

**Article XXVII.—OSTEOLOGY OF *BLASTOMERYX* AND
PHYLOGENY OF THE AMERICAN CERVIDÆ.**

BY W. D. MATTHEW.

In a preliminary contribution upon the Lower Miocene fauna recently discovered in South Dakota (Matthew, 1907), the writer commented upon its importance in supplying the intermediate stages between hitherto disconnected faunæ, and in enabling us to perceive the exact relationships between genera which could until now be connected only in a general or provisional way. One of the most interesting and important of these connecting links is furnished by the complete knowledge of the osteology of *Blastomeryx*. This genus proves to be a very primitive deer, approximately ancestral to the American Cervidæ, and derivable in its turn from the Oligocene genus *Leptomeryx*, whose relationship to the Cervid phylum had not been suspected. We are thus enabled to trace the ancestry of the American Cervidæ back to the Oligocene, by successive stages known from the entire skeleton, and not merely from the inadequate evidence of teeth and jaws. This phylum is thus placed on a plane with those of the Equidæ, Camelidæ and a few other series. It is indeed an approximate phylum: the known species are probably not in direct genetic sequence. But this reservation applies, in my opinion, to all the accepted phyletic series to a greater or less extent. It is a necessary consequence of the general causal conditions of the evolution of the Tertiary mammals.

The evidence for the establishment of this phylogeny can conveniently be presented in the following sequence:

1. A somewhat detailed account of the osteology of *Blastomeryx*, based upon the Lower Miocene species.
2. Specific distinctions and geological occurrence of *Blastomeryx*.
3. Relationship of *Blastomeryx* to the modern Cervidæ, and the evidence on which it is considered approximately ancestral to the American Telemetacarpal deer.
4. Trend of evolution in this phylum, indicating what we should expect to find in the Oligocene ancestors of *Blastomeryx*.
5. Relationship to European Oligocene Selenodonts.
6. Relationship to *Leptomeryx* of the American Oligocene; evidence of the Cervid affinities of this genus and for considering it as ancestral to *Blastomeryx*.
7. The phylogeny of the American Cervidæ and its interpretation.
8. Provisional phylogeny of American ruminants (diagram).
9. Classification of the Selenodonts (key).

1. *Osteology of Blastomeryx.*

The genus *Blastomeryx* has been hitherto very incompletely known. The discovery of several well preserved specimens in the Lower Miocene enables me to give the principal characters of the skeleton and to determine its relationship.

The principal specimens are:

No. 13822, a fairly complete skull and jaws with limbs and feet, and a few vertebrae.

No. 13015, anterior part of a skull with the greater part of the skeleton.

No. 13224, upper and lower jaws, hind limbs, and feet.

No. 13016, lower jaw, atlas and scapula.

No. 13014, lower jaw (type of *B. advena*).

Nos. 13017, 13823-4, etc., upper jaw, several incomplete lower jaws, hind foot, and various isolated bones.

All the above are from the Upper Rosebud beds on Pine Ridge Indian Reservation, South Dakota, excepting No. 13224, which is from Lower Miocene beds south of Lusk, Wyoming. They represent three specimens closely allied to each other and to the typical *B. gemmifer* from the Middle Miocene of Colorado.

Skull.—The general proportions of the skull are much as in *Moschus* or in *Dremotherium*. The face is rather short and deep anteriorly, the cranium comparatively long, with a low sagittal crest and moderately prominent occiput. The orbits are of medium size and not especially prominent, the anterior half of the orbit lies above m^3 and part of m^2 . There is no trace of horns, the upper canines are developed into long, slender laniary tusks, as in *Moschus*, *Cervulus*, *Dremotherium*, etc. The superior branch of the premaxilla is a wide and rather long plate, as in *Moschus*, and much wider than in most of the modern deer. The nasals are long, slender, and narrow, entirely different in form from any modern Cervidæ; more as in *Tragulus*, and very like those of *Leptomeryx*. There was apparently a considerable prelachrymal fossa, but its exact proportions and limits, and the presence or absence of a facial vacuity cannot be determined. The basicranial region shows very primitive conditions, approaching those in *Leptomeryx*. The basioccipital and basisphenoid are long, narrow, and lie in nearly the same plane with the palate. The tympanic bulla is nearly round and strongly inflated, but small, and does not cover the entire mesotympanic fossa, leaving a depressed channel next to the basioccipital at the bottom of which appears the petrosal. The stylohyoid pit is comparatively small; the auditory meatus rather long, cylindrical, and but slightly

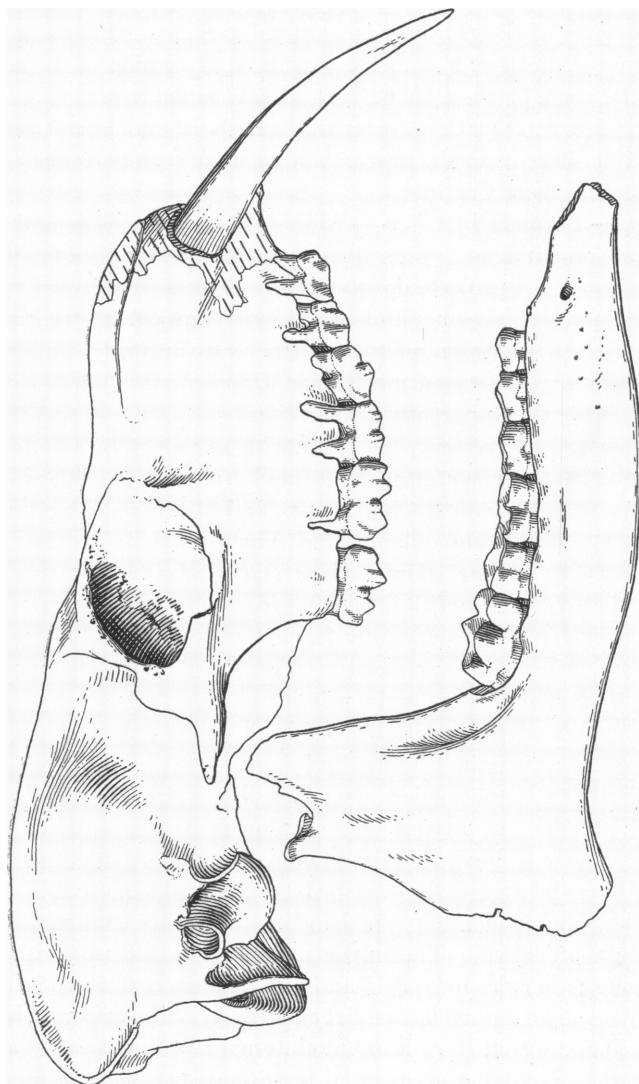


Fig. 1. *Blastomeryx primus*, Type, No. 13822. Side view of skull and lower jaw, natural size. The skull is somewhat crushed in the orbital region, and the upper canine displaced from its natural position.

flattened on its inferior surface. The various modern deer show different degrees of reduction and flattening of the bulla and meatus, with enlargement of the stylohyoid pit; in most of them the internal exposure of the inferior surface of the petrous bone is reduced, partly by widening of the basioccipital, partly by decrease of the petrous bone anterointernally. They also show a varying degree of shortening of the basicranium, elongation of the face, and increase of the angle between basifacial and basicranial axes.

The lower jaw is rather deep, comparatively short, and heavy anteriorly, with broad but short coronoid process and slenderly proportioned condyle as compared with most Cervidæ.

Dentition.—Formula $I\frac{3}{3}$ $C\frac{1}{1}$ $P\frac{3}{4-3}$ $M\frac{3}{3}$. The lower incisors and canines are small and procumbent. The upper canine is as large as in *Moschus*, projects downward, forward, and outward from the alveolus and vertically downward at the tip. The upper premolars are comparatively simple, constructed much as in *Dremotherium*, the second with apparently a small basal cusp representing the inner crescent, the third with an irregular and imperfect inner crescent formed by basal cingula extending from the inner cusp, and the inner cingulum complete only on the fourth premolar. The modern deer show various stages of advance beyond this, *Rangifer* being the most advanced, with the inner crescents fully formed and of identical type on all three premolars. The lower premolars show a correspondingly primitive stage. They are comparatively narrow, with the three internal crests not united internally but separated by open valleys. In the modern deer these inner crests join internally to a varying extent, enclosing basins or lakes. In the Bovinæ this premolar transformation is carried further, the lakes being usually more or less cement-filled.

