Article VII.—A COMPLETE SKELETON OF MERYCODUS.

By W. D. Matthew.

Plate III.

The following description is based on a nearly complete skeleton, very perfectly preserved, found in the Middle Miocene (Pawnee Creek Beds) of northeastern Colorado, by Mr. Barnum Brown of the American Museum Expedition of 1901. The expense of this expedition was defrayed by the generosity of the late Mr. W. C. Whitney. My special acknowledgments are due to Professor Osborn for the privilege of describing this very pretty and interesting animal.

Two groups of the higher ruminants (Pecora) are found in the American Miocene, each combining characters now peculiar to distinct families. The first includes small hypsodont species related to the antelopes, but with branching, deciduous antlers like those of the deer. The second includes brachydont species, mostly of large size, related to the deer, but with horn-cores or antlers unbranched, probably non-deciduous.[1] The hypsodont group includes *Merycodus* (= *Cosoryx*) and the true *Blastomeryx;* the brachydont includes a number of species which have been variously referred to *Dicrocerus, Blastomeryx*, and *Palæomeryx*, and which I leave provisionally under the last-named genus. Neither group can be regarded as directly ancestral to any modern animals; they represent side branches which have not survived.

Most authors have grouped these Miocene genera, along with the European *Palæomeryx, Dicrocerus, Amphitragulus*, and *Dremotherium*, under the Cervidæ, either as allied to the Muntjac (*Cervulus*) or without particularizing their position. Schlosser refers the European genera to a distinct family, the Palæomerycidæ [2]; and would no doubt refer the brachydont American species with them. In view of the relationship of

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[1] But the evidence in regard to this point is not positive.
[2] Proposed by Lydekker in 1883, without definition.—Ind. Tert. and Post. Tert. Vert., II, v, p. 32.

Merycodus with *Antilocapra*, as shown by Professor Scott in 1890 and abundantly confirmed by the complete skeleton here described, it is necessary to separate *Merycodus* and *Blastomeryx* from the Cervidæ and place them as a distinct family or as a subfamily of Antilocapridæ. The former course seems best to express their relationships as at present understood, for the one definite character (the nature of the horns) which separates Antilocapridæ from Bovidæ is not more important than the horn distinction which separates *Merycodus* from either group. Nevertheless, in the writer's opinion, the clearness of this distinction will be broken down when we have a better knowledge of the various allied fossil types, and it will probably then be necessary to unite Merycodontidæ and Antilocapridæ into a single family.

Assuming for the present that the Merycodonts are entitled to rank as a family, the classification will be as follows:

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                                        ( Bovinæ.
                           ┌ Bovidæ    ⟨ Caprinæ.
                           │            ( Antilopinæ, etc.
            ┌ typica      ⟨ Antilocapridæ.
            │              │ MERYCODONTIDÆ, fam. nov.
Booidea ⟨                 └ Giraffidæ  { Sivatheriinæ.
            │                             Giraffinæ.
            │                            ┌ Palæomerycinæ,
            └ cerviformia   Cervidæ     ⟨ Moschinæ.
                                         │ Cervulinæ.
                                         └ Cervinæ.
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BOÖIDEA TYPICA. Teeth hypsodont, premolars reduced, basifacial axis highly inclined to basicranial. Lateral toes much reduced or absent. Horns usually supra-orbital.

> *Bovidæ.* Permanent unbranched horns.
> *Antilocapridæ.* Deciduous horns with permanent cores.
> *Merycodontidæ.* Deciduous branching antlers.
> *Giraffidæ.* Rudimentary permanent horns of primitive type.

BOÖIDEA CERVIFORMIA. Teeth brachydont, premolars large, basifacial axis nearly parallel to basicranial. Lateral toes usually better developed than in preceding group. Horns postorbital.

> *Cervidæ.* Deciduous branching antlers.

The Giraffidæ do not, in fact, fit very well into either of these divisions, being largely an intermediate group. They are regarded by authors as referable rather to the typical Boöidea than to the deer.

MERYCODONTIDÆ, fam. nov.

1. MERYCODUS. Molars, especially m_3, hypsodont. Antlers of two or three tines, without brow tine, forking dichotomously or nearly so. Lateral toes greatly reduced, distal rudiments with phalanges only, no trace being left of metapodials.

M. necatus. $P_{\overline{2}}$ very small, teeth much compressed, antler forked near base. Upper Miocene.

Type, a lower jaw from Bijou Hill, Missouri River. Another specimen figured by Leidy, has p_2–m_3, 53 mm. Antlers and associated jaws from New Mexico, figured by Cope. Upper Miocene.

No. 9825, lower jaw from Little White River, South Dakota. Probably *Cervus warreni* Leidy can be referred here.

M. furcatus. Teeth as in preceding species, antler forked high up. P_2–m_3, 55 mm. Upper Miocene.

Type (*Cosoryx furcatus*), an antler from Niobrara River figured by Leidy. Antlers and associated jaws from New Mexico figured by Cope.

Restoration of the skeleton figured by Scott.

No. 8497, back of skull with antlers and parts of skeleton. Nebraska.

M. osborni, sp. nov. P_2 larger, teeth less compressed, antler forked high up, flattened at fork. P_2–m_3, 50 mm. Middle Miocene.

Type, No. 9476, complete skeleton, mature. Colorado.

No. 9475, fragmentary skeleton, young adult. Colorado.

Nos. 9473, 9474. Feet, etc. Colorado.

M. ? ramosus. Teeth shorter-crowned, p_2 larger, molars with basal tubercle between external columns. P_2–m_3, 50 mm. Upper Miocene.

Type, antler and jaw (association doubtful) from New Mexico.

No. 8561, lower jaw, from Nebraska.

M. teres   { Large species, teeth not known, of entirely uncer-
" *trilateralis* {   tain position. Upper Miocene.

2. BLASTOMERYX. Teeth less hypsodont, molars with anteroexternal cingular cusp, and basal tubercle between external columns.

B. gemmifer. Smaller than any of the above species, p_2–m_3, 42 mm. Middle Miocene.

Type, a lower molar, Am. Mus. No. 8301, from Colorado.

No. 9449, lower jaw, hind leg, etc., from Colorado.

B. wellsi, sp. nov. Larger than *B. gemmifer*, premolars more reduced. P_2–m_3, 1150 mm. Upper Miocene.

Type, a lower jaw, No. 9823, from Little White River, South Dakota.

3. CAPROMERYX. Teeth more hypsodont, crowns as long as in *Antilocapra*, but retaining in part the more primitive premolar pattern of *Merycodus* and *Blastomeryx*. Only the lower jaw is known. Pleistocene.

C. furcifer. Size of *Merycodus*. P_2–m_3, 52 mm.

Type, No. 2771, lower jaw, from Hay Springs, Nebraska. Pleistocene.

ANTILOCAPRIDÆ.

Antilocapra americana is the only species generally recognized. Pleistocene and Recent.

CERVIDÆ.

PALÆOMERYX. Teeth very brachydont, with accessory basal cusps on molars, and "Palæomeryx fold" on lower molars. Typical species supposed to have been hornless, but referred species bear simple antlers. Three premolars in upper and in lower jaw.

P. kaupi, P. bojani, P. eminens. Large species, considered on very uncertain evidence to have been hornless.

P. meyeri. Smaller, with simple antlers.

The above species are from the Miocene of Europe. The American species provisionally referred to the genus are:

P. borealis Cope. P^2–m^3, 79 mm. Antlers supra-orbital, and, as far as known, unbranched, without burr (hence ? non-deciduous), velvet-covered.

