XI. DROMOMERYX, A NEW GENUS OF AMERICAN RUMINANTS.

By Earl Douglass.

In 1878 Professor E. D. Cope described, under the name *Blastomeryx borealis*,[1] the larger portions of two skulls of a ruminant from the Ticholeptus (Deep River) beds of Smith River valley in Montana. Later he published a figure of the skull,[2] which is evidently in part a restoration from the two skulls (Amer. Mus. Nat. Hist., No. 8132 and No. 8133).

The name *Blastomeryx*[3] had been proposed by Cope in 1877 for a posterior lower tooth of a small ruminant, in case the specimen should be found to represent a new genus. The tooth was obtained from the upper Miocene ("Loup Fork") deposits of northwestern Colorado.

In 1879 Dr. J. L. Wortman found in the Mascall (Cottonwood Creek) beds of Oregon some incomplete upper jaws, teeth, and bones of limbs and feet, which Cope referred to *Blastomeryx borealis*.[4]

The Princeton Scientific Expedition of 1891 discovered a smaller, but closely related, species in the same locality and horizon from which Cope's type of *Blastomeryx borealis* had been obtained. To this species Scott gave the name *Blastomeryx antilopinus*.[5] The posterior portion of a skull, a radius, part of an ulna, a nearly complete tarsus, and anterior and posterior canon-bones were figured and described.

Concerning the generic reference of this genus Scott said ("Mam. of Deep River Beds," p. 167): "This Deep River species [*Blastomeryx borealis*] is in many ways similar to the larger species of *Palæomeryx* from the Upper Miocene of Europe, and perhaps should be referred to that genus, though in the present state of knowledge it would be

[1] "Description of New Vertebrata from the Upper Tertiary Formations of the West," *Proc. Amer. Philos. Soc.*, 1878, p. 222.

[2] "The Artiodactyla," *American Naturalist*, Vol. XXII, 1889, p. 129, fig. 19.

[3] Geographical Survey West of the 100th Meridian, Vol. IV, Part II, p. 350.

[4] *Proc. Amer. Phil. Soc.*, 1886, p. 359.

[5] "Mammalia of the Deep River Beds," pp. 168–178.

premature to do so. This doubt is justified by the fact that the mandibular dentition of *B. borealis* is still unknown, and we cannot therefore determine whether the lower molars possessed the very characteristic *Palæomeryx* fold, and it is uncertain whether the type of the European species had developed horns."[5]

While collecting vertebrate fossils from the Upper Miocene deposits in the Lower Madison Valley in Montana (1894–1896) Earl Douglass found portions of lower jaws and teeth of *Blastomeryx*, the last lower molars being nearly like the type of the genus. In the same beds two portions of lower jaws were obtained, which were much larger than those of *Blastomeryx*, and the lower molars possessed the so-called "*Palæomeryx* fold" which was then supposed by him to be characteristic of *Palæomeryx*. These specimens were therefore described under the generic name *Palæomeryx*. The most nearly complete mandibular ramus (Pl. LXII, Figs. 1 and 2) was named *Palæomeryx americanus*.[6] Two upper premolars and the greater portions of the three upper molars of one individual (Pl. LXIII, Fig. 2) were in the original description provisionally referred to this species.[7] In the same deposits, a portion of a brain-case (Figs. 2 and 3) as large as that of *Blastomeryx borealis* Cope, was found, but not described.

Since that time the American Museum of Natural History has recovered sufficient material for the restoration of *Blastomeryx*. This has been described by Matthew in a recent paper entitled "The Osteology of Blastomeryx and Phylogeny of the American Cervidæ."[8] This paper settles doubts, if any existed, with regard to the generic identity of the true *Blastomeryx* and the larger species described in the present paper.

In the spring of 1899, Mr. Earl Douglass found, in the Flint Creek beds (Upper Miocene) near New Chicago in Montana, a skull, the corresponding parts of which do not differ in any important particular, so far as the present writer is able to discern, from the portion of a skull which is the type of *Blastomeyrx borealis* Cope, or from the more complete skull which was found in the same deposits. With the skull from the Flint Creek deposits, were associated the left horizontal ramus of the mandible, and good parts of the skeleton.

[6] "The Miocene Lake-beds of Western Montana," University of Montana, 1899, p. 21.

[7] *l. c.*, p. 22.

[8] *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, 1908, pp. 535–562.

These discoveries showed conclusively that the larger species described as *Blastomeryx borealis* Cope and *B. antilopinus* Scott were very different from the true *Blastomeryx*. I had not access to the European specimens which had been described as *Palæomeryx*, or to the literature describing them, but I judged from the writings of others that the larger American species were *Palæomeryx*.

The above mentioned skeletal remains show by far the greater number of the osteological characters of *Blastomeryx borealis* Cope. A restoration of the skeleton was made by Mr. Sydney Prentice under my direction and a paper was read before the American Society of Vertebrate Paleontologists, on "The Restoration of *Palæomeryx borealis*" in 1906; but on account of the doubt concerning the relation of this animal to the type of *Palæomeryx* and to other European *Palæomerycinæ*, the paper was not published. The author wished, on the one hand to avoid further perpetuating the use of a name that would be misleading, and on the other hand to refrain from creating a synonym.

The generic name *Palæomeryx* was given by Hermann von Meyer in 1834 to various fragments of jaws and teeth found at Georgensmund in southeastern Bavaria. In the paper,[9] which contains the original description, several teeth and portions of the mandible were described. Evidently the specimens do not all belong to the same species and perhaps not to the same genus. Apparently the portion of a mandible with teeth, illustrated on Plate X, Fig. 77, should be taken as the type, as it is the first used in establishing the characters of the genus. Other specimens, in part at least from supposedly different Miocene horizons, have since been variously referred by European authors to *Palæomeryx*, *Dicrocerus*, *Cervus*, *Dromotherium*, *Propalæomeryx*, etc.

The types of *Palæomeryx* are not accessible, and I do not know whether they still exist; but I judged from von Meyer's figures and descriptions that *Palæomeryx* was different from anything that had been found in America; and in fact I was for some time satisfied in my own mind that the fossil remains which were referred to *Blastomeryx* by Cope and to *Palæomeryx* by myself, had been erroneously referred to these genera. Dr. Matthew has entirely removed doubt

[9] *Die Fossilen Zähne und Knochen und Ihre Ablagerung in der Gegend von Georgensmund in Bayern.* Abhandlungen der Senck. Nat. Ges., Supplement zu Band I, 1834, pp. 93–98.

in regard to the former genus, but it has not been so easy, on account of the lack of proper material for comparison, to remove all doubt in regard to *Palæomeryx*.

Some specimens recently received by the Carnegie Museum from Europe, though not belonging to the type itself, and not from the same locality as the type of *Palæomeryx*, enable me, without great danger of serious error, to point out differences which exist between *Palæomeryx* and the American species, which have been referred to that genus. It seems indeed that there is really no very intimate relationship between the American and European forms, and it would be an error to employ them for a close correlation of horizons. This is only another example of the general rule that there are very few mammalian genera common to the Eastern and Western Continents; and as more complete material accumulates and is more carefully studied, the apparent number grows less. I therefore venture, in order to prevent error and misconception, to suggest for the American forms a new generic name. The possession of very complete material permits a very satisfactory definition of the osteological characters of the new genus. Some of the distinguishing features which separate it from the European species, which have been referred to *Palæomeryx*, can be pointed out, and the differences which separate it from the type of *Palæomeryx* can be stated with a large measure of certainty.

The following are the characters which Cope gave for *Blastomeryx borealis*: "The superior dental formula is I.0; C.0; Pm.3; M.3. The molars all have two pairs of crescents excepting the last premolar where the posterior pair are rudimental. The external face of the anterior crescent in all the molars presents a groove, which is bounded posteriorly by a vertical ridge. The posterior crescent is directed a little inward posteriorly on the true molars. The palate is much contracted in front of the first molars. The horns stand above the posterior parts of the orbits; their section is triangular, the posterior angle being rounded, and the external produced and acute, bounding the orbits outwards and backwards. There is no trace of a burr. The temporal fossæ approach so as to be represented only by a rather wide and low occipital crest. . . . This species was as large as the black-tailed deer, *Cariacus macrotis*." [10]

In Volume XVIII of the *American Naturalist* Cope observes that

[10] "Description of New Vertebræ from the Upper Tertiary of the West," *Proc. Amer. Philos. Soc.*, 1878, p. 223.

the molars of *Blastomeryx borealis* differ from *Cosoryx* [*Merycodus*] as much as those of the deer differ from those of the antelope; those of "*Blastomeryx*" and the deer being brachyodont, while those of *Cosoryx*, and the "antelope" (*Antilocapra*) are hypsodont.