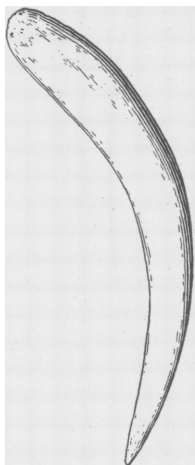


Fig. 2. *Blastomeryx olcottii*. Type, No. 13224. Upper canine, natural size.

The molars are moderately brachyodont, of rather uniform size, and uniform height of crown. The upper molars show the primitive Cervid pattern, strong parastyle, mesostyle and anterior external rib of the paracone, weak metastyle, and metacone flat externally. The upper molars have no internal cingulum but show a minute internal basal cuspule between the inner lobes; the corresponding external basal cusp between the outer lobes of the lower molars is more prominent. These Lower Miocene species of *Blastomeryx* show distinct traces of the "*Palæomeryx* fold" in the lower molars on the posterior face of the anterior inner crescent. The prominent

anterior basal cingulum on the lower molars appears to be characteristic of the genus; it is more developed than in any other primitive deer with which I have made comparison.

In general the teeth correspond very nearly with those of *Dremotherium*

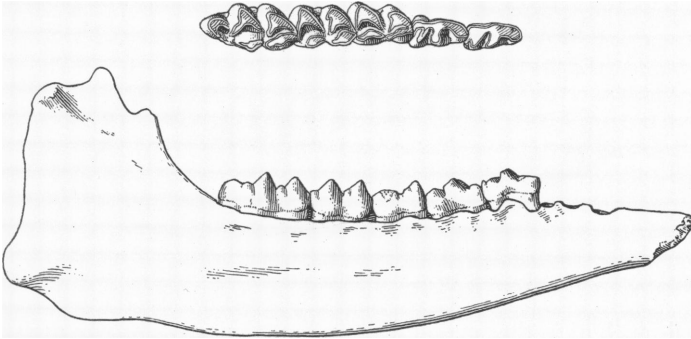


Fig. 3. *Blastomeryx olcottii*, Type, No. 13224. Lower jaw, inside view, and crown view of cheek teeth. Natural size.

and *Amphitragulus*.¹ The basal cuspules of the molars are stronger, the anterior basal cingula on m_{1-3} much more prominent. The premolars are very much the same in construction and proportions; they are intermediate between the simple trenchant type of the Tragulids and the double-crescent type of most modern Pecora. They are more advanced than the genera of the Phosphorites *Prodremotherium*, *Bachitherium*, *Lophiomeryx*,² less than *Dicrocerus* or *Palæomeryx*, decidedly less than the so-called *Palæomeryx* of the American Miocene.³ In comparison with the American Oligocene genera *Leptomeryx* has essentially the same tooth pattern, but the premolars are simpler and more trenchant, their inner crescents very rudimentary, and the molars have shorter crowns and the crescents more obliquely set. In *Hypertragulus* the molar pattern is different, corresponding to that of *Tragulus*, and the premolars are, as also in that genus, much simpler and more trenchant, but more reduced than in the Chevrotain. In *Hypisodus* the molar pattern is also different, more like that of the Camelidæ; the teeth are much more hypsodont; the premolars are relatively small, compressed, and reduced, and the molars peculiarly narrow, as in the Camelidæ.

Vertebrae.—The atlas resembles that of *Merycodus*, especially in the large size and incomplete separation of the cotyli and axis facets, and in the strongly

¹ See Filhol, 1881, pll. xiii-xvi.

² See Filhol, 1876-7.

³ Cf. Matthew, 1904, fig. 21.

marked paired median depressions at the anterior end of the arch for attachment of the occipital muscles. The fifth and sixth cervicals are moderately long, proportioned nearly as in *Mazama*, longer than in *Cervulus*, and much longer than in *Tragulus*. The dorsals, so far as they are preserved, are pro-

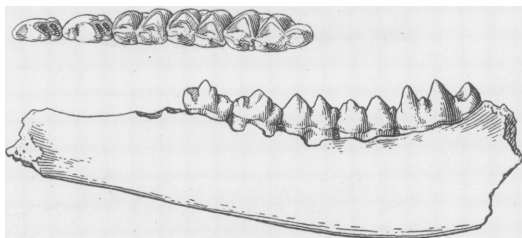


Fig. 4. *Blastomeryx advena*, Type, No. 13014. Lower jaw, inside view, and crown view of cheek teeth. Natural size.

portioned much as in the smaller deer and antelopes. The ribs are strongly curved, the anterior ones broad and flat, the posterior ones quadrate in cross-section proximally and flattened oval distally, the form throughout the series being much as in *Merycodus* and the smaller antelopes. In *Tragulus* the curvature and length of the ribs is much less, and their form more as in the smaller carnivora, narrow, little curved, round oval in section, and but little flattened or broadened in the anterior part of the series.

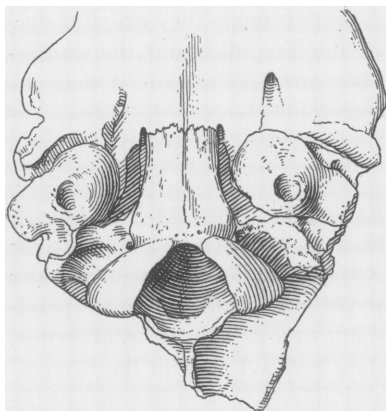


Fig. 5. *Blastomeryx primus*, Type, No. 13822. Basicranial region of skull, natural size.

There are six lumbar, all with short, broad plate-like spines which curve strongly forward in the posterior part of the series. The transverse processes are broad and flat, much shorter than in *Mazama*, somewhat shorter than in *Cervulus*.

The sacrum consists of four vertebrae, whose spines are coössified into a continuous plate, as in *Mazama* and most of the deer; not separate, as in

Cervulus. In *Tragulus* the sacral spines are coössified into a continuous plate, but it is not so high, and differs in various details of form.

Two proximal caudals indicate a very short, small tail.

Fore Limb.—The scapula differs from that of the smaller Pecora chiefly in the prominence of the spine, which is higher than in *Merycodus*, much