Type, a horn and part of a skull from the Deep River Beds (Smith Creek), Montana, No. 8132. Skulls and various fragments of skeletons from the same horizon and locality, and jaws and fragments of skeleton from Pawnee Buttes, Colorado, are referred to this species.

P. antilopinus Scott. P^2–m^3, 79 mm. Type, a skull and fragmentary skeleton from the same locality as the type of *P. borealis*.

P. americanus Douglass. P_2–m_3, 80 mm. Size of preceding species, with which the describer thinks it may be identical.

Type, a lower jaw.

P. madisonius Douglass. About ten percent larger than the preceding species.

Type, part of a lower jaw with three true molars.

Other larger and smaller species are indicated by fragmentary material in the American Museum and other collections, but I refrain from naming them until more complete specimens are available.

Merycodus *Leidy.*

This genus has been described from antlers and jaws by Leidy and Cope, and from incomplete skeletons by Scott and Douglass. The study of the complete skeleton and various fragmentary skeletons in the American Museum collections, and the excellent figures and descriptions of the authors above named enable us to present a fairly complete idea of its characters. Following is a summary of the more important ones:

1. Antlers supra-orbital, deciduous, branched, three-tined in mature, two-tined in younger adult, probably single-tined or absent in earlier stages. Branching dichotomous or nearly so, brow tine absent. Antlers provided with burr.
2. Skull with basifacial axis much depressed on basicranial. Cranium shortened, orbits very prominent.
3. Teeth hypsodont, most nearly resembling those of *Antilocapra*, but retaining certain primitive characters.
4. Lateral toes on both fore and hind feet represented by tiny vestiges of the three phalanges.
5. Detailed characters of vertebræ and limb bones nearest to *Antilocapra*, but somewhat less specialized in most respects.

The above is a curious combination of deer and antelope characters. Two explanations offer: Either *Merycodus* was a deer which paralleled the antelopes in every detail of its skeleton structure, skull, and teeth, or else it was, like *Antilocapra*, an antelope separated from the main line at a date sufficiently early for it to have developed a distinct type of horn structure, namely, antlers in place of deciduous or permanent horns. The former view involves a parallelism too exact and uniform between unrelated types to be at all probable. If the latter view be taken we must regard *Merycodus, Antilocapra*, and the true antelopes as representing three branches of a primitive stock, divergent in horn structure, but parallel in other characters. In theory, if *Antilocapra* deserves to be placed in a family separate from the antelopes and Bovidæ, *Merycodus* has an equal claim. But the various imperfectly known related types from the Loup Fork and Pleistocene of the West are more or less intermediate, and combine in varying degree characters now peculiar to deer, antelopes, and
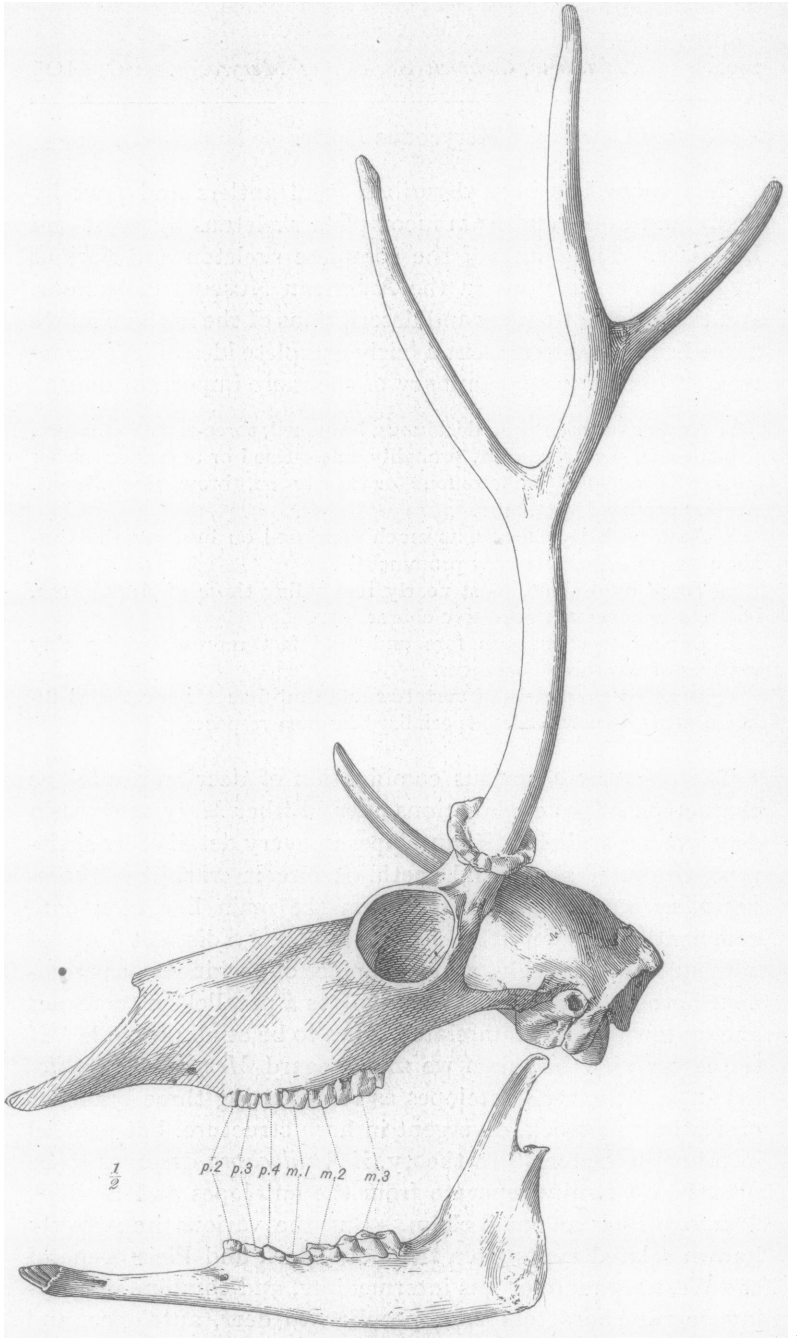
Fig. 1. *Merycodus osborni*. Side view of skull and lower jaw, half natural size. Type specimen, Middle Miocene, Colorado. The anterior part of the skull is mostly restored in plaster, indicated in the drawing by cross-hatching, and the face has been made too long and too heavy.

pronghorns.   The most convenient arrangement seems to be
to leave the very brachydont types, with their European
allies, in the Cervidæ, and to consider *Merycodus* with its
allies, *Blastomeryx* and *Capromeryx*, all hypsodont types, with
reduced premolars, high basifacial angle, and unquestionable
antelopine affinities in skeleton details, either as a distinct
family, or a subfamily of Antilocapridæ.

Merycodus osborni, sp. nov.

Type, a nearly complete mounted skeleton, No. 9476, from the Middle
      Miocene (Pawnee Creek Beds) of northeastern Colorado.
Cotype, a fragmentary skeleton, No. 9475, from the same formation
      and locality.
CHARACTERS: *Antlers* three-tined in mature, two-tined in a younger
      adult, bifurcate some distance above burr, and the posterior
      branch again bifurcate; considerably flattened and expanded at
      each bifurcation.
         Teeth less compressed than in *M. furcatus* and *M. necatus*, pre-
      molar not reduced in size.
         Fore and Hind feet with vestiges of lateral phalanges, but none
      of the lateral metapodials.

