

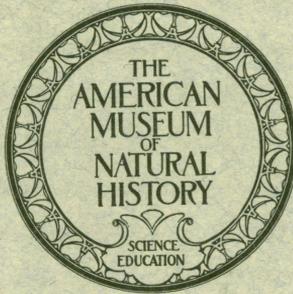
# AMERICAN MUSEUM NOVITATES

No. 1

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## THE EVOLUTION, PHYLOGENY AND CLASSIFICATION OF THE PROBOSCIDEA

BY HENRY FAIRFIELD OSBORN



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## THE EVOLUTION, PHYLOGENY, AND CLASSIFICATION OF THE PROBOSCIDEA

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The following is the quadruple branching indicated in classifications of the Proboscidea previous to 1910 (Osborn, 'Age of Mammals'):

- ELEPHANTIDÆ—Gray, 1821; Zittel, 1891
- MASTODONTIDÆ—?Mastodonadæ Gray, 1821
- DINOTHERIIDÆ—Bonaparte, 1845; Zittel, 1891
- MÆRITHERIIDÆ—Andrews, 1906

### 1.—PRIMARY DIVISIONS

In December 1917, the author presented before the Palæontological Society a paper entitled 'A Long-jawed Mastodon Skeleton from South Dakota and Phylogeny of the Proboscidea.'<sup>1</sup> This included a polyphyletic theory of the Proboscidea more or less fully anticipated by previous authors but more radical. This branching, as extended by Osborn in 1910 and 1917, is as follows:

- MASTODONTINÆ—Osborn, Age of Mammals, 1910, p. 558
- ELEPHANTINÆ—Osborn, Age of Mammals, 1910, p. 558
- BUNOMASTODONTINÆ—Osborn, 1918, p. 134. Defined to contain three main phyla, originally termed (Osborn, 1918, p. 136): 1, *Longirostrinæ*; 2, *Rhynchostrinæ*; 3, *Brevirostrinæ*
- STEGODONTINÆ—Osborn, 1918, p. 135 = Stegodonts of southern Asia
- LOXODONTINÆ—Osborn, 1918, p. 135 = African and Eurasiatic loxodonts
- EUELEPHANTINÆ<sup>2</sup>—Osborn, 1918, p. 136 = Mammoths of Eurasia and North America

Of the above branches it now appears that the Bunomastodontinæ is a group rather than a subfamily and must be split up into the three subfamilies provisionally termed (1, 2, 3) above. Adding the *Mæritheriidæ* and the *Dinotheriidæ*, this would divide the Proboscidea into ten branches.

<sup>1</sup>Bull. Geol. Soc. Amer., XXIX, No. 1, March 1918, pp. 133-137.

<sup>2</sup>The term Euelephantinæ is invalid, because the genus *Euelephas* is invalid; the term *Mammothinæ* (i. e., *les mammons*, the mammoths) may be substituted.

In continuing the study of the Proboscidea since 1917, aided by recent observations of Lull, Matthew, Mayer, Schlesinger, Pilgrim, Barbour, and many others, it is the opinion of the author that the polyphyletic theory of the Proboscidea is not only confirmed but that the phyla are more numerous than the ten branches already named and are geologically far more ancient than appeared in 1917.

As regards the rank of the four primary divisions of the Proboscidea which have hitherto been discovered, they are certainly more profound than the four sections of the Rodentia, viz.: I, Sciuromorpha; II, Myomorpha; III, Hystricomorpha; IV, Lagomorpha. They are also more profound than Osborn's four main divisions of the Perissodactyla, viz.: I, Titanotheroidea; II, Hippoidea; III, Tapiroidea; IV, Rhinocertoidea.

With the reservations, first, that we should not expect to find different orders of mammals subdivided into branches of equal rank and, second, that the subdivisions of the Proboscidea are either of subordinal or of superfamily value, we may adopt as the four primary divisions:

- I. MÆRITHERIOIDEA typified by the *Mæritherium* in the Oligocene of North Africa
- II. DINOTHERIOIDEA typified by the Miocene and Pliocene Dinotheres of Eurasia
- III. MASTODONTOIDEA to include the Bunomastodontidæ, new family, and the Mastodontidæ
- IV. ELEPHANTOIDEA to include the Elephantinæ, Loxodontinæ, Stegodontinæ, and Mammontinæ

#### I.—Mæritherioidea

Renewed study of *Mæritherium* by Osborn and Matsumoto entirely confirms Andrews' original opinion that *Mæritherium* belongs in the order Proboscidea, as well as Osborn's opinion that it stands very far apart from the other proboscideans and is not directly or indirectly ancestral to either of the other three groups. The enlargement of the second upper and lower incisor teeth into mutually abrading tusks, girdled with enamel, presents a firm ground of affinity with a still unknown primitive Lower Eocene proboscidean stem form. There the resemblance ends. These Mæritheres had no proboscis. The face, of brachyopic type, is markedly abbreviated. The cranium is elongated. Thus the facial and cranial proportions are analogous to those of the Sirenia. The upper grinding teeth are bilophodont, pointing to a tetrabunodont ancestry, and different from the bunomastodont grinders of *Palæomastodon*, which point to a hexabunodont ancestry. The lower grinders exhibit a rudimentary third crest. Andrews' opinion that the Mæritheres were amphibious is probably correct.