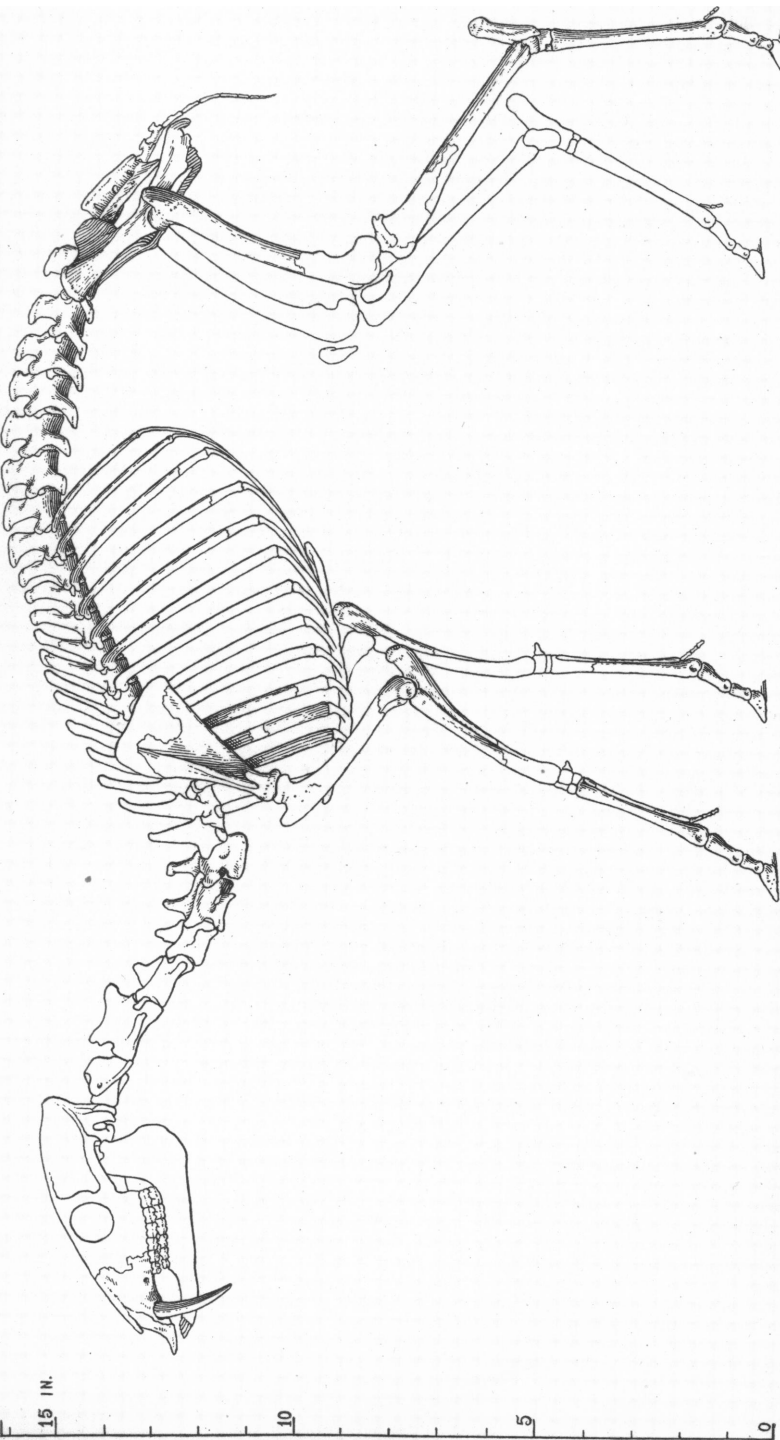


Fig. 6. *Blastomeryx advena*. Restoration of the skeleton, one-fourth natural size. No. 13015, Lower Miocene (Upper Rosebud beds) Pine Ridge, S. Dakota. The missing (unshaded) parts of head and limbs are restored from other specimens of *Blastomeryx* from the same horizon and locality, the missing vertebrae and ribs modified from *Cephalopithecus* and *Cervulus*.

higher than in *Cervulus*, *Mazama*, or *Cephalophus*. The humerus is not completely preserved in any of our specimens, and I do not observe any significant differences from the small modern Pecora.

The radius and ulna are separate throughout, the ulnar shaft very thin and flat, but retaining a considerable depth throughout. The radial shaft is moderately curved, as in *Merycodus*. The carpus is not complete in any of our specimens, the proximal row is preserved in No. 13822, but I do not observe any very significant differences from modern deer except in the greater vertical diameters of the bones.

The metacarpus is remarkably primitive. The lateral digits were apparently complete, and less reduced than in *Tragulus*; the cannon bone, however, is perfectly formed, and of true pecoran type, and the distal keels complete even upon the small lateral metacarpals. In *Dremotherium* the lateral metacarpals are complete¹ but reduced to filiform vestiges; in *Moschus* the lateral digits are comparatively large, but the shafts of the metapodials are not complete in either fore or hind foot, only proximal and distal ends being preserved. In *Merycodus*² the lateral digits in both fore and hind feet are reduced to very small vestigial remnants of proximal and distal ends of metapodials and tiny phalanges with flat facets. In most of the deer and all of the Bovidae the distal remnants of the lateral metacarpals have disappeared, only the phalanges being represented. In *Antilocapra* and *Giraffa* the lateral digits are entirely gone.

The phalanges of the median pair of digits are comparatively long in *Blastomeryx*, as compared with *Merycodus*, in agreement with the Cervine affinities of the one and the antelopine affinities of the other genus.

Hind Limb.—The pelvis is distinctly Pecoran in type, and differs widely from that of *Tragulus* in the angulation between pre- and post-acetabular bars, the eversion of the upper end of the ilium and greater development of its superior plate.

The femur is more primitive than in any modern deer, less so than in *Tragulus*. This is seen especially in the comparatively narrow patellar trochlea facing more anteriorly and less distally than in modern deer, indicating a less horizontal position of the femur and the thigh more free from the flank.

The tibia presents no especial peculiarity. The distal rudiment of the fibula is quite as much reduced as in *Merycodus*, the shaft being represented by a very small, short spine.

The hind foot is decidedly more advanced than the fore foot, the lateral digits being reduced to short splints proximally; presumably distal rudiments

¹ Gaudry, Enchainements, III, p. 108, fig. 142.

² Matthew, 1904, figs. 13-14.

were also present, but they are not preserved in our specimens. The proximal splint of Mts. ii is partially coössified with the cannon bone, the splint of Mts. v is free in all our specimens. The tarsus affords no very significant characters; it is much like that of *Merycodus* and of the smaller Cervidæ. The metatarsus is consolidated into a cannon bone, typically pecoran, somewhat shorter and more robust than in *Merycodus*, the distal keels complete. As in *Merycodus* and in all primitive pecora the median furrow is strong and well defined. This furrow is generally present in modern pecora, but more or less obliterated. It is entirely absent in the Camelidæ, fairly well marked in *Tragul*us, but of somewhat different form. The phalanges, like those of the carpus, are relatively long.

The limb and cannon bones in these Lower Miocene species of *Blastomeryx* are materially shorter and more robust than in *Merycodus*, but in species from the Middle and Upper Miocene the distinction is less apparent.

2. *Species of Blastomeryx*.

Three Lower Miocene species are represented in our collections, as follows:

B. advena Matthew, 1907: smaller, teeth more compressed, p_1 absent, fourth upper and lower pre-molar more rounded or oval in form, limbs and feet very small.

B. primus sp. nov. Larger, teeth broader, p_1 vestigial and spaced. $P \frac{4}{4}$ as in *B. advena*. Limbs and feet nearly two fifths larger.

*B. olcott*i sp. nov. Size of *B. primus*, but $p \frac{4}{4}$ more triangular in outline, p_1 less reduced and in series with p_2-m_3 . Limbs and feet one-fourth larger than in *B. advena*.

The following measurements give the proportionate size of the three species.

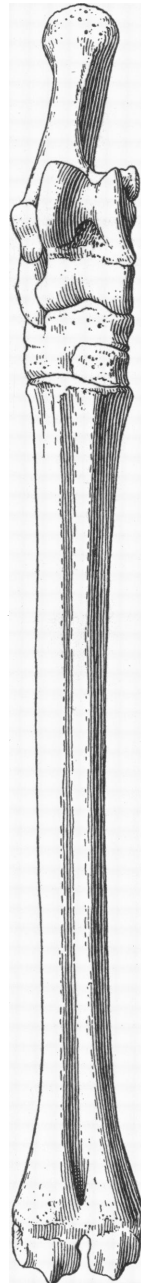


Fig. 7. *Blastomeryx olcott*i, Type, No. 13224. Hind foot, natural size.

	<i>advena</i>	<i>primus</i>	<i>olcottii</i>
	mm.	mm.	mm.
Length p_2-m_3	46	49	49
Transverse diameter of m_3	5.7	6.4	6.1
Length of metatarsus	100	140	125

The type of *B. advena* is a lower jaw, No. 13014. I refer to the same species No. 13015, the anterior part of a skull, fore and hind feet, pelvis, most of the vertebral column and ribs, and parts of limb bones; No. 13823 hind foot; all from the Upper Rosebud of South Dakota.

The type of *B. primus* is No. 13822, skull, jaws, fore and hind limbs and feet, atlas, and other vertebræ. No. 13016, lower jaw, atlas, and scapula,

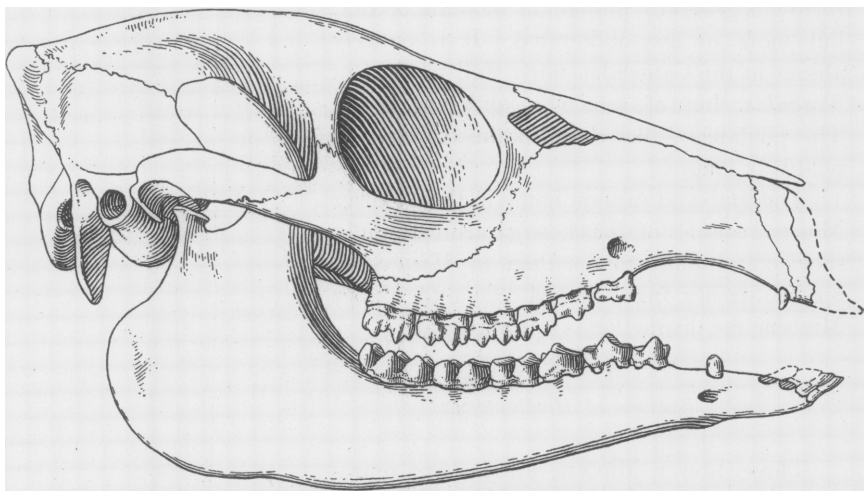


Fig. 8. *Leptomeryx evansi*, skull and jaws, natural size. No. 11870, Middle Oligocene, South Dakota.

is referred to the same species. Both are from the same level and locality as the preceding.