The principal characters of this species are derived from the
nearly complete skeleton of an individual in which the molars
are very much worn.   The first true molar in each jaw is worn
down to the roots, and the others correspondingly.   This
specimen gives the characters of the species in maturity.   The
second skeleton has the antlers, upper and lower jaws, fore
and hind feet, and some limb-bones and vertebræ in good
preservation, and after a careful comparison of all these parts
I have no hesitation in placing it in the same species, especially
as it is from the same horizon and locality.   It is of a younger
but adult individual, the last molar being fully protruded and
moderately worn.

SKULL.—The muzzle anterior to the orbits had been ex-
posed and weathered out when found, and is represented only
by a few fragments, including most of the teeth and nasal
bones.   There is therefore some margin of uncertainty as to
just how much the *basifacial axis* is inclined to the basicranial
axis, but the angle was certainly not less than in *Antilocapra*,

and appears to have been somewhat greater. The *orbits* are large, very prominent, and wide apart, directed chiefly laterally and a little upward. I have seen no modern ruminant skulls in which the orbits are quite so prominent. The *antlers* are the most striking feature of the skeleton; they project from the upper posterior corner of the orbit as in *Antilocapra*
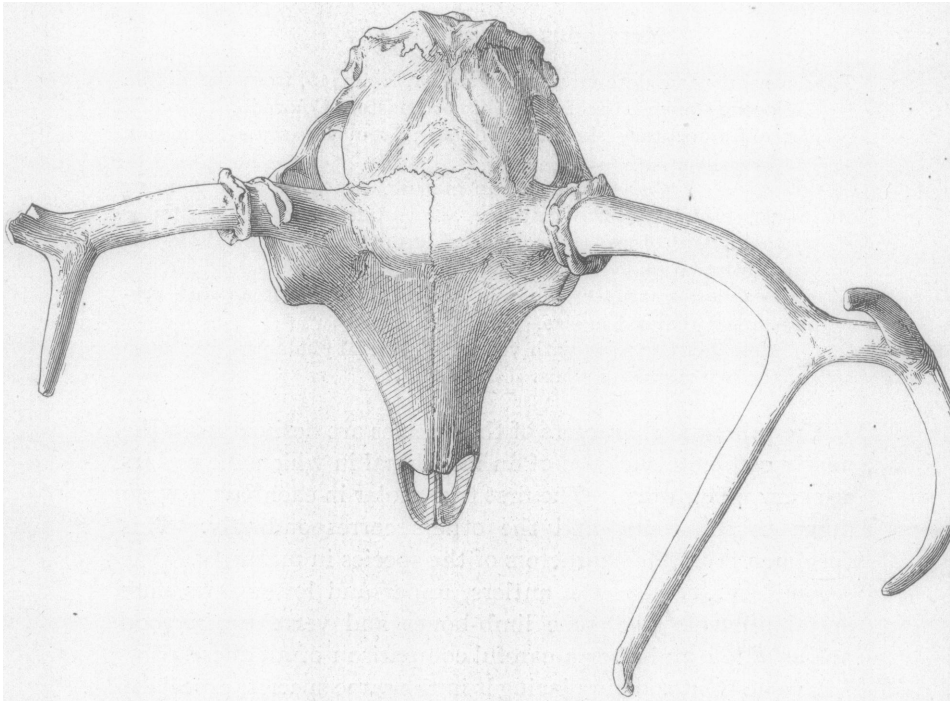

Fig. 2. *Merycodus osborni.* Superior view of skull and antlers, half natural size. Type specimen.

and most of the true antelopes, not from the cranial vault as in the deer. One of them has sustained an injury during the lifetime of the animal; the uninjured antler is directed outward, backward, and upward about equally, being thus intermediate in direction between antelope horns and deer antlers. Its total length on the curve is 300 mm., or approximately one and two thirds the length of the skull. A burr at

18 mm. from the base divides the beam from the stock, but there is no distinction in texture between the two, and where parts of the burr were removed during the preparation of the specimen, it was impossible to determine where the burr had been from any mark, scar, or change of texture on the beam beneath.   The beam continues without branching for 100 mm., curving upwards; it then forks into two almost equal branches, the upper and somewhat smaller branch continuing simple to a length of 120 mm., the lower forking again at a distance of 55 mm. into anterior and posterior tines.   The smaller posterior tine projects backward and upward to a length of 65 mm., having some upward curvature; the larger anterior tine projects upward 87 mm., with a strong inward and backward curvature.   These distances are measured on the chord of the arc, except the total length of the antler. At each bifurcation the antler is considerably flattened and spread; elsewhere it is round-oval in section.

The right antler has been injured during the lifetime of the animal, with the result that the beam is smaller than the left,
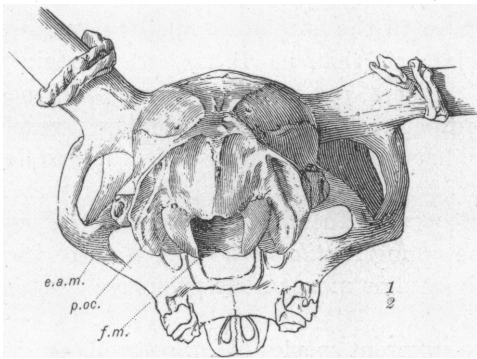

Fig. 3. *Merycodus osborni.* Posterior view of skull showing injured right antler.   Type specimen.

Fig. 4. *Merycodus osborni.* Antler of right side of cotype, No. 9475. External view, half natural size.

bent down so as to project horizontally outward, and forked at 55 mm. from the burr, the upper branch the smaller.   The main branch is broken off just beyond the fork; this probably occurred after death.   But to judge from appearances, the

whole antler was dwarfed by the injury during life, which is also indicated by a second burr formed proximally to the normal burr, and encircling obliquely the upper part of the stock, becoming continuous with the normal burr on the under side. Probably the injury bent down the antler, breaking the stock, or at least the upper part of it, just within the burr, but leaving the velvet unbroken. A second burr would naturally be formed proximal to the break after it was repaired, and mean time the blood supply would be checked to some extent and the size of the antler correspondingly dwarfed.

The cotype illustrates a younger stage in the ontogeny of the antler, which is about 70 mm. in length, the beam flattening and forking at a distance of 40 mm. into two nearly equal tines, each about 40 mm. long.

The *frontals* in the type are strongly convex from side to side as well as anteroposteriorly—more convex than in the young pronghorn, which offers the nearest comparison. This convexity and the large, strongly projecting orbits accentuate the hollow in which the supra-orbital foramina are set, antero-internal to the bases of the antlers.

The *cranium* is short, as in the antelopes, apparently more inclined to the basifacial axis than in *Antilocapra*, certainly much more so than in the deer, resembling the true antelopes most nearly in this respect. The auditory bulla is much larger than in the pronghorn, almost as large as in the gazelle, and the posterior part of the zygomatic arch is less reduced in length than in *Antilocapra*. In both these respects *Merycodus* approximates the young *Antilocapra* more than it does the adult, and probably retains more of the primitive characters of the group.

