THE MASCALL FAUNA FROM THE MIOCENE OF OREGON

BY

THEODORE DOWNS

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(A contribution from the University of California Museum of Paleontology)

ABSTRACT

Three assemblages of fossils from the type Mascall area, the Crooked River area, and from the Gateway area in central Oregon contain identical taxonomic units and are considered to belong to the Mascall fauna. The Crooked River material has provided new specimens for study. Mammals from the Gateway area of Jefferson County are described for the first time. Much undescribed material stored in museums in the eastern and western parts of the United States has been reviewed and figured.

The Mascall formation, particularly in the type area, includes wind-blown and water-laid deposits of variable thickness. It was probably deposited in a shallow synclinal basin bordered by uplands and crossed by streams that meandered across flood plains between forests and grasslands.

A new species of a marmotlike rodent and a heteromyid resembling the Dipodomyinae are described. New material referable to the known carnivores, *Tomarctus rurestris* and *Leptarctus oregonensis*, is described. The study indicates that *Parahippus brevidens* (Marsh) is synonymous with *P. avus* (Marsh) and that *Merychippus insonesus* (Cope) is synonymous with *M. serversus* (Cope). *Merychippus quartus* is considered to be a *nomen vanum.*

The Mascall formation is believed to be transitional Hemingfordian (middle Miocene) and Barstovian (late Miocene) in age. There is no evidence for subdivision of the formation or the fauna.

INTRODUCTION

THE OCCURRENCE of fossil vertebrates in the rocks of the John Day Valley of north central Oregon has been recorded since the early 1870's. We are particularly indebted to Thomas Condon, who first stimulated serious scientific investigation of the ancient life of the John Day Basin. After his pioneer work other paleontologists, including Leidy, Cope, Marsh, Merriam, Gidley, and Stock, published extensive studies on the extinct mammals from the John Day, Mascall, and Rattlesnake formations of this region.

The purpose of the present study is to review the fauna of the Mascall formation. New, accurately documented material and previously undescribed specimens stored in various institutions throughout the country are described. Exact geographic allocations for many little-known localities have been established.

J. C. Merriam (1901, p. 306) was the first to describe the Mascall formation and to specify the type locality: "The typical exposure is near the Mascall Ranch, four miles below Dayville." He stated that the Mascall beds have been referred to as Cottonwood beds, Loup Fork beds, Ticholeptus beds, and Amyzon beds. He also presented an informative history of explorations in the Mascall formation and a list of pertinent literature. In 1907, Merriam and Sinclair gave the first comprehensive list of vertebrates considered to be from the area of the Mascall type fauna.

Maxson (1928) recorded a mammalian tooth from the Crooked River area; otherwise little has been reported from this region. E. D. Cope apparently had been in the general region, as indicated in his original notes in the American Museum. He mentions reaching the Crooked River and Logan's Butte and makes note of white strata equal to "?Loup Fork beds," but his published descriptions of fossils do not specify actual localities. Merriam (1901, p. 274) states that in 1882 Davis and Day worked for Marsh in Oregon and "their work seems to have been confined to the beds south of the Blue Mountains." Marsh's publications do not give enough data on localities to judge the significance of this statement, but examination of the Yale collections and associated data indicates that Davis and Marsh collected many specimens from the area south of the Blue Mountains, particularly in the Crooked River area.

No fossil mammals have been previously described from the Gateway area.

Merriam (1901) was the first to give a detailed account of the geologic relationships of the Mascall formation. Calkins (1902) wrote on the petrography of the John Day Basin, and Collier (1914) published a small generalized map covering much of the John Day Basin area. In 1925, Merriam, Stock, and Moody added data on the structure and geology of the Mascall formation. Coleman (1949), in an unpublished thesis (Oregon State College), completed an extensive study of the geology of the Picture Gorge Quadrangle, including much of the John Day Basin, but his study is concerned particularly with the John Day formation.

In the later 1920's, Merriam and Stock led field parties into the John Day and Mascall areas. Stock's description of a new carnivore, *Leptarctus oregonensis* (1930), is the last published contribution to the Mascall fauna. In a semipopular article (1946), he paid a fitting tribute to the wealth of natural phenomena present in the John Day Basin. He encouraged the Museum of Paleontology of the University of California and me to make use of the California Institute of Technology collections and to adopt the Mascall area as a general problem, although he and others from the Institute had been working in the region for many years.

Acknowledgments

I am much indebted to Lawrence E. Mascall and his family, owners of the property that includes the type area of the Mascall formation, for their many courtesies and hospitality. Other ranchers to whom thanks are extended for permitting our parties to collect on their land are George MacKay, Mrs. Katherine McDonald, E. Roy Moore, and Roy Wells. Philip F. Brogan, of Bend, Oregon, has contributed much to our knowledge of fossils from the Gateway locality. Through his newspaper writings, this friend of paleontology has made others aware of the interests and pleasures to be realized from the study of fossils and has donated valuable specimens to the Museum of Paleontology of the University of California.

I am especially indebted to Robert G. Coleman, formerly at Oregon State College, for the use of his Master's thesis on the "Geology of the Picture Gorge Quadrangle" and for his collaboration on problems concerning the geology of the Mascall formation, and to Dr. W. D. Wilkinson for his counsel. Dr. Thomas P. Thayer of the United States Geological Survey contributed useful information in connection with the field work.

This study was made under the guidance of Dr. R. A. Stirton, to whom I am greatly indebted for encouragement and assistance throughout the work. Dr. J. W. Durham, Dr. D. E. Savage, and Dr. S. B. Benson contributed valuable advice

and criticism, and Dr. R. W. Chaney offered helpful counsel on many phases of the problem. The following colleagues gave valuable assistance in the field and laboratory: Dr. M. Green, L. F. Marcus, F. H. Kilmer, Dr. R. W. Fields, and W. J. Pelletier.

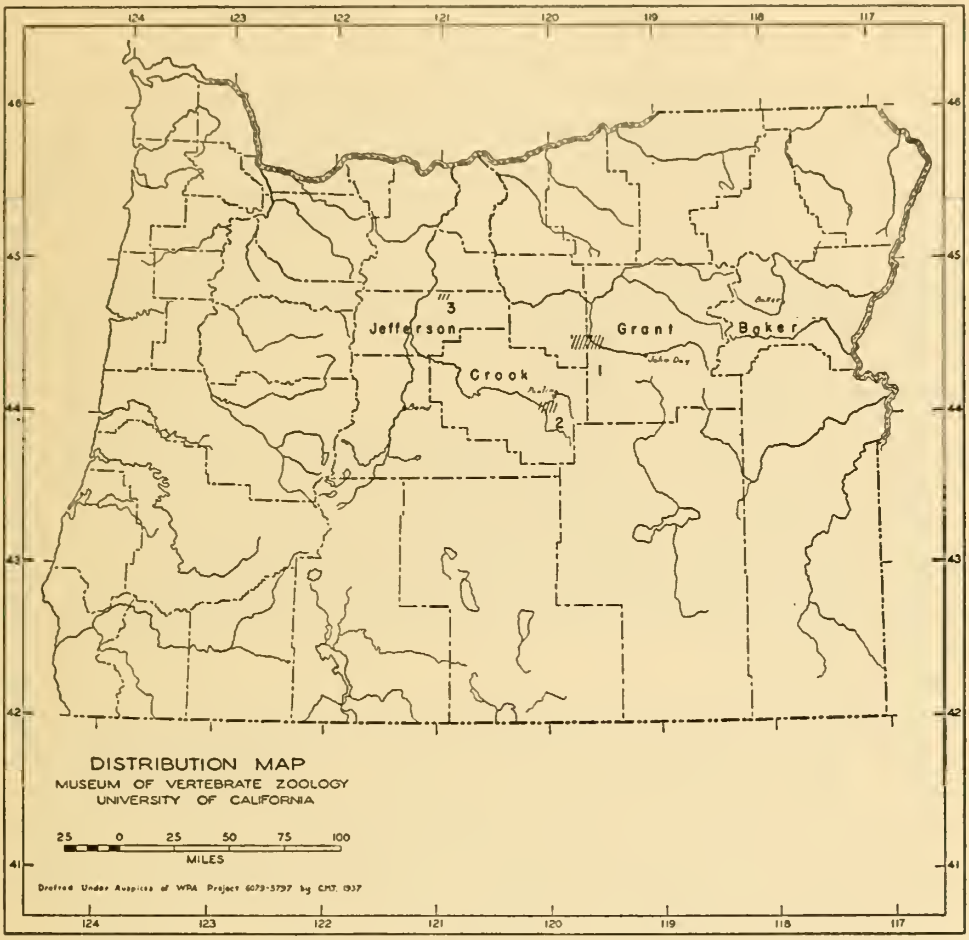


Fig. 1. Outline map of Oregon showing Mascall localities; 1, Mascall type area; 2, Crooked River area; 3, Gateway area. Based on a map prepared for the Museum of Vertebrate Zoölogy, University of California.

Among those who generously supported my study of specimens in various institutions were: the late Dr. Chester Stock, William Otto, Dr. Hildegarde Howard, G. P. Kanakoff, Dr. G. G. Simpson, Mrs. Rachel H. Nichols, Dr. E. H. Colbert, Dr. J. T. Gregory, Dr. A. S. Romer, Miss Nelda Wright, Dr. G. L. Jepson, Dr. David Dunkel, Dr. C. L. Gazin, Dr. Theodore E. White, Dr. J. LeRoy Kay, Dr. R. W. Wilson, Dr. E. C. Galbreath, Dr. J. A. Shotwell, and Dr. A. H. Miller.

After most of this monograph was completed as part of a doctoral dissertation, I was granted the privilege of continuing research on certain species of *Merychippus* under a National Research Council Fellowship. Reference to some material

collected during tenure of this fellowship, as well as some conclusions from subsequent research, are included in this paper. The assistance of my wife, Theda C. Downs, has been invaluable in the preparation of the manuscript. It was extreme good fortune to have Owen J. Poe prepare most of the drawings. The late Miss Annie M. Alexander contributed her deep interest and much appreciated financial support.

Methods

In the systematic section, material in addition to that previously described is recorded in the discussions of *Tomarctus rurestris* (Condon), *Parahippus avus* (Marsh), *Archaeohippus ultimus* (Cope), *Merychippus relictus* (Cope), *Merychippus seversus* (Cope), and *Dromomeryx borealis* (Cope). Detailed description of characters in such specimens is given only when they diverge from the diagnosis or general description or when they represent an element hitherto unknown. Each additional tooth of *M. seversus* is not described, although measurements are included in the statistical data. Where adequate material permits, data on central tendencies or variation in particular characters are presented for the defined populations or groups as a whole.

Tables involving analyses of qualitative and quantitative features (see table 9 for example) have been used to evaluate each character in the several species and to facilitate recognition of disparate materials.

I have attempted to obtain consistent records of mensuration and, whenever possible, have personally measured the specimens discussed. Metric vernier calipers, reading to 0.1 mm., were used for all measurements except those involving lengths beyond the capacity of the instrument (115 mm.). All measurements are given in millimeters.

Histograms have been used in comparing dispersals of quantitative values of like categories. Samples of less than ten were not treated statistically. Species have not been recognized by one statistical result, but by evaluation of all determinable values, both qualitative and quantitative. As a matter of practical application it would seem that if definite average tendencies of differences in two or three characters can be seen in teeth of two populations, there would be probabilities of the same relative degree of difference in soft parts, physiology, and breeding habits of the species or populations when alive.

In general, the criterion for a species determination has been dependent on the amount of knowledge of the group attained through research experience, the information gained from the published work of others, the quantity of material available, and the consideration of geologic and geographic factors. In little known families examined in this study, taxonomic categories do not have as sound validity as better known fossil groups or Recent ones, for example, species of *Tomarctus* as compared with better known species of *Merychippus*.

Terminology and symbols.—For purposes of clarity and consistency the following terms are defined:

Fauna and assemblage: The usage of Stirton (1936, p. 164) is followed in this paper; "... the term fauna is used to designate one or more identifiable fossils from given quarries, localities or stratigraphic levels. Assemblages of fossils from different localities are herein recognized as one fauna when the genera and species are identical." There are no identifiable species or genera from the Crooked River and Gateway localities that are not found in the type Mascall assemblage; therefore these assemblages constitute a part of the Mascall fauna until additional discoveries prove otherwise. The Skull Spring fauna contains some taxonomic units not found in any of the Mascall assemblages; hence it is not considered to be a part of the Mascall fauna though it may have existed as a nearly contemporary assemblage.

Population: "A local population, the essentially homogeneous group of actually or potentially interbreeding organisms at a given locality," Jepsen, Mayr and Simpson (1949, p. 458).

Symbols and abbreviations.

In tables and figures

- X Any individual value.
- N The total frequency of a given sample. Number of specimens examined.
- Σ Summation of quantities designated by a symbol following in parenthesis.
- M Arithmetic mean.
- σ Standard deviation as defined in Simpson and Roe (1939, p. 396).
- OR Observed range of values of a variate.
- V Coefficient of variation (*op. cit.*, p. 121).
- \+ A species is similar to the species compared in a particular feature.
- − A species is not similar to the species compared in a particular feature.
- o A species is nearly intermediate relative to comparison with another species in a particular feature (discussion in text often needed to specify a trend).

In text

- * Denotes species or specimen actually seen and measured by the writer.
- A.M. The American Museum of Natural History, New York.
- C.I.T. The California Institute of Technology, Pasadena.
- C.M. Carnegie Museum, Pittsburgh.
- M.C.Z. Museum of Comparative Zoölogy, Harvard.
- U.C.M.P. University of California Museum of Paleontology, Berkeley.
- U.S.N.M. United States National Museum, Washington.
- Y.P.M. Yale Peabody Museum, New Haven.

Taxonomic abbreviations

- cf. Similar to material compared, on the basis of limited specimens available.
- ? Reference to category uncertain. Placed immediately after category in question.

MASCALL FAUNA LOCALITIES

Type Mascall Area

Highway locality.

3043. U.S.G.S. Picture Gorge Quadrangle, 1925 ed., Grant Co., Oregon; N ½ of NE ¼, Sec. 29, T. 12 S, R. 26 E; grid zone G, 1,118,500–2,488,000; center of quad.; aerial photo, U.S.G.S. Spray

Quad., GS-CK, 1947, no. 20–31; along south bank of John Day River. Specimens found on surface below prominent, hard tuff (unit 6 of geologic section). *Merychippus seversus*, Blastomerycini. Pl. 9.

Type locality.

3059. Picture Gorge Quadrangle, Grant Co., Oregon; SE ¼, Sec. 19, T. 12 S, R. 26 E; grid zone G, 1,118,500–2,487,900; aerial photo, see 3043; North of Rattlesnake Creek. Bones in prominent, massive white to buff tuff (unit 5 of geologic section). *Mylagaulus* sp., ?*Parahippus*, *Archaeohippus ultimus*, *merychippus* cf. *relictus*, *Merychippus seversus*, *Merychippus* cf. *seversus*, *Dromomeryx borealis*. Pl. 9.

Fresh rock samples were taken at the type locality (3059) and a representative columnar section was measured by means of a Brunton compass, hand level, and tape. The localities chosen for the section are indicated on the map (see pl. 12, fig. 53, A-A′ and B-B′). This section differs from previous ones in the position of fossil mammals in the stratigraphic units. Merriam, Stock and Moody (1925, p. 50) state "... the vertebrate remains were obtained at a single horizon, ..." It is true that most of the fossils have been collected from unit 5 of the section which includes the beds commonly referred to as the "mammal horizon," but at V-4945 and V-4824, units 7 and 8 respectively, fragments of mammal bones were found.

In unit 5 of this section the sediments are difficult to interpret, but they are important in explaining how the mammals were deposited. The bed is of uniform lithology and is widespread; being traceable almost continuously from loc. 3059 to V-4943 (see figs. 48 and 50). It is usually 20–40 feet thick with a highly indurated bed above it. The buff-tuff bed (unit 5), characteristic of the type area, is a homogeneous blocky tuff consisting of well-sorted fine particles and minerals. Cross-bedding and graded bedding are lacking and considerable compaction of the tuff grains is evident. Two possible conclusions may be drawn from the evidence:

1. The bed was aeolian ash deposited on the dry land surface of a basin or valley, approximately 5 by 10 miles in area.
2. Alternatively, the ash fell from the air into a small lake or ponded stream.

The second possibility seems the most acceptable. Ash settling on land in the open might be expected to show aeolian-type cross-bedding, a feature which is not evident in the outcrops examined. If the ash fall was rapid or heavy enough and consisted of equigranular material, erosional effects would be negligible, and sorting probably would not be developed even in water. The Mascall beds in the type area may have been deposited in a basin, and some of the lacustrine deposits may have formed as a result of damming drainage channels during accumulation of ash and debris.

Merriam, Stock, and Moody (1925, p. 48) maintained that local variation of the sediments along the strike and frequent changes in thickness below a known horizon (probably unit 5 in the paper) suggest an unconformity between the Columbia River basalt and the Mascall formation. The best attitudes of the Columbia River basalt were obtained by sighting on the basalt flows at Picture Gorge from near the Mascall and McDonald ranches. The basalts dip SSW 15°–16°, whereas the southwesterly dips in the Mascall tuffs are as follows: loc. 3059, 13°; V-4824, 13°; V-4829, 12°; V-4828, 13°; V-4827, 13°; V-4835, 15°, with an average of 13°15′. At V-4833, near Dayville and the John Day River, the Mascall tuffs dip at a 3°–4° angle, but these attitudes may be due to slumping.

GENERALIZED SECTION AT THE TYPE AREA OF THE MASCALL FORMATION

Unit		*Thickness in feet*
11	Gray, buff, and tan, soft to indurated tuff; fine- to medium-grained; contains tuff balls, glass shards, quartz grains, and hornblende; water-laid, in part at least.	170
10	Buff, indurated tuff; basal six inches with rounded sand grains, pebbles, and cobbles, well sorted and cross-bedded; contains glass shards, tuff balls, manganese staining, and quartz grains; water-laid.	3½
9	Reddish to greenish bentonitic tuff.	23
8	Gray, reddish-brown, and green, soft to indurated tuff; dominantly bentonitic; possibly aeolian. *Mammal remains* in top two feet, V-4824.	54
7	Gray to buff, loosely consolidated tuff with prominent narrow lens of white ash containing broken glass shards; aeolian and water-laid. *Mammal remains* near top of unit, V-4945.	32
6	Gray-buff, highly indurated tuff with black, horizontal and vertical veins of psilomelane coated sandstone fill; contains hornblende, glass shards, and quartz grains; possibly water-laid.	9
5	Light buff, fine-grained, consolidated tuff; contains glass shards and quartz grains; characteristic blocky fracturing; aeolian lacustrine; traceable 9–10 miles. *Mammal remains* common; loc. 3059–V-4943.	40
4	Dark gray, fine-grained, laminated and cross-bedded, unconsolidated sandstone; contains glass shards and quartz grains; water-laid.	1
3	Yellow, gray, buff, and brown, soft to indurated tuff; vitric and bentonitic in part; contains glass shards, quartz grains, and some manganese; probably aeolian.	24
2	Blue-gray, vitric, fine-grained tuff; loosely consolidated; contains glass shards; probably aeolian.	1–2
1	Olive-green, gray, buff, and yellow, fine- to medium-grained, soft to indurated tuff; contains glass shards, hornblende, and quartz; bentonitic at base; water-laid and in part possibly aeolian.	33
	Total	390

Thayer and Ray state (1950, p. 89): "At Picture Gorge the later Miocene section consists of 21 olivine-bearing basalt flows totaling about 1500 ft., conformably overlain by about 2000 ft., of water-laid ashy beds that constitute the Mascall formation." The average dip of the beds in relatively undisturbed areas indicates, however, that there is at least a local difference in the attitude of the Mascall and the underlying Columbia basalts. The basalts may have been uplifted to some extent, and perhaps eroded, before the Mascall rocks were deposited. Possibly some folding took place after the extrusion of the Columbia River basalts, but basalts were certainly less deformed at the beginning of Mascall deposition than they are today.

Basin localities

V-4823. Picture Gorge Quardangle, Grant Co., Oregon; E ½ of NW ¼, Sec. 29, T. 12 S, R. 26 E; grid zone G, 1,119,300–2,492,300; aerial photo, see 3043; west of Cottonwood Creek, south of Rattlesnake Creek, and east of Little Rattlesnake Creek; above and south of the hard tuff and "mammal zone" horizon (unit 5 of geologic section). Fragments at various levels of southward-dipping brown to buff tuffs; main part of specimens from surface below brownish tuff. Possibly old loc. 3063. Small equid. Pl. 9.

V-4824. Across relatively level basin, west of V-4823 about 400 yards. Fragments from surface on dark brown and light-colored tuff (see unit 8 of geologic section). *Leptarctus oregonensis*, *Merychippus* cf. *relictus*. Pl. 9.

V-4945. NE ¼, NW ¼, Sec. 29, T 12 S, R. 26 E; N 13° E of V-4824; exposure relatively small, facing southeast and covered by considerable vegetation. Specimens found on surface wash under sagebrush and fragments in place in blocky tuff above; south of and above hard tuff (unit 7 of geologic section), along Rattlesnake Creek. Mylagaulidae. Pl. 9.

Confusion locality

V-4825. Picture Gorge Quadrangle, Wheeler Co., Oregon; S. ½, NE ¼, Sec. 36, T. 12 S, R. 25 E; grid zone G, 1,116,400–2,485,350; aerial photo, see 3043; southward-facing exposure about 100 yards north of road, horizontal, buff-brown tuff and gravels overlying the lighter, inclined Mascall (?) beds. Inclined beds are white, ash-gray, and light brown; most of material found on surface. Probably old loc. 815, possibly old locs. 817, 884, 887, 3042. *Merychippus* cf. *relictus* (records are not clear as to exact location of the *Merychippus* material). Pl. 9.

Birch Creek locality

V-4827. Picture Gorge Quadrangle, Wheeler Co., Oregon; S ½, NE ¼, Sec. 27, T. 12 S, R. 25 E; grid zone G, 1,113,500–2,487,000; aerial photo, U.S.G.S. Spray Quad., GS–CK, 1947, no. 20–32; exposure on both sides of road and Birch Creek. On west side of, and about 200 yards from road, exposure topped by Rhyolite flow of Rattlesnake; dipping, varicolored Mascall exposure. Mammals from the surface and seeds in place in blocky, buff-colored tuff. Probably old loc. 3049. *Merychippus relictus*, *Merychippus seversus*. Pl. 10.

The Birch Creek locality is close to an area of much faulting. Coleman (1949, p. 55) believed this post-Rattlesnake deformation to be caused by "*en echelon* gravity faults." The typical buff-tuff horizon (unit 5) is not positively identifiable in this area; but on the west side of Birch Creek, alternating tuff beds resemble those seen in the lower part of the type section. To the east, across the creek, soft, brown to reddish tuffs predominate. A few horse teeth were collected from a light-colored tuff, two to three feet above the coarse-grained, blue-gray vitric layer in this exposure.

McDonald localities

V-4828. Picture Gorge Quadrangle, Wheeler Co., Oregon; SE ¼ of NE ¼, Sec. 15, T. 12 S, R. 25 E; grid zone G, 1,113,500–2,490,250; aerial photo, see V-4827; North side of Rock Creek, about ½ mi. northwest of MacDonald's ranch and junction of Rock Creek and Birch Creek. Mammals in place or on surface of a light-colored tuff. *Arctomyoides oregonensis* n. sp., *Merychippus seversus*. Pl. 10.

V-4946. Picture Gorge Quadrangle, Wheeler Co., Oregon; SW ¼, NE ¼, Sec. 15, T. 12 S, R. 25 E; aerial photo, U.S.G.S. Spray Quad., GS–CK, 1947, no. 20–32; N 75° W of V-4828 about 1 mi. A specimen taken from surface; light-colored tuffs exposed. *Merychippus* sp. Pl. 10.

The tuffs containing the specimens at V-4828 are relatively soft and fine-grained and vary in color from brown to greenish. Glass shards are present, and in some samples these tuffs appear to be partly altered to bentonite. Limonitic staining is also common in this stratum. Below the mammal level, there is a layer of hard, brittle, shaley, sandy tuff containing glass shards, underlain by a layer of cross-bedded, fine- to coarse-grained sandy tuff. Laminated bentonitic tuffs occur below this sandy level followed by more sandy tuff with fragments of silicified wood stems; under this are layers of soft, yellow, tan, and gray tuffs. West of this locality (see white exposure west of V-4828 on aerial photo), there are more Mascall beds considerably lower in the section than the mammal-bearing bed at V-4828. In these beds there are extensive deposits of reddish tuffs containing crumbled remains of plants.

The vitric, cross-bedded layer of tuff below the mammal-bearing bed at V-4828 suggests similarity to unit 2 of the type section. Nowhere in the type area, however, are there coarse tuffs as thick as this unit. The hard shale between the fine tuff and vitric tuff is suggestive of deposition in a bog or small basin, and its high content of limonite may result from bacterial action (Rogers, 1937). Merriam, Stock, and Moody (1925, p. 51) cite the presence of siliceous shales and "earthy" tuff as evidence for "marginal lacustrine conditions" at a locality east of V-4943, in the MacKay ranch area; similar conditions may be indicated in the McDonald area. There is evidence of faulting and tilting of the Mascall beds between the type area and the McDonald area (V-4828), and as already mentioned, there may be considerable lateral variations in lithology. Perhaps the rocks at V-4828 were deposited in a small basin isolated from the type area.

Rock Creek locality

V-4829. Picture Gorge Quadrangle, Wheeler Co., Oregon; SE ¼, NW ¼, Sec. 24, T. 12 S, R. 25 E; grid zone G, 1,115,700–2,488,500; aerial photo, see V-4827; south of Rock Creek and Hy. 28 between junctions of Rock Creek and Birch Creek and John Day River and Rock Creek. Mammals found on south side of exposure. *Merychippus seversus.* Pl. 10.

Mammal material was found in the region of the prominent colored tuffs at the Rock Creek loc. V-4829 (see pl. 10). The bones were found only as wash at certain levels, but their concentration suggests that they came from near-by rocks. There are alternating beds of soft and hard laminated or nonlaminated tuffs; the mammals may have come from the softer, finer tuffs near the middle of the section. The typical buff-tuff horizon is not detectable. Slumping and faulting of beds is evident, especially east of V-4829. At one point fragments of a mastodont from the Rattlesnake were found scattered in loose gravels approximately 250–300 feet below the undisturbed Rattlesnake exposures.

Old Schneider Ranch localities

V-4830. Dayville Quadrangle, 1936 ed., Grant Co., Oregon; N ½, SW ¼, Sec. 25, T. 12 S, R. 26 E; grid zone G, 1,117,600–2,485,600; NE corner of quad.; aerial photo, U.S.G.S. Spray Quad., GS–CK, 1947, No. 20–29. Prominent exposure of massive, blocky, buff tuff (unit 5 of geologic section) with hard tuff above; fossils found on the west exposure; mammals in place and on slope below buff-colored tuff. *Merychippus seversus, Prodipodomys? mascallensis* n. sp., Carnivora sp. Pl. 11.

V-4831. South of V-4830 at 4.8 mi. point on pasture road to V-4830; an exposure of hard and blocky buff-tuff of mammal zone continuing apparently along strike of beds at V-4830; only a few square feet exposed, much of slope below tuff covered with vegetation. Mammals found on surface exposures. *Dromomeryx borealis.* Pl. 11.

V-4832. S ½, SE ½, Sec. 25, T. 12 S, R. 26 E; southeast of V-4830 along northwest side of intermittent stream; outcrop of hard and vertical, buff-colored tuff beneath part of knoblike surface feature facing south at relatively similar dip as at V-4830. Mammal fragments on surface. *Merychippus* sp., *Dromomeryx borealis.* Pl. 11.

Riverside localities

V-4833. Dayville Quadrangle, Grant Co., Oregon; center of SW ¼, Sec. 26, T. 12 S, R. 26 E; aerial photo, see V-4830; north of John Day River. Prominent typical buff tuff, blocky "mammal horizon" with hard tuff cap, 60–80 ft. lateral extent of exposure, beds flat-lying. Mammals in place and on vegetation-covered slope below tuff. *Hypolagus* cf. *vetus, Heteromyidae, Merychippus seversus.* Pl. 11.

V-4944. Dayville Quadrangle, Grant Co., Oregon; N ½, SE ¼, Sec. 26, T. 12 S, R. 26 E; aerial photo, U.S.G.S. Spray Quad., GS–CK, 1947, no. 20–29; about N 60° E from V-4835;

prominent, light-colored tuff exposures, mostly facing southwest; follow ravine from V-4835 north, going along its main course to the right. Specimens taken from vertical, light-colored tuff and on surface below exposure. *Merychippus?* Pl. 11.

V-4834. W ½, SE ¼, Sec. 26, T. 12 S, R. 26 E; E of V-4833. Tuff weathered and covered with vegetation; mammals on surface wash of slopes below buff tuff. *Hypolagus* cf. *vetus*, *Tomarctus rurestris*, *Parahippus avus*, *Merychippus seversus*, *Merychippus* sp., Oreodonta, sp., small ruminant. Pl. 11.

V-4835. NE ¼, SW ¼, Sec. 26, T. 12 S, R. 26 E; in next valley or gulch NE of V-4833. Mammals in place on slope below typical buff-tuff exposure; also in place in tuff; rounded, gravel-mantled hills above. *Merychippus seversus*, *Merychippus* sp., Oredonta, Camelidae, and *Dromomeryx borealis*. Pl. 11.

Localities V-4830, 4831, 4832, 4833, 4834, and 4835 bear the typical buff-tuff bed (unit 5 of the section). The vitric, granular, blue-gray tuff (probable "pumiceous sand" of Merriam, Stock, and Moody, 1925, and unit 2 of section) may be exposed at V-4830 and V-4832. There is considerable lithologic and stratigraphic resemblance to the type section at these localities.

MacKay Ranch localities

V-4941. Aldrich Mountain Quadrangle, 1943 ed., Grant Co., Oregon; NW ¼, NW¼, Sec. 4, T. 12 S, R. 27 E; grid zone G, 1,131,200–2,484,200, NW corner of quad. Specimen found on surface and above a hard layer of tuff; dip of the beds about 5° SE. *Parahippus?* Fig. 48.

V-4942. NE ¼, NW ¼, Sec. 4, T. 12 S, R. 27 E; grid zone G, 1,135,000–2,484,250; a few hundred feet NE of V-4941. Specimens taken on surface of weathered, light buff-colored tuff below a bed of vertical tuff. *Merychippus relictus*, *Merychippus seversus*, *Merychippus* sp. Fig. 48.

V-4943. SE ¼, NW ¼, Sec. 4, T. 12 S, R 27 E; grid zone G, 1,136,500–2,488,850. About 1 mi. from Stewart's Crossing east of V-4942; west facing, small exposure; specimens found on surface near top of sloping exposure above alternating light and dark-brown soft tuffs; below the tuffs, approximately 60 ft., a layer of gray sandy tuff. *Merychippus* sp. Fig. 50.

The buff tuff found at the type area is also present at locs. V-4942 and 4943. Slumping is again evident. At V-4943 there is a blue-gray, granular tuff, indurated. laminated, and vitric, possibly similar to that in unit 2 of the type area. The mammal remains at these two localities apparently were from a buff-tuff bed like that in the type area (unit 5), but thinner.

CROOKED RIVER ASSEMBLAGE

Beaver Creek locality

V-4948. U. S. Dept. Agriculture, Ochoco National Forest Map, 1942, Crook Co., Oregon: NW ¼, SE ¼, Sec. 18, T. 17 S, R. 23 E; 2.7 mi. west of Paulina, about 200 yards south of Beaver Creek. Specimens in place in white, blocky tuff and from surface of slope immediately to the west. Possibly old loc. 895. *Merychippus* sp. Fig. 50.

South Fork localities

V-4949. U. S. Dept. Agriculture, Ochoco National Forest Map, 1942, Crook Co., Oregon; SE ¼, Sec. 13, T. 17 S, R. 22 E; about ½ mile south of Paulina road, S 60° E from bridge at South Fork, Crooked River, and road leading to Paulina; exposures mostly covered by sage brush and junipers. Specimens on vegetation-covered slopes below scattered exposures of more resistant tuffs. Rhyolite flow at top of hill with most of material from middle of north slope of hill. Possibly old loc. 897. *Parahippus?*, *Archaeohippus ultimus*, cf. *Hypohippus*, *Merychippus relictus?*, *Merychippus?*, Camelidae, *Dromomeryx* sp. Fig. 50.

V-4950. SE ¼, Sec. 13, T. 17 S, R. 22 E; about 200 yards east of V-4949, across small valley. Fragments on surface of sage-covered tuff exposures. Possibly old loc. 896. *Merychippus?*, *Dromomeryx* sp., *Dromomeryx?*, Fig. 50.

Camp Creek locality

V-4951. U. S. Dept. Agriculture, Ochoco National Forest Map, 1942, Crook Co., Oregon; S ½, Sec. 17, T. 17 S, R. 22 E; 1.9 mi. E of U.S.B.M. 3566 on Paulina road and ½ mile S of B.M. no. S-482; on S side of ridge or divide between Camp Creek and Crooked River; S 30° W from B.M. no. S-482. Small bowl-shaped exposure facing south, about 50 yards in diameter; hard, yellow, white, and gray tuffs; specimens on surface. Soft tuffs above covered with talus and a capping of rhyolite flow at summit. Possibly old loc. 900. *Archaeohippus ultimus, Merychippus* cf. *relictus, Merychippus?*, Fig. 50.

Chaney (1927) has emphasized the close relationships of the stratigraphic sequence in the Crooked River Basin to that in the John Day Basin and has noted the lack of faunal evidence from which to interpret their relationships. We now have considerable fossil materials that assist in establishing correlations with the John Day Basin.

The geological relations are obscure at localities where fossils were found. At loc. V-4948 (old loc. 895) a fragment of *Merychippus* sp. was discovered in place in a tuff similar to unit 5 of the type section of the Mascall formation. Beneath this blocky tuff is a layer of gray, laminated, vitric tuff, possibly water-laid. On the slopes above these Mascall exposures are loose gravels of questionable source. North, across Beaver Creek and at the top of the hill, are flows of rhyolite apparently similar to those of the type Rattlesnake formation. At V-4948, the dip of the beds is about 12° to the west. Much buff to yellow, fine-grained tuff is exposed at this locality (V-4949, old loc. 897); the tuffs vary from coarse- to fine-grained and are not greatly indurated. At the crest of the slope is hard rhyolite similar to that of the Rattlesnake formation in the John Day Basin.

GATEWAY ASSEMBLAGE

V-3427. Data from Univ. Calif. Mus. Paleo. vertebrate locality catalogue specify specimens found in sections 32, 33, 34 and parts of sections 27, 28 and 29; T. 9 S, R. 14 E; from Willamette Base line; approximately 3 mi. SE of Gateway, Jefferson Co., Oregon; fossils found at several levels within 300 feet of volcanic ash exposures. Definitely located specimens came from a spot about a mile in a direct line from Gateway on small hill; cut by boundary line of S ½, SE ¼, Sec. 21 and N ½, NW ¼, Sec. 28, Madras Quadrangle, 1931 ed., Jefferson Co., Oregon; grid zone G, 992,150–2,516,650; E central part of quadrangle. Most of specimens from below prominent dark layer of hard, sandy to pebbly, brecciated tuff (?). Mustelidae or Procyonidae, *Parahippus?, Merychippus seversus, Merychippus?, Ticholeptus?, Camelidae.* Fig. 49.

According to Phillip F. Brogan (oral communication), the Gateway locality was found by Warren S. Hodge, now of the State Highway Department in Oregon.

E. T. Hodge, who published on the geology of the Madras Quadrangle and of north central Oregon (1940 and 1942), mapped the area from which the fossils were collected as the Madras formation (upper Pliocene). In the accompanying map legend, he describes the formation as follows: "... Horizontally bedded and partly consolidated sand, silt, gravel, agglomerates, mud flows, and stratified fluviatile deposits of volcanic materials; volcanic debris, mostly basic, resulting from ash showers of volcanoes; and a few beds of diatomaceous earth; several intercalated basalt flows; the highest flow, which forms the base of the Cascan formation." The formation thus differs from the Mascall in the presence of more basic ash, the intercalation of basalt flows, and possibly the greater abundance of gravels and agglomerates.

A partial lower molar of *Merychippus seversus* was collected on the west exposures at loc. V-3427, on the surface at a point between a stratum of coarse, brown tuff and a well-cemented gray-black, breccia (?) layer. The breccia (?), which is 10 feet thick, is a prominent marker. Mr. Brogan informed me that the horse teeth, that is, no. 32753, *M. seversus*, came from a level below this dark brecciated (?) bed.

In the Gateway area the beds containing fossil vertebrates occur above extensive Columbia River basalts. There appears to be much less tuff present in the Gateway rocks than in those containing the Mascall fauna of the John Day Basin. There are channel gravels apparently of later age on the west side of the valley that have yielded part of a rhinoceros mandible and teeth (not available for study). These gravels were probably brought in by torrential stream flow at a later date than the Mascall age material.

The mammals recorded from the various localities described above represent fossils considered to be critical and identifiable; not all specimens collected are listed.

Localities from which material in other museums was collected are not listed above since much of the data for this material is very general and is given in conjunction with the specimen numbers in the systematic part of the text.

Personal letters written by T. S. Davis to O. C. Marsh indicate that the locality called Bully Creek, Baker County, Oregon (see discussion under material of questionable faunal affinity, cf. *Tomarctus rurestris*) on Yale Museum tags probably refers to the large creek in northern Malheur County, Oregon, an area adjacent to and south of Baker County. The letters and accession numbers are associated with the Yale Peabody Museum specimens, and discussed in this study as coming from Bully Creek. Davis notes that the packages containing the fossils with these numbers came from "the Malheur River Region." Since Bully Creek is part of this drainage area and is very near the Baker-Malheur County line, there may have been some confusion as to the county involved when the records were entered. There may be beds of Mascall age in the northern Malheur County area, but to date, the age relationship of the Bully Creek fossils has not been established.

All recorded fossil localities have not been precisely located in the field, particularly those from Yale Peabody Museum and National Museum specimens, but it is believed that there is definite resemblance of fossil material from the general localities—Crooked River, Cottonwood Creek, and Grant County—to material of typical Mascall species. I consider the allocation of these materials to the Mascall as reasonably accurate. Animals poorly represented, though possibly new, have not been included unless definite locality data were available.

MODE OF DEPOSITION OF FOSSILS

As Merriam (1901) observed, teeth and isolated bones comprise the greater part of collections from the Mascall formation. Two discoveries made in 1948 constitute probable associated skeletal material, the *Merychippus* sp. (no. 39183) and *Dromomeryx borealis* (no. 39185). The bones of these animals were arranged in an irregular manner within a bed about a foot in thickness; but in the palaeomerycid, the fragments of ribs and vertebrae were posterior to the head fragments. Fossils varying from fragments to several bones have been found at all levels in the buff tuff (unit 5 of the type section). There was no evidence to show concentration of material at the base of the 20–40 foot stratum or at any other point. In the type section at V-4823 and V-4824, some of the material may have been derived from either water-laid or aeolian beds, but a few were in place in what has been considered a water-laid deposit. However, none of the fossils to be described show much abrasion by water transportation.

Many teeth occur on talus slopes below the blocky tuffs. The tuffs weather and fall as angular blocks, breaking up as they hit the slopes or roll downward. Many fossils in these blocks are thus shattered. Alteration of the Mascall tuffs to soft bentonite promotes rapid erosion, so that many fossils become exposed during and after rainy seasons, and many specimens lie loose on the surface. It is often impossible to state precisely from which stratum they came.

The area occupied by the type Mascall beds was a broad shallow basin, probably occupied by small streams and lakes. Water-laid deposits in addition to aeolian beds suggest that the region may have been flooded during wet seasons, and the plants of the Mascall flora suggest humid conditions. A lake may have been formed in the basin, particularly in the type area and in the Old Schneider Ranch region, as a result of blocking of drainage channels by heavy ash showers. The position of the fossils in the individual beds may be possibly explained by the fact that many animals were overcome by dust storms; some may have died from poisoning by acid waters, from silicosis, or by drowning in flooded streams (Williams, 1948). Many bodies may have floated into the lake, gradually disintegrating and settling to various levels in the tuffs. The bones that were trapped at different levels may have descended through water-suspended ash; but the weight of the body or bone might have caused eventual compaction of ash particles beneath it and thus held it in suspension.

As a consequence of the apparent humid environment, it seems probable that there was relatively continuous sedimentation in the area and that the effects of wind erosion were negligible. The presence of hackberry nutlets in Mascall beds is significant in this connection, for today this plant often frequents stream borders (Chaney, 1925, p. 55). The nutlets in some Mascall localities were found in clusters that were not confined to bedding planes; presumably they floated into a lake and settled to its floor.

MASCALL FAUNAL LIST

Gastropoda†
Lymnea stearnsi Hannibal
Pisces
Plioplarctus septemspinosus Cope
Reptilia
Clemmys saxea Hay
Mammalia
Hypolagus cf. *vetus* (Kellogg)**
Mylagaulus sp.**
Mylagaulidae gen. and sp. indet.**
Arctomyoides oregonensis Downs n. sp.**
Prodipodomys? mascallensis Downs n. sp.**
cf. *Prodipodomys? mascallensis***
Peridiomys cf. *oregonensis* (Gazin)**
Heteromyidae gen. and sp. indet.**
Tomarctus rurestris (Condon)**
Amphicyon cf. *sinapius* Matthew
Leptarctus oregonensis Stock**
Mustelidae or Procyonidae
Carnivora sp.
Parahippus avus (Marsh)**
*Parahippus?***
Archaeohippus ultimus (Cope)**
*Archaeohippus ultimus?***
cf. *Hypohippus*
Merychippus relictus (Cope)**
Merychippus cf. *relictus***
Merychippus seversus (Cope)**
Merychippus cf. *seversus***
Merychippus sp. indet.**
Merychippus?†
Equidae gen. and sp. indet.**
Ticholeptus obliquidens (Cope)**
Ticholeptus?
Oreodonta gen. and sp. indet.**
Miolabis transmontanus (Cope)**
Camelidae gen. and sp. indet.**
Blastomerycini gen. and sp. indet.**
Dromomeryx borealis (Cope)**
Dromomeryx sp.
Dromomeryx?

Crooked River Assemblage List

Tomarctus rurestris
Parahippus brevidens
Parahippus?
Archaeohippus ultimus
Archaeohippus ultimus?
cf. *Hypohippus*
Merychippus cf. *relictus*
Merychippus seversus
Merychippus sp. indet.
Merychippus?
Camelidae
Dromomeryx borealis
Dromomeryx sp.
Dromomeryx?

Gateway Assemblage List

Mustelidae or Procyonidae
Parahippus?
Archaeohippus ultimus
Merychippus seversus
Merychippus sp. indet.
Ticholeptus?
Camelidae

DESCRIPTION OF MATERIAL

Phylum Mollusca
Class GASTROPODA
Family LYMNAEIDAE
Lymnaea stearnsi Hannibal

Stearns (1906) briefly described and figured *Limnaea maxima* "nom. prov." from Mascall beds, three-quarters of a mile east of Belshaw's ranch, John Day Valley. Baker (1911) synonymized *L. maxima* with *Lymnaea stearnsi* Hannibal; Hannibal (1912) declared *Limnaea maxima* a *nomen nudum;* and Henderson (1935) used the name *Lymnaea stearnsi.* Stearns referred to several casts taken with the type; the University of California collections contain a holotype (no. 10002) still im-

† This list is based on fossils collected at all the localities.
** Found in the Mascall type area assemblage.

bedded in a piece of the matrix. Both Stearns and Hannibal concluded that this gastropod was a lacustrine type.

The name *Lymnaea contracosta* Cooper has been applied to specimens supposedly from "Mascall Lake beds, Oregon" by Hannibal (1912). Henderson (*op. cit.*, p. 236) cites the reference as ". . . Mascall Lake beds, Ore., both Miocene (latter doubtful)." The parenthetic phrase apparently questions the age designation for the Mascall. The Mascall is certainly Miocene; however, there may be justification for questioning the allocation of this invertebrate material (U.C.M.P. no. 12147, loc. 904) to the Mascall. This is not a Hannibal locality reference; according to the museum files, loc. 904 is the number for a John Day faunal locality now designated V-4847.

Phylum CHORDATA
Class PISCES
Family CENTRARCHIDAE
Plioplarchus septemspinosus Cope

Cope (1889*b*, pp. 625–626) describes this species as coming from "shales near Van Horn's ranch on the John Day River, Oregon"; probably 12.5 miles east of Dayville.

The cotypes are four individuals, according to Cope. At the United States National Museum the type catalogue shows no. 4996 to be the type, but there are eight separate slabs of rock bearing fossil fish with this number. One tag attached to some scrap material in the tray refers to a locality fifteen miles south of Mt. Vernon, Oregon. It is fairly certain that these fish were not collected near any beds known to contain mammals. There is no evidence of any difference in time between the existence of the mammals and the fish, but the geographic separation suggests a different ecologic facies. Cope did not figure the type specimens, but Eastman (1917) has done so.

Class REPTILA
Family EMYDIDAE
Clemmys saxea Hay

Several plates of the carapace of *Clemmys saxea* were described by Hay (1903, p. 241) with U.C.M.P. no. 2192 as the type specimen. The material was found in beds on Beaver Creek, V-4950 (old loc. 896), which happens to be in the Crooked River region and is a probable Mascall locality.

There is a discrepancy in the literature concerning the stratigraphic position of *C. saxea* from the Mascall and *Clemmys hesperia* from the Rattlesnake. Hay (1903) specifically records the type of *C. saxea* as from the Mascall beds. In 1908 (p. 290) he erroneously recorded *C. saxea* from the Pliocene Rattlesnake formation and *C. hesperia* from the Mascall. The reverse is actually the case and on pages 292 and 294 of the same paper (1908), he has given the data correctly. In this same paper (p. 294) he has indicated that U.C.M.P. nos. 2179 and 522, assigned to *C. hesperia*, may belong to *C. saxea:* "there being some doubt regarding the level in which they occurred." Consequently, the validity of two species might be questioned.

According to Pope (1946) one of the four American species of *Clemmys* is entirely aquatic; the others exhibit amphibious habits tempered by varying degrees of terrestrialism.

Class MAMMALIA
Order LAGOMORPHA
Family LEPORIDAE
Hypolagus cf. *vetus* (Kellogg)
(Fig. 2)

The California Institute of Technology collection has several isolated permanent rabbit teeth which were collected in the Mascall by Tom Weatherford in 1926; C.I.T. no. 4002. The teeth of this genus, other than $P_{\bar{3}}$, are not particularly diagnostic (Dice, 1917). One tooth in the C.I.T. collection is a $P_{\bar{3}}$; Dice considered the Virgin Valley and Thousand Creek specimens of *Hypolagus* to be conspecific although he noted that the shape and size of $P_{\bar{3}}$ in the Virgin Valley specimen might be significantly different. The posterior lophid of the Mascall $P_{\bar{3}}$, C.I.T. no. 4002, has a greater anteroposterior diameter than in the Thousand Creek specimen. In this characteristic it is much like the Virgin Valley form. The lateral grooves extend to the base of the tooth and consist of a large anterior and a smaller posterior reëntrant groove.

Fig. 2. *Hypolagus* cf. *vetus*, C.I.T. no. 4002, loc. Mascall type area (?): *a*, right $P_{\bar{3}}$; *b*, *c*, and *d*, right lower teeth; *e*, upper molar; × 5.

The measurements of no. 4002 indicate that the tooth resembles the Virgin Valley or Thousand Creek specimens, although there may be a slight tendency for closer affinity with Virgin Valley material.

Another specimen collected by a University of California party, no. 39299 from loc. V-4832, an upper molar, and no. 39294, a fragmentary mandible bearing $P_{\bar{4}}$, are very similar to *H. vetus*. The upper teeth have the reëntrant angle extending halfway across the tooth, and the enamel is coarsely folded within the angle much as *H. vetus*. Because of the scarcity of readily identifiable material, I hesitate to assign the fossils to *H. vetus*, but the genus can be recorded from the Mascall since nos. 39299 and 39294 are from known localities.

Measurements.—Anteroposterior and transverse diameter respectively; C.I.T. no. 4002; $P_{\bar{3}}$ 2.9 and 2.8, other lower teeth (a) 2.7 and 2.7, (b) 2.7 and 2.6, (c) 2.7 and 2.6, (d) 2.5 and 2.6, an upper tooth 2.3 and 3.8, U.C.M.P. no. 39299 (an upper), 2.1 and 3.8, (a) lower 2.5 and 2.8; U.C.M.P. no. 39294 $P_{\bar{4}}$, 2.5 and 2.9 with depth of ramus below $P_{\bar{4}}$, 12.2.

Order RODENTIA
Family MYLAGAULIDAE
Mylagaulus sp.[1]
(Fig. 3)

Recent collecting in the Mascall type area has produced a fragment of a mandible bearing $dp_{\bar{4}}$, $M_{\bar{1}}$, and $M_{\bar{2}}$ in place; U.C.M.P. no. 39292, loc. 3059. This specimen

[1] The original reference to *Mylagaulus* (Merriam and Sinclair, 1907) refers to a specimen collected by L. S. Davis for K. A. von Zittel. It may be (or it was?) in a European collection.

is characterized by the impression of part of an alveoli of P_4 in the bone; by a $dp_{\bar{4}}$ with five small lakes and two roots present and no suggestion of hypsodonty; by an $M_{\bar{1}}$ with five lakes and a median internal groove; and $M_{\bar{2}}$ with a mesofossettid recently formed and a hypoflexid still present.

Measurements.—$dp_{\bar{4}}$ anteroposterior diameter 3.4, transverse diameter 3.4; $M_{\bar{1}}$ 3.7, 3.2 respectively; $M_{\bar{2}}$ 2.1, 2.4 respectively.

Matthew (1924, p. 77) believed there were "progressively deciduous molars in the Mylagaulidae." He stated that the rudimentary $M_{\bar{1}}$ drops out in early stages of wear, this being followed by the loss of $M_{\bar{2}}$ and then $M_{\bar{3}}$. Therefore he would have considered the $dp_{\bar{4}}$, described above, to be $M_{\bar{1}}$, the $M_{\bar{1}}$ to be an $M_{\bar{2}}$, and the $M_{\bar{2}}$ to be an $M_{\bar{3}}$. Dorr (1952) has argued convincingly that Matthew's interpretation is in error. I have followed Dorr's system of terminology. Particularly perti-

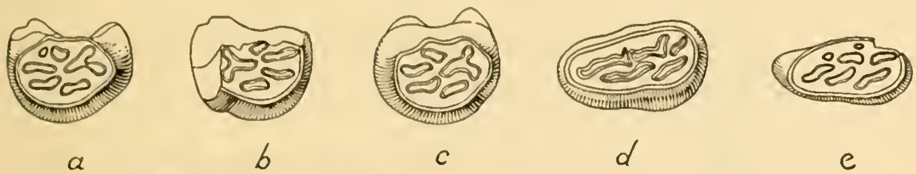


Fig. 3. *Mylagaulus* sp., Y.P.M. nos. 14311 and 14310, loc. Crooked River area: *a*, *b*, and *c*, $P^{\underline{4}}$; *d* and *e*, $P_{\bar{4}}$; × 2.

nent arguments presented by Dorr, which may be applied equally well to the Mascall specimens, are: the $dp_{\bar{4}}$ (Matthew's $M_{\bar{1}}$) is brachyodont, it possesses two distinct roots; and the $M_{\bar{1}}$ (Matthew's $M_{\bar{2}}$) is hypsodont, and the $M_{\bar{2}}$ (Matthew's $M_{\bar{3}}$) is reduced but also hypsodont. Radiographic pictures (X rays) show this to be true of U.C.M.P. no. 39292. The last molar, whatever it be, $M_{\bar{2}}$ or $M_{\bar{3}}$, is not well developed. It seems unlikely that the $M_{\bar{1}}$ (of Matthew's terminology and $dp_{\bar{4}}$ in this paper) would have been first hypsodont, then turned brachyodont (with prominent roots) in its evolutionary history.

Among specimens in the Peabody Museum, there are some isolated teeth, Y.P.M. $P^{\underline{4}}$ no. 14311 and two $P_{\bar{4}}$'s, no. 14310, of a characteristic *Mylagaulus* from the Mascall formation at Paulina Creek in the Crooked River region in Oregon. In no. 14311, $P^{\underline{4}}$ possesses six lakes, one tending to divide. The $P_{\bar{4}}$'s show three large, elongate external lakes, and one specimen has two large and two small internal lakes. The other has two large internal lakes, one beginning to separate.

Comparisons with the figures of *Mylagaulus* cf. *laevis* from the Skull Spring, Gazin (1932), reveal very little difference in tooth pattern. In fact many teeth nearly duplicate the Mascall specimens; for example, C.I.T. no. 516, $P_{\bar{4}}$, and no. 14310; another $P_{\bar{4}}$ bearing the number 14310 is also similar to no. 14311 of the Mascall (see Gazin, pl. 6). In comparing *M. pristinus* from the Virgin Valley, it was found that most of the premolars bear fewer lakes than in the Mascall specimens; but one specimen from the Virgin Valley has seven lakes instead of the usual five. The Mascall specimens are possibly advanced over the Virgin Valley material in pattern, but are not more elongate. Stirton (1939, p. 631) observes that the stages of evolution in the teeth of these rodents are relatively little known and are inadequate for use in correlation.