In his "Mammalia of the Deep River Beds" Scott gave some characters of *Blastomeryx borealis* Cope. He says "The skull is remarkable for the high and narrow occiput the upper portion of which is drawn out into a long backwardly projecting process composed of the parietals and supraoccipitals, which is very similar to the corresponding part of the occiput of the Oreodontidæ. The horns are trihedral at the base gradually becoming rounded distally and are of remarkable length; they are perfectly simple and unbranched, and in no specimen which I have seen is there any trace of a burr. The surface of the horns is faintly marked by vascular impressions, but is on the whole remarkably smooth, much more so than in the antlers of the deer, and, as Cope has suggested, they were doubtless covered with skin during the lifetime of the animal. . . . The upper premolars, three in number, have the internal crescent, deuterocone, complete; P^2 and P^3 are massive and oval in section, while P^4 is more extended transversely. The molars are very brachyodont and are covered with very rugose and strongly wrinkled enamel; the internal crescents are complicated by accessory spurs which invade the valleys. The internal pillar or style is very variable, being sometimes quite large, while in many specimens it is absent from one or the other of the molars."

DROMOMERYX gen. nov.

I propose the name *Dromomeryx* (running ruminant) for this genus of American fossil mammals including *Blastomeryx borealis* Cope, *B. antilopinus* Scott, and perhaps *Palæomeryx americanus* Douglass, and *P. madisonius* Douglass. *Blastomeryx borealis* Cope was the first to be described, so this would become the type-species of the genus. In the collections of the American Museum of Natural History the less complete skull (Fig. 1) but the one which possesses the greater portion of a horn (No. 8132) is marked on the label as the "type" and the more nearly complete skull (No. 8133) is indicated as the "co-type." Cope's original labels do not accompany the specimens, so I do not know whether or not Cope selected one specimen as the type, but he apparently used both skulls in his original diagnosis of the genus and species. There appear to be no important differ-

ences between the two skulls, and they supplement each other very well.

Below is given a summary of the distinguishing characters of *Dromomeryx* as they now appear :

The size was greater than that of an ordinary specimen of *Odocoileus americana* or *Antilocapra americana*, at least the bones are heavier. The skull is long and the crest of the occiput is produced backward. The face is quite long, the orbit is large, and the malar below the orbit projects outwardly. The horn-cores are large and simple, and they expand outward below into heavy lateral wings behind the upper

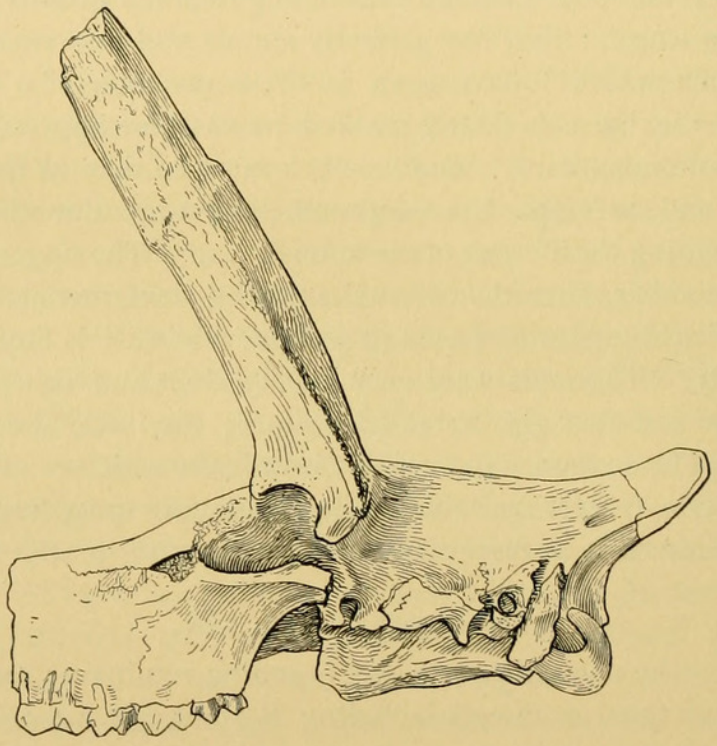


FIG. 1. *Dromomeryx borealis* (Cope). No. 8132, American Museum of Natural History. The specimen marked "Type." One fourth natural size.

portions of the orbits. They stood nearly perpendicular to the upper plane of the skull. There are no lachrymal pits. There is a slit or oblong vacuity in the upper portion of the face anterior to the orbit. The parieto-temporal suture is below the middle of the brain-case. The basi-cranial axis forms a considerable angle with the basi-facial axis. The palate is quite broad between the cheek teeth, but is narrow anterior to them. The mandible is long and not deep and it curves downward beneath the molars and premolars. The teeth are brachyo-

dont with a tendency to become hypsodont. There are quite prominent pillars on the anterior outer portions of all the outer crescents of the upper cheek teeth. The lower molars have median outer pillars on the teeth and "*Palæomeryx*-folds" on the anterior outer crescents. The neck and limbs are long, but heavier than those of *Odocoileus* and *Antilocapra*. There were at least vestiges of the lower portions of the lateral metapodials. The humerus is proportionally larger than in *Antilocapra*. The radius and ulna were separate; but the trapezoid and magnum, the navicular and cuboid were united. The distal heels of the metapodials are high, the ungual phalanges high and narrow.

Comparison of Dromomeryx with Palæomeryx. — As previously stated, it is difficult to make reliable comparison with the type of *Palæomeryx*. From von Meyer's figures I inferred that the teeth of the European genus were lower in proportion to the length and width, the valleys between the crescents shallower, and the outer walls of the teeth more convex vertically. The mandible in von Meyer's figure is deeper posteriorly and narrows more rapidly anteriorly.

There are now in the Carnegie Museum, several specimens from Sansan, France, and Steinheim, Germany, which have been referred to the genus *Palæomeryx* by European paleontologists. Three specimens referred to *Palæomeryx bojani*, the type species, have recently been acquired by the Museum. Whether these specimens are referable to the species *P. bojani*, or not, I see no reason to doubt that they belong to the genus *Palæomeryx*.

No. 2263A (Carn. Mus. Cat. Vert. Foss.) is a portion of a mandible with the last molar tooth complete (Plate LXII, Figs. 7 and 8). This tooth, like all the teeth of *Palæomeryx* which I have seen from Europe, strikes one at once as belonging to a quite different animal from those of which remains have been found in America. The tooth is low, heavy, and broad, the outer and inner crescents are thick transversely, the outer and inner surfaces of the tooth are convex, the valleys between the crescents are shallow, the heel is sub-conical in form, and its outer element is represented by a small, short, antero-posterior ridge resembling a cingulum. There is a quite large internal median conule and the enamel of the tooth is coarsely wrinkled. The last lower molar of *Dromomeryx borealis* is much higher and narrower in proportion to the length, the outer and inner walls are less convex — more nearly perpendicular, the valleys are deeper, the heel proportionally longer and composed of an outer and an inner crescent.

The enamel is more nearly smooth, but is finely wrinkled, and the outer median conule is smaller. The tooth of *Palæomeryx* has the appearance of belonging to a larger, heavier animal with more primitive teeth.

No. 2263 (Carn. Mus. Cat. Vert. Foss.) is part of a maxillary with the last premolar and the three molars complete (Plate LXIII, Figs. 4 and 5). This is also labelled "*Palæomeryx bojani.*" This, like the lower tooth just described, represents an animal approaching in size that of *Cervus canadensis.* To describe their most striking characteristics would be to repeat what has been said concerning those of the lower molars. The teeth are broad, heavy, and low, and the valleys are shallow. Among the other characters of this specimen are the following: All of the teeth which have been preserved have heavy inner cingula. The inner crescent of P^4 has the appearance of having been formed from two cusps or crescents uniting near the transverse median line. The posterior portion of the crescent sends outward two long horns, instead of one, to near the outer crescent. The posterior portions of the anterior inner crescents of the molars end abruptly in a rounded border anterior to the middle of the anterior portions of the postero-inner crescents — that is, the antero-inner crescents do not send long horns outward to near the inner wall of the antero-external crescent parallel with the anterior horns of the postero-inner crescents. The smaller specimen described as *Palæomeryx americanus* (No. 755, Carn. Mus. Cat. Vert. Foss.), which is figured in this paper, has this peculiarity also. On M^2 of *Palæomeryx* the anterior horn of the postero-inner crescent has an accessory spur, and in M^3 there is a small tubercle in the median valley, between the anterior and posterior inner crescents. The outer faces of the postero-external crescents are concave and have only the faintest trace of a median ridge.

