A GEOLOGICAL, PALAEONTOLOGICAL AND PHYLOGENETIC STUDY
OF THE ELEPHANTOIDA OF INDIA, PAKISTAN AND BURMA:
PART 1. GOMPHOTHERIIDAE

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ABSTRACT.—In this paper, the author has recorded his critical observations upon the
leading forms of Proboscidea (with the exception of the single genus, Dinotherium)
known from the fresh-water Cainozoic formations of India, Burma and Pakistan,
the present part dealing with the family Gomphotheriidae only. The study has been
mostly on the basis of published literature, but full advantage has been taken of the
numerous specimens and plaster casts kept in the Indian Museum in Calcutta and
the few specimens in the Geological Museums of the Banaras Hindu University and
of the Government G. M. College at Jammu.

Among changes in nomenclature, the following deserve notice:—Gomphotherium
for Trilophodon or Tetralobodon; Mastolophodon (gen. nov.) for Mastodon turicensis
(Schinz) and Mastodon borsoni (Hays); Mammut americanum for Mastodon americanus
(Pennant); Syncnolophus corrugatus for Tetralophodon corrugatus Pilgrim; Anancus hasno-
tensis for Mastodon hasnoti Pilgrim and Syncnolophus hasnoti (Pilgrim) of Osborn;
Anancus sivalensis for Pentalophodon sivalensis (Falc. et Caut.).

While dealing with the various species, the author has discussed the origin,
phylogeny, and distribution of each and compared it with allied forms known from
other countries.

INTRODUCTION

The author has made a comprehensive study of thirty-three leading species
of Elephantoidea falling under eleven genera
and four subfamilies, the present part dealing
with nineteen species. For each species, its distinctive
characters are surveyed and its geological and geographical distribution studied. Its affinities
with foreign forms have been traced and ultimately its origin
and phylogeny have been discussed. Probable palaeogeographical and palaeoclimatic conditions were considered wherever the question of migration was involved.

The study was based mostly on published literature, but full advantage was taken of the numerous specimens and plaster casts kept in the Indian Museum in Calcutta
and in the Geological Museums of the Banaras Hindu University and of the Government G. M. Science College at Jammu. In the course of this study, necessity was felt for effecting certain changes in nomenclature. These are listed below.

(1) Gomphotherium for Trilophodon or Tetralobodon:—The long-jawed and short-toothed mastodons, found mostly in Europe but also in America (these later proved to be M. andium) were designated as Mastodon angustidens by Cuvier in 1805. To this he had also referred some specimens which later proved to be M. longirostris. Till then the presence of the lower tusks was not known. Burmeister in 1837 (Handb. Naturges., 795) separated M. angustidens from the genus Mastodon and placed it in a new genus, Gomphotherium, which included other long-jawed forms as well. On observing the constancy of a three-fold division of 'the intermediate molars' in some species of Mastodon, Falconer in 1846 first proposed the sectional name of Trilophodon; the rest he referred to Tetralophodon. These were later (Falconer, 1857, 313) given the status
of subgenera. Besides the typical form *M. angustidens*, the former also included *M. americanus*. Many of the modern authors use this term *Trilophodon* as a generic name for long-jawed Miocene mastodons with narrow trilophodont molars. The name *Mastodon* is restored for the American mastodon and other short-jawed mastodons generally, even though some of these had trilophodont molars. Cope (1869, 193) introduced the generic name *Tetralophodon* for four-tusked long-jawed species of mastodon. This included both *Trilophodon* and *Tetralophodon* of Falconer. But the name *Gomphotherium* has the priority and should therefore be used in preference to the other names. It may be recalled in this connection that the name *Gomphotherium* was given by Cope to a Poebrotheriine camel from John Day beds of Oregon, but as this name had been preoccupied, it was substituted by *Paratylopus*.

(2) *Mastolophodon* (gen. nov.) for *Mastodon turicensis* (Schinz) and *Mastodon borsoni* (Hays):—These two species have rightly been regarded as distinct from the rest of the mastodons from Europe in showing a eurycoronine character of molars. This character, exhibited in the straight well-formed crests with transverse valleys free from the growth of accessory conules, is shared by the American mastodon also. On this basis these species might be referred to the genus *Mammut*; but the present author thinks, that the American form, though originally derived from the European stock, had separated early and had since then lived in a different habitat and got modified sufficiently to deserve a generic distinction. Since the generic name *Mammut* was first applied to the American form, a new name has to be given to the European representatives of this branch. The present author proposes the name *Mastolophodon* which he thinks would clearly convey the characteristics of the molars concerned.

