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ON A NEW PRIMITIVE DEER AND TWO TRAGULOID GENERA FROM THE LOWER MIOCENE OF NEBRASKA

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Machæromeryx tragulus, new genus and species

TYPE.—No. 20548, a skull, jaws and nearly complete skeleton.

HORIZON AND LOCALITY.—Lower Miocene (Upper Harrison beds) of Nebraska, found by Albert Thomson, expedition of 1923.

GENERIC CHARACTERS.—Small, hornless, tusked deer, related to *Blastomeryx*, but with much simpler and more trenchant premolars, somewhat more hypsodont

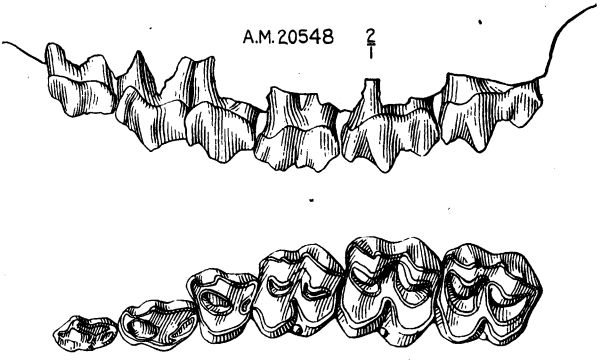

Fig. 1. *Machæromeryx tragulus*, upper teeth, crown and external views, twice natural size.

Type skeleton No. 20548, Upper Harrison beds near Agate, Nebraska.

molars, a distinct coat of cement over the cheek teeth. Neck and limbs of moderate length, anterior ribs very broad, flat and thin, sternal bones broadened but retaining also the primitive narrow, deep keel. Tusks very long, slender and compressed, with knife edge, the enameled crown of the tusk exceeding the series of cheek teeth in length. Basifacial axis moderately bent down from basicranial. line. Bullæ small, inflated and hollow, with a moderately long meatus. Cheek teeth $\frac{6}{6}$, the first upper and lower premolars absent, $p\frac{2}{2}$ simple, compressed and trenchant, considerably reduced in size. P^3 with low, narrow inner crescent, less developed than in *Blastomeryx* and its allies, more than in *Tragulus* or *Hyæmoschus*, rather less than in *Eumeryx*.[1] P_3 with rudimentary transverse crests; p_4 with well developed crests almost as in *Blastomeryx*. Molars longer-crowned than in *Blastomeryx*, the upper ones with the

[1] *Eumeryx* Matthew and Granger, 1923, from Oligocene of Mongolia.

characteristic nearly square form of the early Pecora in contrast to the oblique set in *Leptomeryx*, *Hypertragulus*, *Tragulus* or *Dorcatherium*. Mesostyle and anterior external rib distinct, posterior rib absent, as usually in primitive deer, etc. No clear evidence of *Palæomeryx* fold, but trace of it might be found on unworn teeth. Ulna separate from radius throughout, the shaft gradually decreasing from the rather broad olecranon to a slender, almost thread-like distal portion. Median metacarpals and metatarsals united, the distal ends with sharp dorsal keels as in Pecora generally, but hardly as much modernized as in *Eumeryx*. The lateral metacarpals with complete but very slender thread-like shafts as in *Blastomeryx*. Magnum and trapezoid coössified, the remaining carpals distinct; the ungual phalanges triangular in cross-section, rather short for Cervidæ.

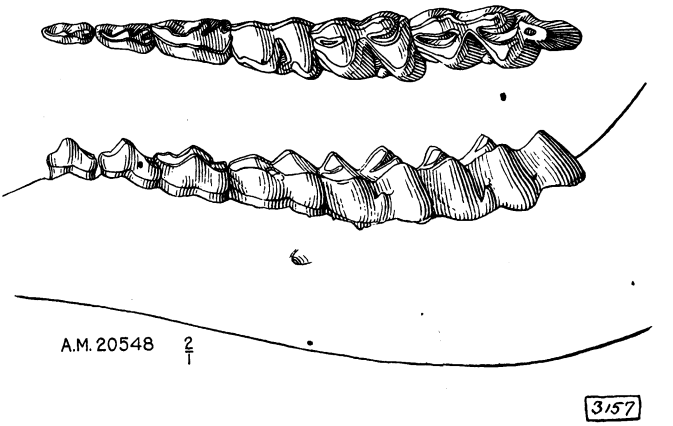

Fig. 2. *Machæromeryx tragulus*, lower teeth, crown and external views, twice natural size. From the type skeleton.

