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Charles D. and Mary Vaux Walcott  
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A REVIEW OF THE UPPER EOCENE  
ARTIODACTYLA OF NORTH  
AMERICA

(WITH 18 PLATES)

By

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INTRODUCTION

Perhaps the most significant feature of life during upper Eocene time in North America is the striking diversity and relative abundance of the Artiodactyla among the mammalian groups. At this time the even-toed ungulates made their first bid for a dominant role in the Tertiary sequence. Their new prominence is in marked contrast to the insignificant position occupied in the preceding middle Eocene Bridgerian interval, during which the Perissodactyla appear to have been unchallenged as the predominating ungulates. The reason for this new deployment is not immediately evident, but it may be described as a noticeable and perhaps rapid diversification of the bunodont types in situ together with the sudden appearance, possibly through migration, of a host of selenodont types. Remains of the latter exhibit a basic resemblance throughout but are already clearly divisible into several of the major groups, such as the hypertragulids, agriochoerids, camelids, and leptomerycids. Explanation for such a marked shift in the proportions of the fauna may lie in environmental changes that were taking place, as indicated in part by the dwindling and disappearance of the extensive lake system which provided the Green River formation. Perhaps it was a setting of the stage causing or permitting a faunal readjustment, encouraging the introduction of new types through migration.

In somewhat greater detail the changes that were accomplished following Bridgerian time include the development and expansion of the homacodont dichobunids into the genera *Bunomeryx*, *Hylomeryx*, *Mesomeryx*, *Pentacemylus*, and *Mytonomeryx*. The helohyids exhibit

striking growth with transition to forms such as *Achaenodon*, and may also have given rise to the Oligocene entelodonts, possibly through the long-snouted *Lophiohyus*. Included in the helohyd line is the closely related *Parahyus*, now generally and probably erroneously attributed to the lower Eocene. The selenodont forms appear in the North American upper Eocene represented by at least five families. These include the hypertragulid, *Simimeryx*; the agriochoerids, *Protoreodon* and *Diplobunops*; two distinctive groups hitherto admitted together in the Camelidae, including on the one hand the poëbrotherine camelid, *Poëbrodon*, and on the other the oromerycids, *Oromeryx*, *Protylopus*, *Camelodon*, and *Malaquiferus*; and the leptomerycids, *Leptotragulus*, *Leptoreodon*, and *Poabromylus*. *Protoreodon* is by all odds the most frequently encountered and most abundantly represented in collections. In lesser numbers, but not uncommon, are *Protylopus*, *Leptotragulus*, and *Pentacemylus*.

Interest in the upper Eocene artiodactyls was stimulated by an exceptionally good representation of these forms obtained by the Smithsonian Institution in 1938 from the upper or "C" horizon of the Uinta formation. The bulk of the material came from a single quarry in Myton pocket, approximately 7 miles east of the town of Myton in the Uinta Basin of northeastern Utah. During routine identification of these specimens for purposes of cataloging, it became evident that there was marked taxonomic confusion and that the systematic arrangement applied to the artiodactyls of this age was in much need of revision.

It may be noted that this study is based for the most part on dental characters, so that it may be looked upon as essentially an odontographic revision. Other details of skeletal anatomy are, of course, extremely important to a better understanding of relationships, but only a few of the forms involved were represented by anywhere near adequate skeletal material so that the additional information obtained of these could not be fully utilized on a comparative basis. A detailed investigation of the skeletal anatomy of the better-represented forms might well form the basis of a separate study, and was indeed planned by Scott<sup>1</sup> (see 1945, pp. 233 and 236).

#### ACKNOWLEDGMENTS

This review has been aided immeasurably by the courtesies extended by various museums and universities in permitting me to borrow for

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<sup>1</sup> A study of the Uinta fauna as a whole was under way by Professor Scott at the time of his death, and considerable manuscript had been prepared.

study type and certain other specimens of upper Eocene artiodactyls. It was also thus possible to make direct comparisons and correctly identify the rather large collection of Uinta C artiodactyls in the U. S. National Museum.

Through the courtesy of Dr. Joseph T. Gregory the Uinta artiodactyls described by Marsh were made available. Drs. George G. Simpson and Edwin H. Colbert kindly permitted me to study various specimens in the American Museum collections described by Osborn, Granger, Scott, and Wortman. Materials described by Scott, or by Scott and Osborn, as well as more recently acquired collections at Princeton University were turned over to me for this investigation by Dr. Glenn L. Jepsen. Pertinent materials in the large upper Eocene collections at the Carnegie Museum were lent through the kindness of Dr. J. LeRoy Kay, these being essentially the specimens studied by Peterson.

The photographs used in plates 1-3, 6-7, and 13-18 were made through the kindness of Dr. G. Arthur Cooper, with a background overlay prepared by William D. Crockett. Those in plates 4, 5, and 8-12 were made by the photographic laboratory of the Smithsonian Institution. Charts 1 and 2 were prepared by Lawrence B. Isham, staff artist for the department of geology. Acknowledgment is also due the Committee on "Nomenclature and Correlation of the North American Continental Tertiary" of the Society of Vertebrate Paleontology for use of terms and composition of ages and subages of the Eocene employed in the charts. These are to be defined in the committee's forthcoming report.

#### HISTORY OF INVESTIGATION

Undoubtedly the earliest exploratory work in the upper Eocene of North America was Marsh's trip of 1870, which resulted in the discovery of fossil remains in the now well-known Uinta formation in northeastern Utah. Marsh gave the name Uinta Basin to this area of Eocene deposition, and from it the designation Uinta was subsequently applied to the beds that, overlying the Green River formation, are well exposed throughout the basin. Materials from here, collected by Marsh in 1870 and by his parties in following years, particularly 1874 and 1877, included the Artiodactyla that he referred to by the generic names *Eomeryx*, *Parameryx*, and *Oromeryx* in a lecture delivered and published in 1877. Inasmuch as the descriptions were inadequate, without figures, and no types were designated, the names were invalid. However, in 1894 he described and figured species of each, adding *Hyomeryx* to the list.

Cope apparently did no collecting in the Uinta Basin but may have been the first following Hayden's exploration to investigate the upper Eocene of the Washakie Basin, although Marsh was likewise prompt in getting into this area, supporting collecting parties here for several seasons. In 1872 Cope obtained the Washakie specimen that in 1873 he described as *Achaenodon insolens*. *Achaenodon* was thus the first artiodactyl named from the upper Eocene and, for that matter, the first mammal known from this horizon in North America.