The type of *B. olcottii* is No. 13224, upper and lower jaws, hind limbs and feet; 13224a lower jaw and hind foot of a younger individual was found associated with the type specimen. Both are from the "Aricaree" formation south of Lusk, Wyoming. This species is more primitive in its premolar construction than the two preceding, and the associated fauna has a somewhat older facies than that of the Upper Rosebud, but corresponds closely with that of the Upper Harrison beds immediately to the eastward, with which this "Aricaree" is probably continuous.

Comparison with the type species, *B. gemmifer*, is difficult on account

of the imperfection of the type. The referred specimen No. 9449¹ is a trifle larger than *B. advena* and differs in the form of p_4 , broader anteriorly and narrower posteriorly, so as to have a more quadrate outline; and in the greater proportionate length of the hind cannon bone, consolidation of Mts. ii with the cannon bone, and other details indicating a more advanced stage. The type specimen of *B. gemmifer* is a third lower molar and is a little larger and more robust, agreeing more nearly with *B. primus* and *olcottii*, and not clearly separable from them; but probably if it were better known its stage of evolution would be demonstrably more advanced, as it is in the referred specimen from the same level and locality, the Middle Miocene, Pawnee Creek beds of Colorado.

*B. wellsi*² of the Upper Miocene differs in more reduced premolars, molars larger and somewhat longer crowned; and a referred specimen shows the jaw to be very long and slender anteriorly.

Professor Scott has described³ and referred to *Blastomeryx* a species from the "Loup Fork," probably Upper Miocene, which is much more advanced in skull and skeleton structure than those on which the preceding description is based. It is of much larger size; bears a small or rudimentary antler; the orbits are more prominent; the ulnar shaft is reduced to "a mere thread of bone"; the lateral digits are much more reduced and the shafts of the lateral metacarpals incomplete. This cannot well be congeneric with the Lower Miocene species, whether or not it be regarded as derived from them. If we do so regard it, *B. gemmifer* would probably represent an intermediate stage, as is indicated, in fact, by the little we know of it. In view of the near agreement in size and other characters between

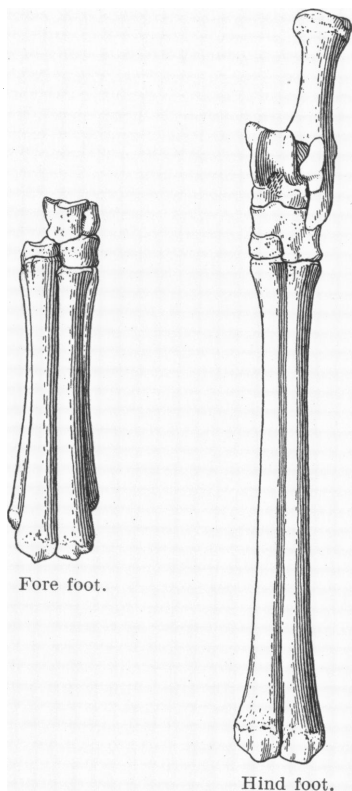


Fig. 9. Fore and hind feet of *Leptomeryx evansi*, natural size. No. 6782, Cope Collection. Middle Oligocene, Colorado.

¹ Matthew, 1904, p. 124, fig. 17.

² *Ibid.*, p. 125, figs. 18-19.

³ Bull. Mus. Comp. Zool., 1890, Vol. XX, p. 76.

B. gemmifer and the Lower Miocene species, it seems preferable to place the latter in *Blastomeryx*, and regard the species described by Scott as referable to a more advanced genus, with rudimentary antlers and with the lateral digits of the fore foot incomplete. It seems inadvisable to name the Upper Miocene genus until we know something more definite of its dentition and skull characters, and its distinctions, if any, from *Mazama*.

Blastomeryx antilopinus Scott, 1894, and *B. borealis* Cope, 1878, with *Palæomeryx americanus* and *madisonius* Douglass, 1900, belong to a larger, more brachyodont phylum of Cervidæ, with supraorbital horns (or antlers) of peculiar type. They are distinct from *Blastomeryx*, probably also from the true *Palæomeryx*, but at present of uncertain relationship.

3. Relationship to the Cervidæ.

Structurally *Blastomeryx* is most nearly related to the musk-deer, but might stand in a general ancestral relation to the Cervidæ and especially to the smaller American deer. Its geological and geographical distribution would prevent its being regarded as actually ancestral to *Moschus* or to the Cervidæ generally, for we find in the Upper Oligocene of Europe genera more nearly representing the hypothetic ancestors of this family. *Blastomeryx* must be regarded, therefore, as a persistently primitive type, which may be ancestral to *Mazama* and perhaps *Odocoileus* but hardly to any of the remaining Cervidæ. Its structural resemblance to *Moschus* is greater than to any other living genus. But in view of the fact that genera closely related to *Blastomeryx* inhabited Europe at a somewhat earlier epoch, it is obviously more probable that *Moschus* is a little altered descendant of one of the primitive Cervidæ of the Old World, than that it is actually descended from the American genus.

The more typical modern Cervidæ have been divided (Brooke, 1878) into two groups. In one (Plesiometacarpalia) the distal end of the lateral metacarpals has entirely disappeared, only short proximal splints remaining. In the other (Telemetacarpalia) the distal ends of the lateral metacarpals are retained as splints of various lengths, the proximal splints are either absent or else fused more or less completely with the cannon bone. The first group includes nearly all of the Old World deer; the second includes all the New World genera together with two or three exceptionally primitive Old World deer. (Of the three holarctic genera, *Cervus* ranks with the Old World, *Alces* and *Rangifer* with the New World deer, in accord with their principal distribution.) The Old World deer therefore are distinguished by the precocious reduction of the lateral metacarpals, while in the New World deer the reduction is retarded. This distinction corresponds to that between

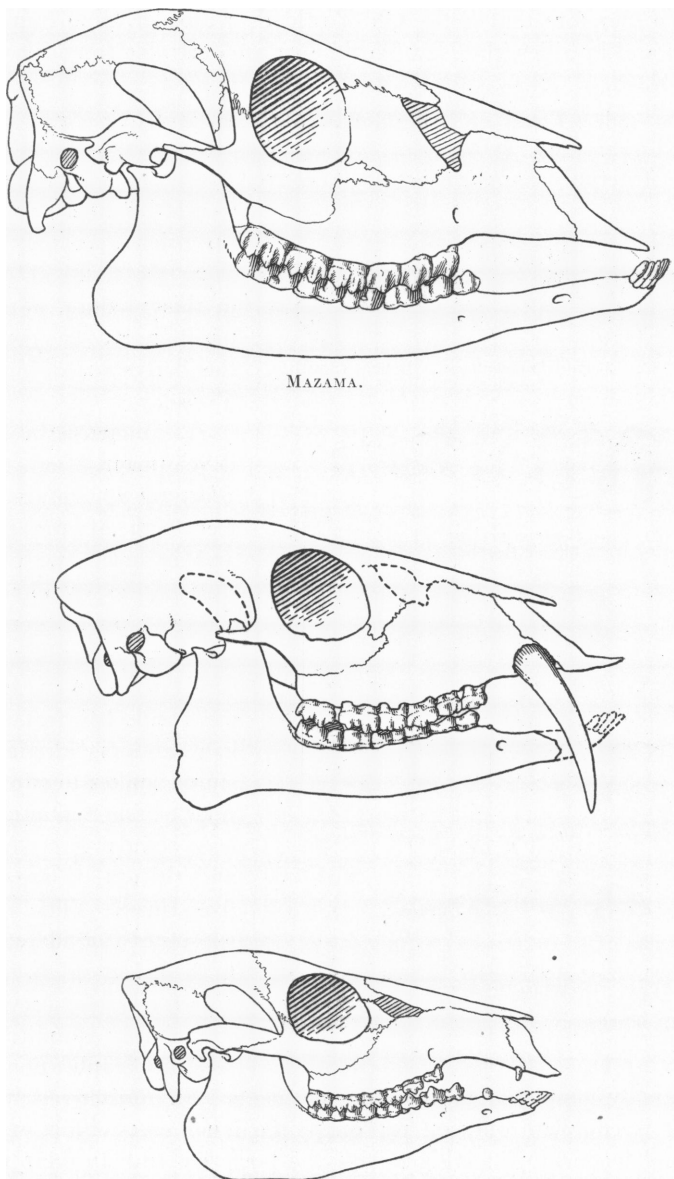


Fig. 10. Phylogeny of American Cervidæ. Skulls, half natural size. *Leptomeryx evansi* No. 11870 Middle Oligocene; *Blastomeryx primus*, No. 13822, Lower Miocene; *Mazama nemorivaga*, No. 15486, Recent (South America).