(3) *Mammut* for *Mastodon* :—The classic American mastodon, commonly known as *Mastodon americanus*, was first recognized by Pennant in 1793 as a distinct species of elephant and was named *Elephas Americanus* in a systematic work of his. It was Blumenbach who first regarded it as a distinct genus and used the name *Mammut Ohioticum* in 1797 in his 'Handbuch der Naturgeschichte'. The generic name 'Mastodon' was first used by Cuvier in 1805 and was applied to elephants with mammillated molars as distinct from those with lamelliform molars. He took the American species as the type and named it *M. giganteus*. This account makes it clear that according to the law of priority of Linnaeus the generic name used by Blumenbach and the trivial name by Pennant should be adopted universally, the combination taking the form *Mammut americanum* (Pennant).

(4) Generic identity of *Anancus perimensis* (Falconer et Cautley), *Synconolophus hasnoti* (Pilgrim) and *Pentalophodon sivalensis* (Falconer et Cautley):—It will be shown in the treatment of the first species, that these three are very closely connected genetically. Hence they should be referred to the same genus *Anancus* and not to three separate genera as was done by Osborn.

(5) *Anancus hasnotensis* for *Mastodon hasnoti* :—The name *Mastodon hasnoti* was proposed by Pilgrim (1913, 293) for certain less-complex molars originally referred to *Mastodon sivalensis*. The trivial name is apparently after the place Hasnot (formerly 'Asnot') in the Potwar near the Salt Range. This name should therefore take the usual form *hasnotensis*. It is a person's name that is followed by the letter 'i' when made into a trivial name in the form of a noun in the genitive case.

Previous workers laid too much stress on the number of transverse crests, sometimes even on the number of cones or conelets forming the crests. The present author regards the structure of the grinding surface of molars as the most important character. The manner of arrangement of cones and conelets forming the enamel crests; the trend of the crests, running straight across the crown or in an oblique direction or in a curve; the height of the crests; the nature of the valleys, open, or obstructed by accessory conules; the relation of such conules with the main cones or conelets; the part played by the cement when present; etc.—are characters which are intimately connected with the mode of comminution of the food material, the movement of the lower jaw,
the nature of the food and hence also with the habitat of the animal race concerned. And habitat plays a most important part in the origin of species.

The present author has further applied to his study the principle of palingenesis, usually known as Haeckel’s biogenetic law (morphogenesis of Hyatt), which implies that characters acquired during the evolutionary history of the race (phylogeny) and conserved by heredity are reproduced in the life history of the individual (ontogeny). According to this principle, the character of the molars in ancestral forms of a race is seen in the premolars of individuals belonging to later generations. This is amply supported by the observed palaeontological facts. The application of this rule, however, cannot be extended to the milk molars, in view of the fact that the nature of the food in the case of young individuals may be different from that of the adult. A study of the palaeontological records reveals another interesting phenomenon which may be called ‘prediction of orthogenesis’. This means that the last true molar in a particular species shows characters which may be staked on the ‘intermediate molars’ in the later species belonging to the same phylum. An application of this principle gives an additional clue to the tracing of the phylogenetic history of apparently divergent forms.

Family GOMPHOTHERIIDAE
Subfamily LONGIROSTRINAE
HEMIMASTODON CREPUSCULI Pilgrim

This form was first announced in a brief notice by Pilgrim (1908, 157) as a new species of Tetrabelodon. Later (1912, 17), he found it necessary to make it the type of a new genus, in recognition of the fact that it represented an intermediate stage of evolution between Palaeomastodon and Tetrabelodon.

The type specimen, a last upper molar, shows three transverse crests and the rudiment of a posterior talon. There are no accessory conelets blocking the transverse valleys. There is just an indication of one at the postero-external corner of the inner cone of the first crest. One milk molar, described and figured by Pilgrim (1912, 20; Pl. IV, fig. 9), is particularly interesting. It is the last milk molar belonging to the left (mentioned as right in the expln. of Pl.) upper jaw of a young individual. Pilgrim called it the fourth milk molar. It may be mentioned by the way that in no case more than three milk molars are known in any member of the Proboscidea. Hence, the old way of naming the milk molars has to be discarded. The tooth in question, the third milk molar according to the correct view, shows a subdivision of the cusps by vertical wrinkles. This character is too advanced to be attributed to a Heminastodon milk molar. The question cannot be settled unless a jaw carrying milk and true molars together is found.

Specimen No. A. 427, Indian Museum, described by Lydekker (1884, 22) under Mastodon (Trilophodon) angustidens palaeindicus, was referred by Pilgrim to the present species. A second specimen, No. A. 417, regarded by Lydekker as the first lower molar of M. angustidens palaeindicus, was identified by Pilgrim as the second lower molar of the present species. But all these paratypes appear to fall within the range of variation observed in Gomphotherium angustidens (Cuvier).