Early investigations by Princeton University were conducted in the Washakie Basin in 1878 by Osborn and others under the leadership of J. B. McMaster. Material from upper or B horizon included the skull and mandible that Osborn in 1883 described as *Achaenodon robustus*. In 1886, led by Francis Speir, Princeton extended its explorations to the Uinta Basin and the collection obtained at that time formed the basis for the 1887 preliminary report by Scott and Osborn, followed by their memoir of 1889. The original descriptions of *Protoreodon* and *Leptotragulus* are a part of the preliminary report, but these forms are more fully described and figured in the memoir. Princeton continued its fieldwork in the Uinta Basin in 1895, at which time Hatcher succeeded in obtaining much of the excellent material Scott described in his preliminary (1898) and final (1899) reports on the selenodont artiodactyls of the Uinta beds. In the preliminary note Scott, evidently hurried, named *Camelomeryx* and *Merycodesmus*, both later found to be synonyms of *Leptoreodon*, and gave the preoccupied name *Agriotherium* to one of his species of *Protoreodon*. Much of this was corrected in the comprehensive 1899 report, and his interpretations were further aided by Wortman's camelid study (see below), although he disagreed with Wortman in certain details. In the later study Scott also included descriptions as new of the genus *Protagriochocerus* and the species *Protoreodon minor*.

Peterson's activity in the Uinta Basin dates from 1893 when he initiated the American Museum's field investigation of this upper Eocene occurrence; however, it was not until 1894 that significant collections were made. Specimens obtained during the latter year were described by Osborn in 1895 and among the forms recognized was a species of *Achaenodon* which he named *Protelotherium uintensis*, regarding it as an elothere. Peterson's collection also furnished the specimens described in the Eocene part of Wortman's 1898 paper on the extinct camelids. In this work Wortman named *Bunomeryx* and *Leptoreodon* as well as the oromerycid *Protylepus*, and added in-



formation on *Leptotragulus* which he considered as a synonym of the invalid *Parameryx*.

In the same year (1893) that Peterson first visited the Uinta Basin, the American Museum had Wortman collecting in the Washakie Basin. Wortman's work here was carried on further in 1895, and then in 1906 Granger, accompanied by Osborn, renewed investigation of these beds. The later Washakie expeditions, however, do not appear to have contributed significantly to our understanding of upper Eocene artiodactyls.

Undoubtedly the most intensive exploration work in the Uinta was that of later years by the Carnegie Museum, and Peterson's 1919 study of the fauna was essentially the result of Douglass' collecting in 1908 and 1909, and of his own in 1912. In this contribution Peterson added *Hylomeryx*, *Sphenomeryx*, and *Mesomeryx* to Wortman's *Bunomeryx*, as representing the homacodonts, and described the large agriochoerid *Diplobunops*, which from foot structure he believed to be related to the European *Diplobune*. New species also were added to *Protoreodon*, *Protylopus*, and *Leptotragulus*. Subsequent exploration for the Carnegie Museum in the Uinta Basin over a number of years has included particularly the collecting of J. LeRoy Kay and John Clark as well as Peterson, and in 1929 resulted in discovery of fossil materials in the relatively barren upper portion of the Uinta sequence. The collections of 1929-1931 from these upper beds were described by Peterson in 1931 as Oligocene in age, and the upper red facies was named the Duchesne formation, later corrected to Duchesne River as the earlier name was found to be preoccupied. At this time Peterson named the homacodont *Pentacemylus* and the leptotragulid *Poabromylus*, believing that the latter was a camelid. In a separate paper that year he added *Diplobunops uintensis* and *Diplobunops ultimus* to the growing list of agriochoerids from the Uinta beds. Peterson's last study of the upper Eocene, which appeared in 1934 as a posthumous paper, was largely concerned with the Duchesne River artiodactyls and included descriptions of *Mesagriochoerus primus*, *Leptomeryx(?) minutus*, and an unnamed species of *Helohyus*, all three of which I am inclined to regard as incorrectly allocated.

A final and detailed summary of the Duchesne River fauna was made by Scott in 1945, and in this he largely retained Peterson's identifications and taxonomic arrangement. Scott, like Peterson, believed the age of these beds to be Oligocene, a conclusion not generally accepted by contemporary and later workers. Unfortunately, for a proper understanding of the sequence and age relationships of the forms involved, Scott listed as in a single fauna all the forms involved

in the study, and it is noted that such forms as, for example, *Camelodon arapahovius*, and possibly others known to be from the Uinta equivalent in the Beaver Divide area, are included with Randlett "*Mesagriochocerus*" *primus*, Lapoint *Poabromylus kayi*, and *Leptomeryx*(?) *minutus* (this is *Simimeryx*), together with Oligocene *Brachyhyops wyomingensis*.

Various institutions have paid visits to the Uinta and Washakie Basins in late years, and mention may be made of that conducted by the writer for the Smithsonian Institution in 1938 which led to the present study. We were indeed fortunate in locating a site which produced an excellent series of specimens representing the smaller Artiodactyla of the Myton or C horizon. The work of Princeton University in recent years has been referred to, and a collection obtained by a group from Harvard University in 1940 was also made available for this study, but unfortunately much of the latter material has yet to be prepared.

#### GEOGRAPHIC AND GEOLOGIC OCCURRENCE

There are essentially but five general areas where mammal-bearing deposits of upper Eocene age are exposed, and all these have produced notable fossil remains of Artiodactyla. Listed in order of importance, they are the Uinta Basin in northeastern Utah, the Washakie Basin in southern Wyoming and adjacent Colorado, the Wind River Basin in central Wyoming, the area in which the Sespe formation is distributed in southern California, and Sage Creek, Montana. By far the most significant area, and that from which remains of most of the known forms have been obtained, is the Uinta Basin. It is here that we have the most nearly complete stratigraphic sequence known for the continental upper Eocene, a sequence that is used rather generally as a standard of reference for studies elsewhere. Two formations are recognized, the lower or Uinta, interfingering below with the Green River beds, and the upper or Duchesne River, based essentially on a facies change from that of the Uinta resulting from a change in source of sediments. Laterally, this facies change transgresses time boundaries, and hence cannot be relied on as limiting horizons or ages except in closely adjacent sections. The Uinta formation is divided into three parts lettered A to C; or into two parts: Wagonhound, including A and B, and Myton, comprising C. The Duchesne River or red facies has been likewise divided into three members. Kay has named these Randlett, Halfway, and Lapoint in ascending order. Remains of Artiodactyla have been obtained from all except Uinta A, with the bulk of the material coming from B and

C. Occurrences in the Duchesne River formation, however, are exceedingly rare.

In the Washakie Basin the upper or B portion of the Washakie formation is regarded as upper Eocene and generally considered to be about equivalent in age to the Wagonhound or lower part of the Uinta formation. So far the only artiodactyl remains known to have been found in the Washakie beds are of *Achaenodon*, a questionable *Protylopus*, and *Homacodon*. The *Achaenodon* and (?)*Protylopus* specimens are from Washakie B, whereas *Homacodon* is from Washakie A, according to Granger (1909). In addition to these, *Parahyus vagus*, as will be discussed in the systematic treatment of the species, was based on a specimen that almost certainly came from the Washakie, and likely from a horizon nearly transitional between A and B.