TABLE 1

Comparative Measurements

(in millimeters)

	Arctomyoides oregonensis		*A. arctomyoides*	*Palaearctomys montanus*	*Protospermophilus quatalensis*		
	U.C.M.P. no. 39093	U.C.M.P. no. 40241	C.M. no. 741	C.M. no. 740	C.I.T. no. 30	C.I.T. no. 32	C.I.T. no. 31
Length of diastema of mandibular ramus (in line with ap. of ramus, nearest point)	10.0	....	12.5	18.1	6.4	....	
Depth of ramus across mental foramen	6.4	....	....	....			
Depth of ramus below anterior end of P_4	8.8	....	11.6	16.4	....		
Depth of ramus below middle of M_1	8.5	....	11.1	16.1	7.4		
Length of mandibular tooth row	11.9	....	15.1	15.3	10.2		
Greatest length, P_4	2.7	2.5	3.1	3.1	2.0	....	2.0
Greatest length, M_1	2.9	....	3.5	3.4	(2.4)	2.6	2.4
Greatest length, M_2	3.2	....	3.7	3.6	(2.5)	2.7	2.7
Greatest length, M_3	4.0	....	4.0	4.2	....	3.7	....
Greatest width, P_4 at hypocone	2.5	2.4	3.1	3.6	2.2	1.8	2.0
Greatest width, P_4 at protocone	2.2	2.0	....	3.1	....		....
Greatest width, M_1	3.3	....	4.2	4.0	2.6	2.8	2.8
Greatest width, M_2	3.4	....	4.3	4.7	2.6	3.0	3.0
Greatest width, M_3	3.3	....	3.8	4.3	....	2.8	....
Depth and width of lower incisor at alveolus	3.7	....	3.5	7.3			
Width of lower incisor at alveolus	2.0	....	2.0	3.5	....		
Width mandibular ramus at mental foramen	3.9	....	6.4	8.2			
Distance from base of P_4 to mental foramen	6.1	....	5.5	3.8			
Depth of ramus to M_2	8.2	....	11.5				
Depth of diastema posterior to mental foramen	6.7	....	....	14.2			
Width of ramus below M_1	5.0	....	....				
Approximate length of symphysis	7.0	....	....				

Measurements.—Anteroposterior and transverse diameter respectively; Y.P.M. no. 14311, P^4 8.6 and 5.3; Y.P.M. no. 14310, P^4 8.1 and 5.5, P^4 10.3 (at base) and 4.3, P_4 9.8 and 5.3.

Mylagaulidae gen. and sp. indet.

A distal part of a humerus, U.C.M.P. no. 40271, loc. V-4945, may be referable to Mylagaulidae. It is smaller than the humerus described by Gregory (1942) from the Big Spring Canyon fauna and possesses an epicondylar foramen. The humerus is wide and has a wide supinator crest. It could belong to an animal the size of a late Miocene *Mylagaulus*.

TABLE 2

Comparative Table of Ratio Indices

	A. oregonensis	*A. arctomyoides*	*P. montanus*	*P. quatalensis*	*S. venturus*	*C. (O) gidleyi*
Mandible						
length diastem / length tooth row	.88	.81	1.18	.62	...	...
depth below M_1 / length diastem	.80	.89	.89	.73	...	...
M_3						
greatest length / greatest width	.84	.95	.94	.76	.92	.76

Family SCUIRIDAE

Arctomyoides oregonensis Downs, n. sp.

(Figs. 4–6)

Holotype.—Left mandibular ramus with complete dentition and without posterior ramus. U.C.M.P. no. 39093.

Paratype.—Left P_4 of another individual. U.C.M.P. no. 40241.[2]

Type locality.—U.C. loc. V-4828.

Fauna.—Mascall. *Age.*—Late Hemingfordian or early Barstovian (transitional).

Diagnosis.—Smaller than *Arctomyoides arctomyoides* (Douglass), larger than *Protospermophilus quatalensis* (Gazin); diastem and alveolus nearly equal length; masseteric crest ascends opposite protoconid of M_3;[3] M_3 relatively much narrower than in *A. arctomyoides* and *P. quatalensis*, M_1 and M_3 with large protolophid or protoconulid and prominent valley between protolophid and metalophid; minute hypoconulid on M_1 and M_2; protoconid and hypoconulid of equal size and height; faint vertical groove on posterolingual side of M_3.

Description.—Anterior mandibular ramus shallow relative to length with ventral part defaced exposing incisor, anterodorsal tip of ramus level with alveolar border; mental foramen midway between anterior extension of ramus and anterior border of P_4 and near dorsal surface, dorsal surface of lateral anterior region of diastem flattened; masseteric fossa, although somewhat defaced, shows depth with a rounded, moderately narrow anterior tip (limits not distinct) fossa situated immediately below posterior border of hypoconid of P_4; ventral masseteric crest more pronounced than dorsal crest; angle of descent of masseteric crest and its continuation as angle of ramus gradual from horizontal axis of ramus; angle of ramus not strongly inflected medially;

[2] Collected a year later than type at the same locality.

[3] Dental terminology follows Bryant (1945) for the most part.

dorsal crest or margin of masseteric fossa ascends along border of vertical ramus opposite protoconid of M_3; mandibular foramen deep with well-developed crests.

Wear on teeth: P_4; slight on posterior side of tip of protoconid and metaconid, median side of hypoconid; M_1, heavy on protolophid, protoconid, and hypoconid, slight on metaconid, mesoconid, and posterolophid; M_2; heavy on protolophid, protoconid, and hypoconid, slight on metalophid, metaconid, mesoconid, and posterolophid; M_3 heavy on protolophid, protoconid, metaconid, and slight on mesoconid of M_3.

Incisor much deeper than wide (depth 3.7 mm., width, 2.0 mm.), finely striated on anterior surface; cheek teeth become increasingly large from P_4 to M_3; M_3 much narrower in proportion to its width than other teeth (see measurements); crowns more hypsobrachyodont then brachyodont.

Fourth premolar: tends to be molariform but still retains somewhat trapezoid outline; smaller than molars; metaconid larger and slightly higher than protoconid; protolophid descends obliquely anteriorly, does not connect with metaconid; protoconulid minute, closely appressed to median side of protoconid (this may be simply the protolophid); ectolophid well in from the labial margins near median line; mesoconid distinct; hypoflexid deep and wide anteroposteriorly; ectostylid absent; posterolophid well developed and crescentic with a slight elevation, possibly an entoconid; mesostylid minute; talonid basin deep and narrow. Paratype P_4, as above but more heavily worn and without protoconulid; protolophid questionable.

First molar: parallelogram shape, but labial border directed more lingually than lingual border; greater width than length (see table 2); metaconid smaller basally but higher than protoconid; protolophid and metalophid enclose a valley and both are separated by grooves from base of metaconid; protoconulid present (or enlargement of protolophi), well worn and adjacent to protoconid; protoconid and hypoconid similar in size and height; ectolophid elevated and well in from labial border; hypoflexid wide anterposteriorly; ectostylid small and mesoconid well developed; mesostylid at the base of metaconid larger than ectostylid; distinct entoconid at anterointernal termination of crescentic posterolophid; talonid basin deep and narrow; a slight indication of a small, worn hypoconulid near base of hypoconid.

Second molar: similar to M_1 except slightly larger in size; labial border parallels lingual border; slightly more prominent ectostylid; smaller mesostylid; somewhat larger hypoconulid near base of hypoconid.

Third molar: longer than wide (see table 2); metaconid only slightly higher than protoconid: protoconid and hypoconid equal in size and height, and larger than metaconid; well-developed protolophid apparently without an enlargement or protoconulid; metalophid only a spur at base of protoconid. Compared with M_1 and M_2: ectolophid elevated but more marginal, ectostylid smaller, hypoflexid V-shaped at base, hypoconid and protoconid larger. In M_3, irregular surface on depression within posterior part of talonid basin; only slightly suggested on surface of basin in M_1 and M_2; small distinct notch on posterointernal margin of posterolophid extending as a groove ventrally to base of crown; mesostylid and entoconid apparently absent; mesoconid as large as in M_2.

Comparisons.—Characters that place the fossil in the family Sciuridae are the vertical angle of the jaw and a squirrellike dental pattern with absence of median transverse loph.

Arctomyoides oregonensis shows the greatest affinity to the terrestrial squirrel and chipmunk division of Bryant (1945) on the basis of the following features: diastemal part of mandible relatively long and shallow; anterior end of mandible level with or above level of alveolar border, M_1 and M_2 hypoconid not larger than protoconid; entoconid indistinct (but present), entoconid region rounded; posterolophid running from hypoconid toward parametaconid in an even arc.

The total number of specimens and species representing the two genera *Palaeaarctomys* Douglass and *Arctomyoides* Bryant is five, but the importance of the criteria for their generic distinction may be overrated when we consider the inadequacy of one sample for each species. Specimens representing Miocene rodents are not common in any fauna. Because the genera might be slightly vague in their identities, an attempt was made to evaluate the distinctions between *Palaearctomys* and *Arctomyoides*.

Palaearctomys differs from *Arctomyoides* in having a skull larger than other North American sciurids except *Marmota*, cheek teeth small in proportion to size of skull, anterior edge of ascending ramus more ventral in position, and a proportionally deep anterior ramus or diastemal region.

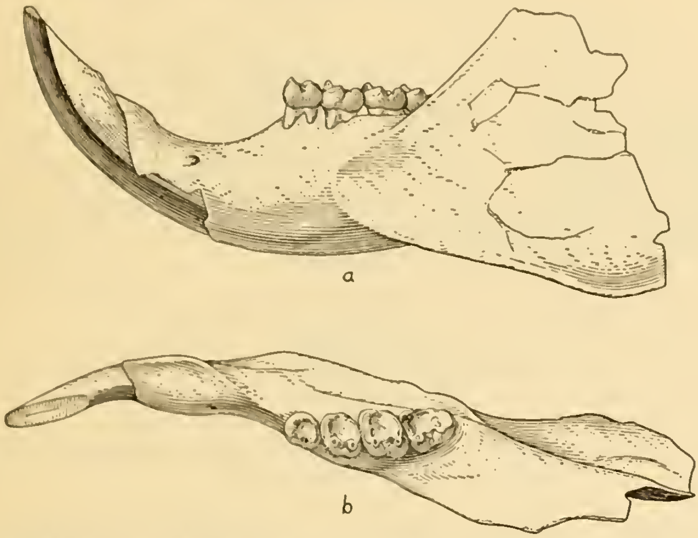


Fig. 4. *Arctomyoides oregonensis* Downs n. sp., holotype, U.C.M.P. no. 39093, loc. V-4828: top, external view of mandible; bottom, occlusal view of mandible; × 4.

Palaearctomys resembles *Arctomyoides* in incisors crenulate with median groove, P^3 small, parastyle on P^4 large, mesostyle similar and well developed, lingual position of ectolophid, and mesoconid and entoconid present.

The difference in proportions of the mandible seems particularly significant; the dentition displays important similarities and suggests that the two genera are related but generically distinct. The resemblance of *Palaearctomys* to *Marmota* has been established (Bryant, 1945), especially in the presence of the strong protolophid as a transverse crest and the parallelogram shape of $M_{\overline{1}}, _{\overline{2}}$. *Palaearctomys* is apparently distinct from *Marmota* in smaller P^4 than M^1, lower-crowned cheek teeth, mataloph on M^1, ^{2} incomplete, and P^4 trapezoid. The species *A. oregonensis* has similar generic tendencies as itemized for the genus *Arctomyoides*, wherein comparable elements are present. The difference between *A. arctomyoides* and *A. oregonensis* in position of the dorsal border of the masseteric crests would be a generic distinction according to Bryant, but I believe, in this instance, that only one character exhibited in one specimen is insufficient for determination of generic status.

Unfortunately the mandible of *Palaearctomys macrorhinus* Douglass* is not

* This symbol denotes a species or specimen that I have actually seen and measured, and so throughout.

known, though Bryant has erroneously figured a mandible of *Palacarctomys montanus* Douglass as *P. macrorhinus*. Even the validity of the species might be questioned. The difference seems to be in the skull proportions. *P. montanus* is described as having a larger and relatively more slender skull and relatively larger incisors than *P. macrorhinus*. It is possible that this difference is a matter of age or sex; the cheek teeth are absent in *P. montanus*, and an age difference is not

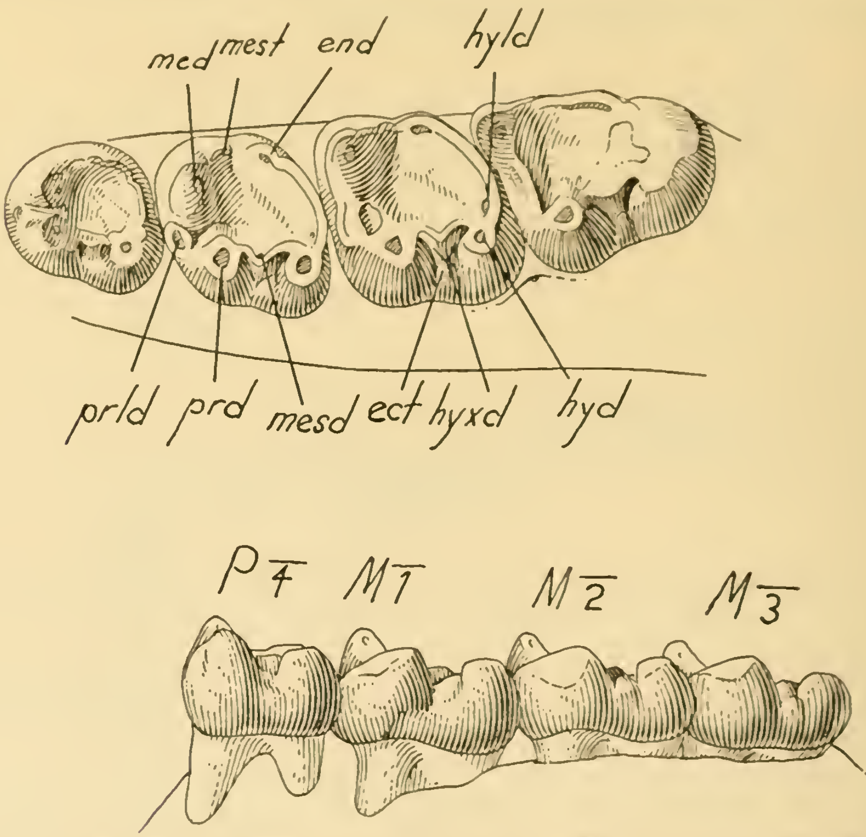


Fig. 5. *Arctomyoides oregonensis* Downs n. sp., holotype, U.C.M.P. no. 39093, loc. V-4828; top, occlusal view of lower dentition; bottom, external view; × 8. Legend: med = metaconid, mest = mesostylid, end = entoconid, hyld = hypoconulid, hyxd = hypoflexid, ect = ectostylid, mesd = mesoconid, prd = protoconid, prld = protolophid, hyd = hypoconid.

readily checked. Without better material at hand, including a mandible, the status of these species might as well remain as it is until more information is available. One point of interest is the presence of two closely related genera, *Palacarctomys* and *Arctomyoides*, in the same fauna. In another part of this study, mention is made of possible evidence for two ages represented in the Madison Valley fauna; the presence of *Pliocyon ossifragus* Douglass may be an example of a possible Pliocene genus. It appears that *Palacarctomys*, too, could be of that age.

Palacarctomys vetus (Marsh)* of the Miocene or Pliocene of Nebraska is of questionable status. Bryant did not examine the specimen. The features of significant resemblance to *A. arctomyoides* are the proportions of the incisors, lingual position of ectolophid, wide hypoflexid, and presence of entoconid. It is particularly distinct in its larger protoconulid and greatly expanded hypoconid on $P_{\overline{4}}$; in the absence of hypoconulid, mestotylid, mesoconid, and ectostylid; shorter diastem with sharp descent of dorsal surface; mental foramen closer to P_4; and greater hypsodonty. The upper and lower incisors are deeply grooved.

Measurements.—*Palaearctomys vetus*, anteroposterior and transverse diameter respectively; Y.P.M. no. 10323 $P_{\overline{4}}$ 3.0, and 3.2, $M_{\overline{1}}$ 3.1 and 4.1, $M_{\overline{2}}$ 3.2 and 4.2.

Many characters are present in *A. oregonensis* that show outstanding resemblance to *A. arctomyoides:* hypsobrachyodont teeth, tendency to parallelogram shape of $M_{\overline{1}}$ and $_{\overline{2}}$, equal size of hypoconid and protoconid, well-developed elevated ectolophid, small ectostylid, large mesoconid on $M_{\overline{1}}$–$M_{\overline{3}}$ and large mesostylid on $M_{\overline{1}}$, ratio of length of tooth row to depth of ramus, and wide hypoflexid. *A. arctomyoides* is particularly distinct in proportions of $M_{\overline{3}}$, ventral position of mental foramen, ascent of vertical ramus opposite $M_{\overline{2}}$, more trapezoid $P_{\overline{4}}$, and greater size.

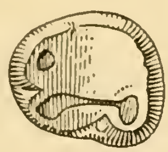


Fig. 6. *Arctomyoides oregonensis* Downs n. sp., paratype, U.C.M.P. no. 40241, loc. V-4828, occlusal view left $P_{\overline{4}}$; × 8.

*Protospermophilus quatalensis** (Gazin) from the Quatal Canyon, Lower Pliocene, Clarendonian, of California, shows some resemblance to *A. oregonensis,* but is distinct in smaller size, more rhomboidal occlusal outline of $M_{\overline{1}}$ and $M_{\overline{2}}$, much shorter diastem in proportion to length of alveolus, more trapezoidal shape of $P_{\overline{4}}$ with slightly more appressed protoconid and metaconid, uninterrupted protolophid and metalophid on $M_{\overline{1}}$ and $_{\overline{2}}$, less elevated and more marginal ectolophid, hypoflexid narrower, smaller protoconulid and protolophid on $M_{\overline{1}}$ and $_{\overline{2}}$, no mesastylid on $M_{\overline{1}}$, separate slip of anterior masseteric fossa (Bryant, 1954, p. 351), and absence of an ectostylid. Characters that tend to show resemblance to *P. quatalensis* are: lack of an inward slant of labial margin of molars, ventral position of anterior and of masseteric fossa, ratio of depth of ramus to length of tooth row, equal protoconid and hypoconid, and presence of mesoconid and entoconid.

Protospermophilus tephrus (Gazin), *P. angusticeps* (Matthew), and *P. malheurensis* (Gazin) from the Upper Miocene, Barstovian, are not represented by mandibles. *P. tephrus,* according to Gazin (1932), is smaller than *P. quatalensis,* nearing *Sciurus ballovianus* Cope in size and therefore possibly smaller than *A. oregonensis. P. malheurensis* and *P. angusticeps* are apparently no larger than *P. quatalensis,* which is smaller than *A. oregonensis.* This can be judged in part by comparing the length of the maxillary tooth row and the mandibular tooth row: *P. quatalensis* lower alveolus, 10.0 mm.; *P. malheurensis* upper alveolus, 10.5 mm.; *A. oregonensis* lower alveolus, 15.4 mm. If Bryant's proposal to place these four species under the same genus is valid, we might assume that features in the mandibles of *tephrus*, *angusticeps*, and *malheurensis* would show similar distinction from *A. oregonensis* as does *P. quatalensis*.

Scharf (1935) has referred a right mandible to Sciurid sp. from Sucker Creek. Bryant has suggested (1945, p. 341) that it is not a member of the family Sciuridae. It differs from *A. arctomyoides* in the heavier ramus, more posterior termination of masseteric fossa with less prominent ventral crest, and more flattened fossa. *Sciurus* cf. *aberti* from the upper Snake Creek apparently has a deeper jaw and is larger.

Citellus primitivus Bryant* of the Lower Madison Valley formation of Montana is distinct from *A. oregonensis* in its smaller size (length diastema 8.5, tooth row 9.2), more acute masseteric fossa, much greater length of mandibular tooth row relative to length of diastem, more posterior mental foramen, more compressed incisor (width 1.2, depth 3.7), shorter and more marginal hypoflexid, absence of ectostylid, and more angular posterolophid.

Citellus ridgwayi Gazin of the Upper Miocene, Barstovian, cannot be compared since it is represented by a skull. It is smaller than *Protospermophilus quatalensis* (see Gazin, 1932) and therefore is probably smaller than *A. oregonensis*.

Discussion.—Bryant has suggested that there are certain features of the dentition possibly indicative of primitive condition in sciurids (1945, p. 365). Of these primitive tendencies, the following correlate to some degree with *A. oregonensis* and, in a lesser extent, with *A. arctomyoides:* hypsobrachyodonty; $M_{\overline{3}}$ longer than wide; appressed protoconid and parametaconid on $P_{\overline{4}}$; small protolophid on $P_{\overline{4}}$; talonid nearly as high as trigonid; presence of mesoconid, mesostylid, entoconid; hypoconid of $M_{\overline{3}}$ large; and possibly small size.

Advanced characteristics are indicated (*loc. cit.*) in a high, well-developed median or lingual ectolophid with consequent reduction in size of talonid; parallelogram-shaped $M_{\overline{1}}, _{\overline{2}}$; tendency for molariform $P_{\overline{4}}$; and anterior position of masseteric crest below $P_{\overline{4}}$. These features are not only advanced, but tend toward characters found in the *Marmota* line or at least in *Palaearctomys* and in *Arctomyoides*.

A. oregonensis is more closely allied to *Arctomyoides arctomyoides* than earlier sciurids, yet it may be not far from the basal stem of the terrestrial squirrel section (see *op. cit.*, p. 384). *A. arctomyoides* comes from the lower Madison Valley formation, which may correlate with late Barstovian or late Miocene (in part) according to Wood *et al.* (1941), whereas *A. oregonensis* is from the earlier Mascall fauna of transitional Hemingfordian—Barstovian or middle to late Miocene age. *Protospermophilus*, living in the late Miocene, and *Arctomyoides* may have been derived from an earlier common ancestor.

A. oregonensis was buried under somewhat different conditions than those indicated in the area containing the greater concentration of mammals at loc. 3059. The lithology suggests (see p. 206) that the rocks in this section were mostly waterlaid in a small basin with a stream outlet. *A oregonensis* may have been living near the water and was simply trying to escape from the volcanic dust and died in the attempt. Since there is so much morphological distinction between this specimen and recent sciurids, it would be logical to assume that habitat preferences and food requirements could have been different.

Family HETEROMYIDAE

Prodipodomys? mascallensis Downs, n. sp.

(Figs. 7–9)

Holotype.—Incomplete left mandible with well-worn I, P_4–M_3, diastem and horizontal ramus with part of external side, only anterior part of angular and coronoid; remainder of mandible absent. U.C.M.P. no. 39094.

Type locality.—V-4830.

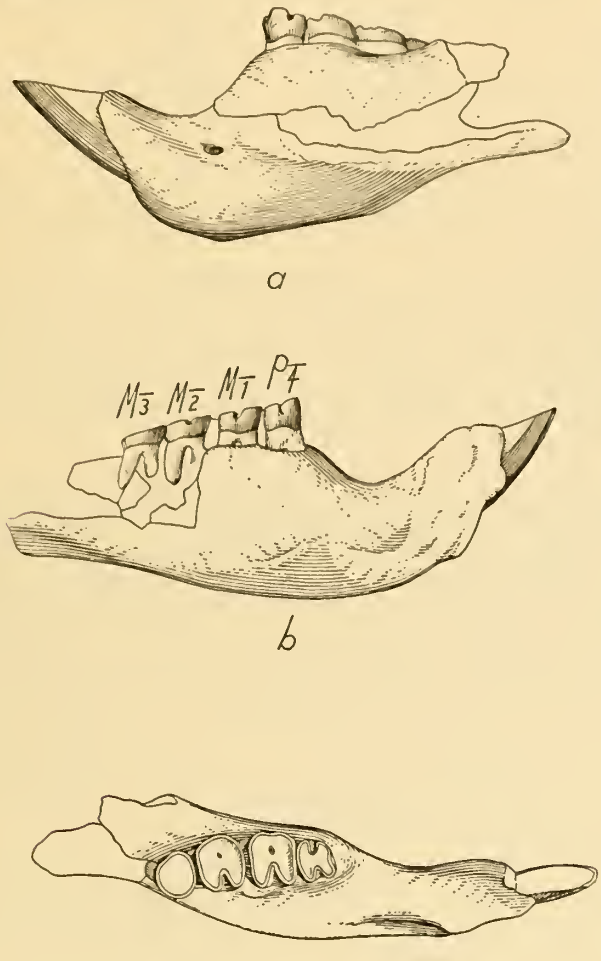


Fig. 7. *Prodipodomys ? mascallensis* Downs n. sp., holotype, U.C.M.P. no. 39094, loc. V-4830: *a*, external view of mandible; *b*, internal view of mandible; *c*, occlusal view of mandible; × 5.

Fauna.—Mascall. *Age.*—Late Hemingfordian or early Barstovian (transitional).

Diagnosis.—Postsymphyseal diastem shorter than length of tooth row; ramus below P_4, nearly as deep as length of tooth row; moderate ridge for masseteric lateralis, mostly horizontal and near mental foramen; brachyodont to hypsobrachyodont though rooted; P_4 with X-pattern, anterior lophid narrower than posterior lophid and with distinct reëntrant on anterior margin, with probable two short roots; M_{1-2} with incipient H-pattern and two (possibly 3) roots; M_3 slightly smaller than M_2 and larger than P_4 with two roots (possibly 3).

Description.—Mandible: diastem relatively stout and angular on ventral margin; mental foramen midway between incisor and $P_{\bar{4}}$ and slightly dorsal to mid-line of jaw; masseteric lateralis ridge moderate size, horizontal and terminating above foramen; internal base of coronoid with moderate depression between coronoid and M_3, but no pit present; masseteric medialis impression moderate, ventral, and horizontal.

Measurements of Prodipodomys ? mascallensis n. sp.

a. Length of tooth row	4 8
b. Length of diastem	4 2
Index b/a	.87
c. Depth ramus at center of diastem	3 5
d. Length of alveolus	5 0
e. Depth ramus below $P_{\bar{4}}$	4 7
Index e/a	9 7
f. Greatest length $P_{\bar{4}}$ (moderate wear)	1 0
Greatest width $P_{\bar{4}}$	1 2
Greatest length $M_{\bar{1}}$	1 4
Greatest width $M_{\bar{1}}$	1 4
Greatest length $M_{\bar{2}}$	1 3
Greatest width $M_{\bar{2}}$	1 5
Greatest length $M_{\bar{3}}$	1 2
Greatest width $M_{\bar{3}}$	1 3
Greatest length incisor (anteroposterior)	1 5
Greatest width incisor	.8

Dentition: Enamel strong on all teeth; brachyodont to hypsobrachyodont; incisor smooth with convex anterior surface;[4] $P_{\bar{4}}$ X-shaped pattern anterior column narrower than posterior column and with inflection, posterior column with very slight reëntrant and no accessory cusps and wider than long, high crowned; $M_{\bar{1}}$ square anterior and posterior external corners, incipient H-pattern on labial side, no extra cusps, nearly same size as $M_{\bar{2}}$, at least two roots but fused deep in jaw; $M_{\bar{2}}$ as in $M_{\bar{1}}$ except wider than long, external corners more rounded, labial lake smaller, two roots distinct lingually and separate to crown, anterior root visible and smaller than posterior; $M_{\bar{3}}$ smaller than $M_{\bar{2}}$ nearly equidimensional and round in outline except for slight external posterior inflection and with two roots distinct to crown, anterior root visible, smaller than posterior root.

Comparisons.—The specimen is referred to the family Heteromyidae because of its tendency for hypsobrachyodont dentition, smaller size than species of Geomyidae, and continuous enamel on cheek teeth.

The absolute designation of a subfamily category is not possible owing to tendencies for characters in these groups to merge in the few Miocene representatives. This species reflects affinity with two subfamilies. It is probable that *P. ? mascallensis* is nearer Dipodomyinae than Perognathinae in the relative depth of mandible, and the slight tendency to high crown, size, and incipient H-pattern[5] in molars.

P. ? mascallensis differs from the Heteromyinae in features listed under Dipodomyinae and in that $P_{\bar{4}}$ lophs unite at center of tooth forming X-pattern, and lophids of molars unite centrally and labially.

It is significant to observe that in some features *P. ? mascallensis* shows neutral

[4] Dr. S. B. Benson pointed out to me that the incisor has been pushed backward in the jaw, possibly reflecting the effects of being lodged in an owl pellet (?). The jaw is not distorted because of this.

[5] Following Wood (1935, p. 123). His paper is also relied on for general definitions of the subfamilies and dental terminology.

relationship to Dipodomyinae and resemblance to Perognathinae in the size of $M_{\bar{3}}$, X-pattern on $P_{\bar{4}}$ with inflection on anterior lophid, presence of at least two roots on $M_{\bar{1}-\bar{3}}$, and moderate development of masseteric crest.

Cupidinimus magnus (Kellogg)* (= *Diprionomys magnus*) Kellogg, from Thousand Creek, Nevada. There is some resemblance to *D. ? mascallensis* in X-pattern and presence of faint anterior notch on $P_{\bar{4}}$; the depth of the mandible may

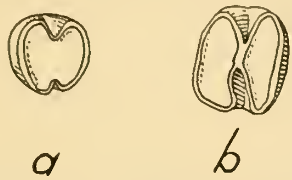


Fig. 8. cf. *Prodipodomys ? mascallensis* n. sp., C.I.T. no. 4002b, loc. Mascall (type area?) : *a*, $P_{\bar{4}}$; *b*, $M_{\bar{1}}$(?) ; × 10.

be similar, but *D. magnus* is too incomplete for a true estimate. Distinctions are evident in the proportionately long $P_{\bar{4}}$ and the greater hypsodonty with enamel pattern wearing away early. The cotype of *C. magnus* is different from the type in the absence of the inflection in the anterior loph. This is an example of the variation in the enamel pattern in the heteromyids and further reason for caution

TABLE 3

Variation in Measurements of Mandible in Two Groups of Heteromyidae

	Number of teeth	Observed range	Mean	Standard deviation	Coefficient of variation
Depth of mandible at $P_{\bar{4}}$					
Dipodomys ordii columbianus	15	4.3 – 4.7	4.50 ± .04	.126 ± .23	2.80 ± .51
Perognathus c. californicus	15	3.0 – 3.3	3.17 ± .03	.115 ± .02	3.60 ± .06
Length of alveolus					
Dipodomys ordii columbianus[a]	15	4.4 – 5.1	4.52 ± .06	.216 ± .39	4.75 ± .86
Perognathus c. californicus[b]	15	3.7 – 4.4	4.01 ± .06	.256 ± .05	6.30 ± 1.14
Depth at $P_{\bar{4}}$					
Cupidinimus sp. Miocene Niobrara River	11	2.5 – 3.2	2.73 ± .05	.178 ± .04	6.55 ± 1.39

[a] *D. o. columbianus* includes recent populations from Malheur County, Oregon, and Bingham County, Idaho.
[b] *P. c. californicus* recent specimens from Alameda County, California. Material in M.V.Z., University of California

in naming a new genus or referring to an established genus. Except for the possible difference in tooth proportions, *C. magnus* appears to be very similar to *Perognathoides* Wood, particularly *P. tertius* Hall.

Specimens of *Cupidinimus* from the Niobrara River fauna in U.C.M.P. collections were compared with *P. ? mascallensis*, and definite resemblance in tooth pattern is indicated, but *P. ? mascallensis* is significantly larger and has a deeper jaw.

Measurements of Niobrara material.—Length of alveolus, U.C.M.P. nos. 36100, 4.1; no. 36687, 3.8, no. 36086, 4.4 (unnumbered), 3.4 and 4.1, no. 36101, 4.1. OR = 3.4–4.4, M = 3.9. Using data from table 3, depth of mandible at $P_{\bar{4}}$ over length of alveolus = 2.74/3.90 = .70.

The Niobrara River materials display a difference from the new species in the depth of the mandible, with an index of .70 compared to index of .97 in *P.* ? *mascallensis. Cupidinimus nebraskensis* Wood* was compared directly with *P.* ? *mascallensis*, and similar relationships were observed as stated above for the Niobrara material. The teeth of *C. nebraskensis* are so little worn that in $P_{\bar{4}}$ the anterior loph has not completely joined. It appears that the lophids of the molars are uniting at the center first. As Wood states (1935, p. 123), the joining of the lophids vary as to buccal or central in their sequence, but in either case there is slight difference in time per tooth. It has been difficult to decide which happened first in *P.* ? *mascallensis*, but it is certain that both points of junction of the lophids occurred.

Prodipodomys kansensis Hibbard,* Edson beds of Kansas. This species, as well as the genus, is like *Dipodomys* in its tendency toward hypsodonty, great reduction of $M_{\bar{3}}$, strong dorsal masseteric ridge, and moderately deep mandible (index, depth mandible over length of alveolus = .89). The pattern of $P_{\bar{4}}$ and the proportions of the molars except $M_{\bar{3}}$ resemble *P.* ? *mascallensis*, but *P. kansensis* differs in less development of roots on molars and on $P_{\bar{4}}$, smaller $M_{\bar{3}}$, and more prominent dorsal masseteric ridge. In the depth of mandible and in size, *P.* ? *mascallensis* seems nearer *Dipodomys* than does *P. kansensis*, but *P. kansensis* is as close to *Dipodomys* in the characters cited above.

Prodipodomys ? *minor* (Gidley)* (= *Dipodomys minor* Gidley) Benson, Arizona. There is resemblance to *P.* ? *mascallensis* in the pattern of $P_{\bar{4}}$, in the prominence of the masseteric ridge, and in the proportions of the teeth, but it differs in depth of mandible (depth at $P_{\bar{4}}$ over length alveolus = .82), absence of roots, greater hypsodonty, and relatively shorter diastem. The referred specimen* at the American Museum may not be *P.* ? *minor* as Gazin (1942) suggests; it differs from *P.* ? *mascallensis* in more prominent masseteric crest, relatively longer $P_{\bar{4}}$ and $M_{\bar{1}}$, and greater hypsodonty. This referred specimen is more like *Dipodomys* in some features than is *P.* ? *minor.*

Dipodomyine (?), n. gen. and sp. Wilson from the Avawatz fauna, California. This is one of the earliest Dipodomyinae recorded and bears strong resemblance to the recent forms in hypsodonty, wide enamel breaks, and relatively large $P_{\bar{4}}$. It is distinct from *P.* ? *mascallensis* in these points and shows similar distinctions from *Prodipodomys.*

Pliosaccomys dubius Wilson from Smiths Valley, Nevada. There are several specimens assigned to this group, and one is in a state of wear similar to that in *P.* ? *mascallensis* and resembles *Cupidinimus magnus* as Wilson has described. This species tends to show resemblance to *P.* ? *mascallensis* in relative depth of jaw (depth below $P_{\bar{4}}$, 5.1 over length alveolus, 6.1 = .84) and moderate masseter medialis ridge. *P. dubius* is distinct in subcircular anterior loph on $P_{\bar{4}}$ (with wear) and much greater hypsodonty.

Perognathus coquorum Wood, Upper Snake Creek beds, Nebraska. This species is distinct from *P.* ? *mascallensis* in its proportionally long $P_{\bar{4}}$, stronger inflection on anterior lophid of $P_{\bar{4}}$, and greater size. This species also reflects a resemblance in the possible depth of mandible (not measurable) an incipient H-pattern, and X-pattern on $P_{\bar{4}}$. The masseteric ridge appears in the drawing to be very prominent anteriorly and dorsal in position, thus resembling *Dipodomys*. The type of *Cupidinimus magnus* resembles this species in dental proportions and pattern. It is unwise to offer an opinion without seeing the specimen, but the impression at present is that this species (*P. coquorium*) shows as much relation to the Dipodomyinae as to the Perognathinae; it is probably distinct from *P.* ? *mascallensis* and possibly advanced over the Mascall species.

*Perognathoides** is a genus with supposedly higher-crowned teeth than the typical *Perognathus*, and it has a proportionally longer and larger $P_{\overline{4}}$ as, for example, in *Perognathoides tertius* (Hall). As Wilson has noted (1939), in some specimens such as his *Perognathoides* sp. indet., there is a resemblance to *Cupidinimus* or *Perognathus*. The genus is distinct from *P.* ? *mascallensis* in these features.

A recent species of *Dipodomys* was studied for the purpose of determining variation in a known group—*Dipodomys ordii columbianus* Merriam from Malheur County, Oregon, and Bingham County, Idaho (stored in the University of California Museum of Zoölogy). Measurements were made on a series of fifteen specimens. In these specimens the following features were observed, and they tend to resemble *P.* ? *mascallensis:* $P_{\overline{4}}$ with X-pattern and anterior inflection, even with considerable wear; relatively deep mandible (see table 3); nearly similar size; and length of diastem. This group is distinct from *P.* ? *mascallensis* in greater hypsodonty, more prominent and more dorsal masseteric lateralis ridge, continuous or broken enamel on molars, and much reduced $M_{\overline{3}}$. As has been stated by Wood (1935), large size does not necessarily imply advancement of character. It is interesting to find a record from the Miocene that shows a size equivalent to some Recent forms and, in addition, similar proportions of the jaw. *D. o. columbianus* is one of the least variable subspecies of *D. ordii* according to Setzer (1949). The material used for data in table 3 came from two different localities not far from the type area of the Mascall; however, the coefficient of variation is not high in the measurements taken and indicates that such dimensions are not highly variable in that group at least (see Simpson and Roe, 1939, p. 123). *P.* ? *mascallensis* is relatively old geologically, and its proportions may reflect individual variation in a population not as stable as in the Recent forms. There are not enough samples from the Mascall to determine the variation at that time, and the Pliocene fossils which have been described are almost as fragmentary. One fossil population of *Cupidinimus* from the Niobrara River shows no significant difference in the degree of variation of the depth of the mandible at $P_{\overline{4}}$ from that shown in *D. o. columbianus*.

One of the larger species of the Recent *Perognathus* was also studied to check its range of variation in characters considered specifically significant. *Perognathus c. californicus* Merriam from Alameda County (see table 3) shows a small dimensional spread or near-average value of V in selected measurements, though slightly greater than in *D. o. columbianus*. *P. c. californicus* resembles *P.* ? *mascallensis* in the $P_{\overline{4}}$ inflection on anterior lophid usually present with X-pattern and two rooted; masseteric ridge with moderate development near mental foramen; and $M_{\overline{3}}$ being slightly smaller than $M_{\overline{2}}$ and both rooted. The species is distinct in the shallow depth of mandible, relatively short diastem, and only a faint suggestion of H-pattern.

These studies of reasonably good samples of related populations show that proposed important characters of the mandible are not highly variable in known populations and that they can be depended upon as significant features when observed in small fossil samples. It thus appears probable that the characters described for this new species, *P.* ? *mascallensis*, will prove to be valid.

Discussion.—The genus *Prodipodomys* is not represented by many samples, and its taxonomic relationship is consequently vague. We might interpret the genus as including those species probably ancestral to *Dipodomys* (see Hibbard, 1937) and as a genus carrying on from late Miocene to Pliocene time. Such a range is not abnormal. From the morphological viewpoint and in the broadest sense the species of the genus *Prodipodomys* would have central tendencies for hypsodonty, reduction of $M_{\bar{3}}$, relatively stout deep mandible, incipient H-pattern, and a prominent masseteric lateralis ridge. *P.* ? *mascallensis* has some of these characters and lacks others. *P.* ? *mascallensis* is not believed to have sufficient characters and representative material for designation as a new genus, nor can it be positively given a generic identification.

The phyletic position of *P.* ? *mascallensis* in the history of the Dipodominae is uncertain. Its presence in the Mascall as possibly the earliest recorded representative of Dipodomyinae supports the view of Wilson (1939) and Setzer (1949) that the subfamily has great antiquity. It would appear that *Cupidinimus* is not necessarily the ancestral group of the subfamily (see Wood, 1935). Setzer (*op. cit.*) has suggested that *Cupidinimus* may be an "aberrant side branch" that parallels the main line of evolution. Wood (*op. cit.*, p. 250) has emphasized that parallelism is the rule in the hetoromyids, and a more complete history of similar structures must be available before conclusion as to descent can be made. *P.* ? *mascallensis* may be nearer the line of ancestry of *Dipodomys* than any record known so far, but the step-by-step history of the structures involved is not available, particularly in Miocene faunas. Therefore, to date, we cannot say whether *P.* ? *mascallensis* is the primitive dipodomyine or a specialized offshoot.

cf. *Prodipodomys* ? *mascallensis*

Two isolated lower teeth, $P_{\bar{4}}$ and $M_{\bar{1}}$?, were found with several lagomorph teeth in a tray in the California Institute of Technology collection, no. 4002b from the Mascall. $P_{\bar{4}}$ differs from *P.* ? *mascallensis* in convex anterior margin but is similar in size and X-pattern of the lophids. $M_{\bar{1}}$? is slightly shorter than in *P.* ? *mascallensis* but shows to better advantage the connection of the two lophids. The labial (?) ends have definitely started to join, and the center union is just beginning. Both teeth show short roots as in *P.* ? *mascallensis*. $P_{\bar{4}}$ is well worn but hypsobrachyodont with one long posterior root (the anterior root broken, but seemingly one root); $M_{\bar{1}}$ also with heavy wear but well-developed roots (one broken which may have consisted of two roots). $P_{\bar{4}}$, anteroposterior diameter 1.1; transverse diameter 1.2; ?$M_{\bar{1}}$ 1.2 and 1.4 respectively.

Peridiomys cf. *oregonensis* (Gazin)
(Fig. 9)

In the California Institute of Technology there are several specimens of rodents which are probably the specimens mentioned by Gazin (1932) in a summary list of the Mascall fauna. C.I.T. no. 4001 is an incomplete left mandible with unworn dentition. It was purchased from T. J. Weatherford who resides within a hundred yards of the type locality of the Mascall. The data on the museum tag reads "Mascall, W. of D. highway, Oregon. Purchased from Weatherford." Since the specimen is so much like *Peridiomys oregonensis* Gazin from Skull Spring and since this fauna correlates with the Mascall, it is considered likely that C.I.T. no. 4001 was taken from Mascall deposits. The ramus of *P. oregonensis*, C.I.T. no. 371, is not preserved, but dentition in *P.* cf. *oregonensis* from the Mascall is similar, especially in the tendency for an H-pattern in the molars and in a prominent groove or separation between the cusps on the anterior lophid of $P_{\overline{4}}$. C.I.T. no. 4001 in addition has $P_{\overline{4}}$ longer than wide; two rooted (possibly three), two outer cusps close, tending to connect; $M_{\overline{1}}$ and $M_{\overline{2}}$ with slight evidence of an anterior cingulum; both center and labial connection of lophids beginning, but central union the nearest to completion, two roots with possibly a third; $M_{\overline{3}}$ with two well-developed lophids and somewhat smaller than $M_{\overline{2}}$, at least two rooted. The specimen is slightly smaller than *P. oregonensis* and lacks the anteroconid of $P_{\overline{4}}$, considered as diagnostic by Wood (1935).

Peridiomys rusticus measures much larger than *P.* cf. *oregonensis* (see measurements, table 4). With more wear on C.I.T. no. 4001, we might recognize even closer affinities with the type of *P. oregonensis.*

Morton Green directed my attention to three rodent specimens of probable Mascall age, U.C.M.P. no. 442, stored with the John Day faunal collection. Unfortunately they are without locality data. There is half of a cranium with part of the snout, most of the narial palate, left tooth row, and another snout with parts of two incisors and part of a skull (part of frontal, nasals, and palate without teeth). No. 442 may be a slightly larger animal than *P. oregonensis* (see measurements). Many features on the teeth are not visible because of wear, but the specimen compares most closely with the subfamily Heteromyinae on the basis (see Wood, 1935) of the pattern partly preserved on teeth in heavy wear; lophs united on lingual side of uppers (not on labial side); a faint suggestion of Y-shaped crest on posterior lophs; and molars with roots. The specimen was compared directly with the type of *P. oregonensis* and was found to agree in available features with the characters noted by Gazin except in the absence of anterointernal fold on posterior column of $P^{\underline{4}}$ and no reëntrants on posterior column of $P^{\underline{4}}$, although in *P. oregonensis* this column tends to lengthen toward the base of the tooth. Since the specimens under no. 442 show some slight differences from *P. oregonensis* it is believed they should be called *Peridiomys* cf. *oregonensis*. It seems probable that when variation in the group is better known, these specimens will prove to be *P. oregonensis.*

C.I.T. no. 3999 from Mascall, Oregon, north of Dayville, includes isolated $P^{\underline{4}}$, $M^{\underline{1}}$, $M^{\underline{2}}$, and $M^{\underline{3}}$. These teeth are similar to U.C.M.P. no. 442 and the teeth of the type of *P. oregonensis*. This record substantiates the opinion that no. 442 did come from the Mascall. It may be stated that the units of measurement fall between the values of specimens of *P. oregonensis* (C.I.T. nos. 370 and 371). The $P^{\underline{4}}$ has a nearly separate cusp on the posterior loph like C.I.T. 370. $M^{\underline{1}}$ possesses one large lingual and two smaller labial roots; $M^{\underline{2}}$ has at least two broken roots; $M^{\underline{3}}$ shows

TABLE 4

a. Comparative Measurements of Mandible of Peridiomys cf. oregonensis and P. rusticus
(in millimeters)

	C.I.T. no. 4001	*P. rusticus* no. 18894
Alveolar length at base of tooth	5.5	7.20
Alveolar length at crown	5.2	...
Length diastem	4.5	...
Depth ramus below P_4	4.7	....
Anteroposterior diam. P_4 (slight wear)	1.5	1.62
Transverse diameter P_4	1.4	1.83
Ap. diameter M_1	1.3	...
Tr. diameter M_1	1.5	...
Ap. diameter M_2	1.3	...
Tr. diameter M_2	1.6	....
Ap. diameter M_3	1.2	....
Tr. diameter M_3	1.3	....

b. Comparative Measurements of Maxilla and Skull of Peridiomys cf. oregonensis and P. oregonensis
(in millimeters)

	Mascall		Skull Spring	
	P. cf. *oregonensis*		*P. oregonensis*	
	U.C.M.P. no. 442	C.I.T. no. 3999	C.I.T. no. 371	C.I.T. no. 370
Depth skull between palate (opp. P^4)	8.7	...	8.3	8.5
Width palate between P^4	3.2	...	2.4	2.4
Length diastem I – P^4	10.8	...	..	9.4
Alveolar length	6.5	...	6.1	5.5
Anteroposterior diameter P^4	2.0	1.4	1.6	1.3
Transverse diameter P^4	2.3	1.6	2.0	1.7
Ap. diameter M^1	1.4	1.2	1.3	1.3
Tr. diameter M^1	2.2	1.5	1.8	1.6
Ap. diameter M^2	1.2	1.1	1.2	1.1
Tr. diameter M^2	2.1	1.4	1.7	1.6
Ap. diameter M^3	1.3	1.1	1.2	1.1
Tr. diameter M^3	...	1.2	1.6	1.3

evidence of three roots broken off. This root structure suggests relation to *P. oregonensis*. One particular feature noted is a tiny cusp on the center edge of the anterior loph of M^1 and M^2; it has the shape of a short J with a lake. Such fragmentary material does not justify a more definite identification.

A recent addition to the University of California collections is no. 39895 from V-4833. Unfortunately only a part of the palate and right P^4 and M^1 are present. The uniting of the lophs of P^4 on the lingual side suggests affinity with the subfamily Heteromyinae, but the lack of union of M^1 on both ends of the lophs suggests Perognathinae relationship. The genus *Peridiomys* as seen in *P. oregonensis* Gazin is probably similar to this specimen, although P^4 tends to be a little more quadrate.

Measurements.—Anteroposterior and transverse diameter respectively, P^4, 1.6 and 2.0; and M^1, 1.3 and 1.8.

Since we have other teeth from the Mascall that can be compared with *Peridiomys oregonensis*, no. 39895 likewise might fall within the range of variation of that species.

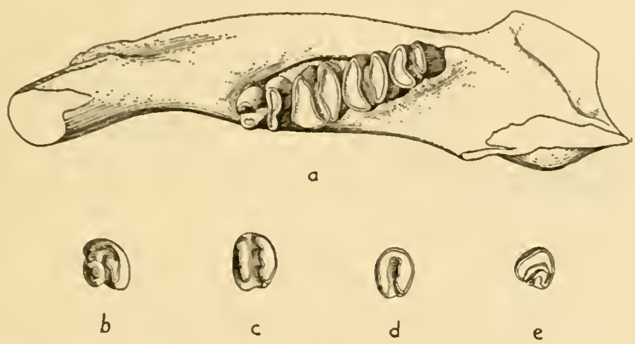


Fig. 9. *Peridiomys* cf. *oregonensis*, C.I.T., loc. Mascall (type area?): *a*, no. 4001 occlusal view of left mandible; *b*, no. 3999 occlusal view of $P_{\bar{4}}$; *c*, no. 3999 occlusal view of M^1; *d*, no. 3999 occlusal view of M^2; *e*, no. 3999 occlusal view of M^3; × 5.

Order Carnivora

Family canidae

Tomarctus rurestris (Condon)

(Figs. 10–12)

1896 *Canis rurestris* Condon, Bull. Univ. Oregon, vol. 2, no. 6, p. 11, 1 pl.

Holotype.—Nearly complete cranium and associated mandible. Condon Museum of Geology, University of Oregon, Eugene; no number.

Referred specimens.—Mascall type area. U.C.M.P.; partial unworn left $M_{\bar{1}}$ no. 39297, loc. V-4834; Y.P.M. left P^4, M^{1-2}, right P^4, left $M_{\bar{2}}$ and $M_{\bar{3}}$ no. 12713, late Miocene (Mascall formation), Cottonwood Creek, John Day Valley, Oregon; right $M_{\bar{1}}$ no. 12720, late Miocene (Mascall formation), John Day River, Oregon, Crooked River area; left M^1 no. 14312 (with Paulina Creek collection).

Type locality.—Condon (1896, p. 11), "It was taken from a light, porous rock, the deposit of a long narrow lake in the Upper John Day Valley. The deposit belongs to the Pliocene period." In personal conversation with Condon, Merriam (1906) obtained fair verification that the specimen came from the type locality of the Mascall. The referred specimen, no. 39297, is known to have come from near the type area (V-4834).

Revised diagnosis.—This diagnosis is based on Merriam (1913, p. 361) and on further observation of the type and referred material. Muzzle short, saggital and occipital crest high; mandible stout, strongly convex posteroventral margin and with deep masseteric fossa; M^1 with large hypocone and M^1 and M^2 with hypocones deflected posteriorly, no anterior cuspule on lower premolars; moderate metaconid on $M_{\bar{1}}$; larger size than *Cynodesmus kellogii* (Merriam).

Supplementary description.—Thorpe (1922, p. 175) briefly refers to the occurrence of the specimens listed above from the Mascall but gives no description or notes on comparisons. Since the species is typical of the Mascall and not abundantly represented, it is desirable to describe this material as compared with the type as follows: No. 12713 relatively smaller but probably not significantly so (see measurements); P^4 unworn right and left, parastyle less prominent, otherwise as in holotype; left M^1 relatively narrower anteroposteriorly across protocone, otherwise similar; M^2 metaconule slightly larger with less deflection of hypocone, otherwise similar; M^1 stronger external cingulum along paraconid and minute cusp between protoconid and hypoconid; M^2 similar. No. 14312 unworn M^1, similar except for smaller size. No. 12720 M_1, similar

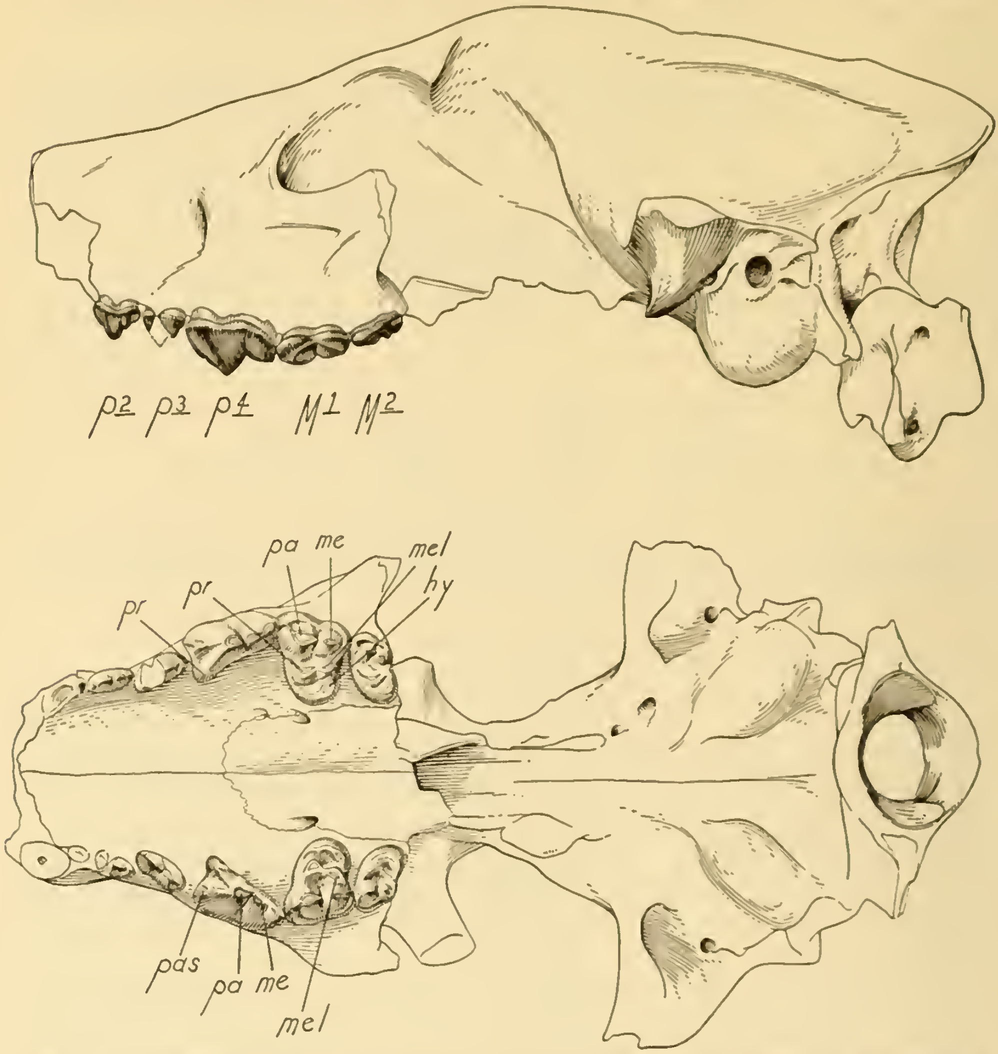


Fig. 10. *Tomarctus rurestris* (Condon), holotype, Condon Museum of Geology, University of Oregon, no number, loc. Mascall type area: top, external view, left side of skull; bottom, occlusal view of skull; × ¾. Legend: pr = protocone, pa = paracone, me = metacone, mel = metaconule, hy = hypocone, pas = parastyle.

except for greater size, possibly more vertical anterior edge of paraconid and presence of minute ridge on posteroexternal wall of paraconid. U.C.M.P. no. 39297 an unworn M_1 is possibly too small to be included in the species (transverse diameter across protoconid, 6.0 mm.), but it may be a young individual; it has relatively similar proportions of protoconid and metaconid.