Another cranium of a different species (*M. furcatus*), coming from a higher horizon, illustrates the characters of a younger individual. In this the antlers are about as much developed as in the cotype of *M. osborni*, but judging from the cranial sutures and epiphyses of the bones, the individual was considerably younger; the teeth unfortunately are not preserved. These antlers correspond almost exactly in form and size with the typical antler of *M.* (*Cosoryx*) *furcatus*, except that the

burr is present. They are placed nearly over the orbit and directed upward; also they are less flattened out at the bifurcation than in *M. osborni*, and the beam is longer than in the younger individual of that species. The cranium, compared with the mature type cranium of *M. osborni*, shows less prominent occipital crests, the occiput sloping forward rather than backward. The frontals are less arched, the orbits less prominent, the distance between the glenoid and occipital condyles is greater, and the tympanic bulla is larger. All the cranial differences appear to me due to the *furcatus* skull having belonged
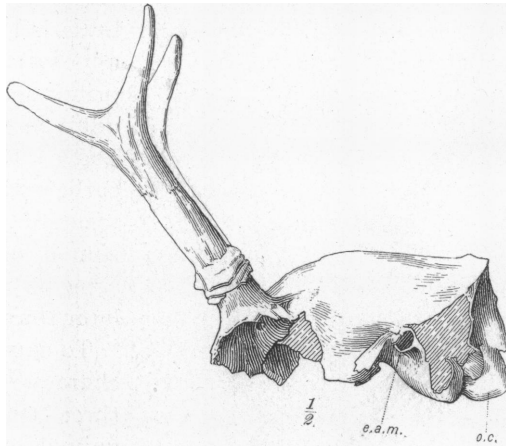
Fig. 5. *Merycodus furcatus.* Skull and antlers, side view, half natural size. No. 8497, Upper Miocene, Republican River Basin, Nebraska.

to a younger animal. All are shown by young antelopes and pronghorns when compared with older individuals of the same species; in all of them the mature *M. osborni* approaches *Antilocapra*, and especially the young *Antilocapra*, more nearly than does the young *Merycodus* from the later Miocene, and departs further from the primitive Cervid characters. The true specific distinctions between *M. osborni* and *M. furcatus* are noted elsewhere in this paper.

A still younger specimen of *Merycodus* is the skull and fragmentary skeleton described by Douglass under the name of *Cosoryx agilis*. This individual was immature, the last molars not yet fully protruded, and the milk dentition just about to be shed. The epiphyses of this specimen, which Mr. Douglass kindly permitted me to examine, are mostly separate. There are no antlers, for which reason Mr. Douglass considers it a female, but it is not improbable that the antlers would not

have appeared in the male at this time of life, so that the sex is indeterminate. The convexity of the frontals behind the orbits is not so great as in the *M. osborni* type. The occipital crests a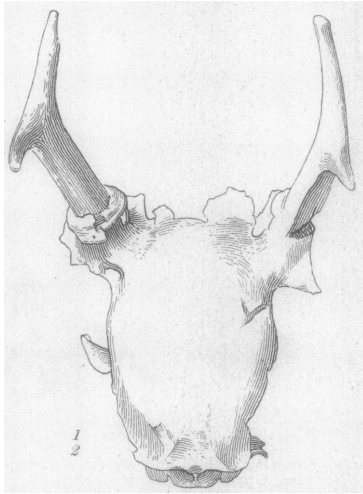re less prominent, the occiput slopes more forward, the orbits are not so wide, the bulla is larger, and the whole appearance of the skull more primitive than in the young adult *M. furcatus*, mentioned above, thus illustrating an earlier stage in the development of the skull. Its horizon is probably about the same as that of *M. furcatus*, later than that of *M. osborni*.

Fig. 6. *Merycodus furcatus.* Skull seen from above, one half natural size. No. 8497, Upper Miocene, Republican River Basin, Nebraska.

To sum up the above skull characters: The antlers are three-tined in the mature animal and two-tined at a younger adult stage, probably unbranched or absent in juvenile stages. They have no brow tine, and branch dichotomously at some distance from the base, the inferior branch again forking. They were deciduous, quite probably annually renewed. All that have been found are smooth-surfaced, as though covered by velvet during life; this condition is also indicated by the character of the burr in all known specimens; this may be best explained by supposing that these deer frequented the plains and watercourses only in spring and summer, while the antlers were still in the velvet, and that during the autumn and winter, when the antlers would be bare, they retired to the higher land, where, of course, their remains are not preserved, on account of the absence of sediment in which they could become buried.[1]

The skull shows progress from the little-altered cervine type towards (and in some respects beyond) the more specialized

[1] I am indebted to Mr. Madison Grant for this suggestion.

pronghorn and antelope type, in the shortening of the cranial region, reduction of the bullæ, bending down of the facial region, and prominence of the orbits. In the last two characters *Merycodus* is more specialized than *Antilocapra*, and the young *Merycodus* resembles the adult *Antilocapra;* in the first two, *Antilocapra* is the more specialized, and the adult *Merycodus* resembles the young *Antilocapra.*

Teeth. — The teeth of *Merycodus* have been carefully and accurately described by Leidy, Cope, and Scott,.so that it is unnecessary to give a full description here. Their most im-portant characteristics are as follows:

Molars and premolars much more hypsodont than in any Cervidæ, considerably less so than in *Anti-locapra* and most true antelopes. The anterior premolars and anterior molars are less hypsodont in
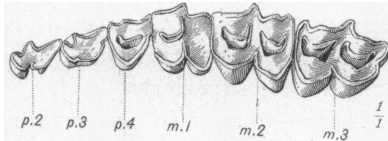

Fig. 7. *Merycodus osborni.* Upper teeth, crown view, natural size. No. 9475. Middle Miocene, Colorado.

proportion to the posterior ones than in the pronghorn, and the milk teeth are comparatively short-crowned. The lower premolars retain the ancient pattern much as is seen in *Leptomeryx* and *Poëbrotherium*, their internal ribs being separated by open valleys, instead of uniting to enclose a
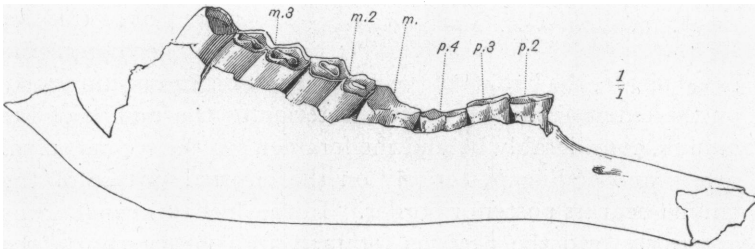

Fig. 8. *Merycodus osborni.* Lower jaw, external view, natural size. No. 9475. Middle Miocene, Colorado.

fossa, as they do for the most part in *Antilocapra* and the true antelopes. This primitive condition is largely retained in the Cervidæ, but the form of their premolars is

quite different. It appears in the second and third milk pre-molars of *Antilocapra*, although lost in the permanent teeth. In the *Merycodus* teeth here figured the premolars are too much worn to show this character, but it is equally seen in *Blastomeryx* and *Capromeryx*, and may be observed in figures 18 and 20. The upper premolars show an analogous incompleteness in the inner crescents, except of the fourth.

VERTEBRÆ. — *Atlas.* Length the same proportionately as in *Antilocapra* and *Odocoileus.* The cotyli are wider than in either genus, the transverse wings more expanded anteriorly. In other respects it most resembles *Antilocapra;* the cotyli and the facets for the axis are continuous or ill-separated inferiorly, while in *Odocoileus* they are well separated; the foramen piercing the transverse wing is single, while in *Odocoileus* it is double superiorly.

Axis.—Longer in proportion than in pronghorn or deer, resembling rather the proportions in the gazelle. The spine is higher than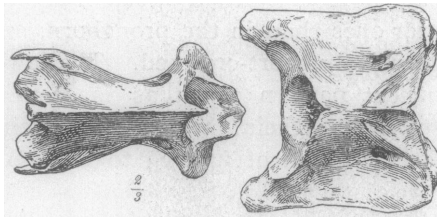 in *Antilocapra*, especially anteriorly, but does not project so far forward. The inferior notch in the atlas facet is less marked than in the prong-horn, much less than in the deer, and is more like *Gazella.*

Fig. 9. *Merycodus osborni.* Atlas and axis viewed from above. Two thirds natural size. Type specimen.

