general size of the jaw now being discussed, good arguments may be advanced for the assignment of the specimen to *Sivatitanops cotteri.*

In its large size and robustness this jaw is somewhat comparable to a new genus from Mongolia, to be described by Granger and Gregory. A further resemblance is to be seen in the very large canines in both the

Burma and the Mongolian forms. In the Mongolian titanothere, however, there is a rather long canine—premolar diastema, a distinct contrast to the jaw from Burma. Parenthetically it might be said that the elongated upper molar of *Sivatitanops cotteri* would point to the probability of an elongated mandible in this species with a consequent post-canine diastema. Naturally, if such should eventually prove to be the case, then the jaw now being described would necessarily be taken out of the genus *Sivatitanops*. On the other hand it may be noted that this lack of a diastema in 20014 would seemingly accord with the condition of the palate of *Sivatitanops birmanicus* as figured by Pilgrim, in which the dental series is continuous, without any breaks.

The large, one might say gigantic, canine of the jaw is its most distinctive character. This tooth is somewhat elliptical in shape, being longer than it is broad, and it occupies a considerable part of the anterior region of the tooth series. It is broken and pushed out of place, due to the crushing of the mandible, so that its true position in the symphysis is difficult to determine. There would seem to be evidence that the canines were almost contiguous to each other along the mid-line, so that the incisors were either reduced to mere insignificance or eliminated altogether. Since there are no incisors present in the specimen, this point cannot be certainly determined.

This jaw is characterized not only by the lack of a post-canine diastema, but also by the proximity of the canine to the first molar, thereby causing the premolars to be very small and crowded. Only the last two premolars are present, so there is a possibility that either one or both of the first two premolars had been eliminated. (In the palate of *S. birmanicum*, as described and figured by Pilgrim, P^1 has been eliminated from the dentition.) If they were present, then they were extremely small.

The molars of 20014 are the only teeth that are at all adequately preserved. They are very large, robust and brachyodont. They show the typical titanothere pattern in being doubly crescentic, and the hypoconulid of the last molar takes the form of a semi-crescentic loop. There are no external cingula, except in M_3, in which there is a faint basal shelf on the hypoconulid. The most characteristic feature of the molars in this jaw is their extraordinary robustness.

The massiveness of the mandibular rami has been alluded to above. The symphysis likewise is very heavy and rather squarish in front. On one side (the left) it is swollen by an extensive exostosis of the bone, as if in life the animal had suffered some injury or disease.

MEASUREMENTS

Amer. Mus. No. 20014

Depth of ramus at M_1		130 mm.
Canine	length	46
	width	32
P_3	length	29
	width	20
P_4	length	33
	width	25
M_1	length	48
	width	30
M_2	length	56
	width	35
M_3	length	85
	width	38

Sivatitanops birmanicum (Pilgrim and Cotter)

Telmatherium (?) *birmanicum*, PILGRIM AND COTTER, 1916, Rec. Geol. Surv. India, XLVII, pp. 72–74.

Sivatitanops birmanicum, PILGRIM, 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, pp. 9–11, Pl. I, figs. 1a–c.

TYPE.—G.S.I. No. C315, five fragments of upper molars.

REFERRED SPECIMEN.—G.S.I. No. C329, a skull.

HORIZON.—Pondaung, Eocene.

LOCALITY.—Myaing area, Burma.

DIAGNOSIS (Revised; Pilgrim).—From the characters which can be distinguished in the specimen, it is evident that we have before us a skull of a brachycephalic type, with an extremely short facial region, due mainly to the great reduction of the premolar series; p^1 is not present and there is no diastema between p^2 and the canine. The incisor series forms an arc of about a quarter of a circle. The upper surface in the frontal region is flat both transversely and antero-posteriorly, from which it would appear that horns, if present, could have been merely incipient. The absence of the nasals prevents us from seeing the actual condition. The front part of the jugal process is stout and jutted out considerably. The infra-orbital foramen is big and situated directly above p^4. The posterior nasal foramina are opposite the last molar.

The structure of the molars agrees closely with that of the type molar of *Sivatitanops cotteri*, except that the breadth index is greater, and the anterior internal cingular cusp is more prominent than in *S. cotteri*, as well as the beaded ridge which runs backward from it along the median valley. The distinctness of this cingular cusp from the protocone becomes more marked in each successive molar from behind forward. In m^1 there is a deep valley, separating it from the protocone, and it has taken on the appearance of an actual cusp, almost comparable with the main cusps of the tooth. The external surface of the outer cusps, paracone and metacone appears to be flat or at any rate less strongly ribbed than in the species *S. cotteri*. M^3 is not inferior in size to m^2; there is a hypocone at the postero-internal angle of the tooth, which is perfectly distinct, though rather smaller than is the case in the two anterior molars.

The breadth index of the premolars is also greater than in *S. cotteri.* So far as one can see, the internal part of p^3 and p^4 consists merely of a single large cusp, the deuterocone, with anterior and posterior cingula which do not extend to the inner margin of the tooth. There is no indication of a tetartocone. The detailed structure of p^2 cannot be made out.

The roots of the canine, and the three incisors are large and indicate that the teeth in question were large and fully functional. The third is the largest of the three and the second is smaller than the first. (Pilgrim, G. E., 1925, pp. 10–11.)

It is unfortunate that the type of this species consists of such extremely fragmentary teeth, and that the referred palate, described and figured by Pilgrim in 1925, has such a badly battered dentition. Nothing very definite can be said about the species, *Sivatitanops birmanicum,* except that it is seemingly a very brachycephalic titanothere in which the dental series is closed and lacks the first premolar. According to Pilgrim the molars of the palate (G.S.I. No. C329) are characterized by a large hypocone, an extraordinarily large upgrowth from the anterior cingulum, and as compared with *S. cotteri* flatter or at least less strongly ribbed ectoloph surfaces on the paracone and metacone, and a greater breadth index. In view of these differences between the molars of *Sivatitanops birmanicum* and *Sivatitanops cotteri* (particularly in the matter of breadth indices) the generic standing of the species now under consideration is certainly dubious.

The measurements for the second upper molars (as given by Pilgrim) and the indices for these teeth are given below.

	Sivatitanops cotteri	*Sivatitanops birmanicum*
M^2	G.S.I. No. C330–332	G.S.I. No. C329
Length	56.3 mm.	71.9 mm.
Width	49.8	69.4
Index	*88*	*96*

Sivatitanops (?) rugosidens Pilgrim

Sivatitanops (?) *rugosidens,* Pilgrim, 1925, Mem. Geol. Surv. India, (N. S.) VIII, No. 3, p. 11, Pl. II, figs. 6, 7.

Type.—G.S.I. No. C339, four associated fragments of upper teeth.

Paratypes.—None.

Horizon.—Pondaung, Eocene.

Locality.—1 mile E.S.E. of the village of Sinzwe, Burma.

Author's Diagnosis.—Four associated fragments of upper teeth of a Titanothere (C.339), found by H. M. Lahiri, 1 mile E.S.E. of the village of Sinzwe, may provisionally be referred to the genus *Sivatitanops,* to which they are allied by the backward position of the protocone of the molars. The crowns of the teeth are, however, lower; the protocone of the molars is smaller and more truly conical, and a greater space intervenes between it and the anterior margin of the tooth. There is a more pronounced protoconule, which is isolated from the cingulum. The cingulum extends to the internal side of the tooth and both it and the surface of the base of the protocone are strongly rugose. This rugosity is even more pronounced in the case of p^4. The deuterocone is smaller than in the corresponding tooth of *Sivatitanops cotteri;* there is a small tetartocone, isolated from the cingulum. The cingulum itself is narrower than in *S. cotteri*, and extends to the inside of the tooth, and the remainder of the broad area on either side of the deuterocone is covered with small pimples or wrinkles. It is not unlikely that it will prove entitled to generic rank, but as so little of the dentition is known, it seems unwise to found another genus on such slender evidence.

This species is based on such very fragmentary material as to be of little or no value.

METATELMATHERIUM GRANGER AND GREGORY, 1938

GRANGER, WALTER, AND GREGORY, WILLIAM KING, 1938, "Addendum" to this paper, page 435.

GENERIC TYPE.—*Metatelmatherium cristatum* Granger and Gregory.

DIAGNOSIS.—See the type description of this genus on page 435 below.

Metatelmatherium (?) browni, new species

TYPE.—Amer. Mus. No. 20008, a left M^3.

PARATYPES.—Amer. Mus. Nos. 20022, a mandible of an immature animal with the permanent molars and the permanent incisors in eruption; 20016, a broken mandible, with deciduous and permanent molars preserved.

HORIZON.—Pondaung beds, Upper Eocene.

LOCALITY.—For 20008, two miles northeast of Gyat (Map, Fig. 8, locality A24); 20022, one mile northwest of Mogaung (Map, Fig. 8, locality 18); 20016, one mile northeast of Gyat (Map, Fig. 8, locality A23). Upper Burma.

DIAGNOSIS.—Upper molar large and brachyodont, with a centrally placed protocone and a well-developed hypocone, in which latter respect this species may be contrasted with *Metatelmatherium cristatum* and *Metatelmatherium ultimum.* There is no external cingulum, in which respect this form resembles the first of the above mentioned species, and likewise there is no cingulum on the internal side of the protocone. There is a slight ridge on the ectoloph of the paracone, as in *Metatelmatherium ultimum.*

The lower incisors are large, longer anteroposteriorly than they are laterally and have postero-external cingular ridges. The lower molars are rather hypsodont, considerably more so than are the comparable teeth in *Metatelmatherium cristatum.* They are characterized by their relative narrowness, in which respect they resemble somewhat the lower molars of *Telmatherium cultridens.* There are no external cingula but the posterior cingula are well developed. There is also a prominent internal ridge, running posteriorly from the metaconid. Perhaps the most characteristic feature of the lower molars in this species is the swollen posterior process on the entoconid, which would seem to be distinctive for the form under consideration.

The mandibular ramus is heavy, the ascending ramus wide and the symphysis short and crowded.

The specimens here designated as *Metatelmatherium* (?) *browni* would certainly seem to be distinct from any titanothere hitherto known from Burma with the possible exception of *Eotitanotherium* (?) *lahirii*. The molar ectoloph, G.S.I. No. C341, is seemingly almost identical with the similar portion of Amer. Mus. No. 20008, and thus there is good reason for considering these two specimens as specifically identical. On the other hand, certain reasons exist, as set forth on page 311, for thinking that the molar ectoloph, G.S.I. No. C341, is not specifically identical with the other specimens included by Pilgrim in *Eotitanotherium* (?) *lahirii*.

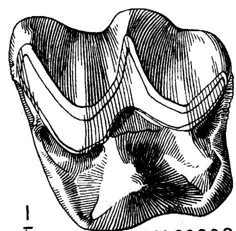


Fig. 17. *Metatelmatherium* (?) *browni*, new species. Amer. Mus. No. 20008, type, left M^3. Crown view, one-half natural size.

In view of certain characters whereby *Eotitanotherium* (?) *lahirii* differs from the typical *Metatelmatherium* (see page 311) and considering the very fragmentary nature of the material comprising Pilgrim's species, it seems best not to identify these new fossils, Amer. Mus. Nos. 20008, 20016, 20022, with the already described species, but rather to set them apart as a new form with truly recognizable characters.

Moreover, G.S.I. No. C341 is hereby considered as being probably referable to the new species now under consideration rather than to *Eotitanotherium* (?) *lahirii*.

The upper molar, No. 20008, is quite different from the single upper molar of *Sivatitanops cotteri*, described and figured by Pilgrim, particularly in its greater breadth index, and the entirely different expression of its ectoloph, protocone and hypocone. The closest comparisons to the tooth now under consideration are to be found in the genus *Metatelmatherium*, from Utah and Mongolia, described elsewhere by Granger and Gregory. For this reason it may be well to consider briefly the resemblances and differences between the last upper molar in *Metatelmatherium* (?) *browni* (Amer. Mus. No. 20008), *Metatelmatherium cristatum* (Amer. Mus. No. 26411) and *Metatelmatherium ultimum* (Amer. Mus. No. 2060).

As to the central protocone, this would seem to be a character common to all species of the genus, and no differentiations may be made on this one point. Concerning the other characters of the molar, the three species may be arranged somewhat in the following manner:

(*a*) *Metatelmatherium ultimum*	(*b*) *Metatelmatherium cristatum*	(*c*) *Metatelmatherium browni*
Uinta	Irdin Manha	Pondaung
Upper Eocene	Upper Eocene	Upper Eocene
(1) Most brachyodont	(1) More hypsodont than *a*	(1) Comparable to *b* in tooth height
(2) No distinct hypocone	(2) Small hypocone, an upgrowth from the cingulum	(2) Large hypocone
(3) Large internal cingulum	(3) Internal cingulum diminished	(3) No internal cingulum
(4) External cingulum present	(4) External cingulum absent	(4) External cingulum absent
(5) Slight ridge on ectoloph of paracone		(5) Slight ridge on ectoloph of paracone

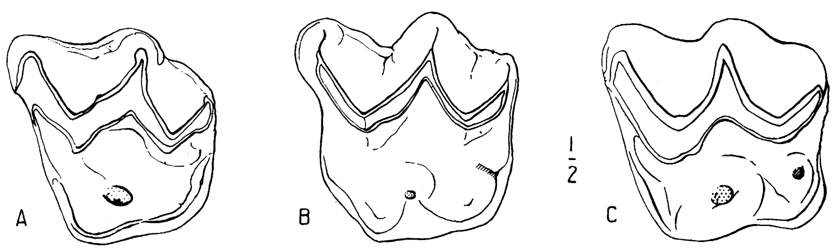


Fig. 18. Comparison of the left M^3 in the types of:

a.—*Metatelmatherium ultimum* (Osborn). Amer. Mus. No. 2060. Uinta formation, Utah.

b.—*Metatelmatherium cristatum* Granger and Gregory. Amer. Mus. No. 26411. Irdin Manha formation, Mongolia.

c.—*Metatelmatherium* (?) *browni*, new species. Amer. Mus. No. 20008. Pondaung formation, Burma.

All one-half natural size.

From this tabulation it may be seen that as regards the upper molars the new titanothere from Burma is more closely related to the Mongolian form, *Metatelmatherium cristatum* than it is to the American species *Metatelmatherium ultimum.* Moreover a distinct progression from the American species through the Mongolian form to the Burma species may be seen in such characters as the hypsodonty of the molar, the de-

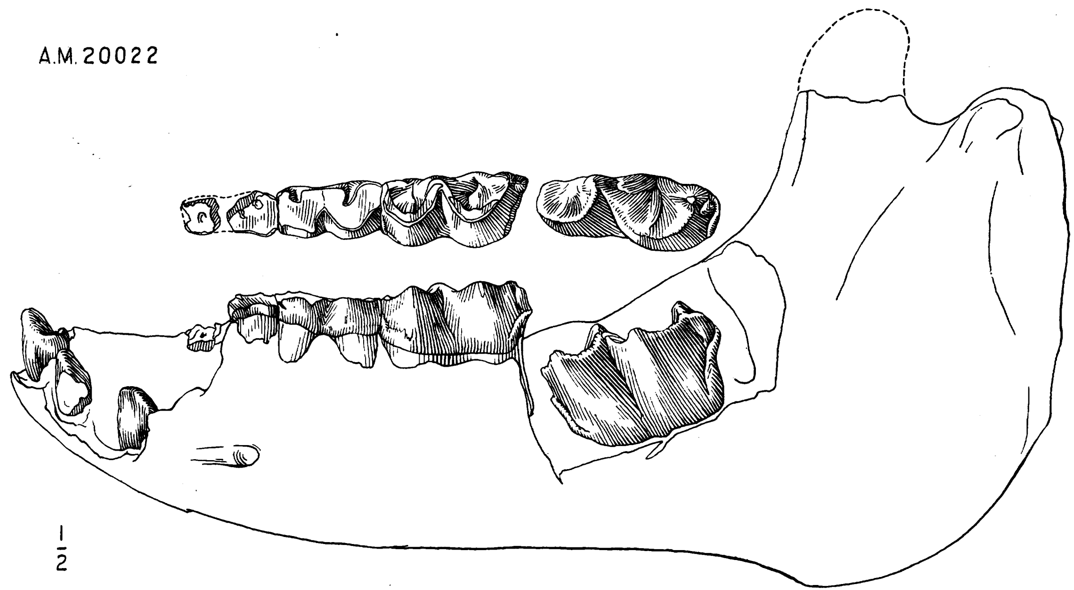


Fig. 19. *Metatelmatherium* (?) *browni*, new species. Amer. Mus. No. 20022_1 paratype. Mandible of immature individual. Left side, and crown views (M, transposed from right side). One-half natural size.

velopment of the hypocone and the reduction of internal and external cingula. All of these species are approximately of about the same age, since the Uinta of America is equal to or perhaps somewhat later than the Irdin Manha of Mongolia, which in turn is perhaps a little earlier than the Pondaung horizon of Burma. Therefore the changes from the American through the Mongolian to the Burmese species cannot be attributed to a progressive evolution through geologic time between these regions, but rather to the fact that there has been a migration from the center of origin for the genus, a migration resulting in the successive differentiation of one species from another as the genus has been geographically dispersed. And it would seem that the center of origin was in America, from whence the genus crossed to Mongolia and continued on until it reached Burma.

Comparative measurements of the upper molars are given below.

MEASUREMENTS

M^3	*M. ultimum* A. M. 2060	*M. cristatum* A. M. 26411	*M. browni* A. M. 20008
Length, pa^s–mt^s	53 mm.	58 mm.	55 mm.
Width, me^s–pr.	56	58	57
Index	*106*	*100*	*104*

The two jaws here considered as the paratypes for *Metatelmatherium browni* are both, curiously enough, of young individuals with the milk molars in place but with the first and second permanent molars erupting. One of them, No. 20016, is very badly shattered, and thus most of the facts must needs be obtained from the other specimen, No. 20022. There is no doubt, however, but that both specimens belong to the same species, for the comparable teeth in them are almost identical as regards size and structure. And there would seem to be no doubt, from the much smaller and narrower first molar of the specimens now under consideration that they belong to a species, and probably a genus, quite distinct from the large mandible described on other pages under the name of *Sivatitanops cotteri*.

The characters of the lower teeth have been set forth in the diagnosis of the species. Briefly they are as follows: the incisors are large with strong postero-external cingular ridges; the lower molars are rather hypsodont, narrow, without external cingula and with a swollen posterior process on the metaconid. The mandibular ramus is heavy, the ascending ramus wide and the symphysis short and crowded.

In the better preserved of the two specimens, No. 20022, the short, mandibular symphysis has caused the erupting permanent incisors to crowd each other in a most abnormal way. The proper identification of these teeth in this specimen is a problem difficult to work out, and the results of any interpretation are open to doubt. After considerable study, however, it would seem that the following solution offers a more or less close approach to the truth.

The incisors on the right side of the jaw have erupted precociously, and due to their large size, there has not been sufficient accommodation for them in the still undeveloped symphyseal region. Therefore they are crowded so that the second member of the series is behind the first and third incisors, the latter two teeth being almost in contact with each other. In front of the two anterior incisor teeth are two small roots that may be regarded as the roots of two deciduous incisors. On the left side of the mandible the incisors are in eruption in the normal way, one tooth, supposedly the left I_1 being contiguous to the erupted

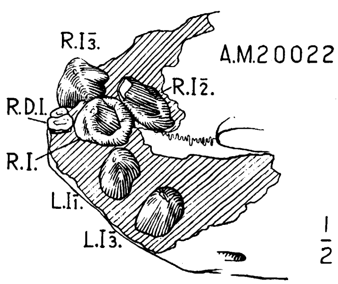


Fig. 20. *Metatelmatherium* (?) *browni*, new species. Amer. Mus. No. 20022, paratype. Symphysis of mandible. Angular view to show abnormal eruption of the permanent incisors. Approximately one-half natural size.

tooth identified above as the right I_1, another tooth separated from this first tooth and located behind it occupying the position of I_3. There is a gap between these teeth in which was undoubtedly lodged the second incisor. The precocious eruption of the right incisors together with the crushing of the jaw has caused a displacement of the mid-line of the symphysis toward the left side of the mandible. The points outlined in the above description are illustrated by the accompanying figure.

In addition to the description of the incisors in the diagnosis and in the above paragraphs, there might be added the fact that the postero-external cingulum on each tooth extends upwardly on the postero-internal side of the crown, to terminate near its tip.

Nothing need be added to the remarks about the lower molars except to stress the hypsodonty of M_1, its narrowness, its lack of an external cingulum and the swollen posterior process on the metaconid. All of these features, which would seem to be distinctive, are shown in the accompanying illustration (Fig. 19).

COMPARATIVE MEASUREMENTS

M_1

	T. cultridens	*M. ultimum*	*M. cristatum*	*M. browni*
	A. M. 1560	A. M. 2060	A. M. 26411	A. M. 20022
Length	30 mm.	39 mm.	37 mm.	38 mm.
Width	18.5	28	26	19.5
Index	*62*	*72*	*70*	*51*

MEASUREMENTS

Metatelmatherium browni, new species

		A. M. 20022	A. M. 20016
Length of mandible, condyle–symphysis		270 mm.	
Depth of ramus below M_1		49	60 mm.
Height of condyle above lower border		135	
Breadth of symphysis		61	
I_1	length	16.5	
	width	12	
	height	20	
I_2	length	15.5	
	width	11.5	
I_3	length	13.5	
	width	11	
	height	18+	
DM_4	length	26.5	26
	width	15	14.5
P_4	length		26
	width		17
	height (me^d)		16
M_1	length	38	33
	width	19.5	18.5
	height (me^d)	24	
M_2	length	49	40
	width	23e	..
	height (me^d)	34	28

Metatelmatherium (?) lahirii (Pilgrim)

Eotitanotherium (?) *lahirii*, PILGRIM, 1925, Mem. Geol. Surv. India, (N. S.) VIII, pp. 11–14, Pl. I, figs. 2, 7, 8.

LECTOTYPE.—G.S.I. No. C342, right maxilla with fragmentary first molar and last premolar.

COTYPES.—G.S.I. No. C340, a second left upper premolar. G.S.I. No. C341, external wall of second or third upper molar.

HORIZON.—Pondaung, Eocene.

LOCALITY.—1 mile E.S.E. of Sinzwe village, Burma.

DIAGNOSIS (Revised).—Skull with heavy maxilla and a strong jugal; the infraorbital foramen is large and situated above the fourth premolar. The second upper premolar resembles that of *Eotitanotherium osborni*, except that the external lobes are less convex in the Burma form, and the deuterocone and tetartocone are not connected; cingula are present on all sides of the tooth. There is a small central tubercle, in the median valley between the deuterocone and tetartocone. The upper molars are relatively broad, a distinct difference from *Sivatitanops*, the protocone is further forward than in this last mentioned genus, and there are no traces of a rudimentary protoconule; the styles of the ectoloph are pronounced, but are less constricted than in *Sivatitanops;* there is a faint buttress on the external surface of the paracone, but the metacone is smooth.

Eotitanotherium (?) *lahirii* is based on such very fragmentary material that definite conclusions as to its taxonomic or phylogenetic position are practically impossible to make. Pilgrim referred the species to *Eotitanotherium* with full recognition that his generic assignment was quite provisional.

From a careful examination of the type figures and description of this form it would seem more likely that it is referable to the genus *Metatelmatherium*, described at some length in preceding pages of this work. The molar ectoloph, G.S.I. No. C341, is certainly close to the complete upper molar in the American Museum, No. 20008, and there is good reason to think that these two specimens are specifically identical. (See page 305.)

The supposed M^1, G.S.I. No. C342, though badly damaged, would seem from its proportions and measurements to be a rather broad tooth, in which respect it is again more like *Metatelmatherium* than it is like *Eotitanotherium*. And the P^2, G.S.I. No. C331, is certainly as closely comparable to the same tooth in *Metatelmatherium* as it is to *Eotitanotherium.*

Some differences from *Metatelmatherium* are to be noted. In G.S.I. No. C342, which, by the way, is very probably an M^2 instead of an M^1, the hypocone is placed somewhat more anteriorly and buccaly than is the case with the hypocone of *Metatelmatherium*. Then again, the P^2, G.S.I. No. C340, is rather longer in comparison to its width, with more of an antero-internal angle than is the case in the P^2 of *Metatelmatherium.*

In view of these differences, and in view of the fragmentary nature of the material comprising *Eotitanotherium* (?) *lahirii*, its generic identity with *Metatelmatherium* cannot be certainly established. Further remarks about this perplexing problem will be found in the discussion of *Metatelmatherium* (?) *browni*, on page 305.

Titanotheres, Genera and Species Indeterminate

In the collection are a few isolated bones and teeth that are referable to the Titanotherioidea, but which cannot be definitely assigned to any particular genus. These specimens are listed below.

Amer. Mus. No. 20009, a left fifth metacarpal. Pondaung beds, one mile north of Koniwa. (Map, Fig. 8, locality A21.)

Amer. Mus. No. 20020, a right humerus. Pondaung beds, one and one-half miles northwest of Myaing. (Map, Fig. 11, locality 7.)

Amer. Mus. No. 32527, a left astragalus. Pondaung beds, one mile west of Zeittaung. (Map, Fig. 8, locality A20.)

Amer. Mus. No. 32528, an upper incisor. Pondaung beds, one mile northeast of Gyat. (Map, Fig. 8, locality A23.)

Amer. Mus. No. 32540, a left scaphoid, a magnum, and the glenoid of a scapula. Pondaung beds, one-half mile northeast of Kyawdaw. (Map, Fig. 8, locality A27.)

Amer. Mus. No. 32542, an incisor tooth, associated with Amer. Mus. No. 20010, *Paramynodon;* the incisor is, however, definitely that of a titanothere. Pondaung beds, one mile north of Koniwa. (Map, Fig. 8, locality A21.)

Brief descriptions of these specimens will now be presented, and comparisons will be made particularly with *Paramynodon*, to illustrate the differences between homologous elements of the two groups of large perissodactyls, titanotheres and amynodonts, in the Pondaung beds.

Of the specimens listed above, the incisor teeth are too large and robust to be referable to *Paramynodon*. One of them (Amer. Mus. No. 32542) although not much larger than the central incisor of *Paramynodon*, is characterized by the rather flat outer surface, the lack of an external cingulum, and the strong lingual ridge or buttress. Because of these decided contrasting characters that set it apart from *Paramynodon*, the tooth in question is considered as that of a titanothere, probably one of the relatively small central incisors. The other tooth (Amer. Mus. No. 32528) is very large, and is most certainly a lateral incisor of a titanothere, quite probably of the genus *Sivatitanops*. It is characterized by the strong concavity on its posterior or lingual surface, a very typical feature in the large lateral incisors of the titanotheres. For illustrations of these specimens the reader is referred to figure 29.

The reference of the humerus (Amer. Mus. No. 20020) to the Titanotherioidea is an identification that may be somewhat debatable. The following description and comparisons may serve, however, to make clear the reasons for this identification.

In size this bone is slightly smaller than the humerus (Amer. Mus. No. 20013) of *Paramynodon*—the difference between them, however, is not great. Thus it is at once apparent that this humerus belongs to a rather small titanothere, probably to *Metatelmatherium* rather than to *Siva-*

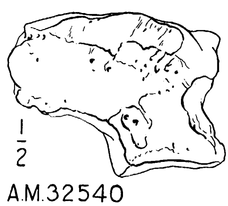
titanops. The deltoid crest is prominent, but not so much so as in *Paramynodon.* The head of the humerus, while resembling in a general way the head in *Paramynodon,* is rounder; that is, it is not quite so broad transversely as the head in the Pondaung rhinoceros, and it is slightly more convex antero-posteriorly.

Of particular significance is the bicipital groove, which is single, as contrasted with the double bicipital groove in the rhinoceros. An examination of the humeri in various genera and species of titanotheres and rhinoceroses would seem to show that in the former the bicipital groove is generally single, while in the latter it is generally double. Thus the single groove in the humerus now under discussion is here considered as one of the diagnostic characters defining the specimen as of titanothere relationships.

Another character of this specimen that would seem to be typical of the titanotheres rather than of the rhinoceroses is the form of the greater tuberosity. In this humerus it is produced upward into a point, rather than being rounded as in *Paramynodon.* On the external side of the head there is a broken surface, that may represent the base of a second tuberosity, similar to the tuberosity in the same position in *Paramynodon.* It is doubtful, however, whether this process in No. 20020 was as prominent as the same process in the rhinoceros. Beneath the greater tuberosity and at the proximal end of the deltoid crest is a rugose surface, probably for the attachment of the infraspinatus muscle. This surface is quite separate, whereas in *Paramynodon* the same surface is connected to the posterior tubercle of the greater tuberosity by a ridge.

The supinator crest is rather prominent at the distal end of the humerus. There are articular surfaces on the olecranon fossa for the anconeal process of the olecranon. The olecranon fossa is comparatively much shallower than the fossa in *Paramynodon.* Of particular significance is the shape of the capitellum and the trochlea of this humerus, as compared to the same features in *Paramynodon;* in the specimen now under consideration there would seem to be a greater disparity in the antero-posterior diameters of these structures than there is in *Paramynodon,* and this again would seem to be a feature whereby the humerus shows titanothere rather than rhinoceros relationships.

The fragment of a scapula and the os magnum (Amer. Mus. No. 32540) are referred to the Titanotherioidea because of their large size and heaviness. Such is the identification of the scaphoid, of the same number. This latter bone is interesting because of its contrasting size 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).



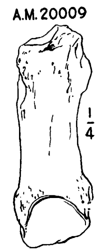


Fig. 21. Left scaphoid of a titanothere. Amer. Mus. No. 32540. Anterior view, one-half natural size.

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

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[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

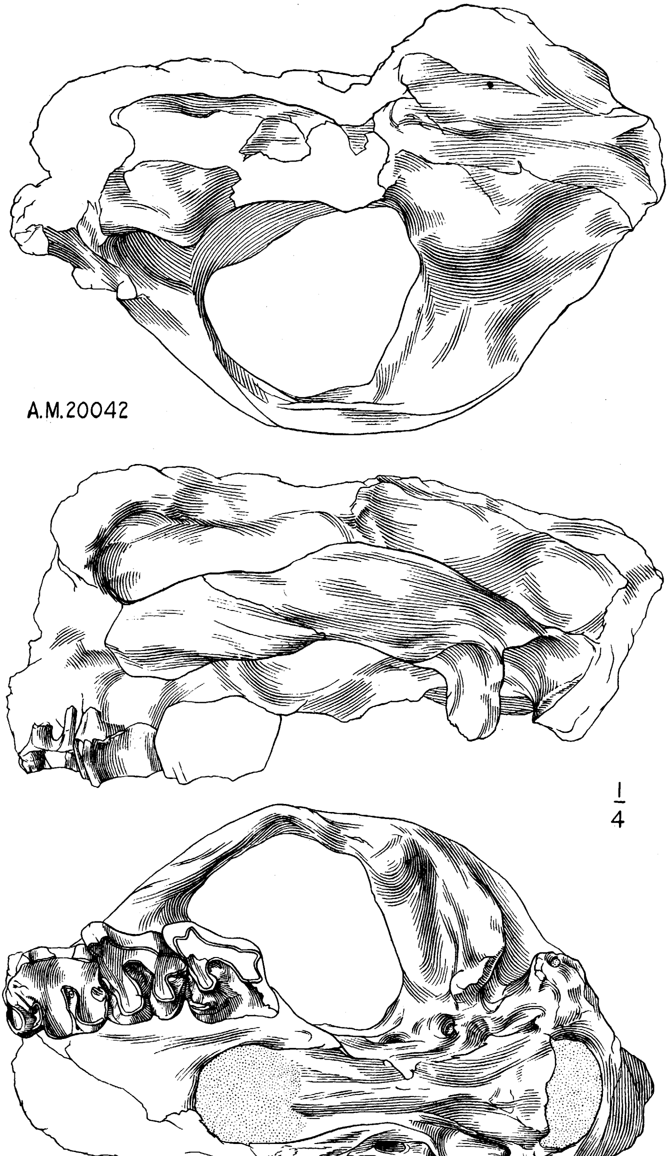


Fig. 23. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20042, skull. Dorsal view above, lateral view of left side in middle, palatal view below. One-fourth natural size.

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.