The importance of small additional cusps or ridges on the species of *Tomarctus* is questionable. A cuspule on the paraconid of *Tomarctus marylandica* Berry* has been described and one on the $M_{\overline{2}}$ of Y.P.M. nos. 12720 (see above). Variation in the presence or absence of cuspules on lower premolars has been observed in *Cynodesmus kelloggi* (Merriam). These tiny cusps are possibly sporadic in appearance intra- and interspecifically and apparently have not been consistently established in a known population. Some additional measurements of the type have been given in table 5, and as a matter of general interest, my measurements are placed with those of Merriam. The differences are not great. The description by Merriam has been checked with the type; the following alterations are offered: hypocone bulbous and well developed on M^{1}; metaconid moderately developed on $M_{\overline{1}}$; cingulum present along a definite paraconid and protoconid on $M_{\overline{2}}$; hypoconid and metaconid may be distinguishable on $M_{\overline{3}}$.

Comparisons.—Matthew (1924) has suggested that there is a definite need for a comparison of the type specimen of *Tomarctus rurestris* with what he regards as neotypes of *T. brevirostris*, the type species of *Tomarctus*. The type of *Tomarctus rurestris* agrees with Matthew's specifications in the generic characters of *Tomarctus:* carnassial heel bicuspid and trigonid relatively large (compressed?), with small metaconid.

A series of measurements and comparisons were made of the "neotypes" of *T. brevirostris* and the type mandible of *Tomarctus optatus* Matthew* at the American Museum (see comparative measurements, table 5). If all three jaws, nos. 18244, 13836 of *T. brevirostris*, and no. 18916 of *T. optatus*, are placed in a series, *T. optatus* falls between the two specimens 18244 and 13836 in nearly every dimension. The morphology in the three specimens is very similar. The specific distinctions between *T. brevirostris* and *T. optatus* given by Matthew are insufficient on the basis of visible standard of differences seen in *T. brevirostris* and *T. rurestris*. True specific relationships within the genus are not clear owing primarily to insufficient sampling, therefore *Tomarctus optatus* Matthew is tentatively considered equal to *Tomarctus brevirostris* (Cope). *T. brevirostris* (plus *T. "optatus"*) is then very like *rurestris* in the posterior extension of premaxillaries, high saggital crest, parastyle prominent on P^{4}, large hypocone on M^{1}, moderate metaconid on $M_{\overline{1}}$, and paraconid and adjacent cingulum on $M_{\overline{2}}$. There is apparent specific difference in *T. brevirostris* in possible smaller size, longer muzzle and less prominent occipital crest, hypocone more in line with center of tooth or less deflection of heel posteriorly in M^{1}, mandible relatively less massive and less convex in ventral margin, and a suggestion of anterior cuspules on $P_{\overline{2}}, _{\overline{3}}, _{\overline{4}}$. The shape of M^{1} and the proportions of the mandible are the most distinctive features.

Tomarctus near *rurestris* from the Barstow (Merriam, 1911, p. 464) is a partial maxilla with a well-worn defaced M^{1} and ^{2}. Although equal in size to *T. rurestris*, it has decidedly less deflection of the hypocones and greater width anteroposteriorly across the protoconule region. Right and left mandibles, U.C. no. 32824, collected from the Barstow since Merriam's publication, are large enough to be *T. rurestris*, but possess certain marked differences in the shallower masseteric fossa, relatively longer jaw, more slender and straighter ventral margin of mandible, less crowding of the premolars, deeper basin in talonid of $M_{\overline{1}}$, and less massive molars.

Tomarctus cf. *brevirostris* (Cope) from Skull Spring, Oregon. Gazin considered this specimen (C.I.T. no. 379*) distinct from *T. rurestris* in the less deflection of

TABLE 5

Measurements of the Holotype of Tomarctus rurestris and Referred Specimens

(measurements in millimeters)

	Holotype		*Tomarctus surestris*				*Tomarctus brevirostris*				*Tomarctus optatus*
	Merriam 1906	Downs 1951	Y.P.M. 12713 left	Y.P.M. 12713 right	Y.P.M. 12720	Y.P.M. 14312	A.M. 18244	A.M. 13836	A.M. 18242	A.M. 18243	A.M. 18916
Length, ant. end orbit to inion (most post. edge)	124.0	125.0	....	....	....	....	119.0	....	121.0	105.2	....
Length, post. orb. process to inion	97.0	97.7	....	....	....	....	96.6	....	95.3	....	....
Width between orbits (least)	38.0	39.2	....	....	....	....	42.5	....	32.8	....	....
Width across snout above middle of sup. canine	38.0	38.4	....	....	....	....	....	....	36.4	....	....
Width of mand. fr. ant. side P_1 to post. side condyle	108.0	111.8	....	....	....	....	....	....	....	....	....
Height mand. below protoconid M_1	20.0	23.9	....	....	....	....	20.9	24.5	....	....	16.7
Length, ant. side P^1 to post. side M^2	60.0	59.5	....	....	....	....	55.7	....	55.4	60.1	....
Anteroposterior diam. sup. canine at base	10.0	10.3	....	....	....	....	10.2	....	11.4	10.0	....
P^2 anteroposterior diameter	8.5	8.3	....	....	....	....	10.0	....	9.5	9.0	....
P^3 anteroposterior diameter	10.0	10.3	....	....	....	....	10.6	....	11.4	10.5	....
P^4 anteroposterior diameter	17.0	17.4	17.1	15.8	....	....	17.7	....	18.9	17.3	....
P^4 greatest transverse diameter	9.5	10.0	9.3	8.8	....	....	10.4	....	9.6	10.4	....
M^1 anteroposterior diameter	13.0	12.7	11.8	....	....	10.8	12.2	....	13.7	13.5	....
M^1 greatest transverse diameter	16.0	17.0	14.7	....	....	14.2	16.5	....	17.3	17.4	....
M^1 anterposterior diameter across protocone	10.0	9.7	8.7	....	....	9.2	11.0	....	9.5	10.2	....
M^2 anteroposterior diameter	7.7	7.6	7.0	....	....	....	8.4	....	7.6	8.0	....
M^2 greatest transverse diameter	12.0	12.4	11.3	....	....	....	12.5	....	12.0	12.8	....
P_2 anteroposterior diameter	7.5	7.3	....	....	....	....	7.7	8.4	....	....	7.2
P^2 anteroposterior diameter	9.0	8.4	....	....	....	....	9.3	9.3	....	....	8.4
P^3 anteroposterior diameter	11.5	11.2	....	....	....	....	12.3	11.6	....	....	10.4
M_1 anteroposterior diameter	20.0	20.0	....	....	21.9	....	21.5	19.7	....	....	17.8
M_1 anteroposterior diameter of heel	6.0	6.0	....	....	5.8	....	6.1	5.6	....	....	5.4
M_2 anteroposterior diameter	11.5	11.0	10.1	....	....	....	11.3	10.3	....	....	9.2
M_2 anteroposterior diameter of heel	4.0	4.4	3.4	....	....	....	4.6	4.3	....	....	3.4
M_3 anteroposterior diameter	5.0	5.3	5.3	....	....	....	5.5	5.5	....	....	5.5
M_3 anteroposterior diameter	5.0	5.3	5.3	....	....	....	5.5	5.5	....	....	5.5
M_3 transverse diameter	....	4.3	4.0	....	....	....	....	....	....	....	....
M_1 transverse diameter of heel	....	8.1	....	....	8.1	....	8.4	8.6	....	....	7.5
M_1 transverse diameter across protoconid	....	8.2	....	....	8.6	....	....	8.5	....	....	7.1
Depth mandible below P_3	....	22.1	....	....	....	....	18.0	21.3	....	....	15.7
Depth mandible below M_1	....	23.2	....	....	....	....	....	....	....	....	....
Length narial notch to ant. edge orbit	....	44.0	....	....	....	....	....	....	....	....	....

the heel on M^1, in the less angulate anteroexternal corner of M^1, and in the less transverse width of M^1. Variations that would include diversities in the Skull Spring specimen can be seen in the material referred to *T. rurestris* from the Yale collection. Since only one tooth is available from Skull Spring it is difficult to judge the specific relationship, and there is a possibility of relationship to *T. brevirostris*. With consideration of geologic and geographic proximity of the faunas this specimen may be *Tomarctus* cf. *rurestris* (Condon).

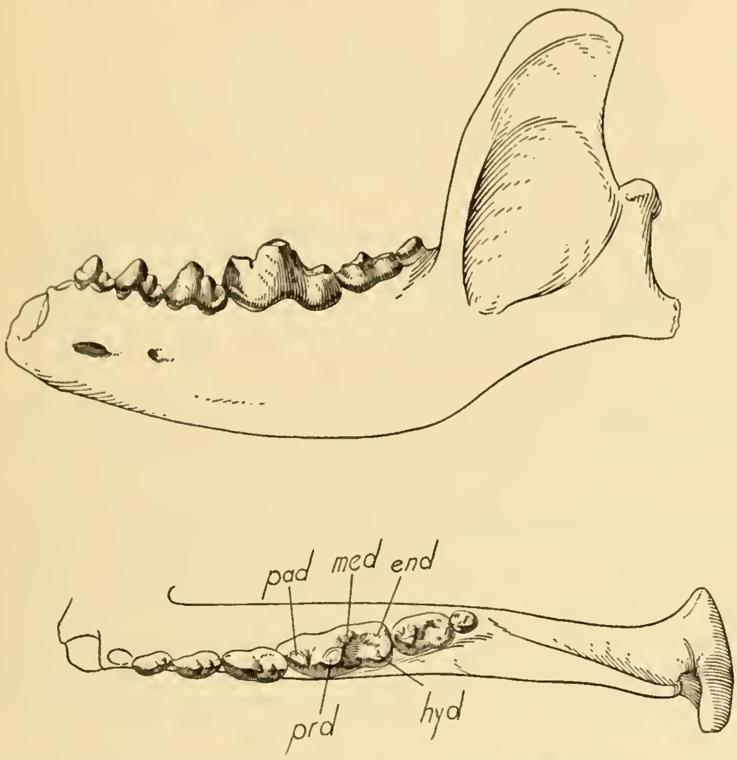


Fig. 11. *Tomarctus rurestris* (Condon), holotype, Condon Museum of Geology, University of Oregon, no number, loc. Mascall type area: top, external view of left mandible; bottom, occlusal view of left mandible; × ¾. Legend: prd = protoconid, med = metaconid, end = entoconid, pad = paraconid, hyd = hypoconid.

Tomarctus robustus Green from Ricardo, California, resembles *T. rurestris* in the massiveness of the mandible and in the deep masseteric fossa, but a greater basal thickness of the teeth and smaller metaconid on $M_{\overline{1}}$ are marked differences from *T. rurestris*. The selection of *T. brevirostris* or *T. rurestris* as nearest to *T. robustus* in ancestry is almost arbitrary. In *T. robustus* the proportions of the mandible are near *T. rurestris*, and the anterior cuspules on $P_{\overline{2}}$, $_{\overline{3}}$, and $_{\overline{4}}$ suggest likeness to *T. brevirostris*. We might choose either as the ancestor or decide that the progenitor was a species somewhat removed from *T. rurestris* and *T. brevirostris*.

Tomarctus euthos (McGrew) from the Burge fauna of Nebraska is probably distinct in much less prominent saggital and occipital crests, relatively longer snout, smaller tympanic bullae, more reduced parastyle on P^4, smaller hypocone on M^1, and less posterior deflection of M^2.

Cynodesmus kelloggi (Merriam)[6] from the Virgin Valley, Nevada, is distinct from *T. rurestris* in much stronger metaconid on $M_{\bar{1}}$, proportionally narrow premolars and molars, and small size. Since the metaconid on M_1 is of significance in other species, this distinction seems particularly valid though skulls are not represented.

The High Rock Canyon fauna may include two species of *Tomarctus* (see Stirton, 1939), but the fragmentary nature of the material renders definite identification a problem. U.C.M.P. no. 24291 is referred to *T.* cf. *optatus* (*op. cit.*). As discussed above there may be some question as to the difference between *T. optatus* and *T. brevirostris*, and without specimens of skulls and jaws it is doubtful if we can assign no. 24291 from High Rock Canyon to *T. brevirostris*. U.C.M.P. nos. 12504 and 12503 are large for *T. rurestris*, but the $P_{\bar{4}}$ and $M_{\bar{1}}$ of these specimens are very similar to *T. rurestris* in the proportions of the metaconid. The small specimen no. 24291 from High Rock Canyon is even closer to the type of *T. rurestris* than to these specimens (nos. 12504 and 12503).

Measurements.—Anteroposterior, transverse (at protoconid) and transverse (at talonid) diameters respectively—U.C.M.P. no. 12504, $M_{\bar{1}}$ 24.3, 8.5, and 8.5; U.C.M.P. no. 24291, $M_{\bar{1}}$ 18.5, 7.5, and 7.6.

Nos. 12503 and 12504 from High Rock Canyon may be advanced as compared to *T. rurestris* in height of protoconid and size, but Y.P.M. no. 12720 from the Mascall represents a tooth intermediate between the type and the High Rock Canyon specimen. Some upper teeth from High Rock Canyon, no. 24292, also are much larger (M^1 anteroposterior diameter 13.4 mm. and transverse diameter 14.7 mm.), proportionally narrower, and have smaller hypocones, but they are similar to *T. rurestris* in the posterior deflection of the hypocone on M^1. It is possible that the large specimens nos. 24291 and 12503 and 12504 represent a large species of *Tomarctus*, phyletically related to *T. rurestris*. *T. robustus* resembles the large High Rock Canyon specimens except for the massiveness at the base of $P_{\bar{4}}$ and $M_{\bar{1}}$ in *T. robustus*.

Tomarctus temerarius Leidy* from the Valley of Niobrara River is represented by teeth that are much smaller than in *T. rurestris*, and M^1 and ^{2} have a straight posterior edge, showing no deflection of the hypocone. It is conceivable that this species could be within the size range of *Tomarctus confertus* Matthew.

Tomarctus thomasi White, Thomas Farm of Florida, and *T. canavus* Simpson are distinct from *T. rurestris* in smaller size, in absence of deflection of the hypocone, in the presence of an internal cingulum on M^1 on some specimens, and in the relatively short trigonid as compared to talonid on $M_{\bar{1}}$ (index = .37 in *T. thomasi* and .26 to .33 in *T. rurestris*).

Tomarctus marylandica Berry* from the Calvert formation, Maryland, looks very like *T. brevirostris* or *T. rurestris*. There is a small cuspule on postero-external wall of the protoconid; a specimen from the Mascall has shown the same feature. Since a true concept of species criteria in this genus seems to be elusive

[6] Green (1948) has included this material in *Tomarctus*. Stirton (1939) refers the species to *Cynodesmus*. The population seemingly represents an intermediate group between *Cynodesmus* and *Tomarctus*.

and so little is known of this population from Maryland, it probably should remain as classified. Its geographic position suggests that a distinct species could be represented.

Tomarctus paulus Henshaw from Tonopah, Nevada, is undoubtedly smaller than *T. rurestris* and with less robust proportions of the mandible. It is considered to be near *T. confertus* but larger; it also has a relatively larger metaconid on $M_{\bar{1}}$. The distinction between *T. paulus* and *T. temerarius* (at least the mandible of *T. temerarius,* regarded as the type by Matthew, 1924) is not clear; *T. paulus* is similar to the Barstow specimens referred to *T. temerarius* by Merriam (1924), especially in the size of the metaconid on $M_{\bar{1}}$.

Discussion.—The new material from the Mascall has substantiated the presence of the deflection of the hypocone in *T. rurestris* and has given a more extensive picture of possible variation in the size and proportions of the teeth. Many species

Fig. 12. *Tomarctus rurestris* (Condon), Mascall type area: *a,* Y.P.M. no. 12713 occlusal view of maxilla with P^4, M^1 and ^{2} and a P^4; *b,* Y.P.M. no. 12720 occlusal view $M_{\bar{1}}$; *c,* U.C.M.P. no. 39297 partial $M_{\bar{1}}$. Crooked River area: *d,* Y.P.M. no. 14312, occlusal view of M^1; × ¾.

of *Tomarctus* are based on relatively minute differences in teeth, and few have associated craniums or mandibles. The most reliable differentiation and determination of variations depends on a combination of cranial, mandibular, and dental features and a good sampling of specimens.

Tomarctus rurestris is just as stout jawed as *T. brevirostris* if not more so and is a western species of near middle Miocene (Hemingfordian) age; it could be the ancestor of *T. robustus* (see Green, 1948, p. 86). Green has indicated only "tentative" relationships in his chart, and any opinions presented here are also tentative. The indication of large *Tomarctus*-like animals in the High Rock Canyon and in the Mascall material suggests a general group relationship of the dogs in the Mascall, High Rock Canyon, and Ricardo faunas. As Merriam (1906) and Matthew (1924) point out, there are many resemblances to the genus *Aelurodin* in *T. rurestris* and *T. brevirostris.* I have not studied species of *Aelurodon* in detail, but the gradual increase in size from $P_{\bar{1}}$ to $P_{\bar{4}}$, characteristic of the group, is suggested in the Mascall species and in *T. brevirostris.*

The presence of the large *Tomarctus* in the High Rock Canyon is additional support for the opinion that this fauna is of later date than the Mascall.

The species *T. rurestris* may not have progressed as far as *T. robustus* in hyaenoid habits but was tending that way. The shortness of the face, strong teeth, and stout jaws with deep masseteric fossa suggest a bone-crushing ability.

Amphicyon cf. *sinapius* Matthew

Stock (1930, p. 47) has compared a fragmentary right ramus, C.I.T. no. 207, with *Amphicyon sinapius* Matthew. Locality data are not available, but Stock stated that the material was collected in Mascall deposits and that he was aware of the problem of mixture of Rattlesnake and Mascall faunas. He has shown the possibility of correlating with *A. sinapius* found in the lower Snake Creek and Pawnee Creek beds.

It is significant to note that Matthew (1924) states in regard to the species *Amphicyon sinapius* from Snake Creek and Pawnee Creek: "Size of *A. major* from Sansan (Middle Miocene of France or Helvetian according to Pilgrim, 1940). Upper teeth very like those of *A. major* throughout, . . ."

This genus is the largest carnivore from the Mascall and may well have been a predator harassing the well-represented ungulates.

Family MUSTELIDAE

Leptarctus oregonensis Stock

(Fig. 13)

A complete analysis and description of this species is included in Stock's paper (1930) on Carnivora from the Mascall. The type was collected north of the east fork of the John Day River, approximately 1.5 miles northwest of Dayville, Oregon. After visiting the Mascall deposits in this area, I conclude that this specimen was taken at one of the localities, V-4830–4835.

Another specimen, U.C.M.P. no. 39102, was recently collected at locality V-4824. The specimen consists of a small part of a maxilla with a well-worn right P^4, on a level above the commonly termed "mammal horizon" (see geologic section). The tooth is similar to the P^4 in *Leptarctus oregonensis* in the presence of external cingulum (the parastyle has been broken off) and well-developed hypocone and protocone. The specimen measures a millimeter greater in size than the type (anteroposterior diameter 7.5 mm., transverse diameter, 6.5 mm.), though probably not beyond the range of size variation in *L. oregonensis*, and is undoubtedly an older adult as witnessed by the heavy wear on the cusps.

Mephititaxis ancipidens White (1941)* from Florida, is distinct from *L. oregonensis* in its relatively stronger parastyle on P^4, greater development of hypocone on P^4, and width greater than length on M^1. These differences are a matter of degree of development but seem specifically important at least. The generic distinction of *Mephititaxis* from *Leptarctus* seems questionable to me.

Mustelidae or Procyonidae

The specimen is a fragmentary mandible, U.C.M.P. no. 33482, from locality V-3427, the Gateway assemblage. It is part of a mandible with heavily worn left P_4 and M_1.

M_1 hypoconid worn flat, entoconid(?), metaconid somewhat smaller than paraconid but probably well developed, moderately deep notch between entoconid and metaconid; P_4 with large central cusp, moderate posterior cusp and definite posterior heel, internal cingulum, and small anterior cingulum. Measurements in millimeters: P_4 anteroposterior diameter, 5.8, transverse diameter, 2.7; M_1 anterioposterior diameter, 8.5, transverse diameter at trigonid, 3.9.

Proportions and size of cones in the lower teeth of Mustelids and Procyonids may be of diagnostic value, but caution is required before decisions can be made on the affinities (see Hall, 1936). When exact size of the cusps is not available, as in this specimen, the genus is not determinable. The metaconid in no. 33482 is much too large for the genus *Martes*. *Mephitis* differs in the same manner. *Spilo-*

gale is most like no. 33482 in the shape of $M_{\overline{1}}$, but the entoconid appears stronger than in no. 33482. The state of wear in the fossil hinders a proper analysis. $P_{\overline{4}}$ in *Spilogale* is markedly shorter and narrower and is without the prominent posterior cusp and heel.

Recent species of *Bassariscus* may be distinct from the fossil in their shorter talonid and in the disjunct alignment of the paraconid and metaconid. *Bassariscus antiquus* Matthew is somewhat similar in the length and proportions of the talonid. The number of cusps and shape of $P_{\overline{4}}$ in *Bassariscus* is like that in the fossil.

Fig. 13. *Leptarctus oregonensis* Stock, U.C.M.P. no. 39102, loc. Mascall type area; occlusal view right P^4; × 1½.

Leptarctus oregonensis Stock from the Mascall is not represented by lower dentition; therefore it cannot be compared. *L. primus* Leidy* may be distinct in its great size, possibly in its more bicuspid talonid on $M_{\overline{1}}$, in the more prominent external cingulum on $M_{\overline{1}}$, and in the less prominent anterior ridge on $P_{\overline{4}}$. *L. wortmani* Matthew* is poorly represented but seems to be distinct in $P_{\overline{4}}$ with more oblique position of cusps, relatively greater width, presence of external cingulum, and larger posterior cusp. Both of these species show these minor differences but their importance is questionable.

The general impression at present is that this fossil is more like the *Leptarctus* or Mustelid groups than like the Procyonids.

Carnivora sp.

A U.C.M.P. specimen, no. 33107, loc. V-4830, is a lower canine, large enough to be *Tomarctus rurestris.* U.C.M.P. no. 35671 includes two canine teeth. The smallest is a short, robust specimen possibly comparable to the size of *Leptarctus oregonensis;* the other is a longer, more slender tooth but smaller than no. 33107. No. 2067, old loc. 903 or V-4830–4835, is the distal section of a metatarsal or metacarpal the size of a canid.

Order Perissodactyla
Family Equidae
Parahippus avus (Marsh)
(Pls. 5–6; figs. 14–16)

1874 *Protohippus avus* Marsh, Amer. Jour. Sci. (3), vol. 7, pp. 247–258, figs. 1–5.

1874 *Anchippus brevidens* Marsh, Amer. Jour. Sci. (3), vol. 7, pp. 247–258, figs. 1–5.

Holotype.—Marsh (1874, p. 253): "A number of teeth from the Pliocene beds of Oregon ... most of these specimens are apparently all from one individual, and consist of a nearly complete series of upper and lower molars and one incisor ... there are six lower molars ..." Marsh gives measurements for "space occupied by" six upper molars, three lower premolars and a true molar. Osborn (1918, p. 81): "The type consists of portions of both lower jaws, the right bearing $P_{\overline{2}-\overline{4}}$, $M_{\overline{1}-\overline{3}}$, the left $P_{\overline{2}-\overline{4}}$ and $M_{\overline{1}}$. There are also nine upper molar and premolar teeth, chiefly of the left side, at least one incisor, and a few tooth fragments." The holotype as seen in the Peabody Museum collection: lower right $P_{\overline{2}}$ - $M_{\overline{2}}$, left $P_{\overline{2}}$, $_{\overline{3}}$, $_{\overline{4}}$ and $M_{\overline{1}}$; upper left P^2 - M^1 and M^2 right P^3, M^2, a canine and fragments, Y.P.M. no. 1128, Cottonwood Creek, John Day, Oregon.

Referred specimens.[7]—Mascall type area. The former type of *Parahippus brevidens;* Osborn (1918, p. 89): "Three upper molar teeth, M^{2} ^{3} of the left side, M^{1}? or P^{4} of the left side; there are three specimens given the same number, probable M^{2} and ^{3} left side and right M-, Y.P.M. no. 11274."

U.C.M.P.: left M^{1}? no. 1701, loc. V-4830–4835 (old 903); upper, partial left premolar or molar no. 40240, loc. V-4834. C.I.T.: upper molars or premolars nos. 406 and 407, Mascall, Oregon.

Crooked River area. U.S.N.M., lower no. 18747. Y.P.M.: upper molars or premolars nos. left 10784, right 14271, lower right no. 14272, Grindstone Creek, Oregon.

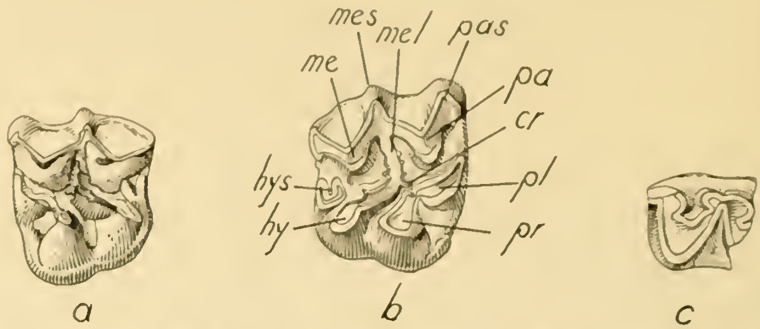


Fig. 14. *Parahippus avus* (Marsh), Crooked River area: *a*, Y.P.M. no. 10784 left upper molar or premolar; *b*, Y.P.M. no. 14271 right upper molar or premolar; *c*, Y.P.M. no. 14272 partial lower; all × 1. Legend: me = metacone, mel = metaconule, mes = mesostyle pas = parastyle, pa = paracone, cr = crochet, hys = hypostyle, hy = hypocone, pr = protocone, pl = protoconule.

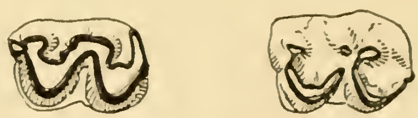


Fig. 15. *Parahippus avus* (Marsh), U.S.N.M. no. 18747, loc. Crooked River area: occlusal view of lowers; × 1.

Type locality.—Marsh (1874, p. 254): "The Pliocene of Oregon." Since referred U.C.M.P. no. 1701 and 40240 are from Mascall localities and C.I.T. has acquired two teeth from the Mascall, it is believed that the holotype of *P. avus* came from near the type area of the Mascall.

Revised diagnosis.—Based on original description, by Bode (1933), and on observations by the writer. Somewhat larger than *Parahippus leonensis* Sellards (mean anteroposterior diam. 15.96 ± .16); hypsobrachyodont; moderate to heavy cement; crochet simple but relatively close to protoloph; styles prominent, and narrow to wide at base; hypostyle large, triangular, isolated and sometimes enclosing a fossette; protoloph separate from ectoloph and constricted or separate from protocone; ribs faint on paracone and metacone; plications on metaloph, usually from one to three anterior or posterior; small cusp on cingulum between protocone and protoconule; external walls of paracone and metacone slant inward; protocone pyriform and larger than ridge-shaped hypocone; internal cingulum on upper cheek teeth often present; metaconid and metastylid widely separate relative to other parahippines.

Supplementary description.—*Parahippus brevidens* (Marsh) is synonymized with *Parahippus avus* (Marsh) on the basis of new material available. In a previous publication, Downs (1951) indicated that *P. avus* is synonymous with *P. brevidens* following the precepts of article 28, International Code of Zoölogical Nomen-

[7] All specimens except U.C.M.P. no. 1701, Y.P.M. 11274, and 1128, and C.I.T. 406 and 407 are reported for the first time in this study.

clature. It was believed at that time that *P. brevidens* was the preferred name although *P. avus* was described on the page preceding the description of *P. brevidens;* the material referred to *P. brevidens* is better represented and can be used more adequately for diagnosis of this taxonomic complex. I believe now that, for purposes of stability of nomenclature, the recommendation of the Commission of the Thirteenth Congress Bulletin of Zoölogical Nomenclature (vol. 4, Jan. 7, 1950, p. 330), should be applied; therefore, since there is page priority in that *P. avus* was described on page 253 and *P. brevidens* on page 254 of the same journal, *P. avus* is the type of the species.

All the material listed under referred specimens, except Y.P.M. no. 11274, U.C.M.P. no. 1701, the specimens at C.I.T., and the holotype of *P. avus,* has not been reported previously from the Mascall. The original figures of the referred

TABLE 6

Summary of Measurements of Transverse Diameter in Parahippus avus and P. leonensis, Including P^3-M^2

	Number of teeth	Observed range	Mean
P. avus, Mascall and N. Coalinga	12	18.8–24.1	22.0
P. leonensis, Florida	30	17.0–22.0	20.2
P. vellicans (leonensis), Texas	9	15.8–19.3	17.5

material (the former type of *P. brevidens*) are accurate in Osborn (1918, fig. 66, plate III) except the following items: Y.P.M. no. 11274, M^2, mesostyle wider at base, protoloph not connected to ectoloph, metaloph with 1 posterior and 4 anterior plications. Y.P.M. no. 1128 (*op. cit.,* fig. 64); M^1 without internal cingulum and posterior part of ectoloph absent.

Osborn (*op. cit.*, p. 89) refers skeletal material and heavily worn cheek teeth to *P. avus* (A.M. no. 14182 from Sheep Creek, Nebraska). An ulna, radius, humerus, tibia, and $P\frac{1}{1}–M\frac{3}{3}$ are figured. There is no skeletal material associated with the type; for the present it seems unlikely that we can assign these parts to *P. avus.* The teeth show greater wear than Y.P.M. no. 1128, and the latter is well worn.

P. avus is believed to be a member of the genus *Parahippus* because of the presence of the following characters (see Stirton, 1940): metaloph connected to ectoloph, crochet present, but not connected to protoloph, brachylophodont teeth, metaconid and metastylid tending to be more widely separate, and marked lingual slant of paracone and metacone walls.

Measurements of teeth in *P. avus* were taken at the base of the tooth as follows: anteroposterior diameter at base of parastyle and metastyle and on inside of lowers, transverse diameter from base of mesostyle to base of protocone, and greatest distance at base of lower teeth. There are few species of *Parahippus* known to me that offer adequate sampling for a reasonable statistical analysis; however, White (1942) has described a relatively large population of *Parahippus leonensis* Sellards from the Thomas Farm in Florida. Measurements of several specimens were made, and these have been compared with *P. avus* (see tables 6 and 7). Table 6 presents the mean for transverse dimension, and table 7 a complete analysis of the antero-

TABLE 7

VARIATION IN ANTEROPOSTERIOR DIAMETER OF PARAHIPPUS AVUS AND P. LEONENSIS, INCLUDING $P^3 - M^3$

	Number of teeth	Observed range	Mean	Standard deviation	Coefficient of variation	Estimated minimum no. individuals
P. avus, Mascall, and North Coalinga	12	16.6 – 19.5	17.86 ± .24	.792 ± .16	4.40 ± .93	6
P. leonensis, Florida	32	13.7 – 17.7	15.96 ± .16	.296 ± .11	5.82 ± .70	9
P. vellicans, Texas	10	12.2 – 16.2	14.28 ± .39	1.25 ± .28	8.00 ± 1.83	5

posterior measurement. The values, 4.40 and 5.82, for coefficient of variation are considered to be about average value (Simpson and Roe, 1939, p. 123). *P. avus* is one of the larger species of *Parahippus.*

Comparisons.—Parahippus leonensis is not greatly different from *P. avus.* Fortunately, the sampling is fairly good in both species. *P. leonensis* from Florida has been considered distinct from a Texas species *P. vellicans.* Except for less development of the ribs on the metacone and paracone and smaller size in the Texas specimens compared to the Florida sample, there is little to distinguish these populations. White (1942) synonymized these species; Stirton (1940 and 1947) lists both *P. vellicans* and *P. leonensis.* Judgment on difference in size of ribs on the metacone and paracone is highly subjective and may have little significance in this instance. Comparison of the material from Texas with the type description of *P. leonensis* revealed smaller size and narrower-tipped styles in the Texas specimens. The type of *P. leonensis* measures length 16.0, width 19.0. The anteroposterior diameters in *P. vellicans* and *P. leonensis* have been compared (see table 7), using the formula (see Simpson and Roe 1939, p. 196): d/σ with ${}^{d}/\sigma_{d} = \sqrt{\sigma^2_{m1} - \sigma^2_{m2}}$ and $d = M_1 - M_2 = 1.68$. Comparison of these populations shows $d/\sigma = 3.95$, surely a significant statistical difference in this dimension. The difference in means of the transverse diameter is 2.7, which would also show significant difference. More material may show a complete integradation of the two populations, yet the data available suggests there may be a specific distinction in the populations, particularly in size.

Comparison of *P. avus* and *P. leonensis* in anteroposterior diameter shows $d/\sigma = 6.55$ with a decided, significant difference; difference in means of transverse diameter is 1.8. Although *P. leonensis* is close to *P. avus,* the important differences in *P. leonensis* are smaller size, T-shaped or more complex crochet, absence of internal cingulum on upper cheek teeth, and external cingulum on lower cheek teeth. The presence of cement and the plications on the metaloph are outstanding resemblances in the two species (see table 9).

Parahippus socius (Hay) may be only a size variant of *P. vellicans;* since the type has not been seen, judgment is restricted.

Parahippus barbouri White* has been considered little different from *Parahippus crenidens* (Scott) (see White, 1942). When *P. barbouri* was compared with *P. leonensis,* it was extremely difficult to see any distinction between these two species from the same fauna. There seems to be no marked difference in size, complication of enamel pattern, or amount of cement, although White considers the amount of cement a significant feature. Cement in *P. leonensis* varies from slight to moderate.

Parahippus crenidens (Scott)* from the Deep River, Montana, has been considered to be very close to *P. avus* by Gidley (1907) and by Merriam and Sinclair (1907). Without more material at hand, it is difficult to judge the status of *P. crenidens.* If we can accept the reference of new material to *P. avus* in this study, there is additional basis for distinction between these species in that *P. crenidens* is without an external cingulum on lower cheek teeth, has no internal cingulum on upper cheek teeth, only a thin coat of cement, and no ribs. Other characteristics of the type are much as in *P. avus* (see table 9).

The type of *Parahippus coloradensis* Gidley is possibly a little smaller than the

TABLE 8

MEASUREMENTS OF PARAHIPPUS AVUS FROM THE MASCALL FAUNA

	Anteroposterior diameter at base		Transverse diameter at base		Height of crown
	Right	Left	Right	Left	
Mascall type area					
Y.P.M. no. 11274 (type) M^2	17.2	....	22.4	....	...
Y.P.M. no. 11274 (type) M^3	16.7	....	20.8	....	12.8
Y.P.M. no. 1128 (former type *P. avus*) P^2	22.8	....	21.7	....	....
Y.P.M. no. 1128 P^3	(22.5)	....	....	....	.
Y.P.M. no. 1128 P^4	....	....	24.1	....	...
Y.P.M. no. 1128 M^1	16.8	....	....	....	...
Y.P.M. no. 1128 M^3	17.0	....	22.1	....	...
Y.P.M. no. 1128 P_2	20.7	20.4	14.7	15.0	...
Y.P.M. no. 1128 P_3	17.7	....	16.5	....	...
Y.P.M. no. 1128 P_4	18.4	17.7	16.5	14.8	...
Y.P.M. no. 1128 M_1	16.6	17.4	14.5	14.5	...
Y.P.M. no. 1128 M_2	17.3	....	14.3		...
U.C.M.P. no. 1701 M^1	17.2	....	21.4	....	8.4
U.C.M.P. no. 31385 lower	18.2	....	14.1	....	11.7
C.I.T. no. 406 PM's or M's, upper	19.5	....	18.8	....	10.6
C.I.T. no. 407 PM's or M's, upper	18.3	.	22.0	....	12.9
Crooked River area					
Y.P.M. no. 10784 PM's or M's upper	16.6	....	21.6	.	12.6
Y.P.M. no. 14272 PM's or M's, lower	18.6		24.0	....	9.8
U.S.N.M. no. 18747 lower	18.0	....	14.3	..	10.3
U.S.N.M. no. 18717 lower	17.2	....	13.5	....	...

TABLE 9

PARAHIPPUS AVUS (MARSH) COMPARED WITH SOME OTHER SPECIES OF PARAHIPPUS AND MERYCHIPPUS

Parahippus avus	*Parahippus cerenidens* (Scott)	*Parahippus leonensis* Sellards	*Parahippus coloradensis* Gidley	*Merychippus primus* (Osborn)	*Merychippus gunteri* Simpson
1. Hypsobrachyodont	1. Possibly lower crowned ○	1. Probably similar... +	1. Probably similar... ○	1. Hypsodont... –	1. Hypsodont ... –
2. Somewhat larger than *P. leonensis*	2. Similar +	2. Somewhat smaller –	2. Similar. +	2. More quadrate and smaller teeth. –	2. More quadrate and smaller teeth... –
3. Cement, moderate to heavy on lakes and between lophs, thin to none external	3. Possibly less –	3. Slightly less prominent. ○	3. Light coat... –	3. Greater.... –	3. Somewhat greater... ○
4. Crochet simple but relatively close to protoloph	4. Similar but weak ○	4. Complex, with one or two plications, T-shaped –	4. Crochet large, close to ectoloph but simple.. +	4. With or without plications, usually one or two, usually connected... –	4. Usually one or two. Sometimes not connected..... ○
5. Styles prominent, wide at base, otherwise narrow	5. Narrower, possibly. ○	5. Smaller.... ○	5. Relatively smaller... –	5. Narrow tips... –	5. Slightly narrower... ○
6. Hypostyle large, triangular isolated and sometimes enclosing a fossette	6. Similar +	6. More elongate on posterior edge, tends to enter post. fossette (a pli hypostyle?).. +	6. Smaller, but triangular, no fossette.. –	6. Triangular but enclosing post fossette and entering posterior portion... –	6. Enters postfossette.... –
7. Protoloph separate from protocone or constricted	7. United to ectoloph but restricted to protocone +	7. Constricted between protocone and protoconule... +	7. Similar. +	7. Tend to enclose pre fossette, constriction at paracone but united... ○	7. Protoloph tends to connect with ecto., protocone conn. to protoconule.. ○
8. Internal cingulum usually on uppers	8. None (also none on lowers, external) –	8. None.... –	8. None.... –	8. None.... –	8. None ... –
9. Ribs faint on paracone and metacone	9. No ribs. +	9. Probably similar... +	9. Ribs prominent on M^3 at least –	9. Possibly similar.... ○	9. None.. –
10. Plications on metaloph vary from one to three anterior or posterior	10. Mostly anterior ○	10. Similar.. +	10. Two ant., small.. –	10. Generally similar ... +	10. Similar +
11. Small cusp or cingulum between protocone and protoconule	11. Similar. +	11. Cusp not common but cingulum present. ○	11. Small on M^3..... +	11. None. –	11. None –
12. External walls of paracone and metacone slant inward at crest	12. Similar +	12. Tend to be more vertical –	12. Similar. +	12. More vertical. –	12. More vertical –
13. Protocone pyriform and larger than hypocone. Separate but close to protoconule	13. Possibly more equal ○	13. Protocone more rounded and nearer size of hypocone... ○	13. Similar... +	13. More elongate ... –	13. More rounded.. –
	Total: +, 6; –, 2; ○, 5; N = 1	Total: +, 5; –, 4; ○, 4; N = 35	Total: +, 6; –, 6; ○, 1; N = 1	Total: +, 1; –, 10; ○, 2; N = 11 (approx.)	Total: +, 1; –, 8; ○, 4; N = 10

average of *P. avus*. The crochet, protocone, and slant of the walls of the ectoloph are similar to *P. avus*, the amount of cement is slight, styles small, ribs prominent, internal cingulum absent, and the metaloph simple (see table 9).

Parahippus cognatus Leidy* from the Niobrara River fauna is listed as late Barstovian age in Wood *et al.* (1941). The type was based on milk teeth which have been compared with *P. avus* (Matthew, 1924). Matthew (*op. cit.*) considers an American Museum specimen no. 14305, also with milk dentition, as near *P. cognatus*. This specimen comes from near Marsland, Nebraska. *P. cognatus* differs from *P. avus* in having the metaloph weakly connected to ectoloph, very little cement (possibly a thin coat), strong ribs, and relatively small hypostyle. There is little in *P. cognatus* to show relationship to *P. avus*, and since it is known only from milk dentition, its true affinity with *P. avus* is obscure.

In Schlaikjer's (1937) phylogeny of species of *Parahippus*, *Parahippus intiger* Matthew is placed near *P. avus*, and the two stem from a common origin. He stated that Matthew (1924, p. 157) had pointed out the affinity of *P. intiger* and *P. avus*. Actually, Matthew was referring to *P. cognatus* in his comparison and not to *P. intiger*. Little data and no figures are presented in Matthew's description of *P. intiger*. Several specimens referred to *P. intiger* by Matthew were examined at the American Museum including paratype nos. 17567 and 17568. Another specimen, A.M. no. 14322, is labeled *P. ? cognatus* but is nearly identical to nos. 17567 and 17568. The entire sample resembles *P. avus* in size and general proportions but differs in the small amount of cement present in fossettes, absence of external ribs on paracone and metacone, hypostyle connected basally with metaloph, no internal cingulum on upper cheek teeth, and no external cingulum on lower cheek teeth.

Parahippus tyleri Loomis may be distinct from *P. avus* in more prominent ribs, hypostyle with posterior notch (?), absence of cement, and probably simpler metaloph.

Parahippus pawniensis Gidley* differs in the absence of internal cingulum on upper cheek teeth and external cingulum on lower cheek teeth, in the absence of cement and ribs, and in the possession of possibly heavier styles.

Parahippus nebrascensis Peterson* is an extremely large species, larger than *P. avus* but basically primitive in some other features such as the absence of cement and the presence of a simple metaloph. It has no internal cingulum on the upper cheek teeth.

Gazin (1932) has described some teeth from the Skull Spring of Oregon as *Parahippus* near *coloradensis* Gidley. He believes *P.* near *coloradensis* differs from *P. avus* in smaller size, less cement on enamel, and simpler metaloph. It is apparent from his figures that the shelflike anterior cingulum and small cusp between the hypocone and protocone are possibly additional differences, yet without more material it is unwise to identify the specimen specifically. The lower tooth from Skull Spring resembles those from the Mascall in a rugose surface, widely separated metaconid and metastylid, and relatively larger hypoconulid.

Parahippus agrestis (Leidy)* is large enough to be *P. avus*. It also has a rugose external cingulum with a very faint deposit of cement. Since the species is based on lower teeth, it is futile at present to form an opinion on its relationships.

The lower teeth referred by Bode (1933) to *P. avus* from North Coalinga probably do not differ significantly from the Mascall even though there is a tendency for the lack of an external cingulum. This feature varies in the Mascall material.

Discussion.—The relationship between *P. avus* and probably primitive species of *Merychippus* is presented in table 9. There is evidence in *P. avus* of tendencies toward *Merychippus* in size, height of crown, shape of hypocone, plications on metaloph, presence of cement, and beginning of enclosure of prefossette. It is probable, however, that neither of the two species *Merychippus primus* (Osborn) or *Merychippus gunteri* Simpson is particularly close to *P. avus*. Stirton (1940) has suggested that *P. avus* and other advanced species of *Parahippus* gave rise to different species of *Merychippus*. Simpson (1932) and White (1942) indicate size to be the only apparent difference between *M. gunteri* and *M. primus;* Simpson states that if they had come from the same locality they could be sepa-

Fig. 16. *Parahippus avus* (Marsh), U.C.M.P. no. 40240, loc. V-4834: occlusal view upper premolar or molar; × 1.

rated only if a large series were at hand. He has also shown that *P. leonensis* practically intergrades with *M. gunteri* in the Thomas Farm and Midway faunas. Schlaikjer (1937) believes the genus *Merychippus* to be derived from *P. leonensis*. Stirton (1947) places *P. vellicans* in line with an undescribed species of *Merychippus* from the Phillips Ranch fauna,[8] and from this *M. primus* is descended. To summarize, it is apparent we have *P. leonensis* or the closely related *P. vellicans* as possible ancestors of the separate species of *Merychippus, M. primus,* and *M. gunteri.*

Results of study in this problem suggest there is another phyletic line in the history of these Miocene horses. *Parahippus avus* could be near the ancestry of the low-crowned, complexly patterned *Merychippus brevidontus* from the North Coalinga fauna of California. One tooth (Y.P.M. no. 14243, see discussion on Merychippus sp. low crowned) from the Mascall has a connected crochet (a merychippine trait), but the specimen bears many parahippine characteristics. It is not as complex in its enamel pattern but has proportions much like *M. brevidontus*. Y.P.M. no. 14279 from Bully Creek, Oregon (see p. 232), in contrast to this simple *Merychippus* tooth (no. 14243) is a complex *Parahippus* but may be referred to *P. avus*. Y.P.M. no. 14272 is another specimen of *P. avus* exhibiting advanced *Merychippus* traits and comes from the Crooked River area. This evidence indicates a probable phyletic sequence from *P. avus* to *M. brevidontus,* or that before Mascall and Virgin Valley times, the two species had a common ancestor. The known species of *Parahippus* are rarely well represented in faunal assemblages, and the genus as a whole seems to be variable, yet few of the species differ widely from each other. Many small populations were possibly genetically stable at the time; these

[8] Since the writing of this paper, Buwalda and Lewis (1955) have published on some of this material and described a new species, *Merychippus tehachapiensis;* they consider it a primitive, middle Miocene *Merychippus,* structurally ancestral to *M. intermontanus* from the Barstow.

closely allied populations of *Parahippus*, as primitive merychippine animals, may have been adapting to various changing environments. By chance preservation and subsequent exposure, some groups have been found at Thomas Farm, Virgin Valley, Garvin Gully, High Rock Canyon, and in the Mascall. In *P. leonensis* and *P. avus* we have close morphologic resemblance; it is conceivable that *M. brevidontus* could have arisen from either of these species, but it is more logical to assume that the western species of *P. avus* is nearer to the ancestor of *M. brevidontus* owing to geographic proximity and very close structural relationship. It may be concluded that *M. primus*, *M. gunteri*, and *M. brevidontus* may have arisen from closely related *Parahippus* species, and "polyphyletic" origins can be recognized at least in a narrow sense (see Simpson, 1932).

P. avus is relatively simple in the complication of the enamel plications on the crochet and might be thought of as "primitive" in comparison with *P. leonensis;* but the greater size, height of crown, and greater complexity of the metaloph in *P. avus,* when compared with other species of *Parahippus,* suggest an advanced condition. *P. avus* is present in the Mascall and North Coalinga faunas where it is associated with more advanced merychippine genera (see fig. 44 on correlation).

Since *P. avus* displays tendencies toward hypsodonty and a coating of cement, it is possible it could have been a plains or prairie dweller and probably did some grazing (see Stirton, 1947). Browsing habits are not excluded since *P. avus* is not a truly hypsodont horse.

Parahippus ?

In the University of California collections there are some upper and lower teeth from Mascall localities that are of questionable taxonomic status. From the type area locality 3059, there is a small milk tooth (U.C.M.P. no. 31987) with stylids widely separate for half the height of the crown. Faint internal and external cingula are present, and anterior and posterior cingula are moderately developed.

An interesting unworn right upper (U.C.M.P. no. 40314) was collected from V-4941 east of the type region. Walls of the ectoloph slant inward as in *Parahippus,* the crochet appears as if it would not connect with protoloph, and cement covers the tips of cusps between lophs.

Measurements.—Anteroposterior diameter at base, 16.2; transverse diameter at base, 21.5; height of crown, 18.5.

From V-4949 (old 897) in the Crooked River area, a part of a left P^2 was obtained (U.C.M.P. no. 40332). The protocone is isolated and crochet bifurcated but not connected to protoloph; small size is suggestive of *Parahippus.*

In the lower premolars collected by P. F. Brogan at Gateway locality V-3427, U.C.M.P. no. 3485, the stylids may be too widely separated toward the base, and more cement may be present than possible in *Parahippus;* external walls of the protocone and hypocone are not rounded as in *Merychippus* but are V-shaped, and the external cingula only faintly suggested. The status of these two specimens is questionable.

Archaeohippus ultimus (Cope)
(Pls. 6–8; figs. 17–20)

1886. *Anchitherium ultimum* Cope. Proc. Amer. Philos. Soc., vol. 23, pp. 357–361.

Holotype.—Cope (1886): "... represented in my collection by a nearly complete superior den-

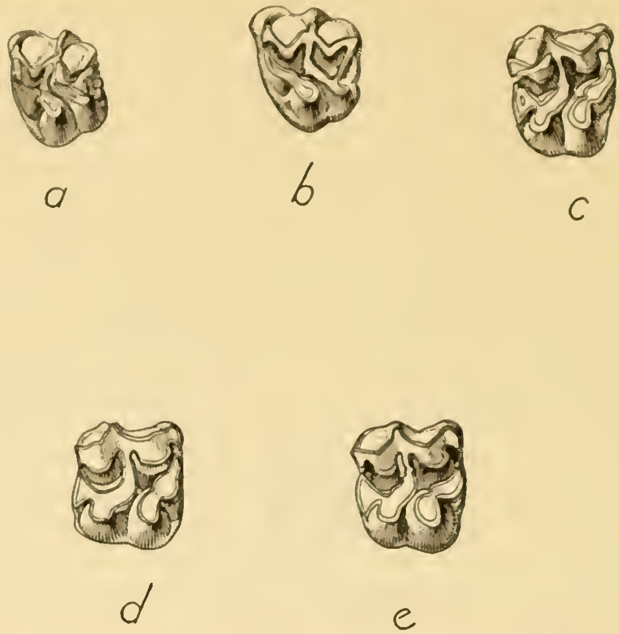


Fig. 17. *Archaeohippus ultimus* (Cope), Crooked River area: *a*, U.C.M.P. no. 39876 molar; *b*, Y.P.M. no. 10420 premolar; *c*, Y.P.M. no. 10418 molar; *d*, Y.P.M. no. 14305 molar; *e*, Y. P. M. no. 10419 molar; × 1.

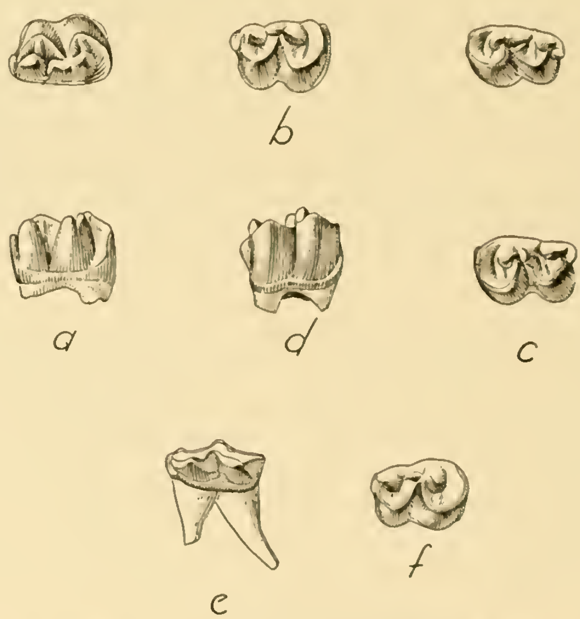


Fig. 18. *Archaeohippus ultimus* (Cope), Crooked River area: *a*, Y.P.M. no. 14309 occlusal and internal view; *b*, Y.P.M. no. 14288 occlusal view; *c*, Y.P.M. no. 14258 occlusal view; *d*, Y.P.M. 14289 external view; *e*, U.C.M.P. no. 39882 occlusal view; *f*, Y.P.M. no. 14256 occlusal view; × 1.

tition, with palate and sides of skull to the middle of the orbits, and top of skull to above the infraorbital foramen." A.M. no. 8174.