## II.—Dinotherioidea

All agree that these animals were chiefly fluviatile and amphibious in habit, in this respect resembling *Mœritheres* but differing in the entire loss of the superior incisor teeth. Early loss of upper tusks released the inferior. In the downturning of the inferior tusks the *Dinotheres* are paralleled by the *Rhynchorostrinæ* among the *Mastodontoidea*. In skull

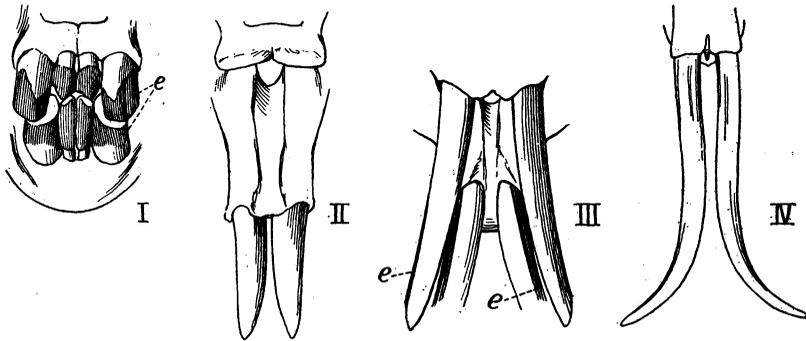


Fig. 1. Fundamental arrangement of the cutting teeth in the four superfamilies of the Proboscidea.

I.—*Mœritherium*. II.—*Dinotherium*. III.—*Rhynchotherium*. Composition of two species. IV.—*Stegodon*. *S. insignis* stage. Scale not uniform.

form and in limb and foot structure the *Dinotheres* parallel the true proboscideans. They diverge very widely from proboscideans in the evolution of the upper and lower grinding teeth. The primitive *Dinotheres* present simple bilophodont grinders, similar to those of *Mœritherium*, and are persistently bilophodont. The upper grinders attain a stage which parallels the molar pattern of the tapir (*Tapiroides*) among the perissodactyls, but shows no tendency to the trilophodont, tetralophodont, or polylophodont structure characteristic of the mastodons and elephants.

## III.—Mastodontoidea

The fundamental character of the front teeth in this superfamily is seen in primitive members of the *Rhynchorostrinæ* and *Longirostrinæ*, namely:

Second superior incisors enlarged, downturned, divergent, with enamel band on the outer side only.

Second inferior incisors downturned (as in *Dinotheres*) with enamel band on outer side (*Rhynchorostrinæ*) or procumbent with no enamel band (*Longirostrinæ*).

The important functional distinction is that for a very long period of time the upper tusks abraded the outer side of the lower tusks; this probably explains the retention of the superior enamel band. In certain lines (Longirostrinæ) the procumbent lower incisors persist and the upper incisors retain their primitive downcurved position as in *Palæomastodon*. In other lines (Mastodontinæ, Brevirostrinæ) the lower incisors practically ceased to function; the upper incisors finally turn upward and inward, but may retain the enamel band for a long period (Mastodontinæ, *vide* Schlesinger, and Brevirostrinæ, *vide* *M. andium*).

A distinctive character of the grinding teeth of the Mastodontoidea is some evidence of the descent from a hexabunodont ancestral grinder (i. e., with intermediate tubercles or conules) as distinguished from the tetrabunodont ancestral type of Mœritheres and Dinotheres. The rudiments of ancestral conules gave rise to various trefoils or paired median outgrowths or crests, so characteristic of all the Bunomastodontidæ whether beak-jawed (Rhynchorostrinæ), or long-jawed (Longirostrinæ), or short-jawed (Brevirostrinæ). In each of these subfamilies the grinders independently undergo a more or less closely parallel evolution, evolving single trefoils in Upper Oligocene and in Miocene time, and double trefoils in Pliocene time.

Unlike the Mœritheres and Dinotheres, the three intermediate molars (i. e., fourth premolar and first and second true molars) invariably become trilophodont, while the third true molars become tetralophodont. At this point there is a divergence into (1) Mastodontidæ, purely forest living, brachyodont, with simply crested teeth, in which the intermediate molars are persistently trilophodont, with arrested trefoils, and into (2) Bunomastodontidæ, which pass into tetralophodonty and polylophodonty in some lines, with evolving trefoils. The grinder evolution is adapted to a leaf-browsing habit, in distinction to the prevailing grazing habit developed among the elephantoids. The development of hypsodonty, and chœrodonty (Schlesinger), among these (longirostrine and brevirostrine) browsers is analogous to that in the hippopotami and the hypsodont suillines.