REMARKS.—This tiny ruminant is considerably smaller than the least species of *Blastomeryx*, the premolars somewhat reduced and of decidedly simpler pattern, the molars higher-crowned, and a thin coat of cement upon all the cheek teeth. It is about the size of *Leptomeryx*, but has reached the pecoran grade in the premolars, molars, reduction of lateral digits and keeling of distal ends of metapodials. These characters separate it from Tragulidæ and *Hypertragulus*, with in addition a different construction of molars.[1] *Hyæmoschus*, *Dorcatherium* and the European Tertiary "Tragulidæ" are all in the earlier stage as respects premolar and molar construction, distal keeling of metapodials, etc.

Although evidently a near relative of *Blastomeryx*, the extraordinary size of the tusks, reduction of premolars, higher-crowned molars and

[1] *Vide* Matthew, 1902, 'The Skull of *Hypisodus*, the Smallest of the Artiodactyls, with a Revision of the Hypertragulidæ, Bull. Amer. Mus. Nat. Hist., XVI, pp. 315, 316.

cementing of the teeth are sufficient to distinguish it generically. It might be ancestral to Lull's *Aletomeryx* (from an unknown but probably later horizon), but if Lull's reconstruction of this genus be correct, there are considerable differences, including the complete loss of the tusks. Lull, however, points out that there is no direct proof of the absence of tusks in his genus. It is inferred from their non-occurrence in the large series of jaws, fragments of skulls and bones upon which the genus was based. I suspect that a careful restudy of *Aletomeryx* in comparison with our complete skeleton might show a nearer agreement. The suggestion may be made in any case that *Machæromeryx* is an early stage with some affinities to *Merycodus* and *Antilocapra*, although less clearly defined than in *Aletomeryx*. The evidence is unsufficient to warrant placing it in any definitely ancestral position.

This species is the smallest of the true Pecora, and represents, along with *Blastomeryx advena*, *primus* and *olcotti* and *Dyseomeryx marshi*, the earliest invasion of that group into America.

The geological horizons of this and related species are shown in the table, pages 5 and 6.

Nanotragulus skull

TYPE.—*N. loomisi* Lull, based upon a specimen from the Lower Harrison.

Lull places the genus in the Hypertragulidæ, but states that "it is not clearly derivable from any known Oligocene form except possibly *Hypisodus*." He distinguishes it from *Hypertragulus* by "the much smaller size and the character of its premolars," and compares it also with *Leptomeryx*, *Merycodus* and *Stenomylus*.

Two specimens in our collection are referred to *N. loomisi*, No. 13821, an incomplete skull and lower jaws, and No. 13012, fragments of lower jaws, from the Lower Rosebud beds of South Dakota, near American Horse Creek and Porcupine Creek respectively. Comparison of these with skulls and jaws of *Hypertragulus calcaratus* from South Dakota and Colorado *Oreodon* beds shows that Lull's genus is quite nearly related. It may be retained as distinct, although upon different grounds from those specified by Lull. The size is almost the same as in *H. calcaratus* and the differences in the premolars are of rather minor character. The molars, however, are notably more hypsodont, and the set of the pairs of crescents less oblique; there is no internal basal cusp between the inner crescents. P^3 differs in the absence of any distinct inner cusp, although the inner root is well developed. *Hypertragulus calcaratus* has a distinct although small inner cusp on p^3; in *Hypertragulus hesperius* it is variable, sometimes well developed, sometimes wholly absent. The tympanic bulla is much larger than in *H. calcaratus* or *hesperius*, overlapping on the paroccipital process behind and the foramen ovale in front; yet the inferior crest of the petrosal, plastered against the basioccipital, is still visible outside (internal to) the inner border of the bulla.

The height and narrowness of the molar crowns, size of bulla and the less defined or constant differences in the premolars serve to distinguish the genus.