The vertebrarterial canal pierces the lamina of the neural arch, beginning anteriorly on the external surface a little anterior to the middle of the lamina, considerably behind the foramen for the second spinal nerve, and ending posteriorly on the internal surface of the lamina near its posterior border. In the deer this canal opens anteriorly into the nervous foramen and posteriorly on the posterior border of the lamina. In the antelopes it seems to be represented only by a very small canal, exterior in both openings; in *Cervulus* it opens anteriorly into the nervous foramen, and posteriorly on the external surface of the lamina. There seems to be in this respect a peculiar modification in

Merycodus of a primitive condition; but this is so inconstant a character that I should not think it of much importance. The transverse processes of the axis are stouter and shorter
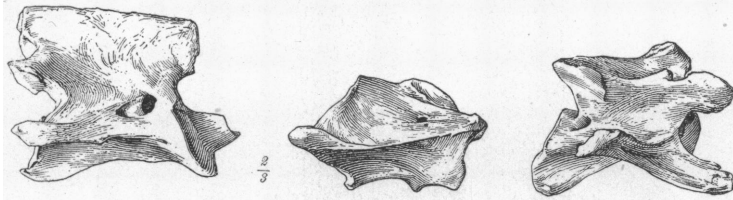

Fig. 10. *Merycodus osborni.* Atlas, axis, and fifth cervical vertebra, side views, two thirds natural size. Type specimen. (The cervical has by error been placed at the anterior end of the series, instead of behind the axis.)

in *Merycodus* than in either pronghorn or deer, and are directed more backwards.

Third to Sixth Cervicals.—Longer than in *Antilocapra* or *Odocoileus*, the inferior transverse lamina more extended into stout processes anteriorly and posteriorly, but not so wide. Superior lamina much as in *Antilocapra*, less developed than in *Odocoileus*, more than in *Gazella*. The neural spine of the fifth cervical is a rudimentary boss; that of the sixth is short but well formed, about 2 centimeters long. The vertebrarterial canal extends from end to end of the lamina of the neural arch in all these cervicals, being longer (more complete) than in any of the genera named. *Gazella* comes nearest in this respect: *Odocoileus* is furthest removed.

Seventh Cervical.—Somewhat longer than in *Antilocapra*, which it rather closely resembles in form and proportions, but the centrum is smaller compared with the arch—smaller also than in *Odocoileus*, much smaller than in *Gazella*. The neural spine is more slender distally than in *Antilocapra*, and directed more backwards; the anterior zygapophysial facets are slightly concave, while in the deer they are strongly concave, and in the gazelle and muntjac convex. The transverse processes are very like those of *Antilocapra*.

Anterior Dorsals.—The spines are shorter, of more uniform width, and directed less backward than in *Antilocapra, Gazella,* or *Odocoileus*, approaching to some extent the muntjac and

other round-backed deer. The difference in size between dorsal and lumbar centra is less than in *Gazella*, somewhat less than in *Antilocapra*, but much more marked than in *Cervulus*.
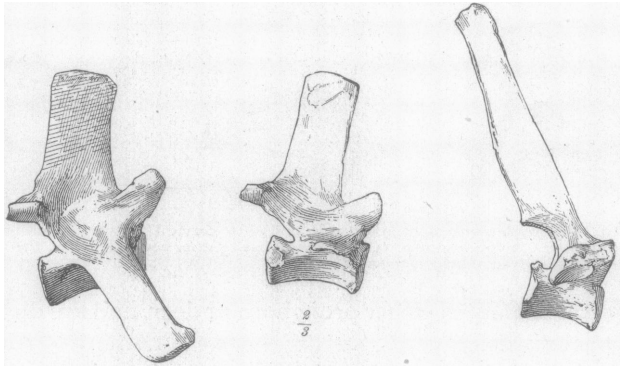

Fig. 11. *Merycodus osborni.* Fourth and twelfth dorsal and second lumbar vertebræ. Two thirds natural size. Type specimen.

Lumbars.—The transverse processes are short, flat, and wide, the first (14th dorso-lumbar vertebra) well developed, so that the dorso-lumbar formula was probably invariably 13–6. The processes resemble those of *Cervulus* in their short, wide proportions, but are larger, and do not curve forward as in the muntjac, having the straightness and direction seen in *Antilocapra* and *Gazella*. The zygapophyses are smaller and less revolute than in the pronghorn. In *Gazella* they are smaller but somewhat more revolute; in *Odocoileus* more revolute and much larger; in *Cervulus* very much simpler.

To sum up the above vertebral characters: *Merycodus* is much more nearly related to *Antilocapra* than to any other living genus in the detailed characters of the vertebræ. The neck is longer, and adapted to carry the larger-antlered head. The back is not so straight as in the more advanced antelopes and deer, but by no means so rounded as in the muntjac. The vertebræ have a few minor specializations peculiar to the genus, but on the whole agree very well with the *Antilocapra* vertebræ, allowing for differences due to smaller size of the animal, its longer neck, and retention of primitive characters in the dorso-lumbar region. There is no indication of any

near relationship with the deer, and one cannot doubt that the position of *Merycodus* is with the Cavicornia, not with the Cervicornia, in spite of its branching, deer-like antlers.
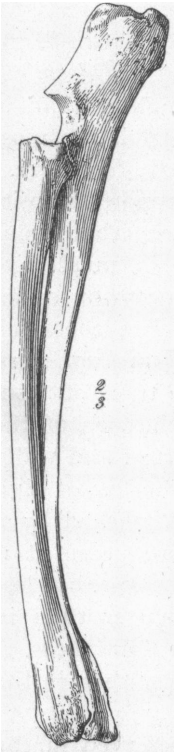

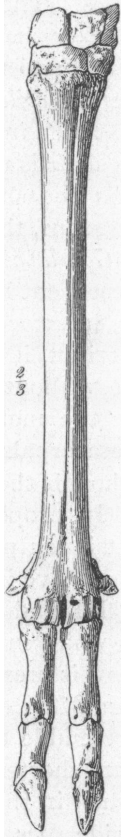Fig. 12. *Merycodus osborni.* Ulna and radius, external view, two thirds natural size. Type specimen.

Fig. 13. *Merycodus osborni.* Anterior view of manus, two thirds natural size. Type specimen.
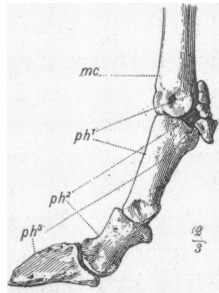
Fig. 14. *Merycodus osborni.* Distal end of manus, external view, two thirds natural size. No. 9475.

FORE LIMB. — The *scapula* is short and wide, with high spine and prominent coracoid process. *Antilocapra* is the nearest in these respects among the genera compared.

The *humerus* is intermediate between *Odocoileus* and *Antilocapra* in straightness of shaft, shortness and prominence of deltoid crest, and some other minor details.