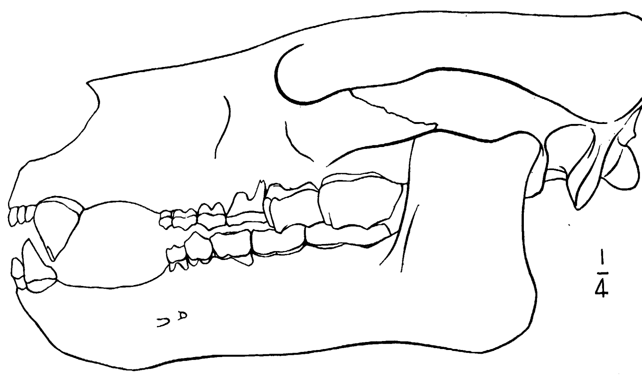


Fig. 24. *Paramynodon birmanicus* (Pilgrim and Cotter). Restoration of skull and mandible, based on Amer. Mus. Nos. 20042, 20010, 32530, 20026 and on G.S.I. No. C344 (type of *P. cotteri*). One-fourth natural size.

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.

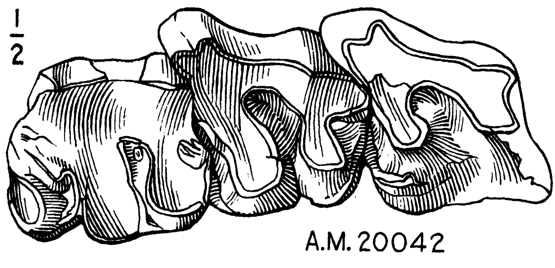


Fig. 25. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20042, left upper molars. Crown view, one-half natural size.

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:

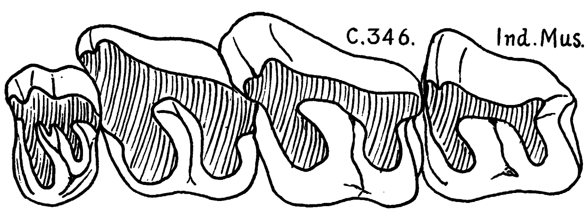


Fig. 26. *Paramynodon birmanicus* (Pilgrim and Cotter). G.S.I. No. C346, right P^4–M^2 and left M^{2-3}. P^4–M^1 reversed in drawing. (From Matthew, 1929.)

"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

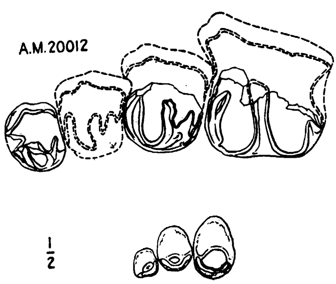


Fig. 27

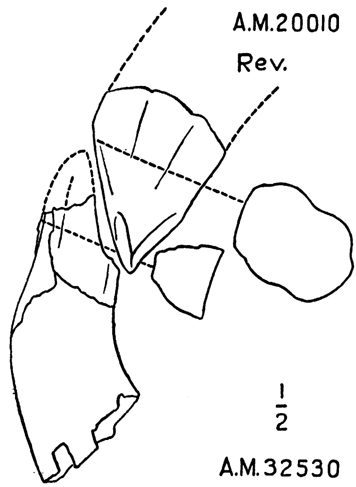


Fig. 28

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 encircling 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-*

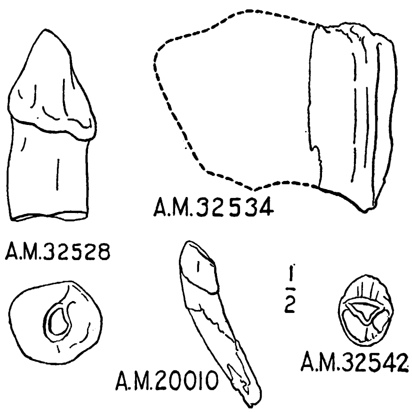


Fig. 29. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 32534, portion of unworn ectoloph of upper molar, showing height of crown. Lateral view. Amer. Mus. No. 20010, incisor tooth, lateral view.

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-

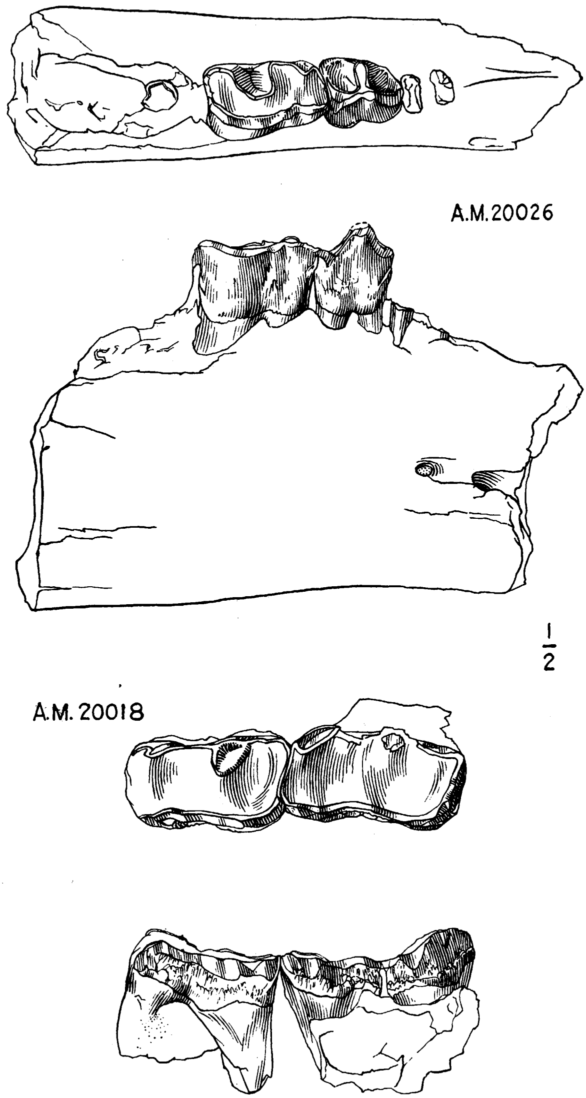


Fig. 30. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20026, portion of right mandibular ramus with P_3–M_1. Crown view above, lateral view below. Amer. Mus. No. 20018, left lower molars. Crown view above, lateral view below. All figures one-half natural size.

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

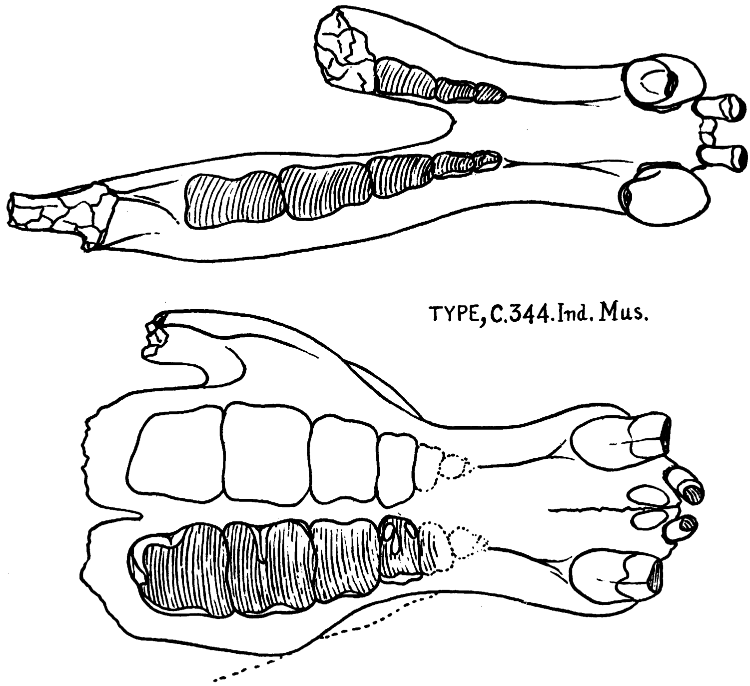


Fig. 31. *Paramynodon cotteri* Pilgrim. G.S.I. No. C344, type skull and mandible. Crown views. (From Matthew, 1929.)

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

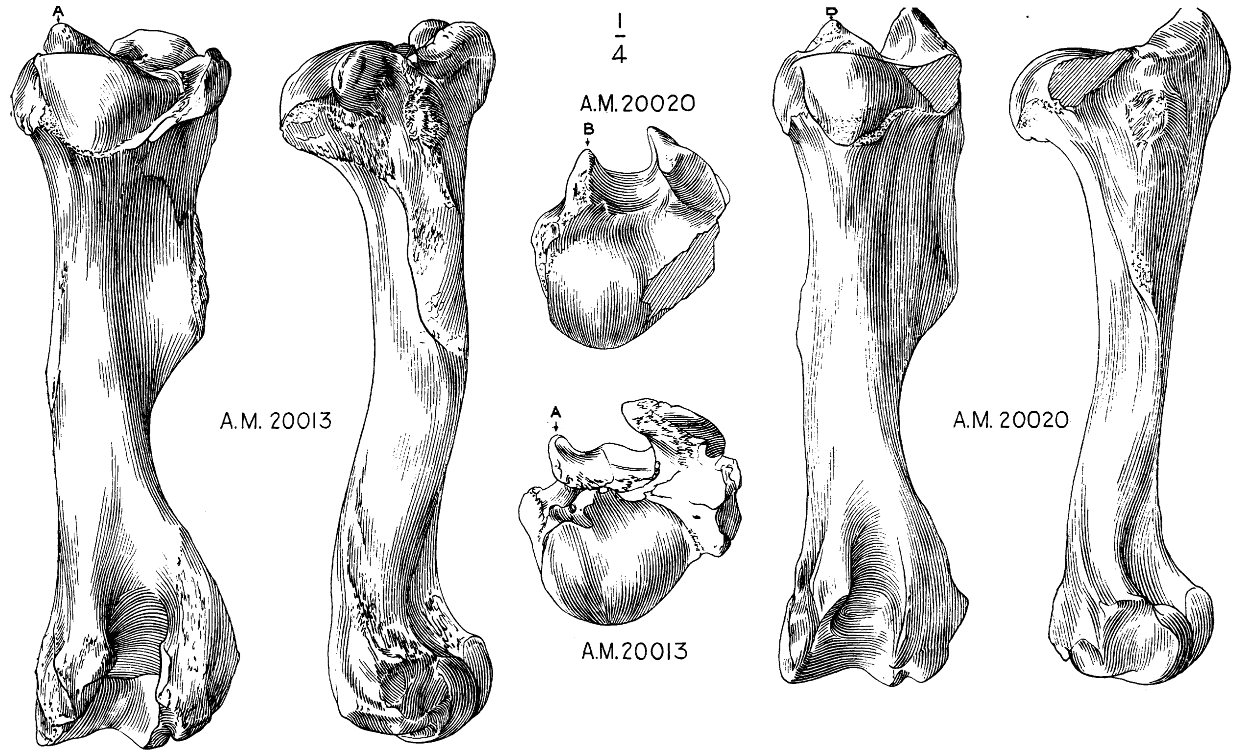


Fig. 32. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20013, right humerus. Dorsal, lateral external and proximal views.

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-

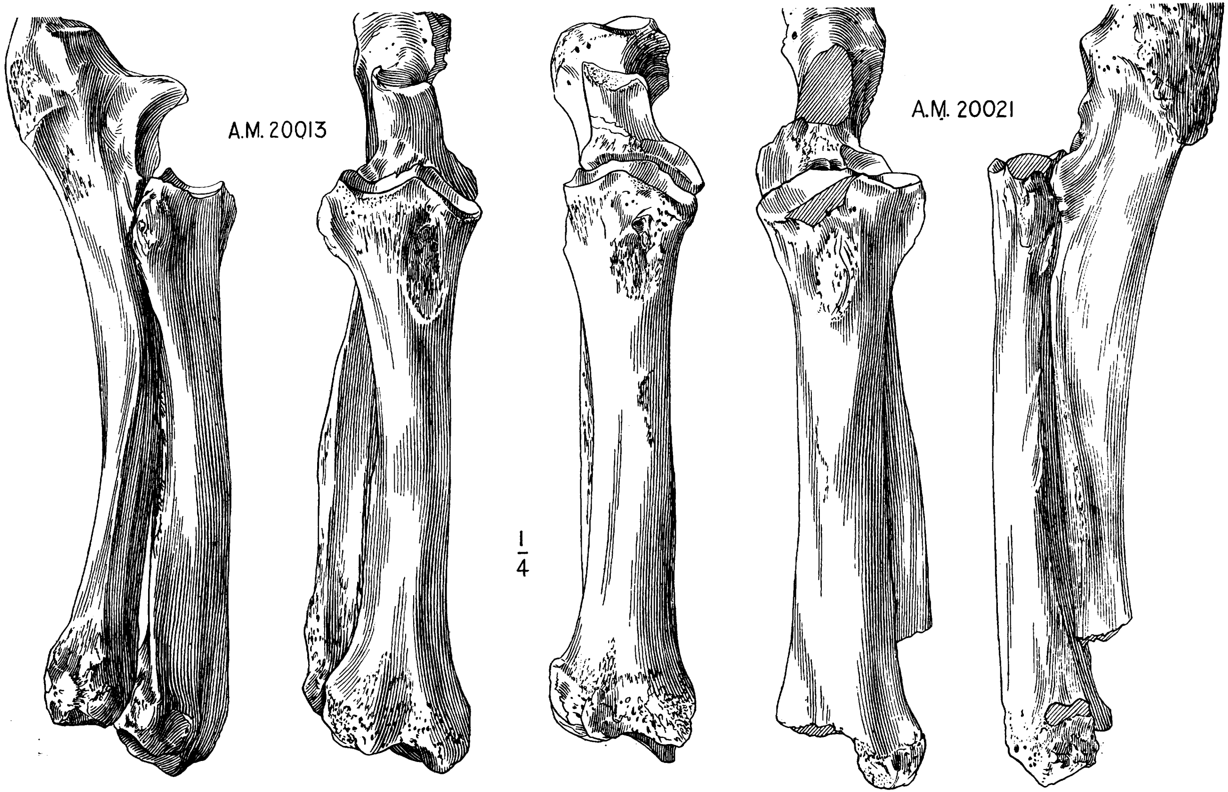


Fig. 33. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20013, right radius and ulna. External lateral and anterior views. Amer. Mus. No. 20032, right radius and ulna. Anterior view. Amer. Mus. No. 20021, left radius and ulna. Anterior and external lateral views. All figures one-fourth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

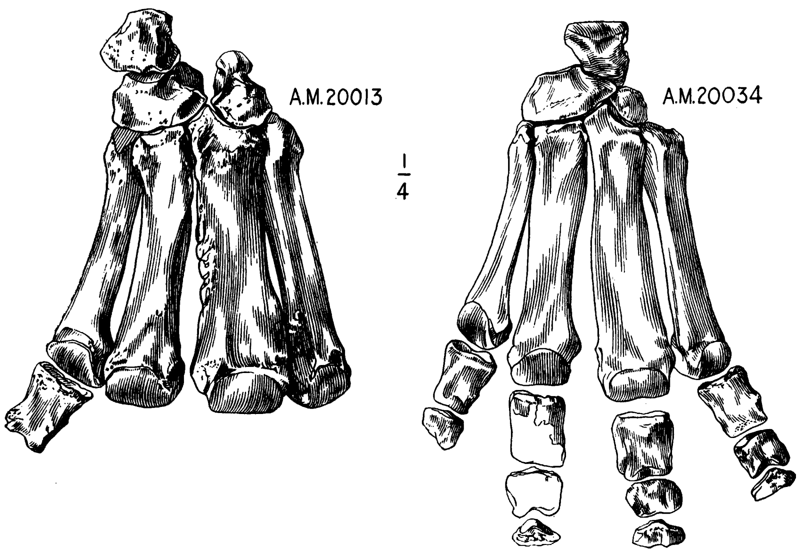


Fig. 34. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20013, right manus, dorsal view. Amer. Mus. No. 20034, right manus, dorsal view. Both figures one-fourth natural size.

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

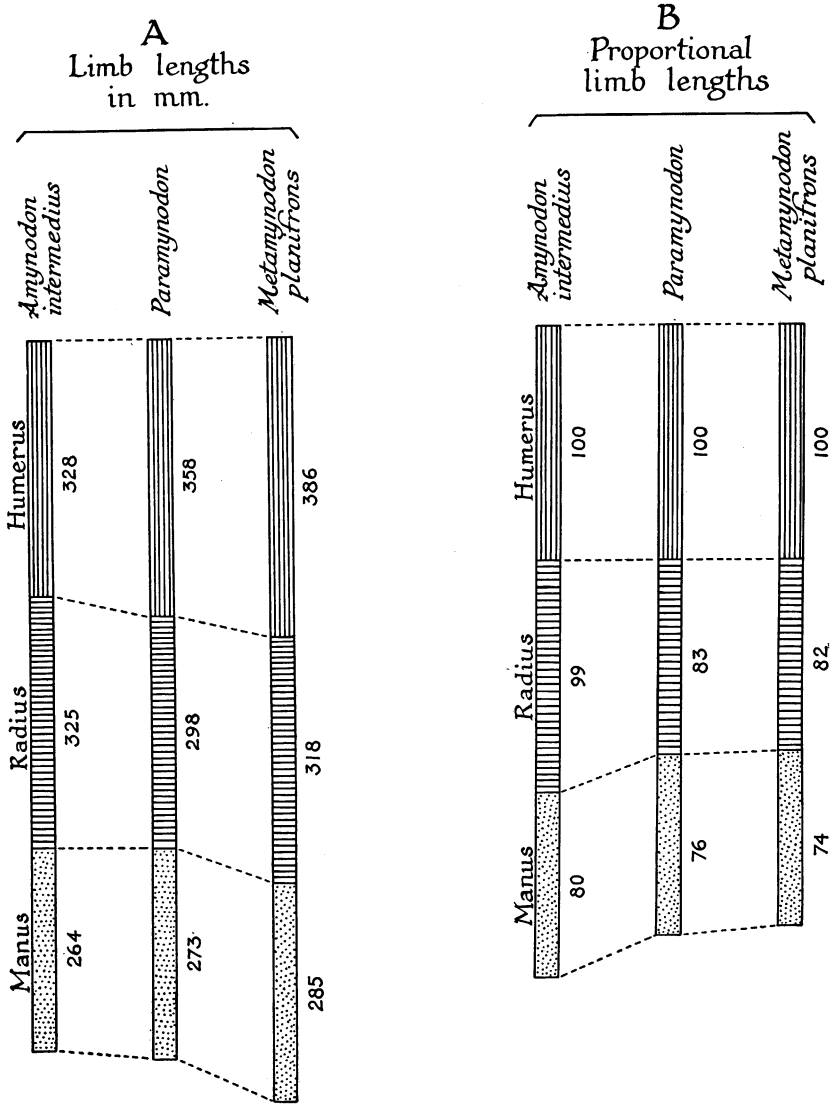


Fig. 35. Diagram to show the comparative lengths of the fore-limbs and their components in three genera of amynodont rhinoceroses.

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

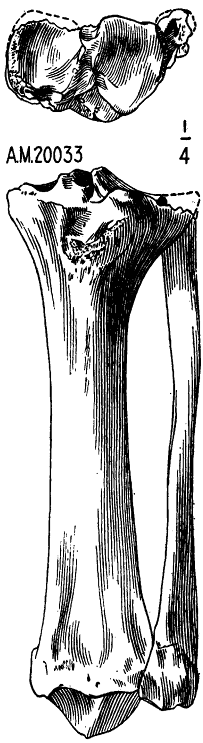


Fig. 36. *Paramynodon birmanicus* (Pilgrim and Cotter). Amer. Mus. No. 20033, left tibia and fibula. Proximal view above, anterior view below; one-fourth natural size.

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.

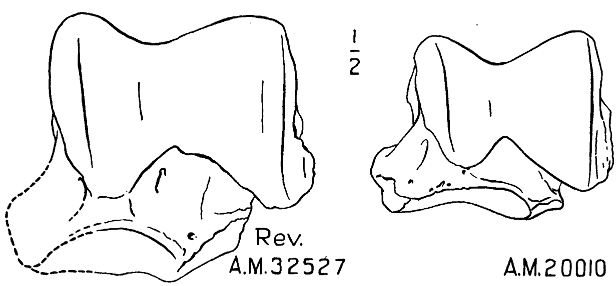


Fig. 37. Astragalus of *Paramynodon* (Amer. Mus. No. 20010) compared with the astragalus of a Pondaung titanothere (Amer. Mus. No. 32527). Figures one-half natural size.

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.

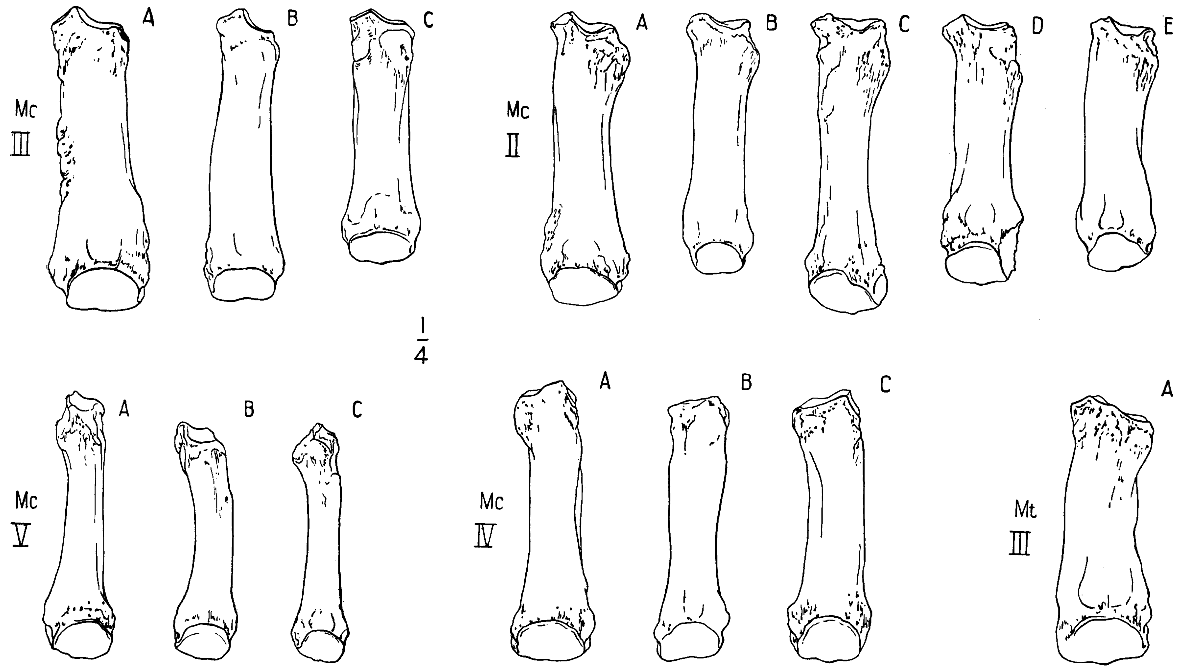


Fig. 38. Variability in the metacarpals of *Paramynodon*. A: 20013. B: 20034. C: (Mc. II) 32539; (Mc. III) 32538; (Mc. IV) 32534; (Mc .V) 32532. D: 32541. E: 32535. A: (Mt. III) probably associated with 20013. All figures one-fourth natural size.

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.)

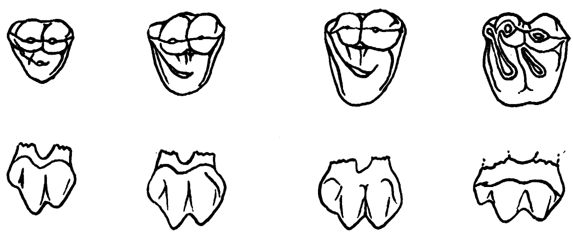


Fig. 39. *Indolophus guptai* Pilgrim. G.S.I. No. C347, type upper premolars and first molar. Crown views above, external views below. Natural size. (From Matthew, 1929.)

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$^1/_2$ 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.

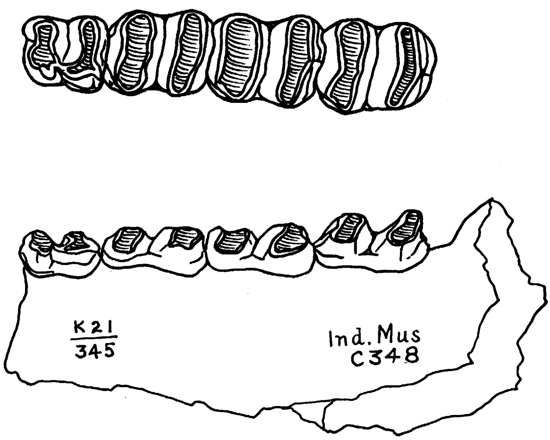


Fig. 40. *Deperetella* (?) *birmanicum* (Pilgrim). G.S.I. No. C348, type left mandibular ramus. Crown view above, lateral view below. Natural size. (From Matthew, 1929.)

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.

ARTIODACTYLA

ANTHRACOTHERIOIDEA

Anthracotheriidae

The artiodactyl element of the Pondaung fauna consists almost exclusively of anthracotheres. In his first description of the Eocene mammals of Burma, Pilgrim made the following remarks about the anthracotheres.

> The family of the *Anthracotheriidae* dominates the fauna of the Pondaung sandstones to such an extent that some 95 per cent. of the total number of specimens contained in the present collection belong to it. This preponderance can be illusory only in as much as the fauna was doubtless one which inhabited the plains and marshes in the neighbourhood of great rivers and from which most of the species of the forests and uplands were excluded. Since, however, similar conditions tend to prevail in all river deposits, we may fairly claim that the extent to which the Anthracotheroids are represented in this formation is excessive when compared with any other fauna at present known to us, with the exception of that of the Upper Aquitanian beds of the Bugti hills, which probably equals it. (Pilgrim, G. E., and Cotter, G. de P., 1916, p. 48.)

These remarks were made, of course, before the numerous amynodonts had been discovered in the Pondaung beds. Nevertheless the anthracotheres are extraordinarily abundant in the Eocene of Burma, and the fact that they represent a river shore facies is upheld by the remains of aquatic rhinoceroses.

ANTHRACOHYUS PILGRIM AND COTTER, 1916

PILGRIM, G. E., AND COTTER, G. DE P., 1916, Rec. Geol. Surv. India, XLVII, pp. 48–51.

PILGRIM, G. E., 1928, Mem. Geol. Surv. India, (N. S.) XIII, p. 6.

GENERIC TYPE.—*Anthracohyus choeroides* Pilgrim and Cotter.

AUTHOR'S DIAGNOSIS.—UPPER MOLARS.—5-cuspidate, paracone and metacone markedly bunodont on account of the entire absence of a parastyle and metastyle, and the very feeble development of a mesostyle. A cingulum encircles the cusps externally, as well as on the anterior and posterior margins.

UPPER PREMOLARS.—Pm^4 bicuspid, both cusps bunodont, cingulum external, anterior and posterior; pm^3 triangular, longer than broad, pointed anteriorly, main cusp with anterior and posterior ridges opposite to one another; inner cusp strong, connected by cingula to the main cusp, but without any broad flattened area between it and the main cusp.

LOWER MOLARS.—Cusps rather bunodont, hinder arm of the postero-external crescent not uniting with the postero-internal cusp. Thus the valley between the two posterior cusps is convex; m_3 talon showing a distinct division into two cusps.

LOWER PREMOLARS.—Pm_4 elongated, main cusp with anterior and posterior ridges, inner ridge separated by a groove from posterior ridge, small flattened area between the two ridges at the hinder end of the tooth, a slight cingulur cusp anteriorly, anterior premolars elongated, main cusp laterally compressed with two blades but without inner ridge, a faint posterior cingular cusp.

LOWER CANINE laterally compressed, premolariform, only slightly larger than pm_1.

LOWER INCISORS three, strongly compressed between their convex buccal and concave lingual surfaces, crowded together without a diastema, incisor region of the jaw broad and not elongated.

REVISED DIAGNOSIS (Pilgrim).—Upper molars bunodont, without parastyle or mesostyle, lateral diameter much in excess of the antero-posterior diameter, the latter diminishing from the inside to the outside of the tooth. Main cusps conical, with the same ridges as in *Anthracothema* but less pronounced, protoconule prominent, metaconule large, no hypocone; no internal cingulum.

As stated under the head of the single species *Anthracohyus choeroides* the genus is now restricted to the genotype, the other species referred to it by Pilgrim and Cotter, being now separated under the generic name of *Anthracothema.* Since a single upper molar is all that is at present known, a complete diagnosis is impossible.

There is no justification afforded by this for placing it in another family than the *Anthracotheriidae.* It differs from *Choeropotamus* by the absence of a mesostyle, of an internal cingulum, by the more prominent metaconule, and by the greater breadth of the upper molars. Its affinities to no other genus seem to be as close as to *Anthracothema*, but the discovery of additional material may tend to disprove this opinion. (Pilgrim, G. E., 1928, p. 6.)

Anthracohyus choeroides Pilgrim and Cotter

Anthracohyus choeroides, PILGRIM AND COTTER, 1916, Rec. Geol. Surv. India, XLVII, pp. 52–55, Pl. II, figs. 1–4.

Anthracohyus choeroides, PILGRIM, 1928, Mem. Geol. Surv. India, (N. S.) XIII, p. 7.

TYPE.—G.S.I. No. B603, an isolated upper molar.

PARATYPES.—G.S.I. No. B604, a P^3; G.S.I. No. B605, a right mandibular ramus with complete dentition.

HORIZON.—Pondaung, Eocene.

LOCALITY.—$^3/_4$ mile W.S.W. of hill 1133 in the Myaing township, Burma.

DIAGNOSIS.—The diagnosis is the same as that given for the genus (above).

As they [Pilgrim and Cotter] have emphasized, neither parastyle nor mesostyle are present; in the position which the mesostyle would occupy, there is only visible a serrated ridge which is not the least elevated above the cingulum which surrounds the paracone and metacone. The antero-posterior diameter of the tooth is less on the outer than on the inner side, and the breadth index is considerable, even supposing the tooth to be m^2, which is quite probable, even though there is no sign of a facet of wear on its hinder margin. In the characters indicated it is so strikingly different from all the other upper molars of these beds, that I feel that it is entitled to generic separation. In that case it alone must retain the name of *Anthracohyus;* the remainder included in the same genus by Pilgrim and Cotter will receive the name of *Anthracothema.* (Pilgrim, G. E., 1928, p. 7.)

ANTHRACOTHEMA PILGRIM, 1928

PILGRIM, G. E., 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 7–10.

GENERIC TYPE.—*Anthracotherium pangan* Pilgrim and Cotter.

AUTHOR'S DIAGNOSIS.—Moderately large Anthracotheroids, with long premolar series, and probably long snout; mandibular symphysis long, probably reaching back to p_3; lower margin of ramus slightly concave behind the molars, but without a descending flange. UPPER MOLARS 5-cuspidate; paracone and metacone conical, not compressed; parastyle either absent or very feeble; mesostyle weak; protocone conical; metaconule crescentic and as large as the metacone; no hypocone; cingulum strong and only absent internally; UPPER PREMOLARS—p^4 bicuspid, cusps bunodont, cingulum only absent internally; p^3 triangular, longer than broad, pointed in front, prominent inner cusp, situated just behind the middle of the tooth, front and hinder ridges in the anteroposterior plane. LOWER MOLARS narrower in front than behind, cusps bunodont, inner walls of metaconid and entoconid sloping toward the centre of the tooth, arms of the outer cusps short, not reaching as far as the inner cusps; talonid of m_3 short, with a shallow valley, hypoconulid low sometimes with a double cusp. LOWER PREMOLARS long, p_2–p_4 double-rooted, p_1 single-rooted, all with anterior convex and posterior concave ridges, p_4 with strong posterior cingulum and with a faint inner ridge, p_3 longer than p_4, with weak posterior cingulum and no inner ridge. LOWER CANINE large, with almost circular cross section, upright, grinding against the upper canine.

Anthracothema pangan (Pilgrim and Cotter)

Anthracotherium pangan, PILGRIM AND COTTER, 1916, Rec. Geol. Surv. India, XLVII, pp. 59–60, Pl. IV, figs. 1–3.

Anthracohyus rubricae (in parte), PILGRIM AND COTTER, 1916, Rec. Geol. Surv. India, XLVII, p. 56, Pl. II, fig. 7; Pl. III, fig. 6.