#### IV.—Elephantoidea

One prime distinction in this superfamily is the very early complete loss of the lower incisor teeth, accompanied by the early development of the upper incisors into horizontal or upturned tusks finally devoid of enamel except at the tips in the young stage. Vestigial enamel bands are recorded in early stages of the stegodonts. A second distinctive

character is the absence of conule development into trefoils, so characteristic of the mastodontoids, and the early tendency to form evenly transverse, more or less mammillate, crests which become in the highest degree hypsodont and polylophodont in adaptation to chiefly grazing habits.

## 2.—EVOLUTION AND PHYLOGENY OF FAMILIES AND SUBFAMILIES

The phylogeny of species is now partly known; the Miocene phyla of Europe are being studied by Schlesinger. Systematic classification will follow a full understanding of the evolution and phylogeny. Forty-four generic names have been proposed for these animals and, as yet, an uncounted number of specific names. Generic and specific synonymy awaits (1) a clear separation of the phyla, (2) a determination of the precise geologic levels of types, and (3) a fuller knowledge of all the characters of the species. None of these data is complete as yet, hence the present contribution is preliminary to the author's revision of the synonymy.<sup>1</sup>

We await also a restudy by Matsumoto of the characters of the *Mœritheres*, soon to be published in the American Museum Bulletin, also a fuller knowledge of the *Dinotheres* from unpublished materials in the British Museum. The positive determination of supposed south Asiatic relatives of *Mœritherium*, as well as of *Palæomastodon*, is very important. Pilgrim (1910, p. 67) provisionally refers to *Mœritherium* a small, primitive proboscidean molar from the Bugti Hills, Upper Oligocene. In the same beds occur *Hemimastodon crepusculi*, a longirostrine more recent in type than *Palæomastodon*. Ancestors of the Rhynchostrines and of the true Mastodontines should also be sought in southern Asia.

### The Rhynchostrinæ

The type of this subfamily (*Rhynchotherium* Falconer, 1868) is a cast (observed in the Genoa Museum by Falconer) of a lower jaw from the Valley of Mexico; the jaw at the time had no specific or generic name. The original genotype may be termed *Rhynchotherium tlascalæ*, new species, from the locality Tlascalá. A similar specimen from Mexico is in the American Museum (Fig. 2 C). The present known range of these animals is Mexico (*R. tlascalæ*), California (*R. shepardi* Leidy), Colorado (*R. brevidens* Cope), and Kansas (*R. euhypodon* Cope). It is note-

<sup>1</sup>There is in preparation an iconographic revision of the known species of Proboscidea to be published in the American Museum Memoirs.

worthy that the Rynchorostrines are geologically the earliest forms of proboscideans known in America, i. e., *R. brevidens*, *R. proavus*. The presence of a species of this subfamily in Middle Miocene beds was recently confirmed by Loomis.

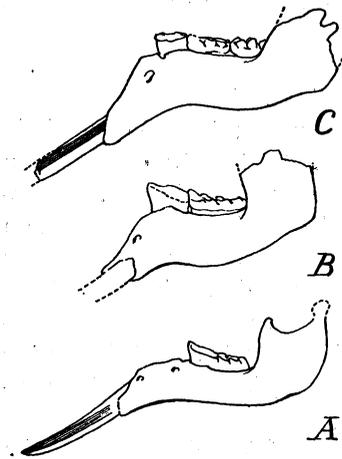


Fig. 2. Rynchorostrine types of lower jaw.

A.—*Rhynchotherium euhypodon* Cope.  
B.—*R. shepardi* Leidy. C.—*R. tlascalæ*,  
new species. All figures  $\frac{1}{4}$  natural size.

The most distinctive feature of this phylum is the downturning of the symphysis, hence the name *Rhynchotherium*, or beak-jawed. A second distinction is the retention of the enamel bands on the lower tusks, to which the specific name *euhypodon* Cope (i. e., perfect lower teeth) refers. A third distinctive character is the relative simplicity and small size of the third grinders, hence the specific name *brevidens* Cope, applied to the most ancient form discovered in America. It would appear that the retention of effective upper and lower tusks relieved the grinding teeth in which the evolution is relatively slow. The known geologic succession of species is:

- Rhynchotherium tlascalæ*, new species, 1921. Valley of Mexico  
" *dinotherioides* Andrews, 1909. N. W. Kansas. Pliocene  
" *euhypodon* Cope, 1884. Lower Pliocene of Kansas  
" *shepardi* Leidy, 1871. Stanislaus County, California. ?Miocene  
" *brevidens* Cope, 1889. Middle Miocene, Deep River, Oregon  
? " *proavus* Cope, 1873. Middle Miocene, Pawnee Creek, Colorado

The maxilla is partly downturned, as well as the mandibular symphysis. Both the superior and inferior incisors are laterally compressed, bending downward and outward. The grinding teeth remain relatively simple, brachyodont, with posterior grinders not exceeding four and a half crests. The intermediate grinders are trilophodont. The grinding series is reduced to  $\frac{2}{2}$ ,  $\frac{1}{1}$  as in *M. mirificus*.