The occurrence of upper Eocene strata in the Wind River Basin is divided between a narrow zone along the north side of the basin and the Beaver Divide forming the rim to the south. To the north, particularly along the south side of Badwater Creek, remains have been obtained of a variety of artiodactyls, including a homacodont, possibly *Pentacemylus*, leptotragulids, and oromerycids, as well as *Protoreodon* and *Diplobunops*. Somewhat farther west near Dry Creek the oromerycid *Malaquiferus* was discovered. As far as can be determined from the fauna as a whole, these Artiodactyla are upper Uintan in age, probably Uinta C, rather than Duchesnean.

Much confusion exists as to the relative ages of horizons represented in the sequence exposed along the Beaver Divide at the southern rim of the Wind River Basin. Uintan beds here have produced *Camelodon arapahovius* and probably several of the specimens of uncertain locality which have been attributed to the Beaver Divide conglomerate. The top of the Uintan sequence is deeply channeled, and the fill has produced remains of Oligocene age. At least one of these, the *Brachyhyops wyomingensis* skull, was described as coming from the uppermost part of the Uintan sequence. I am informed by Dr. Franklyn B. Van Houten<sup>2</sup> that the Beaver Divide conglomerate overlies the channel fill and so is likewise Oligocene in age. The materials of Eocene aspect attributed to the Beaver Divide conglomerate are for the most part uncertain as to locality, particularly the immature specimen described by Scott as *Mesagriochœrus primus*, collected by a local resident. The type of *Protoreodon tardus* was found by J. LeRoy Kay but this is a relatively early protoreodont, presumably not as late as Duchesnean and surely not later than Eocene. For an ex-

<sup>2</sup> Personal communication.

planation, appeal is made to the highly disconformable relationship between Eocene and Oligocene strata. An immature-jaw fragment collected by Van Houten from beds undoubtedly a part of the Beaver Divide conglomerate resembles *Protoreodon*, but the two lower teeth preserved are not truly diagnostic so that a small species of *Agriochcerus* may well be represented. It would seem, from a review of the Beaver Divide materials and occurrences, and from field information furnished me by Van Houten and others, that the Duchesnean interval is not represented by sediments in the Beaver Divide. The hiatus in time is further indicated by the marked disconformity.

A portion of the Sespe formation as exposed to the north of Simi Valley in southern California has been demonstrated by Stock to include strata of at least two horizons of upper Eocene age. The lower of these, as represented by locality 180, also known as Tapo Ranch, produced *Leptoreodon* (*Hesperomeryx*) *edwardsi* and is about equivalent to Uinta C. Significantly higher and possibly equal to Lapoint in age, locality 150 produced the remains of *Simimeryx hudsoni*. No Artiodactyla are known from the earlier Poway conglomerate in San Diego County.

The Eocene on Sage Creek in western Montana, I am informed by H. E. Wood II,<sup>3</sup> is surely Uintan. The collections from here, now in the Carnegie Museum, contain protoreodont remains.

#### ENVIRONMENT

Certain rather general conclusions seem evident regarding the environment that existed during upper Eocene time in the portion of the Rocky Mountain region in which much of our upper Eocene fossil material has been obtained. Perhaps the most significant information forthcoming is derived from the changing lithology observed in the upper Eocene sequence of the Uinta Basin. This pertains to the transition from the lake deposits of the Green River formation, as represented in Utah, to the predominantly greenish-gray sediments of the Uinta formation. The transition is not abrupt, but there is an interfingering between the fluvial or flood plain sediments with the deltaic and lacustrine sediments, denoting a periodic retreat of the lake and an overall reduction and eventual disappearance. Furthermore, the upper part of the Uinta formation intergrades laterally and is superseded by a red facies, the Duchesne River formation, which owes its origin to a transgression of sediments from a different source.<sup>4</sup>

<sup>3</sup> Oral communication.

<sup>4</sup> I am much indebted to Dr. John Clark for an understanding of upper Eocene sedimentation in the Uinta basin.

The overall picture would appear to be one of increasing aridity and one in which there was surely a floristic change effecting the proportions of the various elements that go to make up the food supply of herbivorous groups. Whether this change was a causative factor in a transition in place to a more-selenodont type of dentition in several of the artiodactyl groups represented, or whether the environmental change permitted a faunal readjustment through migration, has not been determined. Nevertheless, there is a correlation between these facts which must be regarded as more than casual.

While there is similar evidence of increasing aridity in a change from lacustrine to fluvial deposition in the Washakie Basin during Eocene time, this change seems to have occurred somewhat earlier, as the Green River lake there evidently disappeared during the middle Eocene. In the Wind River Basin, on the other hand, although the middle and upper Eocene sequence has rather limited surface distribution, there would appear, nevertheless, to be no evidence of a lake accumulation comparable to that of the Green River formation. Presumably, however, the climatic change indicated for the Uinta Basin was of more than local importance.

Faunally, not only was there a shift to more-selenodont types among the Artiodactyla but, as has already been noted, the Artiodactyla, extremely rare in the middle Eocene, have nearly or quite supplanted the Perissodactyla as the more-populous ungulates in the fauna. Associated with the artiodactyls were a rather marked diversity of titanotheres, various rhinos, tapiroids, and horses of the genus *Epihippus* among the perissodactyls; waning groups of creodonts, together with miacid forerunners of modern carnivores; a rather notable assemblage of sciuriform rodents; and, interestingly enough, the first North American lagomorphs.