The *ulna and radius* are entirely separate, as in the deer, not united along the shaft as in the antelopes; the shaft of the ulna is much more slender than in the deer, but not as slender as in the antelopes. The olecranon is somewhat longer and considerably thicker than in either *Antilocapra* or *Odocoileus;* the shafts of ulna and radius are rather strongly bowed forward, while those of *Antilocapra* are nearly straight. The curve is as great as that seen in *Odocoileus;* but in *Merycodus* the upper part of the shaft is most curved, in *Odocoileus* the lower part. In *Gazella* the shaft is straighter than in *Merycodus*, but, as in that genus, the upper part is the most curved. The olecranon of *Gazella* is like that of *Merycodus*.

The *carpus* is about ten per cent higher in proportion to its width than in *Antilocapra*, intermediate between that genus and *Odocoileus*. The trapezium, if present at all, must have been a small nodular bone without distinct facets on either the magnum-trapezoid or the metacarpus. The coössified proximal rudiments of metacarpals II and V are not very clearly distinguishable, although there is more trace of them left than in *Antilocapra*. In proportion to the size of the animal the *metacarpal* shaft is ten percent shorter, and wider than in *Antilocapra*, more concave inferiorly, the line of division between metacarpals III and IV clearly marked by a furrow from end to end, while in the modern genus it is almost obsolete. The furrow is present in *Odocoileus*, but less marked. The *phalanges* in *Merycodus* are shorter than in *Antilocapra*, but in form resemble them more than those of *Odocoileus*. The unguals are shorter and smaller than in the pronghorn, much smaller than in the deer.

The little rudimentary side toes are not preserved in the type specimen, or have been lost in extracting it from the matrix. In the cotype they are preserved in position in the fore foot, and are seen to consist of the distal half of the first phalanx, with the second and third complete. They are extremely small, their combined length about half that of the first phalanx of digit III or IV. The first rudiment lies just outside the first sesamoid series, and the others bend inward, backward, and downward from it. The upper end of the

first phalangeal rudiment is perfectly preserved, and shows that the upper end of the first phalanx was not calcified, and there is no trace left of the shafts or distal ends of the lateral metatarsals. The second and third lateral phalanges are well formed but very short, and with flat articular facets.

HIND LIMB. — *Pelvis.* The superior iliac fossa, lodging the gluteus medius, is more expanded than in any of the forms compared. There is, as in the deer, a deep pit on the inferior surface of the ilium just anterior to the acetabulum, close to the attachment of the rectus femoris, and perhaps serving to increase the area of attachment of this muscle. This is wanting in *Antilocapra*, much less marked in *Gazella*. The ischia and pubes are incomplete, but the parts preserved indicate that they were much like the corresponding parts in the pronghorn, the ischia wide, flattened, laterally expanded, with long, stout processes directed outward. There is a rather marked process on the inferior surface of the ischium, at the proximal end of the attachment of the quadratus femoris, rather more prominent than in *Antilocapra*. The pubic symphysis is shorter and thicker than in the pronghorn; the process for the pectineus is small, well defined, and separate as in the deer, not continued into the anterior border of the pubes as in the pronghorn and true antelopes.

The femora and proximal ends of the tibiæ are missing in the type specimen, and also in the cotype. We do not know, therefore, what the proximal end of the fibula was like. The distal end is much reduced, the shaft represented by a very short, pointed, rudimentary spine at the upper end of the distal segment. This little spine lies in a proportionately short channel on the external border of the distal end of the tibia. The reduction of the fibula at this end is greater than in the pronghorn or gazelle, but less than in *Odocoileus, Cervus*, or any other deer that I have compared. The distal end of the fibula appears to be uniformly more reduced in the deer than in the antelopes: the proximal end, on the other hand, is much more reduced in the antelopes. *Merycodus* stands intermediate between the two groups in the reduction of the distal end of the fibula; as to the condition of the proximal end, we
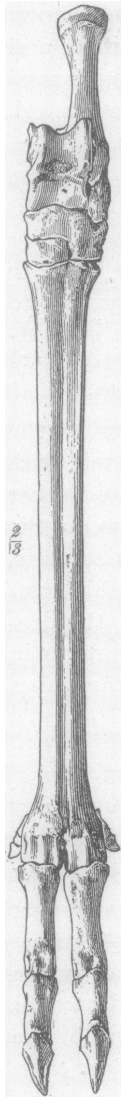
Fig. 15. *Merycodus osborni.* Anterior view of pes, two thirds natural size. Type specimen.

Fig. 16. *Merycodus osborni.* Distal end of pes, external view, two thirds natural size. No. 9475.

have unfortunately no evidence at present. The *tibia* does not appear to show any important distinctions from *Antilocapra*. The metatarsus is shorter in proportion; metatarsals III and IV are more clearly distinguishable than in *Antilocapra* or in *Odocoileus*. The second cuneiform (internal cuneiform, according to Scott) is larger than in *Antilocapra*, considerably larger than in *Odocoileus*, and the small sesamoid-like bone articulating to the inferior surface of the head of the metatarsus is larger and has a more extensive facet than in *Antilocapra*, equalling *Gazella* in this respect.

The vestigial lateral toes are not preserved in the type specimen, but in the cotype the hind foot has associated with it (although not found in position) small rudimentary phalanges, much like those of the fore foot, but somewhat more slender. Except for their much smaller size and somewhat more slender proportions these vestigial toe-bones are much like those in the hind foot of *Odocoileus*.
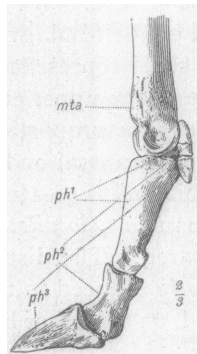
To sum up the above fore- and hind-limb characters:

Merycodus is most nearly related to *Antilocapra*, but in almost all respects more primitive, retaining in greater or less degree characters seen in modern deer, and others which most of the deer have lost.

The lateral toe-bones, entirely absent in *Antilocapra* and the true antelopes, still persist, although much smaller than in the deer. The shaft of the ulna is more reduced than in the deer, but is entirely

separate, while in the pronghorn and antelopes it is still smaller and coössified with the radius. The reduction of the fibula, on the other hand, has gone further than in *Antilocapra* or the true antelopes, at the distal end; and in this respect *Merycodus* is again intermediate between antelopes and deer, although here it is the antelopes that are the more conservative. Most of the minor characters of the limb- and foot-bones relate the animal to the pronghorn and the true antelopes much more nearly than to the deer, but it has not progressed as far in adaptations to speed. The hoofs were small, gazelle-like, and the animal probably stood with the proximal and medial phalanges almost in line with the metapodium, as do the gazelles to-day.

RIBS AND STERNUM. — These are very perfectly preserved in the specimen, but call for no extended comment. The ribs are entirely modernized, wide, flat, and thin, especially the anterior ones, resembling most nearly those of *Gazella*, but somewhat wider in proportion, especially anteriorly. The sternum is of the same type as in the antelopes; parts of the cartilaginous ribs were attached when the specimen was found, connecting the sternum with the vertebral ribs, but so imperfectly preserved that it was not practicable to restore them.

Merycodus necatus *Leidy*.

Merycodus necatus LEIDY, Proc. Ac. Nat. Sci. Phila., VII, 1854, p. 90; Ext. Mam. Faun. Dak. and Neb., 1869, p. 162, pl. xiv, figs. 9, 10.
Cervus warreni LEIDY, Ext. Mam. Faun. Dak. and Neb., 1869, p. 172, pl. xxvii, fig. 12.
Dicrocerus necatus COPE, Rep. U. S. Geol. Survey W. of 100th Mer., 1877, p. 350, pll. lxxxi, lxxxii.