The tooth (Indian Museum, No. A. 452) provisionally diagnosed as an upper molar of a new species of Moeritherium by Pilgrim (1912, 15), appears to me to be a fourth upper premolar of an allied form. The irregular striae seen on the surface of the enamel of this tooth may be due to weathering. This character is peculiar to many specimens from the Bugti bone beds.

The last mentioned specimen was found near Khajuri, Bugti Hills, Baluchistan. The horizon is near the base of the Gaj Series and the age is probably the upper Aquitanian. The other specimens described by Pilgrim were found at Kumbhi in the same formation but from a higher horizon, the age being Lower Burdigalian. Lydekker’s specimens, referred to this form, were also from the same area and stage as revealed by the nature of the matrix (Pilgrim, 1912, 18).

A similar, but slightly more advanced, form is known from the Hiramaki formation of Japan. The third upper molar of this species, Heminastodon annectens, is described by Matsumoto (1926, 6) as being larger.
and longer than its Indian ally, and is given a position intermediate between the latter and Trilophodon angustidens. This relation agrees with facts regarding the geological distribution of the two species and the possible migration of the race concerned. Leaving aside the ancestral stock of mastodons represented by Palaeomastodon and Phiomia known from the Oligocene of the Fayum basin of Egypt, Hemimastodon crepusculi represents the earliest known stage in the evolution of mastodons. The Japanese species moves a step forward and occurs in a horizon which is slightly above the Bugti Stage. This clearly indicates the high probability of a migration of the primitive Ethiopian stock to the Oriental and the easternmost Palaeartic region to have taken place during the earliest part of the Miocene epoch, or even earlier, by way of Arabia and Persia. There is of course sound evidence for a distinct branch of the same stock to have travelled to Europe by way of the hypothetical land bridge connecting Tunis with Sicily and the latter with Italy, and thence by way of Greece to other parts (Lull, 1908, 201), in a period which appears to be later than the previous case of migration cited.

It is rather surprising to find that no part of the material collected by Forster Cooper (1922, 613) from the same locality (where the present type was found) during his two expeditions, gives any evidence in support of the present form. This raises the question as to the validity of this genus. As already mentioned, the paratypes cannot claim generic distinction; and the holotype has only one distinctive character, namely, the crown having one crest less than what are found in G. angustidens. Schlesinger (1918, 48) has suggested that the tooth under consideration had originally four crests of which the front one got broken. This seems quite possible.

**Gomphotherium angustidens palaeindicum**

(Lydekker)

The first notice of the occurrence of Mastodon angustidens Cuvier in India was given by Lydekker (1883, 161) in a short note. The specimens concerned consisted of some molars collected by Blanford from the Kamliia stage (Helvetian) of the Bugti Hills, Baluchistan. Later, this form was discovered in Sind also (Pilgrim, 1917, 100). Lydekker (1884a, 19) described and figured them in a separate memoir under the name of M. angustidens var. palaeindicus. The greater development of the posterior accessory conelets, blocking the transverse valleys as well as the median longitudinal fissure, as seen in the third lower molar, indicates that the form represents a stage more progressive than the European species of which it is regarded as a variety. It should be noted here that the European species occurs earliest in the Orleanian Stage of the Paris Basin, while its Indian variety is known to occur earliest in the Kamliia Stage (Helvetian) which is slightly younger in age. The African representative is known from the Burdigalian of Moghara. The American ally, Gomphotherium conodon, is reported from the Arikaree Stage (Burdigalian), but it is very imperfectly known.

It is very difficult to ascertain at the present state of our knowledge if this form represents an autochthonous development of Hemimastodon crepusculi or a migratory form from North Africa or Europe.

**Gomphotherium angustidens chinjiense**

(Pilgrim)

This variety has not so far been described or figured. While discussing the fauna of the Chinji Zone, Pilgrim (1913, 312) mentioned the occurrence of a variety of Tetrabelodon angustidens in the Lower Chinji stage of Chinji in the Salt Range and named it in an accompanying table as Tetrabelodon angustidens var. chinjiensis (op. cit., 316). For want of a description, the affinity of this form with the European species or with the other Indian varieties of this species cannot be studied.