Blastomeryx and the contemporary European Palæomerycinae. It appears probable therefore that if the Old World deer are derivable from *Dremotherium* and its allies, the New World deer are derivable from *Blastomeryx*.

4. Trend of Evolution in the American Cervidæ.

The structural changes necessary to convert *Blastomeryx* into the modern

Cervid type may be summed up briefly, as they tend to show the trend of evolution in this phylum, a necessary preliminary to considering the derivation of the genus. These are:

1. Increase in size and development of antlers. *Blastomeryx* stands 1 to 1½ feet high at the shoulders and is hornless. Rudimentary antlers appear in the larger Upper Miocene "*Blastomeryx*" according to Scott. The South American *Mazama* stands two feet high and has antlers ranging from simple spikes to two or three tines. The Sonoran *Odocoileus* stands three feet high and the antlers are three to five tined. The Nearctic species of Cervidæ stand four to five feet high, and the antlers are five to seven tined, or variously complicated.

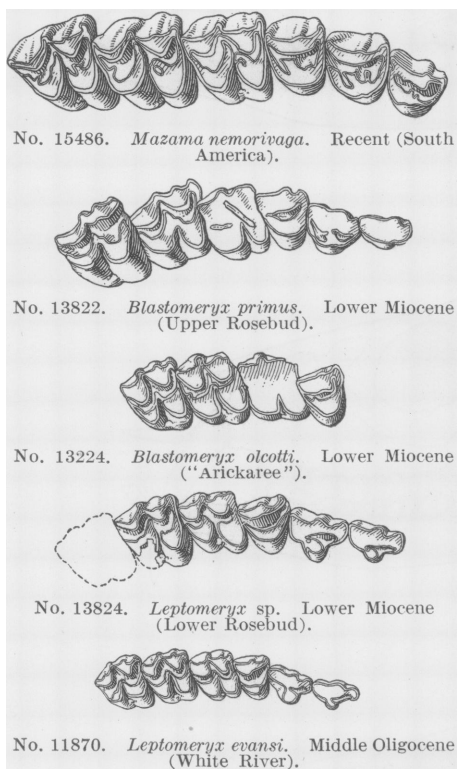


Fig. 11. Phylogeny of American Cervidæ. Upper teeth, natural size.

premolars by completion of their inner crescents. In *Blastomeryx* the inner crescent is complete only on p^4 ; on p^3 the inner cusp is low and partly connected by incomplete ridges with the posterior and anterior margins; on p^2 the inner cusp is low and small, with very rudimentary ridges. In *Mazama* the inner crescent is complete on p^{3-4} , low and imperfect on p^2 . In *Odocoileus* it is complete on p^{2-4} , but still low and a little irregular on

p^2 . In *Cervus* it is more nearly perfected on p^2 , and in *Rangifer* it is quite perfected. The lower molars show a corresponding change in the complication of their inner sides. In *Blastomeryx* there are three marked transverse ridges on the inner side of the tooth, separated by open valleys. In *Mazama* p_4 and the posterior half of p_3 show strong crested inner cusps corresponding to the inner crescents of the molars, partially united with the transverse ridges. In *Odocoileus* the anterior half of p_4 has become completely molariform, the posterior half somewhat degenerate (corresponding to absence of a posterior crescent on the upper premolars); p^3 also shows a strong high pillar on the inner side of the median crest. Evidently this tooth is not exactly analogous in its process of complication with the adjoining one. In *Cervus*, *Alces*, and *Rangifer* the process of complication is carried farther but not by identical methods, so that it is inadvisable to state it in detail.

3. Reduction of the upper canines. In *Blastomeryx*, as in other Miocene Cervidæ and a few modern survivals, they are long, slender laniary tusks. In *Mazama* they are quite small but usually present in the milk, less generally in the permanent dentition; in *Odocoileus* they are never present in the permanent dentition.

4. Disappearance of the "Palæomeryx fold" on m_{1-3} . It is vestigial in the Lower Miocene species, apparently absent in Middle Miocene species, certainly absent in Upper Miocene species of *Blastomeryx*. In the larger and more brachyodont American Miocene species referred to *Palæomeryx* it persists into the Upper Miocene. It is characteristic of all primitive Cervidæ (Palæomerycinæ), according to Schlosser, and absent in any of the late Tertiary and modern Cervidæ.

5. Broadening and shortening of the nasal bones. In *Blastomeryx* the nasals are long and very narrow, as in all the Oligocene ruminants (*Leptomeryx*, *Hypertragulus*, *Poebrotherium*, etc.); in *Mazama* very much shortened and broadened, especially posteriorly; this change is carried a little farther in *Odocoileus*. The Camelidæ show a corresponding change from *Poebrotherium* to the modern types; in *Tragulus*, however, the primitive form is retained.

6. Relative elongation of the lower parts of the limbs, associated with a more horizontal position of humerus and femur. Aside from the length and curvature of the bones, the shortening and more distal position of the patellar trochlea furnishes a convenient index of this change.

7. Reduction of the ulnar shaft.

8. Considerable reduction of the lateral metacarpals. In *Blastomeryx* the lateral metacarpals are slender but apparently complete. In *Mazama* the distal splints are half the length of the shaft. In *Odocoileus*, *Rangifer*

and *Alces* the distal splints are much shorter, and in *Cervus* they have completely disappeared, only the phalanges being left.

9. Very slight reduction of the lateral metatarsals.

10. Sharper definition of the dorsal portions of the distal keels of the metapodials, narrowing and elongation of the metacarpal cannon bone, partial obliteration of the median furrow on the metatarsal cannon bone, and various minor changes which need not be recapitulated.

5. Relationship to European Oligocene *Selenodonts*.

The close resemblance of *Blastomeryx* to *Dremotherium* and *Amphitru-*

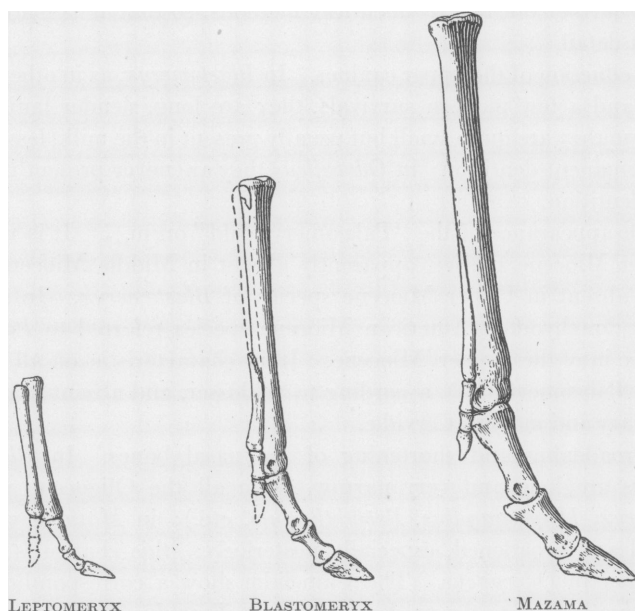


Fig. 12. Phylogeny of American Cervidæ. Fore feet, half natural size. *Leptomeryx evansi*, No. 6782; *Blastomeryx advena* No. 13015; *Mazama nemorivaga*.

gulus in dentition and general skeletal characters has been pointed out. It is, however, somewhat more primitive in dentition, and considerably more primitive in skeleton characters, although occurring in a geologically later stage. The ruminant genera from the earlier Oligocene of Europe are more primitive in dentition, but in none of the better known genera is the condition of the manus and pes such as we should expect to find in an ancestor of *Blastomeryx*. In *Prodremotherium*, although the cannon bones are less

completely formed than in *Blastomeryx*, the lateral metacarpals are much more reduced; and the same is true of the more primitive genera *Lophiomeryx* and *Gelocus*,¹ although the metapodials in these genera are not soldered