#### RELATIONSHIPS

Undoubtedly one of the more interesting aspects of this study has been the attempt to determine the relationships between the various kinds of artiodactyls that lived during Eocene time; to try to visualize something of the phylogenetic arrangement, and relate, where possible, their phyletic groupings to the better-known families of the Oligocene. Heretofore, almost no attempt has been made to demonstrate these relationships on any tangible basis and show pictorially the conclusions obtained. Wortman called attention to the camel-like features of *Protylepus*, and, noting the striking resemblances between the various Eocene forms, regarded most of them as camelid. Scott made an outstanding contribution in his report on the selenodont

artiodactyls of the Uinta, but I find difficulty in accepting many of his conclusions as to relationships, particularly as portrayed in the rather abbreviated synoptic chart given in this work. As far as the bunodont artiodactyls are concerned there appears to have been no previous attempt at ciphering origins and sequence, although much of the groundwork for this was laid by Sinclair and Peterson.

Treating first the bunodont forms, I believe these may be logically regarded as representing a single rather large family, the Dichobunidae. There would appear to be justification for including the North American forms with those of Europe, although distinct directions and tendencies are noted, inasmuch as basic resemblances are evident suggesting a not too remote common ancestry, possibly in early Eocene or late Paleocene time. It is interesting to note, however, that the schism between the Old World and New World groups appears to have widened with advance in Eocene time, and I see no certain evidence of a later interplay between the hemispheres within the period.

While including the Eocene bunodonts within the Dichobunidae there are, nevertheless, cogent reasons for recognizing at least three subfamilies among the North American forms, as may be seen in the accompanying chart. The genus *Eohyus* (Marsh, 1894) is omitted from consideration in this study, as I am unable to determine its relationships or add any information to that brought forth by Sinclair (1914, p. 267), since the type materials are so very incomplete. These are from the lower Eocene (or Paleocene?) of New Mexico.

An early group, and one which I regard as fundamentally distinct, includes *Diacodexis*, *Wasatchia*, and *Bunophorus*. These are separated under the subfamily Diacodexinae. *Wasatchia* and the closely related *Bunophorus* may not much resemble *Diacodexis*, with their much more inflated tooth cusps, but basically their dental structures are rather similar and together seem rather more condylarth-like than other dichobunids. There is no record of any diacodexids after Lost Cabin time but the suggestion is made that the leptochocerids may have originated somewhere in this subfamily. If the leptochocerids are of North American origin, which I am rather inclined to believe, then of the various dichobunids known here, only the diacodexids on the basis of dentition would seem to qualify (not the helohyids as suggested by Scott, 1940, p. 378). Except for relative proportions of the teeth, one cannot escape noticing the basic similarity of the molars. The premolars, moreover, though not so enlarged or so elongate (except in advanced *D. secans*), would seem potentially qualified, particularly those of the upper dentition. In view of the long interval

for which there is no supporting record, this suggestion may seem highly speculative but the resemblance must be more than coincidence.

In conflict with the foregoing hypothesis attention should be called to the reduction of the lateral toes of the hind foot to slender vestiges in certain material of *Diacodexis*, a condition that led Matthew to believe that *Diacodexis* could not be ancestral to any of the later Artiodactyla. However, the extent to which this condition may be variable in the *Diacodexis* complex, in view of the much better developed lateral digits of the fore foot, is not known, and *Diacodexis* certainly shows striking variability in its dentition. Moreover, the hind-foot structure of *Leptochoerus* seems obscure since Scott, as late as 1945, referred to Marsh's statement that in a Yale specimen, "The hind foot resembles that of *Homacodon*, having four usable digits, but the navicular and cuboid are co-ossified, an unexpected feature."

The second dichobunid subfamily group, for which the name Homacodontinae is retained, was certainly not derived from *Diacodexis* or the Diacodexinae. The Wasatchian form *Hexacodus*, which has for its counterpart *Protodichobune* from the lower Eocene of d'Epernay, France, would appear to have been more nearly in the line of descent for later typical homacodonts but was evidently off to one side and, though much less specialized in the dental peculiarities characterizing *Antiacodon*, may well have given rise to that Bridgerian genus. Nevertheless, it is worth noting that within the upper Wasatchian material of *Hexacodus* a certain variant in the dental pattern is strikingly suggestive of *Microsus*. *Microsus* and *Homacodon* are rather alike although the former has teeth with cusps that appear to be more acute. The teeth of *Microsus* are of more delicate and perhaps more primitive appearance and potentially better suited to the ancestral position with respect to the upper Eocene homacodonts than is the large *Homacodon vagans*. Unlike *Homacodon*, the fourth lower premolar of *Microsus* has a pronounced metaconid, but this does not preclude a relationship suggested by the chart.

By upper Eocene time the homacodonts, though still essentially bunodont, had acquired rather marked styles on the outer sides of the upper teeth, and the outer cusps of the lower molars had become a little more crescentic. In one line, represented by *Bunomeryx* and later *Pentacemylus*, the hypocone was early lost and a mesostyle early gained in the upper molars. *Mytonomeryx* is apparently related but was derived from the stock before the hypocone became reduced. It further specialized in a lengthening of the snout. *Hylomeryx* likewise retained the hypocone but did not achieve a mesostyle. As a remain-

ing possibility in the combination of characters, *Mesomeryx* early lost the hypocone but did not develop a mesostyle. In *Mesomeryx*, like *Hylomeryx*, however, a suggested tendency is noted toward the formation of a protoloph at the expense of the protoconule.

As will be discussed in somewhat greater detail in the systematic portion of this paper, there would appear to be some justification for regarding *Simimeryx* and the hypertragulids as derived from the homacodonts at some point near *Mesomeryx*. There is, however, a peculiar resemblance, which probably should not be disregarded, of upper and lower molars of *Simimeryx* to the agriocherids. It is perhaps a similar step in the transition of each from the bunodont to the more-selenodont pattern, so that the change from a bunodont homacodont, such as *Mesomeryx* to *Hypertragulus*, included the *Simimeryx* stage; possibly equivalent to *Protoreodon petersoni* in its suspected relationship to the Oligocene merycoidodonts. Attention is likewise called to the very divergent origins indicated for hypertragulids and leptomerycids. Regardless of an apparent modification toward a similar mode of existence, they show striking dissimilarities in details of dentition. Retaining these in the same family, as pointed out elsewhere, is untenable in view of the polyphyletic origin indicated.