Anthracotherium crassum, (in parte), PILGRIM AND COTTER, 1916, Rec. Geol. Surv. India, XLVII, p. 60, Pl. IV, fig. 4.

Anthracothema pangan, PILGRIM, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 10–13, Pl. I, figs. 1–7.

LECTOTYPE.—Second and third left upper molars. G.S.I. No. B619. (Rec. Geol. Surv. India, 1916, XLVII, Pl. IV, figs. 1, 1a.)

COTYPES.—G.S.I. No. B620, last lower molar. G.S.I. No. B618, a p^3.

HORIZON.—Pondaung, Eocene.

LOCALITY.—Not stated for the types. Referred specimens came from Than-u-daw village, Myaing township, and from Gyat.

DIAGNOSIS (Revised).—A rather large anthracothere. Last upper premolar with a large inner cusp and a single outer cusp. Upper molars five cusped; protocone, paracone and metacone tending to be conical, while the protoconule and metaconule are somewhat crescentic. Parastyle weak; no internal cingulum. Lower canine large, with a nearly circular cross section. First lower premolar single rooted; last three lower premolars double rooted and forming a closed series. Lower premolars simple, with a single central cusp having anterior and posterior ridges, and with a posterior cingular shelf. Lower molars narrower anteriorly than posteriorly; cusps bunodont. Wings of outer cusps short, not reaching the inner cusps. Hypoconulid of third molar rather broad. Mandible seemingly elongated.

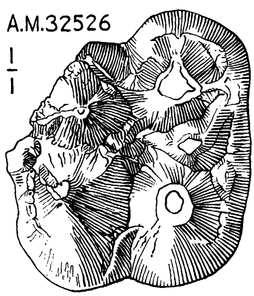
Specimens in the American Museum:

Amer. Mus. No. 20006, a fragmentary left mandibular ramus containing the third molar. (Associated with this specimen were some broken teeth of *Paramynodon.*) From the Pondaung beds, one mile northeast of Gyat. (Map, Fig. 8, locality A23.)

Amer. Mus. No. 32523, a right lower third molar; also the heel of another lower third molar. Doubtfully referred to this species. From the Pondaung beds, one mile north of Koniwa. (Map, Fig. 8, locality A21.)

Amer. Mus. No. 32524, the inner portion of an upper molar. From the Pondaung beds, one and one-half miles northwest of Myaing. (Map, Fig. 11, locality 7.)

Amer. Mus. No. 32526, a right second and third upper molar. From the Pondaung beds, locality unknown.



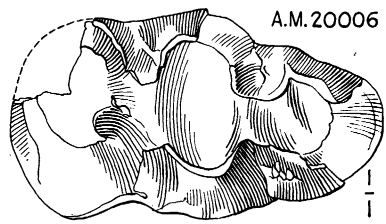


Fig. 41. *Anthracothema pangan* (Pilgrim and Cotter). Amer. Mus. No. 32526, right M^3. Crown view. Natural size.

Fig. 42. *Anthracothema pangan* (Pilgrim and Cotter). Amer. Mus. No. 20006, left M_3. Crown view, natural size.

MEASUREMENTS

Anthracothema pangan

Amer. Mus. No. 32526				G.S.I. No. B619, lectotype			
M^2	length	24 mm.		M^2	length	27.2 mm.	
	width	29			width	27.4	
	index		120		index		100
M^3	length	32		M^3	length	34.1	
	width	36.5			width	36.5	
	index		114		index		107
Amer. Mus. No. 20006				G.S.I. No. B620, cotype			
M_3	length	49 mm.		M_3	length	47.2 mm.	
	width	27			width	25.4	
	index		55		index		54

Little need be said about these additional specimens of *Anthracothema pangan*. They exemplify very well the generic and specific characters of this form, as set forth and illustrated by Pilgrim.

The upper molars are very large, low-crowned and quinquetubercular. The cusps, except the metaconule, are conical. The parastyle and mesostyle are not strongly developed, but there is a heavy anterior, posterior and external cingulum. The enamel is rugose.

The large lower molar (No. 20006) is worn, so that the distinctive characters of the cusps have disappeared. All that can be said of this tooth is that it is very robust and has a wide heel. The other lower molar (No. 32523) is distinguished by its decidedly crescentic outer cusps. This specimen is only provisionally referred to the species under consideration.

Anthracothema palustre (Pilgrim and Cotter)

Anthracohyus palustris, Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, p. 58, Pl. iii, figs. 7–9.

Anthracothema palustre, Pilgrim, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 14–16, Pl. ii, figs. 8–10.

Type.—G.S.I. No. B606, a left upper third molar, also another upper molar.

Paratypes.—G.S.I. No. B608, a third upper premolar; G.S.I. No. B607, a last lower molar.

Horizon.—Pondaung, Eocene.

Locality.—Myaing township, Pakokku district, Burma.

Diagnosis (Revised).—A large species comparable in size to *Anthracothema pangan*. It is distinguished especially by the internal and posterior protuberance or swelling of the base of the upper molars, and by a similar swelling on the anterior and external sides of the lower molars. The protocone and hypocone rise suddenly from this basal swelling or enlarged cingular shelf. Molar cusps very robust and bunodont, teeth brachyodont.

This species is probably synonymous with *Anthracothema pangan*. See below (p. 384) the discussion, "The Pondaung Anthracotheres."

Anthracothema crassum (Pilgrim and Cotter)

Anthracotherium crassum, Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, pp. 60–61, Pl. iv, figs. 4, 5; Pl. v, fig. 1.

Anthracothema crassum, Pilgrim, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 16–18.

Type.—Left first and second upper molars. (1916, Rec. Geol. Surv. India. XLVII, Pl. v, fig. 1.)

Paratypes.—G.S.I. No. B616, fourth upper premolar; G.S.I. No. B617, a mandible.

Horizon.—Pondaung, Eocene.

Locality.—Myaing township, Pakokku district, Burma.

Diagnosis (Revised).—Similar to *Anthracothema pangan*, but smaller and more brachyodont. Heel of lower third molar narrower than in *Anthracothema pangan*.

This species is closely related to *Anthracothema pangan* and *Anthra-*

cothema rubricae. A detailed discussion of its probable relationships is presented below (p. 348), in "The Pondaung Anthracotheres."

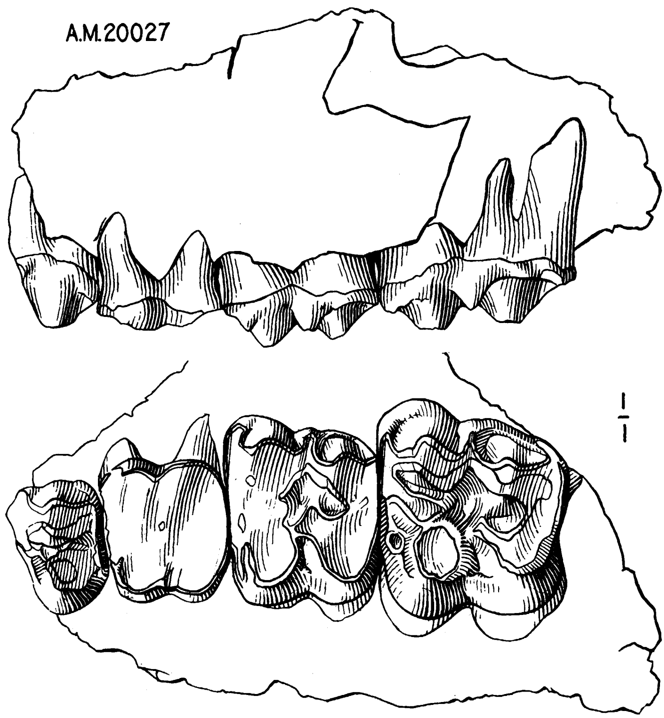


Fig. 43. *Anthracothema rubricae* (Pilgrim and Cotter). Amer. Mus. No. 20027, left P^4–M^3. External view above, crown view below. Natural size.

Anthracothema rubricae (Pilgrim and Cotter)

Anthracohyus rubricae, Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, p. 55, Pl. II, figs. 5–7; Pl. III, figs. 1–6.

Anthracothema rubricae, Pilgrim, 1928, Mem. Geol. Surv. India, (N. S.) XIII, p. 14, Pl. II, figs. 1–7.

Type.—G.S.I. No. B609, a right M^3; G.S.I. No. B610, a right M^2.

Paratypes.—G.S.I. No. B611, a P^4; G.S.I. No. B612, left lower third molar; G.S.I. No. B613, portion of left ramus of mandible.

Horizon.—Pondaung, Eocene.

Locality.—Myaing township, Pakokku district, Burma.

Diagnosis (Revised).—Somewhat smaller than *Anthracothema pangan*, with a distinctly shorter lower premolar series. Parastyle and mesostyle of upper molars very weak or absent.

Specimens in the American Museum:

Amer. Mus. No. 20027, a left maxilla with P^4–M^3. (Associated with this specimen are some broken teeth and foot bones of *Paramynodon.*) From the Pondaung beds, one-half mile northeast of Kyawdaw. (Map, Fig. 8, locality A27.)

Amer. Mus. No. 20029, a right lower third molar. From the Pondaung beds, one mile northwest of Mogaung. (Map, Fig. 8, locality 15.)

Amer. Mus. No. 32525, a fourth upper premolar and a left upper first molar. From the Pondaung beds, one mile north of Koniwa. (Map, Fig. 8, locality A21.)

The maxilla, Amer. Mus. No. 20027, would seem to be referable to the genus *Anthracothema* because of the rounded, conical cusps of the molar teeth. In this specimen the parastyle and the mesostyle are

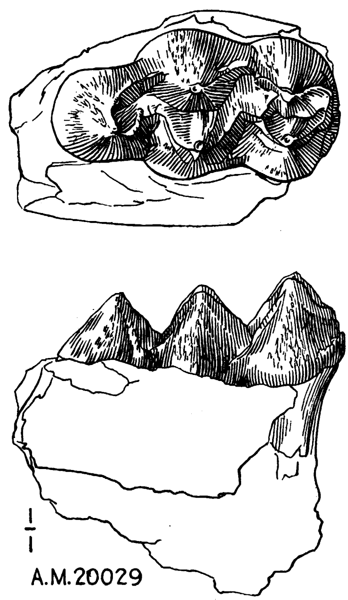


Fig. 44. *Anthracothema rubricae* (Pilgrim and Cotter). Amer. Mus. No. 20029, right M_3. Crown view above, external view below. Natural size.

fairly well developed, more so than in the typical *Anthracothema* but less so than in the typical *Anthracokeryx.* Thus in this one respect the teeth of the present specimen are more or less intermediate between the two genera. It is to be remembered, however, that the development of the styles and the cingula in teeth are subject to a great deal of individual variation, as is evident to anyone studying a large series of teeth of a single species, and so these features must not be given too much importance as diagnostic characters. Thus the specimen now under consideration would seem to be an *Anthracothema* with rather heavy outer styles, in which respect it shows some resemblance to *Anthracokeryx*. It is placed in the species *A. rubricae* because of its size.

The two teeth (No. 32525) are referred to *A. rubricae* more on the basis of their size and general appearance than because of any specifically diagnostic characters shown by them. They are badly broken and weathered so that this identification must be considered as a tentative one.

The single lower molar is a perfect tooth, untouched by wear. The enamel is rather strongly rugose, a character to be seen in the upper teeth also (No. 20027) but not so apparent because those teeth are very much worn. In this tooth the cusps are sharp, as are the arms that lead from the outer cusps (the protoconid and the hypoconid) to the middle of the tooth. The characters of this specimen are shown in the accompanying figure (Fig. 44).

MEASUREMENTS

Anthracothema rubricae

Amer. Mus. No. 20027				G.S.I. Nos. B609, B610, type			
P^4	length	12.5 mm.					
	width	17.5					
	index		140				
M^1	length	16					
	width	19					
	index		119				
M^2	length	19.5		M^2	length	25.3 mm.	
	width	25			width	30.7	
	index		128		index		121
M^3	length	26		M^3	length	31.9	
	width	28.5			width	34.3	
	index		110		index		107
Length of molar series		62 mm.					
Length of M^2–M^3		45.5		Length of M^2–M^3			57.2 mm.

45.5/57.2 = 80/100

Amer. Mus. No. 20029				G.S.I. No. B613, paratype			
M_3	length	38 mm.		M_3	length	38.1 mm.	
	width	20			width	20.5	
	index		53		index		54

Anthracothema sp. indet.

Specimens in the American Museum:

Amer. Mus. No. 32522, fragment of a left mandibular ramus with two lower molars. From the Pondaung beds, one mile north of Koniwa. (Map, Fig. 8, locality A21.)

Amer. Mus. No. 20024, fragment of a right maxilla with two broken molars. From the Pondaung beds, near Kyawdaw. (Map, Fig. 8, locality A26.)

Amer. Mus. No. 20028, fragment of a left mandibular ramus with P_{3-4}. From the Pondaung beds, one mile northwest of Mogaung. (Map, Fig. 8, locality A23.)

In the first two of the above listed specimens the teeth are so badly worn and broken as to make specific identification impossible. The lower premolar teeth are of a medium-sized species of *Anthracothema*, possibly referable to *Anthracothema rubricae.*

ANTHRACOKERYX PILGRIM AND COTTER, 1916

PILGRIM, G. E., AND COTTER, G. DE P., 1916, Rec. Geol. Surv. India, XLVII, pp. 61–62.

PILGRIM, G. E., 1928, Mem. Geol. Surv. India, (N. S.) XIII, p. 17.

GENERIC TYPE.—*Anthracokeryx birmanicus* Pilgrim and Cotter.

DIAGNOSIS (Revised; Pilgrim).—Small Anthracotheroids, with skull rather high but narrow in the parietal region, diminishing fairly rapidly in height and breadth towards the tip of the snout. Snout narrow and elongated; mandibular symphysis long reaching back to p_3; long premolar series; lower margin of ramus slightly concave behind the molars but without a descending flange. UPPER MOLARS 5-cuspidate; paracone and metacone conical but somewhat compressed; parastyle well marked; mesostyle well marked but low; protocone and metaconule crescentic; no hypocone; anterior and posterior cingulum present but varying in intensity, external cingulum strong or almost wanting, internal cingulum present or absent. UPPER PREMOLARS long; p^4 bicuspid, outer cusp crescentic; p^3 longer than broad, blade compressed, inner cusp situated just behind the middle of the tooth, front and hinder ridges approximately in the antero-posterior plane; p^2 longer than p^3, 2-rooted; p^1 separated by long diastemata from p^2 and the canine, probably 1-rooted. UPPER CANINE with a large root somewhat compressed. LOWER MOLARS generally narrower in front than behind, cusps bunodont, inner wall of inner cusps somewhat flattened and vertical, arms of the outer cusps short, not reaching as far as the inner cusps; talonid of m_3 with a shallow valley, hinder cusp either single or double, high. LOWER PREMOLARS long, p_2–p_4 double-rooted, p_1 single-rooted with anterior convex and posterior concave ridges, flattened on the inner side; p_4 with small posterior cingulum and a marked inner ridge; p_3 longer than p_4, with a faint posterior cingulum, with or without an incipient inner ridge; p_2 and p_1 well spaced both from one another and from the canine and p_3, smaller than p_3 similar in structure but without an inner ridge. LOWER CANINE with large root, but reduced crown, laterally compressed, flattened on inner side, procumbent, not grinding against the upper canine but against the last upper incisor. Lower incisors very procumbent. (Pilgrim, G. E., 1928, p. 17.)

Anthracokeryx birmanicus Pilgrim and Cotter

Anthracokeryx birmanicus, PILGRIM AND COTTER, 1916, Rec. Geol. Surv. India, XLVII, pp. 61–62, Pl. v, figs. 2–5.

Anthracokeryx birmanicus, PILGRIM, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 18, 19, Pl. IV, figs. 5, 5a.

TYPE.—G.S.I. No. B621, a right maxilla.

PARATYPES.—G.S.I. No. B624 third and fourth upper left milk molars; G.S.I. No. B623, portion of mandible and last left lower molar.

HORIZON.—Pondaung, Eocene.

LOCALITY.—Myaing township, Pakokku district, Burma.

AUTHOR'S DIAGNOSIS.—The type of this genus and species is a right maxilla (G.S.I. No. B.621; Pl. v, fig. 2) containing the three molars and the two hinder premolars. The molars resemble those of *Microbunodon* in structure, having fairly pronounced outer styles and thus a greater tendency to selenodonty than in the case of *Anthracohyus*. From the latter genus, as from *Anthracotherium*, they differ also by the absence of a protostyle. Pm^4 seems to differ in no essential respect from that of *Microbunodon;* pm^3 has, however, an entirely different shape to the corresponding tooth in that genus. Instead of being almost equilaterally triangular with a broad cingulum on two of these sides and no prominent inner cusp, it is elongated and in outline is almost identical with pm^3 of *Anthracohyus*. The wear of the tooth in its hinder portion prevents us from comparing it in greater detail. *Rhagatherium* and *Haplobunodon* resemble *Microbunodon* in the structure of pm^3.

UPPER MILK MOLARS.—The specimen (G.S.I. No. B.624) figured in Pl. v, fig. 4, containing the last two left milk molars, may reasonably be referred to this species. Mm^4 differs in no respect from the permanent molars which have just been described, and might be that of a *Microbunodon*. Mm^3 differs from that of *Anthracotherium* and *Microbunodon* by the much greater elongation of the front part of the tooth and by the absence, or at all events feeble development, of the mesostyle. . . .

LOWER MOLARS.—The only lower molar which might from its size belong to the upper molars of *Anthracokeryx birmanicum* is the fragment (G.S.I. No. B.623; Pl. v, fig. 5) containing the hinder portion of m_3. The most noteworthy feature about the talon of this tooth is the absence of any distinct double cusp. It agrees in this respect with the various last lower molars from the Lower Siwaliks referred to the species *Anthracotherium* (*Microbunodon*) *silistrense* Pentland, as well as with *Anthracotherium* (*Microbunodon*) *mus* Pilg. The European species of *Microbunodon*, however, appear to have two cusps in the talon.

Specimen in the American Museum:

Amer. Mus. No. 20015, a right M^3 and various fragments of the mandible containing the right M_3 and the left M_3, respectively. From one mile west of Bahin. (Map, Fig. 10, locality 11.)

The upper molar in the American Museum collection referred to this species is somewhat larger than the corresponding tooth of the type. It is clearly referable to the genus *Anthracokeryx*, by virtue of its compressed paracone and metacone, strong parastyle and mesostyle and its somewhat crescentic metaconule. The lower teeth are closely comparable to the lower molars referred by Pilgrim to *A. birmanicus* in his 1928 memoir, although here a direct comparison cannot be made, since there was no third molar in the specimen figured by Pilgrim. The correspondence in size would seem to be very close however, between the second molar of Pilgrim's specimen and the third molar of the American Museum specimen, basing the comparison on the increase of size in the

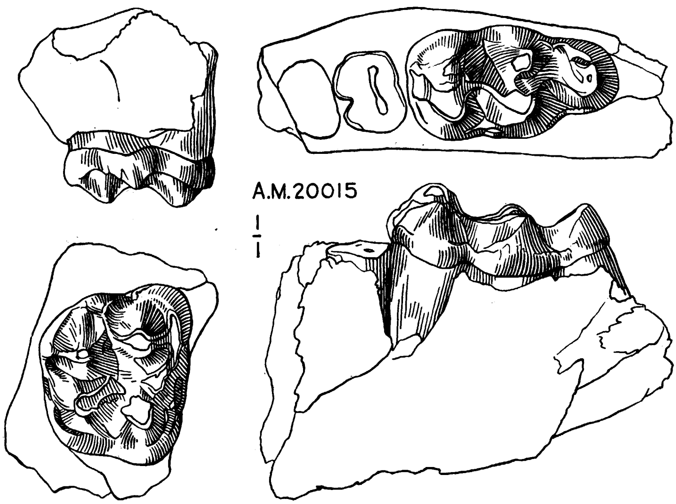


Fig. 45. *Anthracokeryx birmanicus* Pilgrim and Cotter. Amer. Mus. No. 20015. On left; right M^3, external view above, crown view below. On right; left M_3, crown view above, external view below. Natural size.

molars of other species of *Anthracokeryx*. These lower molars now under consideration are somewhat smaller than the lower molars of *Anthracokeryx hospes*, here considered as a large variety of *Anthracokeryx birmanicus* (see below, page 388).

The jaw fragments indicate a heavy, robust mandibular ramus.

MEASUREMENTS

Amer. Mus. No. 20015

M^3	Length	20 mm.	Width	23.5 mm.
M_3		28.5		15

COMPARATIVE MEASUREMENTS, RATIOS AND INDICES

Anthracokeryx birmanicus

G.S.I. No. B621, Type	M^3	Length 16.2 mm.	Width 19.0 mm.	Index[1] 117
Amer. Mus. No. 20015	M^3	20.0	23.5	117
		16.2/20 = 100/123		

[1] Length = 100.

Therefore the M^3 in the American Museum is about one-fifth again as large linearly as the M^3 of the type. The relation of length to breadth in the two teeth is the same.

Anthracokeryx birmanicus				*Anthracokeryx hospes* (= *A. birmanicus*)			
G.S.I., B757	M_1 length	12.7 mm.		G.S.I., B605	M_1 length	13.4 mm.	
	M_2	15.2			M_2	17.4	
			27.9				30.8
Am. Mus.	M_3	28.5			M_3	29.8	
20015		56.4				60.6	
	12.7/15.2/28.5				13.4/17.4/29.8		
	1 1.20 2.24				1 1.30 2.22		
	56.4/60.6 = 100/108				27.9/30.8 = 100/110		

The M_3 in the American Museum holds the same relationship in its length to the M_1 of the jaw referred by Pilgrim to *Anthracokeryx birmanicus* as does the M_3 to the M_1 in the type mandible of *Anthracokeryx hospes.*

The linear difference between the combined length of the lower molars in the type of *Anthracokeryx hospes* and the referred lower teeth of *Anthracokeryx birmanicus* is 8 per cent, considering the molar length in *A. birmanicus* to be 100. In the same way, this difference on the basis of the first and second molar lengths combined, is about 10 per cent.

Anthracokeryx hospes Pilgrim

Anthracohyus choeroides (in parte), Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, p. 53, Pl. II, figs. 3–3e, 4–4e.

Anthracokeryx hospes, Pilgrim, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 29–30.

Type.—G.S.I. No. B605, a mandibular ramus and associated lower dentition.

Paratypes.—None.

Horizon.—Pondaung, Eocene.

Locality.—Myaing township, Pakokku district, Burma.

Author's Diagnosis.—I have on page 7 stated my reasons for regarding the isolated m^3 which was taken by Pilgrim and Cotter as the type of the species *Anthracohyus choeroides* as generically different from all the other upper molars which those authors referred to the genus *Anthracohyus.* No such marked difference can be detected in the case of the mandibular ramus (B.605) and the associated lower dentition which Pilgrim and Cotter provisionally referred to *A. choeroides.* The sole argument for the reference consisted in the agreement in size with the type m^3. The two were not associated, and it now seems to me quite improbable that such a type of m^3 should possess a mandible which differs so little from the others which are found in the deposit. The differences from the mandibular ramus (B.767) figured in Pl. IV, fig.

5, which there is good reason for regarding as belonging to the same individual as the type maxilla of *Anthracokeryx birmanicus*, are so trifling, that I find myself compelled to refer the ramus (B.605) to the same genus, under the name of *Anthracokeryx hospes*, although there are no upper molars either in Cotter's or Lahiri's collections which agree with it in size. All the teeth differ from those of the genus *Anthracothema* by their narrowness, and by the greater height and flattening of the cusps. In particular the internal wall of the molars rises almost vertically to the summit of the cusps, while in *Anthracothema* it slopes perceptibly towards the center of the tooth. The inner ridge of p_4 is more prominent, and in general the outline of the tooth has a tendency to taper more than in *Anthracothema* both in front and behind.

From *Anthracokeryx birmanicus* this species is distinguished by the absence of an external cingulum in the posterior part of p_4, and from *Anthracokeryx ulnifer* by the convex internal wall of p_4. In point of size it exceeds both of these species.

This species is here regarded as being synonymous with *Anthracokeryx birmanicus*. The evidence for this conclusion is presented below, (p. 388) in "The Pondaung Anthracotheres."

Anthracokeryx bambusae Pilgrim

Anthracokeryx birmanicus (in parte), PILGRIM AND COTTER, 1916, Rec. Geol. Surv. India, XLVII, p. 62, Pl. v, figs. 3, 5.

Anthracokeryx bambusae, PILGRIM, 1928, Mem. Geol. Surv. India, (N. S.), XIII, p. 29.

TYPE.—G.S.I. No. B622, a right maxilla containing M^2 and M^3. (Pl. v, fig. 3, Rec. Geol. Surv. India, 1916).

PARATYPE.—G.S.I. No. B623, a hinder fragment of M_3.

HORIZON.—Pondaung, Eocene.

LOCALITY.—Myaing township, Pakokku district, Burma.

AUTHOR'S DIAGNOSIS.—The type of this species is a fragment of the right maxilla containing m^2 and m^3, figured by Pilgrim and Cotter in the paper quoted above under the name of *Anthracokeryx birmanicus*. It is practically certain that the hinder fragment of the left m_3 described by Pilgrim and Cotter on page 62 and figured in Pl. v, fig. 5 of the same paper belonged to the same individual as the maxilla. The two specimens were collected by Cotter in the same locality; they agree exactly in size and in degree of wear; the colour of the bone and the matrix is identical in both. Both the maxilla and m_3 are much too small to belong to the species *A. birmanicus*. The difference of size is more marked in the case of m^2 than in m^3. They are only slightly smaller than the types of *A. ulnifer*, but m^3 differs from that species in the entire absence of an inner cingulum and the weakness of the cingulum on the other sides of the tooth; moreover the parastyle is more prominent. In both these particulars the resemblance is closer to *A. birmanicus*, from which except in regard to the size I can detect no particular difference. The last lower molar equally shows no special points of difference from that of *A. ulnifer*.

The validity of this species is questionable. See the discussion, "The Pondaung Anthracotheres," p. 389, in which it is compared with *Anthracokeryx birmanicus* and *Anthracokeryx tenuis*.

Anthracokeryx tenuis Pilgrim and Cotter

Anthracokeryx tenuis, Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, pp. 62–63, Pl. v, figs. 6–8.

Type.—G.S.I. Nos. B625 and B626, a collection of upper and lower molars.

Paratype.—G.S.I. No. B627, a fragment of a right mandibular ramus.

Horizon.—Pondaung, Eocene.

Locality.—Myaing township, Pakokku district, Burma.

Author's Diagnosis.—We place here a collection of upper and lower molars (G.S.I. Nos. B.625 and B.626; Pl. v, figs. 6, 7) which are much smaller than any hitherto referred to from the Pondaung sandstones, and which one of us collected from a single spot. They are only about one-third of the size of *Anthracokeryx birmanicus*, but differ from the upper and lower molars of that species in no essential points of structure, differing from *Anthracohyus* by the stronger outer styles and by the absence of a protostyle. No specimen of m_3 is included in the collection from this locality.

From another locality comes another fragment of a right mandibular ramus (G.S.I. No. B.627; Pl. v, fig. 8) with m_2 and m_3. This is slightly larger than the molars last described, but this difference in size does not seem beyond the limits of individual variation in the Anthracotheroids. The points in which this specimen differs from the fragment (G.S.I. No. B.623) described under the head of *Anthracohyus birmanicus* are the following:—the ramus is very much shallower; there is no swelling beneath m_3 accompanied nearer the base by a marked groove; the double cusp in the talon of m_3 is quite clearly indicated.

This species is close to *Anthracokeryx ulnifer*. If the two should prove to be synonymous, then the name, *Anthracokeryx tenuis*, would stand. See the discussion below, "The Pondaung Anthracotheres."

Anthracokeryx myaingensis Pilgrim

Anthracokeryx tenuis (in parte), Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, p. 63, Pl. v, fig. 8.

Anthracokeryx myaingensis, Pilgrim, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 30–31, Pl. iii, figs. 4–7.

Type.—G.S.I. No. B759–62, a series of lower teeth.

Paratypes.—G.S.I. No. B627, right mandibular ramus with m_2 and m_3 (Pilgrim and Cotter, 1916, Rec. Geol. Surv. India, XLVII, p. 63, Pl. v, fig. 8). G.S.I. No. B762, a well-preserved crown of a canine.

Horizon.—Pondaung, Eocene.

Locality.—About 3 furlongs N.W. of Than-u-daw village, Burma.

Author's Diagnosis.—The species *Anthracokeryx myaingensis* is intermediate in size between *A. tenuis* and *A. ulnifer*. Structurally I can detect no particular difference between *A. tenuis* and *A. myaingensis*. Certain differences are, however, noticeable between *A. myaingensis* and *A. ulnifer*. The teeth of the former species are relatively narrower, while the talon of m_3 shows a double cusp, which is absent in the latter species. In *A. myaingensis* p_3 is a long narrow tooth tapering at both ends with a flat inner surface and with the cusp bending over to the inside of the jaw, so that the outline is concave in the vertical plane. These teeth are quite unworn and show the posterior ridge which is characteristic of the Anthracotheroids of this deposit. Its edge is slightly concave from summit to base and is serrated. A tiny cusp and small internal and external cingula are present at the base. The anterior ridge has a convex edge and is also serrated. There is no anterior cusp and only the faintest trace of a cingulum. A small but quite distinct internal ridge is visible; this is evidently homologous to the stronger internal ridge which other species of *Anthracokeryx* have on p_4. Whether a similar ridge is present in p_3 of *A. ulnifer* or *A. tenuis* cannot be said, on account of the absence of this tooth in the latter species and the destruction of its crown in the former; it is certainly absent in *A. hospes* and in the genus *Anthracothema.* P_3 is relatively longer than in the species *Anthracokeryx ulnifer.*

Synonymous with *Anthracokeryx tenuis.* See below, "The Pondaung Anthracotheres."

Anthracokeryx ulnifer Pilgrim

Anthracokeryx ulnifer, Pilgrim, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 19–29, Pl. iii, figs. 1–3; Pl. iv, fig. 6.

Type.—G.S.I. No. B755, a mandible; G.S.I. No. B756, a skull; G.S.I. No. B757 a left radius and ulna.

Paratypes.—G.S.I. No. B758, a small canine.

Horizon.—Pondaung, Eocene.

Locality.—$2^1/_4$ miles W. of Paukkaung village, Burma.

Diagnosis (Summarized and Revised).—*Anthracokeryx ulnifer* is a rather small anthracothere, smaller than *A. birmanicus* but larger than *A. tenuis.* The skull is narrow and elongated, with a high sagittal crest. The orbit is open behind and its anterior border is above the anterior edge of the last molar. The occiput is narrow and approximately vertical. The paroccipital processes are very short and they project posteriorly, a condition that holds for the rather large postglenoid processes, as well. The glenoids are shallow and not transversely expanded. The auditory bulla is large and pear-shaped, with the pointed end directed anteriorly. The basicranial foramina would seem to be distinct from each other; not coalesced as in more advanced artiodactyls. The zygomatic arch is slender.

The dental formula is complete. In the upper molars the paracone and metacone are flattened and the parastyle and mesostyle are present, whereby this species resembles the type of the genus. The mesostyle is small; a strong cingulum surrounds each molar. The premolars are relatively long, so that in this respect *Anthracokeryx ulnifer* is comparable to *Ancodon.* The first premolar is separated from the canine and from the second premolar by diastemata. The other premolars are elongated. P^4 is subtriangular, with a somewhat crescentic outer cusp.

The mandible is narrow and long with a shallow ramus, by which characters it resembles *Ancodon.* The lower border forms a fairly straight line rather than a strongly convex edge.