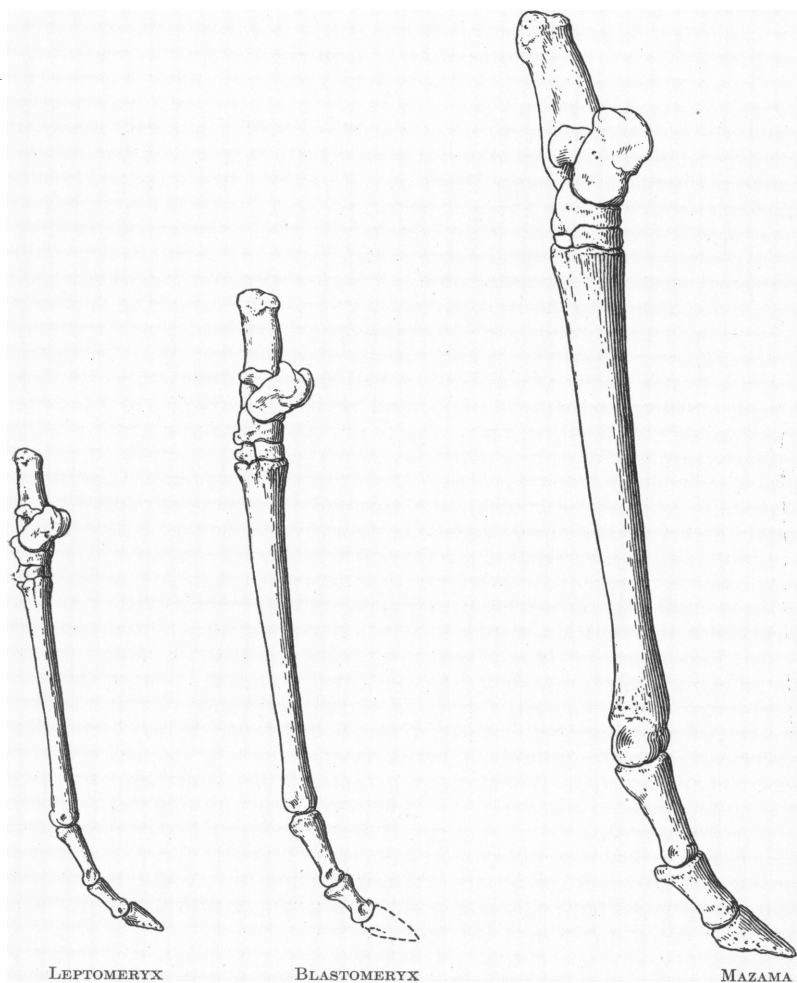


Fig. 13. Phylogeny of American Cervidæ. Hind feet, half natural size. From the same individuals as Fig. 12.

together and their distal keels are confined to the plantar surface. It appears, therefore, that *Blastomeryx*, cannot be derived from any of the known Euro-

¹ Cf. Zittel, 1893; Kowalevsky, 1876.

pean selenodonts, but represents a phylum of Cervidæ in which the reduction of the lateral metacarpals was exceptionally retarded in relation to other progressive characters. This feature, as we have seen, is distinctive of the American deer.

6. Relationship to *Leptomeryx*.

Among the American Oligocene selenodonts *Leptomeryx* appears to fulfil accurately the theoretical requirements for an ancestor of *Blastomeryx*. This interesting little genus has been placed with the Tragulines by Leidy,¹ Cope,² and Scott,³ with the Tylopoda by Rüttimeyer⁴ and by Scott⁵ in his later studies: while Dr. Schlosser⁶ has regarded it as ancestral to the Ovinæ. The present writer has dissented from all these views and regarded it as an independent offshoot of the Pecoran-Traguline stock.⁷ The skeleton characters of *Blastomeryx* throw considerable new light on the question, for they show in one phylum of Cervidæ a marked approximation to the characters of *Leptomeryx* in teeth, skull, and skeleton characters. A re-study of *Leptomeryx* brings out the fact that it has numerous indications of relationship with the Pecora, especially with the primitive Cervidæ, rather than with *Tragulus* or the Camelidæ, although they have been obscured by the broad differences which now appear to be primitive characters, partly bridged over by *Blastomeryx*. These are:

(1) The pattern of the upper molars is that of the primitive Cervidæ, with prominent mesostyle, strongly convex paracone rib, and flat metacone rib. In *Tragulus* and *Hypertragulus* the mesostyle is absent, and both external ribs developed; in *Protoceras*, *Heteromeryx*, and the earlier brachyodont Camelidæ the mesostyle is present and both ribs are usually equally developed, as they are in most modern Pecora.

(2) The lower molars have the Palæomeryx fold peculiar to the primitive Cervidæ. This fold is not present in *Hypertragulus*, *Hypisodus*, *Heteromeryx*, *Protoceras*, *Poebrotherium* or *Paratylopus*. It is present, according to Schlosser, in all the Palæomerycinae but absent in all other primitive Pecora.⁸ It is therefore not a common primitive ruminant character, nor is it found with any brachyodont dentition except in the Cervid phylum. I have not detected it in any of the Uinta selenodonts. Its presence is a strong argument for Cervid affinities.

¹ Leidy, 1869, p. 165 ("Moschidæ" = Tragulidæ of later authors, with *Moschus* included).

² Cope, 1887, p. 389.

³ Scott, 1891.

⁴ Rüttimeyer, 1883, p. 98.

⁵ Scott, 1899, pp. 15 et seq.

⁶ Schlosser, 1904, p. 90.

⁷ Matthew, 1905, p. 25.

⁸ Excepting certain Gelocidæ and early Cervinæ. Schlosser, 1902, 1903.

(3) The premolars are fairly large and their pattern is very much like that of *Blastomeryx*, only more simple and trenchant and the inner crescents of p^{2-3} more rudimentary. The first upper premolar has already disappeared, and the first lower premolar is small and one-rooted. The principal diastema in the lower jaw is in front of p_1 , the lower canine is incisiform. The upper canine is small and so far as known its great development in the primitive Cervidæ is not foreshadowed in *Leptomeryx*. In *Tragulus* the premolar pattern is much simpler and more trenchant; in the camels the premolars are much more compressed, the internal ridges fewer and differently placed, and the teeth are early reduced in number and size except p_1^1 , which are placed more anteriorly and tend to become caniniform instead of disappearing. In *Hypisodus* and *Stenomylus*,¹ which appear to have cameline affinities, p_1 is placed still farther forward and becomes incisiform.

(4) The face is moderately long and agrees very well with *Blastomeryx* in form. It does not show the broadening of the supraorbital region and extreme pinching in beneath the nasals that characterizes the camels, nor the thick, heavy muzzle of the Tragulines. The nasal bones are long and narrow, as in all primitive ruminants, but agree much more nearly with *Blastomeryx* than with *Poebrotherium*, and are entirely unlike any of the later Camelidæ but not unlike those of *Tragulus*. The basicranial region is also much like that of *Blastomeryx*, the bullæ are more inflated than in that genus, and are quite different from the types of bulla characteristic of *Tragulus* and of the camels.

(5) The neck is short and the vertebræ normal, a most important distinction from any of the Camelidæ.

(6) The fore foot is of very primitive type, the metapodials separate, the lateral digits functional, the metapodial keels incomplete. This is in marked contrast with the conditions in the modern Cervidæ, but in view of the remarkably primitive conditions in *Blastomeryx* we may expect that its Oligocene predecessors would be exceptionally primitive in the condition of the manus. On the other hand, in the camels the reduction of the lateral digits occurs very early, and long before the coössification of the median pair. To a less extent the same is true of the Traguline line, and apparently of some phyla of Pecora.

(7) The pelvis of *Leptomeryx* is much like that of *Blastomeryx* and the Cervidæ; well distinguished from that of *Tragulus* and *Hypertragulus* by the characters which I have cited in describing *Blastomeryx*.

(8) The distal rudiment of the fibula remains free, as in Pecora and Camelidæ; in *Tragulus* and its Oligocene relative *Hypertragulus*, and even in certain Bridger selenodonts of unknown affinities, the rudiment is coössified with the tibia.

¹ Peterson, 1907, Ann. Carnegie Mus., Vol. IV, (1906) p. 41.

(9) The magnum is coössified with the trapezoid and the navicular with the cuboid as in Pecora and Tragulina. In the Tylopoda they are invariably separate.