A specimen of a left mandibular ramus with the second and the third molars in situ, collected from the same horizon and locality by Barnum Brown, was doubtfully referred by Osborn (1929, 8) to the genus Rhynchotherium on the basis of its apparently downturned rostrum. The present writer at first thought that the latter character and the warped nature of the alveolus of the tusk were due to distortion superinduced upon the specimen after its entombment. This,
he thought, was corroborated by the fact that the grinding surface of the second molar is at a much lower level than that of the adjoining tooth behind it. But Doctor E. H. Colbert of the American Museum of Natural History, after examining the specimen, assured the author through a private communication that it was not a case of distortion and that the turning down of the symphysis had been correctly shown in the drawing of the specimen (Osborn, 1929, fig. 9). Dr. Colbert himself was inclined to refer this to *Synconolophus*, in which form also the symphysis is known to be turned down. This specimen has been further discussed in a separate paper by the author (Chakravarti, 1936). It may however be noted here that the last molar preserved in this specimen resembles that of *Gomphotherium angustidens* (Cuvier) and as such it should be compared with the Chinji homologue mentioned by Pilgrim, before it is referred to *Rhynchotherium*, a genus confined to the southwestern part of N. America, or to *Synconolophus*.

Besides the specimens from the Kamlial stage of the Bugti Hills and the Lower Chinji stage of Chinji, molars of *Gomphotherium angustidens* have been reported from the Simla Hills, the Bakrala Ridge (Pilgrim, 1910, 200) and from the districts of Attock (Cotter, 1933, 109) and Rawalpindi (Wadia, 1928, 340). The specimens from the latter two localities belong to the Kamlial Stage. None of these have been described or figured, and their specific reference may be regarded as provisional. This species is not reported from any other part of Asia.

**Gomphotherium Pandionis** (Falconer)

The first available description of this species is by Falconer (1868, I, 124, Pl. XXXIV, fig. 6, 7), the specimen being a first upper molar from an unknown locality. Apparently, this form was not represented in the immense collection of fossils by Falconer and Cautley from the Siwalik Hills. Our knowledge of this species is therefore very meagre. It was from a general resemblance of these molars collected by Theobald in the Salt Range Siwaliks with Falconer’s specimen, that Lydekker (1879, 43) referred the former to this species. Except one specimen of a first lower molar collected by Blanford from Dera Bugti, a few others from the same area by Forster Cooper, and some doubtful ones from Sind, all the referred specimens happen to come from the Dhok Pathan Stage of the Potwar or the Piram Island, and show an advanced stage of development when compared with the specimens from Dera Bugti or with Falconer’s type specimen. Pilgrim proposed to refer all these Dhok Pathan specimens to a new species of the name of *Tetrabelodon corrugatus*. The present author finds two distinct types of molars among these. One is
represented by the lower molars figured by Lydekker (1880) in Pls. XXXIV and XXXV, and the other type by the upper molars figured in Pl. XXXX A (1880) and Pl. XVI, fig. 1 (1884b). The third lower molar figured in Pl. XXXV was found in organic association with a mandibular symphysis (Pl. XXXVI, fig. 1) which is even longer than that of G. angustidens. This being a primitive character we can support Lydekker’s reference of this form to Mastodon (Trilophodon) pandionis, whose type representative is supposed to be in an early stage of development. The lower molars referred to are of a much simpler character than the upper molars representing the other type to which the name, Synconolophus corrugatus (Pilgrim) may be rightly applied.

The intermediate molars of this species present three transverse crests and a very prominent hind talon; so that it is a transitional form between trilophodont and tetralophodont types. The inner and outer cones are placed somewhat alternately across the crown. The transverse valleys are completely blocked by accessory conules, which grow as tall as the main cones and have common dentine areas with the latter when sufficiently worn. A trefoil pattern is never exhibited. The valleys are filled with a considerable quantity of cement, which is of course functionless.

This species is known from the Kamlal Stage of the Bugti Hills and Sind, and from the Dhok Pathan Stage of the Potwar and the Piram Island. If G. macrognathum is proved to be a form belonging to this species, its distribution will be extended over the missing age represented by the Chinji Stage.

A closely allied primitive form is reported by Pilgrim (1908, 162) from the Bugti Stage of Sind. A second one is reported by Koken (1885, 37) from Yunnan, China. But so far these have not been supported by any better specimen.

This species seems to have evolved from G. angustidens in early Miocene times, specialising in an elongated symphysis and complex teeth. It gave off a side branch in the Middle Miocene evolving the new generic phylum, Synconolophus Osborn, in which the symphysis got gradually shortened, while the teeth became more complex.

gomphotherium falconeri (Lydekker)