### The Longirostrinæ

This is the most complete and ancient proboscidean phylum known. The four more or less complete skeletons of *T. angustidens*, *T. productus*, and *T. giganteus* prove that these were low-bodied animals, with ex-

tremely broad plevs and short heavy limbs. In the later phases of their evolution they were probably savanna- and stream-dwellers less closely confined to the forests than the Mastodontinæ. The extraordinary traveling powers of this family prove that they were well fed and well defended. The geologic and geographic range is indicated in the following partial list of species. There is an undoubted division of the family into three or four separate phyla, as follows:

I	II	III
Typical Longirostrines: Long, narrow inferior teeth; with typical trefoils; Oligocene to Pliocene. E. g., <i>T. angustidens</i> Cuvier and its successors.	Somewhat broader teeth; with typical trefoils; Miocene of Europe.	Without typical trefoils; Miocene and Pliocene of America. E. g., <i>T. serridens</i> Cope.

Directly ancestral to phylum I appears to be *Palæomastodon wintoni* of the Fayûm Oligocene. The phyla I and II are still to be clearly distinguished in the Miocene of France. Phylum III first appears in the Upper Miocene of America but will probably be found in southern Asia as well as in France.

#### I. *T. ANGUSTIDENS* PHYLUM

PLIOCENE STAGES, double trefoils, intermediate molars four-crested.

*Tetralophodon campester* Cope, 1878. Republican River, Kansas.

" *longirostris* Kaup, 1835. Eppelsheim, Germany.

" *punjabiensis* Lydekker, 1886. Middle Siwaliks, India; Dhok Pathan.

" *corrugatus* Pilgrim, 1913. Lower Pliocene, India.

MIocene AND LOWER PLIOCENE STAGES, intermediate molars three-crested, single trefoils.

*Trilophodon macrognathus* Pilgrim, 1913. Middle Miocene, upper Chinji, India.

" *giganteus*, new species, 1921. South Dakota.

" *floridanus* Leidy, 1886. Lower Pliocene, Florida.

" (*Megabelodon*) *lulli* Barbour, 1914. Snake River, Nebraska.

" (*Tetraelodon*) *osborni* Barbour, 1916. Near Bristow, Nebraska.

" (*Tetraelodon*) *willistoni* Barbour, 1913. Nebraska.

" (*Mastodon*) *obscurus* Leidy, 1869. Miocene, Maryland.

" (*Mastodon*) *productus*, Cope, 1874. Upper Miocene, Clarendon, Texas.

" *angustidens palæindicus*. Manchhar, Middle Miocene, India.

*Trilophodon angustidens* Cuvier. Type. Simorre, Middle Miocene, France.

" *pygmæus*. Lower Miocene, Africa.

UPPER OLIGOCENE, North Africa, India.

*Hemimastodon (Tetralophodon) crepusculi* Pilgrim, 1912. Upper Oligocene. Bugti, Sind.

*Palæomastodon wintoni* Andrews, 1905. Upper Oligocene, Egypt.

### III. *T. SERRIDENS* PHYLUM

*Trilophodon (Mastodon) serridens* Cope, 1884. Upper Miocene, Clarendon, Texas.

" (*Tetralophodon*) *serridens cimarronis* Cope, 1893. Miocene, Clarendon, Texas.

" (*Dibelodon*) *præcursor* Cope, 1893. Blanco, Middle Pliocene, Texas.

? " *turicensis* Schinz. Middle Miocene, France.

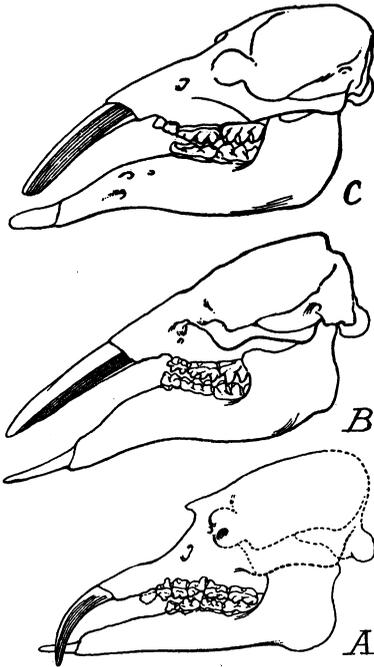


Fig. 3. Longirostrine types of jaw and skull.

A.—*Palæomastodon wintoni* Andrews.  
B.—*Trilophodon serridens* Cope. C.—*Trilophodon productus* Cope. Scale not uniform.