Nearly all of the above characters distinguish the available specimens of *Palæomeryx* from those of *Dromomeryx.*

An astralagus (No. 2263B, Carn. Mus. Cat. Vert. Foss.) from Sansan, indicates a much larger animal than *Dromomeryx* and there are some differences in form. The specimens of teeth in the Carnegie Museum from Steinheim confirm the characters exhibited by the specimens from Sansan.

To sum up, then: As near as I am able to judge *Dromomeryx* differs from *Palæomeryx* (1) in having higher, narrower, more modernized

teeth, the molars have a more decided tendency to become hypsodont, (2) the upper molars are not provided with heavy cingula, (3) the upper molars and last premolars are set more obliquely in the jaw, (4) the postero-internal crescents have slender horns reaching nearly to the outer crescent, and (5) there are median ribs on the outer surfaces of the postero-external crescents. There are numerous other small differences, but we have not sufficient material of *Palæomeryx* for extended comparisons, and so cannot properly estimate the taxonomic value of many of the characters.

It should be stated here that one specimen No. 706 (Carn. Mus. Cat. Vert. Foss.) which was described under the name *Palæomeryx americanus*, though smaller than the known specimens of *Palæomeryx*, is more nearly like that genus in having shorter horns on the posterior portions of the antero-internal crescents, in having the outer faces of the postero-external crescents concave, and in having more coarsely wrinkled enamel. This specimen will be figured and referred to later in this paper.

There are other probable differences between *Dromomeryx* and *Palæomeryx* as for example the supposed absence of horns or antlers in the latter and the presence of large, very unique and characteristic horns in the former. Indeed it appears now that the two genera are not closely related, and had it not been for the differences in the horns it would perhaps be more difficult to separate the American genus *Dromomeryx* from *Dicrocerus*.

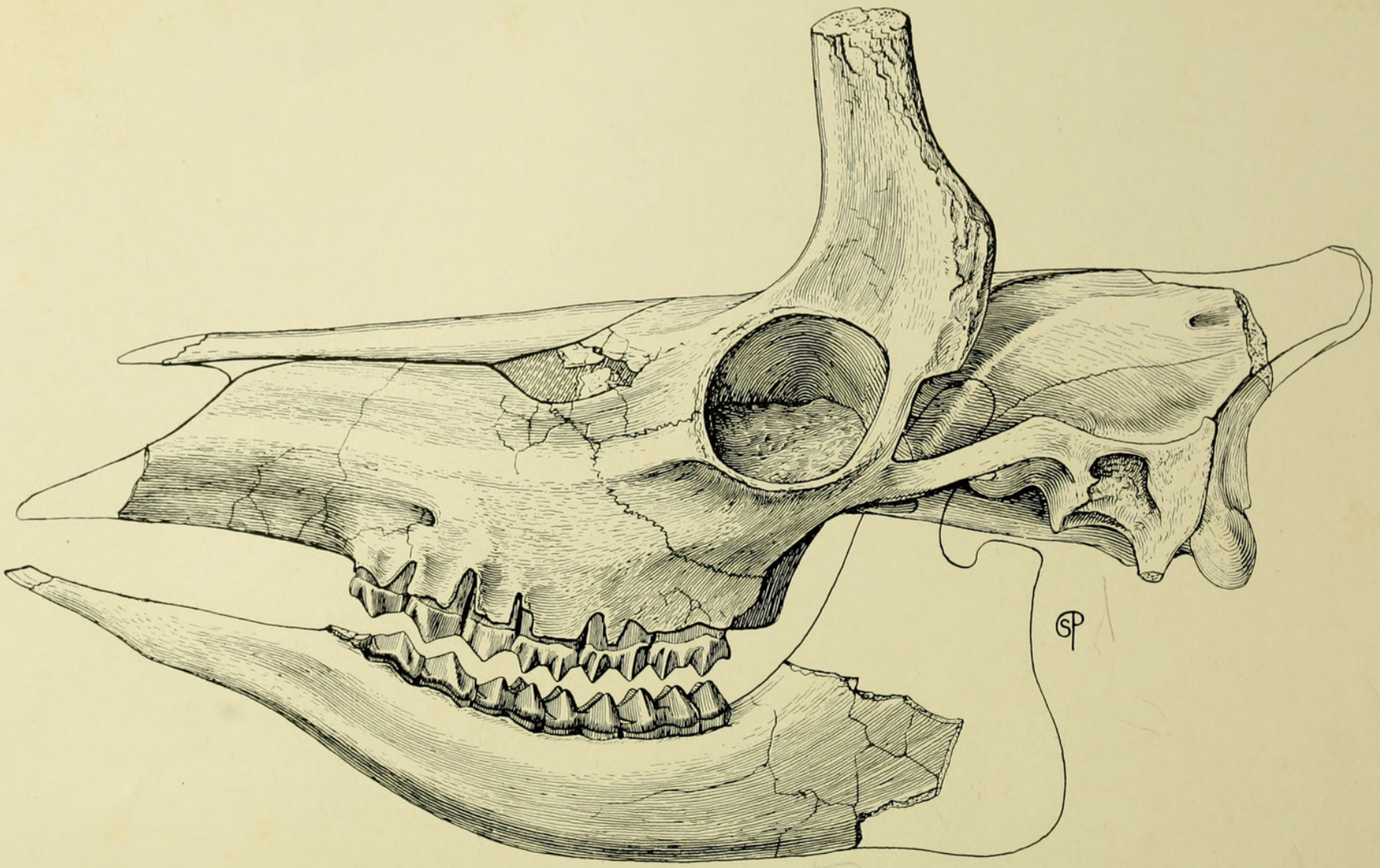
OSTEOLOGY OF DROMOMERYX.

The following descriptions are taken principally from No. 827, Carn. Mus. Cat. Vert. Foss. They are supplemented by descriptions of parts of No. 1542 (Carn. Mus. Cat. Vert. Foss.), which is usually referred to by number when mentioned.

Of No. 827, we have the skull, the left ramus of the mandible, the bones of the neck with the exception of the last two cervicals, five lumbar vertebræ, the sacrum, a large portion of the pelvis, a humerus, a radius, and one anterior canon-bone. Other portions of skulls and skeletons were found in the same deposits. Among these there is a specimen (No. 1542) which consists of large portions of a skull including a complete molar-premolar series, the bones of the neck with the exception of a part of the atlas, the first four dorsal vertebræ, a nearly complete fore limb exclusive of the scapula and a large portion of the hind limb including part of the hind foot.

The Skull. Lateral Aspect. — The skull (Plate LIX) (Carn. Mus. Cat. Vert. Foss. No. 827) is long, yet the face is quite deep anterior to the orbits. The facial portion is rather long, the anterior margin of the orbit being about midway between the extreme anterior and posterior portions of the skull. The muzzle is comparatively slender as seen from above, but has on its sides broad longitudinal convexities. The general upper contour of the cranium is nearly straight, though the forehead is somewhat concave between the orbits, and back of this the top of the brain-case is somewhat convex. The anterior portion of the skull very much resembles that of *Antilocapra*, but the shape and contour of the brain-case are very different. In *Dromomeryx* it is larger and the upper surface does not descend backward as in *Antilocapra*. In the former the low supra-temporal ridges begin at the postero-internal angles of the bases of the horns and converge backward forming a low, broad, sagittal crest about six and one half centimeters in length. The orbits are large and the jugal beneath is produced outward into a shelf which is not so wide nor flat as in *Antilocapra*. The outer border of the jugal is thickened and it is concave transversely beneath. The horns are nearly circular in section above, but are triangular just above the basal wing-like processes. The latter are directed postero-externally. The antero-external faces are concave and the outer borders thickened. The skull is slightly injured in this region, so it is uncertain whether the lachrymal bone reached to the nasal or whether it was separated by the vacuity which lies beneath a part of the posterior portion of the nasals; but apparently the lachrymal was excluded from articulation with the nasals by the antorbital vacuity, as in the *Cervidæ*. The parieto-temporal suture is below the middle of the brain-case which is, according to Brooke,[11] a bovine feature. The temporal ridges are quite heavy and are a little nearer the parieto-temporal suture than they are to the supra-temporal ridges, and they are nearly parallel with both. The zygomatic portion of the squamosal is heavy. The excavation in the squamous portion of the temporal for the external portion of the auditory apparatus (ectotympanic) is large and nearly semicircular in form as seen from the side. The mastoid portion of the temporal is heavy, thickened, and rugose. The infraorbital foramen opens above the anterior portion of $P\frac{3}{}$.

[11] "On the Classification of the Cervidæ, etc.," *Proc. Zoöl. Soc. Lond.*, 1878, p. 885.