Referred specimens.—Mascall type area. U.C.M.P.: right M^2 and left P^2 no. 1689, loc. V-4830–4835; lower right molars no. 31987 and left, 26643, loc. 3059, C.I.T. : premolar no. 424 "from Mascall deposits" (Bode, 1933). Y.P.M. left lowers nos. unworn 14258 and 14259, probably from Mascall though no data attached except "Condon collection." U.S.N.M.: part of ramus with roots of one premolar and part of another, no. 18746 and single lower no. 3909 from "Cottonwood Creek, Oregon."

Crooked River area: U.C.M.P.: M^2 no. left 39876, right lowers nos. 39877 and 39878, loc. V-4949; left lowers nos. 39880, 39879, and left 39882, loc. V-4951. Y.P.M.: right upper molars nos.

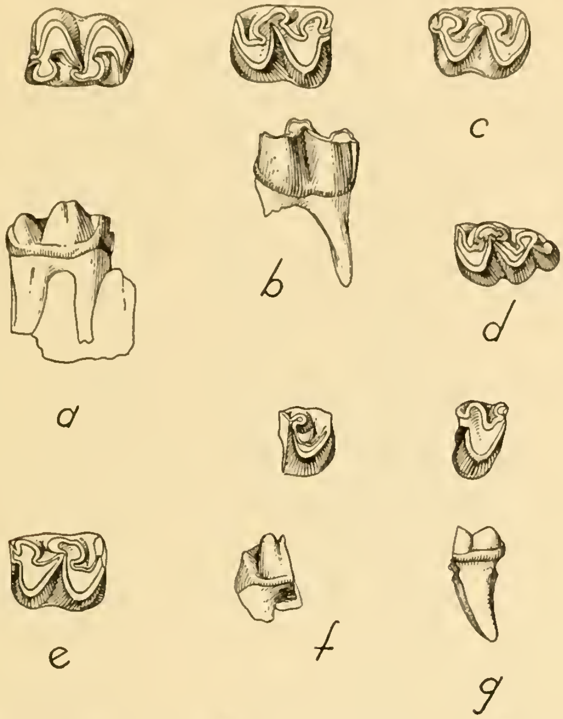


Fig. 19. *Archaeohippus ultimus* (Cope), Mascall type area: *a*, Y.P.M. no. 14259 occlusal and internal view. Crooked river area: *b*, U.C.M.P. no. 39879 occlusal and external view; *c*, Y.P.M. no. 14260 occlusal view; *d*, U.C.M.P. no. 39880 and *e*, U.C.M.P. no. 39877 occlusal view; *f*, U.C.M.P. no. 39878 occlusal and internal view; *g*, U.C.M.P. no. 39878 occlusal and external view; × 1.

10418, 10419, 14305, 14308, left lowers nos. 14307, 14309, 14260, 1426?, 14261, and 14256 from Crooked River region, Oregon, all part of shipment no. 198. Y.P.M. lower right no. 14289 Grindstone Creek, Crooked River region, Oregon.

Gateway area. C.I.T. no. 4095 M_3 and partial upper.

Type locality.—Cope (1886): ". . . the *Ticholeptus* beds of Cottonwood Creek, Oregon." There is enough material found at definite Mascall localities near the type area and near the Crooked River region to justify assignment of the type to the Mascall fauna.

Revised diagnosis.—Based on study of the type and referred material. Smaller than *Archaeohippus mourningi* (Merriam) but close to *Archaeohippus blackbergi* (Hay). Crochet usually absent and minute when present; usually small plication on both sides of metaloph; internal cingulum usually moderate to strong on upper cheek teeth and on lower cheek teeth; external cingulum always moderate or strong on lower teeth; hypostyle triangular and usually small; hypocone smaller than protocone; cement rare on cheek teeth and, when present, only as a thin

TABLE 10

VARIATION IN UPPER MOLARS OF SOME SPECIES OF ARCHAEOHIPPUS

(in millimeters)

	Number of teeth	Observed range	Mean	Standard deviation	Coefficient of variation	Estimated minimum no. individuals
Anteroposterior diameter						
A. ultimus P^3-M^3	11	11.2–13.0	12.06 ± .19	.642 ± .13	5.32 ± 1.13	5
A. blackbergi M^1-M^2	21	10.1–12.8	11.44 ± .15	.688 ± .10	6.01 ± .93	10
Transverse diameter						
A. ultimus P^3-M^3	10	13.0–16.4	15.02 ± .32	.996 ± .22	6.40 ± 1.4	5
A. blackbergi M^1 and M^2 only	22	12.2–15.0	13.75 ± .16	.750 ± .11	5.46 ± .83	11

deposit externally; metaconid and metastylid separate only 1–3 mm. from tips; preorbital fossa forms elongate, deep pit throughout (one skull known).

Supplementary description.—Investigation of collections at Yale Peabody Museum and the National Museum at Washington was particularly compensatory in that several individual teeth of *Archaeohippus ultimus* were found that have not been reported previously. This includes all the referred specimens listed from Y.P.M., U.S.N.M., and C.I.T. U.C.M.P. nos. 39876, 39877, 39878, 39879, and 39882 are also new records for *A. ultimus.* I have transferred some specimens formerly called *A. ultimus* to less definite categories—*A. ultimus?* *Archaeohippus* sp., *Parahippus?*, and *Merychippus?*

TABLE 11

MEASUREMENTS OF ARCHAEOHIPPUS BLACKBERGI

(in millimeters)

Lower dentition M.C.Z.	Anteroposterior diameter	Transverse diameter
No. 3884		
$P_{\overline{4}}$	11.3	9.1
$M_{\overline{1}}$	10.2	7.7
No. 3906		
$P_{\overline{4}}$	11.6	7.8
$P_{\overline{4}}$	10.0	...
$M_{\overline{1}}$	9.5	...
No. 3885		
$P_{\overline{4}}$	10.1	9.1
$M_{\overline{1}}$	9.5	8.1
$P_{\overline{4}}$	10.4	9.3
$M_{\overline{1}}$	10.0	8.3
A. blackbergi		
Observed range	9.5–11.6	7.7–9.3
Mean ($M = \Sigma(X)/N$)	10.3	8.4
A. ultimus		
Observed range	11.4–14.7	7.5–10.2 N = 17 for ap.
Mean	12.7	8.99 N = 18 for tr.
A. penultimus		
Observed range	10.1–10.7	8.1–9.2 N = 3
Mean	10.3	8.76

In addition to the diagnostic features of *A. ultimus* the following characters are noted (as based on the above cited material): Dentition; moderate ribs opposite paracone and metacone, protoconule distinct and smaller than protocone but both connected by ridge; anterior cingulum along protocone and protoconule in upper molars and along protoconid of lower molars, posterior cingulum connects to hypostyle; enamel surface of lower molars rugose; hypoconulid small; postfossette tends to remain open. Skull: elongate, anterior edge of orbit opposite M^3 and narial niche far posterior.

Notes on the figure of the type (Osborn, 1918, fig. 172): In general the figure is an accurate reproduction but the following notations are given: left anterior nasal and all premaxilla absent; preorbital fossae concave on dorsal half of maxilla above mid-point of diastem; anteroposterior axis of incisor III parallel to median plane and not at an angle with it; left canine drawn from right side; left external borders of P^2 and P^3 restored from right side; and internal cingulum broken on left M^2 (pl. 7).

TABLE 12

MEASUREMENTS OF REFERRED ARCHAEOHIPPUS ULTIMUS

(in millimeters)

	Antero-posterior[a] diameter	Transverse[a] diameter	Height[b] of crown
Upper dentition			
U.C.M.P. collection			
No. 1689 M^3.	11.6	14.6	6.3 (unworn)
No. 39876 M^3.	12.2	14.5	7.1 (unworn) M = 7.2
No. 1689 P^2	14.5	13.0	8.2 (unworn)
Y.P.M. collection			
No. 10418 molar (?)	12.8	16.4	...
No. 10419 molar	12.2	16.2	...
No. 14305	12.4	16.4	...
Lower dentition			
U.C.M.P. collection			
No. 26643 molar or premolar	13.0	8.1	8.6 (unworn)
No. 31987 not P_3 or M_3	14.7	9.2	6.7 (unworn)
No. 39879 not P_3 or M_3	12.9	10.2	...
No. 39877 not P_3 or M_3	12.5	10.0	...
No. 39882 not P_3 or M_3...	12.0	9.2	...
No. 31987 not P_3 or M_3	12.0	9.6	...
No. 39880 M_3..	13.7	7.5	6.4 (unworn)
C.I.T. collection			
No. 424....	13.5	9.5	10.3 (unworn)
Y.P.M. collection			
No. 14309 molars or premolars	12.6	9.3	9.4 (unworn)
No. 14307 not P_3 or M_3...	14.3	9.4	...
No. 14260 not P_3 or M_3...	11.7	8.4	...
No. 14261 not P_3 or M_3...	12.0	8.9	8.5 (unworn)
No. 14260 A not P_3 or M_3 ...	13.4	9.8	7.2 (unworn)
No. 14258 not P_3 or M_3 (? locality)	12.5	8.2	8.4 (unworn)
No. 14259 not P_3 or M_3 (? locality)	11.4	7.8	7.4 (unworn)
No. 14289 not P_3 or M_3..	11.4	8.3	8.4
U.S.N.M. collection			
No. 3909 not P_3 or M_3..	13.3	10.7	...
No. 18746 not P_3 or M_3	....	7.5	...
Observed range, lowers	11.4–14.7	7.5–10.2	7.2–10.3
Mean ($M = \Sigma(X)/N$).	12.7	8.99	7.9

[a] Measured at base of tooth, greatest dimension in uppers and lowers.
[b] Tip of mesostyle to edge of enamel.

Measurements.—Type specimen A.M. no. 8174* (also see Cope 1886, original meas.): length diastem I^3–P^1 48.2; length diastem C–P^1 35.3; length tooth row (left) 77.9; distance, posterior edge infraorbital foramen to preorbital bar 26.0; width across nasals anterior to infraorbital foramen 25.0; narial notch to anterior edge preorbital bar 98.5; greatest depth preorbital fossa 14.0 (approx.); width palate at P^1 26.2; width palate at M^2 32.6; least width diameter P^1 10.3; external anteroposterior diameter P^2 14.1; P^3 12.8; P^4 13.0; M^1 11.5; M^2 11.2; M^3 11.3; and I^3 5.8.

Bode (1933) has figured U.C.M.P. no. 26643 (pl. 3, fig. 1, *op. cit.*, but erroneously gives it no. 3059); no. 31987 (pl. 3, fig. 3) and C.I.T. no. 424 (pl. 3, fig. 2).

Comparisons.—*Archaeohippus minimus* (Douglass)* from the Madison Valley fauna is not a readily determined species. More material may decisively justify specific separation of a population from Madison Valley, but on present evidence and with our knowledge of variation in more completely represented species, it is not considered to be well defined. Examination of the comparative chart (table 14) indicates close affinity with *Archaeohippus ultimus*. Even those features with uncertain category (O, table 14) tend to resemble *A. ultimus*. The Madison Valley specimen has internal cingulum on P^4, hypocone broken in most teeth,

TABLE 13
Measurements of *Archaeohippus minimus* C.M. no. 731
(in millimeters)

	Anteroposterior diameter	Transverse diameter	Height of crown
Upper dentition			
P^3	15.5	19.5	....
M^1	13.6	17.4	7.4 (unworn)
M^2	11.4 (inside meas.)	....	....
Lower dentition			
I_2	4.4	3.8	....
I_3	3.7	3.2	....
C	5.7	4.7	....
P_1	6.4	3.3	....
P_2	13.8	7.5	....
P_3	12.6	9.6	....
P_4	11.4	10.3	....
M_1	11.0	9.4	....
M_2	10.6	9.1	....

Least transverse diameter, lower symphysis	12.3
Distance, C to P_1	32.2
Thickness ramus at P_4	10.0

probably equal amount of cement on teeth, presence of crochet debatable but apparently definite on P^4 though absent on other teeth. Individual analysis of the metaloph shows the number of plications present anteriorly and posteriorly respectively; C.M. no. 713, P^4 1 minute and slightly crenulate, M^1 3 and 1 minute M^2 1 and 2 minute plications, M^3 none and very slightly crenulate. It is possible that more material would show the greater size in *A. minimus* as suggested in the measurements of P^3 and M^1 (see table 13). *A. minimus* is notable in the dimensions of the lower jaw (table 13) and particularly in the absence of a marked diastem between I_3 and C. However, these structures are not known in *A. ultimus*.

The type of *Archaeohippus blackbergi* (Hay) from Garvin Gully of Texas was studied by White (1942, p. 15) in his paper on the Thomas Farm fauna of Florida. White was able to take advantage of work done by Hesse on specimens from Garvin Gully, and White concludes that Hay's *Miohippus blackbergi* (Archaeohippus) is similar to specimens taken from the Thomas Farm fauna in Florida. *A. blackbergi* is much like *A. ultimus* in height of crown and in the presence

TABLE 14

ARCHAEOHIPPUS ULTIMUS COMPARED WITH OTHER NORTH AMERICAN SPECIES OF ARCHAEOHIPPUS

(Uppers and lowers)

A. ultimus	*A. minimus*	*A. blackbergi*	*A. mourningi*
1. Smaller than *A. mourningi*	1. Similar size (see meas.) . . . +	1. Probably smaller in transverse diam. of teeth . . . . . . −	1. Larger . . . . . . −
2. Low crowned, Ave. Uppers; 7.2, lowers 7.9, unworn	2. Probably similar . . . . +	2. Probably lower . . . . ○	2. Higher, an upper 9.7, two lowers 10.3 and 9.3 . . −
3. Crochet, absent 80 per cent, minute 20 per cent	3. Varies but probably similar . . . . +	3. Absent, 30 per cent, present 70 per cent but minute . . . −	3. Absent −
4. Metaloph plications, 80 per cent minute 1–3 anterior, 50 per cent minute 1–3 posterior	4. Similar, crenulate or 1–2 distinct 1–3 . . . . +	4. Simpler, 45 per cent none ant., 55 per cent 1–2 ant., 18 per cent none post., 82 per cent 1–3 more post. . . . −	4. None to a few ○
5. Internal cingulum on uppers usually moderate to strong	5. On premolar only . . . . ○	5. None . . . . −	5. None . . . . . . −
6. Hypostyle triangular, usually small	6. Similar (in same state of wear)	6. Probably similar . . . . +	6. Large, with deep pit −
7. Hypocone smaller than protocone	7. Generally similar . . . . . . ○	7. Tend equal size, varies . . ○	7. Equals protocone . −
8. Cement, rare on uppers and only thin spots	8. Similar . +	8. Usually none; rare . . . . . +	8. None . −
9. Internal cingulum, lowers 79 per cent present, mod.–strong	9. Similar . +	9. Present but slight . . . . . ○	9. Variable . . ○
10. External cingulum always moderate or strong	10. Similar . . . . +	10. Usually present . . . . ○	10. Variable ○
11. Cement on lowers not common	11. Not common but present . . +	11. Similar +	11. None −
12. Stylids separate only 2–3 mm. from tips	12. ? . ?	12. Similar +	12. Similar . +
13. Malar fossa forms deep pit throughout	13. ? . . . . ?	13. Possibly . . ?	13. ? . ?
	Total +, 9; −, 0; ○, 3; ?, 2 N = 3 uppers, 9 lowers	Total +, 4; −, 4; ○, 5; ?, 1 N = 22 uppers, 18 lowers	Total +, 1; −, 8; ○, 3; ?, 1 N = 4 uppers, 4 lowers

of thin cement but seems to be definitely distinct in the more frequent occurrence of minute crochet, absence of internal cingulum on upper cheek teeth, simpler pattern on metaloph, and tendency for equal size of hypocone (see table 14). *A. blackbergi*, M.C.Z. no. 3843, appeared to me to have a preorbital fossa as deep as that found in *A. ultimus*. Of the features listed by White (*op. cit.* p. 19), "1. Well developed crochet" and "4. Hypoloph and posterior cingulum closing postfossette" are the two most significantly diagnostic.

By means of a comparison of averages (means) in the two species *A. ultimus* and *A. blackbergi* in anteroposterior diameter $d/\sigma = 2.58$ (see table 10). As a cross check on this, since the *ultimus* sample is small, t was calculated and equals 3.43. This suggests a significant difference in anteroposterior diameter. The difference in means in transverse diameter $(d = 1.27)$ is also significant.

Fig. 20. *Archaeohippus ultimus* (Cope), Mascall type area: top, U.S.N.M. no. 18746; bottom, U.S.N.M. no. 3909; × 1.

The samples of measurements in the lower teeth are small for statistical comparison, but study of the means (table 11) suggests again that *A. blackbergi* is smaller than *A. ultimus* or at least is relatively shorter anteroposteriorly.

Stirton (1940, p. 176) has tentatively synonymized *Archaeophippus minutalis* (Hay), Garvin Gully, Texas, with *A. blackbergi.* I did not see the type of *A. minutalis,* but did observe referred U.C.M.P. no. 32610. It is also my conclusion on the basis of known variation in such features as the crochet, shape of hypostyle, and metaloph plications in well-represented populations that the two species are synonymous.

White (1942, p. 15) has placed *Archaeohippus nanus* Simpson from the Thomas Farm in synonymy with *A. blackbergi* in the same fauna. I have noted some material in the U.C.M.P. catalogued as *A.* cf. *nanus* from the Flint Hill fauna. Many of the features characteristic of *A. blackbergi* are present in these specimens, that is, crochet present or absent, some cement, and no internal cingula. Simpson (1932) has observed an absence of cement and crochet in the type; however, it has been seen that such features vary in one population, for example in *A. blackbergi.* I concur with White's revision.

Archaeohippus penultimus Matthew (1924) is from the Sheep Creek of Nebraska, and the type consists only of lower teeth. Morphologically the teeth may differ from *A. ultimus* and *A. blackbergi* in the absence of an internal cingulum; however, *A. blackbergi* varies in this feature. *A. penultimus* may be smaller than *A. ultimus,* but is close to *A. blackbergi* in size. Several specimens of milk dentition were observed at the American Museum, and these have been referred to *A. penultimus* from the Sheep Creek beds (see Bode, 1933). If the milk tooth, U.C.M.P. no. 2019, a dp^2 (see *A. ultimus?*) is definitely assignable to *A. ultimus,* then a smaller size in *A. penultimus* is indicated, but it is my opinion that there is insufficient evidence for a definite assignment of the Mascall dp^2 to *A. ultimus.*

When consideration is given to the fact that good sampling of adult specimens is essential for sound specific distinctions, it seems logical that specific identification is questionable so far as a few samples of milk dentition are concerned. *A. penultimus* cannot be adequately compared with other species on present evidence. Its geographic position suggests that it is a distinct species, but morphologic evidence does not support this.

Archaeohippus mourningi (Merriam) from the Barstow, California, is a distinct species (see table 14), and is the least like *A. ultimus* of all the known species. The plications on the metaloph and the occurrence of cingula on the lower teeth are like those in *A. ultimus.* On the basis of measurements of the type from the Barstow and referred material from North Coalinga in the U.C.M.P. collection, it is apparent that *A. mourningi* tends to be larger than *A. ultimus,* in the upper teeth at least.

Measurements (Archaeohippus mourningi, Barstow).—Anteroposterior and transverse diameter respectively: U.C.M.P. no. 19840 (type M^1 14.3, ——— ; dp^2 14.1, 14:0; dp^4 (15.0); U.C.M.P. no. 23643 12.6, 16.1; lowers 12.5, 16.3; U.C.M.P. no. 23667? premolars 12.3, 1017; no. 23666 premolars 12.3, 8.5; no. 23664 premolar $_?$? 14.3, 8.5; no. 23665 premolar 12.3, 7.5.

In *A. mourningi* the lack of an internal cingulum on the upper cheek teeth, the probable higher crown, the absence of a crochet, the hypocone as large as the protocone, and the larger hypostyle with an enclosed fossette are significant distinctions from *A. ultimus* and *A. blackbergi* (except for absence of internal cingulum in *A. blackbergi*).

Discussion.—The determination of primitive and advanced features in genus *Archaeohippus* is not easily achieved (see table 15). We might assume, if each character is given equal weight, that *A. ultimus* and *A. mourningi* are almost equally advanced. However, the increased size and the height of crown in *A. mourningi* are particularly significant as probable indications of the advanced evolution (or trend from early to later date) in much of the geologic history of the horse. The conclusion that *A. ultimus* is intermediate in its stage of evolution in the genus *Archaeohippus* is possible, but no actual phyletic sequence is derivable. There is little evidence to judge the phyletic position of *A. penultimus.* It would appear that *A. blackbergi* and *A. ultimus* are more like each other than they are similar to *A. mourningi.*

The generic status of *Archaeohippus* is often questioned. Certainly, there are few species readily determinable and these species were small in population numbers and not comparable to other more widespread and abundantly represented genera of horses; yet there are these few groups of specimens that are worthy of generic recognition. I have considered the following features typical of the genus, and useful in this study: *a*, small size; *b*, low-crowned cheek teeth, probably never more than 11.0; *c*, only a thin external coat of cement when present; *d*, crochet variable, present or absent, but always minute when present; *e*, stylids separate only at tips; *f*, probably deep preorbital fossa.

Stirton (1940, p. 176) notes the features as seen in *a*, *b*, *c*, and *d* above, and adds also: (1) metaloph connected to ectoloph, and (2) ribs between styles as well developed on cheek teeth as in *Parahippus*.

Bode (1933, p. 57) concludes that *Archaeohippus* differs from *Parahippus* in:

(1) absence of crochet (there is good evidence it does appear in *A. ultimus* and *A. blackbergi*), (2) constant thin and straight alignment of protoloph and metaloph (this feature does not seem particularly tenable), (3) "precocious development of crown-height relative to small tooth" size (need more measurable specimens for height of crown), (4) absence of cement (present as very thin coat in rare instances), (5) characteristic preorbital fossa. (Parentheses mine.)

Since *A. ultimus* is low crowned and with little cement, it may have been a browser. Its small size may indicate that it was not an open-range dweller but preferred to use wooded areas for cover and concealment.

TABLE 15

Comparison of Salient Features in Some Species of Archaeohippus

Features	*A. blackbergi*	*A. ultimus*	*A. mourningi*
1. Size	Small (P)[a]	Small (P)	Large (A)
2. Crochet	Present or absent (A)	Present or absent, rare (A)	Absent (A)[b]
3. Crown height	Moderate (P)	Moderate (P)	High (relatively) (A)
4. Metaloph plications	Simple (P)	Moderately complex (A)	Simple to moderate (?)
5. Internal cingulum (Uppers)	None (?)	Present (?)	None (?)
6. Hypostyle	Small (P)	Small (P)	Large (A)
7. Cement	Slight or rare (A)	Slight or rare (A)	None (P)
Totals	A (2) P (4)	A (3) P (3)	A (3) P (2)

[a] P = possibly primitive character as seen in evolution of horse; A = possibly advanced; ? = questionable status in evolution.
[b] One Coalinga specimen with very slight crochet at base of loph.

Archaeohippus ultimus?
(Pls. 6 and 8)

Some of the material, U.C.M.P. no. 2019 from V-4951, consists of one dp^2 and anterior part of dp^3, formerly designated by Gidley (1906) as *Archaeohippus* sp. He considered it too large for *Archaeohippus ultimus*. Since there is now more material to show the total variation, it is possible that these specimens can fall within the range of *A. ultimus*. They are a little larger than the milk teeth referred to *A. penultimus* (Bode, 1933). U.C.M.P. no. 2019 dp^2 measures 17.0 anteroposterior diameter and 13.6 transverse diameter.

Very heavily worn lower teeth, U.C.M.P. no. 1700 from old loc. 903 (V-4830–4835) consisting of parts of $P_{\overline{3}}$ and $P_{\overline{4}}$, have been called *A. ultimus* by Gidley (*op. cit.*). This specimen is probably small enough to be *Archaeohippus;* but since it is so badly marred, its assignment to the species *ultimus* is debatable. The presence or absence of cingula is not accurately determinable.

U.C.M.P. no. 39880, recently found at V-4951, is apparently an $M_{\overline{3}}$. The metaconid-metastylid are not separate (slight wear is present), and there is a slight internal cingulum with no external cingulum. At present there is no other $M_{\overline{3}}$

from the Mascall for comparison, but its size (anteroposterior diameter, 13.5 mm. and transverse diameter, 12.5 mm.) suggests that it is small enough to be near *A. ultimus.*

cf. *Hypohippus*
(Fig. 21)

This horse is represented by a fragment of a molar, U.C.M.P. no. 1702 from V-4949 (old 897), from the Crooked River assemblage.

Fig. 21. cf. *Hypohippus*, U.C.M.P. no. 1702, loc. V-4949; occlusal view partial upper; × 1.

A part of the base of the protocone, one half of the metaloph, a small internal section of the metacone and all the hypostyle are present. In size the specimen may be equivalent to the Virgin Valley, *Hypohippus* near *osborni* Gidley (see Merriam, 1911). The hypostyle does not enclose a fossette in the Mascall specimen and apparently would not do so until heavily worn. The Virgin Valley specimens show a tendency for an enclosure of the fossette. It is too small to be *Megahippus* and possibly too large for *Anchitherium*. The latter possibility is not eliminated; therefore the specimen is called cf. *Hypohippus.*

Fig. 22. *Merychippus relictus* (Cope): *a*, U.C.M.P. no. 23096, loc. V-4827; *b*, U.C.M.P. no. 23090, loc. V-4942. *Merychippus* cf. *relictus*: *c*, U.C.M.P. no. 27238, loc. (?) Mascall. *Merychippus severus* (Cope): *d*, U.Cm.P. no. 27237, loc. Mascall area. Reproduced from Bode (1934, p. 44, fig. 2); Bode designates nos. 27237 and 27238 as *M. relictus*. All × 1.

Merychippus relictus (Cope)
(Pl. 6; figs. 22–23)

1889*a Hippotherium relictum* Cope, Amer. Nat., vol. 23, pp. 253–254.

Holotype.—Cope (1889), "Represented by two superior and three inferior molar teeth." Amer. Mus. no. 8673. Cope (1889) figures an M^1 and M^2.

Lectotype.—A.M. no. 8673; left M^1 and right unworn M^2? (sectioned specimen); see supplementary description.

Referred specimens.—U.C.M.P. left upper molars nos. 23090 and 23096, loc. V-4942 and V-4827. C.I.T. right P^4 no. 4004, loc. Mascall collection?,[9] found stored with material from C.I.T. loc. 113, Mascall type area.

Type locality.—Cope 1889, p. 253, "a lake deposit in Oregon," p. 449, "... Lower Pliocene bed (? Idaho terrane) of the eastern part of Oregon." These locality designations are inadequate. Osborn (1918) has stated that Merriam believed the material may have come from localities not far from the type area (loc. V-4942 and V-4827); therefore, it is probable that the type is from a Mascall locality.

[9] See figure 22 in this study for comments on material referred by Bode (1934).

Revised diagnosis.—Based primarily on features noted in referred material and in M[1] and M[2]? of lectotype. Smaller than *Merychippus seversus* (Cope) but about the same size as *Merychippus primus* Osborn; straight crowned; protocone rounded, relatively small, isloated without spur (or only minute spur); relatively long hypocone; one medium pli caballin and pli protoconule; no pli protoloph; narrow hypoconal groove and one to two small anterior or posterior metaloph plications; narrow styles.

Supplementary description.—The figures of the type are correct in general. It was found that someone had sectioned the unworn tooth M[2]? not included in Cope's figure or designation of the type, but bearing the same number as the type in the American Museum collection. This tooth is typical of *Merychippus relictus.*

There are five upper molars that seem to be definitely *M. relictus*, and in addition to the features noted in the diagnosis, these teeth show high crowns relative to over-all size of teeth as noted in A.M. no. 8673, an unworn M[2]?, 28.1 in height, not far from mean of 27.92 in *Merychippus seversus* (Cope) (see p. 271 for methods of measurements); hypocone with narrow to broad connection and elongate; none to one pli hypostyle; and moderate to heavy cement.

For measurements of the lectotype and referred specimens see the following:

Measurements of Merychippus relictus

	Antero-posterior diameter at crest	Antero-posterior diameter at base	Transverse diameter at crest	Transverse diameter at base	Height of crown	State of wear
A.M. no. 8673						
M[1]	16.4	13.8	17.8	19.2	16.7	moderate
? M[2] (sectioned)	15.3 (at 18.0) 17.4 (at crest)	11.5	14.3 16.4 (at 18.0)	16.5	28.1	none
C.I.T. no. 4004	16.1	14.7	16.5	17.6	14.5	moderate

Some teeth specified as belonging to the type by Cope are not included in the measurements; these include the M[3] and two lower teeth. Two lower teeth instead of three (as stated in the original description) were found in the collection. The American Museum catalogue data is taken from Cope's original shipping list, and from this catalogue it was noted that three upper cheek teeth and two lower cheek teeth comprise the type. In the bottom of the box containing the specimens was this note, in part, "... 8673 with *M. relictus* type M 3." It is probable that this refers to the M[3] discussed and figured by Cope. The lectotype M[2]? (sectioned) may be the third upper tooth mentioned in the museum catalogue. The lower teeth were measured and compared with data on some small lowers of *M. seversus* in the U.C.M.P. collection and manifest a somewhat smaller size than typical *M. seversus.*

A.M. no. 8673	Anteroposterior diameter at 18.0 mm.	Same at base	Transverse diameter at base	Length across stylids	Height of crown at metaconid
M_1 ?	16.1	13.2	9.8	7.0	21.5 (approx.)
M_2 ?	17.9	12.0	11.6	7.3	24.3

There are specimens in the California collection that agree with these specimens in size. In the anteroposterior diameter at the base, $M_{\bar{1}}$? above, agrees with U.C.M.P. no. 39101, which has been called *M.* cf. *relictus* (see p. 265). In occlusal pattern $M_{\bar{1}}$? has an entoconid without the anterior plication and entoflexid is equal to metaflexid in diameter; $M_{\bar{1}}$? has no parastylid. There may be a difference from *M. seversus* in size in the A.M. specimens, but actually nothing can be considered significant in dental pattern. It is not apparent how these lower cheek teeth can be identified specifically.

The M^{2} that was apparently a part of the type is a tooth that could fall within the size range of *M. seversus.* M^{2}'s are not ideal for comparative analysis, but this tooth resembles *M. seversus,* particularly in complexity of enamel pattern, elongate protocone with spur, and proportions of the tooth. It is my opinion that this tooth, though formerly designated as part of the type of *M. relictus,* is *M. seversus* rather than *M. relictus.*

Measurements.—Anteroposterior diameter 17.7 at 18.0 above base of mesostyle, 17.3 at base of tooth; transverse diameter, 16.5 at base, 16.5 at 18.0

Comparisons.—*M. relictus* is like *Merychippus primus* Osborn from Sheep Creek of Nebraska in small size, shape of hypocone, development of single or no pli protoloph and pli hypostyle, one to two metaloph plications, and moderate to heavy cement. *M. primus* differs in lower-crowned teeth, protocone uniting to protoselen in early wear, and protocone with strong spur. Similar features of the protocone in the recently described *Merychippus tehachapiensis* (Buwalda and Lewis, 1955) likewise distinguish *M. tehachapiensis* from *M. relictus.*

M. relictus differs markedly from *Merychippus secundus* Osborn. The teeth in the type of *M. secundus* are well worn, probably more than half way to the base; P^{3}, ^{4}, and M^{1} of the type fit together and seem to belong to the right maxillary of one animal, M^{2} from the left maxillary is evidently part of the same horse. Osborn (1918) characterizes *secundus* by its forked crochet and by the protocone not being united to the protoconule. This is often true in premolars, and occasionally this feature is noticeable in *Merychippus californicus* Merriam (Bode, 1934). The other referred teeth of *M. secundus* have the protocone connected. Other features have little significance because of the state of the wear in the teeth. Plate 39 in Osborn (*op. cit.*) shows A.M. no. 14179 to be *Merychippus isonesus secundus,* but in the text he lists this number as *M. i. primus.* Such a confusion is understandable when we attempt to study the series of species described from the Sheep Creek. The size of the teeth and the size of metapodial III could be within the range of *M. seversus* or even of *Merychippus quintus* Osborn. I cannot identify the type of *Merychippus secundus* beyond its recognition as *Merychippus.*

Merychippus seversus (Cope) is also from the Mascall fauna. There seems to be sufficient evidence to conclude that *M. relictus* may be a distinct but rare species in this fauna. With knowledge of variation as seen in samples of well-defined *M. seversus* and *M. californicus* at hand, it is concluded that *M. seversus* and *M. relictus* may have characters of equal distinction. *M. seversus* differs in larger size; possibly more quadrate teeth; more elongate-oval protocone with larger spur; and greater development of pli protoconule, pli caballin, pli hypostyle, and metaloph plications. These differences are a matter of degree, since in each character there

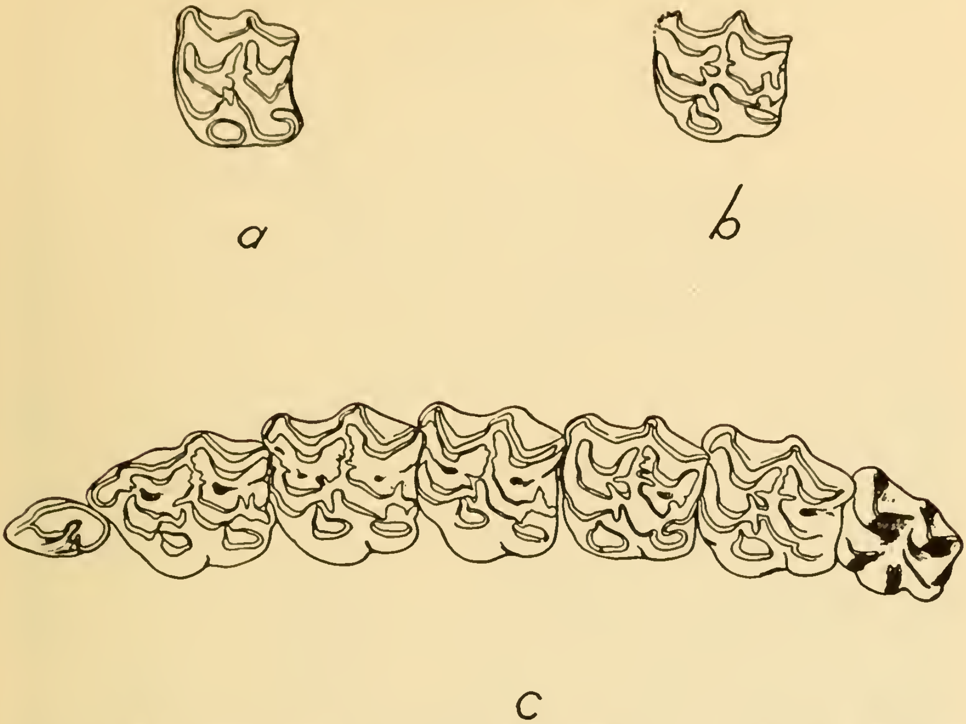


Fig. 23. *a, Merychippus relictus* (Cope), holotype, M^1, A.M. no. 8673, loc. Mascall; *b, Merychippus seversus* (Cope), holotype, loc. Mascall type area, right M^2 (?), reversed; *c, M. seversus* (the former type of *M. isonesus*) A.M. no. 8175, loc. Mascall type. Reproduced from Osborn (1918, p. 13). All × 1.

is a tendency to resemble *M. seversus*. The degree of resemblance in these species is great in the height of crown and in the amount of cement present.

A sample of *M. relictus* can be compared with *M. seversus* in two dimensions by using the "single specimen with a large sample" method of comparison (Simpson and Roe, 1939, pp. 188 and 386). In this test it was found that *M. relictus*, A.M. no. 8673, an M^1, = 16.4 in anteroposterior diameter, therefore:

$$X = 16.4$$

$$d/\sigma = \frac{X - M}{\sigma},\ M = 19.99 \pm .18 \text{ for } \textit{M. seversus} \text{ (see table 22)}$$

$$d/\sigma = \frac{3.59}{.858},\quad \sigma = .858 \pm .12 \text{ for } \textit{M. seversus}$$

$$d/\sigma = 4.18 \qquad P < .01$$

$P < .01$ is always significant according to probability standards (*loc. cit.*). In transverse diameter for the same tooth, $d/\sigma = 1.53$ and $P < .13$, which is not particularly significant. Other *M. relictus* teeth are even smaller in anteroposterior diameter, and transverse diameter measurements show similar size differences.

Merychippus praecocidens Russell (1933) from Wood Mountain, Saskatchewan, Canada, is somewhat geographically isolated and may be older than *M. relictus*.

TABLE 16

MEASUREMENTS, MERYCHIPPUS SEVERSUS (COPE), SKULLS
(in millimeters)

	Mascall type area		Gateway area	
	A.M. no. 8175	C.I.T. 532	C.I.T. 2930	C.I.T. 2929
Greatest length, incisors to occipital condyle	326.0			296.2
Length: incisors to glenoid surface (from base incisor to anterior edge of glenoid)	255.0			260.0
Length: alveolar tooth row P^1-M^3 right side	125.1	115.2	112.2	116.5
Length: alveolar tooth row P^1-M^3 left side	125.2	....	112.1	115.5
Width: from upper edge infraorbital foramen to the other, across skull	54.1	42.0	56.2	....
Depth: skull above P^4 center ($\perp$ to a plane along dorsal surface)	74.1	69.3	60.0	71.8
Length: $C-P^1$ (base)	23.3	43.1	26.1	24.3
Length: P^1-I^3	40.7	65.2	44.3	49.6
Length: I^3, canine right side	8.5	15.0	11.5	9.8
Width: palate between base of canines	34.3		28.0	31.1
Length: narial notch to anterior orbital edge, left side	132.5		112.3	137.0
Least width across nasals (restored)	30.4		27.6	32.2
Width across palate at P^2 (at base of protocone)	28.5		30.2	35.5
Width across palate at P^3 (at base of protocone)	34.7		36.0	37.3
Width across palate at M^1 (at base of protocone)	42.6	28.7[a]	46.8	45.1
Width across palate at M^2 (at base of protocone)	44.6		44.8	45.4
Width (least): internal nares, palatal surface	32.7			33.8
Width across pterygoid wings (on edges)	32.8			38.1
Width: skull at jugal in line with anterior edge of orbit	111.9		111.3	
Width: skull at posterior edge of postorbital bar	54.4		81.0	
Transverse width between external nares, internal edge	38.3		32.0	
Anteroposterior diameter across anterior edge glenoid to posterior edge maxilla	59.9	...		
Diameter (transverse) of occipital condyle at center	51.4			
Diameter (transverse) of foramen magnum	21.5			27.4
Dorsal ventral diameter foramen magnum	22.9			20.4
Depth: skull from intersection temporal ridges to basicranial surface	72.0			74.2
Same at edge of foramen magnum	74.6			79.0
Length: base incisor–ant. edge internal nares (restored)	(151.5) approx.			140.5
Greatest transverse diameter (inside) zygomatic arch	46.6	....		36.7
Transverse diameter jugal opposite posterior edge alveoli for M^3 left side	27.5			15.1
Depth: malar fossa (preorbital fossa) relative to flat plane of preorbital ridge	15.5	(13.0)	(13.0)	20.8
Depth: preorbital fossa above P^2	10.0	(8.0)	(5.0)	4.1
Dorsoventral diameter malar ridge to dorsal border of fossa	63.7	64.6	70.1	68.9
Distance external extremity glenoid to anterior edge of orbit	88.2	...	...	73.5
Dorsoventral diameter of orbit (inner edge as points)	42.6	39.8	46.0	41.6
Anteroposterior diameter of orbit (inner edge as points)	40.1	....	50.7	45.3
Transverse diameter cranium across orbits	...		79.8	79.7
Transverse diameter basisphenoid			...	18.6
Anteroposterior diameter vacuity left side, basisphenoid				33.7
Anteroposterior diameter nasals (posterior edge)		....		345.5
Distance: tip of snout to supraoccipital crest				87.8
Greatest length: frontals (mid-line)				315.1
Distance: base incisor to anterior edge foramen magnum			15.1	16.7
Least anteroposterior diameter premaxilla		19.5	22.5	15.9
Least anteroposterior diameter lacrimal	...	....	43.3	54.7
Distance: posterior edge of infraorbital foramen to ant. edge of preorbital bar	....	...	....	48.0
Distance: ant. edge supraorbital foramen to ant. edge of preorbital bar	....	....		15.5
Greatest anteroposterior diameter paraoccipital process	....		31.2	32.0
Distance narial notch to tip of snout			....	27.6
Least dorsoventral diameter zygoma				20.0

[a] Much distortion in restoration.

In proportions and in the isolation of protocone it resembles *M. relictus*, but the lenticular shape of the protocone suggests *Hipparion* (as Russell notes) or possibly *Nannippus* tendencies.

TABLE 17

MEASUREMENTS OF MERYCHIPPUS SEVERSUS (COPE), DENTITION[a]

(in millimeters)

Anteroposterior and transverse diameters	Mascall type area		Gateway area	
	A.M. no. 8174 at crest	C.I.T. no. 532 at crest	C.I.T. no. 2930 at crest	2929 at crest
I¹ ap	12.7	....	11.9	...
tr	....	....	7.7	....
I² ap	13.3	....	13.6	9.8
tr	....	....	7.5	7.6
I³ ap	11.5	....	12.0	9.3
tr	....	....	6.5	6.2
C ap	....	8.6	7.9	....
tr	....	6.4	5.3	....
P¹ ap	12.6	11.2	13.7	17.0
tr	7.4	....	7.2	10.1 (at base)
P² ap	23.6	22.2	23.7	22.0
tr	20.6	16.6	17.8	21.2
P³ ap	21.0	19.5	20.6	17.2
tr	22.4	20.5	22.3	23.2
P⁴ ap	20.5	19.8	20.5	17.5
tr	22.3	20.9	21.9	24.0
M¹ ap	19.3	16.8	18.5	15.1
tr	20.0	19.6	20.5	23.0
M² ap	20.7	17.7	18.8	15.3
tr	19.5	19.8	20.1	22.5
M³ ap	....	18.8	18.7	19.0
tr	...	17.8	....	20.8

[a] Measurements of teeth in place in skulls; cement included in transverse diameter.

Discussion.—There are several teeth found in the Mascall formation that appear to represent intergrading specimens between *M. seversus* and *M. relictus*. They are U.C.M.P. no. 27237 which I have called *M. seversus*, no. 27238 listed here as *M.* cf. *relictus*, and A.M. no. 8673, an M² discussed previously. No. 27237 (see Bode, 1934, fig. 2, *i*) is like the type of *M. seversus;* but the resemblance to *M. relictus* is in the size and reduction of the protocone. No. 27338 (*op. cit.*, fig. 2, *h*) may be a little large for *M. relictus* but is otherwise similar.

In an attempt to evaluate the characters of the materials assigned to *M. relictus*, three possibilities may be considered in designating their taxonomic position: they represent subspecies of *M. seversus*, a variant of *M. seversus*, or a distinct species.

There is no apparent stratigraphic difference in the position of the two species *M. relictus* and *M. seversus*, and nothing conclusive on horizontal segregation and no evidence that the fossils were washed in from adjacent areas. The area at the type region is probably too limited for coexistence of two subspecies. This is particularly probable with regard to animals as large as these horses. It is more likely that a subspecies would be detected in separate yet adjacent geographic areas or separate succeeding layers of rock.

As a simple variant of *M. seversus*, specimens of *M. relictus* could be small and relatively rare individuals that represent incipient radiation. These individuals might also represent sexual variation. Sexual variation in skeletal parts or in dentition may be reflected in differences in size, but it is less likely that differences between sexes in enamel pattern could be detected.

We may question the possibility of two species, relatively close in the structure of the teeth, existing under the same ecologic conditions in the same general area. *M. relictus* and *seversus* are rather similar in their hypsodonty and thus were both probably grazing animals. However, there may have been additional features such as color, body proportions, or body size, which would have had selective value for survival of each species in certain areas within the faunal realm.

On the basis of present limited information it has been concluded that *Merychippus relictus* could be a distinct species, but it is not as reliably documented nor as well founded as *M. californicus*, *seversus*, or *brevidontus*. Without more material at hand we cannot justify synonymizing *M. relictus* and *M. seversus*, and for the present the name *M. relictus* should be retained.

Merychippus relictus is not particularly useful in correlation since it is known only from the Mascall. It seems to have many more primitive features than *M. brevidontus* or *M. californicus* and thus adds considerable support to the idea that the Mascall fauna is older than the North Coalinga assemblage. *M.* cf. *brevidontus* in the Virgin Valley may be in a stage of evolution similar to *M. relictus*.

Merychippus cf. *relictus* (Cope)

(Fig. 22)

Four isolated teeth in the U.C.M.P. collection could be referable to *Merychippus relictus* (Cope), but they are too poorly represented to be so positively indicated. No. 27238 from loc. ?, Mascall, has been figured by Bode as *Merychippus seversus* (Cope), and in this paper it has been noted as a possible intermediate form. The protocone is much like that in *M. relictus*, but the proportions of the tooth and the pattern resemble *M. seversus*.

An unworn upper tooth, U.C.M.P. no. 39690 from V-4951, the Crooked River area, is a small M^3 (anteroposterior diameter at crest is 15.4, transverse diameter at base 17.2, and height 16.7). The ectoloph is straight but with an abrupt lingual curvature at the apex. This tooth also seems referable to *relictus*.

From the Yale collection of the Crooked River region material there is a left upper premolar, no. 14287, that is relatively small and has a simple enamel pattern; the protocone is narrowly connected.

An American Museum lower no. 8181C is a small worn tooth probably referable to *M.* cf. *relictus.*

A heavily worn C.I.T. no. 1509 is an upper partial molar; although well worn, the protocone is just beginning to connect with the protoconule.

Two lower cheek teeth, U.C.M.P. no. 39101 from V-4824, a level slightly above the "mammal horizon" in the type area, and no. 499 from loc. 884 (?V-4825) are small teeth with metaconids and metastylids separate to the base of the tooth. The size of these teeth suggest they could be assigned to *M. relictus.*

Measurements.—Internal anteroposterior diameter at base: no. 39101, 11.5; no. 499, 13.7. Transverse diameter at base: no. 39101, 9.4; no. 499, 9.3.

The identification of this material remains doubtful without known associated lower cheek teeth of *M. relictus* for comparison. The specimen no. 39101 is apparently not progressive in its dimensions and does not suggest a vertical zonal differentiation in the Mascall beds, although it was found above the typical mammal horizon.

Merychippus relictus ? (Cope)

A small, moderately worn P^2 U.C.M.P. no. 1717 collected at V-4949 is not definitely identifiable. It is small for *Merychippus relictus*, but the ectoloph seems too straight for *Parahippus*. There is a moderate amount of cement on the tooth.

Merychippus seversus (Cope)

(Pl. 6; figs. 24–34)

1879*b*. *Stylonus seversus* Cope. Proc. Amer. Philos. Soc., vol. 28, pp. 63–78.

1886. *Hippotherium seversus* Cope (not Cope 1879 but listed in 1886 and described in 1889 as a distinct species). Proc. Amer. Philos. Soc., vol. 23, pp. 357–361.

1889. *Hypotherium isonesus* Cope. Proc. Amer. Philos. Soc., vol. 26, pp. 429–458, pls. 1–3.

Holotype.—Cope (1879, p. 76) "Two superior molar teeth were accompanied by a number of inferior molars as having been all found together, but whether they belong to one individual is uncertain." Only one tooth is figured and described in the upper series. It is considered to be the type: right M^2? A.M. no. 8180.

Referred specimens.[10]—Mascall type area. The holotype of *Merychippus isonesus* (= *seversus*), Cope 1889, p. 451: "... large part of a skeleton with skull from Cottonwood Creek; parts of maxillary bones with teeth of a second individual from the same locality with some teeth of a third from the same,"[11] loc. Mascall formation, Cottonwood Creek; Cope and Matthew (1915, pls. CXLVII and CXLVIII of A.M. no. 8175) figure: skull with complete dentition, atlas, sacrum in part, pelvis, femur, tibia, right astragalus and calcaneum, navicular, ectocuniform, metatarsals II, III and IV, proximal median, and distal phalanges.

Other specimens referred, U.C.M.P., near type Mascall area: left maxillary series P^2–M^3 and right P^2–M^2 no. 23088, premolars nos. 23091†, 23093, 23103†, nine slightly or unworn upper molars or premolar no. 23089, worn molar no. 23092†, M_3 no. 23108†, M_1 or $_2$ no. 23105†, worn lower premolar no. 23107†, dp_3 or $_4$ no. 26642†, unworn molar no. 23097†, loc. 3059; five worn upper cheek teeth no. 23095†, loc. V-4942; unworn premolar no. 39110†, loc. V-4827; dp_2 and $_3$ no.

[10] All material marked with † is referred to for the first time in print in this study.

[11] Cope apparently means by teeth from second individual: A.M. no. 8177; including left P^1, P^2, P^3 with part of maxilla; right P^2, P^3; right and left I^1, ^{2}, ^{3} and part of maxilla. Right C and P^1 are in same box in collection but no number given; skull characters are probably described from no. 8175; it seems likely that his description of M^1 and ^{2} was derived from teeth in the skull. I cannot be certain of the third specimen he cites; it may be A.M. no. 8179.

39307†, series in mandible or P_{3-4}, M_3 no. 39095†, M_1 no. 39106†; upper molar (?) nos. 39096† and 39105†, loc. V-4830; part upper molar no. 39111†, loc. V-4829; unworn premolars nos. 1715†, 1704†, 1714 (also an M^3 no. 1714)† worn molars (?) nos. 2020†, 1716†, 1708†, six slightly worn lower molars-premolars with parts of mandible and unworn M_3 no. 2028†, mandible with right

TABLE 18

Merychippus seversus Dentition from the Gateway and Crooked River Assemblages*

	Anteroposterior diameter at crest	Transverse diameter at crest
CROOKED RIVER		
Premolars		
C.I.T. no. 40	21.2	19.9
U.C.M.P. 1712	20.3	19.1
Y.P.M. 14267	18.9	15.9
Y.P.M. 14264	20.0	19.7
Molars		
Y.P.M. 14374	20.7	18.4
Y.P.M. 20088	19.3	20.5
GATEWAY		
Premolars		
C.I.T. no. 4916	21.0	22.1
C.I.T. no. 4916	21.3	21.9
C.I.T. 4916a	....	21.4
C.I.T. no. 4914	....	20.2
C.I.T. no. 4914	20.6	20.7
U.C.M.P. no. 32753 (series)		
left P^3	20.6	18.0
left P^4	20.1	21.7
rt. P^3	20.5	21.0
rt. P^4	20.6	21.7
Molars		
C.I.T. no. 4914	....	20.2
C.I.T. no. 4916	....	21.6
C.I.T. no. 4916	....	20.5
U.C.M.P. no. 32753 (series)		
left M^1	....	20.6
rt. M^1	18.8	20.6
rt. M^2	....	19.7

* See table 22 for variation in Mascall type area material.

milk dentition $I_{1, 2, 3}$ (no canine) dp_1–dp_4 and left dp_{2-4} associated with right dp^2–M^1 no. 35674†, loc. V-4820–4835 (old 903); unworn part upper teeth no. 39109†, loc. V-4833; worn upper and unworn lower premolars no. 39296 upper premolar, lower premolar, and partial P_3 no. 40322†, loc. V-4834; partial molar or premolar no. 39100†, unworn upper premolars nos. 39098†, 39099†, broken upper molar 39108†, loc. V-4835; upper premolars nos. 23099† and 23100†, left I_{1-3}, C, and right I_{1-3} in partial mandible, isolated I_3 and two lower premolars no. 23098†, loc. 3043. From uncertain loc. 884, 819, 882, 885, 886, and 3603 but probably Mascall: upper cheek teeth nos. 11784† (including 21 molars and premolars), 23101†, 1621†, 1622†, 27332, 27236, 27237†, 23102†, 739†, 508†, 730†, 511† and 1614†, lower teeth nos. 2070†, 1178†, 518†, 714†, milk teeth nos. 11631† and 732†, adult lowers nos. 1618†, 1620†, 1625†, 1626†, 1627†, and 541†.

A.M., in addition to above citations from near type area: part of upper dentition I^1, ^{2}, ^{3}, P^1 P^2, M^1 no. 8177† (see footnote p. 265), three lower cheek teeth and one upper tooth no. 8181†, upper no. 8182†, lower no. 8187†, P_4–M_3 no. 8188†, upper no. 8179†, loc. Cottonwood Creek, Oregon, Mascall formation.

Y.P.M.: upper cheek teeth nos. 11607† (6 teeth), 11608† (2 teeth), 1608†, 14297†, 14298†, lower cheek teeth nos. 11287†, 11607†, loc. Cottonwood Creek, Mascall, Oregon; upper cheek teeth nos. 10778† (including 6 teeth), 11287† (2 teeth), 11288† (2 teeth), 14262†, 14263†, 14292†, 14293†, 14294†, 14301†, cheek teeth nos. 14252† (2 teeth), 14254†, 14255†, 14256†, 14257†; loc. John Day River, Oregon, Pliocene?, locality data very poor, but believe material definitely *M. seversus* and probably Mascall fauna.

C.I.T.: isolated upper cheek teeth nos. 421†, 412†, 420†, 421, 408, 409, 412, 413†, 414†, 410†–411†, 416† and lower cheek teeth no. 415†, loc. 113; nearly complete skull no. 532†, loc. 183; Mascall type area.