(10) The median metatarsals are coössified into a cannon bone of distinctively pecoran type, except in the incomplete distal keels. The median groove is precisely like that of *Blastomeryx*. This groove is somewhat different in form in *Tragulus*; in the Camelidæ there is no trace of it. The head of the cannon bone has the round-quadrate form of the pecora and tragulines, lacking the long plantar projection formed of the combined proximal plantar processes of the metapodials, which are especially prominent in the earlier Camelidæ but characteristic of the family as a whole. The shaft of the cannon bone is approximately symmetrical, subquadrate in section; in *Tragulus* the dorsal surface of the shaft of Mts. iii is high and crested, and of Mts. iv depressed and obliquely flattened, and the shaft has a trihedral outline.

(11) In both fore and hind feet the distal keels of the metapodials, although completely developed only on the under side, are carried forward on the dorsal side as low, flat ridges, or rudimentary keels, no trace of which appears in any of the Camelidæ. In *Tragulus* the position of the keel is much more lateral—a quite exceptional condition—in *Hypertragulus* the dorsal parts of the distal facets are uniformly convex, as in ungulates; in the successive members of the Camelid series we see the lateral convexity gradually flattened out, as generally among ungulates, but no attempt to extend the plantar keel dorsad.¹

(12) The phalanges of *Leptomeryx* are of the compressed pecoran-traguline type, notably different from those of the later camels, less so from those of *Poebrotherium*.

The above characters appear to me to show conclusively that *Leptomeryx* is of pecoran affinities, not traguline nor tylopod. The features in which it differs from Pecora and resembles either *Tragulus* or the Camelidæ appear on examination and in view of the characters and relations of *Blastomeryx*, to be all primitive conditions lost by the first and retained by the other two groups.

The presence of the Palæomeryx fold in the lower molars is distinctive of the primitive Cervidæ, according to Schlosser, and would exclude the genus from ancestral relationship to any of the Cavicorn groups.² *Leptomeryx* cannot, therefore, by Schlosser's own criteria, be ancestral to the

¹ The eversion of the distal ends of the cannon bone characteristic of the later camels, is said by Scott (1899, p. 17) to occur in a slight degree in *Leptomeryx*; but it is certainly no greater in this genus than in *Blastomeryx*, and, therefore, has no weight as evidence of tylopod relationship.

² Schlosser, 1904, p. 107.

Ovinæ, as he supposes it to be. Dr. Schlosser appears to have been the first to recognize its pecoran affinities, however, and his extensive and thorough studies of the fossil ruminants of the Old World lend especial weight to his opinion.

The above comparisons and contrasts with the Tragulines have been made with *Tragulus* and *Hypertragulus* only, excluding *Dorcatherium* because an examination of that genus leads me to believe that it is, in fact, a very primitive offshoot of the pecoran stock, having no especial relations with *Tragulus*, the common characters being simply persistent primitive features. The relations of the alleged tragulines of the European Oligocene appear to be also open to question. The exact relations of the Uinta selenodonts I am likewise compelled to regard as an unsettled question. Professor Scott is no doubt correct in regarding all of them as comparatively nearly related to each other; but I am not clear that even *Protylopus* is directly ancestral to *Poëbrotherium*, although there is a fair amount of evidence for tylopod affinities. In the other genera the relationship is far from conclusively shown to the primitive Tylopoda as distinct from primitive pecora or tragulines. Indeed it might be better in systematic arrangement to retain the Hypertragulidæ as the primitive group from which the specialized Tylopoda, Tragulina, and Pecora are derived, and to include with them all the Eocene selenodonts with tetradactyl manus, didactyl pes, slender muzzle and four crescents on the molars. This need not prevent our regarding *Leptomeryx* as of pecoran, *Hypertragulus* of traguline, and *Protylopus* of tylopod affinity.

The conclusions may be summed up as follows:

(1) *Leptomeryx* is an extremely primitive, unspecialized genus of pecoran stock.

(2) It is related especially to the primitive Cervidæ.

(3) It fulfils every structural requisite for a direct ancestor of *Blastomeryx*, and no other known genus does so.

(4) Its occurrence in the American Oligocene, contemporary with much more advanced Pecora in the Old World precludes regarding it as genetically ancestral to the Cervidæ as a whole. It may be ancestral through *Blastomeryx*, however, to the American deer.

Occurrence of Leptomeryx.—The genus appears first in the Lower White River, Titanotherium Beds. At least three species are represented (two described) by jaws and teeth, but the structure of the skull and skeleton is unknown. In the Middle White River, Oreodon Beds, *L. evansi* is the only clearly defined type, and the generic characters and comparisons are based upon this species. In the Upper White River, Protoceras and Lep-tauchenia Beds, several undescribed species are represented by jaws and

incomplete skulls. The genus is not found in the John Day, but in the Lower Rosebud occurs a large species, Fig. 11 (No 13824). with the dentition of *Leptomeryx* and intermediate in size between *L. evansi* and *Blastomeryx advena*. A smaller species with more advanced premolar dentition, *L. transmontanus*, is reported by Douglass from supposed Uppermost Oligocene beds in Montana. The skull and skeleton are unknown in these later species; the teeth show but a limited degree of approximation to *Blastomeryx*, so that it is not probable that they are exactly intermediate.

7. Interpretation of the Phylogeny.

If this phylum be regarded as approximately true in a genetic, as it is in a structural sense, we must regard the direct genetic phylum as carried through early species of the genus, probably unknown to us at present, the region of evolution of the race and its centre of dispersion lying far to the north and perhaps Asiatic rather than American. The species known to us represent successive migrations from this boreal center, driven over to the southward before the competition of the higher types evolved in the center of dispersion. These migrant types continue to evolve in certain respects, such as brain capacity, which are advantageous in any habitat, but preserve most of their primitive characters as the environmental pressure is less in amount and more variable in direction. Thus it is obvious that the modern deer of the New World, taken geographically from south to north, represent approximately those stages in the evolution of the group which we would expect to find in the Pliocene to recent formations of the Northwest. Had the connection with South America existed before the Pliocene we might expect to find, far to the south, representatives of still earlier stages. And if there were great islands adjoining South America and connected with it at times during the Tertiary we might find in them living representatives of the Oligocene or Eocene ancestors of our Cervidæ. Such is not the case, however.¹ The New World has preserved nothing of the early Tertiary fauna of the north, and the nearest equivalent stages and representatives of our Eocene and Oligocene faunæ are found in the East Indies and in Madagascar, where they represent rather the Old World divisions of the various holarctic groups of the early Tertiary.

From this point of view it seems fair to say that the genera *Leptomeryx*,

¹ The Antilles and the Galapagos and Falkland Islands might be cited as exceptions to this statement. With regard to the two former it is sufficient to say that their fauna is strictly confined to such types as might conceivably have reached the islands by transportation over sea from South America in the direction of the prevailing ocean winds and currents. Those which could not have done so are absent. The Falkland Islands were almost certainly connected with the mainland at times during the Tertiary, but their small size and the unfavorable physical conditions have prevented the survival of any of the Tertiary types such as have been preserved to our time with but little alteration in the great tropical islands of the Old World.

Blastomeryx, *Mazama*, *Odocoileus*, and the large Nearctic Cervidæ, are structurally and genetically connected but it would be incorrect and misleading to attempt to carry the line through the known species. The fossil species in successive levels in the same locality will show usually successive approximations toward the next higher generic stage. But all are approximately, not exactly, in genetic succession, and we cannot draw from them conclusions as to whether the evolution was spasmodic or continuous, constant or variable in its direction, and in our attempts to discover the underlying causes of the progress of the race, we must keep always in mind that we are dealing usually with an approximate, not an exact phyletic series.

With this reservation, which in my opinion applies equally or more emphatically to most of the accepted phyletic series of fossil mammals, I believe that we can trace the ancestry of the American Cervidæ back to *Leptomeryx*. If Professor Scott is correct in regarding *Camelomeryx* of the Uinta as ancestral to *Leptomeryx*, the series is carried one step farther back. But *Camelomeryx* cannot be directly ancestral to *Leptomeryx*, and I suspect that if it is ancestral to any of the Hypertragulidæ its affinities are rather with *Heteromeryx*, of the Lower White River.

EVOLUTION AND MIGRATION OF THE AMERICAN DEER.

The accompanying diagram attempts to illustrate the succession and southward march of the known stages of this phylum. *Leptomeryx* is the first, ranging through the Oligocene and into the earliest Miocene in the West, precluded from reaching South America by the supposed geographic isolation of that continent during the Miocene. We might look for survivors of this stage in Miocene deposits of Mexico or Central America, if these were better explored.