In the typical Longirostrines (I) the lower jaws progressively elongate; rapidly attain great length in some of the European and American Miocene species, e. g., *T. lulli*, *T. giganteus*; relatively less elongate in the Pliocene species *Tetralophodon longirostris* and *T. campester*, as shown in the accompanying figure (Fig. 4). Throughout, the inferior incisors are without enamel band, spatulate, progressively flattened, horizontally appressed, more or less elongate; as the jaw swings abrading the dentine and inner side of the enamel bands of the superior tusks; the latter are rounded and slightly compressed, never oval as in *Rhynchotherium*. In *T. giganteus*, new species (Fig. 4 C), the two lower tusks turn toward each other.

A characteristic, of all the Miocene grinders observed, is the presence of a single trefoil invariably appearing first on the inner side of the upper teeth and on the outer side of the lower teeth. The double trefoils

(inner and outer) on the upper and lower grinders first appear in the uppermost Miocene and Lower Pliocene stages. The intermediate molars in all Miocene species observed are three-crested; hence these animals fall within the genus *Trilophodon* Falconer. The transition to the four-crested stage is observed in Upper Miocene types of Europe by Schlesinger. In all Pliocene species observed the intermediate molars are four-crested; hence they fall within the genus *Tetralophodon* Warren, Falconer. From the Middle Miocene apparently to the close of the Middle Pliocene there was a steady addition of crests to  $m \frac{3}{2}$ , rising from four and a half crests in the Middle Miocene (*T. angustidens*) to seven and a half crests in the Middle Pliocene (*T. barbouri*, new species). At the same time the crests become subhypsodont partly coated with cement.

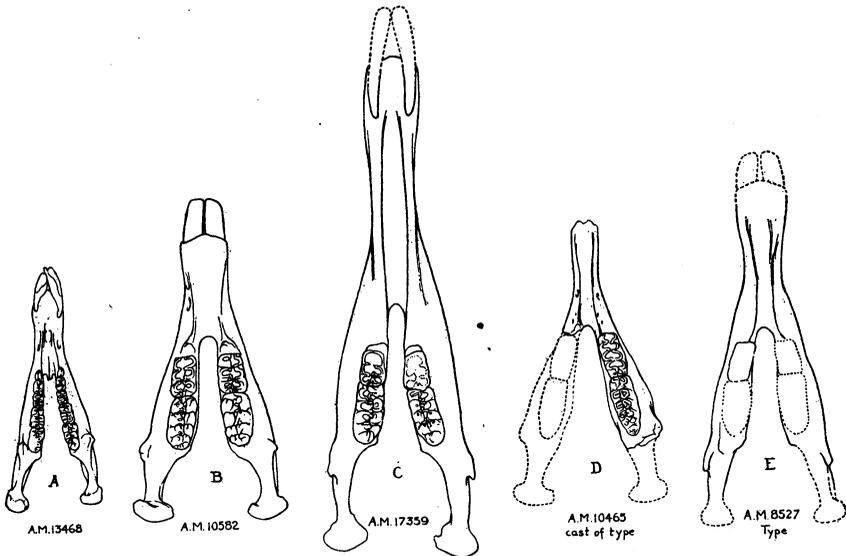


Fig. 4. Lower jaw and grinding teeth in the longirostrine phylum.

A.—*Palzomastodon wintoni* Andrews. Amer. Mus. No. 13468. B.—*Trilophodon productus* Cope. Amer. Mus. No. 10582. C.—*Trilophodon giganteus*, new species. Type, Amer. Mus. No. 17359. D.—*Tetralophodon longirostris* Kaup. Drawn after cast of type. Amer. Mus. No. 10465, Warren Collection. E.—*Tetralophodon campester* Cope. Type, Amer. Mus. No. 8527. All figures  $\frac{1}{4}$  natural size. Grinding teeth in C, *Trilophodon giganteus*, foreshortened in drawing.

There is no evidence that any of the typical Longirostrines (I) were transformed into Brevirostrines by jaw-abbreviation. But it would appear that from certain atypical long-jawed forms (perhaps from phylum II of France with broader molar teeth) arose the *Eubelodon morrilli* type of Barbour, to be described below, without lower tusks, of the Lower Pliocene, Devil's Gulch, Nebraska.

TWO NEW SPECIFIC STAGES.—A new specific stage more recent in character than *T. floridanus* Leidy appears to be represented in the skeleton and jaws (Amer. Mus. No. 17359) discovered in South Dakota by E. L. Troxell in 1916, to which the name **Trilophodon giganteus**, new species, may be applied. It exhibits rudiments of double trefoils and the lower incisors are upturned at the sides so as to face partly inward (Fig. 4 C). A second new species is the **Tetralophodon barbouri**, of which the type (Neb. State Mus. No. 4.22.6.16) is a grinding tooth with double trefoils, seven and a half to eight crests, and cement; thus advanced much beyond *T. campester* with six and a half crests on the superior grinders, without cement.