This is the type species of the genus, and is based on lower jaws, from the Upper Miocene Loup Fork of Bijou Hills and Fort Niobrara, Neb. Professor Cope referred to the same species several specimens from the Loup Fork beds of the Santa Fé valley, of associated jaws and antlers, and distinguished it by the form of the antler, which branches near the base into two equal tines, rather long and curving inward.

Our collections contain several specimens of this type of antler, but none certainly associated with other parts of the skeleton. The teeth are more compressed and hypsodont than in *M. osborni*, the anterior premolars smaller.

Merycodus furcatus (*Leidy*).

Cosoryx furcatus LEIDY, Ext. Mam. Faun. Dak. and Neb. 1869, p. 173, pl. xxviii, fig. 8.
Dicrocerus furcatus COPE, Rep. U. S. G. S. W. of 100th Mer., 1877, p. 350, pll. lxxx, lxxxi, fig. 1, lxxxii, fig. 1.
Cosoryx furcatus SCOTT, Bull. Mus. Comp. Zoöl., XX, 1890, p. 82, pl. i.

Professor Cope in his descriptions of Vertebrata from the New Mexico Loup Fork, points out the identity of *Cosoryx* with the previously described *Merycodus*, but considers them finally as both identical with *Dicrocerus*. Professor Scott, in his description of the skeleton, follows Cope in the use of *Cosoryx* in place of *Merycodus*. Accepting the specific identifications made by these authors, *M. furcatus* is distinguished by the antler branching high up on the beam into two short, straight, equal tines, and the beam very little flattened at the branching. The teeth are very like those of *M. necatus*.

To this species is pretty certainly referred the fragmentary skeleton from the Republican River Loup Fork, of which the skull has already been described in this paper (p. 110, and figs. 5 and 6). The skeleton bones are very like those of *M. osborni*, but the limbs somewhat smaller. Another fragmentary skeleton, in the Harvard Museum, was described by Professor Scott.

Merycodus? ramosus *Cope*.

Cosoryx ramosus COPE, Proc. Acad. Nat. Sci. Phila., 1874.
Cosoryx furcatus COPE, in part, of later publications.

Two specimens from the Upper Loup Fork indicate a species intermediate in several respects between *Merycodus* and *Blastomeryx*. It has the long, straight jaw of the former genus, the molars are intermediate between the two in height of crown, and have well-marked basal colonnettes on the external side between the main crescents as in *Blastomeryx*, but no anterior

fold. The premolars are less reduced than in either M. *fur-
catus* or M. *necatus*.

The type of M. *ramosus* consisted of antlers like those of
•M. *furcatus*, but larger and three-tined, associated with jaws
having the characters just mentioned. Cope appears after-
wards to have come to the conclusion that this association was
incorrect; if so it is very doubtful whether his name can be
used for this species if the rules of nomenclature be strictly
applied.

Merycodus agilis *Douglass.*

Cosoryx agilis DOUGLASS, "Neocene Lake Beds of Western Montana,"
    Univ. of Montana, Missoula, Mont., 1899.

In comparing the skull characters of this interesting speci-
men with those of M. *osborni* and M. *furcatus* described above
(p. 111), it was shown that the chief distinctions are quite
obviously characters of immaturity. Mr. Douglass has not
pointed out, nor do his figures illustrate, any really valid
specific characters.

? Merycodus teres *Cope.*
Merycodus trilateralis *Cope.*

These are large species of entirely doubtful position. They
are known chiefly from the antlers, but Professor Cope de-
scribed some fragments of teeth with his M. *trilateralis* type,
and these, judging from his description, must have been hyp-
sodont. Except for this the two species might be referred to
Palæomeryx.

Blastomeryx *Cope.*

Blastomeryx COPE, Rep. U. S. G. S., W. of 100th Mer., IV, part.ii, 1877,
    p. 350. Not of later publications.
? *Blastomeryx* SCOTT, Bull. Mus. Comp. Zoöl., 1890, XX, p. 76, figs. 7–9.
    Not of later publications.

This genus was based on a last lower molar; and until
recently no better specimens of the type species had been
found. Cope afterwards referred to the genus a large brachy-
dont species which resembles *Palæomeryx*, but differs widely

from the type of *Blastomeryx*. In the 1901 collection from Colorado is a specimen of the type species, *B. gemmifer*, which enables us to characterize the genus more definitely, as follows:

Molars hypsodont, but less so than in *Merycodus*. Anterior cingulum of molars rising into a strong cusp-like ridge externally (absent in *Merycodus*); a well-marked basal cuspule between pr^d and hy^d (absent in *Merycodus* except *M. ramosus*). No trace of the "Palæomeryx fold" on lower molars. Premolars smaller and simpler than in *Merycodus*, much smaller and more compressed than in Palæomerycinæ. Upper teeth unknown. Limbs and feet approaching those of *Merycodus*, but with various minor differences.

It is doubtful whether the fragmentary skeleton which Professor Scott described as *Blastomeryx* in 1890, should properly be placed under the genus. It was identified by the correspondence of a single upper molar to the lower molar of *B. gemmifer*.

Blastomeryx gemmifer *Cope*.

Merycodus gemmifer COPE, Am. Rep. U. S. G. S. Terrs., 1873 (1874), p. 531.

Type, a third lower molar from Pawnee Buttes, Colorado, No. 8301 Cope, Collection, Amer. Museum. I refer to this species, No. 9449, from the same locality and horizon, consisting of a lower jaw with p_2-m_3, most of the tibia and pes, the distal part of the humerus and proximal half of the radius.
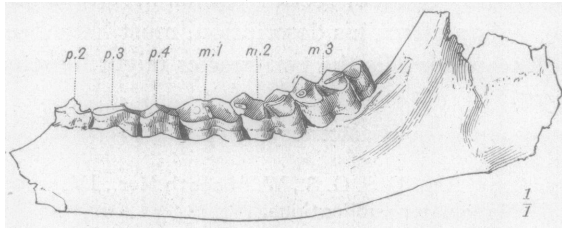

Fig. 17. *Blastomeryx gemmifer*. Lower jaw, external view, natural size. No. 9449. Middle Miocene, Colorado.

It is a little smaller than *Merycodus osborni*, from the same beds, and the proportions of the teeth differ a good deal. The premolars are somewhat smaller, m_1 of about the same size, m_2 and m_3 much smaller as well as shorter-crowned.

Both specimens have the teeth well worn, so that this dispro-
portion is not due to difference in wear.   The jaw under m_{2-3}
is not nearly as deep as in *Merycodus*, and the outline of the
whole inferior border of the ramus is characteristically differ-
ent.   The tibia is smaller than in *M. osborni*, the groove for
the internal flexor tendons (tib. post., flex. long. digit.) is
deeper, the fibula is less reduced, its distal end retaining a
remnant of the shaft about a centimeter in length, coössified
with the tibia in this specimen.   The calcaneum is propor-
tionately longer and of more uniform depth than in *M. osborni;*
the proximal rudiments of mts. II and V are coössified, but
their outlines are clearly defined, the head of mt. V making a
rather strong process on the external side of the head of the
cannon-bone (not present in *Merycodus*).   The shaft of the
ulna is coössified with the radial shaft, beginning at about 3
cm. from the proximal end and extending down for not less
than 2 cm.   This may possibly be pathological, but I hardly
think so from its appearance.   In *Merycodus osborni* the shaft
is entirely separate, even in individuals somewhat older than
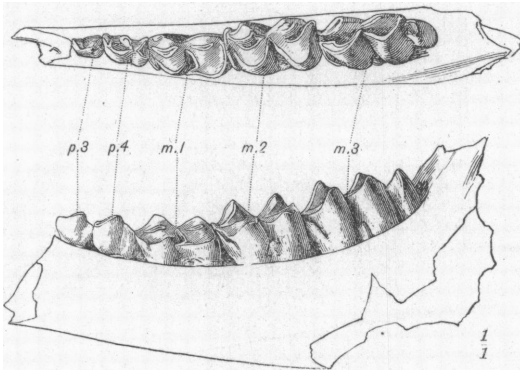this *Blastomeryx* appears to be.