Crooked River area; Y.P.M.: upper cheek teeth nos. 14264†, 14266†, 14267†, 14268†, 14269†, 14280†, lower cheek teeth nos. 14270†, 14273†, 14274†, 14275†, 14290†, 14291†, 14295†, loc. Grindstone Creek or Crooked River area, Oregon.

U.S.N.M.: upper molar ? M^2 and lower R M_1, 3 more lowers no. 20088†, loc. South Fork of Crooked River, Crook County, Oregon (Fld. no. 21). C.I.T.: left P^3 or ^{4} no. 13 (see Maxson, 1928) loc. Crooked River. Oregon.

Gateway area; U.C.M.P.: two lower milk premolars and worn molar no. 34385†, left P_{2-3} associated and seven other lowers no. 32753†, lower no. 32752, upper series left P^2–M^3 and right P^2–M^2 probably same individual no. 32753†, lower no. 40232†, loc. V-3427, Gateway area.

C.I.T.: nearly complete skull no. 2930†, three upper premolars, two molars (no number); complete skull no. 2929†, loc. 368, Gateway.

Revised diagnosis.—Based on original descriptions of *Merychippus seversus* and *M. isonesus* (= *seversus*) and study of referred material. Dentition (P^2_2–M^3_3) hypsodont (height of crown in upper cheek, $M = 29.37 \pm .58$; lower cheek teeth $M = 24.25 \pm .46$); upper cheek teeth P^2–M^3 generally quadrate; moderately curved; protocone oval to elongate with strong anterior spur, not connected to protoconule until more than one half of tooth is worn away; hypocone elongate, usually shorter than protocone, and narrowly to broadly connected with metaconule; pli caballin and pli protoconule usually one and pli cabalin $>$ pli protoconule; metaloph usually one to more than one posterior and one anterior plication; pli protolph usually none or one small plication; pli hypostyle one or two small- to medium-size plications; ante pli hypostyle (plication opposite pli hypostyle, directed lingually) small to large, tending to close posthypoconal groove; usually strong preprotoconal cusp or ridge; cement moderate to heavy on upper and lower cheek teeth; metaconid-metastylid inflection shallow but extends to base of tooth; protoconid and hypoconid walls fully rounded with deep inflection between them; metaflexid narrow anteroposteriorly, parastylid strong. Skull: facial region short; single, deep and large lachrymomalar fossa.

Supplementary description.—All the specimens referable to *Merychippus* in the U.C. collections from the Mascall fauna were mixed, and an attempt was made to sort the collection. Only a few specimens were considered to be distinct from the majority of the material, and they represent the rare *Merychippus relictus* (Cope); the other identifiable teeth fall within the range of one unit. Material formerly referred to *M. isonesus* is better represented in the collections, and that name would probably be more acceptable since it is so well known. However, *M. seversus* is ten years earlier in the date of its description and therefore is the name adopted in this paper.

The size of the type specimen, A.M. no. 8180, is not characteristic of the *M. seversus* population; it is smaller than the mean. Measurement of the type: anteroposterior diameter, 17.0; transverse diameter, 17.8; height of crown (some wear), 23.4. Other specific characters were checked against the revised diagnosis, and no. 8180 was found to be typical in protocone with large spur, metaloph with one large

TABLE 19

Deciduous Dentition, *Merychippus seversus* (Cope), Type Area

(measurements in millimeters)

	Anteroposterior diameter	Transverse diameter	Height of crown at metastyle	Height of crown at metaconid
UPPERS				
U.C.M.P.				
no. 35674 dp^2	26.9	18.3	10.1	
no. 35674 dp^3	22.5	20.6	11.0	
no. 35674 dp^4	22.5	21.2	12.5	
no. 35674 M^1	22.7	...	...	...
LOWERS				
U.C.M.P.				
no. 35674 rt. $I_{\bar{1}}$	12.8	...	...	...
no. 35674 rt. $I_{\bar{2}}$	12.7	...	...	...
no. 35674 rt. $I_{\bar{3}}$	10.6	...	...	...
no. 35674 rt. $dp_{\bar{1}}$	5.0	3.5	...	...
no. 35674 rt. $dp_{\bar{2}}$	23.2	11.5	...	...
no. 35674 rt. $dp_{\bar{3}}$	21.0	12.2	...	...
no. 35674 rt. $dp_{\bar{4}}$	22.8	10.8	...	...
no. 35674 lft. $dp_{\bar{1}}$	5.0	3.5	...	...
no. 35674 lft. $dp_{\bar{2}}$	23.2	11.5	...	...
no. 35674 lft. $dp_{\bar{3}}$	21.9	...	...	...
no. 35674 lft. $dp_{\bar{4}}$	22.1	...	...	...
no. 26642 premolar	19.9	11.5	...	9.6
no. 35673 premolar	17.1	10.2	...	9.2
no. 39307 $dp_{\bar{3}}$	20.7	10.8	...	10.5
no. 39307 $dp_{\bar{4}}$	23.3	12.3	...	11.5
no. 34385 $dp_{\bar{3}}$ or $_{\bar{4}}$	18.7	11.8	...	8.5
no. 34385 $dp_{\bar{3}}$ or $_{\bar{4}}$	19.6	11.5	...	9.8
no. 732 $dp_{\bar{3}}$ or $_{\bar{4}}$	21.5	10.8	...	11.5

anterior and posterior plication, well-developed pli caballin and pli protoconule, reduced pli protoloph, bifurcate pli hypostyle, one large lingual pli hypostyle, probably equivalent hypsodonty, and dimensions slightly wider than long. Since the type was described by Cope (1889), the tooth has been sectioned to show the character of the enamel pattern.

Skull: Referred specimen, no. 8175 (type of *M. isonesus*) was checked with the illustration in Cope and Matthew (1915, pl. 137). The following points are pertinent: preorbital fossa best represented on left side and even there not complete; restoration correct in showing contour of preorbital area; occipital process complete on right side; posterior dorsal outline of skull (seen from lateral view) not present but apparently straight to point opposite glenoid then gently curving downward at about 30° angle; part of basioccipital, basisphenoid, presphenoid, vomer, and much of palatines absent; supraoccipital, most of right jugal, and part of right parietal absent.

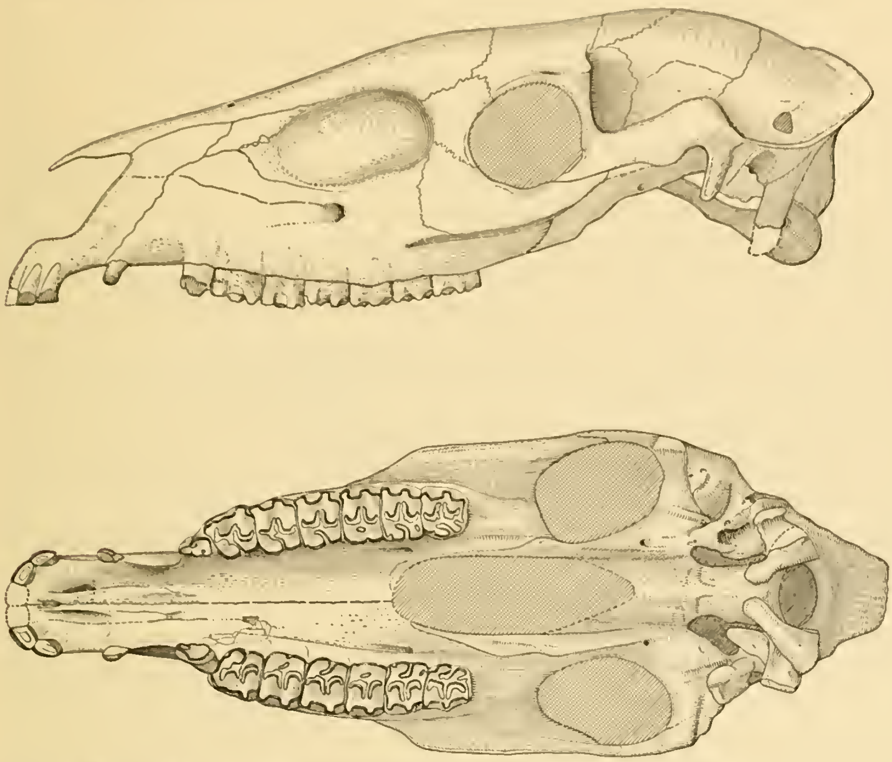


Fig. 24. *Merychippus seversus* (Cope), C.I.T. no. 2929, loc. 368: top, left lateral view of skull; bottom, ventral view of skull; × ⅓. Lateral view shows lacrimal fossa and maxillary foramen from right (and better preserved) side of the skull. Drawing by David P. Willoughby.

The preorbital fossa is a critical area for consideration. The depth of the fossae was measured by placing a straight edge across the fossa and resting it on the nasals and mesostyles of P^2 and M^1 (depth preorbital fossa at point opposite $P^2 =$ 10.0, depth opposite $M^1 = 11.5$). The lacrymal and malar fossa (preorbital bar) may be one large depression from the preorbital bar to above P^2, but there is some suggestion of distinction of the smaller malar fossa on the right side. Other characters of more definite nature in no. 8175 are right postorbital bar with small anterior tubercle 30.4 mm. dorsal to jugal; supraorbital notch (supraorbital foramen, 33.6 from posterior edge to preorbital bar, circular in outline; posttympanic process short (transverse width 11.5, dorsoventral length 9.5); palatine foramen opposite hypocone of M^1; preorbital bar nearly vertical to anteroposterior plane of tooth row; basicranial angle approximately 25° (some distortion); alisphenoid slightly convex and with median groove; sagittal crest reduced (about 2–3 mm. elevation); anteroposterior diameter tympanic bulla 25.0, dorsoventral length 10.0.

Two other skulls from C.I.T. collection, nos. 532 from the Mascall type area and 2930 from the Gateway, do not differ greatly from the known features of A.M. no. 8175, but the following points should be noted: C.I.T. no. 2930 agrees with A. M. no. 8175 in that malar and lachrymal fossa are practically one (slight elevation separates the two); the preorbital fossa is probably somewhat shallower (at point opposite P^2, 5.0, at point opposite M^1, 8.0); there is no anterior tubercle on postorbital bar; dental pattern is similar to typical *Merychippus;* and the palatine foramen opposite hypocone of M^1 (as in A.M. no. 8175) and preorbital bar are similar.

C.I.T. no. 532 is probably a smaller individual than A.M. no. 8175 or C.I.T. no. 2930. It resembles no. 8175 in the relative depth and extension of preorbital fossa (depth opposite P^2 = 8.0–9.0 mm.). The fossa is particularly deep along the margin of nasals to a point opposite P^2. The lachrymal and malar fossa are deep and faintly separated by an elevation. Distortion of the skull in preservation has altered many parts, but no. 2930 may differ from A.M. no. 8175 in its slightly smaller size. It also differs in the somewhat longer diastem. The palate is questionably narrower.

On the basis of features in the skull I would hesitate to consider these specimens to be distinct from *M. seversus.* Perhaps the most significant feature, the deep preorbital fossa, agrees in general in all three specimens.

Another skull, no. 2929 from loc. 368, Gateway area, is an old adult (the M^3 is well worn with the base of the tooth exposed) and a relatively complete, undistorted specimen. Compared to the A.M. no. 8175 it has greater depth of preorbital fossa (greatest measured depth 20.8 mm.), dorsal edge of preorbital fossa sharp as far forward as dorsal juncture premaxilla and maxilla (no evidence for distinction between lachrymal and malar depression); somewhat smaller size; contour outline, flat across frontals, roundly convex at parietals, nasals flat posteriorly but strongly convex anteriorly; and much greater anteroposterior diameter of preorbital bar. Other features to be noticed (also see table 16) are the surface of lachrymal flat; the alisphenoid without median groove; saggital crest much reduced; cavity for tympanic bulla measuring 17.2 anteroposteriorly; anterior extension of frontals at mid-line pointing opposite anterior edge of preorbital bar; supratemporal ridges not prominent except at extreme posterior dorsal part; and internal nares extending to point opposite center of M^1. The measurements of the palate given in table 16 probably present the most accurate measurements of all four skulls described. Since the specimen no. 2929 is an old adult, much of the dental pattern is obliterated. The great size of this specimen probably eliminates the possibility that it could be *M. relictus;* the over-all size, shape of the protocones, and great depth of the preorbital fossa indicate probable affinity with *M. seversus.*

Dentition.—Measurements of fossil skulls are often not desirable since conditions of preservation of parts may alter the true proportions. Teeth, on the other hand, are so resistant that fewer preservation "casualties" result, and those that are isolated are the most suitable for consistent mensuration because there is more freedom of choice in the placement of the calipers. The chances of not recognizing teeth from one individual are greater in isolated specimens, but it has been observed that when measurements or character analyses of a known individual are plotted on standard histograms and contingency tables with isolated teeth (the known individual marked by a distinct color) the dimensions or character categories of teeth of one specimen from one side were dispersed throughout the range of all the units. There seems to be as much variation in one individual as in isolated material from several individuals. Molars and premolars can usually be distinguished as Bode (1931) has shown, but it is not always possible to separate P^4's and M^1's. General comments on dentition refer to P^3–M^2 as a group. The following methods of measurement of upper cheek teeth are itemized:

Anteroposterior diameter: in unworn teeth, in line with a point on mesostyle at ⅓ the average[12] height of crown from edge of enamel below mesostyle and on extreme edges of parastyle and metastyle. At crest in ⅓ wear.

Transverse diameter: at crest, from tip of mesostyle to shortest distance to lingual edge of protocone enamel.

Height of crown in unworn or very slightly worn teeth only: calipers placed on tip of mesostyle and measured to shortest perpendicular distance to lower edge of enamel. V-shape of enamel edge below mesostyle is not always symmetrical; therefore the measurement is taken in a straight line from the tip of the style.

The lower dentition in species of *Merychippus* presents less in the way of diagnostic features than do the uppers. In addition to the features noted in table 21, the following characters (in P_3-M_2) may be pertinent: paralophid usually straight; hypoconulid present; entoconid oval and with anterior spur; metaflexid wider than entoflexid; and upper one-third of protoconid-hypoconid with inflection deep.

There is not enough material available for an evaluation of variation in incisors, in canines, in first premolars, in third molars, or in milk dentition, but some specimens have been studied. U.C.M.P. no. 23098 includes several teeth with the following dimensions (in millimeters at crest):

Measurements.—Anteroposterior and transverse diameter respectively: U.C.M.P. no. 23098 I_2 (isolated) 5.3 and 12.0, left I_1 6.8 and 10.1, right I_1 6.7 and 10.0, left I_2 6.8 and 10.8, right I_2 7.0 and 10.9, left I_3 5.8 and 10.6, left C 4.8 and 3.8 right $P^4/_4$ 14.4 and 7.0, left lower premolar 14.3 and 7.1 left C 8.2 and 6.2; no. 1711 I^1 or ^{2} 6.4 and 14.1.

The well-worn incisors have shallow pits and teeth closely appressed, canine sligtly worn with small internal anterior pocket, narrow ridge on posterior edge with smooth external surface. P^1's are worn on the posterior side of crest, with a pit inside for two-thirds of distance and bounded by internal cingulum.

In second upper premolars there is considerable variation, particularly in the development of the hypostyle, in the crochet, and in the metaloph plications. In general the second premolars are similar to the other teeth, but they are usually too heavily worn to offer useful characters for study. In contrast to this we often find M^3 with little wear. When the pattern is present many features are poorly developed, but frequently the M^3's are similar to the other teeth. Nearly all the M^3's studies show deep pre- and postprotoconal grooves to the base of the teeth. The hypostyle is usually reduced, but the extreme curving forward of the posterior wall of M^3 hinders proper analysis. Neither P^2 or M^3's have proven particularly helpful in this study.

[12] One-third of the average unworn height of crown is 18 mm.; the ⅓ wear range used in this paper constitutes the point at ⅓ less the average height of crown plus ¾ of this ⅓ figure, that is, in *M. seversus* 18.0 + 6.0 = 24.0 mm.; ⅓ range, 18.0–24.0 mm.

Approximately 16 heavily worn upper molars in the U.C.M.P. collections were studied with the view of comparing them with characters noted in relatively unworn teeth. The following conclusions are apparent: Protocone tends to widen at the base of the tooth, becoming nearly round in shape, and moves closer to protoconule and hypocone; pli hypostyle and metaloph plications retain identity longer with wear on the teeth than do pli caballin or pli protoconule.

Fortunately a nearly complete set of milk dentition U.C.M.P. no. 35674 was collected near the type locality of the Mascall. We may question whether this material is not *Parahippus*. It is probable that its large size (see table 19), well-developed crochet (not connected to protoloph), and especially the complexity of the metaloph plications, show relationships to *M. seversus*. The number and development of the plications is as great as in many adult teeth of *M. seversus*. Practically all the lower milk teeth have a prominent cusp between the protoconid and hypoconid at the base of the cusps.

The skeleton: A detailed analysis of skeletal material has not been accomplished. Much work was needed on the dentition, and few skeletal parts are known to be associated with the teeth (the type of *M. isonesus* (= *seversus*) A.M. no. 8175 is an exception). There are four genera of horses in the Mascall fauna: *Parahippus*, *Archaeohippus*, cf. *Hypohippus* (very little known), and *Merychippus* (probably two species of *Merychippus*). I discuss in later pages why I believe some skeletal material is *Merychippus*, but I have not identified many of the skeletal parts as to genus; there is considerable doubt whether any of these isolated elements can be generically assigned. A record of measurements of the American Museum specimens is included (table 20). Cope (1889) has given data on the morphology of these elements and compared them with *Equus* in most cases. Since so great a percentage of the horse dentitions in this fauna represent *M. seversus* it is probable that most of the skeletal parts are also *M. seversus*.

The skull, C.I.T. no. 2930 from the Gateway, was apparently collected in association with at least two skeletons. Dimensions of these parts are included in table 20. The two skeletons are very close in size and proportions as seen in comparable elements of the pes. The close morphologic similarity in these parts gives further support to the belief that the Gateway assemblage contains animals identical to those from the Mascall type area. When more vertebral and girdle elements are collected in association with specifically identifiable teeth, it may be possible to make a composite skeleton representing *M. seversus*.

Comparisons with other assemblages containing referred Merychippus seversus.—The Skull Spring fauna, of southeastern Oregon, Gazin (1932): In addition to characters tabulated in table 28, Gazin notes that the prefossettes are open in early wear, a feature seen in some Mascall material. The degree of closure of the fossettes is sometimes not determinable owing to the type of attrition between the posterior and anterior sides of the teeth. The calcaneum and astragalus measure larger than in any specimens known from the Mascall fauna (calcaneum a.p. length = 86.0; astragalus a.p. length = 43.0 from fig. 11, Gazin 1932); possibly the Skull Spring material represents *Hypohippus* since the trochlear groove is relatively broad and shallow (see Merriam 1919, p. 474), and the external condyle is much smaller than the internal condyle in contrast to the deeper groove and equal condyles in *Merychippus* from the Mascall. The suggested difference in the teeth is in a slightly more complex metaloph and deeper entoflexid than in average *M. seversus,* but the degree is small and is not considered significant. There is some evidence for greater size in the Skull Spring specimens, and this may reflect a subspecific difference from *M. seversus.*

The several teeth assigned to *Merychippus relictus* (Cope) from the Skull Spring by Bode (1934, fig. 2, p. 44) have characters and measurements that fall more definitely within the range of variation of *M. seversus.* There are very few specimens that can be assigned to *M. relictus.* U.C.M.P. nos. 23096 and 23090 shown in Bode (*loc. cit.*) are two of these specimens, but are Mascall specimens.

Gazin (1932) stated that there were several large, low-crowned teeth from the

Fig. 25. *Merychippus seversus* (Cope), C.I.T. no. 2929, loc. 368: dorsal view of skull; × ⅓. Drawing by David P. Willoughby.

Skull Spring that probably represented a distinct species. I have since compared these teeth with *M. brevidontus* from the North Coalinga (see comparisons with *M. brevidontus*).

The Sucker Creek fauna of southeastern Oregon, Scharf (1935, p. 107). The lower canine and $I_{\bar{3}}$, no. 23098, U.C.M.P. collection, confirm the characters for *M. seversus* postulated by Scharf that there is an $I_{\bar{3}}$ present, and it is much larger than the canine in *M. seversus.* The milk teeth described by Scharf are probably like those from the Mascall type area, but there is need for more material from the Sucker Creek. It is unlikely that the specimens of *M. seversus* from Sucker Creek differ from the Mascall material. One specimen, no. 437 $M^{\underline{3}}$, has been compared with *Merychippus sumani* Merriam and in some ways resembles that species; however, the state of wear may obscure the true character of the tooth. The protocone is near the protoconule even though not rounded at this stage of wear as in *M. seversus.* California Institute of Technology no. 437 from loc. 44 was supposedly from an upper fossil horizon and has a preservation of lighter color than other *Merychippus* material from the area. Such evidence does not prove there was a second species present, but it indicates there may have been one at a different level stratigraphically.

The Beatty Buttes fauna of southeastern Oregon, Wallace (1946, p. 127). In specimens from this fauna there is a feature not observed in other known teeth of *M. seversus*—the lack of connection of crochet to the protoselene in one tooth. This

TABLE 20

MEASUREMENTS OF SKELETAL PARTS, MERYCHIPPUS SEVERSUS

(in millimeters)

	Type area A.M. no. 8175	Gateway area C.I.T. no. 2930	
		Right	Left
Lumbar vertebra			
Dorso ventral diameter	15.8	....	....
Transverse diameter	27.3	....	....
Ap. diam. of centrum	32.0	....	....
Innominate bone			
Ap. diam. acetabulum			
left	32.7	....	....
right	34.4	....	....
Ap. diam. obturator			
left	35.5	....	....
right	44.4	....	....
Femur			
Total length	262.0	....	....
Greatest prox. width	30.0	....	....
Least tr. of shaft	24.3	....	....
Least ap. of shaft	29.1	....	....
Ap. across median cond.	60.7	....	....
Tr. 3rd troch.	57.3	....	....
Head to tip of greater troch.	26.0	....	....
Tr. across condyle	54.5	....	....
Tibia			
Greatest length	254.0	....	....
Tr. diam. head	59.5	....	....
Least diam. shaft (tr)	27.4	25.2	....
Least ap. shaft	17.8	18.4	....
Ap. diam. distal	28.0	26.7	....
Tr. diam. distal	39.4	39.5	....
Metatarsal III			
Greatest length	173.0	166.5	....
Ap. prox. diam.	20.4	21.7	22.0
Tr. prox. diam.	24.1	24.2	24.5
Ap. diam. shaft (mid. pt.)	14.4	18.7	17.8
Tr. diam. shaft	17.5	17.2	16.3
Ap. distal diam.	19.6	18.5	....
Tr. distal diam.	22.2	21.0	....
Articulated (?) pes			
Length from prox. end tibia to distal tip of median phalanx	534.7	....	....

TABLE 20—*Continued*

	Type area A.M. no. 8175	Gateway area C.I.T. no. 2930	
		Right	Left
Metatarsal II			
Greatest length	159.0	158.0	....
Ap. diam. prox.	15.1	13.6	....
Ap. diam. distal	12.8	12.2	....
Least ap. shaft	....	4.7	....
Metatarsal IV			
Greatest length	162.0	154.0	....
Ap. diam. prox.	18.9	19.0	....
Ap. diam. dist.	12.4	12.4	....
Least ap. shaft	....	4.3	....
Astragalus			
Greatest ap.	38.0	....	....
Greatest tr.	35.0	....	....
Tr. across trochlea	15.0	....	....
Cuboid			
Greatest ap.	....	24.2	....
Greatest prox.-dist.	....	18.4	....
Calcaneum			
Greatest prox.-distal	69.5	68.7	....
Greatest width	29.4	29.2	....
Greatest ap. diam.	32.1	31.7	....
Ectocuneiform			
Greatest prox.-dist. diam.	7.1	....	....
Greatest tr. diam.	24.2	....	....
Greatest ap. diam.	18.4	....	...
Navicular			
Greatest diam. prox.-dist.	8.2	....	....
Greatest diam. ap.	20.8	....	....
Greatest diam. tr.	28.2	....	....
Proximal phalnax (III)			
Greatest external length	32.9	33.5	34.4
Greatest distal width	18.6	19.7	19.1
Median phalanx (III)			
Greatest length	21.5	24.8	....
Greatest width	19.3	22.6	....
Proximal phalanx (II or IV)			
Greatest length	...	23.4	22.5
Greatest width	....	8.6	8.5

TABLE 20—*Concluded*

	Type area A.M. no. 8175	Gateway area C.I.T. no. 2930	
		Right	Left
Radius			
Greatest length	....		188.5
Greatest prox. tr.	.		40.5
Least tr. of shaft			21.5
Least ap. of shaft			14.5
Greatest distal tr.			36.5
Scaphoid			
Greatest ap. diam.	...	24.5	
Greatest prox.-dist. diam.	....	16.4	
Magnum			
Greatest tr. diam.	....	20.7	
Greatest prox.-dist. diam. at edge	....	11.7	
Metacarpal III			
Greatest length	...	145.0	144.0
Ap. prox. diam.	...	19.7	20.0
Tr. prox. diam.		23.3	23.7
Ap. diam. shaft (mid. pt.)	..	14.6	14.5
Tr. diam. shaft	.	15.7	15.7
Ap. dist. diam.	...	17.3	17.5
Tr. dist. diam.	....	21.2	22.3
Metacarpal II			
Ap. diam. prox.	...	10.7	.
Metacarpal IV			
Greatest length	....	128.5	
Ap. prox.	...	9.4	
Ap. distal	....	12.2	
Least ap. shaft	....	5.4	4.9
Articulated (?) manus			
Length of left manus from prox. tip of radius to distal end median phalanx	...	394.7	..

character has been observed by Bode (1934) in several premolars of *M. californicus*. The teeth have large plications and are possibly simpler in enamel pattern than most *M. seversus* but are not beyond the range of variation of that species. The slight amount of cement on some of the teeth and the larger cross-sectional dimensions compared to the other known specimens of *M. seversus* cast doubt on the specific identity of the material, yet it is not possible to assign it elsewhere on the basis of our present knowledge. A difference in size is not proven on the basis of so few specimens, and it is possible that conditions of preservation or local environmental conditions inhibited deposit of cement. It is probable that the

Mascall species *M. seversus* is present in the Beatty Buttes fauna. C.I.T. no. 3207 from the Beatty Buttes fauna has been called *Merychippus* cf. *campestris*. This specimen is a partial skull with well-worn teeth even in M^3, which measures 17.5 in height of crown. The protocone is narrowly connected in P^3 and P^4 and moderately so in M^1 and M^2. The pli caballin and pli protoconule are present in P^4; the preorbital fossae is large and deep. The protocone was probably isolated to one-half wear. Specific designation is indeed uncertain; it is just as probable that this specimen could be *M.* cf. *seversus*.

The Virgin Valley fauna of northwestern Nevada (Merriam, 1911, and Stirton, 1939, p. 628). Stirton (*loc. cit.*) considered the species in the Virgin Valley to be *M.* cf. *californicus*. The few teeth available are distinguishable from *M. brevidontus* on the basis of height of crown if in nothing else, but the specimens are not so conveniently distinguished from *M. californicus*. As demonstrated by Bode, the two species *M. seversus* and *M. californicus* from the Mascall and North Coalinga, respectively, have individual teeth in both faunas tending either way in their apparent affinities. Comparison of a single unworn specimen, U.C.M.P. no. 11386 (ectoloph absent), with a large sample (this tooth from Virgin Valley measures 22.4 from tip of protocone to base of enamel of protocone compared with a sample of 19 specimens of *M. seversus* with $M = 29.37 \pm .58$) indicates the Virgin Valley tooth is probably not significantly different from the Mascall population in height of crown. One tooth, U.C.M.P. no. 11862, has the isolated protocone, more complex metaloph, and lack of cement that seems prevalent in *M. californicus*, but other teeth are nearer *M. seversus* in numbers of plications and other features. On the basis of the material available, the larger species from Virgin Valley should be designated *Merychippus seversus*. A glance at table 21 shows the Virgin Valley population to have a greater total similarity to the Mascall fauna than do the other populations.

At the California Institute of Technology there is a fairly complete cranium and mandible on display, numbered (S)-41-1185 and (S)-17-333 and labeled from the Virgin Valley. These are much smaller than Mascall specimens of *M. seversus* although the preorbital fossa is deep and extensive as in the Mascall skulls. Measurements such as length from base of occipital condyle to alveolar of incisor, 240.0 and tooth row P^1–$M^3 = 105.2$, indicate a small animal. The protocone is connected in early wear, and the cement is heavy. The enamel pattern may be simpler than in *M. seversus* as indicated by a tally of the number of plications, but the chief difference is size and character of the protocone. This may be a primitive *Merychippus* something like *M. primus* or an early *M. brevidontus*.

The Big Spring Canyon fauna, South Dakota. Gregory (1942) discusses an unusual record of *Merychippus* in this Pliocene assemblage. On the basis of size and height of crown it is probable that this material does fall within the range of *M. seversus* as he suggests, but without more information on the enamel pattern a decision on the species assignment is impractical.

The Deep River fauna, Montana. Osborn (1918) refers to an old adult skull A.M. no. 8105* as *Merychippus isonesus* (= *seversus*) var. The specimen is similar in size and in depth of preorbital fossa to *M. seversus*, but because of extreme wear it is impossible to check the enamel pattern. On the basis of such evidence, no. 8105

TABLE 21

MERYCHIPPUS SEVERSUS (Cope) COMPARED WITH SELECTED SPECIES OF MERYCHIPPUS

Merychippus seversus (Cope) Mascall fauna	*Merychippus californicus* Merriam North Coalinga, Calif.	*Merychippus californicus* High Rock Canyon	*Merychippus sumani* Merriam Barstow
1. Hypsodont, ht. crown (uppers M = 29.37 ± .58, lowers M = 24.25 ± .46)	1. Uppers, M. 34.93 ± .34 Lowers M. 30.9 ± .38..... +	1. Upper M = 34.4......... −	1. Possibly higher than *M. seversus* M = 32.4 ..... O
2. Generally quadrate (M. ap. diam. = 19.35 ± .11; M. tr. diam. = 19.72 ± .13	2. Similar, generally........ +	2. Similar.................. +	2. Ap. M = 20.4; tr. M = 21.3 +
3. Protocone oval to elongate with ant. spur and not connected to protoconule except in more than ½ worn teeth	3. More elongate than oval isolated to base. Minute spur, nipple-like. Protocone with deep pre- and post-protoconal grooves.. −	3. In general similar to Coalinga................ −	3. Elongate, no spur..... −
4. Hypocone elongate, usually < protocone	4. Similar................ +	4. Similar.................. +	4. Similar.............. +
5. Plicaballin, usually 1, and > pliprotoconule	5. Pliprotoconule > plicaballin.................. −	5. Pliprotoconule > plicaballin................. −	5. Similar.............. +
6. Metaloph usually 1–2 or more post. and one ant. plication medium to large size	6. Usually 1–3 ant. 2–4 minute to large post......... −	6. Often more than one ant; more than one post........ −	6. Usually 2–3 ant; 3–4 post. Both dominantly med.-large size.............. −
7. Pli protoloph usually none or one	7. Similar or somehwat more complex................ O	7. One or none............. O	7. Similar (?).............. O

8. Pli hypostyle usually 1 or 2 medium	8. Similar .... +	8. As in N. Coalinga .... +	8. Similar .... +
9. Ante pli hypostyle small to large, tends to close post. hypoconal groove, sometimes none	9. Similar .... +	9. Similar .... +	9. Similar .... +
10. Cement mod. to heavy, rarely slight	10. Slight to moderate ...... −	10. Moderate .... +	10. Heavy, generally .... +
11. Metaconid-metastylid inflections shallow	11. Slightly wider .... ○	11. Similar (?) .... ○	11. ? .... ?
12. Protoconid-hypoconid walls fully rounded, inflection deep	12. Similar .... +	12. Similar .... +	12. ? .... ?
	Total: +, 6; −, 4; ○, 2; N = 65	Total: +, 6; −, 4; ○, 2; N = 18	Total: +, 6; −, 2; ○, 2; ?, 2 N = 9

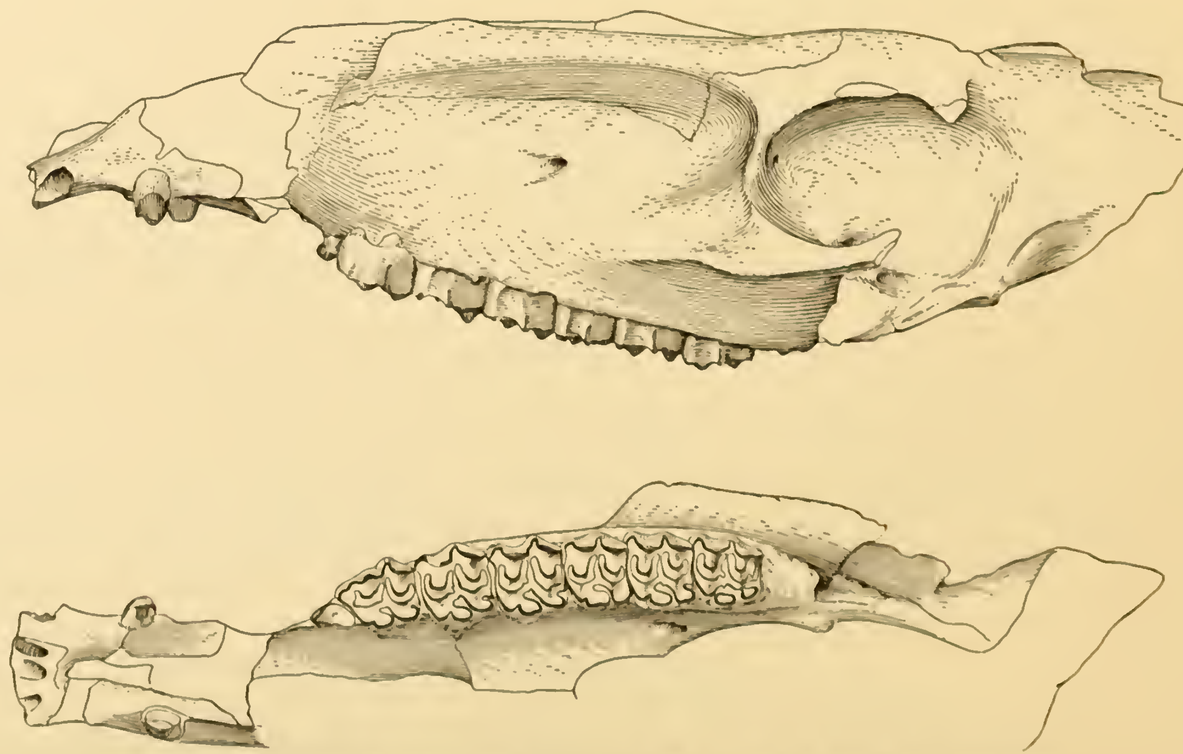


Fig. 26. *Merychippus seversus* (Cope), C.I.T. no. 532, loc. 183: top, partial skull, left side; bottom, occlusal view left side; × ½.

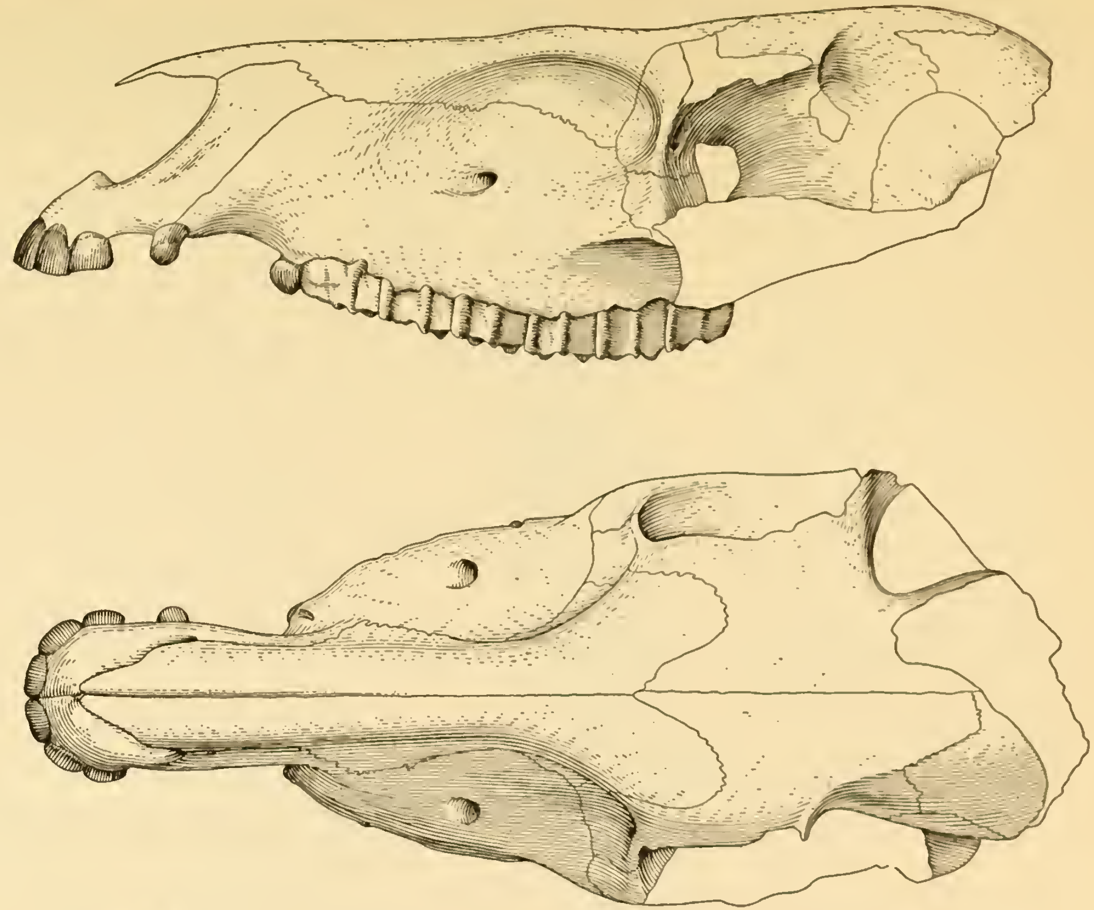


Fig. 27. *Merychippus seversus* (Cope), C.I.T. no. 2930, loc. Gateway area: top, partial skull, left side; bottom, dorsal view of skull; × ½.

TABLE 22

Comparative Variation in Measurements of Merychippus severus and[a] M. californicus

	Number of teeth	Observed range	Mean	Standard deviation	Coefficient of variation	Estimated minimum no. individuals
Upper $P^3 - M^2$						
Height of crown						
M. severus	18	24.6 – 32.3	29.37 ± .58	2.45 ± .41	8.33 ± 1.39	11
M. californicus	39	30.5 – 39.6	34.93 ± .36	2.23 ± .25	6.44 ± .72	5
Upper $P^3 - P^4$						
Anteroposterior diameter						
M. severus	24	18.0 – 21.3	19.99 ± .18	.858 ± .12	4.30 ± .62	8
M. californicus	24	19.2 – 22.4	20.82 ± .18	.873 ± .13	3.11 ± .44	8
			$(M = A + C_1)$[b]			
Transverse diameter						
M. severus	24	16.4 – 21.4	19 437			
M. californicus	42	18.2 – 23.5	21 02			
Upper; $M^{1,2}$						
Anteroposterior diameter						
M. severus	16	17.0 – 20.0	18 66			
M. californicus	14	17.7 – 21.5	20 03			
Transverse diameter						
M. severus	17	16.4 – 20.2	17 85			
M. californicus	20	18.5 – 21.2	19 77			

[a] *M. severus* from Mascall type area only.
[b] See Simpson and Roe, 1939, p. 383, A = assumed mean, $C_1 = \Sigma(fd)/N$.

might be called *Merychippus* cf. *seversus.* Another specimen, A.M. no. 8106,* a nearly complete palate from the Deep River, is possibly advanced over *M. seversus.* The very slightly worn molars are as high as 31.2–32.3; tabulation of plications shows somewhat larger and more numerous foldings of the enamel line than in *M. seversus*, and the protocone possibly has a stronger spur, as seen in the type of *M. quintus* from the Sheep Creek.

Merychippus isonesus (⊨*seversus*) from Rockglen, Saskatchewan, Russell, (1933). A single tooth is figured by Russell. It is not heavily worn but sufficiently so to allow an observation of the characters. It is possible that the protocone unites earlier than the average in *M. seversus*, but otherwise there is not enough material available to prove or disprove the relationship given by Russell.

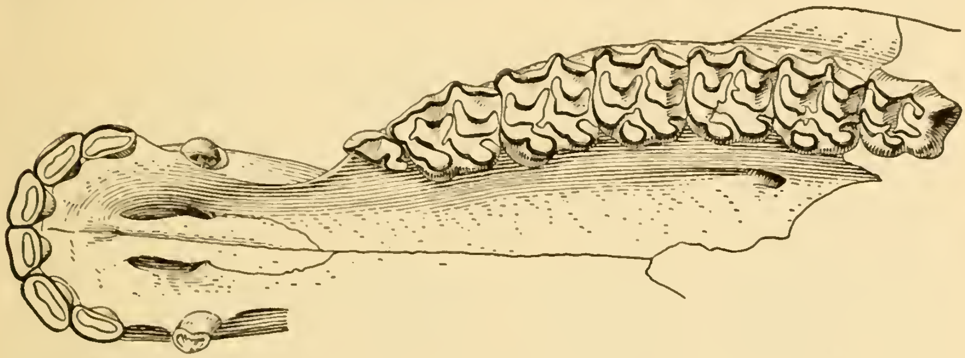


Fig. 28. *Merychippus seversus* (Cope), C.I.T. no. 2930, loc. Gateway area: occlusal view; × ⅔.

Comparisons with other species of Merychippus.—Merychippus californicus Merriam (1915). As Bode (1934) states, the type specimen of *M. californicus*, an M^1, is not typical of the species and is much like *M. seversus* in the deposition of the cement and in the enamel pattern. In the entire representation of material from the two areas there are several differences between *M. seversus* and *M. californicus. M. californicus* as a population is particularly distinct in the greater height of crown in the upper and lower cheek teeth (table 22), slightly greater size, more elongate protocone and the more completely isolated protocone throughout the length of the tooth, absence of a minute spur on the protocone, more complex metaloph, greater size of pli protoconule compared with pli caballin, and in the tendency for greater development of the pli hypostyle. Some other characters of possibly less significance are the larger calcaneum (77.0 a.p. and none more than 70.3 in Mascall calcanea); the cuboid facet of metatarsal III more on a level with ectocuniform facet (see Merriam, 1915); and metacarpal III relatively narrower (a.p.) compared to transverse width and tendency for prefossette to remain open lingually in premolars (Bode, 1934). Bode has also proposed that a difference lies in the milk dentition. Of the features he mentions it seems that the greater amount of cement in the North Coalinga material is more significant than any other character. It is apparent that the two populations are actually close in all the major features; their difference is often one of degree, but with the relatively large sampling available, it is much easier to see the actual trend of characters.

There is not a pronounced difference in size of the teeth in the two species, yet some difference is indicated. All the available teeth of *M. seversus*, representing a state of wear ranging from 18.0 to 24.0 or what may be considered one-third wear, have been measured and compared with a random sampling of teeth from the *M. californicus* population at one-third state of wear. A test of difference of means in the anteroposterior diameter of the premolars shows that there may be a statistically significant difference: $d/\sigma_d = .83 \; .25 \pm 3.31$. The difference in means of transverse diameters is even greater, 1.58, thus suggesting definite difference in this dimension. The molar anteroposterior dimensions show 1.38 difference and 1.92 difference in transverse diameter. All dimensions then suggest a greater size in P^3 to M^2 in *M. californicus* though this is not extreme. The premolars and molars tend to be slightly more quadrate in *M. californicus* than in *M. seversus.* In both species the premolars are larger than the molars, though *M. californicus* tends to have more nearly equal dimensions in the premolars and molars than does *M. seversus.*

The greatest dimensional difference in the two species is in the greater height of crown in *M. californicus;* the mean difference is 5.54.

Merychippus californicus from High Rock Canyon, Nevada (see Stirton, 1939) is supposedly different from the population at the type area in North Coalinga, California, in greater amount of cement, which may actually be owing to less abrasion of the High Rock Canyon teeth during their accumulation. The population from High Rock Canyon shows greater agreement with *M. seversus* in this characteristic. However, the Nevada and California populations are generally similar and the enamel pattern equally advanced in both.

Merychippus sumani Merriam from the Barstow fauna, California. This species is not as well represented as *M. seversus* or *M. californicus* although it appears to be a valid species. It is possibly nearer *M. californicus* than *M. seversus* in height of crown and also resembles *M. californicus* in cross-sectional area, elongate shape, and absence of a spur on protocone and complex metaloph. Resemblance to *M. seversus* is suggested in size of pli protoconule, pli protoloph, and pli hypostyle; it may be distinct in its heavy coat of cement, elongate protocone, and complex anterior metaloph, but future study may force the opinion that *M. sumani* is, at most, a subspecies of *M. californicus.*

Merychippus brevidontus Bode from North Coalinga, *Merychippus* zone, California. This is a distinct species found in association with *M. californicus.* Much difficulty was encountered when measuring the transverse diameter. If the measurement was taken at the crest of the tooth, the characteristic "pinching" together of the protocone and ectoloph walls prevented accurate measurement at one-third wear point, but measurement at the crest is possible. This slanting of the walls of the tooth is typical of *Parahippus.* The species is distinct (as Bode has demonstrated) in the great number and development of plications on the metaloph and pli hypostyle, moderate to heavy cement, and low height of crown. Bode has shown that many of the Coalinga specimens have been well worn and polished by transportation in water. *M. brevidontus* is characterized by well-developed styles which, in turn, could act as a protective buffer against weathering and consequent wearing off of the cement on the walls of the paracone and metacone. There are specimens of *M. californicus* from the North Coalinga that do not have the cement worn away. There is no certainty that differences in degree of occurrence of cement is of genetic significance in these forms.

In the Mascall faunal collection there are some teeth with characteristics suggestive of *M. brevidontus.* A discussion of their affiliation is presented under *Merychippus* sp. low crowned.

The *M.* cf. *brevidontus* material from High Rock Canyon in the U.C.M.P. collection (including nos. 35369, 24295, 24300, 38287, and 11380) is less complex in the enamel pattern with smaller areal dimension and is a little lower crowned than the type, but with the same amount of cement. These High Rock Canyon horses

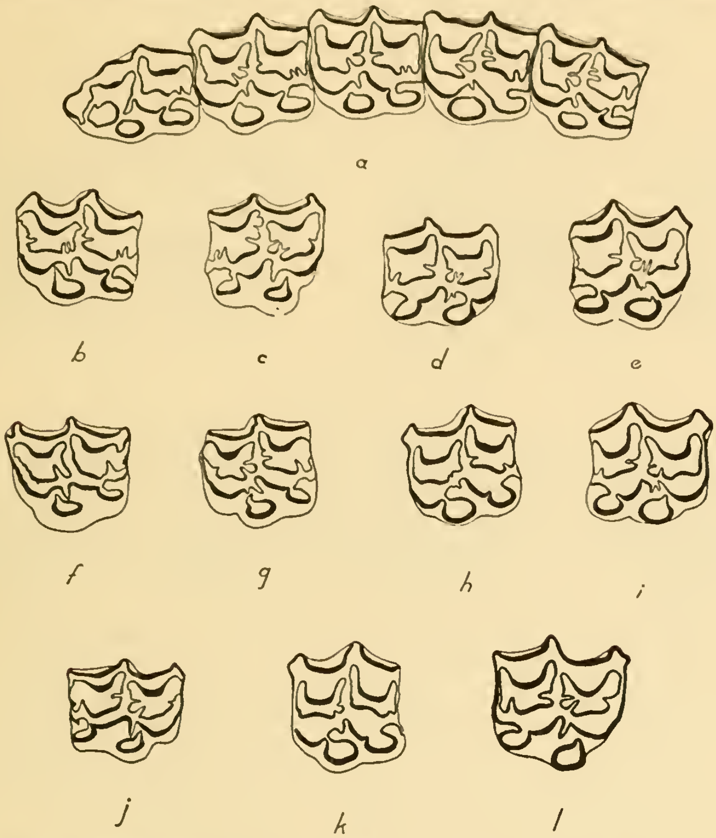


Fig. 29. *Merychippus seversus* (Cope) : *a,* U.C.M.P. no. 23088, loc. 3059; *b,* C.I.T. no. 408, Mascall; *c,* C.I.T. no. 421, loc. 113; *d,* U.C.M.P. no. 23099, loc. 3043; *e,* U.C.M.P. no. 27332, loc. (?) Mascall; *f,* U.C.M.P. no. 23089 loc. 3059; *g,* U.C.M.P. no. 27239 (not 27235 as shown in Bode), loc. (?) Mascall; *h,* C.I.T. no. 412, loc. 113; *i,* C.I.T. no. 409, loc. 3059; *j,* C.I.T. no. 420, loc. 113; *k,* U.C.M.P. no. 23093, loc. 3059; *l,* U.C.M.P. no. 27236, loc. (?) Mascall. Reproduced from Bode (1934, figs. 2 and 3). Bode has incorrectly designated C.I.T. nos. 428 and 1504; no. 428 is from the Virgin Valley, and no. 1504 is from the Skull Spring and not from the Mascall; also C.I.T. no. 1505 is from the Skull Spring and not from the North Coalinga, *Merychippus* zone. All $\times \frac{4}{5}$.

could be ancestral to typical *M. brevidontus* and may even be specifically different from the Coalinga animals. The earlier ancestor might have been like *Parahippus avus* (Marsh). (See discussion under *Parahippus.*) One set of small teeth (U.C.M.P. no. 11380 a, b, c, including P^2–M^3) apparently represents one individual. Stirton (1939) has suggested that these teeth might be referable to *M. gunteri.* They are low crowned and simple in pattern, but I do not believe the individual can be considered more than a small variant of *M. brevidontus* until more material is known. Some characters noted in the *M.* cf. *brevidontus* material are many anterior and posterior plications on metaloph, less than in *M. brevidon-*

tus but similar to *P. avus;* pli caballin and pli protoconule large and complex; protocone isolated but with large spur; and cement moderate to heavy. The last three features strongly resemble *M. brevidontus*, but in general the material is less advanced than *M. brevidontus.*

The Virgin Valley fauna contains several teeth (U.C.M.P. nos. 11386, 21775, 11449, 1–50, 11707, 11714, 11453, 10573, 40989, and possibly C.I.T. nos. 4091, 429, and 428) which may compare with *M. brevidontus* in size (tentatively they are considered to be *M.* cf. *brevidontus*) but are simpler in enamel pattern.

Gazin (1932) mentioned the possibility of another species of *Merychippus* being present in the Skull Spring fauna. This material includes at least C.I.T. nos. 4083 A, B, C, D, and E, 4086, 4080, 4085, 4085 A, 4082 A and B, 5036, and 5036 A. The specimens are large—possibly of greater size than *M. brevidontus*, but of definitely

Fig. 30. *Merychippus seversus* (Cope), A.M. no. 8177, loc. Mascall type area; × 1. Figs. 30–34 are mine.

simpler pattern—with fewer total numbers of plications. The teeth are typical of *M. brevidontus* in cusplike appearance of the paracone and metacone and in internal-external taper of the walls of the tooth.

The presence of a few teeth of *M. brevidontus* in the Sucker Creek fauna of Oregon is significant in that typical *M. seversus* is also present in the same fauna. The teeth referred to *M. brevidontus* are similar to the type in all features, especially in complexity of enamel pattern. This is evidence for a suggestion that there is no great temporal difference between the Sucker Creek and North Coalinga.

Merychippus insignis Leidy, Bijou Hills, South Dakota. If Stirton (1940) is correct in considering the tooth from the Philadelphia Academy of Science, no. 11284, as a topotype of *M. insignis*, there are certain well-defined distinctions from *M. seversus* to be noted, namely, smaller cross-sectional area, oval protocone without spur, and more complex metaloph.

Merychippus stevensi Dougherty (1940) from Caliente Mountain. This is much like *M. seversus* except in the apparent tendency for the protocone to unite early with the protoloph, but the teeth are heavily worn. More comparisons might be made with the *Protohippus* line of *Merychippus* as, for example, *M. sejunctus* or *campestris*. *Merychippus carrizoensis* Dougherty from the same fauna is a short-crowned specimen as seen in the measurements: height of crown C.I.T. no. 2552; M^2 16.8; M^3 15.9; slight to no wear. The protocone in *M. carrizoensis* is similar to that in *M. stevensi*, and there may be a relationship to *M. primus*, *M. gunteri*, or the small species from Phillips Ranch as displayed in the size and the character of the protocone. *M. stevensi* and *M. carrizoensis* are too poorly represented for an accurate interpretation of their relationships.

*Merychippus tertius** Osborn, *M. quartus** Osborn, and *M. quintus** Osborn (all 1918) from Sheep Creek, Nebraska. Stirton (1940) tentatively gave *Merychippus secundus* Osborn, *M. tertius*, and *M. quartus* specific rank. It is my belief that *M. quartus* should be considered a *nomen vanum* (see Simpson, 1945). It is highly improbable that slight differences in size and proportions of the metacarpals and the tibia of this type (no teeth included) are of specific value. On the basis of our knowledge of better-known species it is unlikely that this species can ever be adequately distinguished.