This species was established by Lydekker (1877, 83) under the name of Mastodon (Trilophodon) falconeri on the basis of some molars collected by Theobald from ‘the Salt Range Siwaliks’. The second upper molar (Lydekker, 1880, 204, Pl. XXXII, fig. 1) assigned to this species is considerably more primitive in character than the corresponding lower molar (p. 207; Pl. XXXIII, fig. 4), which may be regarded as the type for the species. The accessory conules, responsible for the trefoil pattern of the worn inner cones of the former, are much less developed than those in the latter; the enamel is much more smooth; and the transverse valleys are more open and are much less obstructed by accessory conules. This tooth should therefore be separated from the material and be referred to a more primitive form. The specimen which has been identified by Lydekker as the first lower molar (p. 206; Pl. XXXIII, fig. 3) is too small to be the next preceding tooth to the second lower molar referred to above. This I consider to be the third lower milk molar. Lydekker’s first upper molar, third upper milk molar, second upper milk molar and second lower milk molar do not belong to this species. Lydekker’s first lower molar, collected by Fedden in the Laki Hills of Sind (p. 206), has exactly the same dimensions as the third milk molar, collected by Theobald from the Punjab (Lydekker, 1877, 83). Obviously the two specimens are identically the same, the earlier diagnosis correct but the source confused.

The type molar carries three stout crests and a very conspicuous hind talon, on the basis of which it may be styled as tetralophodont. There is also a small anterior talonid, the dentine area of which coalesces with that of the first crest after wear. The inner and outer cones are placed in opposite position normally across the length of the crown. The transverse valleys are blocked by accessory conules near the middle, and are narrow.

This species seems to have evolved into G. punjabiense by addition of cones connecting the fundamental inner and outer cones normally across the crown and by a gradual compression of the transverse crests thus formed. This branch travelled to Java.
as known by the remains of *G. huminajense* (Maarel), and also to America having flourished there as *Stegomastodon* Pohlig. A second branch leads to *Anancus sivalensis* and a third to *Gomphotherium cauleyi* (Lydekker). An exactly parallel development took place in Europe as illustrated by the successive forms; *Gomphotherium angustum* from the Vindobonian of Simoree, *G. longirostris* from the Pontian of Eppelsheim and *Anancus arvernensis* from the Lower Pliocene of Montpellier. The last two forms closely resemble the Indian forms *G. punjabiense* and *A. sivalensis* respectively.

Specimens belonging to this form are recorded from the Kamlial Stage of Sind and from the Lower Chinji Stage of the Potwar. *Gomphotherium sinense* (Koken) from Yunnan, China, appears to be closely related to the present species. Osborn (1924, 2) erected a new subgenus, *Lydekkeria*, to accommodate these two forms whose molars show characters intermediate between the genera *Trilophodon* and *Tetralophodon*. As both these genera are included in *Gomphotherium* in the present scheme, this subgeneric distinction may be ignored.

**Gomphotherium cauleyi** (Lydekker)

This species was established by Lydekker (1886, 71) on characters which cannot be regarded as distinctive. The upper molars are said to be relatively wide, with comparatively high crests and obstructed valleys. The trefoil pattern of the worn inner cone is very pronounced. This form has usually been supposed to be the source of origin of the Stegodontinae and is even classed with such forms as *Prostegodon latidens* (Clift) under the same generic name (Pilgrim, 1925, 210). The height of the crests and the number of accessory conelets developed in the valley directly speak against this form being ancestral to *P. latidens* or to any other allied form which is characterized by low crests and open valleys.

The mandibular symphysis of this form was not known to Lydekker, and none has since been described. The systematic position of this form is therefore doubtful. It bears some resemblance with *G. punjabiense* (Lydekker), and *G. longirostris* (Kaup). It is not unlikely that this form evolved from *G. falconeri*.

It was originally known from the Piram Island only. But Pilgrim (op. cit.) mentioned the Simla Hills as a second locality of its occurrence. Both the occurrences are likely to be in the Dhok Pathan Stage of the Middle Siwaliks.

Osborn (1929, 15) reported two allied forms from the Indian Miocene. One of them, which he calls *Stegolophodon cauleyi progressus*, is from the Lower Chinji Stage of the Salt Range. This form is supposed to be more progressive than Lydekker's type which comes from a higher horizon. It is rather unusual that a more progressive form comes from an older formation.

**Gomphotherium punjabiense** (Lydekker)

Lydekker (1888, 60) separated under the name of *Mastodon punjabiensis* some molars and a mandible from the Punjab originally referred by him (1878, 71; 1880, 239) to *Mastodon* (*Tetralophodon*) *perimensis* Falconer and Cautley. The former differs from the latter in having little cement in the bottom of the transverse valleys, in having much thicker crests and in not displaying an alternate arrangement of the inner and the outer cones. Lydekker characterizes the mandibular symphysis as short and in some cases without tusk. But Pilgrim (1913, 293) asserted that it was long and that it was in the case of females only that the lower tusks were missing. From the measurements given by him, it appears that the symphysis was a little longer than that of *Gomphotherium longirostris*. Hence, it should be regarded as a longirostral form.