The lower molars have bunodont cusps, similar in structure to the cusps in *Anthracothema.* The first and second lobes of the molars are approximately equal in width, a difference between this species and members of the genus *Anthracothema.* The hypoconulid of the third molar is distinct, not closely fused to the tooth. The lower premolars are elongated and the inner surface of the fourth premolar is flattened,

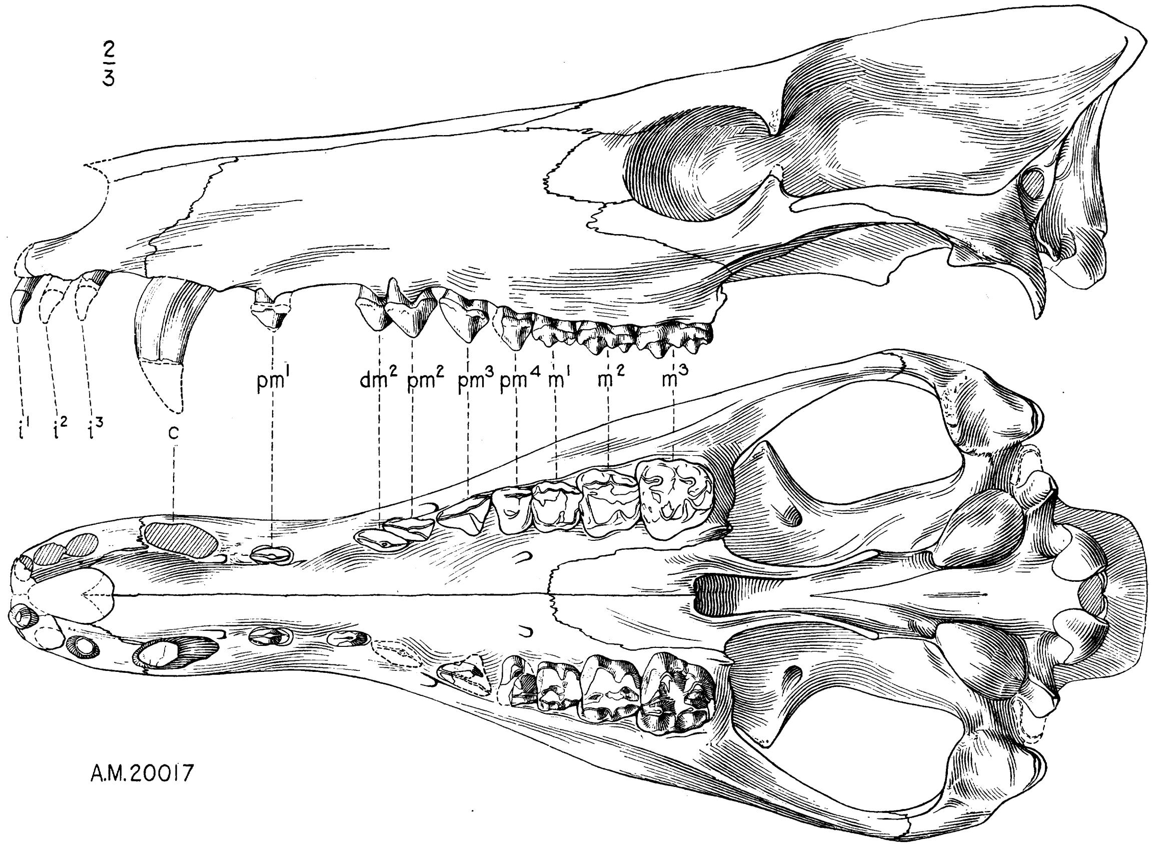


Fig. 46. *Anthracokeryx ulnifer* Pilgrim. Amer. Mus. No. 20017, skull. Lateral view of the left side above, palatal view below. Two-thirds natural size.

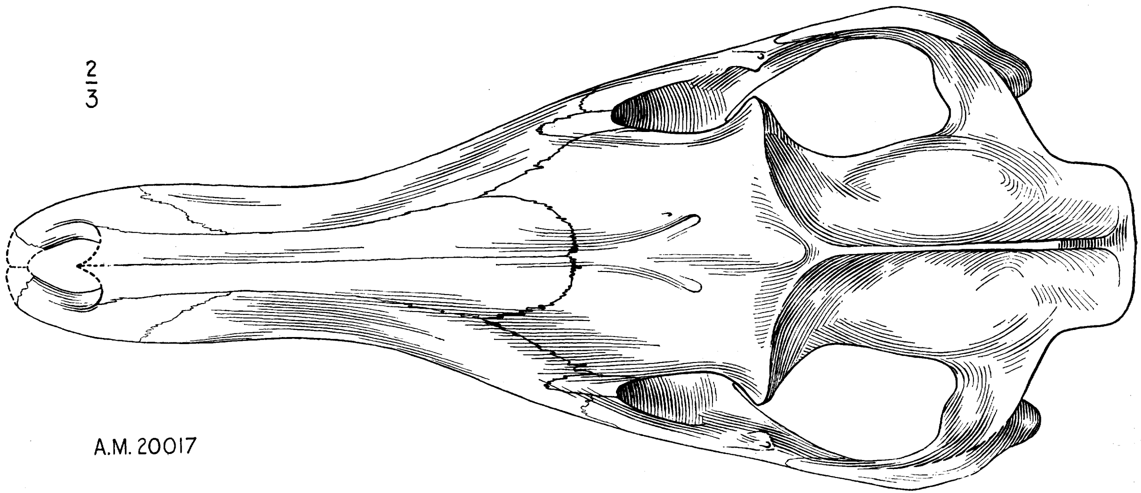


Fig. 47. *Anthracokeryx ulnifer* Pilgrim. Amer. Mus. No. 20017, skull. Dorsal view. Two-thirds natural size.

The canines, above and below are transversely flattened. The incisors are small, peglike teeth, round in cross section.

The radius and ulna are distinct and comparable to the similar bones in *Bothriogenys, Anthracotherium, Ancodon* and *Brachyodus*. The ulna is primitive in that it is relatively heavy and straight, with a vertical olecranon, and is not shifted externally as in more advanced forms.

Specimen in the American Museum:

Amer. Mus. No. 20017, a crushed but almost complete skull and mandible. From the Pondaung beds, 1 mile east of Bahin. (Map, Fig. 10, locality 10.)

Of the Pondaung anthracotheres only the species now being considered is known from really adequate material. The type of *Anthracokeryx ulnifer*, described by Pilgrim, consists of the front portion of a skull, including the muzzle, the orbit and a portion of the frontals and the mandible back to the ascending ramus. The molars are in good condition but the premolars, particularly the anterior ones, the canines and the incisors are for the most part badly shattered. Therefore it is especially fortunate that the skull and jaw discovered by Dr. Brown should be virtually complete, thereby supplementing and adding to the knowledge of this species. The American Museum specimen is crushed, but the crushing has in no way destroyed any essential details of its structure, and by making the proper allowances for crushing, this skull and jaw may be restored to the original condition with a high degree of accuracy. Because of the importance of this specimen a rather detailed description of it will be presented in the following paragraphs.

The Skull

The skull of *Anthracokeryx ulnifer* (Amer. Mus. No. 20017) is elongated and of slender construction. In size it is closely comparable to the type, as described and figured by Pilgrim, which means, of course, that it is relatively small. The orbit is round, open behind, and has its anterior border located above the posterior half of the second molar. The preorbital portion of the skull is slightly longer than the postorbital portion, but the excess of length in front of the eye is so small that the orbit may be considered as occupying a relatively central position. The sagittal crest is very high and the brain case is small. The frontal ridges that run in from the postorbital processes to join the sagittal crest are thick and heavy, and from their somewhat swollen condition it would seem certain that there are rather extensive frontal sinuses beneath them. The zygomatic arch is straight and slender, running in a horizontal line from the glenoid to the last molar. It is thereby evident that the glenoid is low, being on a line with the occlusal surfaces of the cheek teeth. This low glenoid in *Anthracokeryx* is undoubtedly a primitive character, as are many of the other features of the skull in this species, and is not to be attributed to any secondary lowering of the jaw articulation. The glenoid is extremely shallow, and round, so that its antero-posterior and transverse diameters are approximately equal to each other. Here again we see the retention of a very primitive character in this species, for in the more advanced artiodactyls and even in many primitive species more or less contemporary with the animal now being described the glenoids are transversely broad, as an adaptation for the side-to-side movement of the mandible. The articular surface of the glenoid merges into the postglenoid process, which is of medium length and projects somewhat posteriorly. The infraorbital foramen is located above the third premolar.

The occiput is very narrow, as might be expected in a primitive form having a small brain-case, and it is approximately vertical. The lambdoidal crest is high, a correlative development to the high sagittal crest, and it flares transversely into strong, flat plates. Thus there is ample provision for very strong temporalis muscles in this species.

The paroccipital processes are very short, and are situated rather close to the occipital condyles. In front of each paroccipital process and located directly above the postglenoid process is the external auditory meatus, a round opening closed ventrally and directed laterally.

Nothing definite can be said as to the arrangement of the basicranial foramina, because this portion of the skull has been so badly damaged by crushing that the diagnostic characters are more or less obliterated. It would seem probable, however, that the foramina are for the most part separated from each other in *Anthracokeryx,* as is typical of the primitive artiodactyls. Surprisingly enough one bulla, that on the right side, is most excellently preserved. It is large, considering the relatively primitive nature and early geologic age of this anthracothere, and pear-shaped, with the pointed end directed anteriorly. It lies closely appressed to the basicranial roof, so that its ventral surface is somewhat above the level of the glenoid articulation.

The pterygoids are long and well developed. The posterior nasal chonae are opposite the mid-portion of the last molar. The palate is long and narrow, as might be expected.

The Mandible

In keeping with the general configuration of the skull, the mandible is elongated and very slender. The horizontal ramus of the American Museum specimen is particularly slender, being considerably shallower and less robust than the ramus of the type. Pilgrim has emphasized the essentially "straight" lower border of the horizontal ramus in this

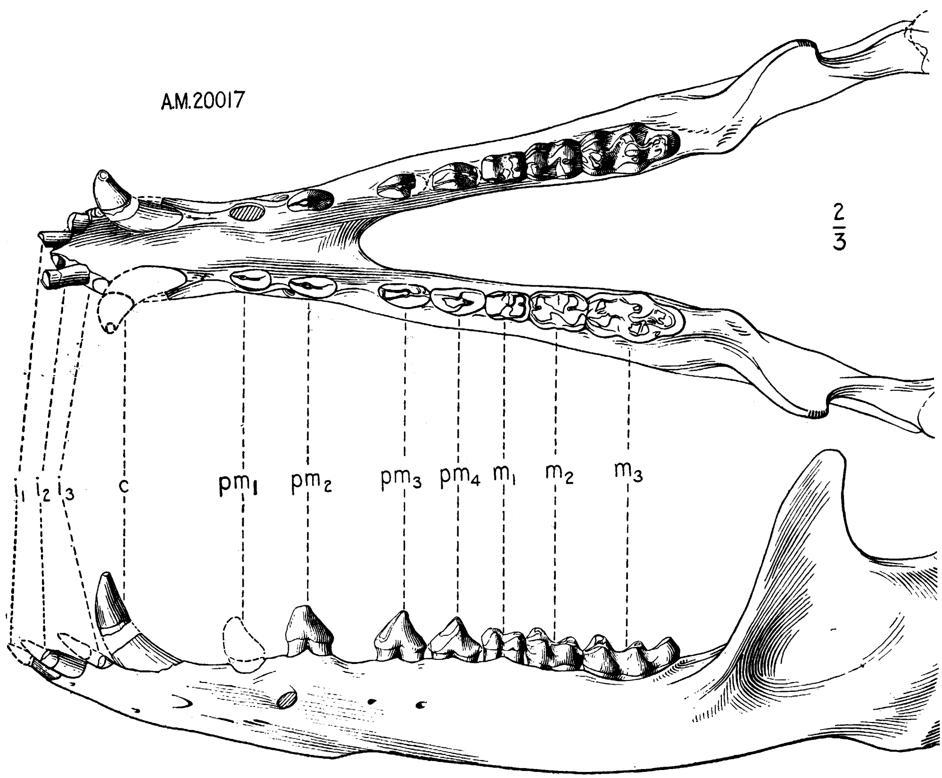


Fig. 48. *Anthracokeryx ulnifer* Pilgrim. Amer. Mus. No. 20017, mandible Crown view above, lateral view of left side below. Two-thirds natural size.

species, showing that there is very little convexity from the region of the last molar to the symphysis. This contour, as shown in the figure of the type, is partly real and partly illusory, due to the fact that the portion of the mandible behind the last molar is missing. In the American Museum specimen the lower border of the ramus is somewhat convex, reaching its greatest depth beneath the last molar. There is a slight concavity in its contour, beneath the second premolar.

The symphysis is long and narrow, extending back to the anterior border of the third premolar. The ascending ramus is very wide and low, with a high, pointed coronoid and with a strong, posteriorly projecting angle. The condyle is relatively low and is not transversely expanded.

The Upper Dentition

The dental formula for *Anthracokeryx ulnifer* is 3/3, 1/1, 4/4, 3/3.

In the American Museum specimen the teeth are well preserved, above and below. In the upper jaw all of the premolars and molars are present, one canine is preserved except for its tip, and two incisors are partially preserved. In the lower jaw the first premolar is missing, but otherwise the cheek teeth are intact, one canine is completely preserved, while the roots of the incisors are retained in their alveoli.

The upper incisors are large and equal in size, each to the other. They are of round cross section, and the crowns are in the form of simple cones. The canine is large and transversely flattened. This tooth is smaller in the American Museum specimen than it is in the type.

The first two premolars are simple, elongated teeth, each with two roots. The crown in these teeth takes the form of a single central conule, from which median ridges run anteriorly and posteriorly to the base of the tooth. Cingula are practically non-existent in these teeth. The first premolar is separated from the canine by a short diastema and from the second premolar by a rather long diastema. The third premolar is an elongated tooth, similar in many respects to the teeth in front of it, but distinguished by an internal basal cusp or swelling located slightly back of the center of the tooth. This internal projection is supported by a third root. The fourth premolar is much broader than it is long, with a sub-triangular crown having a single outer and a single inner cusp. Slight external, anterior and posterior cingula are to be seen in this tooth.

A curious feature of the American Museum specimen is the fact that the deciduous second molars are retained, in a position anterior and internal to the second permanent premolars. These persistent milk teeth are unworn, and it would thus seem that their retention is to be explained by delayed eruption.

In the upper molars the paracone and metacone are conical, with slightly flattened external surfaces and anterior and posterior ridges. The protocone and metaconule are slightly crescentic. There is a well-developed protoconule, which tends to unite with the protocone when the tooth is worn, to form an imperfect protoloph. The parastyle and mesostyle are robust but low, and strong cingula are present on the external, anterior and posterior sides of the teeth. It would seem as if the mesostyle in the American Museum specimen is somewhat larger than the same structure in the type skull, as figured by Pilgrim.

The Lower Dentition

The procumbent lower incisors are similar in cross section and shape to the upper incisors; that is, they are round, and have simple, conical crowns. Immediately behind the third incisor is the large canine, transversely flattened, but not so much so as its counterpart in the upper dentition, and rather strongly curved. As is the case with the upper

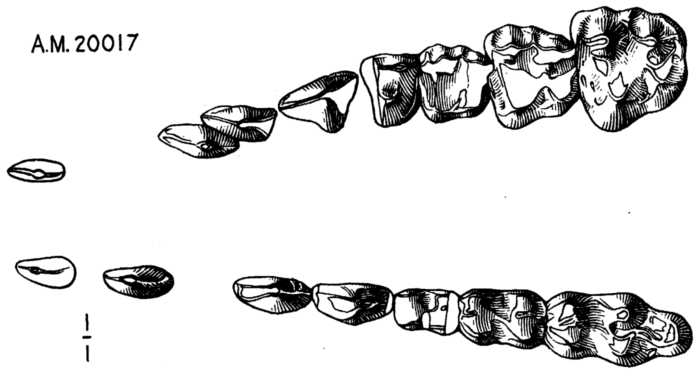


Fig. 49. *Anthracokeryx ulnifer* Pilgrim. Amer. Mus. No. 20017, left upper and lower cheek teeth. Crown views, natural size.

canine, this tooth would seem to be smaller in the American Museum specimen than it is in the type.

The first lower premolar is missing in the American Museum specimen, but from the size and shape of the alveolus this tooth was seemingly rather large, single rooted and antero-posteriorly elongated. It is separated by a diastema from the canine, and from the second premolar, which tooth in turn is separated by a diastema from the third premolar. The second and third lower premolars are simple, two-rooted teeth. In each of these teeth the anterior and posterior borders are ridged, the former being somewhat convex and the latter concave. The fourth premolar is essentially a heavier and more robust replica of the teeth in front of it. It has slight accessory posterior ridges, on either side of and parallel to the central ridge, and there is a very small, almost an incipient talonid.

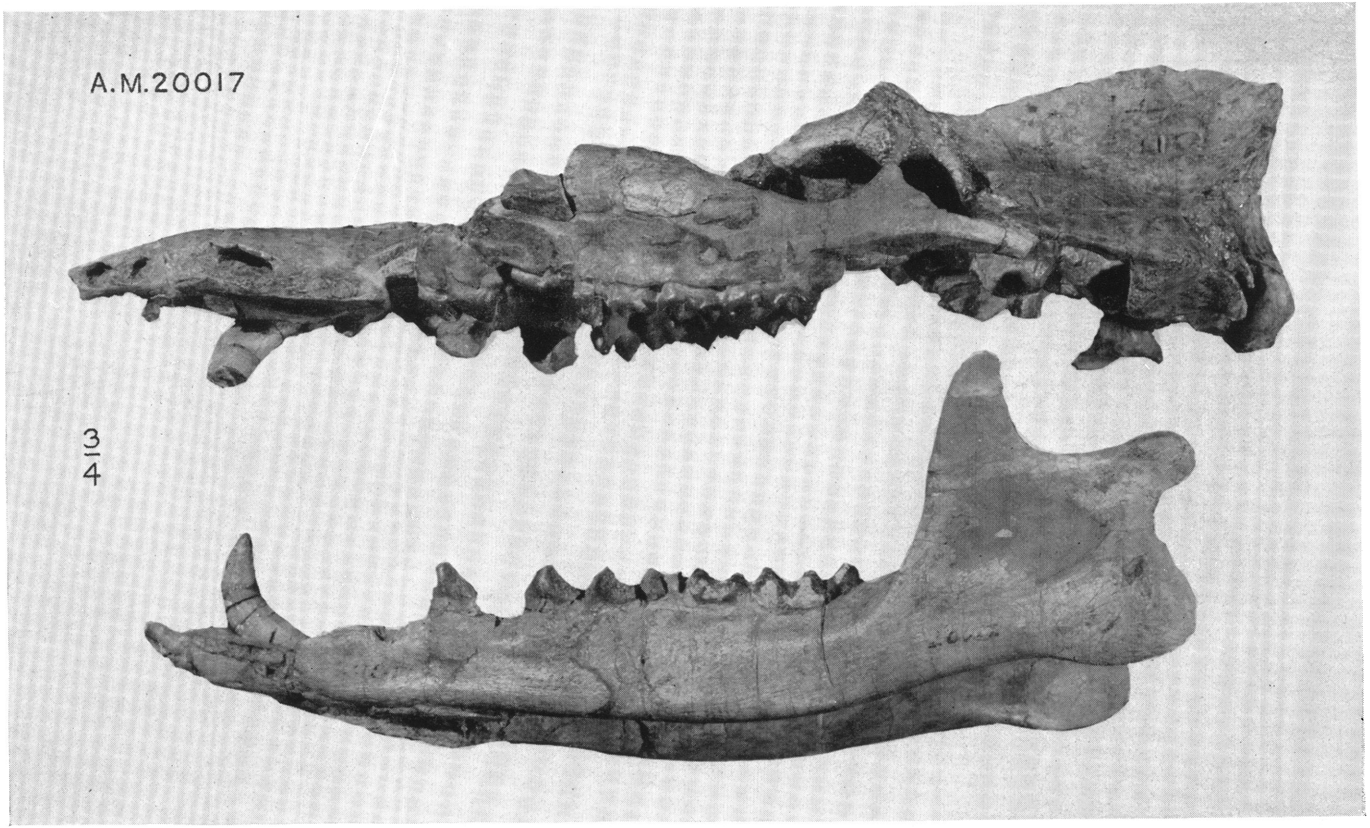


Fig. 50. *Anthracokeryx ulnifer* Pilgrim. Amer. Mus. No. 20017, skull and mandible. Photograph to show the crushed condition of the specimen. Three-fourths natural size.

The lower molars are characterized by their low, bunodont cusps, and by the fact that the anterior and posterior moieties of each tooth are of approximately equal widths. The internal cusps, the metaconid and entoconid are conical, with very slight ridges projecting down their buccal surfaces toward the middle of the tooth. In addition these cusps have internal ridges, one running back from the anterior cusp and one running forward from the posterior cusps to meet and form the inner wall of the median valley. The protoconid and hypoconid are crescentic but their arms are short, reaching only to the middle of the tooth. In the third molar the hypoconulid is distinct and broad, and its crown takes the form of a loop. It would seem to be somewhat wider in the American Museum specimen than it is in the type.

The dentition of *Anthracokeryx ulnifer* is comparable, in many respects, with the dentition of *Gobiohyus*, described by Dr. Matthew from the Irdin Manha, Upper Eocene of Mongolia. A particular resemblance is to be seen in the form and arrangement of the lower teeth of the species described above, with the same teeth in *Gobiohyus robustus*, as was noted by Dr. Matthew. Speaking of these forms, he said:

> This construction of the anterior teeth [of *Gobiohyus robustus*] suggests the primitive Anthracotheriidae and Suidae—not *Choeropotamus* if Stehlin's interpretation of the front teeth in that genus be correct.
>
> The arrangement of the lower premolars [of *Gobiohyus robustus*] is exactly as in the type of *Lophiohyus* Sinclair of the Bridger Eocene; a complete skull and jaws of a small anthracothere from the Eocene of Burma . . . . also agrees in the relations of the anterior teeth. (Matthew, W. D., 1925, Amer. Mus. Novitates, No. 198, p. 10.)

The anthracothere mentioned is Amer. Mus. No. 20017, *Anthracokeryx ulnifer*.

MEASUREMENTS

Anthracokeryx ulnifer

	A. M. No. 20017	G.S.I. Nos. B755–756
Skull, length, occ. cond.-pmx.	220 mm.	
preorbital length	120	
postorbital length	102	
width at glenoids	77	
width of occiput	49	
height of occiput, above condyles	54	
width of condyles	27	
auditory bulla, length	21	
width	13	
glenoids, transverse dia.	16	
ant.-post. dia.	14	
width of frontals, post.-orb. proc.	60	
dia. of orbit (approx.)	27	

	A. M. No. 20017		G.S.I. Nos. B755–756	
Upper dentition	L	W	L	W
I^1		4.5		
I^2 (from alveoli)	5	4.5		
I^3	5.5	4.5		
C	13	6	15.1	8.2
P^1	6	3	11.9	
P^2	10	5	14.6	
P^3	11.5	7.5	11.2	7.4
P^4		10	8.4	10.9
M^1	8.5	10	8.3	10.8
M^2	11	13	11.7	13.8
M^3	14.5	16.5	14.6	17.1
P series (incl. diastema)	55		50	
M series	34		35.2	
Diastema, $C–P^1$	6.5		11.3	
$P^1–P^2$	15 (?)		8	
DM^2	L-10	W-4		

	A. M. No. 20017	G.S.I. Nos. B755–756
Mandible, length, condyle-symphysis	193	
depth of ramus, M_3	19	26.2
symphysis, length	65	71.8
width	18	
asc. ramus, ant.-post. dia.	40	
transverse dia. of condyle	14	
depth, cond.—lower border angle	40	

	A. M. No. 20017		G.S.I. Nos. B755–756	
Lower dentition	L	W	L	W
I_1	4.5	3.5		
I_2	4.5	3.5		
I_3	3	3		
C	8.5	6	13.2	6.5
P_1	7	4	6.7	
P_2	10	4.5	10.4	
P_3	10.5	5	11.7	4.3
P_4	9.5	5.5	11.2	5.5
M_1	8	6	8.5	6.3
M_2	11.5	7.5	11.6	8.1
M_3	19.5	9	21.1	10
P series	50		52.5	
M series	39		41.3	
Diastema, $C–P_1$	7.5		12.1	
$P_1–P_2$	4		7.4	
$P_2–P_3$	7		3.4	

Anthracokeryx moriturus Pilgrim

Anthracokeryx moriturus, PILGRIM, 1928, Mem. Geol. Surv. India, (N. S.) XIII, p. 32, Pl. IV, figs. 1–3.

TYPE.—G.S.I. No. B763, a left upper last molar.

PARATYPES.—G.S.I. No. B764–5, two upper molars.

HORIZON.—Pondaung, Eocene.

LOCALITY.—$^3/_4$ mile W.S.W. of Pangan, Burma.

AUTHOR'S DIAGNOSIS.—The three teeth [LM^1, RM^2, LM^3] . . . are almost twice the size of the corresponding teeth of *Anthracokeryx birmanicus*, and though the disparity in size between them and *A. hospes* is less great, it is nevertheless considerable. The presence of a strong parastyle prohibits their being placed in the genus *Anthracothema*, while the greater height of crown and cusps and the greater flattening of the external cusps equally militates against their being placed in *Anthracotherium*. The outer surface of the paracone is certainly slightly less flattened than in the upper molars which have been referred to other species of *Anthracokeryx* but the difference is hardly appreciable and affords no ground for generic separation.

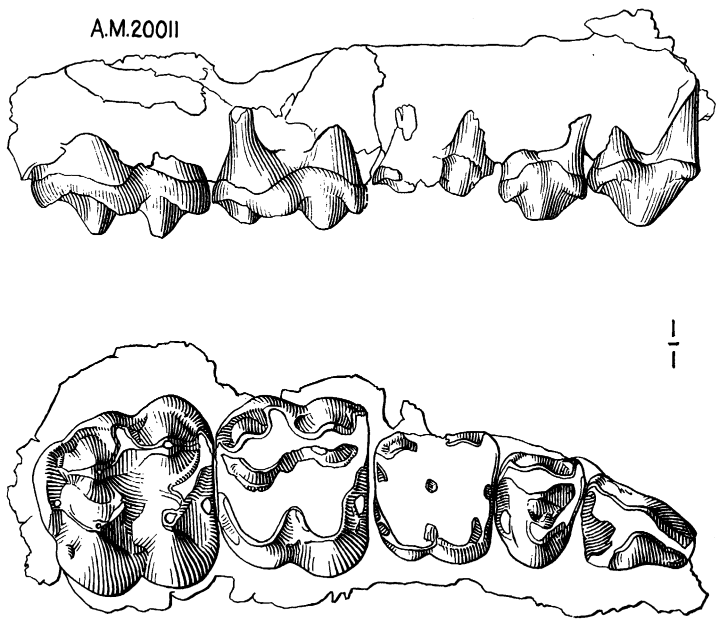


Fig. 51. *Anthracokeryx moriturus* Pilgrim. Amer. Mus. No. 20011, right P^3–M^3. External lateral view above, crown view below. Natural size.

Specimen in the American Museum:

Amer. Mus. No. 20011, a right maxilla containing P^3–M^3 and an associated right mandibular ramus with P_3–M_3. Also a left M^2 and M_3 and a right I_1. From two miles northwest of Mogaung. (Map, Fig. 8, locality 16.)

Considering the very fragmentary nature of most of the anthracothere material from Burma, the specimen now to be considered is unusually complete. In fact, it is surpassed in this respect only by the skull and jaw of *Anthracokeryx ulnifer*, described in another section of this work.

This specimen is referred to the genus *Anthracokeryx* for several reasons. In the upper molars the paracone and metacone are somewhat compressed, the metaconule is crescentic and the parastyle and meso-

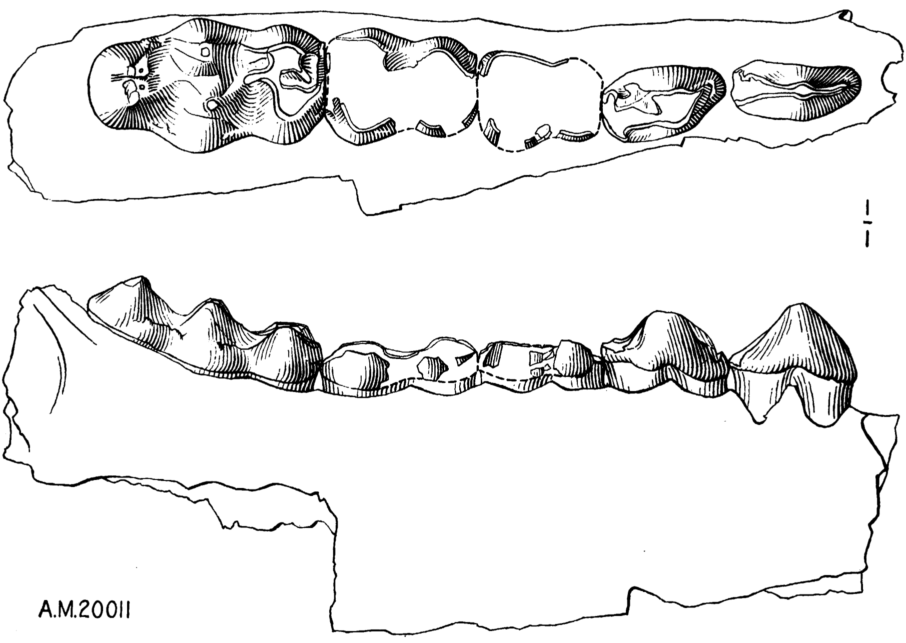


Fig. 52. *Anthracokeryx moriturus* Pilgrim. Amer. Mus. No. 20011, right P_3-M_3. Crown view above, external lateral view below. Natural size.

style are well developed. These are all characters definitive of *Anthracokeryx*. Likewise, other definitive characters shown by the specimen are the somewhat crescentic inner cusp of the fourth upper premolar, the short but well-developed arms on the cusps of the lower molars and the narrowness of the lower molars in their anterior portions.

The large size of the specimen under consideration would seem to place it without question in the species *A. moriturus*. The only form approaching the present specimen in this respect is the type mandible of *Anthracokeryx hospes* (which, as is shown on another page [388] may be considered as probably belonging to the species *A. birmanicus*) and even here there is a considerable difference in size. Moreover, the specimen in the American Museum collection would seem to accord rather well as to size with the type upper molars of *Anthracokeryx moriturus*, described and figured by Pilgrim.

The mandibular ramus of *Anthracokeryx moriturus* is heavy but rather shallow, its depth at the last molar being approximately equal to the length of that tooth.

MEASUREMENTS

Amer. Mus. 20011

	Upper Dentition				Lower Dentition		
P^3	length	16 mm.		P_3	length	16.5 mm.	
	width	12			width	7.5	
	index		75		index		45
P^4	length	11		P_4	length	16.5	
	width	14.5			width	9	
	index		132		index		55
M^1	length	16		M_1	length	17	
	width	17.5			width	12.5	
	index		110		index		74
M^2	length	19.5		M_2	length	20.5	
	width	23.5			width	15.5	
	index		120		index		76
M^3	length	24		M_3	length	31.5	
	width	25			width	17.5	
	index		104		index		55
Length of molar series		60.5 mm.		Length of molar series		69 mm.	
				Depth of ramus below M_1		31 mm.	

Anthracokeryx moriturus, type and paratypes; G.S.I. B763–5.

M^1	length	17.3 mm.		
	width	19.2		
	index		111	
M^2	length	24.1		60.5/70.6 = 86/100
	width	26.2		
	index		109	
M^3	length	29.2		
	width	31.3		
	index		107	
Length of molar series		70.6 mm.		

A small incisor tooth, associated with 20011, would seem without doubt to be of anthracotheroid relationships, and because of its association there is every reason to think that it belongs to the specimen now under consideration. This tooth is determined as a lower right median incisor because of its flattened shape and because of the arrangement of the facets on either side of the tooth, there being a small facet located near the cutting edge on the median side of the tooth, obviously a contact with the left median incisor, and an elongated facet on the external side of the tooth, where the right second incisor was in contact with it. The occlusal edge of the tooth is truncated obliquely in a straight line by the wear of an overhanging upper incisor.

MEASUREMENTS

Amer. Mus. No. 20011—Right I_1

Thickness at base	5.0 mm.
Width	6.2 mm.

Anthracokeryx (?) **lahirii** Pilgrim

Anthracokeryx (?) *lahirii*, PILGRIM, 1928, Mem. Geol. Surv. India, (N. S.), XIII, pp. 32–33, Pl. IV, figs. 4, 4a.

TYPE.—G.S.I. No. B766, a right mandibular ramus containing the molar dentition only.

PARATYPES —None.