#### The Brevirostrines of South America

It now appears that the South American Brevirostrines, *M. andium* and *M. humboldtii*, were not derived directly from the Eurasiatic Brevirostrines, typified by the Eurasiatic *M. arvernensis* and *M. sivalensis*, nor were the South American forms descended from the *M. mirificus* Leidy, which appears to be an Eurasiatic migrant.

The reason for this opinion is that the molar pattern of *M. andium* and *M. humboldtii* is of simple bunomastodont type, with single trefoils (*M. andium*) and double trefoils (*M. humboldtii*), a type familiar in the typical American Longirostrines and Rhynchostrines only. The Eurasiatic Brevirostrines and the American *M. mirificus*, on the other hand, have molar grinding teeth, which Schlesinger aptly terms *chærodont* (pig-like, covered with tubercles).

Another typical longirostrine character in *M. andium* is the broad enamel band on the superior tusks. It is not known in any European Brevirostrine. Consequently, it appears probable that the South American bunomastodonts independently abbreviated the jaw and that they may possibly be related to the only American form known in which the jaw is abbreviated, namely, *Eubelodon morrilli* Barbour. The phylum thus appears to be as follows:

- Mastodon humboldtii* Cuvier. Lower Pliocene
- “ *andium* Cuvier. Upper Pliocene. Andean region
- “ (*Dibelodon*) *tropicus* Cope, 1884. Valley of Mexico
- “ *successor* Cope, 1892. Blanco, Middle Pliocene, Texas
- ?*Eubelodon morrilli* Barbour, 1913. Devil's Gulch, Lower Pliocene, Nebraska

*Eubelodon morrilli* exhibits an abbreviated lower jaw, no lower tusks, superior tusks without enamel band (Barbour, 1920). Thus it differs from *M. andium* in one important character, namely, in the absence of the enamel band.

## The Brevirostrines of Eurasia and North America

Suddenly in the Lower Pliocene of the Siwaliks, India, appears *M. hasnoti* Pilgrim, in the Dhok Pathan horizon, stage of Pikermi, of Eppelsheim. According to Pilgrim this differs from the true *M. sivalensis* Falconer of the Middle Pliocene, Tatrot horizon, in having  $m\frac{2}{2}$  tetralophodont and in the slightly marked alternation of the cones. The Middle Pliocene *M. sivalensis* has a pentalophodont  $m\frac{2}{2}$  and the cones are more alternate. The closely related Brevirostrine (*M. arvernensis*) of southern Europe ranges from the lignites of Casino (Middle Pliocene) to the First Interglacial stage in England (Crag). Similarly, the *M. mirificus* of Leidy was first described in association with *Elephas imperator* and determined by Hay as of the Aftonian, i. e., First Interglacial stage. The known succession of described forms in these browsing, forest-living elephants of the warm zones is as follows:

- Mastodon arvernensis*. Norwich fluviomarine crag, Norfolk, England  
 " *arvernensis* Croizet et Jobert. Typical. Upper Pliocene of Auvergne  
 " *mirificus* Leidy. Typical of *E. imperator-Equus* zone of Nebraska  
 " *chapmani* Hays, 1834. Geologic level unrecorded  
 " *sivalensis* Falconer. Tatrot horizon, Middle Pliocene, Siwaliks, India  
 " *brevirostris* Gervais, 1846. France  
 " *pentelici* Wagner. Pikermi, Lower Pliocene, Greece  
 " *hasnoti* Pilgrim. Dhok Pathan horizon, Lower Pliocene, India

The unique feature of the members of this phylum is the alternation of the inner and outer cones of the grinding teeth, which are placed obliquely instead of opposite each other. A further distinctive character is the brevirostral, brachycephalic skull, which parallels that in all the Elephantoida. The jaws rapidly abbreviate and lose the lower tusks in an early stage. The upper tusks, at first elongate and horizontal (*M. arvernensis*), are upturned and out-turned (*M. mirificus*). No enamel band has been observed. The grinding action of the teeth, like that of the pigs, peccaries, and hippopotami, explains the early evolution of double trefoils and finally of accessory tubercles; hence the apt term cherodont, applied by Schlesinger. The intermediate grinders, at first trilophodont, become tetralophodont (*M. hasnoti*), pentalophodont (*M. sivalensis*). The posterior grinders  $m\frac{2}{2}$  evolve six and a half crests (*M. arvernensis*), the cones becoming subhyposodont.

Within the Brevirostrinae are at least two phyla: I. *Mastodon arvernensis*, termed *Dibunodon* by Schlesinger; and II. *Mastodon pentelici*, termed *Charolophodon* by Schlesinger, with a longer symphysis, represented in Samos and in Maragha, Persia. III. To a third

phylum may belong *M. hasnoti*, *M. sivalensis*, India (see Schlesinger,<sup>1</sup> pp. 224-229), *M. mirificus*, North America.