The teeth called *M. tertius* by Osborn are properly figured, but they are fairly well worn. The several characters given by Osborn could all be included in the variation as seen in *M. quintus,* as for example, size, early uniting of the protocone to protoloph, elongate protoloph, and pattern of metaloph. *M. tertius* could be a worn *M. quintus,* but a more critical study of better documented Midwest material is needed before final opinion is given.

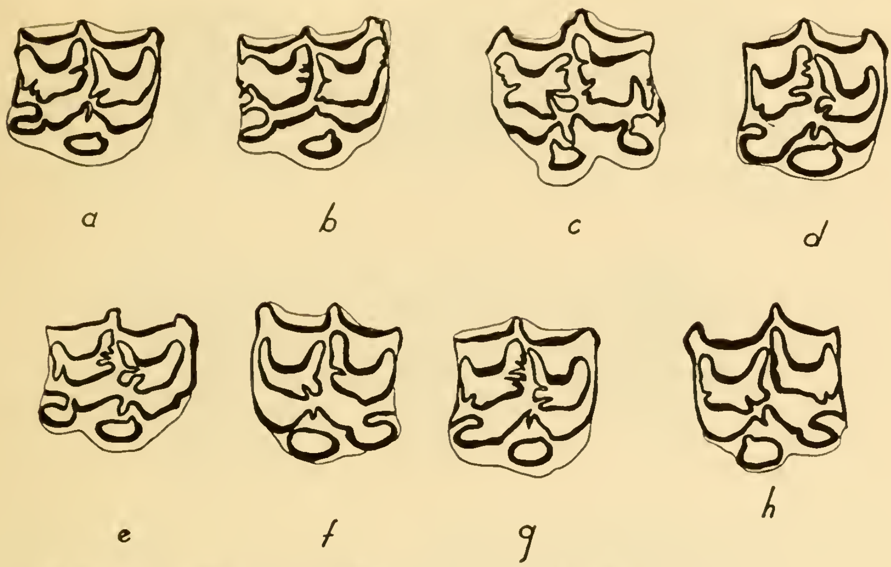


Fig. 31. *Merychippus seversus* (Cope), Mascall type area; Y.P.M. nos.: *a*, 11607; *b*, 11607 b; *c*, 11607 c; *d*, 11607 d; *e*, 11607 e; *f*, 11607 e; *g*, 11607; *h*, 14298; all × 1.

The type of *M. quintus* is possibly larger and higher crowned than *M. seversus* and has an early connection of the protocone with the protoloph in the premolars, but the fairly well-worn M^1 has an isolated protocone thus indicating Merychippine subgeneric affinity.

*Merychippus paniensis** (Cope) from the lower Pawnee Creek, Colorado. This species differs in protocone without spur and possibly simpler enamel pattern. The type is well worn and offers no particularly diagnostic features. A review of the Pawnee Creek, Sheep Creek, and Snake Creek faunas may reveal what might be considered true *M. paniensis* characters.

Merychippus sphenodus, Merychippus calamarius (Cope), and *Merychippus republicanus* Osborn are all larger species and with more complex enamel pattern than *M. seversus* and *M. californicus.* This complexity is particularly evident in the dominance of two pli caballin and pli protoconule plications, a greater number of metaloph plications, and a larger size in these plications.

*Merychippus ? missouriensis** Douglass, from Montana. Since the type specimen is an immature skull and partial skeleton with very heavily worn milk teeth, it is doubtful that it can be determined a distinct species. It is probably *Merychippus* since the crochet appears to be connected and the specimen is large enough. It does not disagree with *M. seversus* except possibly in an early connection of the protocone. The lack of depth of the preorbital fossa is owing to the presence of permanent premolars in the skull and their crowding dorsally into the preorbital region. There is resemblance to *M. quintus* and *M. seversus*, but it would be much more logical to relegate the specimen to *Merychippus* sp. indet.

Discussion.—Bode (1934) has emphasized the affinities of three species: *M. seversus*, *M. californicus*, and *M. sumani*. *M. californicus* might be considered less advanced than *M. seversus* in the amount of cement deposited, but greater hypsodonty is more significant in the trend in the evolution of horse teeth; also a more

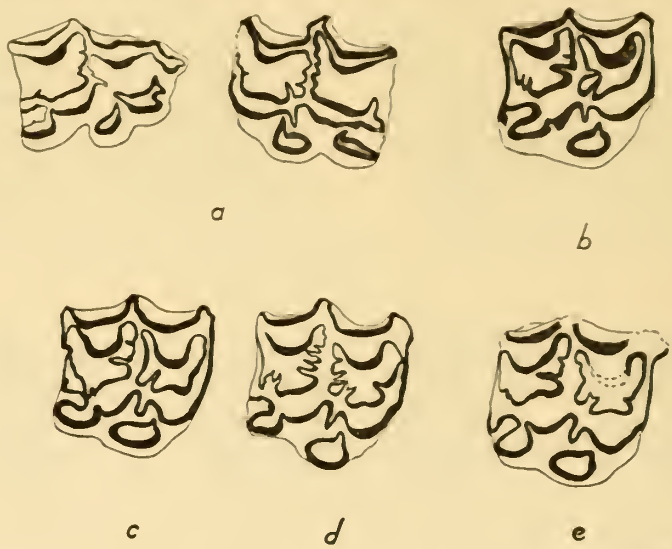


Fig. 32. *Merychippus seversus* (Cope): Mascall type area; Y.P.M. nos.: *a*, $\frac{10778}{3}$; *b*, $\frac{10778}{1}$; *c*, $\frac{11608}{0}$; *d*, $\frac{11608}{1}$; *e*, $\frac{11608}{2}$. All × 1.

isolated protocone and complex metaloph are more advanced features than found in *M. seversus*. The two species are relatively closely allied, and it is difficult to determine how far apart they might have been chronologically, but we may say that *M. californicus* was a later species and a probable descendant of *M. seversus*. *M. sumani* has definite trends toward the isolated elongate protocone, high crown, and large size, but it is not greatly advanced over *M. seversus* and *M. californicus*.

M. insignis is advanced in its metaloph plications, in its isolation of the protocone, in the development of pli caballin and protoconule, and in its hypsodonty. It may have been derived from *M. californicus* (Stirton, 1947), but the species is not represented adequately enough for general appraisal.

Suitable specimens of *M.* (*M.*) *calamarius*, *republicanus*, and *sphenodus* were not studied, but the consistently complex enamel pattern and size in these groups set them apart as advanced species. *M. calamarius* material from Tonopah, Nevada (being studied critically) presents data that uphold the above opinion.

M. brevidontus is exceptional in possessing the primitive trait of low-crowned teeth but displays an advanced condition in the complexity of the enamel pattern. It is like *M. seversus* in the proportions of the crown cross section and in the presence of a spur on protocone, but is less hypsodont and has a much more complex

Fig. 33. *Merychippus seversus* (Cope), Mascall type area: *a, b,* and *c,* U.S.N.M. no. 7721; *d,* 3910. Crooked River area: *e,* U.S.N.M. no. 20088. All × 1.

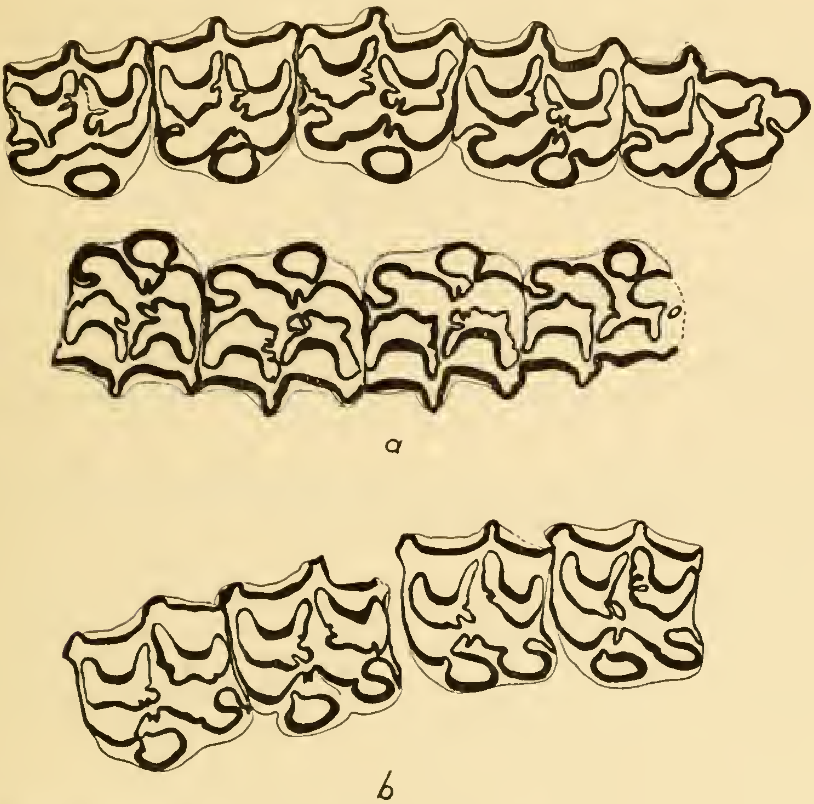


Fig. 34. *Merychippus seversus* (Cope): Gateway area; *a,* U.C.M.P. no. 32753; *b,* C.I.T. no. 4916. All × 1.

pattern. Conceivably, *M. brevidontus* was derived from the common ancestor of *M. seversus* and *M. quintus,* but more likely from a *Parahippus avus* type of animal. The population from North Coalinga is so much more complex in the tooth patterns than *M. seversus, californicus, sumani,* or *M.* cf. *brevidontus* that I feel justified in thinking *M. brevidontus* may have been dominant no earlier than *M. seversus* and was probably dominant later. It is a contemporary of *M. californicus.*

The relationships discussed above demonstrate that middle and late Miocene horses, at least merychippine types, were genetically variable with the potential to diversify. One species emphasizes a trait such as complexity of enamel pattern and another species greater or lower height of crown.

The fact that *M. seversus* does have hypsodont teeth, or that teeth something like *M. brevidontus* have very complex enamel suggests that these animals were eating food requiring more resistant enamel than that found in animals of simpler pattern or lower height of crown. Possibly the Mascall specimens represent some of the first true upland grass-eating horses of western North America.

Merychippus cf. *seversus* (Cope)

At the American Museum several teeth were found under the number 8181 including "? milk teeth." Since the identifying features of milk teeth in *Merychippus seversus* are not as surely perceivable as characters in adult teeth, it is believed logical to consider these teeth as *M.* cf. *seversus*. The catalogue number ? 8181D has been designated for the three upper milk teeth formerly numbered 8181. It is probable that these teeth are *Merychippus* because of height of crown, absence of ribs, and connection of hypostyle to metaloph. The material shows some difference from milk dentition of *M. seversus* in less complex pattern of the metaloph.

U.C.M.P. no. 2070, from ? locality, is a defaced lower M_3 with a narrow metastylid-metaconid inflection possibly resembling *M. seversus*.

Merychippus sp. indet.

A U.S.N.M. specimen no. 3912 from the Mascall is represented by an extremely large upper tooth very heavily worn. This may be *M. seversus* since it is characterized by heavy cement, and has a connected crochet and lophs; but in size and slight V-shape of the paracone and metacone walls, it suggests Hyppohipine features.

The following measurements are available: anteroposterior diameter, at base, 22.3 (heavy cement); anteroposterior diameter, at crest, 22.2; transverse diameter, at base, 26.6; transverse at crest 25.2; at paracone 1.4; at metacone 1.4; at protoconule 1.3; and at protocone 1.4. The protocone is connected to both the protoconule and hypocone.

An incomplete manus, A.M. no. 8174a, is referred to *Merychippus isonesus* (= *seversus*) by Osborn (1918, p. 103). The type of *M. seversus* has no associated manus to be compared. It was noted on the museum tag that no. 8174a is called a topotype; however, there is need for associated material, and this specimen could be referred to *Merychippus relictus*, but is probably *M. seversus*. For the present the indeterminate category will be applied.

There are many skeletal elements and fragments of teeth from the Mascall that seem to be related to *Merychippus*. None of the material is associated with a specifically identifiable specimen. One particularly interesting situation was the discovery of several skeletal elements in association in the typical "mammal" horizon (see unit 5 of geologic section). The material apparently consists of two individuals of nearly similar size, U.C.M.P. no. 39183, loc. V-4835. These bones were all found within an area of about 2 by 3 feet by 1 foot vertical depth; there were no bones in articulation. The various elements were scattered as though considerable shuffling of the material had occurred after death and desiccation. Most of the elements are parts of the hindquarters or limbs. Compared to the type skeletal material of *Merychippus seversus*, these elements average slightly smaller (see table 23).

On the basis of comparison with skeletal elements of *Parahippus* from the Flint Hill fauna this Mascall material differs from *Parahippus*. The distal shaft of the tibia is relatively wide with flat anterior surface with more prominent external condylar surface; the radius has greater curvature and is narrower distally; metatarsals are relatively deep anteroposteriorly; and the calcaneum, astragalus, and phalanges show little difference.

Other skeletal parts in the National Museum collection have been labeled *Merychippus isonesus* Cope. U.S.N.M. no. 7717 is specified on the museum tag as consisting of limb and foot bones from Cottonwood Creek; however, the museum catalogue shows this number as *Merychippus* sp., received from Marsh and collected by L. S. Davis with parts of fore and hind limbs, feet, and upper and lower cheek teeth. Measurements of the various elements indicate slightly greater size than the *Merychippus seversus* specimen. (See table 23.) Since no teeth were found with this number, this material will be referred to as *Merychippus* sp.; it comprises under no. 7717 a manus including right and left metacarpals III, left metacarpal IV, broken radius and magnum, a scaphoid, proximal, median, and distal phalanges; pes, including right and left metatarsal III, right metatarsal IV and II, astragalus, distal phalanx, and proximal phalanx.

Another U.S.N.M. number 7719 includes specimens taken at "Cottonwood Creek, John Day River Valley, Oregon," supposedly with upper and lower teeth (the teeth were not located). This material includes a pes with a left metatarsal, an astragalus, a distal phalanx, and distal tibia. As in no. 7717 this material is slightly larger than the *M. seversus* specimen. Neither of these individuals represented by foot elements appears to be significantly distinct from *M. seversus* in their dimensions.

Parts of a palate and skeleton were found associated according to U.S.N.M. data attached to no. 20087, found at the south fork of the Crooked River, 25 miles above the junction. The teeth in the palate are very heavily worn, the greatest height of crown being 5.5 mm. The protocone in all the teeth is broadly connected to the protoloph except in M^2 which is narrowly connected. The length of the tooth row is slightly less than in any skull referred to *M. seversus*. This would suggest a small species of *Merychippus* is represented, yet the length of metatarsal III (209.0 mm.) is greater than any other from the entire fauna by about 30 mm. (see table 24). Fortunately a nearly complete set of cervicals with the first thoracic were recovered (the atlas is missing). By measuring from the anterior tip of the axis to the posterior edge of the postzygapophyses and from the anterior tip of the prezygapophyses to the posterior tip of the postzygapophyses in each of the cervicals, a total of 346.0 mm. length was determined (this includes cervical 2 through 7).

Compared with *Equus*, the first thoracic of this specimen has a narrower postzygapophyses, and the articular surfaces for the capitulum and tuberculum of the first rib are separate instead of continuous as in *Equus*. Cervical 7 in the specimen may be relatively narrower transversely at the centrum than *Equus*, and numbers 4, 5, and 6 have a relatively shorter prezygapophyses with less lateral extension of these processes. The axis has the crest of the spine separating into two lateral crests more posteriorly than in *Equus*. There is no basis for assigning this material to a particular species.

TABLE 23

MEASUREMENTS OF SKELETAL PARTS MERYCHIPPUS SP., TYPE AREA

(in millimeters)

	U.C.M.P.			A.M.	U.S.N.M.			
	39183		39300	8174a	7717		7719	
	left	right	left	right	left	right	left	right
Humerus								
Tr. distal diam......	....	38.2	....	....	....		....	....
Distal depth........	....	39.7	....	....	....	....	....	....
Radius								
Greatest length......	....	181.0	....	....	....	....	....	....
Tr. prox. diam......	....	37.8		....	....	....	....	....
Tr. distal diam....	....	34.5	....	....	....	....	....	....
Ap. distal diam.....	....	20.2	....	....	....	....	....	....
Greatest depth through ulna......	....	33.2	....	....	....	....	....	....
Metacarpal III								
Greatest length.....	....	....	....	160.0	162.5	163.0	....	....
Tr. prox. diam......	....	....	....	23.7	24.7	24.3	....	....
Tr. distal diam......	....	....	....	24.2	23.5	23.6	....	....
Least tr. diam. shaft	....	....	....	17.3	17.6	16.7	....	....
Metacarpal II								
Greatest length.....	....	....	....	147.0	....	....	....	....
Ap. prox. diam......	....	....	....	11.6	....	....	....	....
Ap. distal diam.....	....	....	....	12.3	....	....	....	....
Metacarpal IV								
Greatest length.....	....	....	....	144.0	....	....	....	....
Ap. prox. diam......	....	....	....	11.6	....	....	....	....
Ap. distal diam.....	....	....	....	12.3	....	....	....	....
Phalanx, proximal								
Greatest length.....	....	....	....	33.3	23.7[a]		....	....
Tr. distal diam......	....	....	....	19.9	19.4		....	....
Median phalanx								
Greatest length.....	....	....	....	....	27.4		....	....
Tr. distal diam......	....	....	....	....	21.2		....	....
Distal phalanx								
Tr. prox. diam......	....	....	....	....	28.8		....	....
Scaphoid								
Tr. distal diam......	....	....	....	....	39.6		....	....
Ap. diam. shaft.....	....	....	....		16.2		....	....
Unciform								
Prox. distal diam....	....	....	....	....	15.1		....	....
Tr. diam............	....	....	....	....	12.6		....	....
Magnum								
Tr. diam.........	....	....	....	....	21.3		....	....
Prox. distal diam....	....	....	....	....	12.6		....	....

[a] Right or left not determined in this column.

TABLE 23—*Continued*

	U.C.M.P.			A.M.	U.S.N.M.			
	39183		39300	8174a	7717		7719	
	left	right	left	right	left	right	left	right
Tibia								
Greatest length....	239.0	....	....	....	....	....	....	....
Tr. prox. diam....	54.3	....	....	....	....	....	....	....
Ap. prox. diam.....	47.0	....	....	....	....	....	....	....
Tr. distal diam.....	37.5	26.8	38.5	....	....	....	....	....
Ap. distal diam.....	24.7	24.3	25.2	....	....	....	....	....
Least tr. shaft....	25.2	....	....	....	....	....	....	....
Least ap. shaft.....	17.4	....	....	....	....	....	....	....
Astragalus								
Greatest length.....	....	34.5	....	....	....	....	....	....
Tr. diam...........	....	30.6	....	....	....	....	....	....
Tr. across trochlea..	....	15.8	....	....	....	....	....	....
Metatarsal III								
Greatest length.....	160.0	161.5	....	179.0	182.0	180.0	166.0	182.0
	172.0							
Prox. ap. diam....	19.6	19.5	....	17.6	....	....	21.5	20.0
	27.8							
Tr. prox. diam......	21.9	22.0	....	....	26.0	25.4	24.6	25.1
	23.8							
Ap. distal diam.....	16.9	16.6	....	12.2	19.3	21.4	18.5	18.2
	18.6	....	....	....	....	....	....	....
Tr. distal diam......	21.8	21.9	....	....	25.5	25.9	25.3	24.2
	21.7							
Least tr. shaft......	15.7	16.3	....	....	16.6	17.0	17.6	17.5
	17.0							
Metatarsal II								
Greatest length.....	....	....	....	166.8	148.0[a]		....	....
Ap. distal diam.....	....	....	....	12.8	....		....	....
Calcaneum								
Greatest length.....	68.2	....	....	....	....		....	....
Tr. diam............	25.1	....	....	....	....		....	....
Ap. diam............	29.2	....	....	....	....		....	....
Proximal phalanx								
Greatest length.....	....	....	....	33.5	35.4		....	....
Tr. distal..........	....	....	....	20.6	19.3		....	....
Distal phalanx								
Greatest tr..........	....	....	....	....	20.7		22.1	
					21.7			
Pelvis								
Ap. across acetabulum............	31.5	....	....	....	....		....	
Tr. across acetabulum............	24.0	....	....	....	....		....	
Tr. across shaft.....	16.5	....	....	....	....		....	

[a] Right or left not determined in this column.

TABLE 24

MEASUREMENTS OF MERYCHIPPUS SKELETON

(U.S.N.M. no. 20087, associated, from Crooked River area)

(in millimeters)

AXIS	
Greatest length at centrum (approx.)	89.2
Transverse diameter across postzygapophyses	
Transverse diameter across neural canal (post.)	15.8
Transverse diameter across posterior centrum	29.5
Dorsoventral diameter across posterior centrum	22.8
Depth, dorsal crest of neural spine to base of centrum (greatest)	61.6
Anteroposterior diameter, right postzygapophyses	24.6
Transverse diameter, right postzygapophyses	18.3

THORACIC VERTEBRA 1	
Greatest length at centrum	43.6
Transverse diam. across prezygapophyses	57.8
Transverse diam. across postzygapophyses	37.7
Transverse diam. across neural canal	20.8
Anteroposterior diam. (extreme edges at zyg.)	50.4

LEFT METATARSAL III	
Greatest length	209.0
Anteroposterior diam. proximal	(26.3)
Transverse diam. proximal	
Anteroposterior diam. shaft (midpoint)	18.4
Transverse diam. shaft	20.1
Anteroposterior diam. distal	22.7
Transverse diam. distal	28.2

CERVICALS

	3	4	5	6	7
Greatest length at centrum	75.6	73.7	75.0	71.1	(54.5)
Tr. diam. across postzygapophysis	52.7			61.7	57.6
Tr. diam. right postzygapophysis					21.6
Tr. diam. left postzygaphophysis	18.7	19.8	20.2	21.7	20.8
Tr. diam. neural canal (post.)	17.0		17.5	17.3	23.6
Anteropost. diam. right prezygapophysis					24.6
Anteropost. diam. left prezygaphophysis	22.1	26.4		25.3	25.9
Tr. diam. right postzygapophysis	18.0		20.2	22.5	19.7
Tr. diam. left postzygapophysis	18.5		20.2	22.2	19.4
Anteropost. diam. right postzygapophysis	23.3	28.0		26.3	19.7
Tr. diam. left postzygapophysis	23.7		25.3	26.2	21.3
Anteropost. diam. ant. edge prezyg. to post. edge postzyg.	76.8	73.5	80.0	68.8	59.8
Tr. diam. centrum, posterior	29.3	29.7		28.1	27.3
Tr. diam. centrum, anterior	21.8		21.5	29.0	20.5
Dorsoventral diam. centrum, ant.	22.2	28.4	19.8	21.0	22.5
Dorsoventral diam. centrum, post.		20.0	27.2	25.7	26.7
Depth (least) at center of vertebra (incl. neural arch)	38.1	43.2			

Other elements from localities near the Mascall type area include: U.C.M.P. no. 40319, several fragments of upper teeth, loc. V-4942; partial upper molar no. 40329, loc. V-4946; no. 11631, including six lower teeth that may actually represent a small *Merychippus*, loc. ?, Mascall beds; no. 515, a broken upper tooth, no. 516 including a broken lower premolar and heavily worn upper, loc. 882; nos. 493 and 500, fragmentary lowers, loc. 884; no. 23094, a part of a heavily worn molar from loc. 3059; and no. 39296, an upper molar fragment, loc. V-4834.

From old loc. 903 (which might include V-4830–4835) there are several limb and foot elements and one large lower premolar. One tooth, no. 2021, seems high crowned for its state of wear, the styles are separate, but not extremely so; for this reason it is placed with *Merychippus*. It is possible that no. 2021 represents a Rattlesnake species, but it is not probable.

Several skeletal elements, donated by Phil Brogan, were collected at the Gateway locality V-3427. These include, under no. 32752, a femur; associated radius-ulna; distal metacarpals II, III, and IV; a proximal phalanx; and part of a pelvis. No. 34385 includes a very small distal metapodial (III) that may represent a small *Merychippus* or even *Parahippus;* also under this number the following elements are noted: a median phalanx, distal and proximal metapodials, two lateral phalanges, and a part of a vertebra. The femur (no. 32752) is smaller than *M. seversus,* A.M. no. 8175, and the radius is larger than *M. seversus* C.I.T. no. 2930 from the Gateway (see table 25). Metacarpal III and the proximal phalanx are larger in no. 32752 than in no. 2930. The median phalanx is larger than in no. 8175 and 2930. In the C.I.T. collections several skeletal elements are given the number 2929. Although locality data specify these bones came from one location, including the *M. seversus* (no. 2929) skull, there are instances of two right or left elements of the same type under this number (see table 25). Consequently specific skeletal parts of one individual cannot be assigned to skull no. 2929. None of the three skeletons from the Gateway (no. 32752 and two individuals of no. 2929) are similar in size, and could conceivably represent a part of the range of variation of skeletal parts of the species *M. seversus.*

U.C.M.P. no. 2027 Crooked River, old loc. 896, V-4950, is a low-crowned lower tooth that has widely separated stylids, very little cement, no internal or external cingulum, and no small cusp between the outer walls. It may be a milk tooth of *Merychippus,* but it is not exactly like others from the Mascall. It measures 16.4 mm. in height of crown at the metaconid. From this same locality there is a fragment of a maxillary no. 2026 containing a newly erupted M_3 that may be a small *Merychippus.* U.C. no. 39104, loc. V-4949, is a well-worn upper of *M.* sp. indet. category.

From old loc. 900 or V-4951, no. 2019, there is one-half of a lower milk tooth as large as teeth known to be *Merychippus seversus.* Also there is a partial upper molar (?) no. 40325, loc. V-4948 (old 895).

Merychippus sp., low crowned
(Fig. 35)

There is some evidence of the presence of teeth like the low-crowned *Merychippus brevidontus* in the Mascall. This is particularly notable in a tooth from the Crooked River area. U.C.M.P. no. 2077, loc. V-4949, a partial molar, has low height of crown (inside height of crown, at protocone, 10.4 mm.) with deep transverse grooving, a

TABLE 25

MEASUREMENTS OF SKELETAL MATERIAL OF MERYCHIPPUS SP. FROM GATEWAY ASSEMBLAGE
(in millimeters)

	C.I.T. 2929a		C.I.T. 2929b		U.C.M.P. 32752	U.C.M.P. 34385
	right	left	right	left		
Humerus						
Greatest distal ap.	47 2	46 6	44 0	43 7		
Greatest distal tr.	(44 0)	43 5	42 6	....		
Radius						
Greatest length	194 0	....	....	....	209 0	
Prox. tr.	47 0				39 9	
Tr. shaft (least)	23 3				23 8	
Ap. shaft (least)	14 7	....	....	....	15 3	....
Distal tr.	38 5	....	....	39 5	41 4	45 2
Metacarpal III						
Greatest length	141 0	....	....	140 0		....
Ap. prox.	19.7	....	....	19 5		....
Tr. prox.	....	....	....	23 0		....
Ap. shaft	(12 2)	....	....	13 4	....	....
Tr. shaft	17.4	....	....	17 8	....	....
Ap. dist.	18.7	....	....	18 3	....	....
Tr. dist.	22.5	....	....	24 6	....	....
Metacarpal II						
Greatest length	127 0	....	....	....		....
Ap. prox.	14 7	....	....	....		....
Ap. dist.	13 0	....	....	....	....	....
Least ap. shaft	7 4	....	....	....	....	....
Metacarpal IV						
Greatest length	125 0	....	....	126 0		....
Ap. prox.	10 0	....	....	12 0	....	....
Ap. dist.	13 7	....	....	....	....	....
Least ap. shaft	6.5	....	....	8 2		....
Scaphoid						
Prox. dist. diam.	18.5	....	....	18 7		....
Ap. diam.	24 2	....	....	23 7	....	....
Femur						
Length capitulum to edge of condyle	....	....	....	....	251 0	....
Distal width	....	....	....	....	(56 8)	....
Ap. across capitulum	....	....	....	....	32 0	....
Least tr. diam. shaft	....	....	....	....	24 0	....
Least ap. of shaft	....	....	....	....	30 0	....
Tibia						
Distal tr.	41 3	....	....	46 5		....
Distal ap.	26 9	....	....	35 2		....
Astragalus						
Ap. diam.	43 2	....	....	37 8	....	....
Tr. diam.	40 6	....	....	34 0	....	....
Tr. trochlea	18 9	....	....	15 3	....	....
Calcaneum						
Length, prox. dist.	71 2	....	....	72 0	....	....
Tr. diam.	30 0	....	....	31 3	....	....
Ap. diam.	31 5	....	....	38 3	....	....

TABLE 25—*Continued*

	C.I.T. 2929a		C.I.T. 2929b		U.C.M.P. 32752	U.C.M.P. 34385
	right	left	right	left		
Cuboid						
Prox. dist. diam	18.2	....	....	....	....	....
Ap. diam	26.6	....	....	....	....	....
Navicular						
Greatest tr	18.5	....	....	....	....	....
Least prox. dist	8.2	....	....	....	....	....
Ap. diam	23.3	....	....	....	....	....
Metatarsal III						
Length	154.0	....	....	....	....	....
Ap. prox	20.0	....	....	19.6	....	....
Tr. prox	23.7	....	....	24.7	....	....
Tr. shaft	17.5	....	....	....	....	....
Ap. dist. diam	19.4	....	....	....	....	....
Tr. dist. diam	22.0	....	....	....	....	....
Metatarsal II						
Greatest length	....	....	....	138.0	....	....
Prox. ap	15.3	....	....	....	....	....
Distal ap	....	....	....	14.7	....	....
Least ap. shaft	....	....	....	6.5	....	....
Metatarsal IV						
Greatest length	141.0	....	....	....	....	....
Prox. ap	18.8	....	....	....	....	....
Distal ap	(13.5)	....	....	....	....	....
Least ap. shaft	(6.8)	....	....	....	....	....
Vertebrae[a]						
Atlas:						
Tr. diam	26.2	....	....	....	....	....
Inside diam. neural arch	13.5	....	....	....	....	....
Cervicals:						
Greatest length at centrum	56.5	....	....	(57.0)	....	....
Tr. across neural arch (post.)	15.5	....	....	15.6	....	....
Tr. left prezygo	13.3	....	....	11.3	....	....
Dorso ventral diam. of centrum (ant.)	15.8	....	....	17.1	....	....
Dorso ventral diam. of centrum (post.)	21.2	....	....	....	....	....
Tr. post. zygo. (left)	....	....	....	12.0	....	....
Distal phalanx[a]						
Greatest length	43.0	....	....	....	....	....
Greatest tr	32.3	....	....	....	....	....
Greatest ap	44.5	....	....	....	....	....
Proximal phalanx[a]						
Greatest length	38.0	....	34.8	....	36.8	....
Distal tr	19.3	....	29.2	....	....	....
Median phalanx[a]						
Greatest length	27.5	....	....	....	....	29.8
Greatest tr	19.6	....	....	....	....	27.5

[a] Right or left not determined in this element.

prominent preprotoconal cusp, a long hypocone at an angle with the anteroposterior axis, and double pli caballin and pli protoconule. In addition, Y.P.M. no. 14243 from Grindstone Creek, Crooked River area, is a tooth possessing the following features: ectoloph of paracone and metacone tending to slant inward as in *M. brevidontus*, internal or anterior cingulum or cusp absent, protocone elongate with large spur, ribs absent, pli protoconule and pli caballin large, one anterior and one posterior metaloph plication, and cement heavy in fossettes and between cusps. The enamel pattern is much like *M. primus*.

Measurements.—Y.P.M. no. 14243, anteroposterior diameter at base 17.5, height of crown 16.4, and transverse diameter at base 17.9.

U.C.M.P. no. 39691 is a heavily worn left molar from V-4949, Crooked River area, and may represent another tooth like *M. brevidontus,* but retaining characters of *Parahippus* (possibly *P. avus*), particularly in the very narrow connection of the crochet to the metaloph.

Fig. 35. *Merychippus* sp., U.C.M.P. no. 14243, loc. Grindstone Creek, Crooked River area: left upper molar; × 1.

Merychippus ?
(Pl. 8)

Gidley (1906) refers U.C.M.P. specimen no. 1709, from old loc. 900 (V-4951), to *Archaeohippus ultimus* (Cope). These include, $I_{\bar{1}}$, $_{\bar{2}}$, and $_{\bar{3}}$ all of which could fall within the size range of *Merychippus* or at least a small *Merychippus.* The pits on the surface of the incisor are similar to known incisors of *Merychippus.*

From the type area region many skeletal elements have been found and are now stored in the University of California Museum: from loc. 3059, no. 29982, including two proximal and one median phalanges, a distal metapodial, possibly metatarsal IV, and a left navicular; no. 39306, a distal phalanx and two calcanea, loc. V-4832; no. 39312, including a part of a medium phalanx, two distal radii, and an astragalus, loc. V-4834; and no. 39318, a distal metapodial, loc. V-4835. From loc. V-4944 east of the type area, three elements were found including no. 40318 a left astragalus, left navicular, and part of an ulna.

From the Crooked River assemblage, old loc. 896, V-4950, there have been found several foot elements that are rather small for *Merychippus,* but in view of the presence of a small species of this genus in the Mascall, we may assume that the material could be *Merychippus.* A particularly interesting set of foot bones is no. 2048 (a median phalanx) and no. 1755 including metacarpals II, III, and IV, digit three, proximal, and distal phalanx, digit two proximal phalanx, digit IV proximal, and distal phalanx. All these elements fit as a possible associated foot where the respective articulating surfaces are present. Other elements from this locality and with this number are a right scaphoid, mangum, and a pisiform; left mangum, left lunar, left trapizoid and these elements of the manus articulate; left navicular;

left calcaneum; right metacarpal IV or left II; proximal, anterior thoracic rib; right and left astragali; right metacarpals III and IV; left radius, right and left distal tibia (see table 26). A magnum no. 40330 is from loc. V-4948.

There are many more foot elements that have been collected from V-4950 including phalanges, astragali, calcanea, naviculars, pisiforms, unciforms, metatarsals, and carpals. Their numbers are as follows: 37a, 1747, 1748, 1749, 1750, 2034, 2036, 2037, 2038, 2039, 2040, 2041, and 2042, 2047, 2051, 2053, 2054, 2056, 2057, 2058, and 2059, 2062, 2063, 2065, and 2067, 2079, 2082, 2085, 2086, and 2087. The total number of specimens included in the material listed above from this locality is 85 elements collected by a University of California party in 1900.

From old loc. no. 897 or V-4949, Mascall type area, there were several foot and limb elements taken; these include nos. 1431, 40334, 40335, 40336, 40337, 40338, and 40339. Other specimens include no. 2072, a distal ulna; no. 2031, a distal radius; no. 1678, an articulated left calcaneum and astragulus; no. 2030, a right navicular; no. 2031, a partial metapodial; no. 2073, a broken calcaneum; no. 2029, a distal metapodial; no. 2074, a distal left metatarsal IV; and nos. 1205 and 2075, median phalanges; no. 1204, two proximal phalanges.

Forty-one miscellaneous skeletal elements included in the University of California collection are from localities poorly designated, but may represent *Merychippus.*

Equidae gen. and sp. indet.

From loc. V-4834, U.C.M.P. no. 39316 includes two lateral median phalanges possibly the size of *Merychippus*, and from V-4823, fragments of a small lower tooth possibly like *Archaeohippus*, U.C.M.P. no. 40340. A distal lateral metapodial possibly equal in size to *Merychippus* was found at V-4829, U.C.M.P. no. 39112.

The articular part of a sacrum U.C.M.P. no. 1735, loc. V-4949, and very heavily worn lower tooth, U.C.M.P. no. 39881, represent a genus of Equidae.

Order ARTIODACTYLA

Family MERYCOIDODONTIDAE

Ticholeptus obliquidens (Cope)

Cope (1886, p. 359) described this species from Cottonwood Creek, Oregon. Additional identifiable material that can be assigned to this species has not been positively found in Mascall beds. Scharf (1935) designates a California Institute specimen (no. 1730) as the first record of *Ticholeptus* in the Mascall. He figures a jaw fragment with $P_{\overline{4}}$ and $M_{\overline{1}}$. This is not the first record because the type of *T. obliquidens* was described earlier. The record of no. 1730 does help substantiate the conclusion that *Ticholeptus* is found in the Mascall.

The type specimen was examined at the American Museum, and Cope's characterization is sufficient, but a few additions might be made: symphyseal suture 28.0 in dorsoventral diameter; masseteric fossa approximately 28.0 in anteroposterior diameter; metastylid of $M_{\overline{3}}$ not much longer than mesostylid or parastylid. (See table 27 for measurements.)

Schultz and Falkenbach (1941) believe that *T. obliquidens* may be a synonym of *Ticholeptus hypsodus* from Lower Snake Creek. The only difference I noted when the types were compared, was the lesser internal extension of the anterior crest on $P_{\overline{4}}$ of *P. obliquidens.* Since there is so little material representing both

TABLE 26

MEASUREMENTS OF SKELETAL PARTS, MERYCHIPPUS?, CROOKED RIVER AREA
U.C.M.P. no. 1755
(in millimeters)

	left	right
Metacarpal III		
Greatest length	133.0	135.0
Tr. prox. diam.	19.4	19.4
Ap. prox. diam.	16.5	16.1
Tr. distal diam.	21.5	21.4
Ap. distal diam.	14.4	...
Least tr. diam. shaft	15.2	...
Metacarpal II		
Greatest length	121.0	...
Ap. distal diam.	10.4	...
Ap. prox.	11.2	
Metacarpal IV		
Greatest length	...	119.0
Ap. distal diam.	...	11.0
Ap. prox.	...	10.0
Left distal tibia		
Tr. diam.	35.5	...
Ap. diam.	23.5	...
Astragalus		
Tr. diam.	31.3	29.3
Ap. diam.	30.9	31.8
Tr. trochlea	13.7	12.9
Lunar, left		
Ap. diam.	15.1	...
Cuneiform, left		
Ap. diam.	11.7	...
Radius		
Tr. distal diam.	31.5	33.2
Humerus, right distal		
Tr. diam.	...	35.9
Ap. diam.	...	33.3
Phalanx, proximal		
Greatest length	33.2	32.7
Tr. distal diam.	16.3	16.4
Calcaneum, left		
Ap. diam.	27.2	...
Scaphoid		
Ap. prox-dist.	15.3	15.1
Magnum, right		
Tr. diam.	...	17.5
Ap. diam.	...	18.5

species, it is rather difficult to judge whether the difference is due to individual variation or not; there is no basis for synonymy on present state of knowledge.

Thorpe (1937) has figured the type. This species is meagerly represented in the Mascall fauna. There are some uncertain records that might be attributed to the Mascall, but the evidence is not conclusive.

Ticholeptus ?

A part of an upper tooth, M^{2}?, U.C.M.P. no. 34386, loc. V-3427, the Gateway assemblage, is possibly assignable to *Ticholeptus*. The mesostyle is strong and larger than the metastyle. There is a moderately developed internal cingulum and well-developed posterior cingulum. Measurements: anteroposterior diameter 22.1, transverse diameter 18.3.

TABLE 27

Measurements of Ticholeptus obliquidens, Holotype

(in millimeters)

	Cope (1886)	Downs (1951)
Length of ramus at line of mental foramen	150.0	151.0
Length molar series (center at base)	96.0	55.6
Length premolar series	42.0	54.8
Length $P_{\overline{3}}$ (at crest, center)	12.5	13.4
Length $P_{\overline{4}}$ (at inner edge)	13.0	12.8
$M_{\overline{2}}$ anteroposterior diameter	16.5	16.3
$M_{\overline{2}}$ transverse diameter (greatest)	12.0	12.7
$M_{\overline{3}}$ anteroposterior diameter	25.0	26.0
Depth ramus at $P_{\overline{3}}$ (below center of tooth)	30.0	30.7
Depth ramus at $M_{\overline{1}}$ (below center of tooth)	....	30.0
Depth ramus at $M_{\overline{3}}$ (below center of tooth)	35.0	34.8

Oreodonta gen. and sp. indet.

An isolated P^{4}, U.C.M.P. no. 39298, loc. V-4834, measures 10.7 anteroposterior diameter and 13.4 transverse diameter. From Mascall beds not far from this locality, an astragalus was found, U.C.M.P. no. 39313. Measurements are anteroposterior diameter, 33.8 (approx.), transverse diameter 22.0 (approx.). An isolated premolar U.C.M.P. no. 35670 was taken at loc. ?, Mascall fauna. It measures anteroposterior diameter 8.0 and transverse diameter 6.6 mm. A possible $P_{\overline{2}}$, U.C.M.P. no. 39302, loc. V-4835, unworn tooth measures; anteroposterior diameter 10.2 and transverse diameter 5.3.

Family CAMELIDAE

Miolabis transmontanus (Cope)

The type. the only known specimen definitely referable to this species was collected by C. H. Sternberg at Cottonwood Creek in so-called Loup Fork beds and is A.M. no. 8196.* Cope (1879, p. 69) presents a detailed description. Other material may be referable to this species.

The teeth are heavily worn in the type; therefore the character of lower-crowned teeth in *Miolabis* as compared with *Protolabis* is not determinable (see Matthew, 1924). The figure of the type in Cope and Matthew (1915) is reasonably good, but some notations relative to the published illustration have been made with the type at hand. I^2 actually extends more anteriorly or horizontally, I^3 is a little large, should be near the size of I^2; from dorsal view, the nasals are incomplete with anterior, convex, dorsal surface, expanding posteriorly where present on right side; frontals incomplete, left mid-part present and with flat surface; mid-part of cranium flat, supratemporal ridges beginning on top of skull in line with post-

TABLE 28

MEASUREMENTS OF HOLOTYPE, MIOLABIS TRANSMONTANUS

(in millimeters)

	Cope's measurements no. 8196	Downs
Length dental series from base 1st incisor	257 0	
Length incisors (anteroposterior)	28 0	12 7
Space between 3d incisor and canine	6 0	5 6
Length, crown 3d incisor (inside height)	13 0	14 1
Length interval between canine and 1st pm	11 0	12 2
Length interval between P^1 and P^2	20 0	20 7
Length P^2-P^4 (ap.)	35.0	35 6
Length P– (ap.)	14 0	14 0
Width P^3 (greatest)	7	8
Length M^1-M^3 (at crest, external)	57 0	55 7
M^2 ap. diameter	18 0	. .
M^2 tr. diameter	18 0	18 5
M^3 ap. diameter	22 0	. . . .
M^3 tr. diameter	19 0	. . .
Width across nasals (least)	. . . .	19 1
Width between M^3 across palate	38 0	. . . .
Width skull between orbits	. . .	95 8
Diameter of orbit	. . .	42 8

orbital bar and meeting dorsally 51.0 mm. posterior to the bar; right side, much of orbit present, but without posterior part, maxillary and nasals less complete compared to left side. (See table 35 for original measurements with some added to those taken by Cope.)

Other faunas of comparable time seem to have few specimens adequate for comparison at present. This species and the camels in general were not as common in this fauna as were the horses. They may have possessed low-crowned teeth and were probably browsing animals.

Camelidae gen. and sp. indet.

In the material borrowed from the California Institute of Technology, there are two specimens representing camels. These were collected for that institution at the Mascall type area and at the Gateway area. C.I.T. no. 4003 is a fragmentary mandible with part of P_2, all of P_3, alveoli for P_4 and M_1, all of M_2, and a part of M_3. *Miolabis transmontanus* (Cope) has no associated mandible; therefore it is not advantageous to compare this material (no. 4003) with the type. No. 4003 is characterized by relatively short diastem from $P_{\bar{2}}$ to the symphysis and apparent alveolus of $P_{\bar{1}}$; $P_{\bar{2}}$ smaller than $P_{\bar{3}}$; and $P_{\bar{3}}$ compressed with small anterior cusp (shape much as in *Procamelus courtatus* Stirton). The specimen could be within the size range of (?) *Miolabis californicus* Maxson from Tick Canyon, Jahns (1940). The type of *Miolabis californicus* is smaller than *M. transmontanus*. Under the circumstances we cannot judge fairly whether the Tick Canyon specimen is smaller than *M. transmontanus* (see measurements, table 29).

TABLE 29

MEASUREMENTS OF CAMELIDAE FROM GATEWAY ASSEMBLAGE

(in millimeters)

MANDIBLE, C.I.T. NO. 4003	
Length ant. edge alveolus $P_{\bar{2}}$ to post. edge symphysis	16.7
Length alveolus $P_{\bar{2}}$	11.2
Length alveolus $P_{\bar{3}}$	10.8
Length crown $P_{\bar{3}}$ (greatest)	12.7
Length alveolus $P_{\bar{4}}$	12.2
Length alveolus $M_{\bar{1}}$	(14.5)
Length crown $M_{\bar{2}}$ (at crest)	20.4
Transverse width $P_{\bar{2}}$ (at crown)	4.7
Transverse width $P_{\bar{3}}$ (at crown)	5.5
Transverse width $P_{\bar{4}}$ (at alveolus)	6.0
Transverse width $M_{\bar{2}}$ (at base)	14.1
Depth ramus below ant. edge $P_{\bar{1}}$	25.3
MAXILLA, C.I.T. NO 4913	
Length M^{1-3} at crest	78.4
Length M^2 at crest	31.5
Length M^3 at crest	28.6
Width ant. column M^3	23.1

Another specimen C.I.T. no. 4913 from the Gateway assemblage includes a part of a maxilla with $M^{\underline{1}}$, $^{\underline{2}}$, and $^{\underline{3}}$. This specimen is moderately worn and larger than the type of *Miolabis transmontanus* (see table 29). It is so much larger than this species that it may be distinct, but there is a considerable variation in size in camels; therefore apparent greater size of such a fragment of a specimen may not be significant.

There are several foot elements and isolated teeth in the U.C.M.P. collections representing the camels. The foot elements may represent a species smaller than comparable elements in the Virgin Valley and in the Rattlesnake faunas. A lower molar, unworn, U.C.M.P. no. 29984, loc. ? from the Mascall, is characterized by reduced stylids, faint ribs on paraconid and metaconid, and strong anterior and weak posterior cingulum. Measurements: anteroposterior diameter 17.7, transverse diameter 12.3, height of crown at mesostyle 12.0.

A larger broken molar U.C.M.P. no. 39097, loc. V-4835, is suggestive of a fairly high-crowned tooth, possibly like that in *Protolabis*.

A cuneiform U.C.M.P. no. 40341, probably referable to camelidae, was taken at loc. V-4949. Also a navicular, no. 2068, V-4950, is referable to the camels.

Measurements.—U.C.M.P. loc. V-4949; no. 1739 left lunar, greatest proximodistal diameter, 25.0; no. 1732 astragalus, greatest proximodistal diameter, 37.6, greatest transverse diameter, 24.6; no. 2049 median phalanx, greatest proximodistal diameter, 34.5; no. 1734 metapodial, greatest distal transverse diameter, 23.2; no. 1733 proximal phalanx, greatest transverse diameter, 34.6, and no. 40341 cuneiform, greatest proximodistal diameter, 3.0.

Blastomerycini gen. and sp. indet.[13]

A fragmentary ramus with a heavily worn M_2 and $_3$, U.C.M.P. no. 39309, and isolated P^4 and M^1, no. 39310, were collected at locality V-3043 of the type area. The external surface of the teeth is crenulate and the teeth are probably brachyodont, especially the less worn upper. No. 39310 has a simple M^1 with a small pillar between the protocone and metaconule, a small anterior cingulum, and no crochet. P^4 is a simple crescent-shaped tooth with a prominent style and no anterior cingulum. No. 39309 is so worn that the presence of a *Palaeomeryx* fold is not determinable; the protostylid is present, and there is a complete loop on the posterior lobe of M_3.

Measurements.—Anteroposterior and transverse diameter respectively, U.C.M.P. no. 39310 P^4 5.8 and 6.7; M^1 7.3 and 8.4; U.C.M.P. no. 39309 M_2 ? and 6.4, M_3 13.7 and 6.2.

Yale Peabody Museum no. 14314* is a partial mandible with P_4, M_1 and $_2$ in place. This material represents the Palaeomerycidae (Stirton, 1944) and is characterized by open lingual flexids on P_4, mid- to basal part of protolophid on P_4 expanded, reduced mesostylids, *Paleomeryx* fold present, and teeth brachyodont.

Measurements.—Y.P.M. no. 14313; greatest anteroposterior and greatest transverse diameter respectively, P_4, 10.2 and 5.0; M_1, 11.7 and 8.3; and M_2, 12.4 and 9.1. This specimen is larger than the size trend in the Virgin Valley *Parablastomeryx mollis* (Merriam, *op. cit.*), but conceivably within the possible range of that species. U.C.M.P. no. 39309 is a smaller specimen, more like the size of the Virgin Valley material. The features as presented above show greatest affinity with *Parablastomeryx* on the basis of analysis of characters as set up by Stirton. The locality data attached to this specimen is uncertain; it specifies "Probably John Day River, Oregon. Down river from cove," but it is called Miocene-Mascall formation.

Another small specimen probably referable to this subfamily Blastomerycini is a lower molar in the U. S. National Museum collection, no. 7720. It is a slightly worn tooth with a *Palaeomeryx* fold, and with reduced stylids and moderate ribs on the paraconid and metaconid. The specimen measures anteroposterior diameter 13.8 and transverse diameter 10.5. This is another example of a large individual.

It would appear from the fragmentary evidence at hand that there is a species of *Parablastomeryx* represented in the Mascall fauna. Because of a tendency to greater size in the Mascall specimen as compared to the Virgin Valley, there is reason to believe that the Mascall specimens are advanced over the Virgin Valley material.

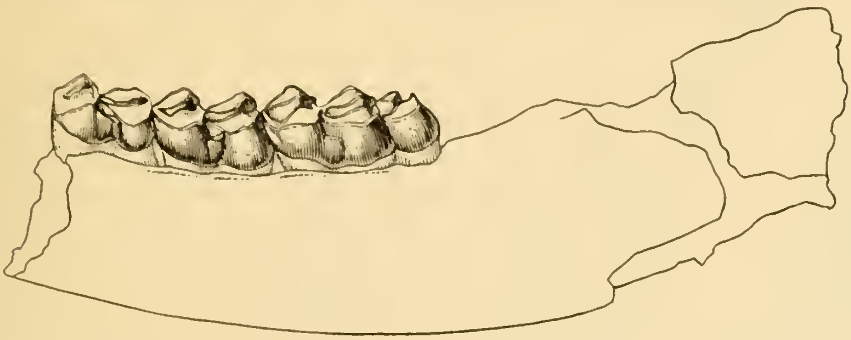
Dromomeryx borealis (Cope)
(Figs. 36–43)

Part of a cranium associated with some of the skeleton of this species had been collected by former University of California field parties (U.C.M.P. no. 1486). More material from the Mascall in the American Museum and National Museum collections was made available to me.

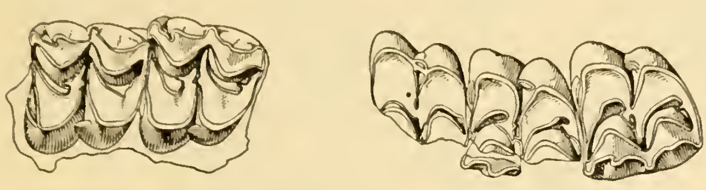
[13] R. A. Stirton informs me some *Blastomeryx*-like material was sent to the University of California Museum and thence to the American Museum, but has not been located since then.

Merriam and Sinclair (1907) listed the species as from a doubtful Mascall locality. According to Douglass (1909), Matthew had written to him that referred material from the Mascall was very close to *Blostomeryx* (= *Dromomeryx*) *borealis* (Cope).

It was noted at the National Museum that on several museum tags associated with *Dromomeryx* material, J. W. Gidley had apparently intended to name a new species from the Mascall although no description was published. Dr. D. H. Dunkle permitted me to search through all of Gidley's personal notes on file in the museum, but no manuscript was found either illustrating or describing these specimens.



a



b

Fig. 36. *Dromomeryx borealis* (Cope), U.C.M.P. no. 1486, loc. 3059: *a*, external view of mandible; *b*, upper dentition; × ¾.