HORIZON.—Pondaung, Eocene.

LOCALITY.—3 furlongs N.W. of Than-u-daw village, Burma.

AUTHOR'S DIAGNOSIS.—The type of this species is a right mandibular ramus (B.766), containing the molar dentition only. The teeth are in an advanced stage of wear and only in the case of m_3 is the structure clearly exhibited. In size it comes nearest to *Anthracokeryx myaingensis* but differs very markedly from this in many details of structure, as indeed it differs from all the other species of Anthracotheroid which are found in the Pondaung Sandstones. The teeth are of the regular Anthracotheroid pattern, but the indications are insufficient to enable me to decide in what genus it should be placed and the reference to *Anthracokeryx* is quite provisional. The chief point in which it differs from other species of *Anthracokeryx* is the extreme shortness of the molars and especially of m_3 relative to the stoutness and depth of the ramus. The breadth index of the molars is also greater than in any other species. M_2 is almost precisely of the same length as in *Anthracokeryx tenuis*, but the breadth of that tooth and the size and depth of the ramus makes it quite impossible for the two species to be confused. In many of these points it seems to agree with *Lophiohyus alticeps* from the Bridger Eocene, though a smaller species. There is however no trace of a paraconid. The cusps are remarkably low but less so than in *Gobiohyus*, while the talonid of m_3 displays the same kind of loop as in other species of *Anthracokeryx* though it is shorter and broader.

ANTHRACOKERYX OR ANTHRACOTHEMA

Specimen in the American Museum:

Amer. Mus. No. 20031, an incomplete left hind limb. The parts present are; the femur, tibia and fibula, all badly shattered; the astragalus and calcaneum, complete;

the third, fourth and fifth metatarsals, broken; and various phalanges. From the Pondaung beds, one-half mile northeast of Kyawdaw. (Map, Fig. 8, locality A27.)

One of the most interesting specimens in the American Museum collection from Burma is the anthracothere hind limb, listed above. Anthracothere limb bones and feet are rare, even from some of the abundantly fossiliferous beds of Europe and North America; consequently the discovery of a hind leg in the Pondaung beds of Burma may be regarded as one of the major achievements of Dr. Brown's work in Burma. The specimen is rather fragmentary, but even so enough of it is preserved to enable us to make a fairly accurate restoration.

It is not possible to assign this specimen, with any degree of certainty, to a particular genus or species of the Pondaung anthracotheres, especially in view of the fact that among these animals there are no definite associations of teeth with foot bones. From the size and the general appearance of the specimen now under consideration a few deductions as to the probabilities of its relationships may be drawn.

The several bones constituting the specimen are of medium size, comparable in a general way to the limb and foot bones of *Sus*. Thus they would seem to be representative of a medium-sized anthracothere, an animal considerably larger than the smaller species of *Anthracokeryx*, but considerably smaller than the largest species of *Anthracothema*, or of large members of other genera such as *Anthracotherium*. The foot of the specimen now under consideration is notable because of its length, due to the great attenuation of the metatarsals. Thus it is very slender, much more so than the foot of *Anthracotherium* as figured by Kowalesky, and more recently by Roman and Boucher (1936), and comparable in this respect to *Hyopotamus*.

Now a study of anthracotheres in which the skull and feet are associated will show that as a general rule the feet are comparatively small usually being less than one-half the length of the skull. The same relationship holds for other primitive artiodactyls, such as the entelodonts, anoplotheres and suids. Thus it would seem that small feet are more or less characteristic of the bunodont and bunoselenodont artiodactyls.

The anthracothere foot from Burma is somewhat longer than is the skull of *Anthracokeryx ulnifer*, and consequently it would seem obvious that it can not be assigned to this species or to the other smaller species of *Anthracokeryx*. Since it is very slender, it is probably not referable to the larger species of *Anthracothema*, such as *Anthracothema pangan*. Therefore it would seem probable that the limb and foot under consideration are probably referable to one of the smaller species of *Anthracothema*, such as *Anthracothema rubricae* or to one of the large forms of *Anthracokeryx*, such as *Anthracokeryx moriturus*. Of course it might belong to *Anthracohyus*, but so little is known of this genus that it may be properly left out of this discussion.

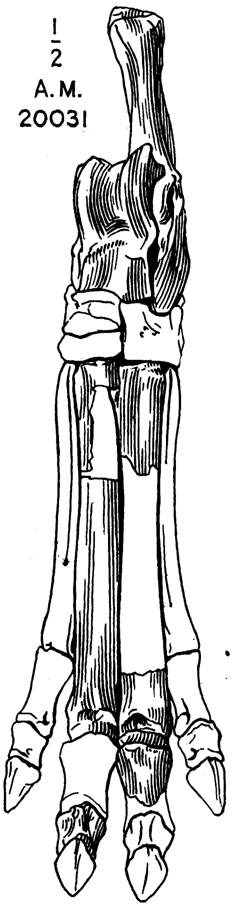


Fig. 53. *Anthracokeryx* or *Anthracothema*. Amer. Mus. No. 20031, left pes. Dorsal view. One-half natural size.

The femur is closely comparable in size to the femur of *Sus*, not only with regard to its general weight but also as to its probable length. The head, which is circular, rests on a short neck, which projects almost at a right angle from the axis of the shaft. Near the internal border of the head, and somewhat removed from its center, is a well-marked pit for the ligamentum teres. The great trochanter is rather massive, but it does not rise above the level of the head of the femur. Along the anterior surface of the bone it is attached to the head by a transverse ridge, and posteriorly it is excavated by a deep digital fossa. Distally the femur is characterized by a long trochlea, set at somewhat of an angle to the shaft while as a correlative development the two condyles are placed obliquely to each other. This is a typical artiodactyl characteristic. Due to the crushed and fragmentary condition of the shaft, nothing can be said as to its configuration.

Only the extreme proximal and the distal ends of the tibia are preserved. Proximally there are the usual two articular surfaces for the condyles of the femur. The inner articulation is somewhat higher than the outer one, a relationship that follows from the arrangement of the inner and the outer condyles of the femur. The distal articular surface shows a narrow internal groove and a much wider external groove, to fit the condyles of the proximal trochlea of the astragalus. Although the internal malleolus is broken away, it would seem from the size and shape of the broken surface that this portion of the bone extended ventrally to a considerable degree. On the external malleolus is a broad, roughened surface that articulates with the distal portion of the fibula.

The fibula is expanded proximally and distally, while in its mid-portion the shaft is very small. On the expanded distal end of the bone there is a long articular surface that makes a contact with the calcaneum.

The astragalus is elongated, and it has the proximal trochlea set at a slight angle to the distal trochlea. The proximal trochlea is characterized by a broad external condyle, that rises to an appreciable height above the narrower internal condyle. The distal trochlea shows a relatively broad surface for articulation with the navicular, and a narrow surface for articulation with the cuboid. On the plantar surface of the bone are the articular facets for the sustentaculum of the calcaneum; a broad outer facet and a very narrow inner facet that makes an obtuse angle with the large facet. Both of these facets are strongly convex in an antero-posterior direction. On the external surface of the bone are three very small facets for the calcaneum, one proximal in its position, one ventral and a third one in the middle of the bone, at the distal termination of the outer condyle of the proximal trochlea.

The calcaneum is very long and slender. Much of its length is due to the elongation of the tuber, which forms considerably more than half the length of the bone. Proximally the tuber is slightly expanded in a transverse direction, and on the plantar surface ot its tip there is a well-defined groove, the sulcus plantaris. Distally there is a long facet for articulation with the cuboid. The sustentacular facet has two faces, to fit the facets of the astragalus, described above. The fibular facet is placed on a raised process, occupying the base of the tuber on the outside of the bone. The external surface of the calcaneum is traversed by a long, deep groove that runs from the cuboid facet to the proximal expansion of the bone.

The remaining tarsal bones are missing in this specimen. They were probably elongated, in keeping with the general configuration of this foot.

The metatarsals are greatly elongated, as was mentioned above, being in their general shape and slenderness comparable to the metatarsals of *Hyopotamus* as figured by Kowalevsky. The second metatarsal and its accompanying phalanges are missing. The third and fourth metatarsals, which are present but fragmentary, have the shafts flattened somewhat anteroposteriorly. This may be due in part to crushing, although it would seem to be the typical form of these bones. The fourth metatarsal is somewhat wider than the third one, as is common among the less specialized artiodactyls, and it has a median proximal process that articulates with a corresponding groove or indentation in the third metatarsal. The distal articular surfaces of the metatarsals have very strong, prominent posterior keels.

There is a small fragment, presumably of the shaft of the fifth metatarsal, showing that this bone was very slender. The lateral toes were probably complete, but it would seem rather certain that they were for the most part non-functional.

A proximal phalanx is rather long, with a proximal articular surface that is somewhat broadened transversely. There is a deep notch in the plantar portion of this articular surface, to receive the keel of the metatarsal articulation.

A median phalanx is short and slender, with the distal articulation arranged in quite an asymetrical manner in its relationship to the proximal articulation. Both articulations of this bone show inner and outer facets, those of the proximal end being concave and those of the distal end being convex.

Measurements

	A.M. 20031
Calcaneum, greatest length	83 mm.
breadth	24
Astragalus, length	41
breadth	22

	A.M. 20031
Metatarsal III, length (estimated)	101
Proximal phalanx, length (estimated)	25
Median phalanx, length	18
Pes, extended length (estimated), top of calcaneum	245
breadth, astragalus-calcaneum	30

COMPARATIVE MEASUREMENTS AND RATIOS

	A. M. 20031	*Hyopotamus*[1]	*Ancodus*[2]	*Brachyodus*[3]	*Anthracotherium*[4]
Extended length of pes (top of ast.)	210	280	249	244	298
Width of pes cal.-ast.	30	41	39	41	82
Pes, breadth index	14	14.5	15.5	17	27
Length of Mt. III	101	117	99	103	114
Breadth of Mt. III	12	18	15	14	32
Index	12	15.5	15	13.5	28

THE PONDAUNG ANTHRACOTHERES

A study of the anthracotheres from the Pondaung horizon is fraught with many difficulties, for these are numerous mammals in the Eocene of Burma, comprising practically the entire bulk of the artiodactyl element of the fauna, and they show intergradations of size and characters that make their differentiation into species a problem of unusual difficulty. Dr. Pilgrim, as the result of his studies on the Pondaung anthracotheres, created three genera and thirteen species of anthracotheres. They are as follows:

Genus *Anthracohyus*, one species:	*A. choeroides.*
Genus *Anthracothema*, four species:	*A. pangan; A. rubricae; A. palustre; A. crassum.*
Genus *Anthracokeryx*, eight species:	*A. birmanicus; A. ulnifer; A. bambusae; A. hospes; A. tenuis; A. myaingensis; A. moriturus; A.* (?) *lahirii*

Now it is a well-established principle in the study of mammalian ecology that two or more species of a single genus are more or less incompatible in the same area and the same environment. That is, each species has its own ecological niche, and for the most part this niche is not shared with any other species of the same genus. If several species of the same genus occupy a certain restricted area, it is usual for each

[1] From Kowalevsky. [2] From Scott. [3] From Geais. [4] From Roman and Boucher.

species to be restricted, in turn, by certain environmental limitations. Thus, one species may occupy highlands, while another one is found in the lowlands. Rarely do the ranges of species overlap, and this statement together with the ones preceding it holds, in the main, for subspecies, also.

With these considerations in mind, there immediately arises the question as to whether the two genera, *Anthracothema* and *Anthracokeryx*, should contain between them the grand total of twelve species. Certainly this is a large number of species to be included in two genera from one geological horizon confined to a relatively small geographical area. To justify this long list of species in one stratigraphic level certain conditions must needs be shown by the physical expression of the beds, thus:

1.—The horizon must show either by its thickness or by its sedimentary content that it covers a considerable time period, thereby introducing the possibility that the several species were not all contemporaneous with each other;

2.—The beds must be exposed over a wide area, thereby affording the possibility of several species being mutually compatible by their geographic separation, or;

3.—The sediments must show by their content that the region was one of topographic or environmental differences, thereby affording the possibility of the several species living in a state of geographic contiguity, but separated by differences of habitat.

What does the physical expression of the Pondaung deposits show in the light of the above stipulations?

As to thickness, the Pondaung beds in their entirety cover a vertical range of about six thousand feet. It must be noted, however, that the lower portion of the Pondaungs are of marine origin and that the continental facies are restricted to the upper portion of the formation in the more northerly reaches of its exposure. Moreover, the fossil vertebrates are found in certain clay members of the formation, indicative of the fact that they were deposited in freshwater lagoons or streams. Thus it would seem probable that the Pondaung vertebrates do not represent any great range of geologic time, but rather that the various genera and species are generally contemporaneous each with the other.

This supposition would seem to be strengthened by the sedimentary characters of the Pondaungs, which indicate that these beds were formed as part of a deltaic flood-plain that existed during a short portion of upper Eocene times.

The present geographic extent of the Pondaungs is quite restricted, and on the basis of geological considerations there do not seem to be any sound reasons for supposing that these beds were ever of very great distribution. It has been shown in preceding pages of this paper, following

Stamp and others, that the Tertiary history of Burma is a record of the infilling of the ancient Burmese gulf by marine sediments to the south and by southwardly encroaching continental deposits from the north. Thus the old Eocene valley of upper Burma, where the continental Pondaungs were formed, was limited (as it is today) by the ancient Arakan Yoma on the west and by the ancient Shan Plateau on the east. In upper Eocene times the continental Pondaungs formed the floor of a valley that could not have been more than one hundred to one hundred and fifty miles in width and, at the most, a few hundred miles in length. This is a relatively small area to serve as the habitat for moderate-sized hoofed animals, such as the anthracotheres, capable of moving about freely and more or less extensively. Consequently, from the aspect of geographic extent, it would seem that the habitat of the Pondaung anthracotheres was not widespread enough to permit the contemporaneous existence of a large number of species belonging to a single genus.

Considering now the physical expression of the Pondaungs at the time of their deposition, the arguments again would seem to militate against the mutual existence of a great number of species representative of a single genus of anthracotheres. Evidently the Pondaungs were deposited on a rather low, flat valley floor. There is no evidence of any great amount of topographic relief in the region where the Pondaung sandstones were deposited, nor is there any reason to think that the ancient valley of upper Burma was hilly. This was a flood-plain region on a large delta, and such regions are notoriously flat.

During upper Eocene times the climate was extraordinarily equable, and this factor, combined with the lack of relief and the consequent uniform physical environment, would again militate against numerous species of a single genus living together.

Thus it becomes apparent that all of the probabilities are against the existence of a large number of species for any single genus of mammal in the Pondaung beds. Here was a region of comparatively small extent, with a uniform climate and featureless topography, an environment ideally suited to the presence of a single, wide-spread assemblage of the larger mammals. Only the question of time duration comes in to complicate the picture, and this is the one consideration to be seriously studied in the matter of the numerical relation of species to genera. Perhaps there was a certain time lapse during the deposition of the Pondaung sandstones and clays, thus allowing the presence of several species of a single genus in the Pondaung beds. It seems to me, however, that even if this be the case, the presence of more than a very few species for any one genus must be a condition subject to critical examination. Perhaps there were several species of *Anthracothema* and of *Anthracokeryx* living throughout the duration of Pondaung times, but it seems to me that in the case of the latter genus eight species does represent a rather high number.

All of these foregoing arguments constitute *a priori* evidence against the great proliferation of anthracothere species in the Pondaung horizon. It must be remembered that if there are valid distinctions to show the existence of a great number of species, then this evidence is not to be denied. The question, of course, is just what constitutes valid distinctions between fossil species, particularly species based for the most part upon teeth.

With the exception of one species, *Anthracokeryx ulnifer*, the Pondaung anthracotheres are known only from upper and lower teeth. Naturally the distinctions between the several species are based on the differences in their dentition. These differences are of two kinds, namely those of character and those of size. Many of the species are defined and differentiated from other species by the characters of their teeth, but some of them are based mainly on size differences alone. For instance the description of *Anthracokeryx myaingensis* reads in part as follows:

> The species *Anthracokeryx myaingensis* is intermediate in size between *A. tenuis* and *A. ulnifer*. Structurally I can detect no particular differences between *A. tenuis* and *A. myaingensis*. (Pilgrim, G. E., 1928, p. 30.)

Thus, since certain species have been separated on the basis of size differences it becomes evident that a study of size variations within the Pondaung anthracothere genera may help in an understanding of the relationships of the various species.

By making a graph of the Pondaung anthracothere molar teeth, plotting the molar lengths along the horizontal axis of the chart, and the breadth along the vertical axis, a comparative picture of tooth sizes in the several species may be obtained. In a comparison of species by this method, it is feasible to use only the molar teeth, since in a number of forms the premolars are incompletely known. The accompanying figure (Fig. 54) shows the results obtained by plotting the tooth dimensions in this fashion.

An examination of the graph readily shows that the Pondaung anthracotheres fall into two groups, one large and the other small. The large group is made up of the several species of *Anthracothema*, while the various species of *Anthracokeryx* constitute the small group. It is to be noted, however, that these groups overlap, due in large part to the unusually great size of *Anthracokeryx moriturus.* If this one species is left out of account it may be seen that the size ranges of the two genera under consideration are more nearly independent, each of the other. (*Anthracohyus*, restricted by Pilgrim to a single species based on a single specimen, is not considered in this discussion of size variations.)

Anthracothema pangan is seemingly a well-defined species of large size, while *Anthracothema rubricae* appears to be equally well defined and smaller than the generic type. Now there comes the question of the validity of *Anthracothema palustre* and *Anthracothema crassum.* The former species, known from a few scattered teeth, is probably synonymous with *Anthracothema pangan;* at least as far as size differences go, there are no very good reasons for considering these species separable. As to structural distinctions, the only characters distinguishing *Anthracothema palustre* from the generic type are the swollen internal basal region of the molars and the flatter slopes of the buccal sides of the paracone and metacone. These are differences that would seem to be of small import in the definition of a species. Consequently *Anthracothema palustre* is very probably a variant of *Anthracothema pangan*—a large variant in which the molar teeth are especially robust.

Anthracothema crassum is somewhat more difficult to place. In its size range, it falls within the limits of both *Anthracothema pangan* and *Anthracothema rubricae.* Pilgrim and Cotter recognized the fact that *Anthracothema crassum* is smaller than *Anthracothema rubricae* (thereby becoming the smallest member of the genus) and they went on to show that the cusps of the teeth are lower than in any other species of this genus. Subsequently Pilgrim compared this species with *Anthracothema palustre* and between the two forms he saw a great deal of similarity. On the basis of size *Anthracothema crassum* might be considered as more or less comparable to *Anthracothema rubricae;* on the basis of tooth characters it may be linked with *Anthracothema palustre,* which in turn may be considered as equal to *Anthracothema pangan.* Thus *Anthracothema crassum* is possibly a valid species, but there exists a probability that it may be synonymous with *Anthracothema palustre,* and therefore with *Anthracothema pangan.*

Now coming to a consideration of *Anthracokeryx,* it will be seen that the generic type, *Anthracokeryx birmanicus,* is a large species, the largest of the genus with the exception of *Anthracokeryx moriturus.*

Closely comparable in size to the generic type is *Anthracokeryx hospes,* known only from the lower teeth. Since there is a close agreement in size between these two species, and since Dr. Pilgrim characterizes the structural differences between them as "trifling" it would seem probable that this form now under consideration is synonymous with *Anthracokeryx birmanicus*.

Several species, namely *Anthracokeryx tenuis, ulnifer, bambusae* and *myaingensis* are closely comparable to each other on the basis of molar dimensions. Of these forms, *Anthracokeryx bambusae* is like *A. ulnifer*, with regard to size, and like *A. birmanicus* in the structure of the teeth, points that were demonstrated by Dr. Pilgrim. Therefore the validity of this species may be questioned. There are good grounds for believing it to be identical with one of the above mentioned forms.

Anthracokeryx myaingensis is similar to *A. tenuis*, except for slight differences in size, as was admitted by Pilgrim. Therefore it is very probable that these two forms are synonymous.

Anthracokeryx tenuis is in turn quite similar to *A. ulnifer*, and thus there is a strong probability that these two species are synonymous. If so, the name *Anthracokeryx tenuis* would have to stand, and this would be too bad, for *A. ulnifer* is the one Pondaung anthracothere known from really adequate material.

Anthracokeryx moriturus is, curiously enough, a large form, more nearly comparable in size to some of the species of *Anthracothema* than it is to the typical *Anthracokeryx*. It is evident, however, that there are valid structural differences between this form and the various species that characterize *Anthracothema*. These differences are to be seen in the crescentic protocone of the form under discussion, and the development of its parastyle and mesostyle in the manner typical of *Anthracokeryx*. Therefore it would seem best, for the present, to consider *Anthracokeryx moriturus* as a valid species—a very large member of the genus, comparable in size to the typical species of *Anthracothema*.

Coming finally to *Anthracokeryx lahirii*, the evidence favors the probability that this species is quite different from any other members of the genus. As Pilgrim surmised, it may be referable to some other genus, probably new.

To recapitulate, a study of the size differences and structural differences in the molar teeth of *Anthracothema* and *Anthracokeryx* (the only anatomical features whereby all of the species may be directly compared with each other) point to the following probable assumptions.

There are probably two species of *Anthracothema*, possibly three:

Large—*Anthracothema pangan* (*A. palustre*, *A. crassum* (?)—this latter form possibly distinct)

Small—*Anthracothema rubricae*

There are probably four or five species of *Anthracokeryx:*

Large—*Anthracokeryx birmanicus* (*A. hospes, A. bambusae* (?))

Small { *Anthracokeryx tenuis* (*A. myaingensis, A. bambusae* (?), *A. ulnifer* (?))
Anthracokeryx ulnifer (Synonymous with *A. tenuis*?)

Very large—*Anthracokeryx moriturus*

Very small—*Anthracokeryx* (?) *lahirii*

Unfortunately, none of these conclusions can at the present time be definitely stated. Until more and better material is discovered, the systematic taxonomy of the Pondaung anthracotheres must remain in this rather confused and uncertain condition.

KEY TO NUMBERS ON GRAPH

Anthracohyus choeroides
1. G.S.I. B603

Anthracothema rubricae
2. G.S.I. B609
3. G.S.I. B610
4. G.S.I. B612
5. G.S.I. B613
6. G.S.I. B751
7. A.M. 20027
8. A.M. 20029

Anthracothema palustre
9. G.S.I. K18/847
10. G.S.I. B607
11. G.S.I. B752

Anthracothema pangan
12. G.S.I. B619
13. G.S.I. B620
14. G.S.I. B750
15. G.S.I. B745
16. A.M. 32526
17. A.M. 20006

Anthracothema crassum
18. G.S.I. B615
19. G.S.I. B617

Anthracokeryx tenuis
20. G.S.I. B627

Anthracokeryx birmanicus
21. G.S.I. B621
22. G.S.I. B767
23. A.M. 20015

Anthracokeryx ulnifer
24. G.S.I. B755–756
25. A.M. 20017

Anthracokeryx bambusae
26. G.S.I. B622

Anthracokeryx hospes
27. G.S.I. B605

Anthracokeryx myaingensis
28. G.S.I. B759–760

Anthracokeryx moriturus
29. G.S.I. B763–765
30. A.M. 20011

Anthracokeryx lahirii
31. G.S.I. B766

Dr. Pilgrim has presented a full discussion of the taxonomic and phylogenetic relationships of the Pondaung anthracotheres in his 1928 memoir on the Pondaung artiodactyls. In this paper he shows that the Burma anthracotheres are the most primitive types as yet known, certainly very close to and probably to be derived from *Gobiohyus*, a primitive dichobunid-like form from Mongolia, and undoubtedly ancestral to some of the Oligocene anthracotheres of Eurasia.

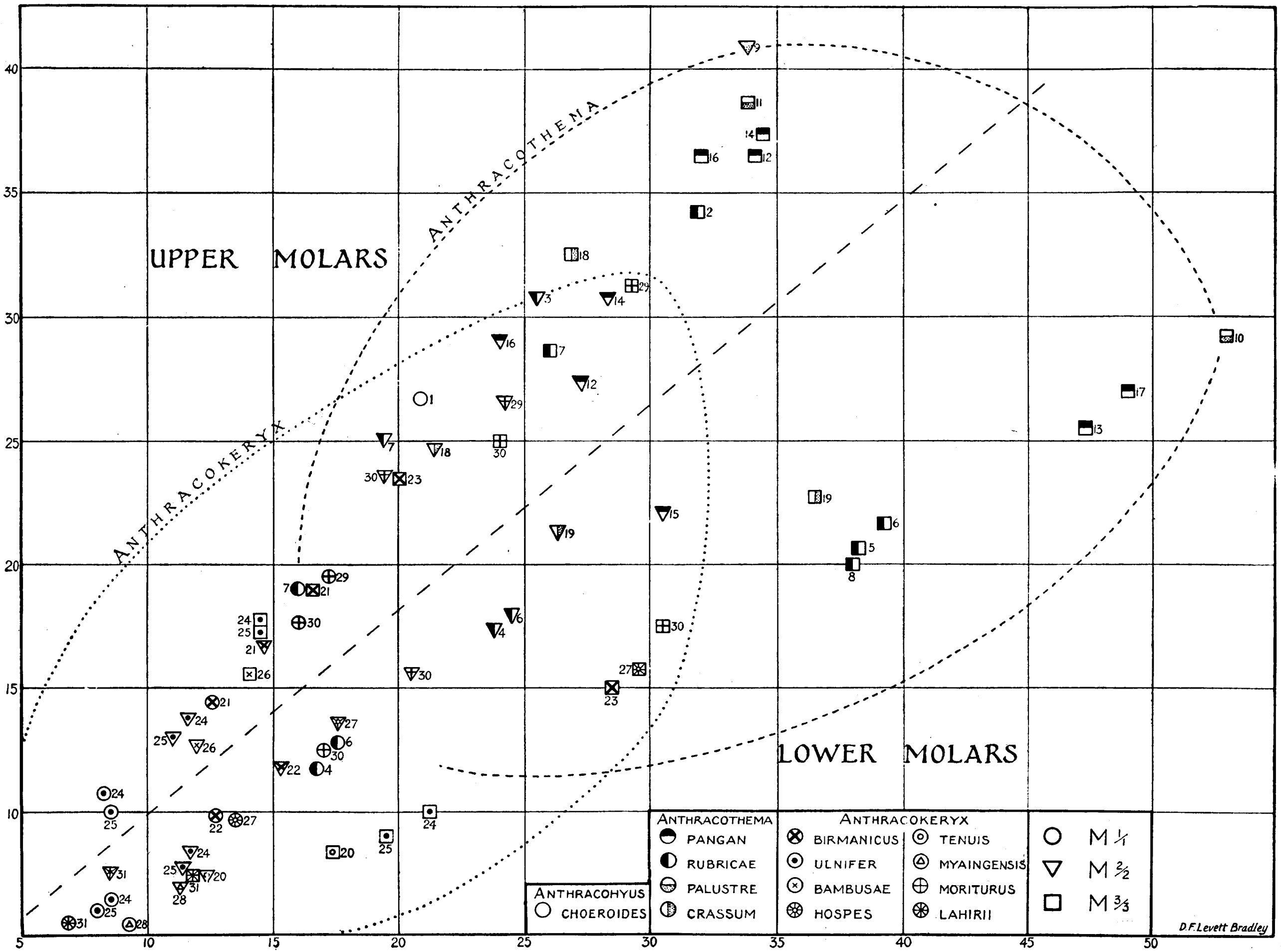
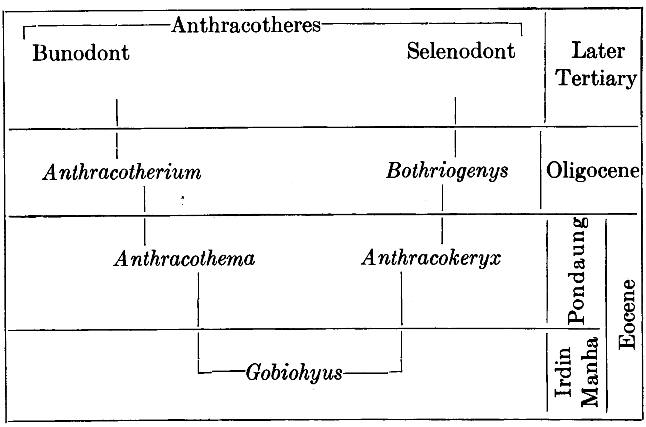


Fig. 54. Diagram to show the degree of variability in size in the upper and lower molars of the several species of Pondaung

The resemblance between *Anthracokeryx* and *Gobiohyus* is remarkably close, and considering the Pondaung formation of Burma to be slightly later in age than the Irdin Manha beds of Mongolia, the derivation and southward migration of the former genus from the latter would seem to be logically sound. *Anthracokeryx*, with its relatively long muzzle and a tendency toward a flattening of the molar cusps might easily have given rise to the later long-jawed, crescentic-cusped genera such as *Bothriogenys* and *Ancodon*. *Anthracothema*, on the other hand, a form in which the teeth show a general trend toward robustness and in which the premolar region becomes short, might very well have given rise to *Anthracotherium* and later related forms.

Perhaps the relationships of the Pondaung anthracotheres might be expressed in the following way.



TRAGULOIDEA

Hypertragulidae (?)

The only artiodactyl other than anthracotheres known from the Pondaung beds is a small, primitive type of ruminant. Our knowledge of this form, consisting of a single genus, is exceedingly scant, because it is based upon a few very fragmentary lower jaws.

INDOMERYX PILGRIM, 1928

PILGRIM, G. E., 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 33–35.

GENERIC TYPE.—*Indomeryx cotteri* Pilgrim.

DIAGNOSIS (Revised).—A small primitive member of the Pecora. Lower molars quadritubercular, the outer cusps being selenodont and the inner ones bunodont but laterally compressed. The entoconid may have a double ridge on its anterior face, or it may be smooth. External cingulum either present or absent. Talonid of third molar consisting of a single loop. Fourth lower premolar simple, elongated, being made up of a single cone, having on its posterior portion double ridges running down to form a basined heel. On the inner ridge there is a very small cusp; the "metaconid." Mandibular ramus seemingly shallow.

Indomeryx cotteri Pilgrim

Indomeryx cotteri, PILGRIM, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 33–35, Pl. IV, figs. 7, 9.

TYPE.—G.S.I. No. B768, a right mandibular ramus with P_4–M_3.

PARATYPES.—None.

HORIZON.—Pondaung, Eocene.

LOCALITY.—Seven furlongs E.S.E. of Sinzwe, Burma.

AUTHOR'S DIAGNOSIS.—The outer cusps of the molars are simple crescents; of these the anterior and posterior horns of the protoconid run in to join the metaconid, and the posterior horn of the hypoconid runs in to join the entoconid, while the anterior horn of the hypoconid meets the protoconid instead of joining the entoconid. The second arm, which runs back from the protoconid in *Dorcatherium* and *Dorcabune* is here absent. The inner cusps of the molars are not crescentic but merely compressed, closely resembling those of *Dorcatherium* and *Dorcabune*, except that the adjacent ridges of the hypoconid and entoconid are single instead of double as is the case in those genera; in *I. arenae* a distinct indication of such a double ridge can be seen on the entoconid of m_3. The cusps of the molars are low and the valleys are consequently shallow as compared with *Dorcatherium* or even *Dorcabune*. The talonid of m_3 consists of a single loop, with a hypoconulid which is just as high as the cusps in the preceding part of the tooth; this loop contains a shallow, forwardly directed valley and is united to the entoconid without the intervention of small cusps such as are present in *Dorcatherium* and *Dorcabune*. There is a cingulum externally as well as anteriorly and posteriorly; in the fragmentary m_3 of *I. arenae* I can see no trace of an external cingulum, except between the hypoconid and the talonid; it is also absent in *Dorcatherium* and *Dorcabune*.

P_4 is a long slender tooth, apparently as long as m_3, though the fracture of the front part of the tooth does not permit either the actual length or the structure of that portion to be ascertained with certainty. It consists of a high main cusp with two prominent ridges running steeply down to the rear; these continue into a long heel in which they form prominent rims encircling a basin-shaped area. On the inner side of the innermost of these two ridges there is a small but distinct internal cusp which can be traced as a bulge to the very base of the crown. I am not aware of any known Artiodactyl which possesses such a p_4 and this alone entitles it to generic differentiation.