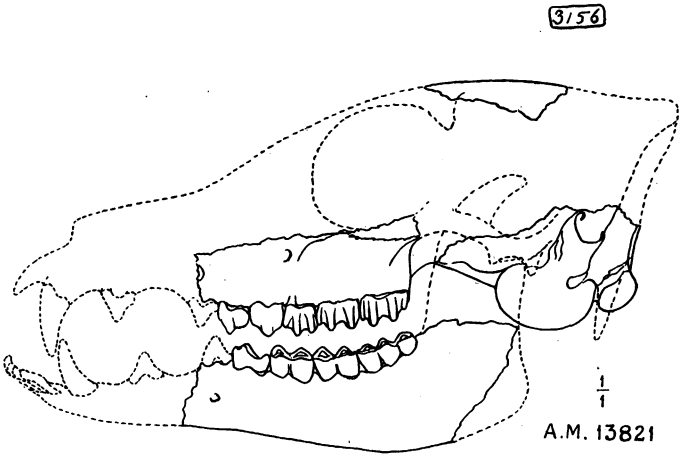

Fig. 3. *Nanotragulus loomisi*, skull and jaws, natural size; restored from No. 13821, Lower Rosebud beds near American Horse Creek, Pine Ridge, S. Dak.

The restored outlines are based chiefly on skulls of *Hypertragulus calcaratus* of the White River in the Amer. Mus. Coll., which differs from *Nanotragulus* in smaller bullæ and shorter-crowned molars, but is nearly related, probably ancestral.

To this genus is to be referred *Hypertragulus ordinatus* Matthew, 1907, distinguished by the somewhat larger size and absence of any diastema between p_2 and p_3. Skull unknown.

Leptomeryx obliquidens Lull

No. 13824, an upper jaw with p^2-m^2 well preserved, is slightly smaller than Lull's type, which is a poorly preserved skull and jaws from the *Protoceras* beds. The molars, however, do not show the markedly oblique set of the crescents noted by Lull in his type. The present specimen is from Lower Rosebud beds near No Flesh Creek, Pine Ridge Indian Reservation, S. Dakota.

Lull does not compare his type with *L. drummondanus* Douglass from Montana, which, however, does not seem much different from *L. evansi*. Other fragmentary specimens from the Lower Rosebud are smaller than No. 13824, but still notably larger than *L. evansi*. I am unable to see any progressive changes in the construction of the premolars such as Douglass has noted in *L. drummondanus*, but his description of them applies to our specimens of *L. evansi*, so that it may not be a valid species character. At present it is only possible to say that the *Leptomeryx* phylum survived into the Lower Rosebud horizon, its known range being the same as that of the hypertragulines.

The table shows the geologic range of American traguloid genera from the *Titanotherium* beds to the Lower Harrison. The Uinta genera referred to the Hypertragulidæ are omitted, pending a restudy of their

GEOLOGICAL OCCURRENCE OF HYPERTRAGULIDÆ, PRIMITIVE CERVIDÆ AND ANTILOCAPRIDÆ IN NORTH AMERICA

EQUID ZONES	OLIGOCENE					MIOCENE										PLIOCENE	PLEISTOCENE		
	Mesohippus		*Miohippus*			*Parahippus*			*Merychippus*			*Hipparion*				*Equus*			
FORMATIONS	*Titanotherium*	*Oreodon*	*Leptauchenia*	John Day	Lower Rosebud	Lower Harrison	Upper Harrison	Upper Rosebud	Lower Sheep Creek (Mascall)	Lower Snake Creek (Pawnee Creek)	Barstow and Santa Fé	Valentine	Upper Snake Creek (Republican River)	Thousand Creek	Blanco	Eden	Sheridan	Later Pleistocene
HYPERTRAGULIDÆ																			
1. *Hypertragulus*	×	×		×															
Nanotragulus[1]					×	×													
2. *Hypisodus*		×																	
3. *Heteromeryx*	×																		
Portoceras			×																
Syndyoceras						×													
4. *Leptomeryx*	×	×	×		×	×													

[1]Lull, R. S., 1922, Am. Jour. Sci., IV, p. 116.

GEOLOGICAL OCCURRENCE OF HYPERTRAGULIDÆ, PRIMITIVE CERVIDÆ AND ANTILOCAPRIDÆ IN NORTH AMERICA—(*Continued*)

EQUID ZONES	OLIGOCENE					MIOCENE									PLIOCENE	PLEISTOCENE		
	Mesohippus		*Miohippus*			*Parahippus*			*Merychippus*			*Hipparion*				*Equus*		
FORMATIONS	*Titanotherium*	*Oreodon*	*Leptauchenia*	John Day	Lower Rosebud	Lower Harrison	Upper Harrison	Upper Rosebud	Lower Sheep Creek (Mascall)	Lower Snake Creek (Pawnee Creek)	Barstow and Santa Fé	Valentine	Upper Snake Creek (Republican River)	Thousand Creek	Blanco	Eden	Sheridan	Later Pleistocene
CERVIDÆ																		
Machæromeryx							×											
Blastomeryx							××	×	××	××	×	××	××					
Dyseomeryx							×		××	××		×××	×××					
Dromomeryx										××	×	×××	×××					
Aletomeryx[1]												×××						
ANTILOCAPRIDÆ																		
Merycodus									×	×	×	×	×					
Sphenophalos														××				
Illingoceras														××				
Capromeryx																	×	
Tetrameryx[2]																	×	
Neomeryx[3]																		×
Antilocapra																	×	×