Material and localities.—Mascall type area. U.C.M.P.: incomplete cranium including complete horns, posterior part of orbits, most of mid-part of frontals and anterior parietals, complete occipital condyle and basioccipital (restored off-center relative to axis of head owing to absence of most of squamosal and supraoccipital area on both sides of skull), left lateral anterior part of parietal and inner part of glenoid; incomplete left mandible including worn M_1–M_3 with approximately 70 mm. of dorsal part of ascending ramus; isolated M_1 and M_2 (undoubtedly of another individual since unworn) in partial mandible; left M^2 and M^3 and right M^1, ^{2}, and ^{3} moderately worn; atlas three-quarters complete and one-half of axis; proximal end of tibia; distal end of left tibia; left metatarsals III and IV; left astragalus; left and right radii; left and right distal humeri; proximal phalanx; fragments including parts of ulna, ? tibial shaft, skull, and several vertebrae, all no. 1486; unworn P^4 no. 29985; both numbers from loc. V-3059. Anterior part of left mandible with complete postsymphysial diastem, well-worn P_2, $_3$, $_4$ and M_1 and $_2$, parts of three lumbar vertebrae no. 39185; worn P^4 no. 39301, loc. V-4835. Unworn M_1, no. 39293, loc. V-4831. Poster half calcaneum and distal tibia, no. 39305, loc. V-4832. Worn lower cheek teeth in partial mandible, unworn P_3 and slightly worn P_2, fragments lower molar no. 39984; broken M^2 or M^3

TABLE 30

Measurements of the Skull and Mandible in Dromomeryx

(in millimeters)

	D. borealis Mascall			*D. borealis* Montana					*? Dromomeryx*	
	U.C.M.P. no. 1486	U.C.M.P. 39185	U.S.N.M. 5517	A.M. 8133	A.M. 8132	C.M. 3349	C.M. 817	C.M. 827	Virgin Valley U.C.M.P. 41001	High Rock Canyon U.C.M.P. 41044
SKULL AND HORNS										
Transverse width from external edge of flange on horns across top of skull	214.0	...	....	145.0	....	....	...	....		
Left horn length from posterior edge of orbit to tip of horn	230.0	....	..	....	...	..	...	....		
Same, right horn	237.0	....	...	....	....	....	...	...		
Width across frontals, in line with supraorbital foramen	110.0	....	....	84.0	...	....		97.0		
Anteroposterior diameter at base of horn	36.0	....	....	29.5	35.6	31.2		.	41.0	35.6
Least thickness basal flange of horn	10.0	....	.	5.7	9.5	.		.		
Transverse diameter 3 inches from top of orbit	34.6	...	.	....	...				36.5	35.7
Distance of supraorbital foramen from center of skull	25.0	.		.				27.3		
Greatest available diameter of orbit, left	48.2	.		45.0	.			.		
Same, right	47.5	...	..	....						
Diameter of supraorbital foramen	5.2	...	...	....	.			.		
Greatest outside transverse diameter of occipital condyle	56.5	.	.	55.0	56.5			...	..	.
Transverse diameter foramen magnum	22.7	...	...	27.2	26.0	....		....	...	
Diameter from internal base of horn to most external edge of basal flange	88.7	....	...	65.7	..	72.0	81.0	60.0	....	
MANDIBLE										
Depth below center M_2 outside	.	29.7	27.3	....						
Depth below center P_3 outside		29.6	26.2		.			29.2		
Depth below center P_4 outside		28.4						27.4		
Depth below center M_1 outside	26.5	30.3			.			29.8		
Depth beloff center M_2 outside	26.8	31.4						30.4		
Depth below heel M_3	28.5	.	30.1	.				31.3		
Length from posterior edge M_2 to posterior edge of alveolus of C	..	182.0	....		.					
Length from posterior edge of C to anterior edge P_2	.	94.7	..		..					
Thickness (transverse width) mandible under M_1	..	15.6	17.1		...			17.0	...	
Thickness (transverse width) mandible under M_2	.	16.4	18.3	.	..		....	18.5	....	
Thickness (transverse width) mandible under M_3	16.4	....	19.4	....	....	...	....	18.8	....	

no. 14412; worn M^2 no. 2205; well-worn P^4 and M^1 no. 1710, loc. ? Mascall. Navicular-cuboid no. 524; well-worn M^2 or ^{3} and fragment no. 540; distal metapodial no. 709; proximal phalanx no. 713, locs. 882, 885, and 886 all questionable localities but probably Mascall.

C.I.T.: nearly complete horn (right) with part of orbit and cranium no. 799, loc. 184, Mascall.

U.S.N.M.: heavily worn right P^3, M^3 no. 5515; heavily worn left P^2–M^3, right P^2–M^3, well-worn left P_3–M_1 and isolated M_3, proximal and distal ends of humeri, proximal end of radius, proximal end of ulna, proximal and distal end of femur, right and left distal ends of tibia, astragalus,

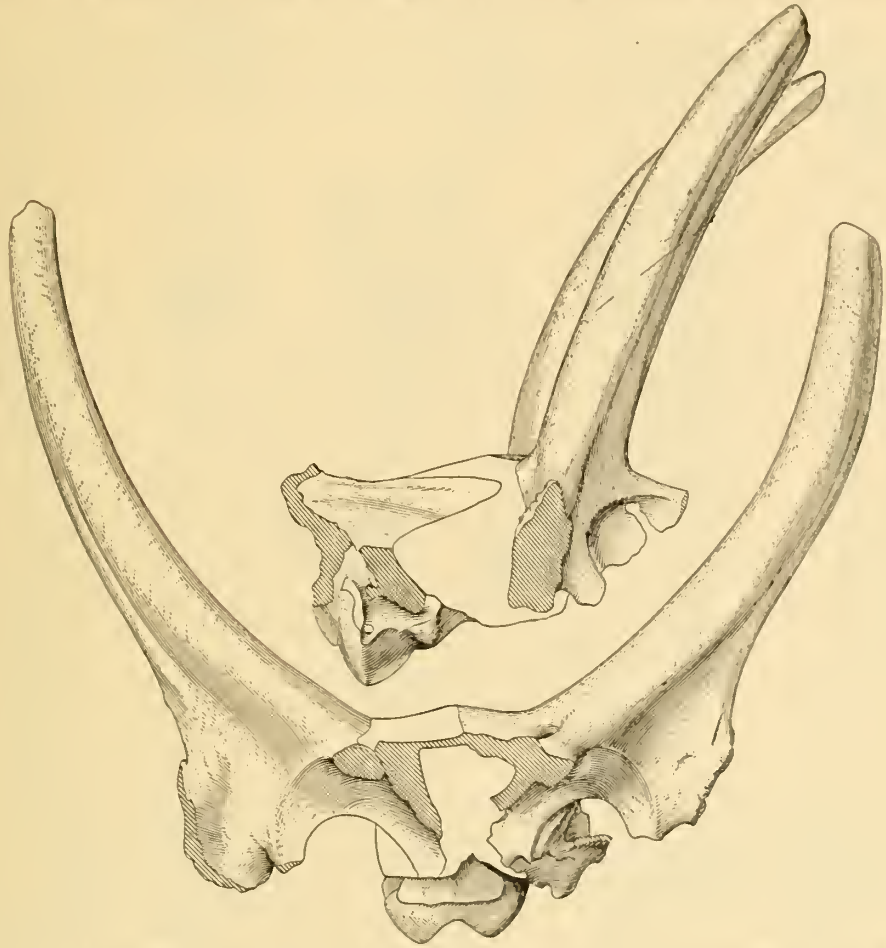


Fig. 37. *Dromomeryx borealis* (Cope), U.C.M.P. no. 1486, loc. 3059: top, right lateral view partial skull and horns; bottom, anterior view; × 1/3.

partial calcaneum, navicular-cuboid, and two proximal and two median phalanges, no. 5516; slightly worn I_1, $_2$, $_3$ and canine (?) associated, part of mandible with right P_2–M_3, distal end of tibia, upper part of shaft of tibia, metapodial, two proximal and one median phalanges, right and left calcanea no. 5517; loc. Cottonwood Creek, Grant County, Oregon.

A.M.: left M^{1-2} and right P^4–M^2, astragalus, distal end of tibia no. 8204; isolated M^1 and M^{1-2} no. 1486; loc. Cottonwood Creek, Oregon, Mascall beds.

Crooked River area U.C.M.P.: five complete astragali nos. 1721, 1722, 1723, 1725, 1724, loc. V-4950 (old, 896).

Description of U.C.M.P. no. 1486.—Postorbital horns: elongate, heavy, moderate grooving on most of surface with deep longitudinal anteroexternal groove, rounded at tip; base triangular, but oval in anteroposterior direction at center and tips; basal flange prominent behind orbits, concave anteriorily and directed perpendicular to longitudinal axis of skull; horns curve forward 10°–20° relative to dorsoventral axis, internal arc of horns, gradual from cranium to tip.

Cranium: occipital crest directed mostly posteriorly, orbit as large or larger than horn diameter; dorsal profile of cranium somewhat convex; supratemporal ridges low, beginning at postero-internal angle of horn converging to a minimum of 6.6 mm. from each other on cranial surface; supraorbital foramen circular and in line with anterior edge of horn; temporal ridge moderately heavy, descends prominently below flange of horn, a deep groove in lateral parietal, parallel and above temporal ridge; visible part of glenoid fossa narrow anteroposteriorly and somewhat deeply convex; basioccipital possibly broad, terminating posteriorly in heavy transverse ridge; foramen magnum with greater dorsoventral than transverse diameter and with ventral and dorsal notches broad; external auditory meatus oval in cross section with axis directed dorsoventrally.

Mandible: semioval in cross section below M_1, but tends to flatten medially, beginning of

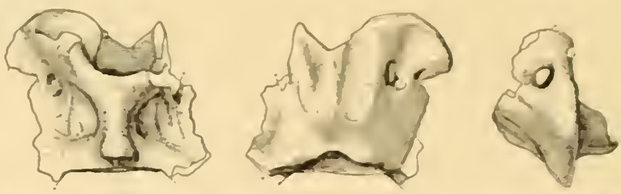


Fig. 38. *Dromomeryx borealis* (Cope), U.C.M.P. no. 1486, loc. 3059: left, ventral view of atlas; center, dorsal view of atlas; right, lateral view of axis; × 1/3.

Fig. 39. *Dromomeryx borealis* (Cope), U.C.M.P. no. 1486, loc. V-3059: *a*, distal humerus anterior view; *b*, distal view of tibia; × 1/3.

ascending ramus broad and flat on external surface and internally slightly convex; shallow groove with narrow median ridge on anterior surface of coronoid; shallow elongate depression on ventral internal surface below M_1 and $_2$. (See table 30 for measurements.)

Dentition: Brachyodont; upper cheek teeth wider than long, M^2 and M^3 with prominent mesostyle and well-developed parastyle; large rib on paracone, small on metacone; metastyle small; fold or cingulum on anterior side of protocone, crochet on external tip of protocone extending into prefossette; valleys between internal and external crests shallow or pinched at base. Lower cheek teeth with moderate wear, longer than wide, mesostylids moderately developed, faint indication of *Palaeomeryx* fold on molars; M_3 with posterior lobe large and bulbous externally, smaller internal crescents not forming complete loop until worn, prominent protostylid between protoconid and hypoconid on all molars. (See table 31 for measurements.)

Skeleton: Atlas with ventral arch deep and with rounded strong ridge ending anteriorly in broad tubercle and with deep concavity on each side of ridge; dorsal arch flat to slightly convex, shallow dorsoventrally; intervertebral foramen and alar foramen uniting as one dorsally.

Axis, with odontoid process extending nearly 20 mm. from face of flat articular surface, median ventral notch on articular surface broadly V-shaped, internal anteroposterior diameter of intervertebral foramen 8.1 mm.

Distal humerus with lateral condyle and angular ridge on surface, medial epicondyle robust and in line with longitudinal axis of shaft, median trochlear groove broad and deep, coronoid fossa wider than long and not deep, olecranon fossa deep and broad, distal shaft narrower anteriorly than posteriorly with external surface nearly flat.

Radius with ulna separate as splintlike bone in medial and distal region, grooves for extensor tendons 1 and 2 deep with long angular ridge separating them, also a ridge lateral to 2, ridge between 1 and 2 terminates in narrow groove, shaft generally compressed anteroposteriorly and curving broadly with convexity anterior, styloid process sharp extending below articular surface, facet for medial condyle of humerus broader and shallower than facet for lateral condyle.

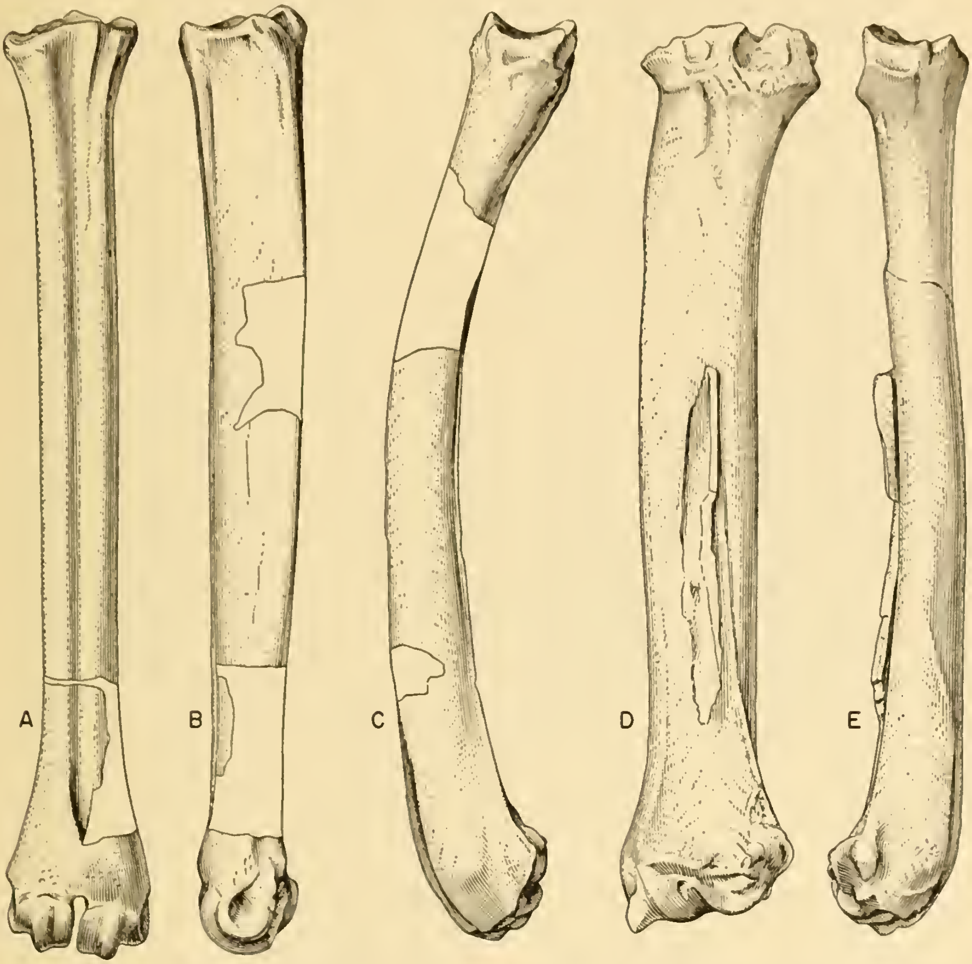


Fig. 40. *Dromomeryx borealis* (Cope). A–B: U.C.M.P. no. 1486, loc. 3059: anterior and lateral views of metatarsal; × ½. C: lateral view of radius, × ½. D–E: U.C.M.P. no. 66, loc. 3059: front and lateral views of radius; × ½.

Distal end of tibia with internal malleolus narrow and slightly longer than anterior median tubercle of articular facets, articular facets parallel and directed anteroposteriorly, external facet broader than internal facet; groove for flexor digitalis longus 9.4 mm. wide distally, moderately deep and smooth.

Metatarsal with external and internal face of median and proximal shaft flat, vascular groove deep for entire length of shaft except broader and shallower at proximal end, condylar ridges prominent and continuous over entire articular surface, posterior surface slightly concave throughout length of shaft.

TABLE 31

Measurements of Dentition in Dromomeryx borealis (Cope)

(in millimeters)

	U.C.M.P. no. 1486		U.S.N.M 5516	U.C.M.P. 39185	U.S.N.M. 5507	Holotype		C.M. 1542	C.M. 847	C.M. 827
	Right	Left				A.M. 8133	A.M. 8132			
MAXILLARY TEETH										
Anteroposterior diam. M¹ (at base)	....	....	17.0	....	....	20.4	....	18.8	(18.4)	16.0
Transverse diam. M¹	22.5	....	21.7	....	....	24.4	....	21.1	(19.6)	20.7
Ap. diam. M²	20.7	20.1	21.6	....	....	21.6	....	22.8		21.5
Tr. diam. M²	22.0	22.7	23.6	....	....	25.2	....	23.7	....	21.2
Ap. diam. M³	21.2	20.7	21.9	....	....	21.2	22.6	23.3	....	20.0
Tr. diam. M³	22.8	22.6	21.3	....	....	23.3	24.8	22.6	....	21.3
Ap. diam. P²	....	....	....	....	....	....	....	15.2	15.6	
Tr. diam. P²	....	....	....	....	....	....	....	12.4	14.4	
Ap. diam. P³	....	....	16.6	....	....	....	....	16.2	15.8	14.0
Tr. diam. P³	....	....	17.0	....	....	....	....	14.5	16.7	14.5
LOWERS										
Greatest ap. diam. P_2	....	....	....	11.9	12.2	....	....	....	....	
Greatest tr. diam. P_2	....	....	....	6.5	6.6	....	....	....	....	6.2
Greatest ap. diam. P_3	....	....	15.4	15.7	15.5	....	....	....	....	15.2
Greatest tr. diam. P_3	....	....	9.7	9.3	10.4	....	....	....	....	8.3
Greatest ap. diam. P_4	....	....	16.2	16.8	16.2	....	....	....	....	16.5
Greatest tr. diam. P_4	....	....	11.4	10.6	11.3	....	....	....	....	9.5
Greatest ap. diam. M_1	16.7	17.7	....	18.0	16.8	....	....	....	....	17.3
Greatest tr. diam. M_1	12.3	13.5	14.0	13.7	13.5	....	....	....	....	12.5
Greatest ap. diam. M_2	19.2	20.7	....	20.5	20.6	....	....	....	....	(20.0)
Greatest tr. diam. M_2	13.7	14.2	....	15.7	15.6	....	....	....	....	14.3
Greatest ap. diam. M_3	31.0	....	....	....	33.2	....	....	....	....	17.8
Greatest tr. diam. M_3	13.6	....	....	....	14.5	....	....	....	....	13.8

Astragalus longer than wide, no keel on distal facets, trochlea deep with nearly flat central surface, external tibial condyle twice as large as internal condyle, calcaneum facet broadly convex. (See table 32 for measurements.)

Description of additional Mascall material.—This is based on remaining specimens listed above. Only the salient features exclusive of those previously noted for no. 1486 are given. The discovery of a mandible with an entire diastem has contributed much to our knowledge of *D. borealis*. U.C.M.P. no. 39185 is an old individual with teeth heavily worn; mandible becomes much narrower dorsoventrally from M_1 anteriorly (see fig. 43), diastemal region transversely compressed and becomes narrower dorsoventrally near symphysis, diastem relatively long (45.0 mm.), internal ventral furrow deeper than in no. 1486; dentition from P_2–M_3 represented, premolars with lingual and slight posterior inflections, metaconid nearly closing fossetid on P_4, lingual expansion of protolophid of P_3.

C.I.T. no. 799, a nearly complete horn and a partial cranium (see fig. 43). U.S.N.M. no. 5516, P_3–M_1 as in no. 1486 but larger. Isolated M_3 partly worn but posterior lophid incomplete. Upper check tooth series on both sides with cerviform P^4 and with mesostyle, P^{2-3} tending to be elongate; other teeth as in no. 1486 (see fig. 42).

U.S.N.M. no. 5517 with mandible slightly thicker than in no. 1486 and no. 39185, but with similar proportions, diastem anterior to P_2 only partly present but shows definite tendency to taper as in no. 39185. Dentition as in no. 1486 or 39185 except M_3 with small accessory cuspule on posterior edge of third external lobe.

Frick (1937) presents an illustration of a mandible F. A.M. no. 31509 identified as *Dromomeryx whitfordi*, with an M_3 bearing a cuspule. Gazin (1932) figures an M^3 from the Skull Spring fauna C.I.T. no. 449 with a small lobe on the posterior side. None of the illustrations of specimens Frick (1937) designates as members of the family Cervidae show accessory cuspules on the upper or lower molars except no. 31509. This rare occurrence might be considered as evidence of a mutant character seldom appearing and apparently not established in the selection of consistent traits in any of these groups, at least in *Dromomeryx*.

The first known incisor and canine teeth ascribed to this species includes U.S. N.M. no. 5517. Since they were apparently found with other identifiable teeth it is probable they are from the lower jaw of *D. borealis*. No. 5517, I_{1-3} and C, which may be a complete set, is slightly worn on the tips; I_1 is the largest incisor with prominent longtitudinal ridge along medial curvature, and flat anterior and posterior surfaces, thickest at base anteroposteriorly, lateral edge angular with small longitudinal ridge; I_2 as in I_1 but relatively narrower; I_3 narrower anteriorly, otherwise as in I_1; canine incisiform and smallest of the set.

Measurements.—Greatest tranverse diameter, inner anteroposterior diameter, and anteroposterior thickness at base respectively: U.S.N.M. no. 5517, I_1 6.1, 9.2 and 6.1; I_2 6.0, 9.9 and 5.7; I_3, 4.4, 10.3 and 5.1; C 4.1, 9.7 and 5.2.

Most of these additional elements offer few differences from the material in the U.C.M.P. collection or from the Carnegie material from Montana.

The proximal end of an ulna U.S.N.M. no. 5516 is new to the Mascall. The specimen is sturdy, with a transversely compressed shaft and deep groove on the anteroproximal end. The tibia of the same number is more complete than the University of California specimen and reveals a deep groove for the flexor digitalis which continues proximally as a prominent ridge for more than one-half of the length of the shaft.

Comparisons.—Holotype of *Dromomeryx borealis* (Cope) A.M. nos. 8133* and 8132* (see Douglass, 1909). Includes parts of cranium and palates. Features were compared in detail, and a general similarity seemed probable though differences could be detected such as horns slimmer in proportion and less massive toward the base; styles and ribs on M^2 less prominent than on M^3. The specimens from New Chicago, Montana, referred to *D. borealis* by Douglass (*op. cit.*), show proportions of the horns much like *D. borealis* from the Mascall. It is believed that the range of variation in proportions are enough to include the type and the Mascall material under the one taxonomic unit, and the difference in size of the styles is negligible. The forward direction of the horns and perpendicular extension of the basal flange are probably diagnostic of the species.

Dromomeryx borealis (Cope)* from New Chicago, Montana, in Carnegie Museum. A description of this relatively complete skeleton is given by Douglass (*op. cit.*). Although the illustration (*op. cit.*, pl. LIX) shows the relative length of the diastem of the mandible, it was found on examination of the specimen that the length cannot be determined because of damage in the anterior area. It was also observed that much of the left horn has been reassembled, and some of it is missing. At a point where restoration was necessary, it is apparent that the exact position of the horn was not preserved; consequently, the posteroexternal direction of the basal flange seen in the figure is not a natural distinction from the Mascall material. In general the following conclusions were derived concerning the New Chicago specimens as compared with the Mascall: Cranium and mandible, U.C.M.P. no. 39185 displays diastemal region most accurately; mandibular curvature similar; same size range though New Chacoga specimens are slightly smaller. Skeleton, with ventral notch on articular surface of axis of variable size; sigmoid shape of radius exaggerated in C.M. no. 1542 (as in one of U.C.M.P. specimens), but other specimens show practically no sigmoid form; olecranon of ulna thicker transversely than in Mascall specimen, lateral condylar ridge of humerous more rounded than in the Mascall specimen. The general impression from an analysis of the Carnegie specimens is that sexual or individual variation could have played a considerable part in the development of slight differences noted in the bones from the same population.

Dromomeryx near *borealis* (Cope),* Skull Spring fauna, Oregon (Gazin, 1932). The material as described by Gazin is limited, but specimens have since been added (C.I.T. no. 1828), and are much like *D. borealis*. Gazin suggests that the horn core he describes is more robust and markedly curved with a forward concavity. As seen by me these variations are present in the type and referred material from Montana as well as in material from the Mascall. The additional cusp on M^2 in the Skull Spring specimen may be significant but this is doubtful. There is a suggestion of a deeper mandible in C.I.T. no. 1828 than that seen in Mascall specimens, but not deeper than that found in the Montana material. For the present, until a better horn is found, it seems most logical to refer the Skull Spring samples to *Dromomeryx* cf. *borealis* (Cope).

Dromomeryx borealis (Cope)* from Beatty Buttes, Oregon. Wallace (1946) describes a nearly complete skull with peculiar facial fossae or pits in the maxillaries (the areas not available for comparison in known material of *D. borealis*). The teeth are heavily worn and the horns are broken off near the base. It is probable, as Wallace notes, that this specimen is like *D. borealis* in its size and in its dentition. The horns may have been directed in a straighter line from the skull than in *D. borealis;* the facial fossae are peculiar to this specimen. Since this specimen is so similar to *D. borealis* from Montana and to the Mascall specimens in comparable parts, it also may be referable to *D. borealis.*

Virgin Valley Palaeomerycidae. Stirton (1944) has referred a horn, U.S.M.P. no. 11628,* to *Cranioceras* because of its vertical supraorbital horns. Some species

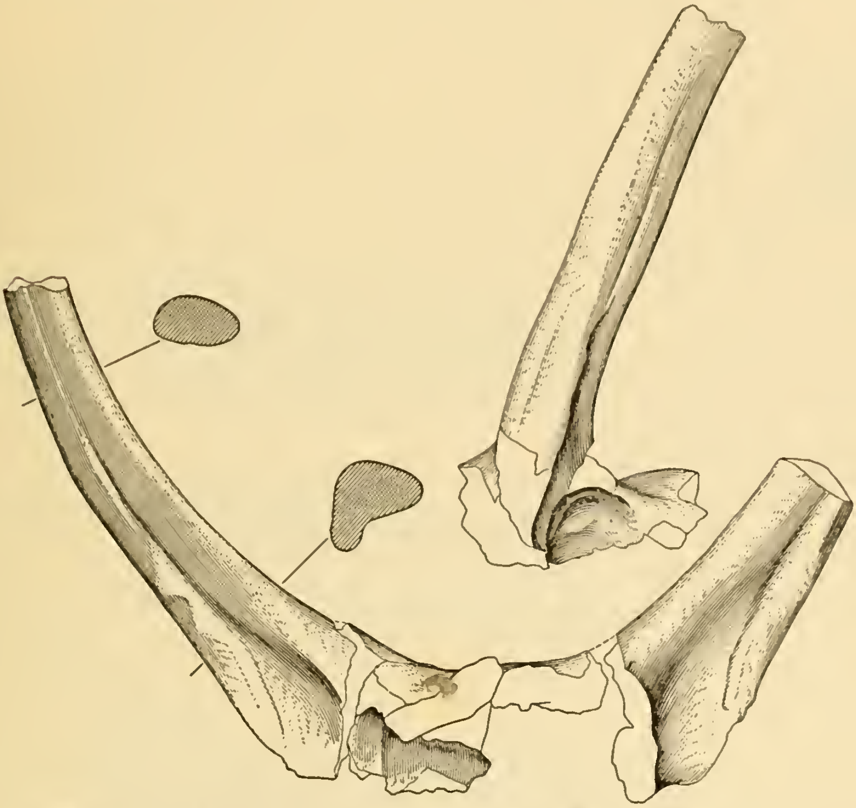


Fig. 41. *Dromomeryx borealis* (Cope), C.I.T. no. 799, loc. 184: bottom, anterior view partial cranium and horns; top, external view right horn, × ⅓.

of *Dromomeryx* have relatively straight supraorbital horns compared to *D. borealis,* for example *Dromomeryx antilopinus* Scott; but none of the species have the supraoccipital horn which Stirton (*op. cit.*, p. 640) shows is diagnostic of *Cranioceras.* The external basal part of the Virgin Valley supraorbital horn is missing. This horn (no. 11628) is straight at the base, more so than in species of *Dromomeryx,* and there is no anterior concavity at the base of the horn. As Stirton has noted (longhand note in U.C.M.P. tray containing the specimens), $P_{\overline{3}}$ and $_{\overline{4}}$ have a distinctive formation of the hypolophid as a posterior loop. Other teeth resemble *D. borealis* in pattern. Merriam (1911) considered most of the Virgin Valley material to be near *Dromomeryx.* No. 11628 is possibly distinct from the Mascall material and closer to *Cranioceras*. There are only a few identifiable elements of ? *Dromomeryx* from the High Rock Canyon fauna of Nevada, but collecting in 1951 resulted in recovery of a supraorbital horn core, U.C.M.P. no. 41044. The anterior basal surface is concave but the inner border is relatively straight. Generic designation of the horns from Virgin Valley (no. 11628 and no. 41001, see below) and no. 41044 from High Rock Canyon, is highly conjectural on available data. A recently acquired supraorbital horn (collected, 1951) from the Virgin Valley, U.C.M.P. no. 41001, is nearly identical in size and shape to the C.I.T. horn no. 799 which was collected from the Mascall. It is broadly curved at the base with shallow anterior concavity and probably referable to *Dromomeryx*.

Dromomeryx whitfordi Sinclair,* Lower Snake Creek, Nebraska. The younger mandible as indicated by the well-worn $dp_{\overline{2}}$, $_{\overline{3}}$, and $_{\overline{4}}$ in P.U. no. 12089, has a more slender and straighter form than the adult material from the same locality. Curvature in the mandible of Mascall specimens reflects individual variation. The Mascall and Snake Creek populations intergrade in characters of the mandible. The horn in *D. whitfordi* may be specifically distinct in smaller size; anteroposterior diameter at base 29.3 mm.; heavier, more angular flange; the internal profile much straighter since slope of horn is nearly straight to base; and a strong suggestion that horn ascends more directly from skull rather than curving forward as in *D. borealis*. The evidence for specific differences between *D. whitfordi* and *D. borealis* is not conclusive but on the basis of present knowledge, the two should be regarded as distinct species.

Dromomeryx pawniensis Frick from Pawnee Creek, Montana. I did not see the type, but it seems probable that this species is distinct from *D. borealis* in its smaller size and more perpendicular horns. It might be conspecific with *Dromomeryx antilopinus* Scott.

Dromomeryx antilopinus Scott* from Deep River, Montana. This is a small species of *Dromomeryx* and like other species of the genus is similar to *D. borealis* in its dentition. There is a valid difference from *D. borealis* in straighter, more slender horns that do not curve forward from the base of skull (they also ascend abruptly from top of skull in internal profile), and in the reduced basal flange compared to *D. borealis*. Scott has presented a detailed comparison of the skeleton of *D. antilopinus* with that of the deer. The skeleton of *D. borealis* is not different in any important features except possibly size. The more sigmoid shape of the radius was thought to be distinct in *D. antilopinus*, but it was found in this study that this character is present in varying degrees in *D. borealis*.

Dromomeryx americanus (Douglass) Madison Valley, Montana. This species is based on a mandible that is probably distinct in its small size from *D. borealis*. The presence of an inferior external groove along the ramus and a short protolophid on $P_{\overline{4}}$ may differentiate it from *D. borealis*. The type was not available, but on the basis of figures and descriptions it is possible that *D. americanus* is very like *D. antilopinus*. *Dromomeryx madisonius* (Douglass), a part of a mandible from Madison Valley, is probably as small as *D. americanus*. It is supposedly characterized by greater "hypsodonty," but this is more a matter of difference in wear than difference in true height of crown. It is also distinct (?) in its smaller protostylids. Both of these species, *D. americanus* and *D. madisonius*, are difficult

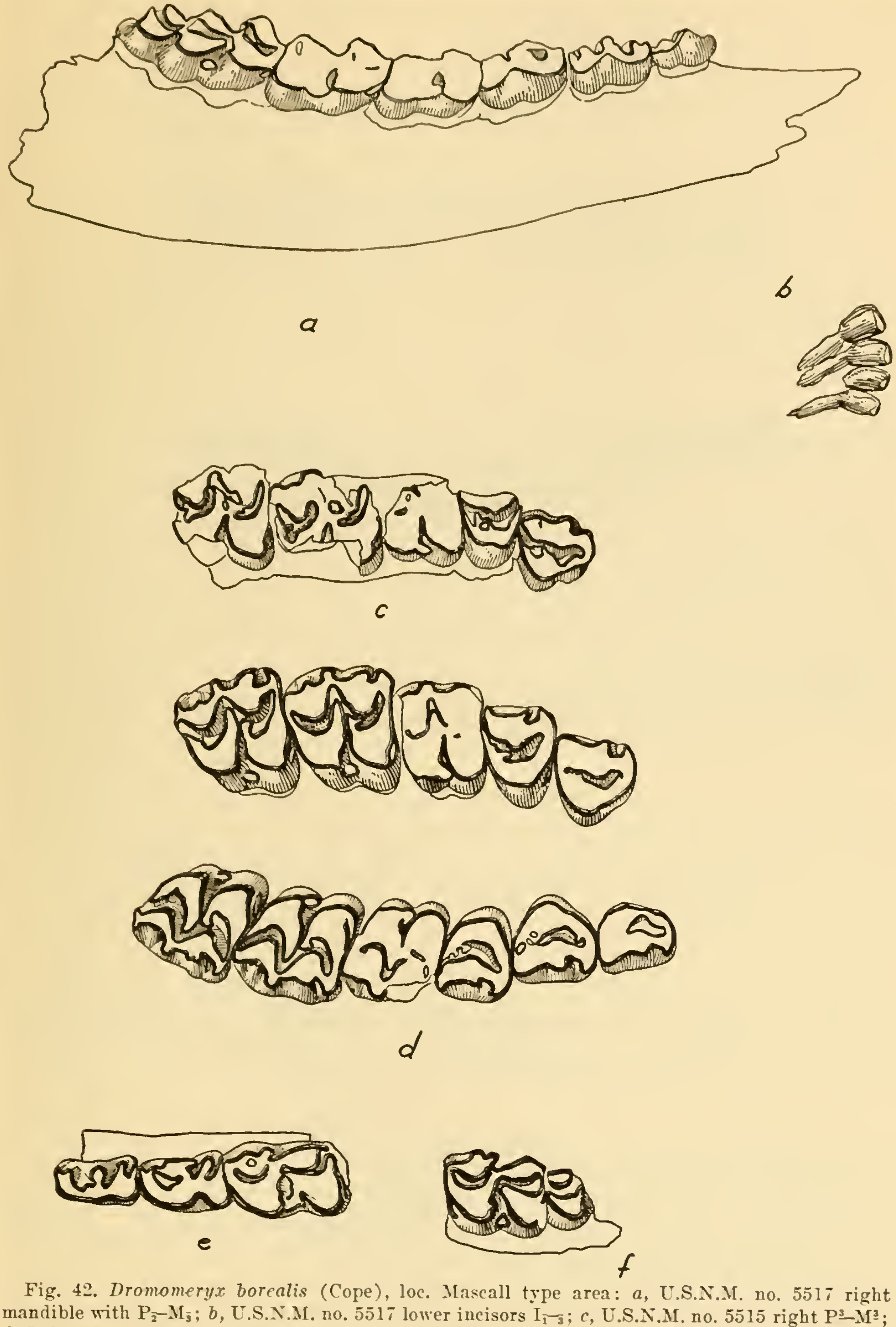


Fig. 42. *Dromomeryx borealis* (Cope), loc. Mascall type area: *a*, U.S.N.M. no. 5517 right mandible with $P_{\overline{2}}$–$M_{\overline{3}}$; *b*, U.S.N.M. no. 5517 lower incisors $I_{\overline{1}-\overline{3}}$; *c*, U.S.N.M. no. 5515 right P^3–M^3; *d*, U.S.N.M. no. 5516, right P^3–M^3 and left P^2–M^3 (not necessarily associated); *e*, U.S.N.M. no. 5516 left $P_{\overline{3}}$–$M_{\overline{1}}$ and *f*, isolated left $M_{\overline{3}}$. All occlusal view and × ¾.

to evaluate, and since neither type was seen it is not wise to propose a synonymy. It is believed, however, that *Dromomeryx antilopinus, americanus,* and *madisonius* represent closely related populations.

The subgenus *Subdromomeryx* Frick, including the species *S. scotti* and *wilsoni*, is distinct from *D. borealis* and possibly similar to *Barbouromeryx* in the slight

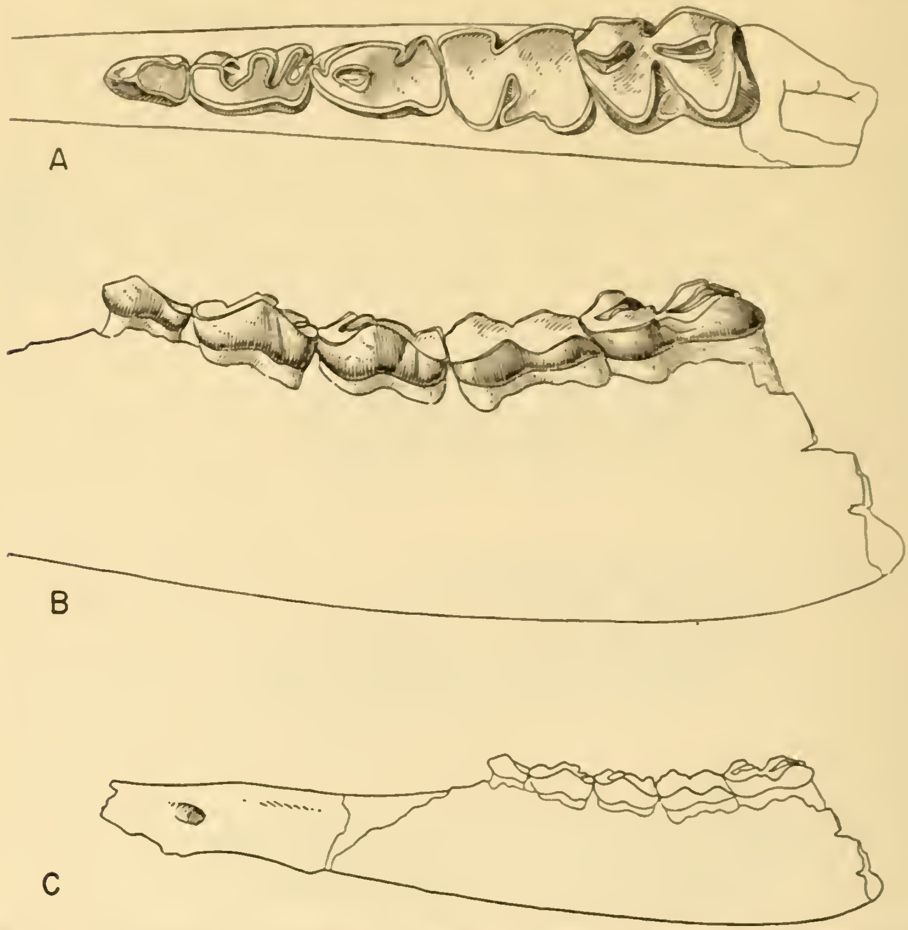


Fig. 43. *Dromomeryx borealis* (Cope), U.C.M.P. no. 39185, loc. V-4835: A: occlusal view P_2–M_3; × 1. B: Labial view, P_2–M_3; × 1. C: Labial outline of mandible, showing length of antepremolar diastem and depth of horizontal ramus; × ½.

development of basal flange on horn, absence of the *Palaeomeryx* fold, short diastem, and presence of upper tusk (see Stirton, 1944).

Discussion.—Compared to the status of species in *Merychippus*, the relationships of species of *Dromomeryx* are relatively tenuous. It is difficult to perceive any grouping of the species or their evolutionary tendencies. I have attempted here to summarize the evidence.

a. *Dromomeryx antilopinus* Scott: horns small, relatively straight, flange much reduced; smaller than b or c.

b. *Dromomeryx borealis* (Cope) possibly diagnostic in: horns large, strong, curve forward and with moderate flange perpendicular to skull; diastem long and slender; ramus moderately curved.

c. *Dromomeryx whitfordi* Sinclair: horns large, strong, relatively straight, heavy angular flange; other characters as above.

The other species, *D. americanus, madisonius,* and *pawniensis,* have been considered as probably like *D. antilopinus.* The tendency for larger and stronger horns in *D. borealis* and *whitfordi* compared to *D. antilopinus* suggests that the former are possibly advanced over the latter (also see chart in Stirton, 1944).

By comparing the characters in the Mascall specimens with tendencies in early and late genera as outlined by Stirton (*op. cit.*), we find in the Mascall species these advanced conditions: horns strong, well developed; cerviform P^4 with prominent mesostyle and slightly elongate P^2 and ^{3}; strong tendency for metaconid to close fossetid on $P_{\overline{4}}$, and $P_{\overline{2}}$ small; inner cusp of posterior lobe in $M_{\overline{3}}$ smaller than outer cusp; and moderate curvature of horizontal ramus.

These features in the Mascall specimens and others in the table (*op. cit.*) are indicative of advanced species in the genus *Dromomeryx. Dromomeryx* is apparently prominent in the middle and late Miocene. It seems very likely *D. borealis* is one of the latest representatives of the genus.

Palaeomeryx from Europe may be considerably removed from *D. borealis* of the Mascall in palmate horns, massive premolars, metaconid not developed, incomplete loop on posterior lobe of $M_{\overline{3}}$, relatively long diastem, and slight curvature of the ramus. As Stirton suggests, the relationship may extend back to an early common ancestor, but both evolved independently. *D. borealis* from the Mascall and some species of *Palaeomeryx* could have been contemporaries but on different continents. The rate and stage of evolution represented in the Mascall material cannot be determined accurately enough to allow correlation with the stage of evolution in the European genus.

Douglass (1909, p. 470) dealt with the restoration and the possible habitat of *D. borealis.* The evidence from new material reported in this paper does not greatly change this view but may add something to the picture. The size of the limbs and their proportions suggest a fairly stocky animal; the slim, elongate diastemal region of the mandible, moderate curvature of the ramus, and delicate incisors support the idea that the animal was primarily a browser. It may have been a good open country runner as Douglass points out; but the assets of well-developed horns, not necessarily long nor slender limbs, and large eyes could be beneficial in an environment of woodland and brush. The animal may have been the customary nocturnal browser and capable of protecting itself with its stout horns while feeding in at least partly forested areas.

Dromomeryx sp.

From loc. V-4949 (old 897) there are isolated elements probably belonging to the genus *Dromomeryx.* This material includes U.C.M.P. no. 40342, a broken astragalus; no. 1740, nearly complete small astragalus.

From loc. V-4950 (old 897) a median phalanx, no. 2052. This is a very small specimen compared to other *Dromomeryx* material but has a similar form.

At loc. 882 (a poorly documented locality) several isolated foot elements, U.C.M.P. no. 792, were collected including a pisiform; a broken and complete median phalanx; an articulating series of lunar, cuneiform, trapezoid-magnum, and unciform; and two fragments of vertebrae.

Dromomeryx ?

From loc. (?), U.C.M.P. no. 29984 Mascall fauna, there is an isolated $dp_{\overline{3}}$ or $_{\overline{4}}$ that seems to be large for a Blastomerycini mammal. The styles and ribs are very reduced, and there are three distinct crescentic cusps present.

From the Crooked River locality assemblage, V-4950 (old 896) a very small astragalus U.C.M.P. no. 1727 was collected. This bone has been thoroughly chewed by some creature on all the articular surfaces. It may have been a young animal.

Small Ruminant

A median phalanx, U.C.M.P. no. 39317, from V-4834, measures 15.5 mm. anteroposteriorly and 5.6 in. distal diameter. There are also two astragali, nos. 1726 and 1728, loc. V-4950 (old 896) one of which is badly defaced. The other measures 18.1 mm. anteroposteriorly and 11.2 mm. in transverse diameter. These may be the size of the Blastomerycini material.

U.C.M.P. no. 39113 may be a heavily worn deciduous premolar of a small ruminant.

U.C.M.P. no. 40333 is part of a small calcaneum from V-4834. It would seem likely that it may belong to the Blastomerycini.

ENVIRONMENTAL INTERPRETATIONS

Specific comments have been made relative to certain groups of animals as to possible correlation of form with habits and habitat preferences. It is important to note the possible interpretations of environments that may be derived from the Mascall flora as a unit. Chaney (1925, p. 47) compared the Mascall assemblage with the oak-madroña forest of the West. Since that publication, recent discoveries have brought to light a better understanding of the fossil flora. Chaney (1951) has revised the fossil *Sequoia* and *Taxodium* of western North America on the basis of new information on Recent *Metasequoia. Sequoia langsdorfi* from the Mascall is now known as *Metasequoia occidentalis. Taxodium dubium* is another plant well represented in the Mascall. The deciduous conifer *Metasequoia* inhabits what Chaney describes as summer-wet type of climate in interior China today. In the Columbia Plateau the Tertiary swamp cypress *Taxodium* ". . . is associated with other swamp and floodplain trees in deposits, frequently diatomaceous, which are of a lacustrine type. The volcanic events of the Miocene in this area appear to have produced a terraine which was especially suited to *Taxodium*, long since restricted (*T. distichum*) to the eastern United States with its best development southward" (*op. cit.*, p. 234).

The first specimens I collected in the type Mascall beds were fossil "seeds" of *Celtis*, found in small blocks of tuff from the buff-tuff horizon (unit 16) of the section. There is no previous record of the collection of *Celtis* nutlets from this horizon. Chaney (1925) has not listed the hackberry in the Mascall flora, but he has informed me that in the forthcoming revision with D. I. Axelrod, leaves of the hackberry will be discussed as part of the flora from Van Horn's Ranch, sixteen miles east of the mammal beds. As many as sixty whole and half nutlets have been collected at the type area with some isolated "seeds," but more often they are in close clusters. Nutlets were found at every locality bearing mammal remains in the Mascall type area. At V-4948 (old 895) in the Crooked River region, one nutlet was found; at the Gateway locality there was evidence for their presence.

According to Chaney (1925) and Bailey (1936) *Celtis douglassi* is found today along streams and rivers of eastern Oregon. Chaney has described a fossil species from the Bridge Creek flora including leaves, which suggest that the fossil plants were more like those in existence in western Washington today. Leaves were not found in the Mascall mammal horizon.

The causes for death of the mammals preserved in the Mascall deposits were probably from natural predation or accidents in some cases, but the effects of ash-dust storms and volcanic gases on the respiratory systems of the animals and their food sources may have caused more animals to die than would have done so normally. The concentration of bones in the buff-tuff horizon seems to support this idea.

The approximate order of dominance of animal life as represented by the fossils in the Mascall fauna is as follows: *Merychippus seversus* (by far the most abundant), *Dromomeryx borealis, Parahippus avus, Archaeohippus ultimus, Tomarctus rurestris,* Rodents, Lagomorphs, Camels, Oreodonts, and others (see faunal list).

The ecologic relationships of the plants and animals in the Mascall is not readily determinable in most instances since so many of the animals are now extinct. The larger horses with higher-crowned teeth must have been capable of eating grass on the uplands. The smaller horses and artiodactyls could have been browsers in the protective forest areas; this may have been true of the large *Dromomeryx borealis* although it is possible that this species inhabitated both forested and open country. The abundance of small and large perissodactyls and artiodactyls would be an excellent source of food for predaceous carnivores such as *Tomarctus* and *Amphicyon.* At some localities and especially V-4951, many elements of equids and paleomerycids were thoroughly gnawed or chewed by some type of animal, possibly *Tomarctus, Amphicyon,* or some rodents. (See U.C.M.P. no. 40343.) The rodents might represent forms that were dependent on meadow grass.

As a general summary of the available evidence the following outline is presented:

Probable Environment of the Mascall Fauna and Flora

Valley and near-by uplands. Evidence
- Geologic: synclinal structure, wind-blown pockets and continuous strata.
- Biologic: grass-eating mammals (dominance of *Merychippus seversus*), hackberry nutlets.

Small lakes, streams, flood-plain or even swamp areas. Evidence
- Geologic: water-laid deposits, laterally continuous strata, bog deposits, diatomaceous deposits.
- Biologic: position of preserved material, swamp-dwelling and moisture-requiring plants, lacustrine gastropods, fresh-water fish.

Wooded areas in the valley at least, and grasses on probable uplands or meadows. Evidence
- Biologic: the Mascall flora deposited in lacustrine sediments but presence of hackberry nutlets with the mammal remains, and the great dominance of *Merychippus seversus.*

TABLE 32

MEASUREMENTS OF SKELETON, DROMOMERYX BOREALIS, U.C.M.P. no. 1486
(in millimeters)

Radius, left		
Greatest length	242.0	
Transverse diam., distal	43.3	
Anteroposterior diam., distal	30.0	
Transverse diam., proximal	37.5	
Anteroposterior diam., proximal	26.2	
Greatest transverse diam., shaft	29.1	
Greatest anteroposterior diam., shaft	18.4	
Least transverse diam., shaft	23.8	
Least anteroposterior diam., shaft	16.5	
Metapodial, left metatarsus III and IV		
Greatest length	248.0	
Transverse diameter, distal	37.7	
Anteroposterior diameter, distal	25.8	
Transverse diameter, proximal	35.0	
Anteroposterior diameter, proximal	34.2	
Least anteroposterior diam., shaft	18.5	
Least transverse diam., shaft	20.0	
Humerus, left		
Greatest transverse diam., distal	51.5	
Greatest anteroposterior diam., distal	45.4	
Humerus, right		
Greatest transverse diam., distal		51.3
Greatest anteroposterior diam., distal		46.9
Tibia, left distal		
Transverse diameter	43.3	
Anteroposterior diameter	31.9	
Tibia, proximal		
Transverse diameter	69.1	
Atlas		
Anteroposterior diameter through dorsal arch		38.2
Anteroposterior diameter through centrum		37.3
Dorsoventral diam., occipital condylar facet		32.5
Internal diam., neural canal		27.1
Axis		
Greatest transverse diameter, proximal		63.4
Internal transverse diameter, neural canal		25.7
Astragalus		
Greatest length		46.5
Greatest width		31.5
Proximal phalanx		
Distal width		14.8

Compared to the Recent faunal and floral relationships of east central Oregon, the Mascall presented a different ecologic situation. Bailey's (1936) study on the mammals and life zones of Oregon shows that all the areas in which Mascall assemblages are found are characterized today by semiarid and arid faunas. The mammals found in the Mascall fauna do not in themselves indicate that more humid conditions were present at that time; however, the combined evidence from geology, paleobotany, and mammalian paleontology demonstrates the contrast between the past (Mascall) and the present.

CORRELATION AND AGE OF THE MASCALL FAUNA

The Mascall fauna existed within Hemingfordian (middle Miocene) and Barstovian (late Miocene) time. Two of the genera may be restricted to Barstovian (*Arctomyoides* and *Mylagaulus*); if evidence presented here is accepted, they may extend into the Hemingfordian or at least the Hemingfordian-Barstovian transition. Two genera, *Miolabis* and *Dromomeryx*, are as early as Hemingfordian in chronologic range, but *Miolabis transmontanus* is so little known, particularly in its relationships to other camels, that species of the genus are not particularly significant in this discussion. *Dromomeryx* may be present in the Barstow fauna

TABLE 33

Chronologic Range of Significant Mascall Genera in North America

Provincial age (Mascall genera)	Arikareean (early Miocene)	Hemingfordian (middle Miocene)	Barstovian (late Miocene)	Clarendonian (early Pliocene)	Later
Tomarctus		———	———	———	
Amphicyon		———	———		
Hypolagus		———	———	———	———
Mylagaulus		- - -	———	———	
Arctomyoides		- - -	———		
Peridiomys		———	———		
Archaeohippus	———	———	———		
Parahippus	———	———	———		
Merychippus		———	———	- - -	
Ticholeptus		———	———		
Miolabis		———			
Dromomeryx		———	— ? - - -		

Dotted lines, extension of ranges based on this paper and other authors. Solid lines, after Simpson (1945).

(Merriam, 1919); but the lack of *Palaeomeryx* fold in the Barstow specimen casts doubt on its affinity, as Merriam suggests. The lower Snake Creek of Nebraska has an apparently valid species in the occurrence of *Dromomeryx whitfordi* Sinclair. Except for smaller size this species is just as "advanced" as the Mascall material. It is not possible to depend on the range of genera to decide on a more precise age for the Mascall; other evidence must be taken into account.

The greatest degree of refinement from a vertebrate paleontological viewpoint can be achieved in comparison of critical species of Great Basin and Pacific Coast faunas. Consideration will be given those faunas containing significant species, or faunas with comparably representative material.

Table 34 gives a listing of occurrences of selected species[14] in the various faunas, including a complete list of species in the Mascall. The Skull Spring fauna is probably of similar age if consideration is given the resemblances of critical species. From the viewpoint of ecology it has more variety in genera and species than the Mascall; perhaps there were barriers preventing complete mixture of populations. The apparent general similarity to the Mascall is evidenced by the presence of

[14] The terminology of taxonomic category follows either the original author or that proposed by me in the systematic discussion.

Tomarctus cf. *rurestris*, *Amphicyon* cf. *sinapius*, *Mylagaulus* cf. *laevis*, *Peridiomys oregonensis*, *Dromomeryx borealis*, and *Merychippus seversus*. The common occurrence in the Virgin Valley and Skull Spring faunas of *Liodontia*, *M.* cf. *brevidontus*, chalicotheres, rhinoceroses, and *Merycodus* and their absence in the Mascall suggest a possible close chronologic and faunal resemblance between the Virgin Valley and the Skull Spring; yet the evolutionary stage of development in these animals from the two faunas is not readily determinable. The horses from the Skull Spring give the best criterion for judgment of the stage of evolution. I could find no satisfactory basis for considering *M. seversus* in the Skull Spring to be distinct from the Mascall form. The specimens of *M.* cf. *brevidontus* are very large and probably more advanced than those found in the Virgin Valley.

Liodontia, which is present in the Virgin Valley and Skull Spring, may have been excluded from the Mascall because of environmental restrictions. Further collecting may prove the definite presence of *M. brevidontus* type animals in the Mascall. If so, it will certainly add support to the idea of close affinity among the three faunas.

The Beatty Buttes fauna of Oregon shows a general resemblance to the Mascall in the presence of *Mylagaulus* cf. *laevis*, *Periodiomys* sp., *Archoeohippus* cf. *ultimus*, and *Parahippus* cf. *avus*. *Archaeohippus* cf. *ultimus* is believed by Wallace to be near *A. mourningi* in size of hypostyle and lack of cement, but it is equal to *A. ultimus* in size, and there seems to be an internal cingulum present in the figure which leads me to think it may be like *A. ultimus*. The specimen of *P.* cf. *avus* is too fragmentary for positive identification, but the features that are present in the lower cheek teeth fall within the variation seen in the Mascall specimens. The occurrence of *M. seversus* and *D. borealis* in the two faunas is significant.