#### The Mastodontinæ

Forest-living animals are rarely found fossil, e.g., the forest-living Chalicotheres of the entire Tertiary. The massive, low-bodied, low-headed, well-defended Mastodontinæ probably evolved chiefly in the north temperate forests of Eurasia. That they were cold-loving animals is shown by their avoidance of southern Eurasia, except for the single appearance of *M. borsoni* in the Upper Pliocene of the Val d'Arno in northern Italy. Of one of the oldest known forms (*M. tapiroides* Cuvier) of the Middle Miocene of France, according to Schlesinger, occasional descendants are found in Europe. All are zyglorhodont; the cones of the grinders turning into transverse crests, the intermediate conules remaining rudimentary, no trefoils forming. Superior incisors (Miocene) retain enamel bands (Schlesinger), but, released from apposition with the lower incisors, turn upward and outward; the lower incisors persisting as abbreviated, horizontal, rounded tusks. The jaws and skull abbreviated, brachycephalic. Intermediate grinders persistently trilophodont. Posterior grinders progressing to a tetralophodont stage only. The vertical chopping motion of the jaws, as distinguished from the grinding motion in the Longirostrines and the Brevirostrines, explains the retention of simple crests and the non-development of trefoils and tubercles.

All ancestral stages will doubtless be found in northern Eurasia. The *M. borsoni* of the Upper Pliocene forests extends into Russia and is directly or indirectly ancestral to the *M. americanus*, a Pleistocene arrival in North America. The chief known specific stages are:

	<i>Mastodon americanus</i> .	Pleistocene
	"	<i>progenium</i> Hay. Missouri Valley, Iowa
	"	<i>borsoni</i> Hays. Upper Pliocene, Val d'Arno, Italy
?	"	<i>turicensis</i> ( <i>tapiroides</i> ). Middle Miocene, Simorre, France
?	"	<i>pyrenaicus</i> . Middle Miocene, France
	"	<i>tapiroides</i> Cuvier. Middle Miocene, France

These six outstanding species are doubtfully placed in one phylum awaiting further evidence.

#### The Stegodontinæ of Southern Eurasia

We observe that the Stegodonts are persistent browsers, probably tropical, forest-living proboscideans. According to Pohlig, from the

<sup>1</sup>1917, Denksch. K. K. Naturhist. Hofmuseums, I, Geol.-Paläontol., Reihe 1, pp. 1-230.

skeleton discovered in Trinil, Java, they have short, massive bodies like those of the Mastodontinæ of the north temperate forests. The skull and tusks do not lead into either the Elephantinæ or the Mammontinæ types. The phyletic succession of species is clarified by Pilgrim's geologic subdivisions of the Siwaliks and by his observations on the succession of specific types, which provisionally may be arranged as follows:

- Stegodon ganesa* (male), *S. insignis* (female). Upper Pliocene and Lower Pleistocene, southeastern Eurasia
- “ *stegodontoides* Pilgrim, 1913. Lehari, Upper Siwaliks. ?Middle Pliocene
- “ *cliftii* Falconer. Dhok Pathan horizon, Lower Pliocene, India
- “ *bombifrons* Falconer. Dhok Pathan, India
- “ *caulleyi* Lydekker. Perim Island. Upper Miocene
- “ *latidens* Clift. Irawadi River, Asia

The distinctive feature of the grinding teeth is the rapid multiplication of transverse crests which rise from the formula 4.5.6.6.7-8 in *S. cliftii* (Lower Pliocene) to 5.9.10.12.13 in *S. insignis* (Lower Pleistocene). Jaw rapidly abbreviated. Upper tusks straight, parallel, slightly up-curved (adapted to dense forests). Grinders brachyodont to subhypso-dont, crests breaking up into small mammillæ, valleys filling with cement.

#### The Loxodontinæ

The late appearance (Upper Pliocene) of these Loxodonts in Italy, the dwarfed evolution in all the Mediterranean islands, the still later geologic appearance (Lower Pleistocene) in Asia, and the existing exclusive occupation of Africa by a great variety of Loxodonts, point to Africa as the original center of adaptive radiation of the Loxodontinæ. This phylum is abundant in the Pleistocene of northern Africa, e.g., *L. atlanticus*.

There is, on the other hand, no trace of these animals in the Pliocene Siwaliks of India; Pilgrim records the first occurrence of *L. antiquus namadicus* in the Lower Pleistocene of Godávári and Narbada, which also contains *Stegodon ganesa* and *S. insignis*.