Specimens in the American Museum:

Amer. Mus. No. 20023, a fragmentary piece of the right mandibular ramus, containing a broken third molar. From the Pondaung beds, one-half mile northwest of Mogaung. (Map, Fig. 8, locality 17.)

Amer. Mus. No. 32521, a fragmentary piece of the left mandibular ramus, containing M_1 and the anterior half of M_2. From the Pondaung beds, one mile north of Koniwa. (Map, Fig. 8, locality A21.)

The specimens here referred to *Indomeryx cotteri* would seem to agree fairly well with Dr. Pilgrim's description and figures of the type. The first molar, No. 32521, agrees very closely with the type in size, whereas the third molar, No. 20023, is some twenty per cent. larger, linearly, than the corresponding tooth of the type specimen. This difference in the third molar is here considered to come within the limits of individual or subspecific variation.

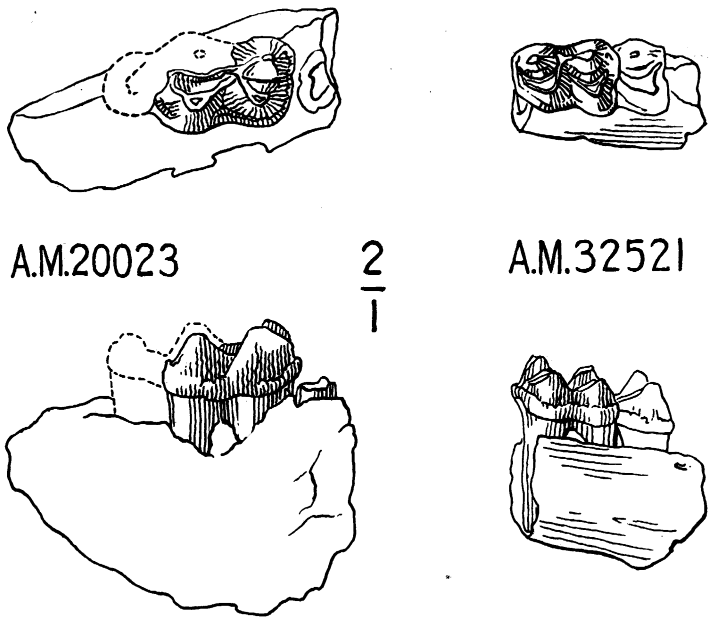


Fig. 55. *Indomeryx cotteri* Pilgrim. Left, Amer. Mus. No. 20023, right M_3. Crown view above, external lateral view below. Right, Amer. Mus. No. 32521, left M_{1-2}. Crown view above, external lateral view below. All twice natural size.

The specimens under consideration represent a fairly large Eocene pecoran; that is, they are considerably larger than typical Eocene forms such as *Archaeomeryx* (to which *Indomeryx* has been compared) and are more comparable in size to some of the Oligocene genera such as *Gelocus*, *Prodremotherium* and *Hypertragulus*. Both of the American Museum specimens are characterized by the very rugose enamel of the molars. The molars are comparatively broad, as in the Oligocene traguloids, but the tips of the cusps, when unworn, are rather closely appressed laterally, a character distinguishing this genus from some of the smaller

Eocene genera such as *Archaeomeryx*. The contiguity of the tips of the molar cusps is due to the fact that the ectoloph surfaces of the protoconid and the hypoconid slope inwardly to a considerable degree. There is a well-developed external cingulum along the external surface of the first molar and on the anterior portion of the second molar that is present in No. 32521, but in the third molar, No. 20023, the cingulum is developed only on the antero-lateral surface of the protoconid, the posterior surface of the hypoconid and across the valley between the protoconid and the hypoconid. Thus this latter tooth differs somewhat from the type, in which the cingulum is continuous along the outer surface of the molar.

In Pilgrim's description of *Indomeryx cotteri*, the third lower molar is distinguished by:

a.—Crescentic outer cusps.
b.—Anterior and posterior horns of the protoconid run in to join the metaconid.
c.—Posterior horn of hypoconid joins the entoconid; anterior horn joins the protoconid.
d.—There is no second posterior crest on the protoconid.
e.—The inner cusps of the molars are compressed.
f.—The adjacent ridges of the hypoconid and entoconid are single.
g.—The molar cusps are relatively low and the valleys comparatively shallow.
h.—An external cingulum is present.

All of these characters apply to the specimens in the American Museum collection. The only real difference to be noted is in the development of the cingulum, on M_3, discussed immediately above.

Measurements of the American Museum specimen, with comparative measurements of the specimens described by Pilgrim and of *Archaeomeryx optatus*, from Mongolia, are given in the following table.

MEASUREMENTS

		Indomeryx cotteri	*Indomeryx cotteri*	*Indomeryx arenae*	*Archaeomeryx optatus*
			Type	Type	Type
		A.M. 32521	G.S.I. B768	G.S.I. B769	A.M. 20311
M_1	length	6.5 mm.	6.6 mm.		5.9 mm.
	width	4.4	3.4		3.4
M_2	length		6.9		5.7
	width	4.5	4.2		4.0
	height (me^d)	3.9			3.3
		A.M. 20023			
M_3	length	11.5 (est.)	9.7	9.2 mm. (est.)	9.9 mm.
	width	5.4	4.3	4.1	4.4
	height (me^d)	4.7			3.8

Dr. Pilgrim provisionally referred *Indomeryx* to the Tragulidae, but he qualified this position for the genus by pointing out the fact that it is extremely difficult to be certain of the relationships of the primitive Eocene selenodont artiodactyls. Then, in a subsequent paragraph of his discussion, he indicated that *Indomeryx* is probably closely related to *Gelocus*, of the Oligocene traguloids and to *Archaeomeryx*, of the upper Eocene genera.

Gelocus may be considered as belonging to a separate group of the tragulids, the Gelocinae or the Gelocidae, depending on whether the tragulids are placed in an inclusive family, Tragulidae (an obviously bad procedure) or in a superfamily Traguloidea. Matthew placed *Archaeomeryx* in the Hypertragulidae.

Simpson, in 1931, designated a superfamily Traguloidea, consisting of five families, the Amphimerycidae, Hypertragulidae, Protoceratidae, Tragulidae and Gelocidae. Of these, the first family consists of very small, primitive Eocene genera while the third is made up of rather large, specialized, Oligocene and later Tertiary forms. Thus these two families may be safely excluded in a consideration of the relationships of *Indomeryx*.

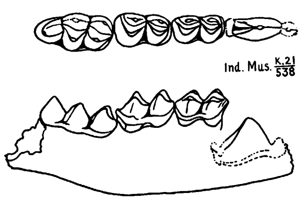


Fig. 56. *Indomeryx cotteri* Pilgrim. G.S.I. No. B768, type. Right mandibular ramus with P_4, M_{1-3}. Crown view above, external lateral view below. Natural size. (From Matthew, 1929.)

The Tragulidae are characterized, among other things, by the presence of a second crest or ridge on the posterior surface of the protoconid (and usually on the metaconid as well) of the lower molars. It may be noted, however, that there is no such crest in *Indomeryx* ("*f*" in the above list of characters). Consequently it becomes apparent that the Burmese form may be placed either in the Gelocidae with *Gelocus* or in the Hypertragulidae with *Hypertragulus* and *Archaeomeryx*.

In certain respects *Indomeryx* is similar to *Gelocus*, a point that was developed by Pilgrim. Thus, the general size of this form, the structure of its lower molars—consisting of robust inner cusps and crescentic outer cusps—the rugosity of the enamel and the development of the cingulum are all characters that tend to link *Indomeryx* with *Gelocus*. On the other hand, it would seem that the fourth lower premolar in *Gelocus* is somewhat more advanced in its structure than is the same tooth in the Burma genus.

Archaeomeryx of the Shara Murun formation of Mongolia likewise resembles *Indomeryx* in many of its characters. It is smaller than *Indomeryx*, has smooth enamel and lacks an external cingulum on the molars. Thus, it may be regarded as perhaps slightly more primitive than the Burmese form in its molar structure. On the other hand, the last lower premolar in *Archaeomeryx* has a well-developed internal cusp, as is the case in *Gelocus*. *Archaeomeryx* was placed by Matthew in the Hypertragulidae.

All in all, it would seem probable that *Indomeryx* is a primitive ruminant, showing certain resemblances to *Gelocus*, but being on the whole more primitive than this latter genus, and showing other resemblances to *Archaeomeryx*, but being perhaps slightly more advanced than this Mongolian genus. Because of its generally close resemblance to the Mongolia form, it is included provisionally in the family Hypertragulidae. In view of the fragmentary specimens on which our knowledge of *Indomeryx* is based, the precise determination of its family relationships must wait until some future time, when more adequate material is discovered.

Dr. Matthew made the following remarks about the type of *Indomeryx cotteri*. At the time he made his observations (1926) the specimen had not been described, so it was designated by him as an "undescribed ruminant."

> A lower jaw fragment, Fig. 40, represents a small primitive ruminant about the size of *Archaeomeryx* (Eocene, Mongolia) or *Tragulus*. Molars rather brachydont; premolar has doubled posterior ridge as in *Leptotragulus*, some camels, some "tragulids," etc. There is a slight trace of a metaconid on the inner ridge of p_4. Affinities are with Traguloidea or Tylopoda, exact position indeterminate. (Matthew, W. D., 1929, p. 516.)

Indomeryx arenae Pilgrim

Indomeryx arenae, Pilgrim, 1928, Mem. Geol. Surv. India, (N. S.) XIII, pp. 35–36, Pl. iv, figs. 10, 10a.

Type.—G.S.I. No. B769, a fragment of the left mandibular ramus containing the hinder half of M_3.

Paratypes.—None.

Horizon.—Pondaung, Eocene.

Locality.—1/4 mile W. of Pangan, Burma.

Author's Diagnosis.—This species is founded merely on a fragment of the left mandibular ramus containing the hinder half of m_3 (B769), collected by Cotter, $^1/_4$ mile W. of Pangan. It belongs presumably to the same genus as the type mandible of *Indomeryx cotteri* but is smaller and differs from it in certain details of structure. The lower border of the ramus behind m_3 shows a less degree of concavity; there is no external cingulum in m_3; the front side of the entoconid shows a distinct trace of a double ridge which is absent in *I. cotteri*. There are no other differences between the two species, so far as the available material permits of a comparison. Since the ramus, unlike that of *Indomeryx cotteri*, belongs to a mature animal, its depth may be taken as correct. We gather that this was moderately great, about three times that of the height of the molars. It agrees with *Archaeomeryx optatus* in regard to this.

Of the differences whereby Pilgrim distinguishes *Indomeryx arenae* from *Indomeryx cotteri*, only one may be considered as affording sufficient grounds for separating the species. This is the presence in *Indomeryx arenae* of "a distinct trace of a double ridge" on the front side of the entoconid. Unfortunately the type figure does not show this feature distinctly.

The size differences between the specimens are not large enough to warrant separation into two species. Thus the length of the third lower molar in *Indomeryx cotteri* is 9.7 mm.; the estimated length in *Indomeryx arenae* is 9.2 mm.; the variability or dispersion around the mean length is five per cent—a figure well within the range of subspecific or individual variation.

The differences in the lower border of the ramus, cited by Pilgrim, are nullified by the fact that the ramus of *Indomeryx cotteri* is that of a young animal, while that of *Indomeryx arenae* indicates a fully adult individual. As to the difference in the development of the cingulum, this may very well come within the range of individual variation. On the other hand, it is possible that this difference is indicative of a real specific distinction.

Therefore, in spite of certain differences between them, it is probable that *Indomeryx arenae* is synonymous with *Indomeryx cotteri;* certainly, considering the fragmentary specimen on which the former species is founded, it cannot be considered as a well-established form.

B.—FOSSIL MAMMALS FROM THE FRESHWATER PEGU SERIES

A few exceedingly fragmentary remains of fossil mammals have been found at various levels in the Freshwater Pegu beds, and they would seem to indicate that this series of deposits ranges in age through the Oligocene and the Miocene. It is even quite possible that the Pegus extend into the Pliocene, for *Dorcatherium* found near the top of the series is typically a Miocene and Pliocene genus. More extensive remarks as to the correlative significance of these fossils are to be found on a preceding page of this paper (p. 275).

From the above remarks it is readily apparent that the fossils from the Pegu series are not members of a single fauna, although they are treated together as a matter of convenience in the following pages. Rather, these Pegu fossils are the meager indications of at least three separate faunas, one of upper Oligocene age, one of lower Miocene age and one of middle or upper Miocene age. It is to be hoped that future explorations will increase our knowledge of fossil mammals from the Pegu beds.

PERISSODACTYLA

RHINOCEROTOIDEA

Amynodontidae

Cadurcotherium sp.

Cadurcotherium, PILGRIM, 1910, Rec. Geol. Surv. India, XL, p. 197; p. 205, (*Cadurcotherium indicum*).

ADDITIONAL REFERENCES.—PILGRIM, G. E. AND COTTER, G. DE P., 1916, Rec. Geol. Surv. India, XLVII, p. 45. STAMP, L. D., 1922, Geol. Mag., LIX, p. 497.

SPECIMENS UNDER CONSIDERATION.—Two fragments of molars, presumably in the collections of the Geological Survey of India.

HORIZON.—Pegu beds, provisionally correlated in part with the Aquitanian.

LOCALITY.—Twelve miles west northwest of Myaing, near the village of Kyaukwet, Burma.

REMARKS.—From the Pegu beds above the Yaw stage, about 12 miles WNW of Myaing, near a village named Kyaukwet, two fragments of molars of *Cadurcotherium* were found by Mr. Lister James, owing to which occurrence one of us suggested an Aquitanian age for the beds in which they were found. Unfortunately this area has not hitherto yielded any more specimens of mammalia. (Pilgrim and Cotter, 1916, p. 45.)

The *Cadurcotherium* from the Pegu beds of Burma was listed as *Cadurcotherium indicum* by Pilgrim in his correlation chart of the Tertiary deposits of India and adjacent regions, published in 1910. In no other place, however, does Pilgrim indicate that the Burma form is specifically identical with the Gaj species. Therefore it is designated in this present paper as *Cadurcotherium* sp., according to the manner in which it has been most often published.

ARTIODACTYLA

ANTHRACOTHERIOIDEA

Anthracotheriidae

Telmatodon (?) sp.

Telmatodon (?) sp., PILGRIM, 1910, Rec. Geol. Surv. India, XL, p. 68.

SPECIMEN UNDER CONSIDERATION.—A lower molar, presumably in the collections of the Geological Survey of India.

HORIZON.—"Slightly lower than that of Noetling's mammalian teeth." That is, the upper portion of the Pegu series. Miocene.

LOCALITY.—Maingyaung, Pakokku district, Upper Burma.

A small and fragmentary upper molar from Sind provisionally referred by Lydekker to *Agriochoerus* has a structure so similar to that of *Telmatodon bugtiensis* as to suggest that it belongs to the same or a closely allied genus. A lower molar found by Mr. Cunningham Craig in the upper beds of the Pegu series of Burma may belong to the same species. (Pilgrim, G. E., 1910, p. 68.)

TRAGULOIDEA

Tragulidae

Dorcatherium birmanicum (Noetling)

Anoplotherium birmanicum, NOETLING, 1901, Pal. Indica, (N. S.) I, Pt. 3, p. 378, Pl. xxv, figs. 24, 25.

Dorcatherium birmanicum, PILGRIM, 1910, Rec. Geol. Surv. India, XL, p. 203.

ADDITIONAL REFERENCE.—VREDENBURG, E., 1921, Rec. Geol. Surv. India, LI, Pt. 3, pp. 255–257.

TYPE.—A third lower molar and another lower molar, described and figured by Noetling in the above cited work. Number not given.

PARATYPES.—None.

HORIZON.—"Zone of *Anoplotherium birmanicum*, Yenangyaung." This is in the Pegu series, and is correlated more or less with the Lower Siwaliks, by Pilgrim (1910). See also Vredenburg, *op. cit.*, pp. 255–257.

LOCALITY.—Yenangyaung, Burma.

AUTHOR'S DESCRIPTION.—The larger molar may probably represent the third molar of the lower jaw, while the smaller one represents a more anterior one. So far it seems to me that in its character it does not agree with any of the described species.

C.—THE LOWER IRRAWADDY FAUNA

Remarks as to the age of this fauna and the mammals comprising it will be found in an earlier section of this paper.

PERISSODACTYLA

EQUOIDEA

Equidae

HIPPARION CHRISTOL, 1832

CHRISTOL, J., 1832, Ann. Sci. Indust. du Midi de France, I, p. 215.

GENERIC TYPE.—Apparently no type was named in the original description. Lydekker includes 4 species: *Equus* (*Hippotherium*) *gracilis* Kaup (1833), from Europe; *Hippotherium antelopinum* Falconer & Cautley (1849), from India; *Hipparion richthofeni* Koken (1885), from China; and *Sivalhippus theobaldi* Lydekker (1877), from India. (Palmer, T. S., 1904, 'Index Generum Mammalium,' No. Amer. Fauna, No. 23, p. 325.)

GENOTYPE: *H. prostylum* Gervais, 1849, from the Miocene of Cucuron, Vaucluse, France. (Osborn, H. F., 1918, Mem. Amer. Mus. Nat. Hist., (N. S.) II, Pt. 1, p. 173.)

DIAGNOSIS.—Protocone separate to base, or nearly so; round-oval; crown of upper molars of moderate height; mesostyle progressively heavy; cement lake borders simple to much folded; curvature of upper molars slight; size progressively large. Inner pillars of lower molars rounded; intervening valley deeply rounded; outer crescents convex; protostylid slight. Face short, with a deep lachrymal fossa; no malar fossa. Metapodials moderate to stout; cuboid facet wide; mesocuneiform facet well developed; lateral digits (II and IV) well developed; fifth digit and trapezium in the form of nodules.

This diagnosis is adapted from: MATTHEW, W. D., AND STIRTON, R. A., 1930, Bull. Dept. Geol. Sci., Univ. Calif., XIX, No. 17, pp. 368–369. It applies to *Hipparion sensu stricto*, as distinguished from *Neohipparion* and *Nanippus*.

Hipparion antelopinum (Falconer and Cautley)

Hippotherium antelopinum, FALCONER AND CAUTLEY, 1849, 'Fauna Antiqua Sivalensis,' Pls. LXXXII–LXXXV.

Hipparion antelopinum, LYDEKKER, 1885, 'Cat. Siwalik Vert. Ind. Mus.,' pp. 57–58.

Hippodactylus antelopinum, PILGRIM, 1910, Rec. Geol. Surv. India, XL, p. 201.

Hipparion punjabiense, LYDEKKER, 1886, 'Cat. Foss. Mam. Brit. Mus.,' III, p. 60.

ADDITIONAL REFERENCES.—For the synonymy and a complete list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, pp. 129–132.

TYPE (LECTOTYPE).—B.M. No. 2647, a right maxilla with P^2–M^3.

COTYPES.—B.M. Nos. 16170, a portion of a cranium; M2652, a mandible; M2653, a mandible; M2648, fragment of an upper molar; various limb bones, etc., figured by Falconer and Cautley, 1849, Pls. LXXXIII–LXXXV.

HORIZON.—Middle Siwaliks, typically from the Dhok Pathan zone, Pliocene Lower Irrawaddies, Pliocene.

LOCALITY.—Siwalik Hills and the Salt Range, Punjab. Vicinity of Yenangyaung, Upper Burma.

DIAGNOSIS.—A large species of *Hipparion*, characterized by the oval protocone and the crenulated fossette borders of the upper molars, by the well-developed preorbital fossa of the skull and by the slender medial metapodials of the feet. (Colbert, E. H., 1935, p. 131.)

COTYPES OF *Hipparion punjabiense*.—G.S.I. No. C139, a left maxilla with P^3–M^2; G.S.I. No. C138, a left maxilla with a milk dentition and M^1; B.M. No. M2646, a maxilla with the milk dentition and M^1.

Stamp, in 1922, recorded "*Hipparion punjabiense*" as coming from the lower, or Pliocene, level of the Irrawaddies. Since this species is here considered as being synonymous with *Hipparion antelopinum*, the record for the genus in Burma is presented as above.

Specimen in the American Museum:

Amer. Mus. No. 20035, a single lumbar vertebra. From the Beme dome, one half mile southeast of Yenangyaung. (Map, Fig. 12, locality 6.)

This fragmentary centrum of a lumbar vertebra is the only specimen in the American Museum collection that is definitely recorded from the lower, or Pliocene horizon of the Irrawaddy beds. Careful comparisons would seem to show that it is definitely referable to *Hipparion*.

RHINOCEROTOIDEA

Rhinocerotidae

ACERATHERIUM KAUP, 1832

KAUP, J., 1832, Oken's 'Isis,' pp. 898–904, Pl. XVIII, fig. 1 [*Rhinoceros (Acerotherium) incisivus*].

KAUP, J., 1834, Oken's 'Isis,' p. 314 (*Acerotherium incisivum*).

GENERIC TYPE.—*Rhinoceros incisivus* Cuvier.

DIAGNOSIS.—Dolichocephalous. Nasal bones small, projecting freely above the narial openings, hornless; frontal bones smooth above; mastoid process (post-tympanic) independently developed and separated from the postglenoid process by a furrow. Dental formula: $\frac{2\text{-}1.0.4.\ \ 3.}{2\text{-}1.0.4\text{-}3.3.}$. Upper incisors with low laterally compressed crowns elongated antero-posteriorly and with the wear oblique. Lower inner incisors diminutive, deciduous, chisel-shaped; outer very large, procumbent, triangular, with wear posterior. Premolars less complex than the molars. Manus often still tetradactyl, pes tridactyl. (von Zittel, K. A., 1925, p. 139.)

Aceratherium lydekkeri Pilgrim

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

ADDITIONAL REFERENCES.—For the synonymy and a list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 200.

TYPE.—Not definitely designated.

COTYPES (by inference).—G.S.I. Nos. C1, C2, C3, C4, C7, C14, C18, C238. One of these specimens might be picked as a lectotype. See Colbert, E. H., *op. cit.*, p. 200.

HORIZON.—Middle Siwaliks, Pliocene. Lower Irrawaddies, Pliocene.

LOCALITY.—Northern Punjab, particularly from the vicinity of Hasnot. Yanangyaung, Upper Burma.

DIAGNOSIS.—Like *Aceratherium perimense*, but smaller and more dolichocephalic. (Colbert, E. H., p. 200.)

This species is cited by Stamp (1922) as coming from the lower, or Pliocene, level of the Irrawaddies.

ARTIODACTYLA

SUOIDEA

Suidae

TETRACONODON FALCONER, 1868

FALCONER, H., 1868, Pal. Memoirs, I, pp. 149–156.

GENERIC TYPE.—*Tetraconodon magnus* Falconer.

DIAGNOSIS.—A gigantic suid in which the last two premolars are extremely large, conical, and with very rugose enamel.

Tetraconodon minor Pilgrim

Tetraconodon minor, PILGRIM, 1910, Rec. Geol. Surv. India, XL, p. 67.

ADDITIONAL REFERENCES.—For a complete list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 230.

TYPE (LECTOTYPE).—G.S.I. No. B677, portion of a mandible, containing the last two left premolars.

COTYPES.—G.S.I. Nos. B676, maxilla with right P^4–M^3; G.S.I. No. B534, mandibular ramus with right M_{2-3}.

HORIZON.—Near the base of the Irrawaddy series, Pliocene.

LOCALITY.—Below Yenangyaung, Burma.

DIAGNOSIS.—Smaller than *T. magnus,* but much larger than *Conohyus*. The premolars are relatively much smaller than in *T. magnus*, but much larger than in *Conohyus*. Teeth hypsodont, palate wide. Skull similar to skull of *T. magnus*. (Colbert, E. H., p. 230.)

GIRAFFOIDEA

Giraffidae

HYDASPIDOTHERIUM LYDEKKER, 1876

HYDASPITHERIUM LYDEKKER, EMEND., 1878

LYDEKKER, R., 1876, Rec. Geol. Surv. India, IX, Pt. 4, p. 154. 1878, Pal. Indica, (X) I, p. 159.

GENERIC TYPE.—*Hydaspitherium megacephalum* Lydekker.

AUTHOR'S DIAGNOSIS.—The distinctive characters of the cranium are the possession of one common horn-base on the vertex, and the absence of anterior horns; the profile is concave, the orbit depressed, and separated by a long interval from the horn core; the teeth resemble those of Bramatherium.

Hydaspitherium birmanicum Pilgrim

Hydaspitherium birmanicum, PILGRIM, 1910, Rec. Geol. Surv. India, XL, p. 70.

ADDITIONAL REFERENCES.—For a list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 362.

TYPE.—G.S.I. No. B517, a right upper molar.

PARATYPES.—None.

HORIZON.—Irrawaddy series, equivalent to the Middle Siwaliks.

LOCALITY.—Near Singa, Upper Burma.

AUTHOR'S DIAGNOSIS.—A single upper molar, found near Singu in Upper Burma, differs little from *H. megacephalum* except by its much smaller size. The front horn of the second crescent is not so long and the enamel folds penetrate the crown less deeply.

VISHNUTHERIUM LYDEKKER, 1876

LYDEKKER, R., 1876, Rec. Geol. Surv. India, IX, Pt. 3, pp. 91, 103.

GENERIC TYPE.—*Vishnutherium iravaticum* Lydekker.

AUTHOR'S DIAGNOSIS.—Genus founded on a portion of a left mandible discovered by Mr. W. T. Blanford in Burma; the specimen contains the first and second true molar teeth. The general form of the molars is like those of *Camelopardalis*, *Sivatherium* and *Bramatherium*, and the enamel has the same rugose character; the teeth are, however, distinguished from those of either of the above genera by the following characters:—

Along the whole of the external surface of each molar there is a well-marked sinuated cingulum; this extends halfway across the posterior and anterior surfaces, where it is very conspicuous; it is produced into a number of cusps on the anterior surface; there is a prominent tubercle at the entrance to the main valley between the barrels: the other characters differ but slightly from those of the teeth of the above genera.

This genus is distinguished from *Sivatherium* and *Bramatherium* by its small size, and by the presence of the cingulum and tubercle; from *Camelopardalis* by the presence of a cingulum, and by the tubercle being pointed and present in both molars, instead of being blunt and only present in the first molar.

Vishnutherium iravaticum Lydekker

Vishnutherium iravaticum, LYDEKKER, 1876, Rec. Geol. Surv. India, IX, p. 103.

ADDITIONAL REFERENCES.—For a complete list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 364.

TYPE.—G.S.I. No. B168, a left mandibular ramus.

PARATYPES.—None.

HORIZON.—Lower levels of the Irrawaddy series, Pliocene.

LOCALITY.—Burma.

DIAGNOSIS.—Since this is a monotypical genus, the generic and specific diagnoses are the same. See the generic diagnosis, above.

The type of the genus . . . . appears very doubtfully separable from *H. megacephalum.* In absence of adequate topotypes the genus and species are practically indeterminate. (Matthew, W. D., 1929, p. 544.)

BOVOIDEA

Bovidae

PACHYPORTAX PILGRIM, 1937

PILGRIM, G. E., 1937, Bull. Amer. Mus. Nat. Hist., LXXII, p. 766.

GENERIC TYPE.—*Cervus latidens* Lydekker.

AUTHOR'S DIAGNOSIS.—Boselaphinae of small to large or very large size; closely allied to *Strepsiportax* but differing from that genus by the much more massive skull, with horn-cores longer, stouter, more twisted and less curved inwardly; occipital condyles and foramen magnum larger; mastoid process and squamosal shelf more developed; supraoccipital exposed on the upper surface of the occiput as a narrowly elliptical area much extended transversely; basioccipital approaching a rectangular shape, with posterior tuberosities not greatly expanded; upper molars strongly hypsodont but less so than in *Selenoportax*, quadrate, with strong basal pillars, external folds weaker and less divergent than in *Selenoportax*, external ribs weaker than in *Selenoportax*, in particular the median rib of the posterior lobe flattened, enamel rather thick, somewhat less rugose than in *Selenoportax*, with traces of cement.

Pachyportax latidens (Lydekker)

Cervus latidens, LYDEKKER, 1876, Pal. Indica, (X) I, p. 65, Pl. VIII, figs. 7, 10.

Oreas (?) *latidens*, LYDEKKER, 1884, Pal. Indica, (X) III, p. 111, Pl. XIII, figs. 12, 13.

Taurotragus latidens, PILGRIM, 1910, Rec. Geol. Surv. India, XL, pp. 196, 204.

Pachyportax latidens, PILGRIM, 1937, Bull. Amer. Mus. Nat. Hist., LXXII, p. 766, Fig. 18.

ADDITIONAL REFERENCES.—LYDEKKER, R., 1884, Pal. Indica, (X), III, p. 127; 1885, 'Cat. Siwalik Vert. Ind. Mus.,' I, p. 18. PILGRIM, G. E., 1913, Rec. Geol. Surv. India, XLIII, p. 287.

TYPE.—G.S.I. No. B219, an isolated M^3.

PARATYPES.—None.

HORIZON.—From the Lower Portion of the Upper Siwaliks, Tatrot Zone.[1] (Pilgrim, G. E., 1937, p. 767.)

LOCALITY.—Hasnot and adjacent localities, Punjab. (Pilgrim, G. E., 1937, p 767.)

DIAGNOSIS.—A *Pachyportax* of extremely large size; upper molars with relatively strong external folds, median ribs broad and relatively prominent, internal basal pillar much extended transversely. (Pilgrim, G. E., 1937, p. 767.)

On page 196 of his 1910 paper, listed above, Pilgrim presents a list of presumably Lower Irrawaddy species. Included in this list is "*Taurotragus latidens*, Lyd." So far as I have been able to determine, no sub-

[1] This species is more typically a Middle Siwalik form than an Upper Siwalik one.

sequent descriptions of material referable to this species from the Lower Irrawaddies have been published. Thus our knowledge of this bovid in the Lower Irrawaddies is based on a published name.

Proleptobos birmanicus Pilgrim (*nomen nudum*)

Proleptobos birmanicus, Pilgrim, 1913, Rec. Geol. Surv. India, XLIII, Pt. 4, p. 304.

This name was based on a skull in the British Museum, apparently from Ava on the Irrawaddy River. Since, however, no adequate definition or indication of the species was presented, the name (as of 1913) must be regarded as invalid.

As compared to the pontian of Europe a rather modern look is given to the Dhok Pathan zone by the supposed presence of an ancestral form of *Leptobos*. This specimen is labeled "Ava" and it seems probable that it belongs to the Middle Siwalik of Burma. Even should this be found correct, it is no matter for surprise that a species of the most primitive of the oxen which shows features still more akin to the antelopes than the Upper Siwalik *Leptobos falconeri* should appear as early as the pontian outside of Europe. I venture to name the specimen *Proleptobos birmanicus*. (Pilgrim, G. E., 1913, p. 304.)

Another interesting skull which had apparently been overlooked for some years bears a label containing the word "Ava." If the specimen really came from Ava its age is presumably Middle Siwalik, since numerous Middle Siwalik species have been obtained from that locality. If this is so, its presence is interesting, since Dr. Pilgrim regards it as undoubtedly an ancestral form of the Pliocene *Leptobos*. He also found that it possessed decided antelopine affinities. (Hayden, H. H., 1912, p. 14.)

D.—THE UPPER IRRAWADDY FAUNA

Remarks as to the age of this fauna and the mammals comprising it will be found in an earlier section of this paper.

It might be said here, that Pilgrim's list of Lower Irrawaddy species, published in 1910,[1] certainly includes some forms of definite Upper Irrawaddy affinities. As Stamp pointed out in 1922, *Stegolophodon latidens* and *Hexaprotodon iravaticus*, included by Pilgrim in his list of Lower Irrawaddy forms, are confined to the Upper Irrawaddies. Accordingly these species, because of their obvious Pleistocene affinities, are included in the following pages dealing with the Upper Irrawaddy fauna. Likewise, *Merycopotamus dissimilis*, listed by Pilgrim as a Lower Irrawaddy form, is here placed in the Upper Irrawaddy fauna, because this species is a typical Upper Siwalik fossil in India. However, since *Merycopotamus* does seem to extend down into the Middle Siwaliks, it is very probable that it may have been present in the Lower Irrawaddy beds.

[1] Pilgrim, G. E., 1910*b*, Rec. Geol. Surv. India, XL, p. 196.