Fig. 18.   *Blastomeryx wellsi.*   Lower jaw, external view, natural size.   Type specimen.
Upper Miocene, South Dakota.

Blastomeryx wellsi, sp. nov.

A species of *Blastomeryx* considerably larger than *B. gem-
mifer* occurs in the Upper Miocene of the Republican River

and Little White River valleys. I take as type a lower jaw, No. 9823, found by Mr. Wells of the American Museum Expedition of 1902, in the Loup Fork Beds near Rosebud Agency,
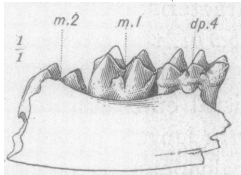

Fig. 19. *Blastomeryx ? wellsi.* Part of young lower jaw showing milk premolar. External view, natural size. No. 8498. Upper Miocene, Republican River Basin, Nebraska.

South Dakota. The premolars are relatively smaller and simpler than in the type species; the molars are very similar, and the jaw shorter and heavier in general outline. Two specimens show the milk dentition, which is quite brachydont, the unworn crown of dp_4 hardly any higher than the width of the tooth. In *Merycodus*, on the other hand, dp_4 is hypsodont, the height of the crown being two or three times the width of the tooth.

Measurements of *B. gemmifer* and *B. wellsi:*

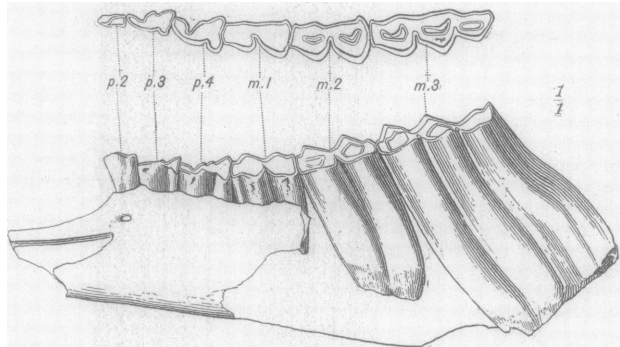|		
Length of molar series, $m_1 - _3$	26 mm.	38 mm.
" " two premolars, $p_3 - _4$	11.5 "	11 "
Anteroposterior diameter of m_1	8 "	11 "
Transverse " " m_1	5 "	6 "
Anteroposterior " " m_3	11.7 "	16 "

Fig. 20. *Capromeryx furcifer.* Lower jaw, natural size, external view, and crown view of teeth. Type specimen. Pleistocene, Nebraska.

Capromeryx *Matthew.*

Bull. Am. Mus. Nat. Hist., 1902, p. 318.

In this genus the teeth are as hypsodont as in *Antilocapra*, but the premolars are of more primitive pattern, approximat-

ing those of *Merycodus* in form.   Unfortunately nothing but
the lower jaw is known, so that we are unable to say whether
it is in any other respects intermediate between the two.

Capromeryx furcifer *Matthew.*

Bull. Am. Mus. Nat. Hist., 1902, p. 318.

About the size of *Merycodus osborni*, two thirds the lin-
eal dimensions of *Antilocapra americana*.   Pleistocene, Hay
Springs, Nebraska.

FAMILY CERVIDÆ.

Sub-family PALÆOMERYCINÆ.

The presence of the "Palæomeryx fold" on the lower molars
and the extreme brachydonty of the teeth, are the principal
characters by which Dr. Schlosser appears to distinguish this
group.   I am not sure, however, that I have seen his original
descriptions.

Palæomeryx.

Douglass has recently described under this genus two large
American species, closely allied to the large brachydont forms
referred to *Blastomeryx* by Cope and Scott.   Professor Scott
had stated in regard to the latter that they would probably
have to be removed to *Palæomeryx* if the lower jaw were
known to possess the characteristic fold of the anterior cres-
cent of the molars, and this is the chief reason given by Mr.
Douglass for referring his species to the European genus.   As
indicated above, this character is common to many or all of
the Miocene deer with very brachydont molars; it occurs in
Dicrocerus, Dremotherium, and *Amphitragulus,* as well as in
Palæomeryx.   All the American species that I have seen differ
considerably in their dentition from any of the European
genera, and appear to possess a different type of antler from
any, perhaps a more primitive one.   Unfortunately all the
known specimens are more or less damaged in this part; all
appear to be in the velvet, unbranched, and without burr, but

whether this was a permanent condition it would not be safe to say. The specimens in this museum, though numerous, are mostly fragmentary, and the correlation of parts more or less uncertain. For the present, therefore, it is better to leave this group of brachydont American species under *Palæomeryx.*

Palæomeryx borealis *Cope.*

The typical specimens are more or less complete skulls and many fragments of the skeleton. The species is about the size of the caribou. The antlers were not branched, and apparently not shed; whether they were covered by velvet or by horn I am unable to determine, but the soft, irregular sur-
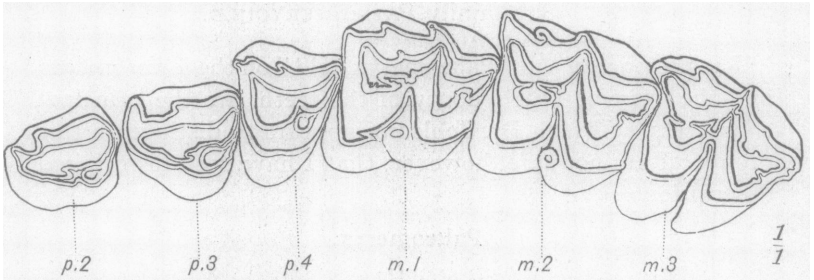

Fig. 21. *Palæomeryx borealis.* Upper teeth, crown view, natural size. Type specimen. Deep River Beds of Montana.

face towards the tip suggests the latter. There was no burr. The basicranial and basifacial axes are parallel, or nearly so. The antlers are supra-orbital, directed forward rather than backward, wide apart at base, and have a peculiar postero-external wing projecting from near the base behind the orbit.

To this species I refer lower jaws associated with several foot-bones from the Colorado Miocene. They show the characteristic "Palæomeryx fold" on the lower molars, and agree in size and proportions with the typical specimens from the Deep River Miocene, among which the lower teeth have not been found. Unfortunately they do not clearly show the most characteristic distinctions in the feet, the presence or absence of lateral toes, and the development of the fibula. The tuber calcis is peculiarly long and of uniform width throughout. The distal end of the radius is deer-like, with a sharp,

clean-cut ridge between scaphoid and lunar facets; in the pronghorn the ridge is round-topped, permitting some lateral movement in the carpus.   The scaphoid is smaller than in the deer, but has the same proportion of height to breadth; in the prongbuck it is not nearly so high.

Palæomeryx, sp.

A small species of *Palæomeryx* is indicated by teeth and various fragmentary remains in uncertain association from the Colorado Miocene.   It is about the size of *Dicrocerus furcatus* specimens from Steinheim; somewhat larger than *Merycodus* or *Blastomeryx*, and easily distinguishable from those genera by the wide, short-crowned molars.