Specimens referred to this form are reported by Lydekker and Pilgrim (1919, 200) to have come from the Dhok Pathan Stage (Pontian) of 'the Salt Range' only. From this it would appear that the whole of the material, collected by Theobald from the Punjab and originally referred by Lydekker to *M. perimensis*, has been transferred to the present species. In that event, it is curious to note that a second right upper molar from the Punjab (Lydekker, 1880, Pl. XLI, fig. 4) shows an alternate arrangement of inner and outer cones as seen in the Piram species. It is difficult to explain how this character is found in the second molar while it is absent in the first and the third. On the other
hand, a homologous molar from the Piram Island, collected by Fedden and described by Lydekker (1884b, 150 and Pl. XVI, fig. 2) agrees with the first and third upper molars from the Punjab (Lydekker, 1880, Pl. XL and Pl. XLIV fig. 1) in having tall crests; deep and narrow transverse valleys and in not showing the alternate arrangement of the inner and outer cones. From the above circumstances it appears that both the species ranged from the Piram Island to the Punjab and had descended from a common ancestral form, one branch retaining a more or less normal transverse arrangement of the crests, and the other evolving an alternate arrangement of the inner and outer cones finally reaching the stage of *Anancus sivalensis* (Cautley). It should be mentioned here, that a third upper molar from Lehri described and figured by Lydekker (1880, 253; Pl. XLIV, fig. 1) under the name of *Mastodon sivalensis* was regarded by Pilgrim (1913, 293) as belonging to his new species *Mastodon (=Anancus) hasnoti* (along with two other specimens described and figured by Lydekker). This molar is of an entirely different type from a corresponding lower molar (Lydekker, 1880, 254; Pl. XLIV, fig. 3) which of course answers the short description given by Pilgrim to characterize his new species. The transverse crests in the former are not oblique as expected in all Brevirostrines, the inner and outer cones are connected by intermediate cones to form regular straight crests, and the transverse valleys are much more open, the accessory conules being inconspicuous in size and number. One should assign this tooth to the species under consideration, as also the second upper molar (Lydekker, 1884b, Pl. XVI, fig. 2) from the Piram Island referred to before and the third upper milk molar figured by Lydekker in the next plate (Pl. XVII, fig. 3). In profile, the latter tooth resembles a second upper molar of *M. perimensis* figured in Falconer's Memoirs (1868, I, Pl. IX, fig. 3) except in having one crest less. But they differ in the coronal view.

This species is thus known from the Dhok Pathan Stage of the Potwar and the Piram Island and from the Sub-Himalayan Siwaliks. *Gomphotherium bhumiajense* (Maarel) from Java, described by Maarel (1932, 108), appears to be very closely related to *G. punjabiense* and to have evolved from it. *Gomphotherium longirostris* of Europe resembles the present species. This apparent similarity in form is due to parallel development.

**Serridentinus prochiniensis** Osborn

The present species and the four following ones were referred to this new genus, *Serridentinus*, by Osborn. The generic name was created by Osborn (1923, 2) with *Mastodon productus* Cope as the type. According to him it is distinguished from the trilophodont *Gomphotherium* by having no intermediate accessory conules in the centre of the transverse valleys and by having 'the serrate crests ascending on the outer cones of the lower molars and on the inner cones of the upper molars'. It was also claimed to have had a different habitat. Mathew did not recognize the distinction. If we recognize this genus and the included species as distinct from the already described forms, it would be difficult to explain the occurrence of eight different mastodon species recorded from the same horizon and locality, namely, the Lower Chinji Stage of Chinji in the Potwar. It may further be mentioned that in *Gomphotherium falconeri* also the accessory conules are not in the centre of the transverse valleys, but are placed on the inner side of the median longitudinal valley closely applied to either side of the inner cones in the case of upper molars and the reverse in the case of lower molars. Until we have a more detailed description of these species, we may regard them as a distinct genus but not as belonging to a distinct subfamily, Serridentinae, as Osborn (1936, 730) did.

*S. prochiniensis* (Osborn, 1929, 6) is a small, primitive representative of the group. The conules responsible for the trefoil shape of worn cones are in a rudimentary state of development. The main cones do not subdivide into conelets.

In *S. chinjieni* (Osborn, 1929, 5) the trefoils are sharply defined, the main cones are connected by conelets to form crests, the latter being still brachydont.

*S. browni* (Osborn, 1926, 4) also has low brachydont crowns with obtuse cones. The fourth crest in the second upper molar and the fifth crest in the third upper molar
are still in a rudimentary stage of development.

*S. metachinjensis* (Osborn, 1929, 4) has subhypodont crowns, but the transverse valleys are free from cement. The third lower molar, besides having four crests, has a talonid consisting of a main cone and many conelets.