The gigantic, wide-spreading upper incisors implanted in the maxillo-premaxillary rostrum are quite distinct from those of either the Stegodontinæ, Mammontinæ, or Elephantinæ. The height attained at the shoulder (*L. namadicus*) is estimated at sixteen feet (Pilgrim), five feet taller than the existing *L. africanus*. The affinity of *L. namadicus* to *L. antiquus* (Upper Pliocene to Middle Pleistocene, Europe) and to *L. africanus* has been pointed out by Falconer, Leith Adams, Pohlig, and Pilgrim. Within the subfamily Loxodontinæ there are a great number

and variety of species undoubtedly belonging to more than two phyla, namely:

- |                              |  |
|------------------------------|--|
| <i>Loxodonta africanus</i> . | Recent, Africa, including fifteen species and subspecies |
| “ <i>antiquus</i> .          | Upper Pliocene to Middle Pleistocene, Europe             |
| “ <i>namadicus</i> .         | Lower Pleistocene, India and southern Eurasia            |
| “ <i>creticus</i>            | } Mediterranean Islands                                  |
| “ <i>melitensis</i>          |  |
| “ <i>mnaidriensis</i>        |  |
| “ <i>atlanticus</i> .        | Pleistocene of northern Africa                           |

Another fossil member of this race has recently been recorded in German West Africa.

#### The Mammontinæ. The Mammoths

It is a striking fact that the oldest geologic appearance of a member of the true Elephantoidæ is the *Elephas planifrons* occurring in the Pinjor horizon, Upper Siwaliks, Middle to Upper Pliocene, India. All the fauna of the great Siwalik deposits underlying this geologic level, according to Pilgrim, contain only Stegodonts, Longirostrines, and Brevirostrines. This is significant of a north Eurasian center of adaptive radiation of both the Mammontinæ and the Elephantinæ. The chief distinction between these two subfamilies lies in the flattened forehead of the Mammoths, to which the specific name *planifrons* refers, a forehead which becomes increasingly concave and compressed antero-posteriorly until it reaches the high, narrow peak of *E. imperator*.

Again, the succession of species is probably polyphyletic, awaiting analysis. In descending order the main geologic succession is as follows:

- |                            |  |
|----------------------------|--|
| <i>Elephas primigenius</i> | Blumenbach. Northern Eurasia and North America,<br>Upper Pleistocene                               |
| “ <i>columbi</i>           | Falconer. Middle Pleistocene, North America  |
| “ <i>imperator</i>         | Leidy. Lower Pleistocene, North America  |
| “ <i>trogontherii</i>      | Pohlig. Lower Pleistocene, Europe  |
| “ <i>hysudricus</i>        | Falconer. Uppermost Pliocene, India  |
| “ <i>meridionalis</i>      | Nesti. Upper Pliocene, Val d'Arno, Italy   |
| “ <i>planifrons</i>        | Falconer. Pinjor horizon, Middle to Upper Pliocene, India,<br>also Austria and Bessarabia (Russia) |

The position of *E. hysudricus* in this phylum is doubtful. The cranium referred to this species by Falconer is not of the mammontine type. In 1913 Pilgrim traced back *E. planifrons* to the Upper Miocene *Stegodon cautleyi*, but it would appear at present that none of the known Stegodonts gave rise to the Mammoths. Extreme cranial abbreviation,

hyperbrachycephaly, and acrocephaly are great characteristics of all the phyla in this subfamily (excepting possibly that to which *E. hysudricus* belongs). There is a wide range of divergence in the thickness and multiplication of the lamellæ of the grinders. *Elephas imperator* may be derived from the *E. meridionalis* type, with very few lamellæ, composed of thick enamel bands and with a great coating of cement, or from the *E. planifrons* Falconer type. The *E. primigenius* phylum presents the highest lamellar formula known, with relatively little cement; this phylum is also distinguished by the loss of a digit in the pes, becoming tetradactyl, a unique character among proboscideans. Very great shoulder height, estimated at thirteen feet, is attained by *E. imperator* in the favorable environment of the southern United States and Mexico, as compared with the height of nine feet six inches attained by *E. primigenius* in the frigid north.

#### The Elephantinæ

*Pleistocene*  
 Like the Mammoths, these animals suddenly appear in the Upper ~~Pliocene~~ of India. They are not found in the Lower Pleistocene, where their place in the fauna is taken by the invading loxodont, *L. namadicus*. In distinction from the Mammoths, the forehead is prominent, convex, in adults highly convex. The upper tusks extend forward and outward, slightly upcurved, not crossing each other in old age as in the more recent Mammoths *E. primigenius* and *E. imperator*. Unlike *E. primigenius*, five digits persist on the fore and hind feet. Skull brachycephalic. Jaws abbreviated. Vestigial lower incisors, enamel remaining on the tips only in young stages. Mammillæ more numerous than in the Loxodonts; less numerous than in *E. primigenius*.

#### The Unknown Home of the Elephantoidea

It appears from the above preliminary studies that the proboscidean phylogeny is still subject to many emendations, transpositions, and corrections. It is in the rocks of the great unexplored regions of Eurasia and of Africa—nearly a hundred-fold greater than the regions explored and known—that we must look for the ancestry of the four great branches of the Elephantoidea, namely, the Stegodonts, the Loxodonts, the Mammoths, and the true Indian elephant type.

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