A third subfamily of dichobunids, the Helohyinae, is represented by what appears to be a nearly continuous sequence from *Helohyus* to *Achaenodon*. The surprising increase in size is foreshadowed in *Helohyus lentus* of Bridger D, and the interval between *Helohyus* and *Achaenodon* is nicely bridged both in size and tooth characters by *Parahyus vagus*, the type of which is almost certainly from the Washakie beds. A simplicity of premolars is evident throughout, possibly with the loss of one between *Helohyus* and *Parahyus*. The bunodont character of the *Helohyus* molars is further emphasized and simplified in *Achaenodon* with the reduction of the protoconule and loss of the vestige of a hypocone in upper teeth of *Achaenodon* and with the loss of the paraconid (vestigial in  $M_1$  of *Parahyus*) and hypoconulid (except  $M_3$ ) in the lower molars. *Helohyus* would appear to be most like *Homacodon* of the various homacodonts in the simplicity of the premolars, but is unlike *Homacodon* in the near absence of a hypocone in the upper molars and the presence of a paraconid in the lowers. The Helohyinae might well have had roots converging with those of *Homacodon* before loss of the paraconid and the development of so prominent a hypocone in the latter. The early helohyids are perhaps structurally intermediate between diacodexids and homacodonts.

The entelodonts were not, of course, derived from *Achaenodon*,



as the directions taken in dental specialization, though similar as to adaptation, are entirely different in detail. Both are large bunodont forms, but in *Archaeotherium* the snout is very elongate, all the premolars are retained, and the secondary cuspules, lost or reduced in *Achaenodon*, are as much emphasized as the primary cusps. If *Archaeotherium* is related to the Helohyinae, it is through an earlier form, possibly *Lophiohyus*, possessing a dental structure and formula that had not gone too far in the direction of *Achaenodon*. I suggest *Lophiohyus* only because this form had already developed an elongate snout. Its dentition is very much like that of *Helohyus*.

The Tayassuidae is shown in the chart, not because of any particular conclusions as to origin in the dichobunids, but because it might well have been derived from North American forms. However, in this instance, the European cebochoerids must not be overlooked as potential ancestors. Its origin may lie somewhere in the middle Eocene homacodonts rather than in the helohyids as suggested by Pearson, inasmuch as the posterointernal cusp of the upper molars in *Perchoerus*, unlike *Helohyus*, would appear to be the hypocone, and as the metaconule is much reduced—that is, unless the small cusp in the position of a metaconule in *Perchoerus* was newly acquired and not the original metaconule.

Directing our attention to the selenodont families, we find the agriochoerids and oromerycids, though with highly crescentic appearing molars, somewhat intermediate between the dichobunids on the one hand and the leptomerycids and poëbrotherine camelids on the other, in the perhaps retarded or differently developed protocone above and hypoconid below. For the agriochoerids I have shown a rather simplified version of their relationship in the general chart, but their lineage within upper Eocene time may have been somewhat more complex in detail, as suggested in chart 2 (p. 67). I do not believe that more than two genera are represented, but within *Protoreodon* there appears to have been at least two distinct sequences of species or mutants that can be carried from middle through upper Uinta levels. The larger of these was evidently derived from or was close to *P. parvus* and carried through Uinta C as *P. pumilus*, culminating in *P. pumilus annectens*. This may well be the line that gave rise to *Agriochoerus*. A sequence of smaller forms can be recognized in *P. minor* of lower Uinta C, culminating in *P. petersoni* in upper Uinta C. If *Merycoidodon* was derived from any of the known forms of *Protoreodon*, the line represented by *P. petersoni* is surely the most likely source. Nevertheless, this is an agriochoerid that cannot be

separated even generically from the complex that includes the large *Protoreodon pumilus annectens*.

*Diplobunops*, the larger of the two Eocene agriochoerids, has much enlarged and widely separated caniniform teeth but is further characterized by cheek teeth rather more primitive appearing than in contemporary protoreodonts. As an aberrant line *Diplobunops* would appear to have separated from *Protoreodon* not much earlier than lower Uinta time, or possibly even as late as Uinta B. It is known only from Uinta B, C, and Randlett horizons.

Removed from inclusion with the poebrotherines, in the Camelidae, are a group of genera closely related to the Chadronian *Eotylopus*, here distinguished as the new family Oromerycidae. Their camelid resemblances, I believe, are largely adaptive, as differences in molar tooth structure from that in the poebrotherines seem fundamental and indicative of a rather remote differentiation, suggesting a heretofore unnatural family grouping. I find no close relationship indicated between the oromerycids and any of the other families, and their origin in the bunodont forms, while uncertain in position, may have been quite independent of other selenodonts. *Eotylopus* is evidently the last of the line.

The poebrotherine forms, like the leptotragulids, show early acquisition of a distinctly selenodont tooth structure, suggesting perhaps a closer relationship with the latter group than with oromerycids, although this is not demonstrated, inasmuch as the early development of P<sub>1</sub> as a caniniform tooth in the leptotragulids is a significant difference. In the absence of any distinctive lower caniniform tooth the poebrotherines are most like the Eocene oromerycids; however, this also characterizes the homacodonts. Although like others of the upper Eocene selenodonts in having obscure pre-upper Eocene antecedents, the poebrotherines nevertheless distinguished themselves by the well-documented diversity and geologic longevity of their descendant forms.

The Leptomerycidae as represented by the leptotragulids would, together with the poebrotherines, appear to be the most advanced and specialized in the attainment of crescentic or selenodont molars among the upper Eocene forms. The Oligocene forms were surely derived from the leptotragulines, but it is not clear that either *Leptoreodon* or *Leptotragulus* gave rise to *Leptomeryx*. Its origin may have been from an intermediate and perhaps earlier but closely related form. There is, however, an even better case for *Protoceras* and the Protoceratidae, and I find that *Leptotragulus*, as far as it is known, completely meets the requirements. In addition to the similar molar structure, the premolars in *Protoceras* are entirely similar to those

PALEOCENE	WASATCHIAN	Grayb	Lysite	Lostc	BRIDGERIAN	Bridg	Bridg	Bridg	Bridg	UINTAN	Uinto	Uinto	Uinto	DUCHESNEAN	Halfw	Lepol	OLIGOCENE	CHADRONIAN	ORELLAN		