[1]Lull, R. S., 1920, Amer. Jour. Sci., L, p. 85.
[2]Lull, R. S., 1921, Am. Jour. Sci., II, p. 163.
[3]Parks, W. A., 1925, Bull. Geol. Soc. Amer., XXXVI, p. 432.

affinities. True Pecora (Cervidæ) appear suddenly in the Upper Harrison (*Blastomeryx*, *Dyseomeryx*, *Machæromeryx*) and Antilocapridæ in the Mascall (*Merycodus*).[1] In both cases they appear to be an invading group, not derived from autochthonic predecessors. *Odocoilæus* may also be an invading type from the north; it is not recorded earlier than the Pleistocene; but in this instance the evidence is unconvincing, as there are several imperfectly known deer-like animals in the American later Miocene and Pliocene which may when better known be shown to be ancestral.

The evidence conforms to the viewpoint taken by the author in 1907 that the American deer were derived by a succession of invasions from a northern center of dispersal, and that certain common peculiarities in their succession were due to their being derived from the American side of this Boreal center. This view, although plainly stated (*loc. cit.*, p. 556), has been persistently misunderstood by writers who cling to the older palæogeographic methods of interpretation, and I have been repeatedly cited as believing that the American Cervidæ form an independent line of descent, distinct from the beginning of the Oligocene from the Old World Cervidæ. Such a conclusion would be quite untenable in view of the close osteological affinities between the New World and Old World genera at each successive stage in their geological succession. They can be explained only by a succession of invasions. But the evidence appears to me to point not to migrations from western Europe to the United States or *vice versa* (as the older interpretation explained it), but to a succession of waves of dispersal into these known regions from an intermediate region. This intermediate region comprises northeastern Europe, northern Asia, Alaska and Canada, and of its Tertiary faunal history we have no record. The recent discoveries in Mongolia afford some aid, however, in locating the center of dispersal of different groups, for the Mongolian faunas would be closely related geographically to a north Asiatic center of dispersal, but not to a northern American center.

Preliminary studies upon the Mongolian faunas indicate, however, that the environmental factor of dispersal which has been neglected in nearly all palæogeographic studies[2] has played a very important part. This is, for land animals, the distribution of rainfall and consequently of

[1]Suddenly, that is to say, not preceded by nearly related more primitive species in the horizon immediately below. Phyla that are so preceded are considered autochthonic. It is of course possible that absence of such preceding stage of the phylum may be due to the accident of collecting; but this is very unlikely in the present instance, as the distribution data are based upon the records of over 300 jaws of Pecora from these horizons in the American Museum collection.. Most of them are from the three Snake Creek levels.

[2]Case's studies of the Permian land vertebrates may be noted as an exception.

forest, plain and desert conditions. (In marine faunas the amount of tide and location of ocean currents, controlling the temperature of the surface waters, would play a correspondingly important part in the past, as they do in the present distribution.) Berry has quite properly emphasized the important part played by the rain-forests in limiting or facilitating dispersal of different races of mammals.

It will be necessary, therefore, to recognize that the evolution and dispersal of the ruminants have been largely controlled by the primary adaptation of their ancestral group in the early Tertiary and the diverse adaptations of the several families in the later Tertiary; by the distribution of forest, plain and desert in the successive Tertiary epochs, in addition to the land connections and ocean barriers of the older palæogeographers; by the progressive refrigeration of the polar regions during the Tertiary, and cyclic changes of climate in previous periods, which I emphasized ten years ago.[1] I hope to essay an interpretation along these lines when the Mongolian faunas have been more fully studied. For the present it will be sufficient to note that *Archæomeryx* of the Mongolian Upper Eocene is the nearest approach to an ancestral type for the tragulines, and *Eumeryx* of the Mongolian Middle Oligocene for the Pecora.

[1] 1915, 'Climate and Evolution,' Ann. N. Y. Acad. Sci.