PROBOSCIDEA

STEGODONTOIDEA

Stegodontidae

STEGOLOPHODON SCHLESINGER, 1917

SCHLESINGER, G., 1917, Denkschriften des K. K. Naturhistorischen Hofmuseums, Band I, Geol.-Pal. Reihe I, p. 115.

GENERIC TYPE.—*Mastodon latidens* Clift.

AUTHOR'S DIAGNOSIS.—Ich schlage für *M. latidens*, das sich durch seine kurze Symphyse von dem Subgenus *Bunolophodon*, durch seinen Molarenbau von *Dibunodon* entfernt, den Untergattungsnamen *Stegolophodon* vor. Der Name bringt einerseits die nahen Beziehungen zum Genus *Stegodon*, anderseits die Loslösung der Untergattung von *Bunolophodon* und ihre Sonderstellung gegenüber *Dibunodon* zum Ausdruck. (Schlesinger, G., 1917, *op. cit.*, p. 115, footnote.)

Stegolophodon latidens (Clift)

Mastodon latidens, CLIFT, W., 1828, Trans. Geol. Soc. London, (2) II, Pt. 3, pp. 371, 372, Pl. XXXVII, figs. 1, 4; Pl. XXXVIII, fig. 1; Pl. XXXIX, figs. 1, 2, 3.

Stegolophodon latidens, SCHLESINGER, 1917, Denkschr. des K. K. Naturhist. Hofmuseums, Band I, Geol.-Pal. Reihe I, p. 115.

ADDITIONAL REFERENCES.—FALCONER, H., AND CAUTLEY, P. T., 1846, 'Fauna Antiqua Sivalensis.' Pl. XXX, fig. 6; XXXI, figs. 1–8.

FALCONER, H., 1868, 'Palaeontological Memoirs,' I, pp. 83, 461, 463, Pl. VI, fig. 2.

LYDEKKER, R., 1880*a*, Jour. Asiatic Soc. Bengal, XLIX, Pt. 2, p. 31; 1880*b*, Pal. Indica, (X) I, pp. 227–239, Pl. XXXVII, figs. 1–2, 4–8; Pl. XXXVIII, fig. 2; 1885, Cat. Siw. Vert. Ind. Mus., Pt. I, p. 94; 1886, Cat. Foss. Mam. Brit. Mus., IV, pp. 74–78.

PILGRIM, G. E., 1910, Rec. Geol. Surv. India, XL, pp. 196, 200; 1913, Rec. Geol. Surv. India, XLIII, p. 294.

STAMP, L. D., 1922, Geol. Mag., LIX, pp. 497–498.

OSBORN, H. F., 1936, 'Proboscidea,' publ. by Amer. Mus. Nat. Hist., I, p. 700.

TYPE (LECTOTYPE).—An upper jaw containing RM^2, RM^3. Original in Geol. Soc. Coll.; Brit. Mus. cast, B.M. No. M2888–9. Pl. XXXVII, fig. 1, Clift.

COTYPES.—Fragments of tooth, Clift, Pl. XXXVII, fig. 4, B.M. cast 7391; right lower jaw, Pl. XXXVIII, fig. 1, Geol. Soc. Coll., Brit. Mus. cast 7394; Pl. XXXIX, figs. 1, 2, 3.

HORIZON.—Irrawaddy series, Upper Irrawaddy beds.

LOCALITY.—Near Yenangyaung, Burma.

AUTHOR'S DIAGNOSIS.—Each tooth of the lower jaw consists of seven denticules, which are elevated, rounded and mammillated: the mammillae being from three to four in number. The dentition both in this species and in *M. elephantoides*, very much resembles that of the elephant. We have the molar tooth gradually protruded forward, and rising as the fangs are added, according to the demand made by the abrasion of the exposed crown, and the consequent absorption of the anterior fang; the posterior part of the tooth not having cut the gum, while the anterior portion is completely worn away. The relics of the preceding tooth, the place of which the tooth in use was progressively supplying, are plainly to be seen.

The exposed grinding surface is considerably larger than that of the molar tooth of any elephant which I have seen, especially in breadth; and the enamel of the tooth is not so thick as it is in *M. giganteum*. And here we cannot fail to be struck with the similarity which the worn surface bears to the worn surface of an elephant's tooth.—The denticules are less elevated than those of other mastodons, and the whole form

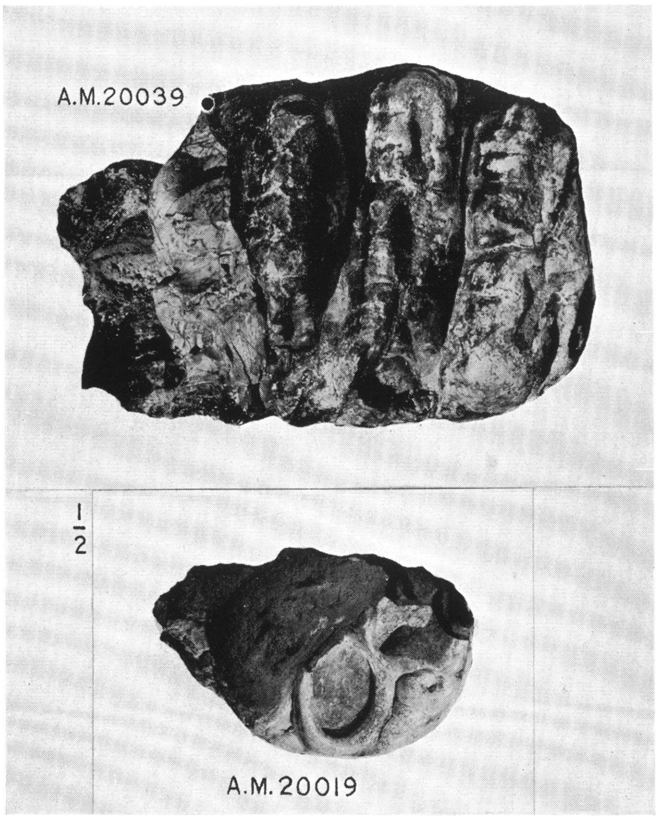


Fig. 57. Above. *Stegodon elephantoides* (Clift). Amer. Mus. No. 20039, upper molar. Crown view, one-half natural size.

Below. *Stegolophodon latidens* (Clift). Amer. Mus. No. 20019, fragment of molar. Crown view, one-half natural size.

indicates an approach to the structure of the teeth of the elephant. The lower jaw too, in this species, is deeper and less angular than it is in *M. giganteum;* and approaches in its contour to the form of the lower jaw of the elephant. But on examining the cranium we shall find still stronger indications of an approach to the elephant; for the palate is so very narrow when compared with the palate of *M. giganteum,* as to strike the most casual observer.

The tusks, judging from the alveoli, must have been of equal volume with the tusks of the largest living elephant. The portions of fossil ivory, however, found with these remains, do not appear to have belonged to the individual which furnishes this description.

Specimen in the American Museum:

Amer. Mus. No. 20019, a fragment of a molar tooth. From the Upper Irrawaddy beds, one mile southwest of Yegyaw. (Map, Fig. 8, locality A35.)

This very fragmentary specimen may, in spite of its imperfect condition, be definitely assigned to *Stegolophodon latidens.* It is a bunodont tooth, showing the remains of two large, well-worn and distinct cones. In addition there are three small conelets comprising a posterior cingulum.

STEGODON FALCONER, 1857

FALCONER, HUGH, 1857, Quar. Jour. Geol. Soc., London, XIII, Pt. 4, pp. 314, 318, synoptic table.

GENERIC TYPE.—Species, 4: *Elephas cliftii* Falconer & Cautley, *E. bombifrons* Falconer & Cautley, *E.* ? *ganesa* Falconer & Cautley, and *E. insignis* Falconer & Cautley, from the Miocene and Pliocene of India. (Palmer, T. S., 1904, p. 643.)

DIAGNOSIS.—Lower incisors absent, upper incisors powerfully developed, without a band of enamel. Molars composed of from six to twelve low, roof-shaped, slightly convex, and usually multipapillose transverse crests, the intermediate valleys being partially filled with cement. In a given jaw, the first and second molars as a rule have an equal number of crests; the teeth of the mandible usually exhibit more ridges than the corresponding upper molars. (von Zittel, K. A., 1925, p. 261.)

Stegodon elephantoides (Clift)

Mastodon elephantoides, CLIFT, 1828, Trans. Geol. Soc. London, (2) Pt. 3, II, pp. 372–373, Pl. XXXVI, fig. 1, Pl. XXXVII, figs. 2, 3; Pl. XXXVIII, fig. 2; Pl. XXXIX, fig. 6.

Elephas cliftii, FALCONER AND CAUTLEY, 1846, 'Fauna Antiqua Sivalensis,' Pl. XXX, figs. 1–5. (A synonym.)

Elephas insignis (in parte), FALCONER AND CAUTLEY, 1846. 'Fauna Antiqua Sivalensis. Pl. XX, fig. 9, 9a.

Elephas cliftii, FALCONER, 1868, Pal. Memoirs, I, pp. 81–82, 113–114, 461–462.

ADDITIONAL REFERENCES.—LYDEKKER, R., 1880, Jour. Asiatic Soc. Bengal, XLIX, Pt. 2, p. 31. (*Stegodon cliftii*); 1883, Rec. Geol. Surv. India, XVI, p. 92. (*Stegodon cliftii*); 1885, 'Cat. Siwalik Vertebrata Ind. Mus.,' Pt. I, p. 88. (*Elephas clifti*); 1886, 'Cat. Foss. Mam. Brit. Mus.,' IV, pp. 79–82 (*Elephas clifti*).

PILGRIM, G. E., 1910, Rec. Geol. Surv. India, XL, p. 200 (*Stegodon clifti*); 1913, Rec. Geol. Surv. India, XLIII, p. 284 (*Stegodon clifti*).

LECTOTYPE.—Left lower jaw figured by Clift, 1828, Pl. XXXVIII, fig. 2.

COTYPE.—Upper molar, Pl. XXXIX, fig. 6. (Geol. Soc. Coll., Cast Brit. Mus. No. 7388.)

HORIZON.—Upper Irrawaddy beds, Pleistocene.

LOCALITY.—Yenangyaung, Burma.

AUTHOR'S DIAGNOSIS.—This species must have been smaller than the last; and though we have one fine example of the lower jaw, showing the tooth in the highest degree of perfection, that is the only portion of the animal from which we can safely draw any inference as to its structure and habits. The tooth, which is eleven inches long and three inches and a half broad, has no less than ten denticules, and each of these denticules is mammillated with small points; five being the smallest number, and eight the greatest on any one denticule. In front of this beautiful tooth we have a remnant of the preceding one, nearly worn down and disappearing; and behind it, we have the cavity in which the young tooth which was intended as a successor to that in existence, must have been in the course of formation.

The denticules of the tooth are much more compressed than those in the species last described; they are closer together, and the enamel appears to be not so thick. They form a series of plates mucronated with small points. There is no apparent commissure, neither is there any central depression; on the contrary, the plates rather rise in the middle.

This tooth approaches still more nearly to that of the elephant, and the contour of the jaw is in unison with the appearance of the tooth. Perhaps we should not be far from the truth, if we were to conclude that the species to which this tooth belonged, formed the passage from the Mastodon to the Elephant. It is not impossible, however, that there may yet be a link wanting, which might be supplied by an animal having a tooth composed of a greater number of denticules, increasing in depth, and having the rudiments of crusta petrosa,—that necessary ingredient in the tooth of the elephant, — (for it is the animal mortar, as it were, by which the plates or denticules are cemented together)—the entire absence of which, distinguishes the tooth of the mastodon.

Eight denticules of *M. elephantoides* occupy the same space as five denticules of *M. latidens.*

Specimen in the American Museum:

Amer. Mus. No. 20039, a fragmentary upper molar. From the Upper Irrawaddy beds, about 4500 feet above their base. Bank of the Irrawaddy River, below B.B.P. office, Yenangyaung. (Map, Fig. 12, locality 5.)

This tooth would seem to be closely comparable to the upper molar of *Stegodon elephantoides* first described and figured by Clift. For this reason it is referred to this species, rather than to *Stegodon insignis birmanicus*, of which latter form no upper teeth are known.

In the specimen at hand only the anterior three ridges are preserved, and of these the first two are worn. From the broken posterior portion of the tooth it would appear that there were probably six or seven ridge crests in all, thereby making this tooth resemble the figured upper molar of *Stegodon elephantoides.* The specimen under consideration is rather brachyodont for a stegodont, perhaps slightly more so than the tooth figured by Clift. The difference is, however, not great.

Stegodon insignis birmanicus Osborn

Stegodon insignis birmanicus, OSBORN, 1929, Amer. Mus. Novitates, No. 393, pp. 15, 16, Fig. 16.

TYPE.—Amer. Mus. No. 20002, a very large and massive left mandibular ramus, containing the left third inferior molar.

PARATYPES.—None.

HORIZON.—Upper levels of the Irrawaddy series; Pleistocene.

LOCALITY.—Mingun, opposite Mandalay, Burma. (Map, Fig. 6, locality 20.)

AUTHOR'S DIAGNOSIS.—The ridge-crests of $1.M_3$, namely $\frac{\quad}{12^1/_2}$, are the same in number as in *Stegodon insignis*, but the elongation of this inferior molar and the open character of the ridge-crests are quite distinctive from *S. insignis;* the jaw is more massive and the inferior grinding teeth surpass in length measurement those of any other stegodont type known; the grinders are larger and exhibit fewer conelets. The conelets are stout and vary in number from four to twelve on each ridge-crest. Cement is present all the way back.

Additional Specimen in the American Museum:

Amer. Mus. No. 20001, a right mandibular ramus with the anterior portion of the third molar preserved. From the Upper Irrawaddy beds, three miles west of Chongsongyi, Upper Burma. (Map, Fig. 9, locality 9.)

The type of *Stegodon insignis birmanicus* is an extraordinarily large and massive jaw, containing the remnants of the second molars, on the right side the anterior portion of the third molar and on the left side the complete third molar. As Professor Osborn pointed out in his type description of this form, the tooth is unusually large, particularly as to its length. In this tooth there are twelve full ridge-crests, with the very rudiment of another posterior crest. The crests are spaced at an approximate ratio of slightly more than three to 100 millimeters, which may be compared with the ratio of four crests to 100 millimeters that is typical of the Siwalik *Stegodon insignis*. Thus, as Osborn demonstrated, the ridge-crests of this Burma species are rather widely spaced, and this makes the tooth very long. A form that may be compared with *Stegodon insignis birmanicus* is *Stegodon orientalis grangeri*, in which the third lower molar is fully as long as the same tooth in the Burmese species, and like it, has a ridge-crest ratio of slightly more than three to 100 millimeters. The type molar of *Stegodon insignis birmanicus* is characterized by rather tall ridge-crests composed of stout conelets, and the posterior portion of the tooth is invested with a very thick coat of cement.

Certain differences are to be seen between the molars in the type of the form under discussion and the specimen (Amer. Mus. No. 20001) that has been referred to it. In the first place, the ridge-crests of the type would seem to be somewhat taller than those of the referred speci-

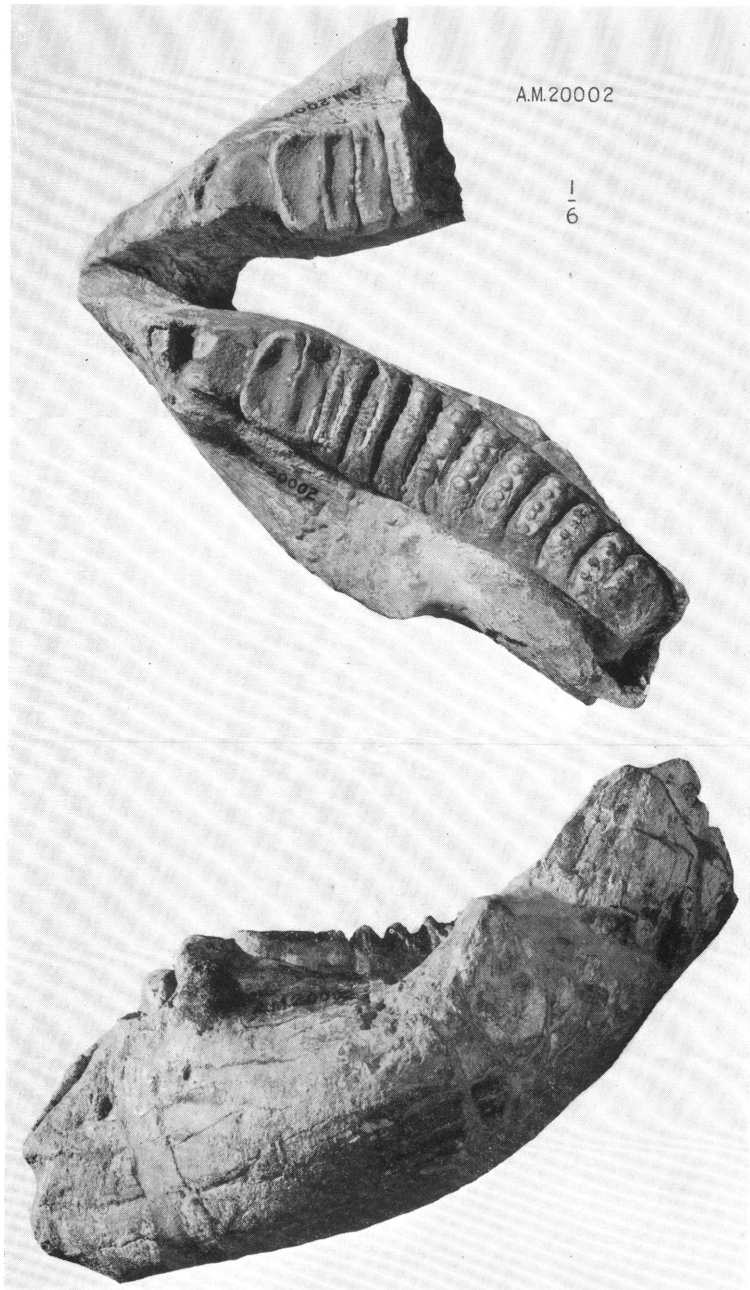


Fig. 58. *Stegodon insignis birmanicus* Osborn. Amer. Mus. No. 20002, type mandible. Crown view above, lateral view below, one-sixth natural size.

men, the difference between them amounting to about twenty five per cent of the total height of the crests in the type. Then, the outer surface of the type tooth is rather strongly rugose, whereas in the referred specimen it is smooth.

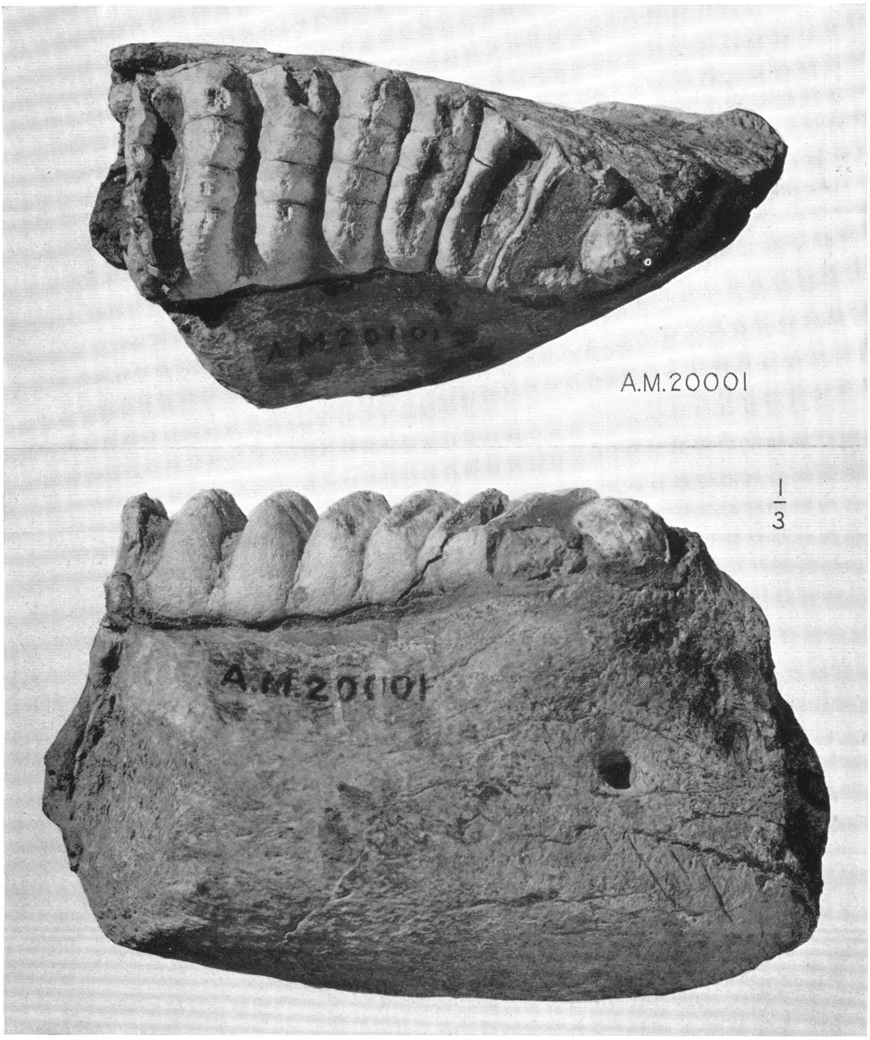


Fig. 59. *Stegodon insignis birmanicus* Osborn. Amer. Mus. No. 20001, right mandibular ramus with portion of third molar. Crown view above, lateral view below, one-third natural size.

On the other hand there are many resemblances, such as similarity in size and in the ratio of three and a fraction ridge-crests to 100 millimeters. Moreover the number and the development of the conelets that compose the individual ridge-crests would seem to be the same in the two specimens. Then again, the mandibular rami of the two specimens are similar to each other, by reason of their great massiveness and the closely comparable shapes of the symphyseal region.

Because of these similarities, No. 20001 is referred to *Stegodon insignis birmanicus*, the differences between the referred specimen and the type being ascribed to factors of individual variation.

Just what the relationship is between *Stegodon insignis birmanicus* and *Stegodon elephantoides* constitutes a question that cannot be definitely settled at the present time. Certainly these two forms are extraordinarily similar to each other.

MEASUREMENTS

Stegodon insignis birmanicus

	Type A.M. 20002	Referred A.M. 20001
Depth of mandibular ramus, ant. border M_3	222 mm.	189 mm.
Width (thickness) of ramus	195	160
M_3, length	359	
width	98	99
height (sixth crest)	72	49
Ridge crests per 100 mm.	$3^1/_2$	$3^1/_2$

ELEPHANTOIDEA

Elephantidae

HYPSELEPHAS OSBORN, 1936

OSBORN, H. F., 1936, 'Proboscidea,' published by the Amer. Mus. Nat. Hist., I, pp. 12, 793. (On page 793 is a bibliographic reference to the following citation: 1934, Proc. Amer. Philos. Soc., LXXIV, No. 4, p. 285.)

GENERIC TYPE.—Genotypic species: *Elephas hysudricus* Falconer, 1845, 1846, and *Elephas platycephalus angustidens* Osborn, 1929. (Osborn, H. F., 1936, p. 12.)

AUTHOR'S DIAGNOSIS.—*Hypselephas*, gen. nov., primitive elephants of India with elevated cranium. (Osborn, H. F., 1934, *op. cit.*, p. 285.)

The name *Hypselephas* was first published in 1934, with the definition or diagnosis quoted above. At that time, however, no type species was named, nor were there any included species listed. Therefore the genus had the status of a *genus caelebs*. In 1936, the name was again published, and two species were named as belonging to it. In this publication there was a bibliographic reference to the publication of 1934—thus the definition became valid under Article 25 of the 'International Rules of Zoological Nomenclature.' But the genus dates from 1936.

Hypselephas hysudricus (Falconer and Cautley)

Elephas hysudricus, Falconer and Cautley, 1846, 'Fauna Antiqua Sivalensis,' Pls. i, fig. 3; iv; v; vi, figs. 1–3; vii; viii; letterpress, p. 41.

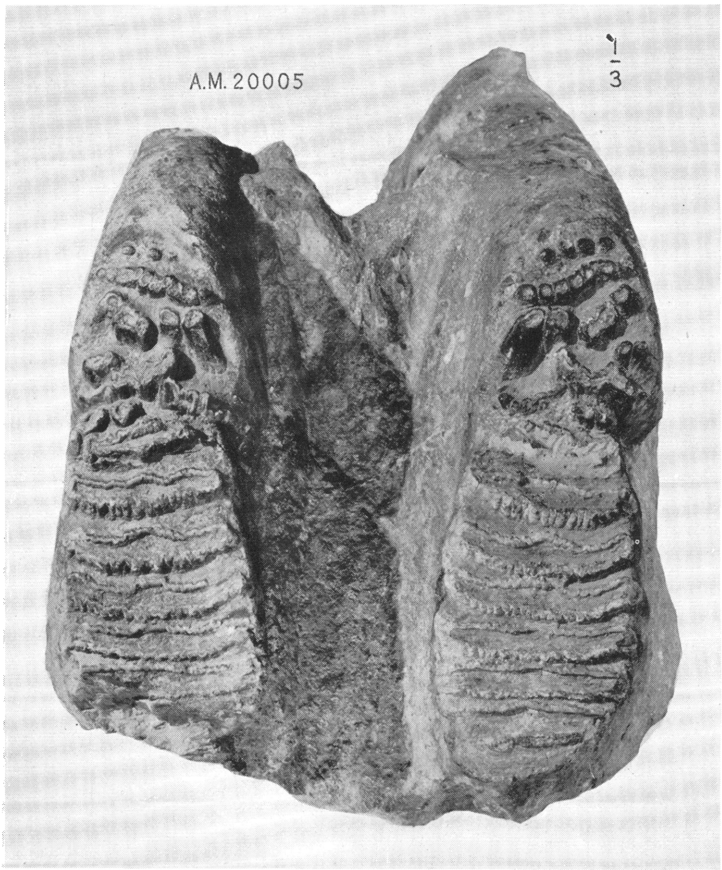


Fig. 60. *Hypselephas hysudricus* (Falconer and Cautley). Amer. Mus. No. 20005, palate with right and left second and third molars. Crown view. One-third natural size.

Euelephas hysudricus, Falconer, 1857, Quar. Jour. Geol. Soc., London, XIII, Pt. 4, pp. 315, 317–318.

Elephas meridionalis, Pohlig, 1884, Sitz. Niederrhein Gesellsch., Bonn, pp. 47–61.

Hypselephas hysudricus, OSBORN, 1936, 'Proboscidea,' I, p. 12. (Special Publ., Amer. Mus. Nat. Hist.)

ADDITIONAL REFERENCES.—FALCONER, H., 1868, Pal. Mem., I, pp. 112–113, 422–430.

LYDEKKER, R., 1880, Jour. As. Soc. Bengal, XLIX, p. 31; 1880, Pal. Indica, (X) I, pp. 278–280; 1883, Rec. Geol. Surv. India, XVI, p. 90; 1884, Pal. Indica, (X) III, p. 133; 1885, 'Cat. Siw. Vert. Ind. Mus.,' Pt. I, pp. 74–77; 1886, 'Cat. Fos. Mam. Brit. Mus.,' Pt. IV, pp. 116–121.

PILGRIM, G. E., 1910, Rec. Geol. Surv. India, XL, p. 200; 1913, Rec. Geol. Surv. India, XLIII, p. 324, Pl. XXVI.

COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 33 (*Hypselephas hysudricus*).

COTYPES. The numerous specimens figured by Falconer and Cautley in the above cited plates of the Fauna Antiqua Sivalensis.

HORIZON.—Upper Siwaliks, Pinjor zone. Also Upper Irrawaddy beds. Lower Pleistocene.

LOCALITY.—Siwalik Hills and adjacent regions. Northern Burma, along the Irrawaddy and Chindwin rivers.

DIAGNOSIS (After Lydekker).—Ridge formula of molars, 9–12, 10–12, 13–17/ 9–12, 12–13, 14–18. Crowns of molars rather wide in comparison to their length; ridge plates numerous, tall and thin; enamel of medium thickness and plicated. Skull similar to that of *E. indicus;* high.

Specimens in the American Museum:

Amer. Mus. No. 20005, a palate with both second and third molars. From the Upper Irrawaddy beds near Than-udaw. (Map, Fig. 11, locality 8.)

Amer. Mus. No. 32543, a portion of an upper molar, unworn. From the Upper Irrawaddy beds along the Chindwin River, about three hundred miles north of Mandalay. Presented by Mr. Arthur Vernay, 1935.

The well-preserved palate, Amer. Mus. No. 20005, has the second and third molars of the right side complete, while on the left side the anterior portion of the second molar and the posterior part of the third molar is broken away. The second molars are well-worn, and since they are composed of eight plates each it would seem probable that about three or four plates have been eliminated from the front portion of each tooth during the process of eruption and wear. The complete third molar has thirteen plates, of which the four anterior ones are worn.

The ridge plates are characterized (particularly in the worn teeth) by their relatively thin and highly plicated enamel. In the unworn molar the plates are seen to consist of about eight (sometimes more, sometimes less) transversely arranged columns with rugose surfaces. When these columns are worn they tend to merge each into the other, and this produces the plicated enamel plates of the worn molar surface. The cement in this specimen is very heavy, completely investing the unworn tooth.

The ridge plate frequency varies from six to 100 millimeters in the worn tooth to seven to 100 millimeters in the unworn tooth.

The single upper molar found by Mr. Vernay, Amer. Mus. No. 32543, contains ten ridge plates comprising the anterior portion of the tooth. It is quite evident that at least three and probably four or five plates are missing, so that the total ridge plate count of this tooth was between thirteen and fifteen or sixteen plates. The frequency is seven plates to 100 millimeters.

The latter of the above described specimens is interesting because it shows the presence of Pleistocene Upper Irrawaddy sediments far up the Chindwin drainage of Upper Burma.

Measurements are given in the following table.

MEASUREMENTS

		A.M. 20005	A.M. 32543
M^2,	length	138 mm.	
	width	78	
	ridge plates per 100 mm. (worn)	6	
M^3,	length	211	
	width	74	76 mm.
	height (4th plate)	212	178
	ridge plates per 100 mm. (unworn)	7	7

PERISSODACTYLA

RHINOCEROTOIDEA

Rhinocerotidae

RHINOCEROS LINNAEUS, 1758

LINNAEUS, CARL, 1758, 'Systema Natura,' 10th Ed., p. 56.

GENERIC TYPE.—*Rhinoceros unicornis* Linnaeus.

DIAGNOSIS.—*Rhinoceros* s. str. Gray (*Zalabis* Cope). $\frac{1.0.4.3.}{1.0.3.3.}$ Cheek teeth mainly hypsodont. Nose with but one horn. Occiput inclined forward. Post-tympanic and post-glenoid processes anchylosed. (von Zittel, K. A., 1925, p. 141.)

Rhinoceros sivalensis Falconer and Cautley

Rhinoceros sivalensis, FALCONER AND CAUTLEY, 1847, 'Fauna Antiqua Sivalensis,' Pl. LXXIII, figs. 2, 3; Pl. LXXV, figs. 5, 6.

ADDITIONAL REFERENCES.—For the synonymy and a complete list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 180.

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, Pleistocene. Upper Irrawaddies, Pleistocene.

LOCALITY.—Siwalik Hills, northern India. Irrawaddy River, Burma.

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. (Colbert, E. H., 1935, p. 180.)

Specimen in the American Museum:

Amer. Mus. No. 20040, a mandibular symphysis with the incisor alveoli, but without the teeth preserved. From the Upper Irrawaddy beds of Lower Pleistocene age; from the east bank of the Irrawaddy River, about one mile below Yenangyaung. (Map, Fig. 12, locality 1–5.)

This specimen needs no elucidation beyond that given by the above description. Naturally its specific determination is at best very provisional.

ARTIODACTYLA

ANTHRACOTHERIOIDEA

Anthracotheriidae

MERYCOPOTAMUS FALCONER AND CAUTLEY, 1847

FALCONER, H., AND CAUTLEY, P. T., 1847, 'Fauna Antiqua Sivalensis,' Pls. LXVII–LXVIII.

GENERIC TYPE.—*Hippopotamus dissimilis* Falconer and Cautley.