Skull of *Dromomeryx borealis* (Cope). (One half natural size.)
(Car. Mus. Cat. Vert. Foss. No. 827.)

In skull No. 1542 the summit of the occiput is produced about 4 cm. posterior to the occipital condyles.

Palate View. — The palate (No. 827, Carn. Mus. Cat. Vert. Foss.) is quite broad between the cheek teeth, but narrows rapidly anterior to them. The anterior portion of the palatal notch is between the last molars. The posterior narial opening is deep vertically on account of the elevation of basi-cranial elements of the posterior portion of the skull — the upward trend forward of the basi-cranial axis. The optic foramen, the sphenoidal fissure, the foramen ovale, the anterior lacerated foramen, the anterior portion of the tympanic bullæ, and the posterior lacerated foramen are in nearly straight lines converging forward and bordering the basi-occipital and the convex portions of the basi-sphenoid and presphenoid. There is a short process on the sphenoid just antero-external to the large sphenoidal fissure.

The glenoid articular surface is convex antero-externally. Between this and the post-glenoid process the surface is concave antero-posteriorly, but a broad antero-posterior convex ridge divides it into two depressions. The post-glenoid process is rather small and low. The tympanic bulla is small, but the anterior portion of the tympanic was large. What I suppose to be the pit for the tympano-hyal is large. The paroccipital process is low and flattened. It is directed antero-internally and postero-externally. The antero-external face is concave while the postero-internal one is convex.

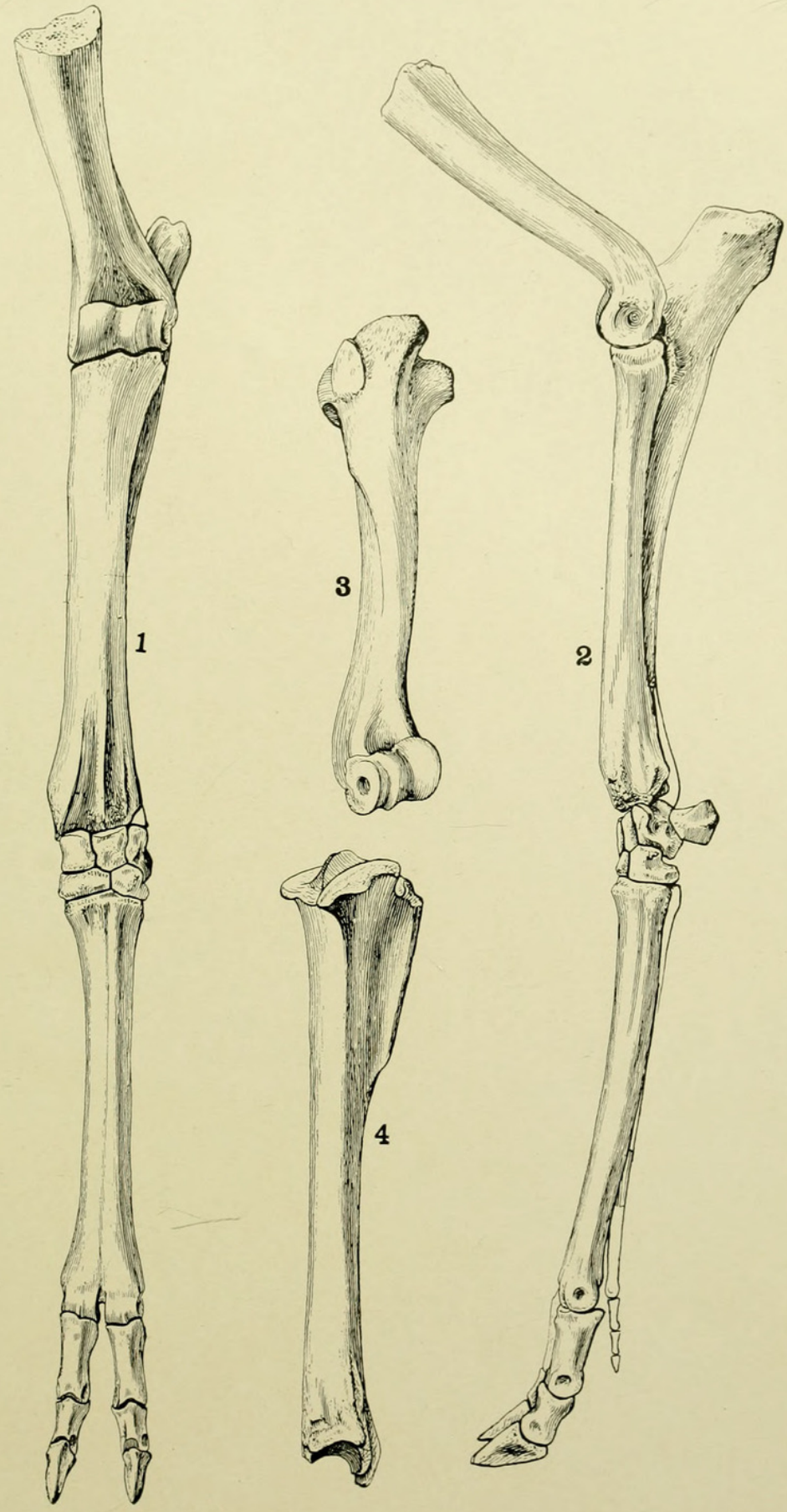
Dentition. — In specimen No. 827 (Carn. Mus. Cat. Vert. Foss.) the most of the cheek teeth are in a good state of preservation (Plate LXIII, Fig. 6). They are not greatly worn. They are not high-crowned and the valleys between the internal and external crescents are not deep. The inner crescents of the upper premolars are comparatively simple. The internal cusps are quite heavy. The anterior outer pillar of P^4 is well developed. On the outer faces of the molars there are prominent anterior and median outer styles and they project outward. The outer faces of the external crescents are very convex. There are cingula on the anterior faces of the antero-inner cusps and small accessory cusps or pillars on the antero-inner faces of the postero-inner crescents. The teeth are not as large as those of Carnegie Museum specimen No. 1542 (Plate LXIII, Figs. 1 and 3) or the types of the genus (Nos. 8132 and 8133 of the Amer. Mus. Nat. Hist.). The teeth of No. 1542 (Carn. Mus.) are somewhat complicated by spurs extending into the median valleys from the inner crescents as is the case in the types.

Lower Teeth (Plate LXII, Figs. 2 and 3). — $P_{\frac{3}{3}}$ is rather long antero-posteriorly and is not broad. It has five loops or lobes on the inner side. The last two enclose a small lake. In $P_{\frac{4}{4}}$ the folds are larger except the first and the last three enclose two lakes. The median inner fold has developed into a large antero-posterior cusp, the anterior portion of which is larger than the posterior portion. The lower molars increase in length from the first to the last. All have small, low, basal cusps between the two external crescents. These are oval in horizontal section. All the molars have the "*Palæomeryx*-fold" on the posterior faces of the anterior outer crescents.