Blastomeryx ranges through the Miocene of the western United States, and it is possible that the later species may have reached South America, and may yet be discovered in the Pliocene of that country.

Mazama is known from the Pleistocene of South America and still inhabits that country. It should appear in the Pliocene faunæ of North America, which are as yet very imperfectly known.

Odocoileus appears in the early Pleistocene of North America and is a typically Sonoran genus in its present range.

Cervus (*canadensis* group), *Rangifer* and *Alces* first appear in America in the later Pleistocene and their typical range is holarctic.

It is hardly necessary to say that these evolutionary stages and generic ranges are approximate, not exact. They are sufficiently so to prove the-

progressive southward movement of successively higher stages in the evolution of the American Cervidæ, and to indicate their origin as on the Nearctic side of a Holarctic centre of dispersion.

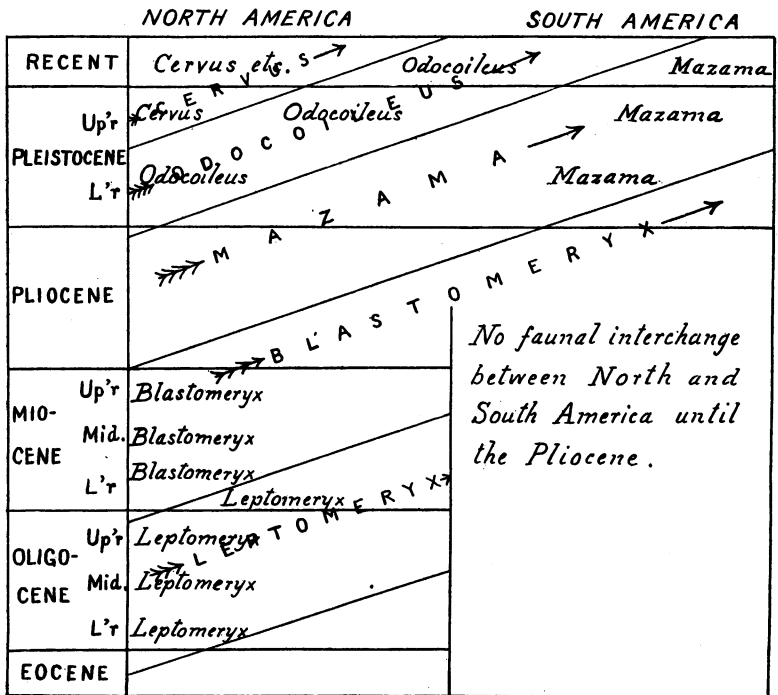


Fig. 14. Evolution and Migration of American Cervidæ.

The evolutionary history of the American Cervidæ is paralleled by that of most of the phyla of the Tertiary mammalia, as I interpret them. With a very few exceptions they can best be understood as a general movement of dispersal from a Holarctic, Nearctic or Palæarctic center of evolution. The geographic distribution of modern mammals taken by itself has long been understood in this way; and so far as the imperfect records of palæontology go, they appear to me to verify, as accurately as could be expected, the inferences from modern distribution and to indicate northern Asia as the great center of dispersion of the mammalia. Our lack of knowledge of the older Tertiary faunæ of Asia has obscured the force of this agreement, and militates against the exactness of all of our accepted phylogenies. When this gap is filled we may have exact phylogenetic series; until then they are approximate. Thus it happens that in Europe, on one side of this centre,

in America, on the other side, we have parallel series of approximate phylogenies; sometimes closer in the one country, sometimes in the other. The southern continents, cut off during the early Tertiary from the northern, developed their faunæ independently; but these faunæ originated from primitive types which are certainly present in the early Eocene faunæ of the northern world, and may quite well be regarded as a similar but earlier dispersal from a northern origin. This subject is too broad to be considered here, however.

PHYLOGENY OF AMERICAN RUMINANTS.

8. *Phylogeny of American Ruminants.*

In the diagram (Fig. 15) I have attempted to show the occurrence and approximate phylogeny of the American ruminants, together with a few of the more important Old World types. The Old World genera are in brackets, and Old World phyla in dotted lines.

9. *Key to the Classification of Ruminants.*

In the following arrangement I have indicated the primary progressive stages by numerals (I, II, III; 1. 2.) the divergent group characters by letters (A, B, C; a, b, c; α , β). The characters selected are merely those necessary for an analytical key; they are not the whole nor always the most important or distinctive characteristics of the several groups.

Dorcatherium and *Hyæmoschus* would in this arrangement fall more readily in the second division under the Hypertragulidæ, as a distinct subfamily. It will readily be understood that the horizontal (numerical) divisions are of necessity arbitrary lines. With a complete knowledge of fossil Artiodactyla every intermediate stage would appear, and the point at which the lateral digits become vestigial rather than functional is not easy to define.

The families of the higher Artiodactyla may be defined as follows:

Molars selenodont, quadricuspid.

I. Manus and pes functionally tetradactyl.

1. Upper molars with strong parastyle and mesostyle and usually a metastyle, but no external ribs on paracone or metacone. Muzzle short and broad, c' and p' stout, caniniform, diastemata short or absent

Agriochaeridæ (*Oreodontidæ*).

II. Manus tetradactyl, pes functionally didactyl. Muzzle slender, as in the following groups *Hypertragulidæ*.

1. Podial bones separate.

- a. Upper molars with parastyle, mesostyle and both external ribs prominent *Leptotragulinae*.
- 2. Navicular-cuboid and magnum-trapezoid coössified.¹
 - b. Upper molars with parastyle, mesostyle and anterior external rib prominent. Premolars well developed *Leptomerycinae*.
 - c. Upper molars with parastyle, mesostyle and both external ribs prominent. Premolars well developed *Protocerotinae*.
 - d. Upper molars without mesostyle, both external ribs prominent. Premolars simpler, trenchant *Hypertragulinae*.
 - e. Molars narrow, hypsodont, premolars much reduced, p_1 incisiform. *Hypisodontinae*.

III. Manus and pes didactyl.

A. (Tylopoda) Podials separate. I^{1-2} disappearing, i^3 , $c\frac{1}{2}$; $p\frac{1}{2}$ becoming canini-form. Principal diastema behind $p\frac{1}{2}$. Molars very narrow, premolars small, progressively reduced. Digitigrade with progressive development of plantar pad

Camelidæ.

B. Navicular-cuboid and magnum-trapezoid coössified. I^{1-3} absent. Molars broader, premolars less reduced. Unguligrade.

- 1. Distal keels of median metapodials incomplete dorsally (Tragulina).

- a. Upper molars as in *Hypertragulinae*. *Tragulidæ*.

- b. Upper molars as in *Protocerotinae* *Gelocidæ*.

- 2. Distal keels of metapodials completed dorsally (Pecora).

- a. Upper molars as in *Leptomerycinae*, premolars more or less complicated, p_1 behind principal diastema, vestigial or absent. Progressive development of antlers.

Cervidæ.

- b. Upper molars as in *Protocerotinae*; premolars more or less complicated; dentition brachyodont. Progressive development of bony bosses on the skull.

Giraffidæ.

- c. Molars usually more hypsodont, but apparently derived from same pattern as in *Protocerotinae*. Face depressed upon cranial axis.

- a. Progressive development of antlers or deciduous horns *Antilocapridæ*.

- β. Progressive development of true horns *Bovidæ*.

The Pecora and Tragulina are derivable from the higher groups of *Hypertragulidæ*, which in common with the *Camelidæ* may be derived from the *Leptotragulinae*. The *Cervidæ* are derivable from *Leptomerycinae*, the *Tragulidæ* from *Hypertragulinae*, the remaining Pecora more nearly from *Protocerotinae*. The *Hypisodontinae* are allied with the Tylopoda, and apparently not ancestral to any of the later groups.

The successive stages of specialization may be summed up as follows:

Toes 2-2	Camelidæ	Giraffidæ	Cervidæ	Bovidæ	Selenodont; upper molars 4-cusped
Toes 4-2	Tragulidæ	Hypertragulidæ	Gelocidæ	Antilocapridæ	
Toes 4-4	Oreodontidæ	Dichobunidæ	Bunodont.	Upper molars	
	Trigonolestidæ	"	"	"	6-cusped tritubercular

¹ Variable in *Protoceros*.

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