In *S. hasnotensis* (Osborn, 1929, 2) the crown of molars are subhypodont, with massive crests and with valleys with cement at the bottom. The main cones present strong internal, and rudimentary external, trefoils in the upper molars.

*S. hasnotensis* is known from the Dhok Pathan Stage of Hasnot and Dhok Pathan in the Potwar, and the rest are all from the Lower Chinji Stage of Chinji farther south in the Potwar. It is interesting to note that this phylum is represented by *Serridentinus mongoliensis* Osborn (1924a, 1) in the Loh formation of outer Mongolia. The age of this formation is Helvetic (Osborn, 1930, 541) which is represented in India by the Kamliial Stage. From this it would appear that Central Asia was the centre of adaptive radiation of this phylum, and from here they dispersed to Europe, India and to south and southeast parts of U.S.A. But it did not leave the centre altogether, because it is found again in the Khumuk formation of Upper Pleistocene age (Osborn, 1930, 542), the species being named *S. florescens* by Osborn (1929, 6).

There are great breaks in the sedimentary record of the Cainozoic era of this region. These are either unrepresented or have yet to be discovered. Osborn and Granger are of opinion that other centres of mammalian evolution still remain to be explored. Mathew (1915, 254) had long before expressed the opinion that the centre of dispersal was more likely in Asia than in Africa. “The principal lines of migration in later geological epochs have been radial from Holarctic centres of dispersal” (op. cit., 172).

Subfamily BREVIROSTRINAE

SYNCONOLOPHUS PTYCHODUS Osborn

The genus *Synconolophus* was erected by Osborn (1929, 9) to accommodate three species of a distinct phylum first brought to light by the collections of Barnum Brown from the Potwar Siwaliks. A part of the material, separated from *Gomphotherium pandionis* by Pilgrim under the name *Tetrabelodon corrugatus*, is also referable to this genus. This is characterized by oblique transverse crests and by a progressively increasing number of accessory conules, which are responsible for a complex choerodont type of molars.

Osborn referred *Mastodon hasnoti* Pilgrim also to this genus. This cannot be accepted. Pilgrim’s species is very closely related to *Anancus perimensis* and *Anancus sivalensis*, and moreover, it does not show the typical choerodont type of *Synconolophus* molars.

The present species represents the most primitive stage in the development of this genus. The molars are smaller, the alternate position of the inner and outer cones is less marked, and the transverse valleys are encroached by a much smaller number of accessory conules. It is found in the lower Chinji Stage of the Potwar.

I am rather doubtful about the generic reference of *Synconolophus prophathanensis* Osborn. The inner and outer cones are placed directly opposite each other, instead of alternately as usual with all the Brevirostrines. This type is known from the Dhok Pathan Stage of the type area.

**SYNCONOLOPHUS CORRUGATUS** (Pilgrim)

Out of the material separated from *G. pandionis* by Pilgrim (1913, 293) and referred to *Tetrabelodon corrugatus*, I consider only three molars as properly belonging to the present species. Two are from the Potwar figured by Lydekker (1880) in Pl. XXXV A, and the third by the same author (1884b) in Pl. XVI. All these three teeth belong to the upper jaw. They are much broader and are much more complex in the pattern of worn surface than the other molars described by Lydekker under *G. pandionis*. For a particular individual the upper molars may be a little broader and a little more specialized in structure than the lower molars, but in the present case the difference is too pronounced to be explained this way.

This species is known from the Dhok Pathan Stage of the Potwar and the Piram Island.
This represents the most advanced stage in the development of this generic group. It is a highly specialized successor of *S. phychoeus* and is even more complex in tooth structure than *S. corrugatus*. The number of transverse crests (five and a hind talon) exceeds that of any other member of the group. This is known from the Dhok Pathan Stage of the type area in the Potwar plateau.

It is only a preliminary account that is given by Osborn (1929, 9-13) for these species. A fuller account of these will no doubt form a valuable contribution to Proboscidean palaeontology.

**Anancus perimensis** (Falconer and Cautley)

The generic name was proposed by Lartet in 1859 for the type species *A. macroplus* Lartet, which is a synonym for *Mastodon arvernensis* established by Croizet and Jobert in 1828.

Certain specimens of jaws and molars from the Piram Island were figured by Falconer and Cautley (1846, Pl. XXXI, figs. 9-11) under the name of *Mastodon perimensis*. Specimens Nos. 1 and 2, originally preserved in the Museum of the Asiatic Society of Bengal, were mentioned by Falconer as characteristic ones for the species. These have been figured in Falconer’s Memoirs (1868, I, Pl. IX, figs. 3-6), but have not been described anywhere. Those that were described by Lydekker (1880 and 1884b) under this name have later (1886) been assigned to the closely related species, *G. punjabiense*. But, one right upper second molar (Lydekker, 1880, Pl. XLI, fig. 4), referred to in the preceding discussion on *G. punjabiense*, shows the characters of *A. perimensis*. A corresponding lower molar (op. cit. fig. 1) has also to be retained in this species.