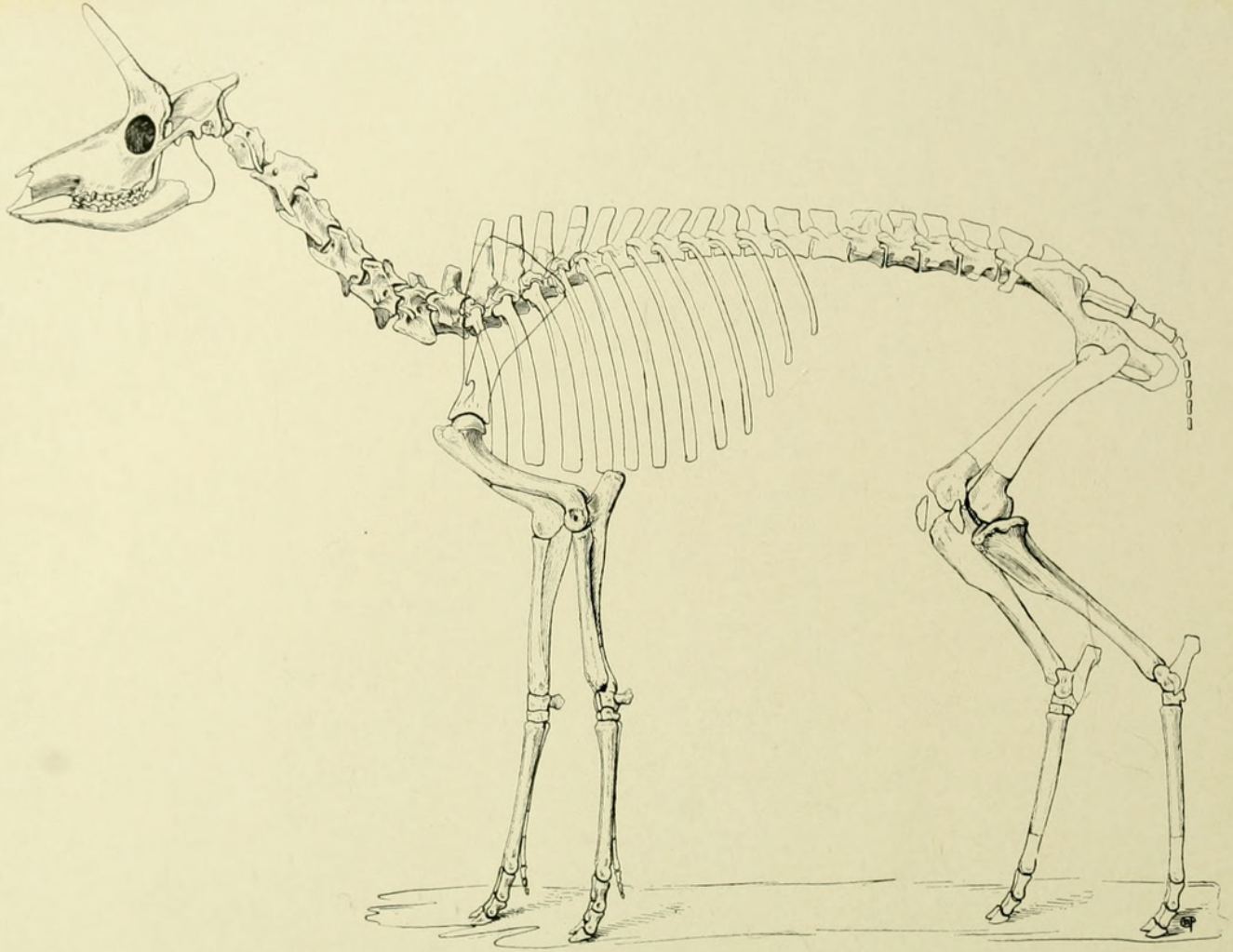
The Spinal Column (Plate LXI). — The neck is long — a little longer than the head. The individual vertebræ are heavy and none of the transverse processes are long. This gives to the cervicals posterior to the axis a square or block-like appearance, much as the cervicals of *Antilocapra* would appear were the transverse processes shorter. The spine of the axis is only moderately high. It is low in front, curved upward antero-posteriorly on the upper margin, and is higher behind; the upper posterior portion is overhanging. The inferior median keel on the posterior portion of the centrum and the descending borders of the transverse processes do not form such deep concavities as they do in the axis of *Antilocapra*. The neural spine in No. 827 is represented by low tubercles while on No. 1542 there are two separate spines, low and unequal in size, situated on either side of the median line of the vertebra. In this vertebra the element which forms the prominent upper branch of the transverse process in the succeeding cervicals is a long ridge, anterior to the middle of the centrum. The base of the spine of C4 is fairly large, but its full height is not shown in any of the specimens. The lower branches of the transverse processes are not very high.

The Limbs (Plate LX). — The humerus and the radius are nearly equal in length. The radius is slightly sigmoid as seen from the front. It is broad transversely and flattened antero-posteriorly. The radius and ulna were separate. The latter was broad antero-posteriorly above, and it narrows rapidly downward. It is thin transversely behind the radius.

The lower portion of the ulna is not preserved in any of the material that has been worked out, but, judging by the contiguous bones, it was quite large. The canon-bone of the fore foot is shorter than the radius in No. 1542. In this specimen part of the distal portion of



Limbs of *Dromomeryx borealis* (Cope). (One fourth natural size.)
Figs. 1–2. Left fore-limb (No. 1542, Car. Mus. Cat. Vert. Foss.).
Fig. 3. Humerus (No. 827, Car. Mus. Cat. Vert. Foss.).
Fig. 4. Tibia (No. 1542, Car. Mus. Cat. Vert. Foss.).



Restoration of *Dromomeryx borealis* (Cope). (One twelfth natural size.)

one of the metapodials is preserved. It lies in the matrix just posterior to the metacarpal. It is flat, and 8 cm. above the distal end of the metacarpal it is 6 mm. in width. The trochlear keels of the metapodials are high and narrow on the palmar side, and they extend as far upward on the dorsal side as do the distal articular surfaces. The

MEASUREMENTS.

	Dromomeryx borealis.	
	No. 827.	No. 1542.
	mm.	mm.
Length of portion of skull preserved	307	
Total length of skull, partly estimated	375	
Width of skull including wings of horns	190	
Height of skull anterior to orbit	100	
Vertical diameter of orbit, about	45	
Height of occiput, about	83	92
Depth of mandible under $P_{\frac{2}{2}}$	29	
Depth of mandible under $M_{\frac{1}{1}}$	30	
Depth of mandible under heel of $M_{\frac{3}{3}}$	32	
Length of upper molar-premolar series	99	109
Length of upper premolar series	45	46
Length of upper molar series	59	63
Length of lower molar-premolar series	110	
Length of lower premolar series	43	
Length of lower molar series	67	
Length of neck articulated		390
Length of atlas	77	77
Length of axis including odontoid process	91	87
Length of third cervical including processes	74	74
Length of cervical 4	80	80
Length of cervical 5	80	80
Length of cervical 6		80
Length of cervical 7		67
Length of humerus	237	
Greatest diameter of head of humerus	63	
Transverse diameter of distal end of humerus	46	51
Length of radius	237	246
Antero-posterior diameter of olecranon of ulna	46	
Length of metacarpal		215
Length of proximal phalanx		47
Length of medial phalanx		28
Length of ungual phalanx		40
Height of ungual phalanx		21
Length of tibia		305
Length of astragalus		47
Width of astragalus		31

ungual phalanges are high and narrow. The tibia is long and is slender below.

Throughout the skeleton there is a general resemblance to that of *Antilocapra*, though the bones are all heavier. There are, of course, many differences in detail. The most striking differences are in the teeth and the posterior portion of the skull.

Restoration and Habitat.

The restoration of *Dromomeryx* here given (Plate LXI) was made from two portions of skulls and skeletons, numbers 827 and 1542 of the Carnegie Museum Catalogue of Vertebrate Fossils. The scapulæ, most of the dorsal vertebræ, the caudal vertebræ and the length of the femur and the size and proportions of the lateral metapodials are conjectural. The bones of the skeleton are individually heavier than those of *Antilocapra* and the Virginian deer, but the skeleton is gracefully proportioned. Evidently *Dromomeryx borealis* was about 5 feet (1.5 meters) long, over 3 feet (97 cm.) high at the shoulder. The head, neck, and limbs are long, but not extremely so in proportion to the size of the body. The only features which are very striking are the long heavy horns with thin, peculiar wing-like processes behind the orbits. These must have given to the animal a very peculiar appearance, especially when viewed from in front. The eyes were evidently large.

Dromomeryx was well adapted to life in the open country. It could undoubtedly run swiftly, quickly detect the approach of danger, and, with its powerful horns, defend itself against its carnivorous adversaries. It had not, like *Pronomotherium* of the same beds, strongly hypsodont molars, and, like nearly all of the *Merycoidodonts* (Oreodonts) a deep mandible for the attachment of heavy muscles which were used in the mastication of coarse vegetable food. It probably occupied, in part, the same habitat as the camels (*Procamelus*, etc.) and the horses (*Merychippus?*), etc., which were found in the same beds.

Dromomeryx from the Lower Madison Valley in Montana.

In the collection from the Lower Madison Valley in Montana, a portion of a skull (Figs. 2 and 3), which was found in a bed of pure stream-sand may belong to the species *Dromomeryx borealis*. The size is nearly the same as that of the type, and of the various specimens

from Montana which have been referred to this species, as the fragment shows no characters which would distinguish it from the type-species, though it can only be referred provisionally to *Dromomeryx borealis*. It is much larger than any of the other specimens from the deposits in the Lower Madison Valley.

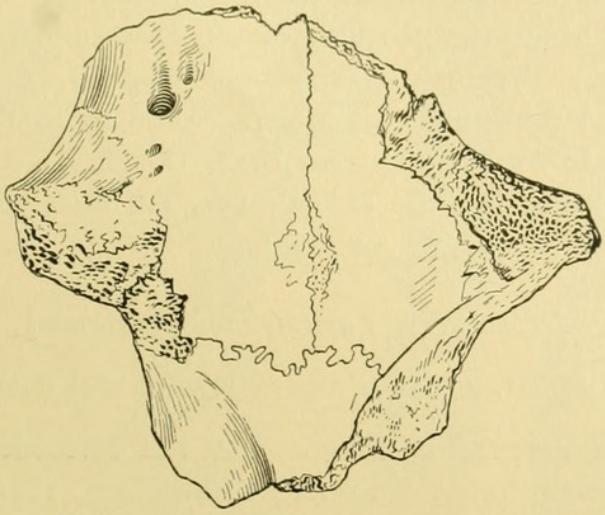


FIG. 2. *Dromomeryx borealis* (?). Portion of brain-case. Carnegie Museum Catalogue of Vertebrate Fossils No. 806. From Miocene deposits, Lower Madison Valley, Montana. One fourth natural size.