DIAGNOSIS.—A large genus of advanced anthracotheres. Upper molars selenodont, and quadricuspid. Skull with a heavy muzzle and elevated orbits; mandible with broad symphysis and very deep angle. Skeleton heavy.

Merycopotamus dissimilis (Falconer and Cautley)

Hippopotamus dissimilis, FALCONER AND CAUTLEY, 1836, Asiatic Researches, XIX, pp. 49–51.

Merycopotamus dissimilis, FALCONER AND CAUTLEY, 1847, 'Fauna Antiqua Sivalensis,' Pls. LXVII–LXVIII.

ADDITIONAL REFERENCES.—For a complete list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 275.

TYPE (LECTOTYPE).—Brit. Mus. No. 18441, a skull.

COTYPE.—Brit. Mus. No. 18442, a right mandibular ramus.

HORIZON.—Upper Siwaliks. This species is occasionally found in the Middle Siwaliks.

LOCALITY.—Siwalik Hills. Also from the Salt Range, Punjab.

DIAGNOSIS.—See generic diagnosis, above.

This species is included here because it was listed by Pilgrim in 1910 as coming from the Irrawaddies. Pilgrim considered it as coming from the Lower Irrawaddy beds, and it is very possible that such is the case. On the other hand, Pilgrim included several Upper Irrawaddy forms, such as *Stegolophodon latidens* and *Hexaprotodon iravaticus* in his Lower Irrawaddy fauna, so it is equally probable that *Merycopotamus* comes from the Upper Irrawaddy beds.

To the best of my knowledge the actual specimen or specimens from Burma were never described. Therefore our knowledge of the genus and species in the Irrawaddy beds is based on Pilgrim's faunal list.[1]

HIPPOPOTAMOIDEA

Hippopotamidae

HEXAPROTODON FALCONER AND CAUTLEY, 1836

FALCONER, H., AND CAUTLEY, P. T., 1836, Asiatic Researches, XIX, Pt. I, p. 51.

GENERIC TYPE.—*Hippopotamus* (*Hexaprotodon*) *sivalensis* Falconer and Cautley.

DIAGNOSIS.—Like *Hippopotamus* except that there are six incisors of sub-equal size and the first premolars are large; the brain-case is relatively small; there is a high sagittal crest; the lachrymal reaches the orbit and is separated from the nasal by the frontal.

Hexaprotodon iravaticus Falconer and Cautley

Hexaprotodon iravaticus, FALCONER AND CAUTLEY, 1847, 'Fauna Antiqua Sivalensis,' Pl. LVII, figs. 10, 11.

ADDITIONAL REFERENCES.—For a complete list of references for this species, see: COLBERT, E. H., 1935, Trans. Amer. Philos. Soc., (N. S.) XXVI, p. 280.

TYPES (LECTOTYPE).—Brit. Mus. No. 14771, a mandibular symphysis.

COTYPES.—A fragmentary mandibular symphysis, figured in the 'Fauna Antiqua Sivalensis,' Pl. LVII, fig. 11.

HORIZON.—From the Upper Irrawaddy beds, Pleistocene.

LOCALITY.—Irrawaddy River, below Mandalay, Burma.

DIAGNOSIS.—Like *H. sivalensis*, but very much smaller. (Colbert, E. H., 1935, p. 280.)

Specimens in the American Museum:

Amer. Mus. No. 20037, a skull, lacking the premaxillae, the anterior premolars, canines and incisors and the brain-case. The molars on both sides are well preserved; the last premolar and the last molar erupting and unworn. From the Irrawaddy beds, some 4000 feet above their base; on the east bank of the Irrawaddy River about one mile below Yenangyaung. (Map, Fig. 12, locality 1–5.)

Amer. Mus. No. 20038, a left upper canine. From the same level and locality as the above specimen. (Map, Fig. 12, locality 1–5.)

Hexaprotodon iravaticus was first published by Falconer and Cautley in the 'Fauna Antiqua Sivalensis' as a plate figure, but no written diagnosis or definition of the species was given by these authors. It was not until Lydekker's revision of the Siwalik Bunodont Suina was issued in 1884, that an adequate diagnosis and discussion of the species was

[1] Pilgrim, G. E., 1910*b*, Rec. Geol. Surv. India, XL, p. 196.

presented. Lydekker, basing his observations on the cotype mandibles, defined and described the species in the following way.

> The type mandible, to which the reference has been already given, is a sub-adult specimen, with $\overline{\mathrm{pm.\,2}}$ half protruded. It is distinguished from the mandible of *H. sivalensis* by its inferior size, proportionately longer symphysis, laterally compressed $\overline{\mathrm{i.3}}$, as well as by the circumstance that the six incisors, instead of forming a straight line between the canines, are placed irregularly; the second being above the first, and the third below both the others. The alveoli of the three first premolars also show that $\overline{\mathrm{pm.1}}$ and $\overline{\mathrm{pm.2}}$ were separated by proportionately longer intervals. (Lydekker, R., 1884, p. 42.)

To these enumerated characters there may be added the following, as derived from a study of the skull and the upper canine tooth in the American Museum collection.

The partial skull, Amer. Mus. No. 20037, is closely comparable to the Pleistocene and sub-recent species, *Hippopotamus madagascariensis* as to size, both in its linear dimensions and in its relative massiveness. It is approximately three fourths as large as the Siwalik species, *Hexaprotodon sivalensis*. Certain structural characters of this skull are distinctive, and they show it to be quite definitely referable to the genus *Hexaprotodon*.

Of particular significance are the rather central position of the orbit and its seeming lack of elevation to the same degree typical of the recent *Hippopotamus*, the topographic position of the lachrymal, which borders the orbit and is separated from the nasal by an anterior projection of the frontal, and finally the relatively unexpanded brain-case. All of these cranial characters are developed to a degree that is practically identical to their condition in *Hexaprotodon sivalensis*, and are relatively primitive as compared with the same characters in *Hippopotamus*. They afford supplementary evidence to that set forth by Lydekker (and based entirely on mandibular characters) concerning the true genetic relationships of the Irrawaddy hippopotamus.

As to the upper molar teeth in *Hexaprotodon iravaticus*, they are closely comparable to those of *Hexaprotodon sivalensis* in their relative degree of hypsodonty. They show certain characters by which they differ from the molars of *Hexaprotodon sivalensis*, these being their less complex enamel patterns due to the lesser expansion of the outer trefoil loops, or in other words due to the fact that these outer loops have not pushed out to encroach on the transverse alleys of the molars. This difference between the molars of *Hexaprotodon iravaticus* and *Hexaprotodon sivalensis* is, however, mainly attributable to size differences; that is,

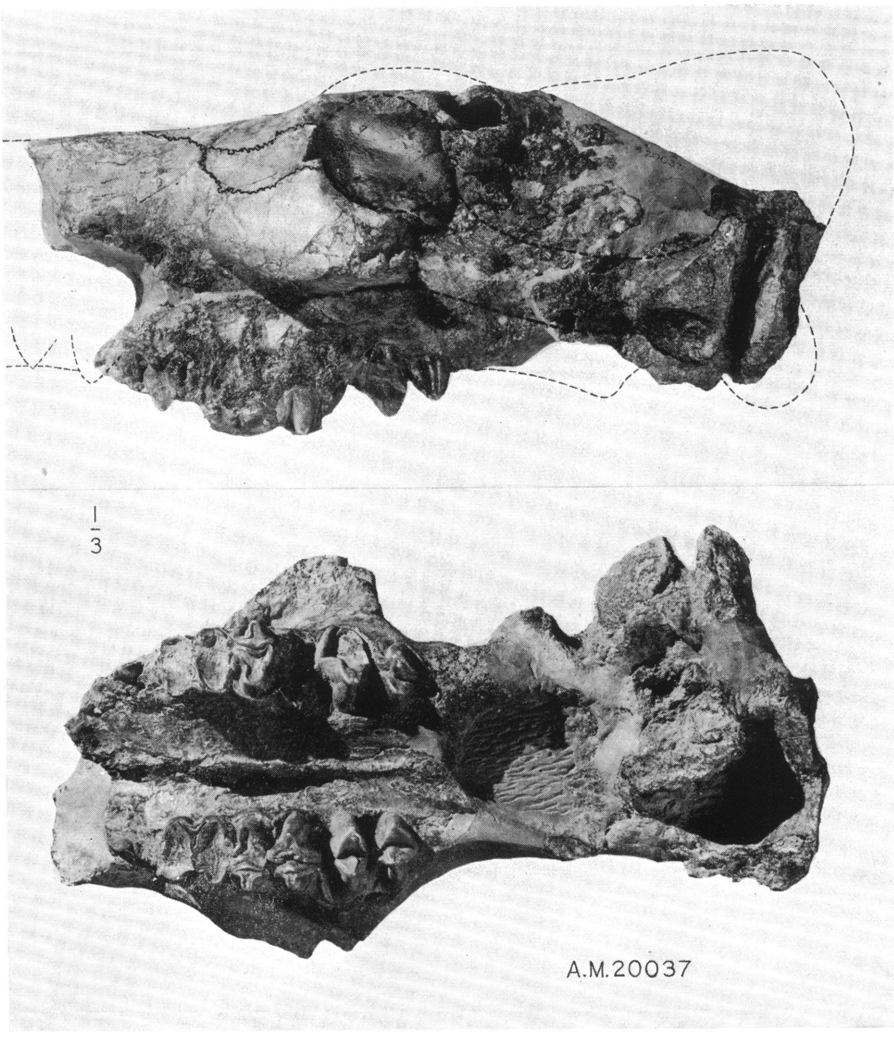


Fig. 61. *Hexaprotodon iravaticus* Falconer and Cautley. Amer. Mus. No. 20037, partial skull. Lateral view above, palatal view below. One-third natural size.

the smaller teeth of the former species are less robust and therefore less expanded in their individual parts than are the large, heavy teeth of the latter species. It might be noted, too, that basal accessory pillars are not so strongly developed in the Burma species as they are in the Siwalik form, but this is a difference of minor import. Therefore, the differences between the molars of *Hexaprotodon iravaticus* and *Hexaprotodon sivalensis* may be assigned, for the most part, to the greater size and robustness of the Indian species.

The canine of *Hexaprotodon iravaticus* is much smaller than the same tooth in *Hexaprotodon sivalensis*, as might be expected, but it is considerably larger than the canine of the comparably sized *Hippopotamus madagascariensis*. It is characterized especially by its unexpanded internal lobe or pillar, which causes the posterior groove to be much more open than is the case in *Hexaprotodon sivalensis*. There might be mentioned the fact, too, that the canine in the Irrawaddy species lacks the heavy, longitudinal enamel ridges, so characteristic of *Hexaprotodon sivalensis* and *Hippopotamus*.

The material in the American Museum collection referred to *Hexaprotodon iravaticus* would seem to support Stamp's contention that this species is of Pleistocene age, rather than Pilgrim's view that it is a Pliocene form. In the first place, the American Museum specimens are undoubtedly from the upper levels of the Irrawaddy series, and therefore of Pleistocene age. Moreover they were associated with other definite Pleistocene mammals. Then again, these specimens are most certainly referable to this Burma species, by reason of their small size, and the characters of the skull set forth in some preceding paragraphs.

According to Stamp, *Hexaprotodon iravaticus* is found only in the upper or Pleistocene levels of the Irrawaddy beds.

MEASUREMENTS

	H. sivalensis A.M. 19781, 19817	*H. iravaticus* A.M. 20037	*H. madagascariensis* A.M. 30006
Length of skull	610 mm.[1]	450 mm.[2]	425 mm.
Width of palate at M^1	47	44	35
Length of molar series	130	102	96
M^1, length	41[3]	28	25
width	40	28.5	26.5
M^2, length	53	36	32
width	47	33.5	33
M^3, length		39	38
width		37	36.5
	A.M. 19972		
Upper canine, ant.-post.	52	38	23
transverse	44	33	16

[1] This and following measurements from A.M. 19781.
[2] Estimated.
[3] This and following measurements from A.M. 19817.

If, however, one consults Noetling's account (Mem. G.S.I., XXVII, pt. ii, 1897, especially pp. 57, 58 and 59) one finds he says "specimens are particularly common along the river bank between Yenangyaung and Nyounghla ..."; again, "I am absolutely sure that certain species are restricted in the neighbourhood of Yenangyaung to the lower parts of the division . . . "; then, after separating a lower "zone" of *Hippotherium antelopinum* and *Aceratherium perimense* from a higher "zone" of

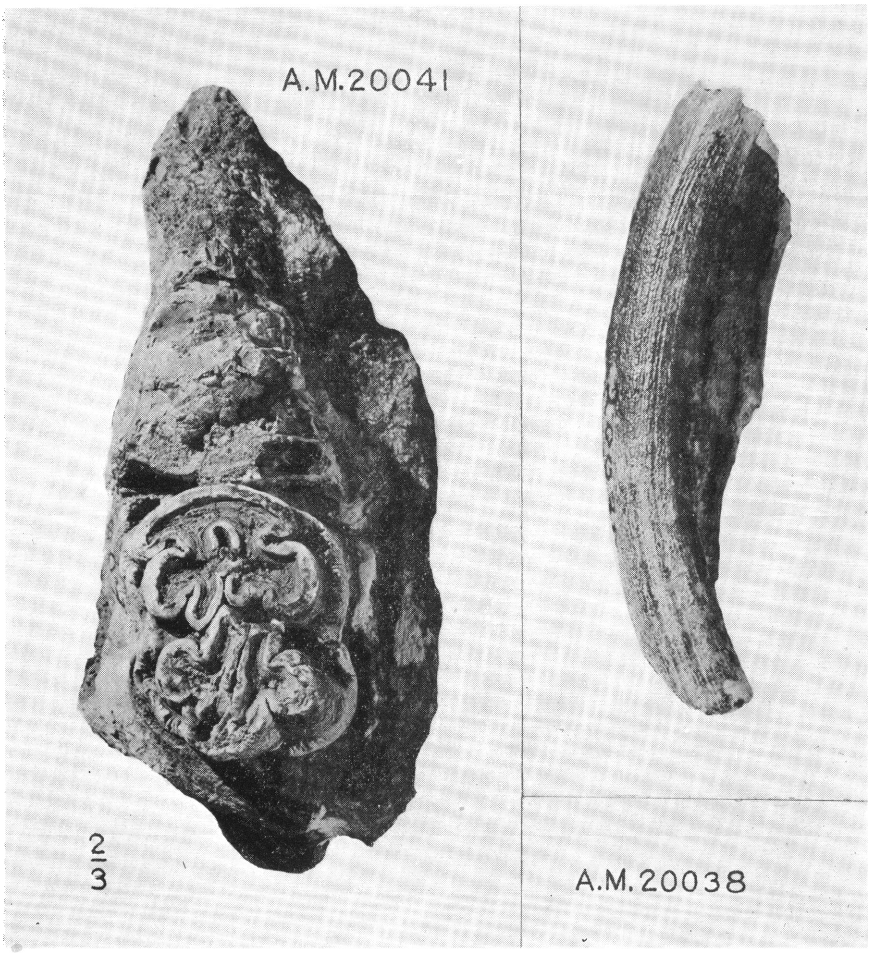


Fig. 62. Left. *Hexaprotodon* or *Hippopotamus* sp. (probably *H. sivalensis*). Amer. Mus. No. 20038, right maxilla with M^2 (roots) and M^3. Crown view, two-thirds natural size.

Right. *Hexaprotodon iravaticus* Falconer and Cautley. Amer. Mus. No. 20041, left upper canine. Lateral view, two-thirds natural size.

Mastodon latidens and *Hippopotamus iravaticus* he says that the two latter almost certainly do not occur lower. (Stamp, L. D., 1922, p. 498.)

Hexaprotodon (?) sp.

Specimen in the American Museum:

Amer. Mus. No. 20041, a right maxilla with M^{2-3}. From the Irrawaddy beds, sixteen miles below Mandalay on the left bank of the Irrawaddy River. (Map, Fig. 6, locality A28.)

This specimen cannot be given a definite generic identification because of the possibility that it may be referable either to *Hexaprotodon* or to *Hippopotamus*. It is much too large to be *Hexaprotodon iravaticus*, and it is closely comparable both as to size and as to the structure of the single, well-preserved third molar, to *Hexaprotodon sivalensis*. The probabilities are that this Burma specimen is referable to *Hexaprotodon sivalensis*, not only because of its size and general form, but also because of its contemporaneousness with and its contiguity to the Siwalik species. This would militate against its reference to the genus *Hippopotamus*. The specimen is illustrated by the accompanying figure and by the measurements given below.

MEASUREMENTS

	A.M. 20041
M^3, length	53 mm.
width	45

BOVOIDEA

Bovidae

BOVIDS, GENERA AND SPECIES INDETERMINATE

Amer. Mus. No. 20003, a right upper molar and a fragment of a mandibular ramus with right M_{2-3}. Also a fragment of a horn-core, of which the association with the teeth may be doubtful. From the upper Irrawaddy beds near Mingun, opposite Mandalay. (Map, Fig. 6, locality 20.)

Amer. Mus. No. 20007, broken teeth. From the upper Irrawaddy beds, one-half mile northwest of Mogaung. (Map, Fig. 8, locality 17.)

Amer. Mus. No. 20036, a horn core. From the upper Irrawaddy beds, near the river, below the B.B.P. office, Yenangyaung. (Map, Fig. 12, locality 4.)

These fragmentary bovid remains from the Upper Irrawaddy beds are exceedingly difficult to identify with any degree of satisfaction. Consequently no generic or specific determinations are attempted here, but rather empirical descriptions and figures are presented and comparisons are made as far as is possible.

It would seem pretty certain that all of these specimens came from the Upper Irrawaddy beds, and therefore are of Pleistocene age.

The two lots of teeth, Nos. 20003 and 20007 are undoubtedly specifically identical. They are tall crowned teeth, as might be expected in a bovine of Pleistocene age. In the upper molars there are very strong styles running from the base of the tooth to the crown, and the ectoloph surfaces of the paracone and metacone are strongly ribbed. The parastyle and metastyle are robust and join at the base of the tooth the paracone and metacone ribs, respectively. The mesostyle is somewhat thin-

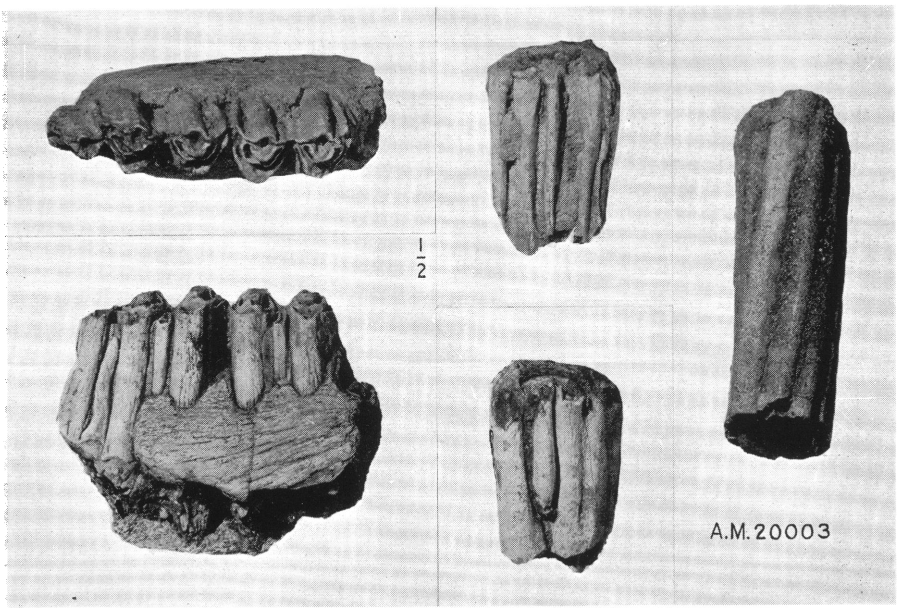


Fig. 63. Bovid. Amer. Mus. No. 20003. Left, right mandibular ramus with M_{2-3}. Crown view above, external lateral view below. Middle, right upper molar. External lateral view above, internal lateral view below. Right, fragment of horn-core. All figures one-half natural size.

ner than the above mentioned styles, and it joins the metacone rib at the base of the tooth. Internally there is a strong median pillar. One upper molar, No. 20003, is somewhat elongated, but this is very probably a third molar. The lower molars are hypsodont, with strong internal ribs and stylids, and with heavy median external pillars.

These teeth are much less hypsodont than the cheek teeth in *Bos* or

Bubalus. Moreover, the internal median pillar of the upper molars has not developed in height so that it reaches the crown of the tooth, as is the case in the advanced genera just named. Thus it is evident that the teeth now under consideration—though representative of a true bovine—

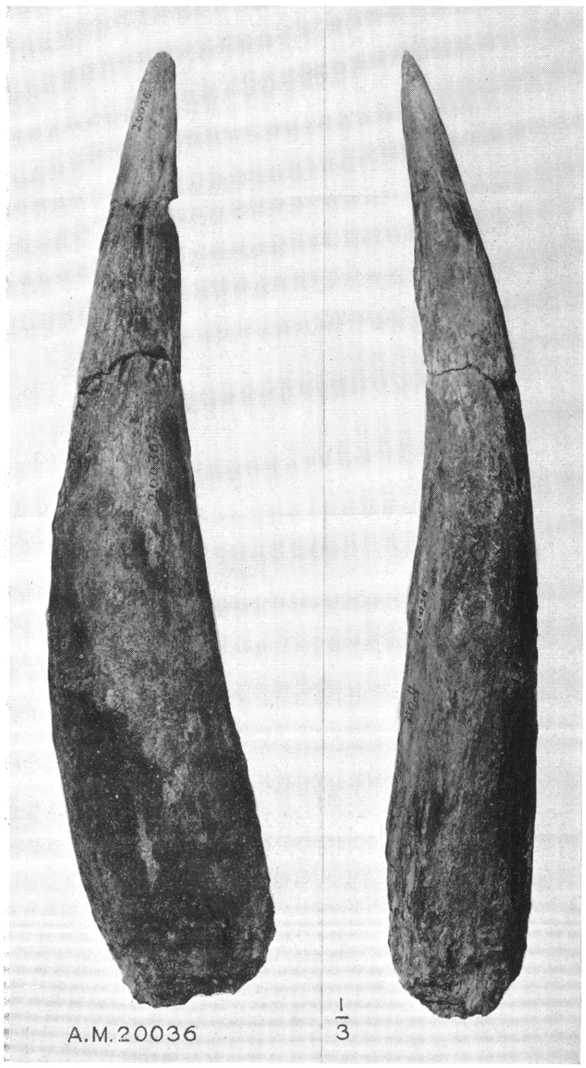


Fig. 64. Bovid. Amer. Mus. No. 20036, left horn-core. External lateral view on left, anterior view on right. One-third natural size.

belong to a relatively more primitive stage of development than that typified by the Pleistocene *Bos* or *Bubalus*. A comparative study would seem to indicate that of the bovine genera these teeth are perhaps most closely comparable to the Upper Siwalik genus, *Leptobos*. As far as may be determined, the upper molars of this Siwalik form are closely comparable to the upper molar, No. 20003, not only with regard to the hypsodonty, but also as to the details of the tooth structure, such as the development of the styles and ribs on the ectoloph surface, and the height of the internal median pillar. It might be said in passing that the teeth now under consideration are quite different from the same teeth in the Upper Siwalik genus, *Hemibos*, a form contemporaneous with *Leptobos*. Further comparisons of these teeth do not show any closer identities than are to be seen in the molars of *Leptobos;* therefore it is reasonable to think that they represent a type of bovine closely related to if not identical with this Upper Siwalik genus.

As for the horn-core, No. 20036, no very close comparisons have been found. As seen from the side it is very large at its base (along the antero-posterior diameter of the horn-core) and it tapers rapidly to the tip. The posterior surface of the horn-core is but slightly concave, whereas the anterior surface is strongly convex, thereby causing the horn core to curve slightly toward the rear. As seen in the anterior view this horn-core is much narrower basally than it is as seen laterally; in other words, the transverse diameter is less than the antero-posterior diameter. There is a strong anterior keel, beginning at the base of the horn-core somewhat inside of the median axis, and twisting slightly to the outside of the median axis about halfway up the horn, finally to curve inwardly to the tip. This slight spiraling of the anterior keel is shown by the accompanying figure (Fig. 64). On the posterior surface of the horn-core there is a rather faint keel that runs straight, from the base to the tip of the core. The external face of the horn-core is relatively flat, while the internal face is strongly convex. Thus it may be seen that in cross section, particularly at the base, this horn-core has an anterior and a posterior keel, of which the former is much the strongest, a flat external and a strongly convex internal surface. All of these remarks are based on the identification of this horn-core as coming from the left side of the skull, which would seem probable; in fact, it would be difficult to imagine this as being a right horn-core.

This horn-core is not closely comparable to any other type of horn-core, either of fossil or of living bovids. In a general way it resembles the horn-core of a *Hemibos* skull in the American Museum collections, but is differentiated by its much shorter length, its more rapid tapering and especially by the twisting of the anterior keel.

A short section of horn-core is numbered "20003" and thus would seem to have been associated with the teeth of this same number, discussed above. It is difficult to imagine, however, that this section of horn-core is from the same type of bovid as that represented by the teeth. This fragment is rather small, being some thirty millimeters in diameter, approximately round in cross section, and with a series of heavy carinae that show strong twisting. If this fragment is truly associated with the teeth, then we must imagine some sort of a large bovine with very small, long and slender and twisted horns, something quite different from *Leptobos*, the genus to which the teeth show the closest resemblances.

From its general size and robust character, the horn-core discussed above, No. 20036, might be supposed to be associated with the teeth that have been considered on preceding pages. But then again, this horn-core is nothing like *Leptobos*. So at present the problem would seem to be left up in the air. Here are some teeth from the Pleistocene levels of the Upper Irrawaddies that show resemblances to the teeth of the Upper Siwalik form, *Leptobos*. Supposedly associated with these teeth is the fragment of a horn-core, of small size, round in cross section and probably rather strongly spiraled. From the same beds there is a large, robust horn-core, tapering rapidly to a point and with a strong, slightly spiraled anterior keel. Which horn-core really is to be associated with the teeth, or are either of them to be so associated? How many types of Upper Irrawaddy bovids are represented by this material?

Measurements

A.M. 20003			
Upper molar	Antero-posterior diameter, at base	35	mm.
	Transverse diameter at base	25	
	Height	51	
	Height of internal pillar	33	
Lower molars	M_2, antero-posterior diameter	29	
	transverse diameter	17.5	
	M_3, antero-posterior diameter	40	
	transverse diameter	17.5	
	height	52	
Horn-core fragment, diameter		30	

A.M. 20007		
Fragment of lower molar, unworn—height		61.5 mm
A.M. 20036		
Horn core	Length along anterior keel	390 mm.
	Length along posterior keel	370
	Antero-posterior diameter, at base	75
	middle	54
	50 mm. from tip	23
	Transverse diameter, at base	55
	middle	43
	50 mm. from tip	18

E.—POST-IRRAWADDY FOSSILS

In the introduction to this paper mention was made of a giant panda skull, found in a cave at Mogok, Burma, and described by Smith Woodward in 1915. Because of the occurrence of this fossil in a superficial cave deposit, and because of the fact that the bone is not mineralized (as was pointed out by Smith Woodward) there is little doubt but that the specimen is of a relatively late geologic date. It is certainly post-Irrawaddian in age, probably late Pleistocene, and possibly sub-recent.

CARNIVORA

ARCTOIDEA

Procyonidae

AELUREIDOPUS WOODWARD, 1915

WOODWARD, A. S., 1915, Proc. Zool. Soc. London, 1915, pp. 425–428.

GENERIC TYPE.—*Aelureidopus baconi* Woodward.

DIAGNOSIS.—"Ailuropodinae in which the muzzle is shorter and blunter than in *Ailuropoda;* the frontal profile steeper; mastoid process irregularly ridged instead of smooth; the foramen which in *Ailuropoda* pierces the inner wall of the lachrymal pit, situated behind the lachrymal pit; P^1 absent; P^2 small and single-rooted." (Pilgrim, G. E., 1932, p. 48.)

Aelureidopus baconi Woodward

Aelureidopus baconi, WOODWARD, 1915, Proc. Zool. Soc. London, 1915, pp. 425–428, Pl. I.

ADDITIONAL REFERENCE.—Pilgrim, G. E., 1932, Pal. Indica, (N. S.) XVIII, p. 48.

TYPE.—B. M. No. M 10971, a skull.

HORIZON.—Probably late Pleistocene.

LOCALITY.—A cave near Mogok, Ruby Mines, Upper Burma.

DIAGNOSIS.—The specific diagnosis is the same as that for the genus, given above.

Smith Woodward considered the differences separating the fossil from the recent form as of sufficient importance to justify the creation of a new genus and species for the Burma skull, Although there seems to be sufficient reason for considering *Aelureidopus baconi* as a distinct species, its reference to a separate genus may be questioned. The differences between this and the recent species are at best small, and it is probable that both belong to a single genus, *Ailuropoda.*

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IV. 'On the Fossil Hippopotamus of the Siwalik Hills.'

V. 'Description of a Fragment of a Jaw of an unknown extinct Pachydermatous Animal, from the Valley of the Murkunda.'

XXIV. 'Note on certain Specimens of Fossil Animal Remains from Ava.'

XXVII. 'A description of the Plates in the "Fauna Antiqua Sivalensis."'

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ADDENDUM

A NEW TITANOTHERE GENUS FROM THE UPPER EOCENE OF MONGOLIA AND NORTH AMERICA

BY WALTER GRANGER AND WILLIAM KING GREGORY

The diagnosis of a new genus of titanotheres is presented at this place in order that the name may be made available. A detailed discussion of this genus will be presented in a forthcoming paper on the titanotheres of Mongolia.

METATELMATHERIUM, NEW GENUS

GENOTYPE.—*Metatelmatherium cristatum*, new species.

REFERRED SPECIES.—*Telmatherium ultimum* Osborn.

GENERIC CHARACTERS.—Skull long, narrow and high; zygomata large, deep decurved, middle portion widely arching transversely but without buccal swellings, infraorbital portion with prominent longitudinal fossa for insertion of suborbital portion of masseter; supraglenoid processes of zygomata rounded, not acuminate; sagittal crest present, high, undivided, lambdoidal crests thin and prominent, the occiput as a whole being relatively high and narrow; free nasals, short, not upturned, subnasal notch short; fronto-nasal horn swellings absent or at most feeble; frontals transversely arched with relatively small and pointed postorbital processes; supraorbital portion of frontals not forming a projecting shelf above orbits; preorbital surface of maxilla anteroposteriorly short and bearing a large shallow depression in front of the infraorbital foramen; postglenoid processes located relatively far back, near the occipital condyles, which are relatively delicate; basioccipital narrow, with high median keel and very prominent tubera basioccipitalia; upper incisors $\frac{3}{3}$, large, heavily cingulate, i^3 almost subcaniniform, with a relatively high, recurved, pointed tip; upper canines large, with high tapering, recurved crown and sharp anterior and posterior cutting edges, the roots in the male skull being extremely massive; a short postcanine diastema; p^1 relatively large, not compressed, with broad posterior lobe; p^2, p^3, p^4, close to those of *M. ultimum*, except that the relative width of p^4 is less, p^3 with low tetartocone ridge, p^4 without recognizable tetartocone; upper molars all relatively wide; lower jaw short, deep and relatively thick (in male type), with gently inflected angular region and short space between m_3 and the low coronoid process; lower incisors (at least in male) relatively small, strongly procumbent, arranged in a nearly transverse row; lower canines with very massive roots and recurved, sub-erect crowns; a prominent postcanine diastema and apparently a short diastema behind p_1; p_1 with thick oval crown; lower molars short anteroposteriorly; p_3 with talonid decidedly wider than trigonid; cusps of cheek teeth conic, swollen; cheek teeth with external cingula faint or absent.

Metatelmatherium cristatum, new species

HOLOTYPE.—Amer. Mus. No. 26411, a skull and lower jaw.

LOCALITY AND HORIZON.—Camp Margetts; Irdin Manha formation, Upper Eocene of Mongolia.

Specific Characters.—Size larger than that of *M. ultimum;* p^1 very large, roundly compressed; p^2 large, asymmetric; p^3, p^4 moderately wide with but slight cingulum; occiput relatively broad. Lower jaw differing from that of *M. ultimum* in its short low, broad coronoid process, relatively deeper ramus, longer and more sloping symphysis.