The present species is distinguished from *G. punjabiense* by molars showing an alternate arrangement of the inner and outer cones and by comparatively short jaws, the lower being without tusks. This form evolved into *Anancus hasnotensis* (Pilgrim), which in turn gave rise to the end form *Anancus sivalensis* (Cautley). Long before reaching this final stage the line seems to have sent off a branch to America represented by *Stegomastodon* Pohlig. Osborn, in his conclusions on ‘the Phylogeny and Evolution of the Proboscidea’ (1925, 27), regarded the present form to be the root from which all the Brevirostrines have evolved. But the discovery of the new species, *Anancus properimensis* (Osborn, 1936, 647), from the Potwar, ranging from the Lower Chinji to the Dhok Pathan Stage, has now made the study of the phylogeny of this group more complex. The root has now to be looked for in this latter or some still earlier form.

The present species is known from the Dhok Pathan Stage of the Piram Island and the Potwar. A molar from Yunnan, China, was referred by Koken (1885, Pl. VII, fig. 1) to the present species under the name of *Mastodon perimensis* var. *sinensis*. This appears to be specifically distinct from the present species and to be more closely related to *Gomphotherium* (*Lydekkeria*) *falconeri* (Lydekker).

**Anancus hasnotensis** (Pilgrim)

The name *Mastodon hasnoti* was proposed by Pilgrim (1913, 293) to accommodate some molars which show characters more primitive than those of the typical *Anancus sivalensis* (Cautley). Some molars, collected by Theobald in the Punjab Siwaliks and figured by Lydekker (1880, Pl. XLIV) under the name of *Mastodon sivalensis*, are taken as representing the new type. It differs from Cautley’s type in the intermediate molars being tetralophodont instead of pentalophodont, in the inner and outer cones alternating in a less marked manner, and in the worn crown presenting a less complex pattern. As I have already pointed out, the third upper molar figured in the plate mentioned appears to me to be referable to *Gomphotherium punjabiense*, while the third lower molar figured in the same plate does really represent the type of the present species.

This species is known from the Dhok Pathan Stage of Jammu Siwaliks, and is apparently not found in Hasnot after which the trivial name is given. There is of course a specimen from Hasnot which Lydekker (1880, Pl. XLI, fig. 4) had first referred to *Mastodon* (*Tetralophodon*) *perimensis*, but later corrected to *Mastodon*...
sivalensis But I think this specimen is better referred to the species *A. perimensis* as it now stands after the separation of some of its material to *G. punjabiense*.

**ANANCUS SIVALENSIS** (Cautley)

This form was first announced and described by Cautley (1836, 294). He considered it to be very similar to a fossil found near Asti in Italy, which Cuvier referred to a variety of *Mastodon angustidens* and which was named as *Mastodon arvernensis* by Croizet and Jobert. Cautley anticipated a specific distinction for this form and provisionally gave it the name of *Mastodon sivalensis* (=*Pentalophodon sivalensis* of many authors). Of the specimens of molars figured by Falconer and Cautley (1846, Pls. XXXIV, XXXVI etc.), the last upper molar of the left side represented in fig. 6, Pl. XXXVI, may be regarded as the type for the species. It has six crests and a hind talon. The molars are narrow. The inner and outer cones alternate in position, thereby completely blocking the transverse valleys. The cones are tall. The intermediate molars of this species show five crests. The species is further characterized by the great elevation of the vertex of the skull. The mandible is short and with a very short tusksless spouting symphysis. In all these characters the present species shows close affinity with *Anancus arvernensis* (Croizet & Jobert) although the latter is somewhat less specialized in certain characters.

This species is confined to the Tatrot Stage of the Upper Siwaliks and is found from the Sub-Himalayan regions of the Punjab and from the Siwalik Hills.

**ANANCUS FALCONERI** (Osborn)

Teeth represented in Pl. 32 and in figs. 1 and 2 of Pl. 33 of Fauna Antiqua Sivalensis (Falconer & Cautley, 1846) referred to originally as *Mastodon sivalensis*, are regarded by Osborn (1936, 653) as belonging to a new species which he named *Pentalophodon falconeri*. According to Osborn (op. cit.) this species is very much more progressive than *Anancus sivalensis*, representing a much more advanced stage of evolution. With this species (reported doubtfully from the Tatrot stage) as the last and the most special- lized representative of Gomphotheriidae, this family seems to have become extinct in the Indian region.

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