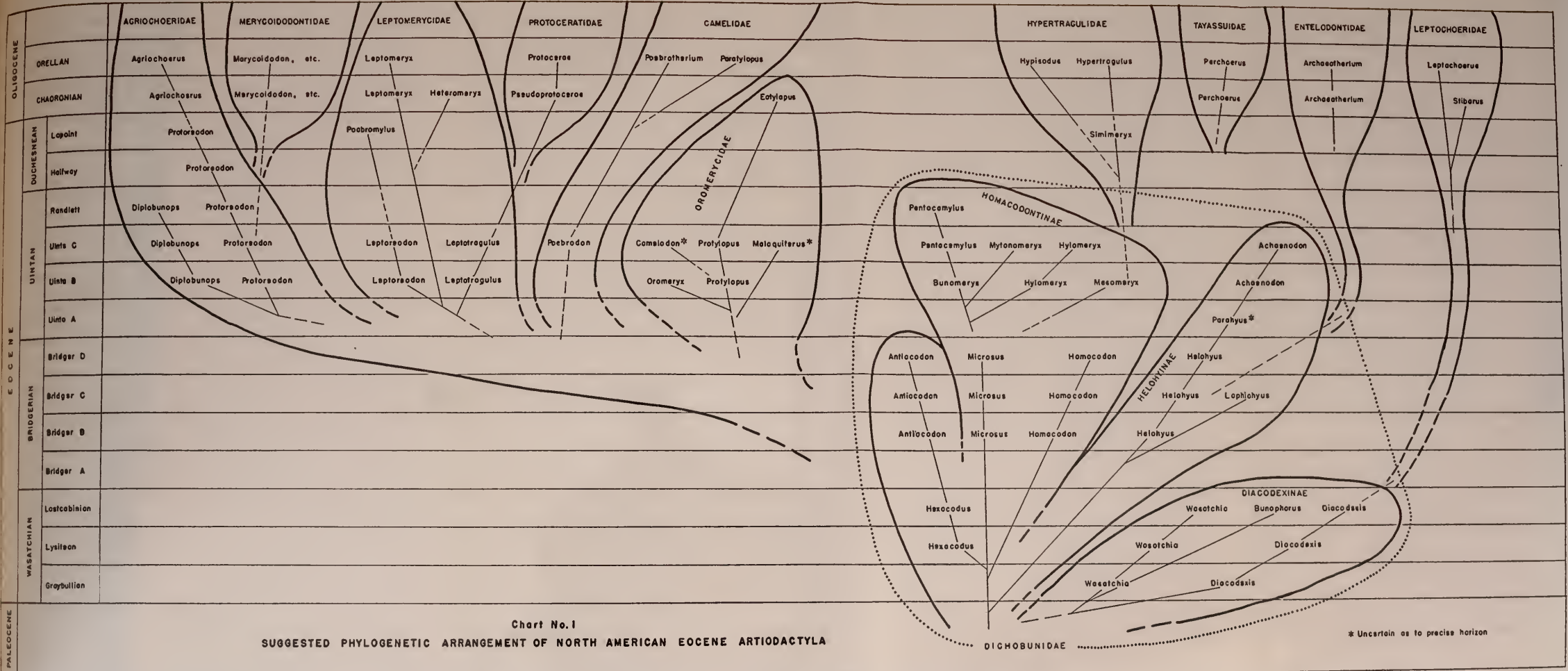


Chart No. 1  
 SUGGESTED PHYLOGENETIC ARRANGEMENT OF NORTH AMERICAN EOCENE ARTIODACTYLA

\* Uncertain as to precise horizon

PALEOCENE



of *Leptotragulus*. Scott (1899) regarded *Leptoreodon* in this relationship, but the premolars in this form are rather distinctive and not like those in *Protoceras*. Instead, Scott indicated with a query that *Hypertragulus* may have come from *Leptotragulus*, but this suggestion is likewise unacceptable. It may be further noted in the chart presented here that Peterson's *Poabromylus* is removed from the Camelidae and tentatively aligned with *Leptoreodon*. This, of course, is not certain, but I am convinced from the molar structure that it is leptotraguline rather than camelid.

Reviewing the various Eocene artiodactyls of North America, with the amazing array of Old World forms in mind, one is impressed by the resemblance of certain North American groups to others in the European assemblage. The division of the dichobunids has been noted, and the similarity between early Eocene *Hexacodus* and *Protodichobune* is possibly the closest actual approach between the two major portions of the family, although these genera appear to have distinctive premolars. In the middle Eocene, *Homacodon* is rather like *Dichobune*, though with simpler premolars, and perhaps like *Mouillacitherium*, but again with simpler premolars and in addition a better-developed protoconule on the upper molars, to judge by Stehlin's (1906) excellent illustrations. Some of the earlier *Dichobune* species, however, with a weaker hypocone are more suggestive of *Helohyus*. It should be noted, moreover, that much of the European middle Eocene dichobunid material shows a precocious tendency toward selenodonty not seen in any of our Bridger forms. Furthermore, the more-distinctive selenodont groups such as the anthracotheres and anoplotheres also appear in the middle Eocene assemblages of Europe, and a comparable though independent development in North America is not seen until upper Eocene.

Although there is a rough similarity between our upper Eocene selenodonts and those of Europe, as for example between the agriocherids and anoplotheres, or between our camelids and the xiphodonts, there are fundamental differences between these groups, and I fail to find any direct line between them or any justification for considering our selenodont stocks as derived from those of Europe. The trend toward selenodonty has surely progressed independently, in parallel though not strictly identical ways, in the two areas. More adequate information on the origin of the North American selenodont groups will possibly be revealed when faunas of Uinta A time or intermediate horizons in the Washakie are discovered. It is highly probable that no interchange of faunas took place between the two continents from about the beginning of the Eocene to its end. There is, however, as at the beginning of the Eocene, ample evidence for

faunal exchange initiating Oligocene time, with the appearance on this side of anthracotheres, choeropotamids, and probably other forms.