The Sucker Creek fauna resembles the Mascall in the presence of *Mylagaulus* cf. *laevis*, *P. avus*, and *M. seversus*, but the records of *M. brevidontus* and supposed *Moropus* confuse the situation. Readily identifiable material representing *Moropus* in North America is confined to early and middle Miocene faunas (Simpson, 1945). The single tooth reported in this fauna is fairly well worn, and it is possible it represents a molariform deciduous P^3 or P^4 such as described in *Moropus petersoni* by Holland and Peterson (1914). The reliability of generic identification by a single tooth is questionable; possibly the Sucker Creek specimen represents *Macrotherium* known in later Miocene faunas, but it is considered best to designate the tooth as Chalicotheriidae sp. indet. As stated previously, the specimens of *M. brevidontus* are very similar to those from North Coalinga. The presenee of typical *M. brevidontus* might suggest that the Sucker Creek fauna is younger than the Mascall, but at present its stratigraphic position is considered questionable.

The Virgin Valley has been judged equivalent to the Mascall (Gazin, 1932) or older than the Mascall (Stirton, 1937). Critical species are not well represented in the Virgin Valley fauna, but the available comparable material is not believed to differ greatly from the Mascall. *Cynodesmus kelloggi* is probably an earlier canid than *Tomarctus rurestris*, and *Mylagaulus pristinus* may be less advanced than Mascall forms of *Mylagaulus*. There is no absolute assurance of the presence of *Dromomeryx borealis* in the Virgin Valley, but the one horn core collected is a good indication of it. The Blastomeryeini may reveal a more primitive condition

TABLE 34

SELECTED COMPARATIVE FAUNAL LISTS[a]

	Mascall	Skull Spring	Beatty Buttes	Virgin Valley	Sucker Creek	Stewart Spring	High Rock Canyon	North Coalinga
Hypolagus vetus	..	..	..	×	..	..	..	..
Hypolagus cf. *vetus*	×	..	..	..	..	..	..	..
Liodontia alexandrae	..	×	..	×	..	..	..	..
Liodontia cf. *alexandrae*	..	..	×	..	..	..	..	..
Liodontia sp.	..	..	..	..	..	×	..	..
Mylagaulus pristinus	..	..	..	×	..	..	..	..
Mylagaulus cf. *laevis*	..	×	×	..	×	..	..	..
Mylagaulus sp.	×	..	..	..	..	×	..	..
Mylagaulus ?	..	..	..	..	..	..	×	..
Prodopodomys ? *mascallensis*	×	..	..	..	..	..	..	..
Peridiomys oregonensis	..	×	..	..	..	..	..	..
Peridiomys cf. *oregonensis*	×	..	..	..	..	..	..	..
Peridiomys sp.	..	..	×?	..	..	..	..	..
Arctomyoides oregonensis	×	..	..	..	..	..	..	..
Tomarctus rurestris	×	..	..	..	..	..	..	..
Tomarctus cf. *rurestris*	..	×	..	..	..	..	..	..
Tomarctus sp.	..	..	..	..	..	..	×	×
Cynodesmus kelloggi	..	..	..	×	..	..	..	..
Cynodesmus cf. *kelloggi*	..	..	..	..	..	×	..	..
Amphicyon sinpius	..	×	..	..	..	..	..	..
Amphicyon cf. *sinapius*	×	..	..	..	..	..	..	..
Amphicyon sp.	..	..	..	..	..	..	..	×
Miomastodon merriami	..	..	..	×	..	..	..	..
Mastodont	..	..	..	..	×	..	..	×
Parahippus avus	×	..	..	..	×	..	×	×
Parahippus cf. *avus*	..	..	×	×	..	..	..	..
Hypohippus cf. *osborni*	..	..	..	×	..	×	..	..
Hypohippus near *osborni*	..	..	×	..	×	..	..	..
Hypohippus sp.	..	×	..	..	..	..	×	×
cf. *Hypohippus*	×	..	..	..	..	..	..	..
Archaeohippus ultimus	×	..	..	..	..	..	..	..
Archaeohippus cf. *ultimus*	..	..	×	..	..	..	..	..
Archaeohippus mourningi	..	..	..	..	..	..	..	×
Merychippus relictus	×	..	..	..	..	..	..	..
Merychippus brevidontus	..	..	..	..	×	..	..	×
Merychippus cf. *brevidontus*	..	×	..	×	..	×	×	..
Merychippus seversus	×	×	×	×	×	..	..	..
Merychippus cf. *seversus*	..	..	..	..	..	×	..	..
Merychippus californicus	..	..	..	..	..	..	×	×
Chalicotheriidae	..	×	..	×	×	×	×	..
Rhinocerotidae	..	×	..	..	×	..	..	×
Aphelops	..	..	×	×	..	..	×	..
Ticholeptus obliquidens	×	..	..	..	..	..	..	..
Ticholeptus sp.	..	×	..	..	×	..	..	..
Miolabis transmontanus	×	..	..	..	..	..	..	×?
Dromomeryx borealis	×	..	×	..	..	..	..	..
Dromomeryx cf. *borealis*	..	×	..	..	..	..	..	..
Dromomeryx ? *borealis*	..	..	..	×	..	..	×	..
Dromomeryx near *borealis*	..	..	..	..	×	..	..	..
Cranioceras	..	..	..	?	..	..	..	..
Merycodus nevadensis	..	..	..	..	..	×	×	..
Merycodus cf. *nevadensis*	..	..	..	..	×	..	..	..
Merycodus sp.	..	×?	×?	×	..	..	..	..
Blastomeryx	..	×?	..	..	..	..	..	..
Parablastomeryx mollis	..	..	..	×	..	..	×	..
Blastomerycini	×	..	..	..	..	..	..	..

[a] The Mascall faunal list is complete but the other faunal list includes only groups pertinent for comparison with the Mascall.

than found in those from the Mascall. The teeth of *Parahippus avus* are similar to the lowers as now known in the Mascall. *M.* cf. *brevidontus* is a simple tooth but some specimens are as large as those found in the North Coalinga. *M. seversus* in the Virgin Valley does not appear to be significantly distinct from the Mascall *M. seversus.* The Virgin Valley is particularly distinct from the Mascall in the presence of a well-represented *Miomastodon merriamii* (Osborn) and in the presence of several specimens of *Aphelops* and a greater proportion of *Hypohippus.* The character of the Chalicothere material suggests middle Miocene relationship. There is undoubtedly a very close chronologic relationship between the Mascall and the Virgin Valley, but on the basis of the combined evidence from the known genera and species, the Virgin Valley may be considered slightly older than the Mascall.

Rhinoceroses are actually little known in the Skull Spring and Beatty Buttes faunas and are yet to be found in the Mascall. *Merycodus* has a chronologic range, from the Hemingfordian on into the Pliocene. *Dromomeryx* is well represented in the Mascall and possibly could have been the dominant artiodactyl in that particular fauna. The grazing and browsing horses are fairly well represented; the two general sources of food, grassland and forest or semiforest, may have been occupied in that region by the horses, *Dromomeryx*, and the camel in the Mascall. It is surprising that no record of *Archaeohippus* is present in the Skull Spring and, as Gazin has pointed out, rodents are dominant in the Skull Spring whereas grazing animals are poorly represented. The apparent differences in faunal content in at least the Mascall and Skull Spring may reflect ecologic instead of chronologic distinctions.

It is apparent that the three faunas, the Virgin Valley, the Skull Spring, and the Mascall are very close faunistically and chronologically. No positive chronologic distinction can be made, but it is suggested that the Virgin Valley is slightly older than either the Skull Spring or Mascall, and the Skull Spring may be intermediate between the two. To me the resemblance in these faunas is as significant as the differences so far as time designation is concerned. Geologically speaking it may be more reasonable to state that all three faunas must be considered as representing a part of one general period of time, the transition between late Hemingfordian and early Barstovian.

The Stewart Spring is a small Nevada fauna that shows resemblance to the Virgin Valley. The canid species can be compared with *C. kelloggi;* it is my belief that the lower-crowned *Merychippus* teeth may be compared with *M. brevidontus.* They are not as complex in enamel pattern as in the type specimens but retain other similar features seen in the Virgin Valley teeth. An M^2 of a larger *Merychippus* may be compared with *M. seversus* and probably is related to that species; more specimens would assist considerably in deciding the relationships.

The High Rock Canyon fauna of Nevada is probably younger than the Mascall and older than the North Coalinga. It was mentioned previously that there are teeth similar to *T. rurestris* in this fauna, but there are also some much larger teeth, more like *T. robustus. M.* cf. *brevidontus* has a simpler tooth than the North Coalinga types, but the specimens of *M. californicus* are very high crowned and similar to the North Coalinga population.

The North Coalinga fauna of California is younger than the Mascall and older than the Barstow. The presence of a small *Tomarctus* sp., typical *P. avus,* and *Miolabis ?* suggests that the Mascall and North Coalinga are not far removed in time. The presence of *A. mourningi*, very complex *M. brevidontus,* and high-crowned *M. californicus* indicates later time than the Mascall, if we follow the concept of stage of evolution in correlation.

The Barstow fauna of California has two species particularly useful for comparison with the Mascall; *Merychippus sumani* has been observed to have more advanced features than *M. seversus,* and the presence of the large high-crowned *M. intermontanus* and possibly *M. calamarius* in the fauna is particularly indicative of a younger age than the North Coalinga and Mascall. Other genera suggesting a later date than the Mascall are *Aelurodon* or *Hemicyon, Pseudaelurus,* and *Prosthennops.*

The Tonopah fauna of Nevada is distinct in the presence of *Merychippus calamarius* (see Henshaw, 1942). The teeth are very high crowned and have more complex enamel pattern than *M. intermontanus.* The presence of the smaller species of *M. sumani* in the Barstow suggests that the Barstow may be older than the Tonopah.

Buwalda and Lewis (1955) have given evidence to indicate the presence of a middle Miocene, Hemingfordian fauna in California in their description of a new species, *Merychippus tehachapiensis,* from the Phillips Ranch. The small teeth of *Merychippus carrizoensis* Dougherty might be related to the Phillips Ranch horse, but there are very few samples of *M. carrizoensis* upon which to base adequate comparisons. There is, however, definite evidence of Miocene mammalian faunas earlier than the Mascall in the California province.

It is important to mention at this point that there is extreme difficulty in denoting fine chronologic differences on a subage or stage level. In this study reasonable assurance can be established that such faunas as the High Rock Canyon, North Coalinga, and Barstow are later than the Mascall, Skull Spring, Beatty Buttes, Sucker Creek, or Virgin Valley. Therefore I have added the term "estimated correlation" in figure 44 where "fine" correlations are attempted.

A more conservative approach might be to consider the Virgin Valley Mascall, Skull Spring, Sucker Creek, and Beatty Buttes as representing transitional middle to late Miocene faunas of the West, the High Rock Canyon and Barstow middle, late Miocene, and the Tonopah and Niobrara River as very late Miocene.

There are three taxonomic groups in the Mascall that have equivalents in the Great Plains Miocene faunas, *Amphicyon* cf. *sinapius, Hypolagus* cf. *vetus,* and *Mylagaulus* sp. These occur in the Lower Snake Creek (Matthew, 1924). In addition there are species distinct from those of the Mascall but possibly in the same general stage of evolution, for example, *Tomarctus brevirostris, Leptarctus primus, Peridiomys rusticus, Parahippus integer, Merychippus paniensis,* and *Dromomeryx whitfordi.* The Pawnee Creek fauna also shows resemblance to the Mascall in the presence of many closely related species including *M. paniensis, Parahippus coloradensis, Tomarctus brevirostris, Amphicyon sinapius,* and *Mylagaulus leavis.* This fauna in turn has been correlated with the Lower Snake Creek (*op. cit.*). The presence of large "advanced" species *M. sejuntus* and *Eohipparion* in the Snake

Creek and Pawnee Creek and *M. sphenodus* in the Pawnee Creek suggests possibly that these faunas, in part, are later than the Mascall. This is substantiated by Galbreath's work (1953) on the stratigraphic position of fossils from the Pawnee Creek fauna. He has given positive evidence of vertical zonation of the Pawnee Creek formation and fauna of previous authors. The Mascall would appear to be nearest the Eubanks local fauna of Galbreath, which he considers to be early Barstovian (*op. cit.*, p. 37.)

The Deep River fauna of Montana shows resemblance to the Mascall in the presence of *Dromomeryx borealis* and a species of *Merychippus* like *M. seversus* or *M. quintus*.

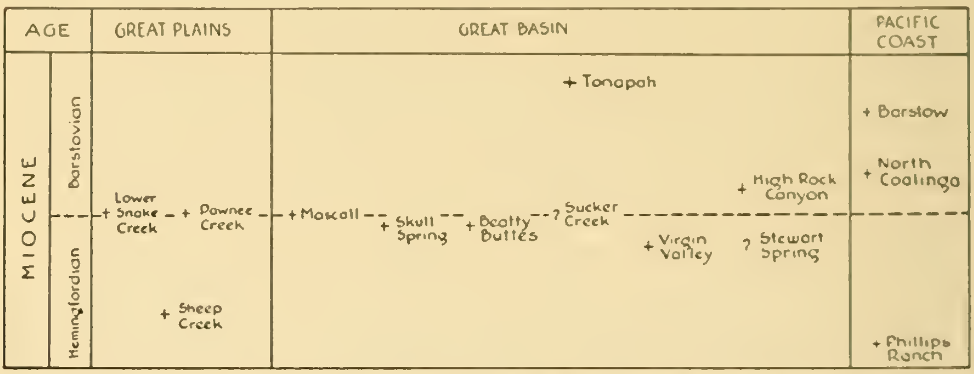


Fig. 44. Estimated correlation of critical North American terrestrial faunas. Pawnee Creek refers to the Eubanks local fauna of Galbreath (1953).

The Sheep Creek of Nebraska with *Merychippus primus* and the Thomas Farm of Florida with *M. gunteri* are early middle Miocene and older than the Mascall. The species *Parahippus leonensis* in the Thomas Farm is probably less advanced than *P. avus* in the Mascall.

The fauna of the *Merychippus* zone, North Coalinga, containing *Merychippus californicus* and first recorded by Merriam, has been carefully studied by Bode (1934). He has shown there are marine formations and land mammals in close association. Bode has correlated the *Merychippus* zone with the marine sections at Domengine Creek, Coalinga eastside oil field, north dome of Kettleman Hills, and on Carneros and Chico Martinez Creek. He correlates the *Merychippus* zone with the *Valvulineria californica* zone. Kleinpell (1938, p. 155) states "... the '*Merychippus* zone' vertebrates of the north Coalinga area may possibly be within the uppermost limits of the Relizian Stage rather than in the lower Luisian.... [they] occur definitely above beds which represent the *Siphogenerina branneri* zone, uppermost zone of the Relizian." This would correspond to late middle Miocene of the Pacific Coast or late Burdigalian (European stage name) on the basis of foraminferal zoning (see Weaver *et al.*, 1944). The megafossil concept of age differs; the metazoan zone equivalent to the *Siphogenerina branneri* zone is the *Echinarachnius merriami* zone which is placed in upper Helvetian (*op. cit.*), or in early middle Miocene. Kleinpell (1938, p. 173) has stated, "It is doubtful whether any Middle Tertiary correlation between Europe and California more refined than one derived by the Lyellian method (percentage of occurrence) can be made on the basis of faunal evidence alone." In a later paragraph (*loc. cit.*) he states that probably the "best direct faunal tie between any two Middle Tertiary stages in the two areas, however, is provided by the geographically widespread and stratigraphically restricted terrestrial mammal fauna of the Miocene-Pliocene transition." *Hipparion* is considered to be the critical genus that would indicate lower Pliocene in both continents (also see Stirton, 1951).

What may we consider as evidence for correlation of the Mascall with old world faunas? The genus *Amphicyon* is often believed to have arrived in North America from Eurasia in early or middle Miocene (Simpson, 1947). Stirton (1951) states that the genus may have arrived in North America shortly before *Miomastodon* and that true *Amphicyon* is present in the Sheep Creek. There is apparently some doubt as to the origin of the genus (*op. cit.*), and Pilgrim (1940) states that because of poorly represented remains in Europe it is not possible to "affiliate the fauna of Amphicyoninae in the two continents." The species of *Amphicyon* in the Mascall is not positively recognized, but it probably shows some change since representations of the genus arrived in North America. On the basis of this evidence the Mascall could not be earlier than middle Miocene. Pilgrim (*op. cit.*, p. 19) notes that Frick has "provisionally" referred a "fragmentary" mandible in the Pawnee Creek to *Ursavus:* "This identity if substantiated would be evidence of a Helvetian or Tortonian age for the Mascall horizon." In Pilgrim's chart he has placed the Mascall opposite the Helvetian, but he has not attempted to apply epoch terminology in his correlation. Since the *Ursavus* record is questionable, the indirect correlation of Mascall–Pawnee Creek—Helvetian or Tortonian—is questionable on this evidence alone. Pilgrim states on page 19, ". . . from the top of the John Day to the Lower Snake Creek we have no direct faunal evidence bearing on the European correlation . . ." Accordingly, it is not surprising to note that there is little direct basis for correlating the Mascall with the type section of the Miocene in Europe. Lyell's (1833) type of the Miocene (middle Miocene) is in the marine beds at Superga Hills in Italy. Kleinpell (1938) and Stirton (1951) include the Burdigalian and Vindobonian (Vindobonian equals the Helvetian and Tortonian stages) in the Miocene. Burdigalian and early Helvetian may be considered as middle Miocene and Tortonian late Miocene in age; but we must always bear in mind that the original subdivisions were on a Series-Epoch level and not Stage-Age.

An indirect basis for a general correlation with European mammal beds may be established on *Miomastodon merriami* Osborn in the Virgin Valley. Osborn (1935) and Stirton (1951) consider this as the first record of the genus in North America. Osborn thinks it is closely related to, and descended from, the more primitive *Miomastodon depereti* Osborn from the lower Miocene of Cheville, Sables de L'Orleanais in France. Stirton (1951) designates the Sables de L'Orleanais of Cheville, which contained *M. depereti*, as Burdigalian or middle Miocene in age, and I am following this opinion. *M. merriami* is not a large mastodon and bears much resemblance to *M. depereti*. The species *M. merriami* from Virgin Valley could not have evolved before its ancestor *M. depereti;* therefore it would probably be late Burdigalian or late middle Miocene in age. It is believed that the

Virgin Valley is possibly slightly older than the Mascall (see correlation chart) or upper Hemingfordian in age (the North American provincial age name). The conclusion is, on the basis of vertebrate evidence, that the Mascall is most nearly transitional in age, or Hemingfordian to Barstovian.

Greater refinement of age relationships seemingly can be attained with the more rapidly evolving and dispersing mammals than from paleobotanical material; however, a suggestion on age can be obtained from the type Mascall flora in the deposits about 16 miles westward where mammals have been found. According to the geologic evidence (see Merriam, Stock, and Moody, 1925), there was a settling and warping of the Columbia River basalt after extrusion. Lateral variations in the lithology, difference in the dip of the Mascall, and the basalt rocks suggest that there may have been an irregular topography after the basalts flowed over eastern Oregon. Since there is probability of varying types of terrain at that time, it is my belief that the flora at the type floral locality could have existed contemporaneously (in general geologic time concept at least) with the mammals. Chaney (1951) dates the Mascall flora as middle Miocene. More specific assignment on the basis of the flora is probably impractical. Earlier he referred the flora to middle or upper Miocene (1925, p. 48) which he considered consistent with the then available vertebrate faunal evidence.

The general conclusions to be derived from this discussion on correlation and dating may be as follows: There is no means of accurately correlating the fauna by typology. On the basis of the relationships to other North American mammalian faunas, the known occurrence or chronologic range of genera, the fossil flora, the relationship to marine sequences, and the world-wide dispersal of some mammalian genera, I believe the Mascall may be most logically designated as middle to late Miocene, or Hemingford-Barstovian age. This implies that there is no evidence for a break in the mammalian fossil record from Hemingfordian to Barstovian, and it appears that the Miocene may not be divided into the three stages on the basis of marked distinction of terrestrial faunas—a conclusion already suggested by Stirton (1951, p. 79). As already pointed out, the Virgin Valley, Skull Spring, and Mascall are very closely related mammalian faunas and, as a group, represent a transitional phase in Miocene faunal succession. I might arbitrarily place the Mascall as late Hemingfordian, but such a move would be purely arbitrary. A less specific designation (as used here) reflects the situation more assuredly.

Thayer and Ray (1950) traced the Mascall formation 22 miles east of the type area, including the locality of the Mascall flora. This extension of the Mascall formation would seem to substantiate my belief that the beds containing the Mascall flora and the mammal-bearing beds have the same geologic age. Thayer and Ray also state that there is definite interbedding of tuffs and flows between Mt. Vernon and Prairie City, areas east of the type section. This supports their final contention that the Mascall and the Columbia River basalts are correlative. If the conclusion is accepted that the Mascall and Columbia River basalts are, in part at least, lateral equivalents and if my faunal correlations are valid, then the laterally equivalent parts of both formations in this area are of the same approximate age and may be dated as transitional between middle and late Miocene.

MATERIAL OF QUESTIONABLE FAUNAL AFFINITY

The following discussion is concerned with material cited in publications on Mascall mammals, especially Matthew (1899), Merriam and Sinclair (1907), Matthew (1909), and Gazin (1932). Recent collecting and study of material from Oregon has supplied information on these forms. Their status as part of the Mascall fauna is doubtful or in error.

Megalonychidae

Stock (1925) has conclusively shown that ground sloth remains once described (Sinclair, 1906) and referred (Merriam and Sinclair, 1907) to the Mascall actually came from the Rattlesnake formation. Ameghino (1912) named one of these specimens, an ungual phalanx, *Sinclairia*.

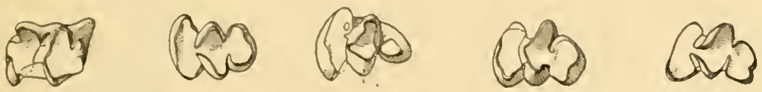


Fig. 45. Leporidae gen. and sp. indef., C.I.T. no. 4002a, loc. Mascall type area (?); occlusal view deciduous premolars; × 5.

Leporidae gen. and sp. indet.
(Fig. 45)

Five isolated teeth were stored with the C.I.T. specimens, no. 4002 referred to *Hypolagus* (see p. 214). These teeth (I designate no. 4002a) were collected by J. T. Weatherford at the type locality of the Mascall according to the museum tag.

I have not found teeth like no. 4002a at any Mascall localities, nor are there any other references to such material. It is probable that the teeth are deciduous premolars. Preliminary comparisons were made with milk dentitions in *Sylvilagus, Hypolagus,* and *Ochotona* (also permanent dentition in *Ochotona*) at the M.V.Z. These specimens (no. 4002a) show three columns to each tooth, the anterior column with a small anterior inflection, a median column with a V-shaped posterior margin, and a straight or convex posterior margin on a third column.

The $P_{\overline{3}}$ in *Ochotona* adult dentition differs in the absence of an anterior inflection on column one, in the less distinct second column, and in a straight posterior margin on the third column. The milk dentition shows a smaller anterior lophid without an inflection, but the lophids are distinct as in no. 4002a and with a V-shaped margin on the second lophid.

Lepus $DP_{\overline{3}}$ has a much more elongate anterior column and straighter posterior margins of the columns. *Sylvilagus* milk dentition suggests a closer relationship in that the V-shaped margins are present and the columns are distinct, but it differs in the absence of an anterior inflection on the first column. Milk teeth of *Hypolagus* have not been seen by me and therefore cannot be compared, but it is possible that these specimens are milk teeth of *Hypolagus*. The genus has a rather extensive geologic range.

Lepus ?

Dice's work (1917) indicates it is more probable that the leporid is *Hypolagus* rather than *Lepus* (see discussion of *Hypolagus* cf. *vetus*.)

Chalicomys sp.

Chalicomys sp. is apparently listed as *Steneofiber* by Merriam and Sinclair (1907). Simpson (1945) shows this is in turn synonymous with *Paleocastor*, and consequently it is possible the genus may refer to a specimen from the John Day fauna.

Heteromyidae gen. and sp. indet.

This is another specimen from the California Institute of Technology collection. Bode collected the material from Mascall beds in 1921 according to the data on the museum tag. It is possible that this specimen, C.I.T. no. 400, was taken from Mascall strata, but it is somewhat questionable whether such a hypsodont heteromyid was living at that time.

The specimen is a partial lower jaw with $P_{\overline{4}}$ and $M_{\overline{1}}$ in place. The following features are apparent: hypsodont though well worn; $P_{\overline{4}}$ pattern present, anterior column smaller than posterior column, anterior surface convex, almost as long as $M_{\overline{1}}$; lophids on $M_{\overline{1}}$ connecting first at center forming definite H-pattern, labial ends beginning to connect, no roots showing; $M_{\overline{2}}$ with definite H-pattern and small roots deep in mandible.

Measurements in millimeters.—$P_{\overline{4}}$ anteroposterior diameter and transverse diameter respectively 1.4 and 1.5; $M_{\overline{1}}$, 1.3 and 1.6; $M_{\overline{2}}$, 1.3 and 1.6.

This specimen resembles *Perognathoides* in the relative large size of $P_{\overline{4}}$ and its simple pattern with rounded anterior lophids and in the great height of the crown. U.C.M.P. no. 12568 from the Barstow assigned to *Cupidinimus magnus* (Kellogg) is much like *Perognathoides tertius* Hall, and the same may be said for this specimen, no. 4000. The referred specimen of *P. tertius* is more worn than no. 4000, but no. 4000 could wear to the same pattern.

As a general rule nearly every fossil heteromyid from the Miocene and Pliocene beds shows some individual difference even in the supposedly diagnostic $P_{\overline{4}}$. Under these circumstances and owing to the meagerness of the sample and somewhat doubtful locality designation, it is not considered advisable definitely to assign this fossil to the genus *Perognathoides* or even to the Mascall fauna. If it is Mascall in age, it will further indicate the antiquity of the heteromyids.

Peromyscus (?) sp.

Merriam and Sinclair (1907) express doubt concerning their identification of *Peromyscus*. I have not been able to locate the specimen or specimens.

Canis (?) sp.

The type specimen of *Canis davisi* Merriam, possibly *Vulpes* (Stirton, 1940), was considered to be Mascall (?), but Merriam, Stock, and Moody (1925) show that the locality is probably Rattlesnake.

cf. *Tomarctus rurestris* (Condon)
(Fig. 46)

From the little-known locality, Bully Creek in Malheur County, Oregon, there are two teeth, $M_{\overline{1}}$ and $_{\overline{2}}$, in the Yale collection, no. 14320. $M_{\overline{1}}$ is very similar to Y.P.M. no. 12720, from a definite Mascall locality, in the shape of the paraconid. It is distinct from the holotype of *T. rurestris* in the presence of a small ridge or cusp on the posteroexternal wall of the protoconid and in a small cusp between the metaconid and the entoconid. No. 14320 may be compared with *Tomarctus rurestris.*

Measurements.—Y.P.M. no. 14320, $M_{\bar{1}}$ anteroposterior diameter 21.2, transverse diameter 8.2, anteroposterior diameter talonid 5.5, transverse diameter at protoconid 8.8; $M_{\bar{2}}$ anteroposterior diameter 11.5, transverse diameter 7.4.

cf. *Pliocyon ossifraga* (Douglass)

An isolated left P^4 U.C.M.P. no. 39948 from V-4948 (old 895) was found on the surface above the Mascall beds in similar circumstances as those associated with the rhinoceros material (see p. 332). It is characterized by the protocone somewhat anterior to paracone; metacone with long-shearing crest, elevated to posterior tip; paracone broken at peak but with anterior ridge; moderate constriction between paracone and metacone; and three roots.

Fig. 46. cf. *Tomarctus rurestris* (Condon), Y.P.M. no. 14320, loc. Bully Creek, Malheur County (?), Oregon: top, external view $M_{\bar{1}}$ and $M_{\bar{2}}$; bottom, occlusal view; × ¾.

Measurements.—Anteroposterior diameter, 34.6; transverse diameter at protocone, 21.6; transverse diameter at metacone, 17.3; height (no wear on crest) at center of metacone, 14.8.

In general morphology, the tooth is like *Amphicyon frendens,* but it was found to be much smaller. *Pliocyon gidleyi* may be of similar size and shape. *Pliocyon ossifraga* (Douglass)* from Madison Valley was found to be nearly identical in size and shape except for a slightly more robust base to the cusps in *P. ossifraga.* This close resemblance in the single tooth strongly suggests that a late Miocene or Pliocene genus is represented at this particular locality, V-4948.

? *Bassariscus* sp.

Cope described a fragmentary mandible from the "Loup Fork of Cottonwood Creek, Oregon." The type has been lost but was figured by Cope and Matthew (1915, pl. 119c). Matthew (1904, p. 254) refers to the Oregon species as *P.* ("lutrictus") *Lycopotamicum* Cope and mentions that no other specimens have been found. He considered it a small species, "about the size of a mink." In 1915 Cope and Matthew suggested that the species was related to *Sthenictis.* Evidence has been presented to show that the type of *P.* ? *lycopotamicum* could have been *Bassariscus* (Gregory and Downs, 1951).

The conclusion is that on the basis of our present knowledge *P.* ? *lycopotamicum* could be Miocene or Pliocene in age and could be assigned to the genus *Bassariscus* just as well as to *Potamotherium,* and it is better designated as ? *Bassariscus.*

Mastodont sp.

Exact locality data are lacking on the supposed Mastodont sp. The citation in Hay's bibliography (1930) suggests that the specimen came from the Pliocene of Oregon.

cf. *Parahippus avus*
(Fig. 47)

Specimens were taken from the Bully Creek area in Malheur County—Y.P.M. nos. 14279, a left upper molar, and no. 14296, heavily worn upper. No. 14279 is a complex tooth; the crochet is not connected to the protoloph but is divided into five plications, the metaloph has six minute and two large posterior plications with one large anterior plication; cement is present only in fossettes or on the pre- and postfossette and deposited thinly between the protocone and hypocone. It is believed that this tooth is a specimen showing the phyletic affinity between *Parahippus avus* and *Merychippus brevidontus* (see discussion under Mascall *P. avus*).

Fig. 47. cf. *Parahippus avus* (Marsh), Y.P.M. no. 14279, loc. Bully Creek, Malheur Co., Oregon (?): occlusal view, left P^4; × 1.

Merychippus insignis Leidy

Matthew (1899) and Gazin (1932) list *Merychippus insignis* from the Mascall. There is no evidence to support the occurrence of a high-crowned species like *insignis* in the fauna.

Rhinocerotidae gen. and sp. indet.

Diceratherium oregonense (Marsh, 1873, p. 409) was recorded by Marsh as ". . . A second new species of this genus, much larger than either of the Miocene species . . . found by Yale party, in 1871, in the Pliocene deposits of Oregon." Cope's measurements of this "penultimate" tooth show the anteroposterior diameter to be 41 mm. and transverse diameter as 48 mm. It is probably a larger specimen than the new material to be discussed.

Matthew (1932) reviewed the status of the type and called it an imperfect upper molar. He thought it was not *Diceratherium* but agreed more closely with *Teleoceras* and differed from *Aphelops* or *Peraceras* in the presence of a "medifossette." In conclusion he states if it were certain that it came from the Mascall or the Rattlesnake it might be safer to refer topotypes. The results of my work throw no light on this problem.

In the collection at the University of California there are several foot elements and parts of limb fragments, the majority of which were taken at V-4948 (old 895). As mentioned previously, this locality may contain rocks and mammals referable to the Rattlesnake or to the Mascall. Many fragmentary elements were found loose on the surface of the densely covered slope above beds of probable Mascall age. At locs. V-4949 (old 897) and V-4951 (old 900) some fragments of rhinoceros were collected on the surface, but again, these materials could have come from beds later than Mascall. One specimen is a part of a maxilla with M^1

and M^2 in place. These teeth show moderate wear and are smaller than the rhinoceros described from the Rattlesnake (see Merriam, Stock, and Moody, 1925). In M^1 there is a moderate development of the anterocrochet and a strong crochet. M^2 has a well-developed parastyle with a large rib posterior to it. The crochet is larger than on M^1 and is bifurcate at the tip. If we follow the specifications of Matthew (1932, p. 434) it would seem that the teeth may be referred to *Aphelops* because of the apparent absence of a "midifossette." An isolated, relatively short calcaneum is more like *Teleoceras*.

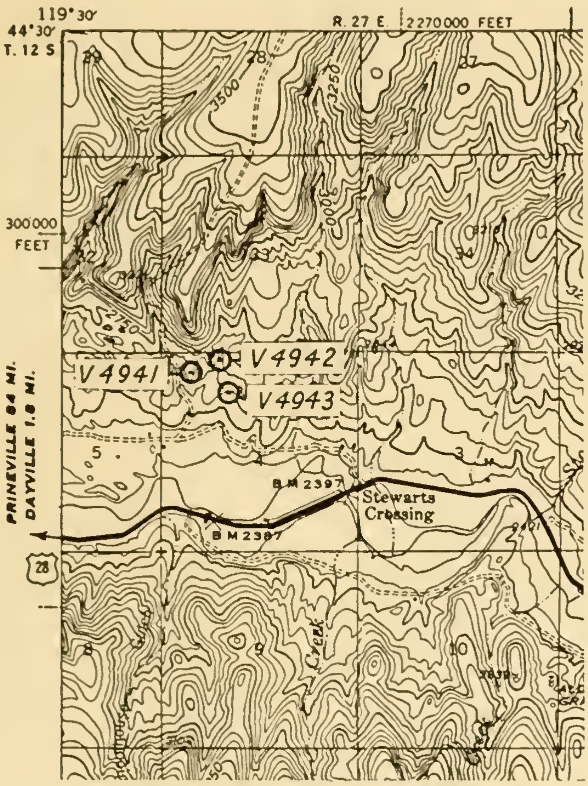


Fig. 48. A part of Aldrich Mountain Quad., Grant County showing locs. V-4941, V-4942, and V-4943. Scale, 1:62,500.

Measurements of Rhinocerotidae Material

M^1 transverse diameter	35.8
M^2 anteroposterior diameter	44.2
transverse diameter	40.0

A very small magnum of a horse, possibly *Merychippus*, U.C.M.P. no. 40326, was found among the other float materials at this locality. It has been noted that a very large Amphicyonid was found in the same area. No identifiable rhinoceros material has been collected in place in positive Mascall beds. I conclude, therefore, that the presence of a rhinoceros in the Mascall has not been established.

Tayassuidae

A recent addition to the University of California collections is no. 39295, loc. V-4829. The specimen included $I_{\overline{1}}$ and $_{\overline{2}}$ of the left side. The circumstances of the collecting suggest the specimen may have come from the Rattlesnake formation. It was lying in loose weathered tuff, actually on Mascall beds, but this particular

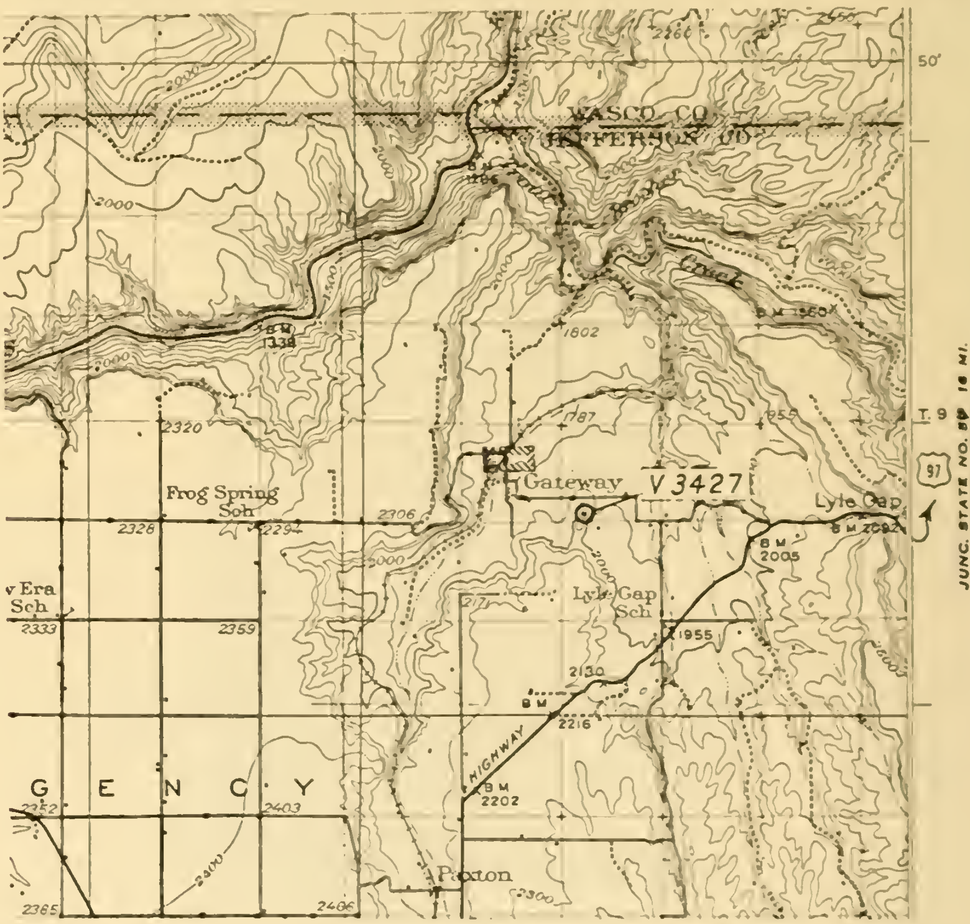


Fig. 49. A part of Madras Quad., Jefferson County, Oregon, showing loc. V-3427. Scale, 1:125,000.

area shows evidence of considerable slumping. In size, the teeth resemble the recent peccary or *Prosthennops* from the Rattlesnake (see Merriam, Stock, and Moody, 1925).

Merycochoerus sp.

Merriam and Sinclair (1907) list this genus with probable Mascall material, but they cite Matthew (1899) as a reference. Matthew has checked the genus as present. There is no further evidence.

According to Merriam and Sinclair (*op. cit.*) a mandibular fragment and milk dentition of a Merycoidodont were collected from the Mascall by U.C. field parties. Also they refer to a caniniform premolar from the Mascall beds "between Camp

Creek and Crooked River." No museum numbers are given and none of this material has been found in the University of California collection.

Alticamelus altus (Marsh)

Alticamelus altus (Marsh) 1894 is based on a calcaneum. It came from so-called Pliocene deposits near the John Day River. There is no evidence to show that it came from the Mascall.

Paleomeryx ? sp. *a* and sp. *b*

As Gazin (1932) suggests, this probably refers to *Dromomeryx* and specifically as now interpreted, *Dromomeryx borealis*. Merriam and Sinclair (1907) do not specify any museum numbers nor do they discuss the material.

Evidence (?) for Post-Mascall or Pliocene in the Crooked River Area

The above reference to a rhinoceros and the large bear dog, cf. *Pliocyon*, is considered as suggestive of the presence of a fauna later than the Mascall in the Crooked River area. As discussed earlier, the geologic sequence and lithology suggest there may be later beds overlying the Mascall rocks. Extensive field work at locs. V-4948, V-4949, V-4950, and V-4951 should reveal more conclusive evidence on the geology and particularly the source of the fossils. It would be especially helpful to obtain horse teeth at these localities. If continued collecting fails to disclose genera such as *Pliohippus* and *Hipparion* in these wash deposits, we might doubt the existence of later beds in this area. At present I believe that there are later deposits.

SUMMARY

Three assemblages of fossils in central Oregon, including the Mascall type area, the Crooked River area, and the Gateway area, contain some identical taxonomic units and are considered part of the Mascall fauna. The Crooked River assemblage has provided new material for study, and this is the first account of the assemblage from Gateway, Jefferson County, Oregon. New and old localities have been mapped. Evidence is presented suggesting a possible new Miocene locality in northern Malheur County, Oregon, near Bully Creek (see p. 210), and there is a probable post-Mascall fauna from the Crooked River area. Much previously undescribed material, stored in museums throughout the country, has been reviewed and figured in this report.

Geologic structure and lithology, particularly in the type area, indicate that the Mascall was probably deposited in a shallow yet irregular basin with many water-laid and some wind-blown units. There is much horizontal variation in many parts of the strata. The environment of the Mascall fauna, particularly near the type area, probably included a valley or basin and adjacent uplands with small lakes and streams or flood plains. Forests and grasslands were probably present, with swamp conditions in the region of the floral deposit.

Determination of the probable validity of diagnostic features in poor samplings of critical fossil species has required quantitative analysis of variation in related and more completely represented recent and fossil populations, especially in the species of Heteromyidae—*Tomarctus*, *Parahippus*, and *Merychippus*.

Previously unknown Mascall rodents and lagamorphs are described, including the new species *Arctomyoides oregonensis*, a form of terrestrial squirrel intermediate between the marmotlike *Arctomyoides arctomyoides* and the early terrestrial squirrel stock. *Prodipodomys ? mascallensis* is a new species of kangaroo ratlike rodent which demonstrates considerable antiquity for this group of Heteromyids.

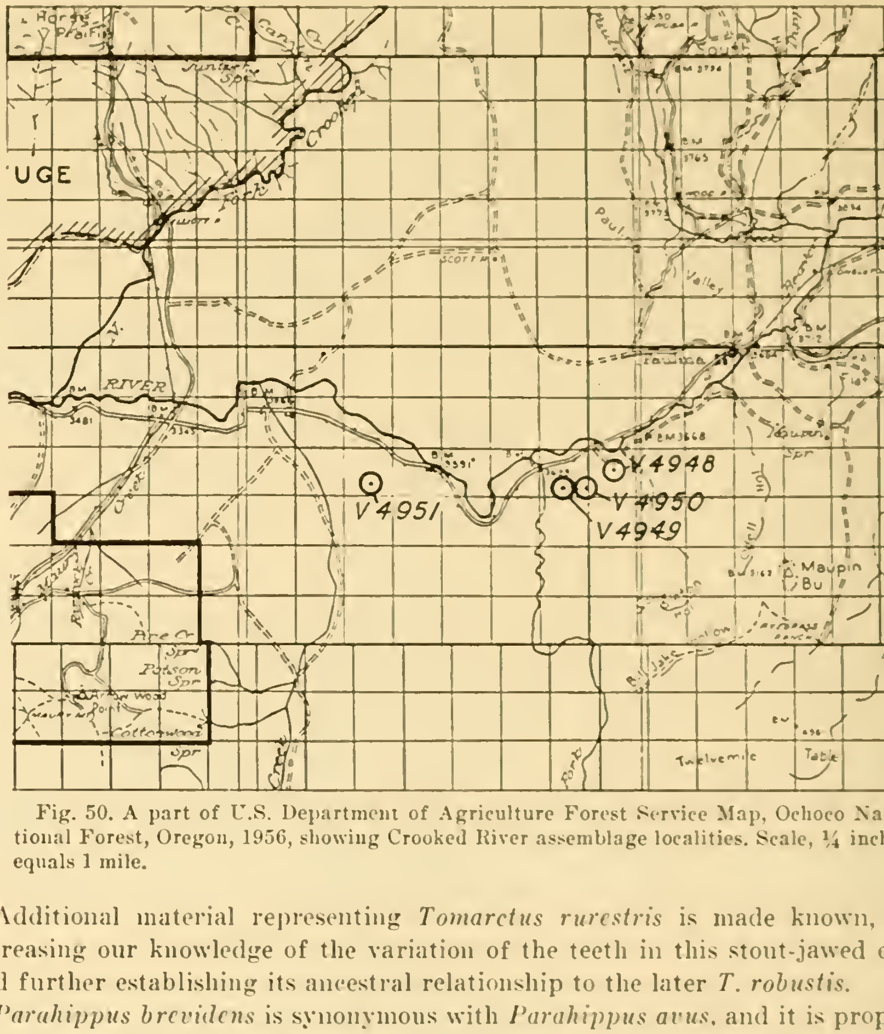


Fig. 50. A part of U.S. Department of Agriculture Forest Service Map, Ochoco National Forest, Oregon, 1956, showing Crooked River assemblage localities. Scale, ¼ inch equals 1 mile.

Additional material representing *Tomarctus rurestris* is made known, thus increasing our knowledge of the variation of the teeth in this stout-jawed canid and further establishing its ancestral relationship to the later *T. robustis*.

Parahippus brevidens is synonymous with *Parahippus avus*, and it is proposed that this species of horse is ancestral to, or closely related to, a common ancestor of *Merychippus brevidontus*. *Archaeohippus ultimus* is now established as one of the better represented species in this genus and aids considerably in the recognition of characters diagnostic of the genus.

Merychippus relictus is tentatively retained as a distinct species. *Merychippus isonesus* is a synonym of *Merychippus seversus*. *Merychippus quartus* is a *nomen vanum*. Critical study of relatively large samples of the species *M. seversus* and *M. californicus* reveal probable close affinity and phyletic line of descent from *M.*

seversus to *M. californicus.* It is believed that many species of *Merychippus* have been injudiciously named in the past on the basis of limited samples and too heavily worn dentition.

Newly described material referable to *Dromomeryx borealis* establishes this species as one of the most completely represented members of the genus and indicates that valid specific distinctions in this group are at present dependent on adequate specimens of horn corns with limited reliance on dental characters and skeletal parts.

The Mascall is believed to be transitional in age between Hemingfordian and Barstovian or middle and late Miocene; it is probably older than the Merychippus zone, North Coalinga fauna, and slightly younger than the Virgin Valley fauna. It is emphasized that all three of the faunas—the Virgin Valley, the Mascall, and the Skull Spring—may more accurately represent a transitional period between Hemingfordian and Barstovian and cannot be distinguished chronologically on the basis of the type of evidence at hand. There is no evidence for vertical time differentiation or separate zones in the Mascall fauna and formation.

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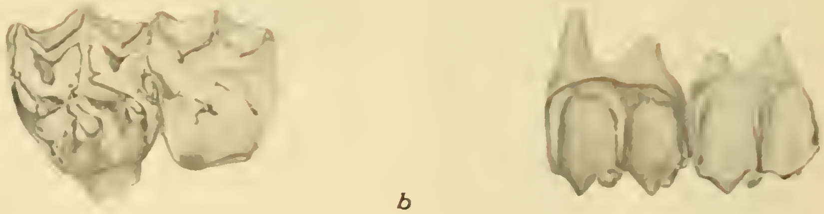
PLATES

PLATE 5

Parahippus avus (Marsh), holotype Y.P.M. no. 1128, loc. Mascall type area; upper and lower dentition. Reproduced from original drawings by B. Yoshihara and by permission of the American Museum of Natural History; also published in Osborn (1918, fig. 64). × 0.80.

a



b

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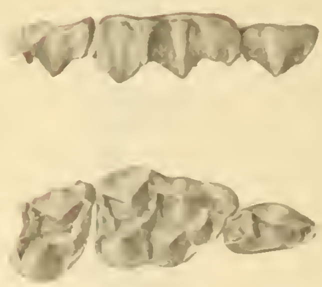

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PLATE 6

Mascall type area: *a*, *Merychippus relictus* (Cope), holotype, A.M. no. 8673; *b*, *Parahippus avus* (Marsh), Y.P.M. no. 11274, left M² and ³; *c*, *P. avus* referred U.C.M.P. no. 1701; *d*, *Archaeohippus ultimus ?*, U.C.M.P. no. 2019 loc. Crooked River area. Reproduced from original drawings by permission of American Museum of Natural History; *a* and *b* by S. Oka, *c* and *d* by B. Yoshihara; *a* and *d* not previously published, *b* and *c* published in Osborn (1918, fig. 66); × 1.

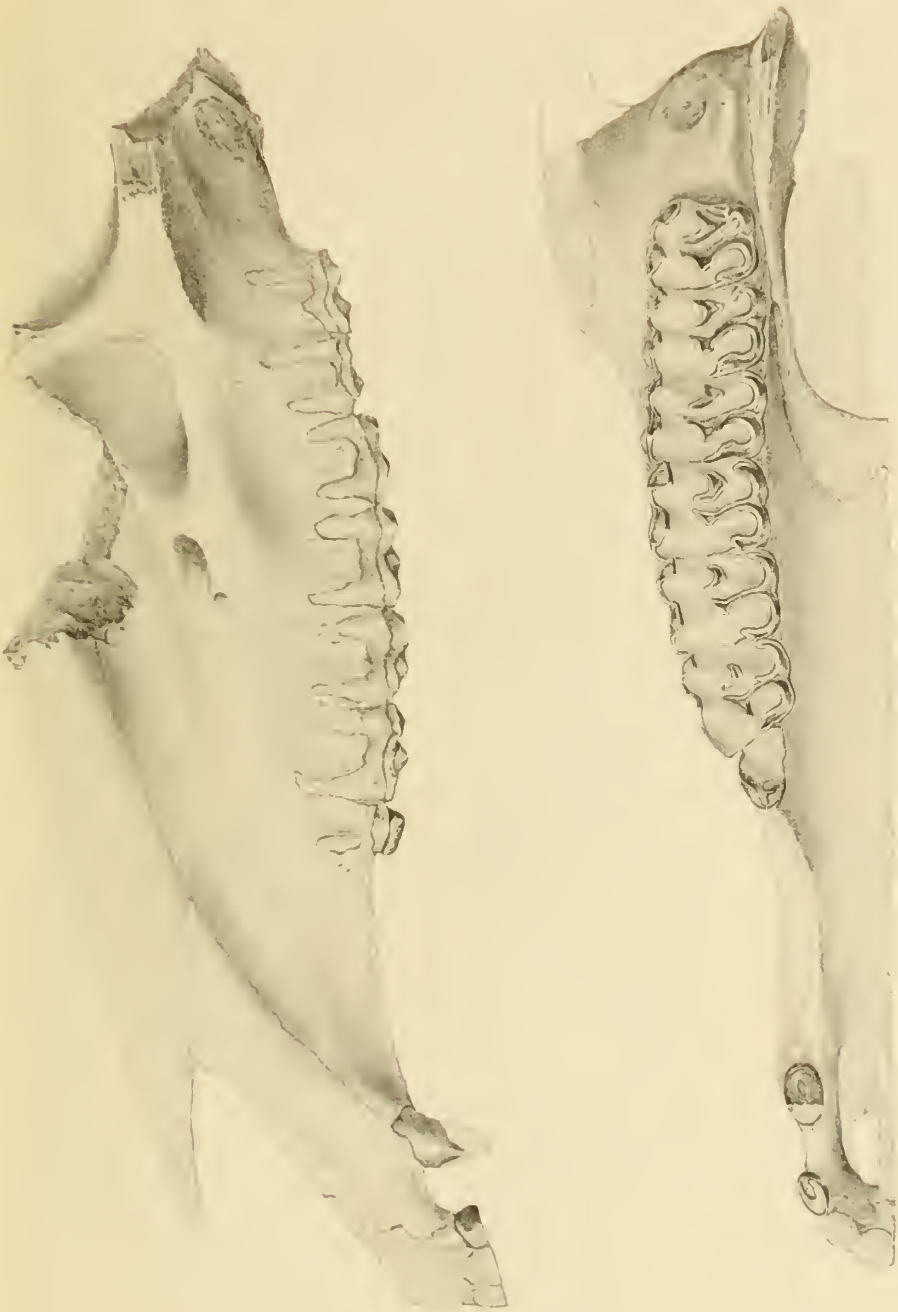
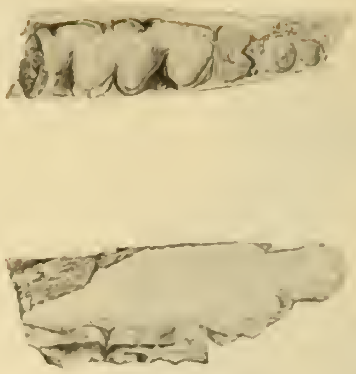


PLATE 7

Archaeohippus ultimus (Cope), holotype, A.M. no. 8174, loc. Mascall type area, lateral and occlusal view. Reproduced from original drawings by B. Yoshihara and by permission of the American Museum of Natural History, also published in Osborn (1918, fig. 172); × 1.

a



b

c

PLATE 8

a, *Archaeohippus ultimus* (Cope), U.C.M.P. no. 1689, loc. Mascall type area: right M^2; *b*, *Archaeohippus ultimus ?*, U.C.M.P. no. 1700, loc. Crooked River area; *c*, *Merychippus ?*, U.C.M.P. no. 1709, loc. Crooked River area. Reproduced from original drawings by permission of American Museum of Natural History, drawings by B. Yoshihara; × 1.

PLATE 9

A part of aerial photo., U.S.G.S. Spray Quad., G S = C K, 1947, nos. 20–31 showing type U.C. loc. 3059 and adjacent localities. Scale, 1:17,400.

PLATE 10

A part of aerial photo., U.S.C.G. Spray Quad., G S = C K, 1947, nos. 20–32 showing area near McDonald's ranch and localities. Scale, 1:17,400.

PLATE 11

A part of aerial photo., U.S.G.S. Spray Quad., G S = C K, nos. 20–29 showing localities near point 2.9 miles east of Mascall ranch. Scale, 1:17,400.

PLATE 12

A part of aerial photo., U.S.G.S. Spray Quad., G S - C K, 1947, nos. 20–30 showing position where the generalized section was taken at points A A' and B B'. Scale, 1:17,400.