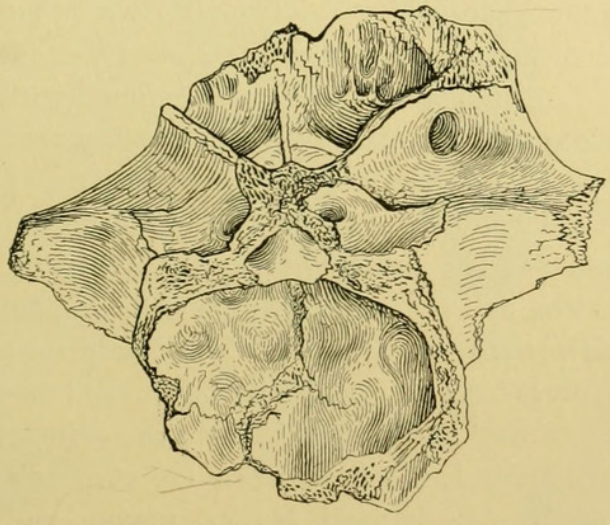


FIG. 3. *Drymomeryx borealis* (?). Portion of brain-case. Carnegie Museum Catalogue of Vertebrate Fossils No. 806. From Miocene deposits, Lower Madison Valley, Montana. One fourth natural size.

Four other specimens from the Lower Madison Valley are referred provisionally to *Dromomeryx*. They are in the collections in the Carnegie Museum and have the following numbers:

No. 705. Ramus of mandible with molar and premolar teeth. Type of *Palæomeryx americanus* Douglass.

No. 706. Last two upper premolars and greater portions of molars. Provisionally referred in the original description to *Palæomeryx americanus* Douglass. The reference of this to *Dromomeryx* is more doubtful than that of the other specimens.

No. 755. The greater portions of the lower molars in fragment of mandible. Type of *Palæomeryx madisonius*.

No. 2146. A third upper premolar. Referred in the original description to *Palæomeryx americanus* Douglass.

These specimens indicate animals very much smaller than *Dromomeryx borealis*.

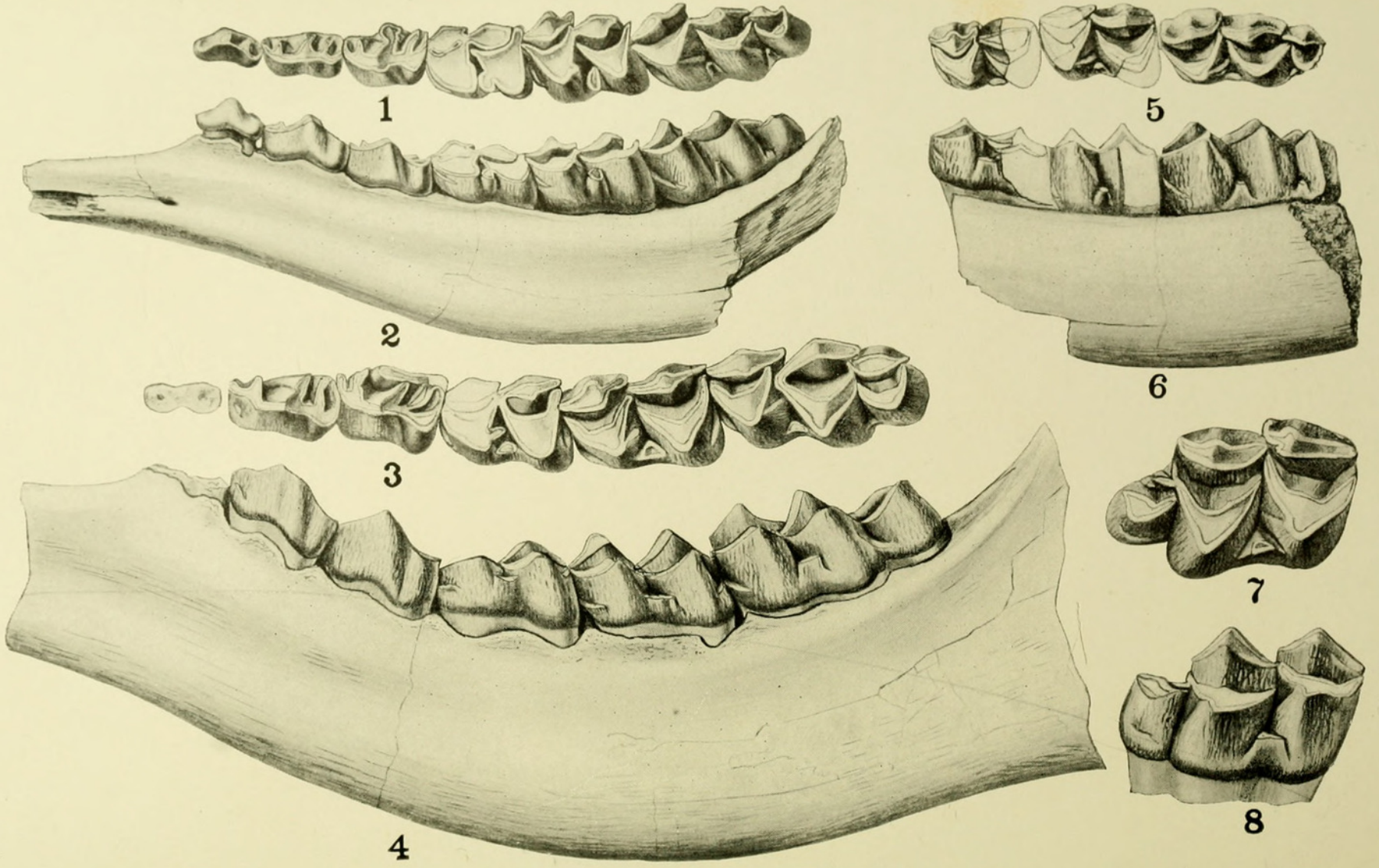
Dromomeryx ? americanus (Douglass).

(PLATE LXII, FIGURES 1 AND 2; PLATE LXIII, FIGURE 2.)

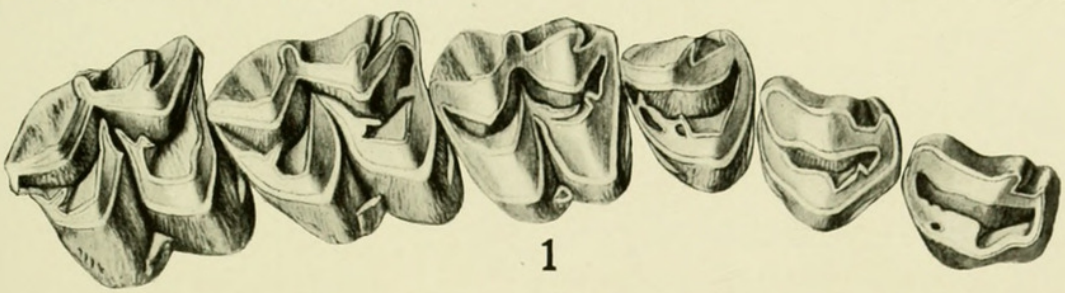
Palæomeryx americanus Douglass. "The Miocene Lake Beds of Western Montana," etc., University of Montana, 1899, Pages 20–23. Plate IV, Fig. 3.

The type of this species is the left ramus of a mandible (No. 705, Carn. Mus. Cat. Vert. Foss.) with the molars and premolars complete. The associated specimen consists of the last two premolars and the greater portions of the molars of the upper jaw (No. 706, Carn. Mus. Cat. Vert. Foss.). This specimen was associated with the type on account of its close similarity in size. The measurements of the teeth approximate those of *Dromomeryx antilopinus* Scott.