#### CLASSIFICATION

The following is the revised classification of the upper Eocene artiodactyls as adopted in this study:

##### DICHOBUNIDAE Gill, 1872

###### HOMACODONTINAE, Peterson, 1919

*Bunomeryx* Wortman, 1898

*Bunomeryx elegans* Wortman, 1898

*Bunomeryx montanus* Wortman, 1898

*Hylomeryx* Peterson, 1919

Synonym: *Sphenomeryx* Peterson, 1919

*Hylomeryx annectens* Peterson, 1919

*Hylomeryx quadricuspis* (Peterson), 1919

*Mesomeryx* Peterson, 1919

*Mesomeryx graugeri* Peterson, 1919

*Pentacemylus* Peterson, 1931

*Pentacemylus progressus* Peterson, 1931

*Pentacemylus leotensis*, new species

*Mytonomeryx*, new genus

*Mytonomeryx scotti*, new species

##### HELOHYINAE (Marsh, 1877, as Helohyidae)

*Achaenodon* Cope, 1873

Synonym: *Protcolotherium* Osborn, 1895

*Achaenodon insolens* Cope, 1873

*Achaenodon robustus* Osborn, 1883

*Achaenodon uintensis* Osborn, 1895

*Parahyus* Marsh, 1876

*Parahyus vagus* Marsh, 1876

##### HYPERTRAGULIDAE Cope, 1879

###### HYPERTRAGULINAE Matthew, 1908

*Simimeryx* Stock, 1934

*Simimeryx hudsoni* Stock, 1934

*Simimeryx minutus* (Peterson), 1934

##### AGRIOCHOERIDAE Leidy, 1869

*Protoreodon* Scott and Osborn, 1887

Synonyms: *Eomeryx* Marsh, 1894

*Hyomeryx* Marsh, 1894

*Agriotherium* Scott, 1898 (not Wagner, 1837)

*Chorootherium* Berg, 1899

*Protagriochoerus* Scott, 1899

*Mesagriochoerus* Peterson, 1934

*Protoreodon pumilus* (Marsh), 1875

Synonyms: *Protagriochoerus annectens* Scott, 1899

*Protoreodon medius* Peterson, 1919

?*Protoreodon tardus* Scott, 1945

*Protoreodon parvus* Scott and Osborn, 1887

Synonym: *Hyomeryx breviceps* Marsh, 1894



- Protoreodon paradoxicus* (Scott), 1898  
*Protoreodon minor* Scott, 1899  
*Protoreodon primus* (Peterson), 1934  
*Protoreodon petersoni*, new species  
*Diplobunops* Peterson, 1919  
*Diplobunops matthewi* Peterson, 1919  
 Synonyms: *Diplobunops uintensis* Peterson, 1931  
*Diplobunops ultimus* Peterson, 1931  
*Diplobunops crassus* Scott, 1945  
*Diplobunops vanhouteni*, new species  
 OROMERYCIDAE, new family  
*Oromeryx* Marsh, 1894  
*Oromeryx plicatus* Marsh, 1894  
*Protylopus* Wortman, 1898  
*Protylopus petersoni* Wortman, 1898  
*Protylopus? annectens* Peterson, 1919  
*Camelodon* Granger, 1910  
*Camelodon arapahovius* Granger, 1910  
*Malaquiferus*, new genus  
*Malaquiferus tourteloti*, new species  
 CAMELIDAE Gray, 1821  
 POEBROTHERIINAE Zittel, 1893  
*Poebrodon*, new genus  
*Poebrodon kayi*, new species  
 LEPTOMERYCIDAE Scott, 1899  
 LEPTOTRAGULINAE Zittel, 1893  
*Leptotragulus* Scott and Osborn, 1887  
 Synonym: *Parameryx* Marsh, 1894  
*Leptotragulus proavus* Scott and Osborn, 1887  
 Synonyms: *Parameryx laevis* Marsh, 1894  
*?Parameryx sulcatus* Marsh, 1894  
*Leptotragulus medius* Peterson, 1919  
*Leptotragulus clarki*, new species  
*Leptoreodon* Wortman, 1898  
 Synonyms: *Merycodesmus* Scott, 1898  
*Camelomeryx* Scott, 1898  
*Leptoreodon marshi* Wortman, 1898  
 Synonyms: *Merycodesmus gracilis* Scott, 1898  
*Camelomeryx longiceps* Scott, 1898  
*Leptoreodon (Hesperomeryx) edwardsi* Stock, 1936  
*Poabromylus* Peterson, 1931  
*Poabromylus kayi* Peterson, 1931

In an attempt to simplify characterizations or present them in a usable form there is given on the following pages a synoptic arrangement in the form of a key, including all the recognized genera for the North American Eocene. The key is divided into two parts: First a systematic arrangement is made conforming in a general way to the classification, and following this a topical presentation is given in which the various Eocene genera and subfamilies are listed accord-

ing to compliance with cited characters. One should bear in mind that even the best of keys are essentially arbitrary and often misleading, and it is with some trepidation that the following is included in this study.

- A. Cheek teeth essentially bunodont.....DICHOBUNIDAE
1. Hypoconulid of  $M_1$  and  $M_2$  developed from cingulum distinctly posterior to saddle between hypoconid and entoconid.  $P_1$ , C, and probably  $I_2$  subequal as far as known.....HOMACODONTINAE
    - a. Trigonid somewhat elevated and anterointernal cusp of lower molars twinned (or paraconid distinct from metaconid).  $P_4$  with metaconid. Talonid of lower molars broadly basined.
      - (1) Paraconid and metaconid about equal and close together  
*Hexacodus*
      - (2) Metaconid more reduced than paraconid and crista obliqua joins higher on metaconid. Upper molars with hypocone (may be double), small cusp anterior to protocone, and small mesostyle on external cingulum.....*Antiacodon*
    - b. No paraconid on lower molars, except possibly  $M_3$ .  $P_4$  without metaconid. Cusps noncrescentic.  $M^1$  and  $M^2$  with parastyle but no mesostyle.
      - (1) Hypocone on  $M^1$  and  $M^2$ .....*Homacodon*
      - (2) No hypocone on upper molars (lower molars not known, see also 1d (2) (b)).....*Mesomeryx*
    - c. Paraconid on  $M_1$  and vestigial or absent on other lower molars.  $P_4$  with metaconid. Cusps high and noncrescentic.....*Microsus*
    - d. Lower molars with subcrescentic outer cusps.  $P_4$  with metaconid.
      - (1) Upper molars with mesostyle and distinct protoconule.
        - (a) Hypocone on  $M^1$  and  $M^2$ . Marked diastemata separating anterior premolars .....*Mytonomeryx*
        - (b) Hypocone on  $M^1$  only (vestige on  $M^2$ ). Short or no diastemata separating anterior premolars.....*Bunomeryx*
        - (c) No hypocone on upper molars. Short or no diastemata between anterior premolars .....*Pentacemyllus*
      - (2) Upper molars without mesostyle (or very weak). Protoconule indistinct or forming a loph with protocone.
        - (a) Hypocone on  $M^1$  and  $M^2$ .....*Hylomeryx*
        - (b) No hypocone on upper molars. (Lower molars not known, see also 1b (2)).....*Mesomeryx*
  2. Hypoconulid of  $M_1$  and  $M_2$  weak (and double) in early stages and absent in later stages. C not known in early stages but caniniform in advanced stages.  $P_4$  without metaconid. Hypocone of upper molars vestigial or absent.....HELOHYINAE
    - a. Four lower premolars? Paraconid distinct from metaconid. Hypoconulid of  $M_1$  and  $M_2$  weak and may be developed from cingulum posterior to saddle between hypoconid and entoconid, and as a second small cuspule in the saddle very close to the hypoconid.
      - (1) Lower premolars in close sequence.....*Helohyus*
      - (2) Lower premolars separated by marked diastemata.....*Lophiohyus*