The ramus of the mandible is slender, nearly uniform in depth under the molar-premolar series, and curved downward as in *Dromomeryx borealis*. $P_{\overline{2}}$ is low and not large. From its principal cusp a sharp ridge extends downward and forward to the anterior portion of the tooth, where it curves inward. A similar but much longer and heavier ridge extends downward and backward from the principal cusp, sending a lobe inward about half way between the cusp and the posterior border of the tooth. $P_{\overline{3}}$ is much higher, longer, and broader, and there are two inwardly directed lobes before and two behind the principal cusp. The lobe which projects inward from the protoconid is directed backward. On $P_{\overline{4}}$ this element is much larger and forms a subcylindrical cusp opposite the protoconid. $M_{\overline{1}}$ and $M_{\overline{2}}$ have large median outer pillars attached to the anterior outer walls of the pos-



Figs. 1–2. Lower dentition of *Dromomeryx americanus* (Douglass).
Figs. 3–4. Lower dentition of *Dromomeryx borealis* (Cope).
Figs. 5–6. Lower dentition of *Dromomeryx madisonius* (Douglass).
Figs. 7–8. Lower dentition of *Palæomeryx bojani* H. von Meyer.
(All figures natural size.)



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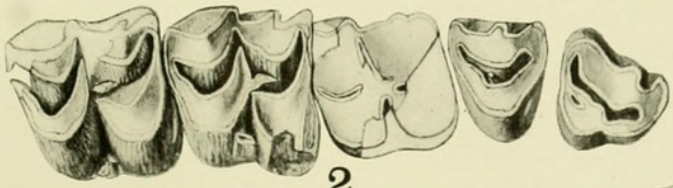

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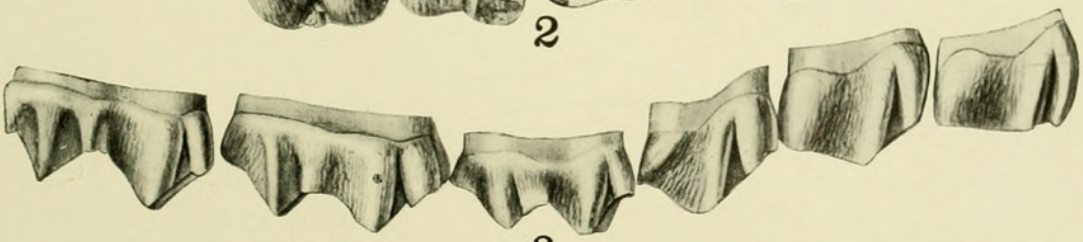

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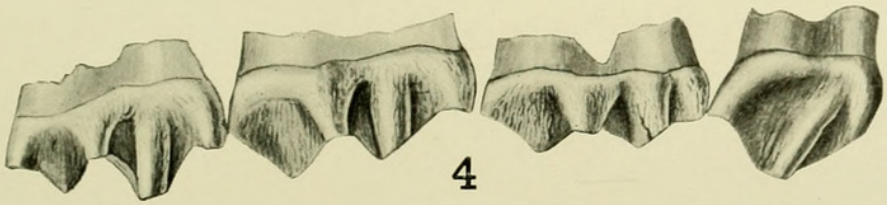

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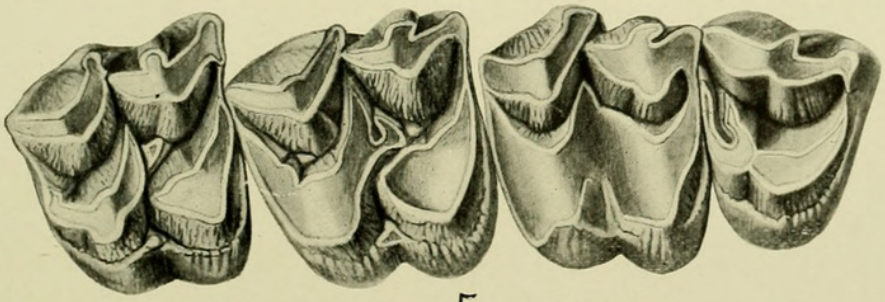

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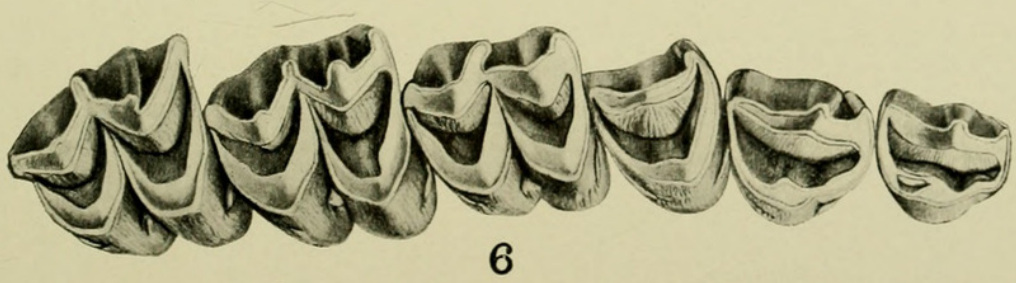

6

Figs. 1, 3, 6. Upper dentition of *Dromomeryx borealis* (Cope).
Fig. 2. Upper dentition of *Dromomeryx americanus?* (Douglass).
Figs. 4, 5. Upper dentition of *Palæomeryx bojani* H. von Meyer.
(All figures natural size.)

terior outer crescents. On $M_{\frac{3}{3}}$ the pillars between the outer crescents are small. In all the molars the antero-external crescents are connected with the postero-internal crescents on the triturating surfaces of the teeth. The first molar is much worn and the last molar slightly abraded.

The associated teeth (No. 706, Carn. Mus. Cat. Vert. Foss.) are very well shown in the figure. All of the teeth show a good deal of wear. The median inner pillars are fairly large. The enamel is more coarsely wrinkled than in the other specimens in the Carnegie Museum. The external surfaces of the postero-external crescent of $M^{\frac{2}{2}}$ is concave (not much ribbed) and the antero-internal crescent has not a long posterior horn. It is doubtful whether this is a species of *Dromomeryx*.

DROMOMERYX MADISONIUS Douglass.

(PLATE LXII, FIGURES 5 AND 6.)

Palæomeryx mædisonius Douglass. "The Miocene Lake Beds of Western Montana," University of Montana, 1899, p. 23.

The type of this species is a portion of a mandible with the three molars incomplete (No. 755, Carn. Mus. Cat. Vert. Foss.). Though this specimen undoubtedly represents a species distinct from *Dromomeryx americanus*, yet it is perhaps unfortunate that so small a fragment should be made the type of a species. The teeth in this species are proportionately higher than those of the other species from Montana, in fact there is a pronounced tendency in the teeth to become hypsodont, and the "*Palæomeryx*-fold" is unusually high and sharp. The median outer pillars are not large. The last tooth is worn nearly as much as in *Dromomeryx americanus*, but in all the molars the inner crescents are unconnected by wear with the outer crescents, except in the anterior portion of $M_{\frac{1}{1}}$. The enamel on the outer surfaces of the teeth is very much wrinkled, being completely covered with narrow ridges and valleys of about the same diameter.

A third upper premolar (No. 2146, Carn. Mus. Cat. Vert. Foss.) is provisionally referred to this species on account of its size.

AFFINITIES OF DROMOMERYX.

In his original description of "*Blastomeryx borealis*" Cope said: "While *Dicrocerus* [*Merycodus*] was probably the ancestor of *Antilo-*

capra, *Blastomeryx* was the ancestor of *Cervus* or *Cariacus*.''[12] In Volume XX of the *American Naturalist* (1886, p. 369) he calls ''*Blastomeryx*'' one of the deer-antelopes with persistent horns and deer-like dentition. Scott in his ''Mammalia of the Deep River Beds'' (page 167) says that the Deep River species ''is in many ways similar to the larger species of *Palæomeryx* from the Upper Miocene of Europe, and perhaps should be referred to that genus, though in the present state of knowledge it would be premature to do so. This doubt is justified by the fact that the mandibular dentition of *B. borealis* is still unknown, and we cannot therefore determine whether the lower molars possessed the very characteristic '*Palæomeryx*-fold,' and it is uncertain whether the type of the European species had developed horns.'' In 1899 Earl Douglass[13] expressed the opinion that the so-called *Blastomeryx borealis*, *B. antilopinus*, and the species which he described were really *Palæomeryx*.

In his paper, ''A Complete Skeleton of *Merycodus*,'' Matthew says: ''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. 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.''[14] On page 127 of the same paper Matthew says: ''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 crescent 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

[12] ''Descriptions of New Vertebrates from the Upper Tertiary of the West,'' *Proc Amer. Philos. Soc.*, Vol. XVII, 1877, p. 223.

[13] ''The Miocene Lake Beds of Western Montana,'' 1899, p. 20.

[14] *Bull. Amer. Nat. Hist.*, Vol. XX, Art. VII, March, 1904, p. 101.

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 velvet, unbranched, and without burr, but whether this was a permanent condition it would be unsafe 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*."

In the paper[15] from which I have just quoted, Matthew proposed *Merycodontidæ* as the name of a family equal in rank with the *Bovidæ*, *Antilocapridæ*, and *Giraffidæ* in the *Bovidæ typica*. In this new family he put the two extinct American genera *Merycodus* and *Blastomeryx* — not including the species which are described in the present paper as *Dromomeryx*. These he put in the family *Cervidæ*.

In a more recent paper by Matthew is the following: "*Blastomeryx antilopinus* Scott, 1894, and *B. borealis* Cope, 1878, with *Palæomeryx americanus* and *madisonius* Douglass, 1900, belong to a larger, more brachydont 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 are of uncertain relationship."[16]

Without a long and painstaking study of the Ruminantia I would not wish to give an opinion as to the relationship of *Dromomeryx*. I may say, however, that I agree with Dr. Matthew in his last statement, quoted above. *Dromomeryx* at present undoubtedly stands, like *Antilocapra*, by itself, and it may well be that the ancestors of the latter were no very distant relatives of the former, but the proof is wanting. As before implied the general skeletal structure of the two is very similar, the most striking differences being in the teeth, the brain-case, and the proportions of the bones. For comparison with *Palæomeryx* a re-study of the European in connection with the American forms is needed. The ruminants however illustrate very well the

[15] *Ibid.*, pp. 103–104.

[16] "Osteology of *Blastomeryx* and Phylogeny of the American Cervidæ," *Bull. Amer. Mus. Nat. Hist.*, Vol. XXIV, June, 1908, p. 546.

fact that the very wealth of individuals and species brings one into confusion when forming phylogenetic trees. When there were fewer known, this seemed a comparatively easy matter, but the discovery of more complete material and of hitherto unknown forms nearly always destroys hypothetical genealogies and shows that they are only approximations to the truth.

If we class *Dromomeryx* with the existing *Cervidæ* it agrees with the Telemetacarpalia in possessing the distal ends of the lateral metacarpals. This group, according to Matthew, includes all of the *Cervidæ* of the new world. If Matthew's contention [17] be true, that *Leptomeryx*, *Blastomeryx*, *Mazama*, *Odocoileus*, and the large Nearctic Cervidæ are structurally and genetically connected, and were separated from the Cervidæ of the Old World; then there is no reason to believe that *Dromomeryx*, the affinities of which are doubtful, has any very intimate connection with European forms. It seems to the writer more probable, then, that instead of *Dromomeryx* furnishing any evidence of Miocene migration from Europe to America, it was derived from some unknown forms either from America, or from some other region outside of Europe; though, of course, the fossils that have been recovered from the most favored regions represent only a fraction of the many forms that lived in these regions, so that we cannot depend too much upon negative evidence.

GEOLOGICAL RELATIONS OF DROMOMERYX.

In Volume XX of the *American Naturalist* (1886, pp. 368 and 369) Cope gives lists of the faunæ of the Deep River beds of Montana and of the Cottonwood Creek (Mascall) beds of the Miocene of Oregon, both of which he includes in his Ticholeptus beds. *Blastomeryx borealis* is the only name common to these two lists. Professor W. B. Scott, however, doubts the specific identity of the specimens from the two localities. He says: "The presence of *Blastomeryx* would of itself be insufficient for the correlation of the two localities, but the identification of the species is not at all certain. Besides certain minor differences in the teeth, the limb bones from the Oregon beds indicate the existence there of two species, both of which are heavier than the Montana forms and more like others from the Loup Fork of Kansas." [18]

[17] *Ibid.*, pp. 546, 556, etc.

[18] "The Mammalia of the Deep River Beds," *Trans. Amer. Philos. Soc.*, Vol. XVII, 1893, p. 60.

In a recent letter to me Dr. W. D. Matthew writes: "The referred material from Oregon (Mascall) consists of upper jaws more or less incomplete, teeth, and limb and foot bones. It is very close to *B. borealis* although not identical specifically in my judgment."

Professor Scott found *Dromomeryx borealis* and *D. antilopinus* in the Deep River beds of Montana. Mr. Douglass found part of a skull not distinguishable from *Dromomeryx borealis* and two or three other species, referred to *Palæomeryx americanus* and *Palæomeryx madisonius* in the Miocene deposits of the Lower Madison Valley in Montana. He also found part of a skeleton of *Dromomeryx antilopinus* in the typical locality of the Deep River beds. In 1899 he found large portions of skeletons in the Flint Creek beds in Montana. Dr. Matthew has listed "*Palæomeryx*" in the Pawnee Creek beds of Colorado and the Santa Fe beds of New Mexico.

I give below a table showing the deposits in which the species, referred in this paper to *Dromomeryx*, have been found with some of the associated fossils which appear to be most characteristic. I think there is little doubt that these beds are, comparatively speaking, nearly related in time, though no two of the faunas may be exactly contemporaneous.

	Deep River, Montana.	Flint Creek, Montana.	Madison Valley, Montana.	Pawnee Creek, Colorado.	Mascall, Oregon.	Sante Fe, New Mexico.
Mylagaulus	X	X	X?	X		
Trilophodon	X?		X	X		X
Aphelops		X	X	X	X	X
Merychippus		X	X	X	X	X
Hypohippus	X	X?	X?	X		
Protohippus	X	X	X		X	
Pronomotherium		X	X			
Protolabis			X	X		
Procamelus		X	X	X		X
Blastomeryx		X	X	X		
Merycodus		X	X	X	X	X
Dromomeryx	X	X	X	X	X	X
Dromomeryx borealis	X	X	X			

I would for the present place these various deposits in the Upper Miocene, though some may be found to belong to the uppermost portion of the Middle Miocene of America. On account of the differences existing in the faunas of the Miocene of Europe and America

it may lead to confusion and misunderstanding to attempt to correlate the minor divisions of the American strata with those of Europe. The most of the fossils which are used in correlation appear, on closer study, to have been wrongly identified.

EXPLANATION OF PLATES.

PLATE LIX.

Dromomeryx borealis (Cope). One half natural size. (No. 827, Carn. Mus. Cat. Vert. Foss.)

PLATE LX.

Dromomeryx borealis (Cope).

Fig. 1. Left fore limb, front view. (No. 1542, Carn. Mus. Cat. Vert. Foss.)

Fig. 2. Left fore limb, external view. (No. 1542, Carn. Mus. Cat. Vert. Foss.)

Fig. 3. Humerus. (No. 827, Carn. Mus. Cat. Vert. Foss.)

Fig. 4. Tibia. (No. 1542, Carn. Mus. Cat. Vert. Foss.)

(*All figures one fourth natural size.*)

PLATE LXI.

Restoration of *Dromomeryx borealis* (Cope). One twelfth natural size. (Restored from specimens Nos. 827 and 1542, Carn. Mus. Cat. Vert. Foss.)

PLATE LXII.

Dromomeryx americanus (Douglass). Type of the species, from the Lower Madison Valley, Montana. (Carn. Mus. Cat. Vert. Foss. No. 705).

Fig. 1. Top view of teeth.

Fig. 2. Outer view of mandible.

Dromomeryx borealis (Cope). (No. 827, Carn. Mus. Cat. Vert. Foss.) This mandible was associated with the skull which is figured on Plate LIX.

Fig. 3. Top view of teeth.

Fig. 4. Outer view of mandible.

Dromomeryx madisonius (Douglass). Type of the species, from the Lower Madison Valley, Montana. (No. 755, Carn. Mus. Cat. Vert. Foss.)

Fig. 5. Top view of molars.

Fig. 6. Outer view of portion of mandible.

Palæomeryx bojana H. von Meyer. Sansan, France. (No. 2263A, Carn. Mus. Cat. Vert. Foss.)

Fig. 7. Top view of last molar.

Fig. 8. Outer view of same.

(*All figures natural size.*)

PLATE LXIII.

Dromomeryx borealis (Cope). From Madison Valley, Montana. (No. 1542, Carn. Mus. Cat. Vert. Foss.)

Fig. 1. Top view of molars and premolars.

Fig. 3. Outer view of the same.

Dromomeryx americanus? (Douglass).

Fig. 2. Top view of molars and last two premolars. (No. 706, Carn. Mus. Cat. Vert. Foss.)

Palæomeryx bojani H. von Meyer. From Sansan, France. (No. 2263, Carn. Mus. Cat. Vert. Foss.)

Fig. 4. Outer view of molars and last premolar.

Fig. 5. Top view of the same.

Dromomeryx borealis (Cope). Teeth of nearly complete skull. Lower Madison Valley, Montana. (No. 827, Carn. Mus. Cat. Vert. Foss.)

Fig. 6. Top view.

(*All figures natural size.*)