- b. Three lower premolars.  $P_4$  enlarged. Paraconid and hypoconulid (except  $M_3$ ) vestigial or absent. Lower C caniniform.
- (1) Molars relatively elongate.....*Parahyus*
- (2) Molars broad and premolar series relatively long.....*Achaenodon*
3. Hypoconulid of  $M_1$  and  $M_2$  developed on crest between hypoconid and entoconid. Talonid broadly basined.  $P_4$  without metaconid

## DIACODEXINAE

- a. Cusps sharply defined, paraconid and hypoconulid distinct. Hypocone of upper molars weak or absent.....*Diacodexis*
- b. Cusps inflated (both  $M^1$  and  $M^3$  believed to have hypocone).
- (1) Paraconid and hypoconulid distinct.....*Wasatchia*
- (2) Paraconid weak or absent and hypoconulid less distinct..*Bunophorus*
- B. Cheek teeth moderately to highly selenodont.

I.  $P_1$  and lower canine approximately equal

## OROMERYCIDAE and probably Eocene CAMELIDAE

- a. Entoconid of lower molars isolated. Protocone of upper molars bilobed posteriorly .....OROMERYCIDAE
- (1) Enamel rugose. Upper molar teeth oblique, transversely compressed posteriorly, and increasing in size from  $M^1$  to  $M^3$ . External styles prominent.....*Oromeryx*
- (2) Enamel rugose to smooth. Upper molar teeth more nearly rectangular and increasing in size from  $M^1$  to  $M^3$ . No significant diastemata between premolars. External styles prominent
- Protylepus*
- (3) Enamel rugose. Upper molar teeth nearly rectangular, not oblique, and more nearly equal in size from  $M^1$  to  $M^3$ . External styles reduced and ribs much emphasized (lower teeth not known)
- Malaquiferus*
- (4) Enamel comparatively smooth. Marked diastemata between  $P_2$  and  $P_3$  (upper teeth not known).....*Camelodon*
- b. Posterior crest of protoconid joined to metaconid and anterior crest of hypoconid joined to entoconid so that the trigonid and talonid columns of the lower molars are separate enamel loops, joined only by the lingual wall. Protocone of upper molars completely crescentic, not bilobed posteriorly.....POËBROTHERIINAE
- (1) Lower molars with weak metastylid flexure on lingual wall and this surface is somewhat convex lingually over metaconid and entoconid.  $M_3$  with hypoconulid loop. Upper molars with compressed, outstanding parastyles and mesostyles.....*Poëbrodon*
2.  $P_1$  caniniform. Lower canine similar to incisors.
- a. Upper molars with prominent parastyle and ribs, but no mesostyle.  $P^2$  and  $P^3$  without accessory cusps.  $P_4$  with metaconid and simple talonid basin .....HYPERTRAGULINAE
- (1) Posterior crest of protocone of upper molars directed toward metaconule. Anterior crest of hypoconid of lower molars directed toward posterior crest of protoconid so as to leave a small median pocket or basin between the crest of the hypoconid and the lingual wall of the tooth.....*Simimeryx*
- b. Upper molars with prominent parastyle and mesostyle, and ribs prominent (early) to weak (later). Posterior crest of protocone

directed toward metaconule. Protoconule present but may be weak. In lower molars anterior crest of hypoconid directed toward posterior crest of protoconid, and lingual cusps of these teeth with prominent styles.....Eocene AGRIOCHOERIDAE

- (1) Snout not elongate. Canine above and  $P_1$  not greatly enlarged. Primary cusp of  $P^4$  may be twinned. Early forms somewhat bunodont but increasingly crescentic in time.....*Protoreodon*
  - (2) Snout elongate and very broad between the much enlarged canines. Primary cusp of  $P^4$  with lingual ridges but not twinned. Upper molars transversely broad and not high crested....*Diplobunops*
- c. Upper molars with prominent ribs and styles externally and highly crescentic lingual cusps. Posterior crest of protocone directed laterally toward valley between paracone and metacone. Lingual styles of lower molars subdued, but outer cusps highly crescentic, with anterior crest of hypoconid directed lingually toward saddle between metaconid and entoconid.....LEPTOTRAGULINAE
- (1)  $P^2$  and  $P^3$  with prominent tritocone.  $P_2$  and  $P_4$  with posterolingually directed crest from apex or near apex of protoconid and well-developed parastylid .....*Leptotragulus*
  - (2)  $P^2$  and  $P^3$  with weak or no tritocone.  $P_2$  and  $P_4$  with prominent metastylid and usually prominent entoconid, but parastylid not separately defined .....*Leptoreodon*
  - (3) Lower premolars and molars distinctly hypsodont. Metaconid of  $P_4$  weak though distinct (upper teeth not known)...*Poabromylus*

$P_1$  is caniniform: AGRIOCHOERIDAE, HYPERTRAGULIDAE, and LEPTOMERYCIDAE.

$P_1$  and lower C approximately equal: HOMACODONTINAE (as far as known), OROMERYCIDAE (except *Eotylopus*), and POEBROTHERIINAE.

Lower C is caniniform: HELOHYINAE (not verified for *Helohyus*).

Upper molars with posterior crest of protocone directed toward hypocone: AGRIOCHOERIDAE and *Simimeryx*.

Upper molars with posterior crest of protocone bilobed or bifurcate: OROMERYCIDAE.

Upper molars with posterior crest of protocone directed toward valley between paracone and metacone: POEBROTHERIINAE and LEPTOMERYCIDAE.

Protocone of upper molars essentially conical: HOMACODONTINAE, HELOHYINAE, and DIACODEXINAE.

Upper molars with mesostyle distinct: *Bunomeryx*, *Pentacemylus*, *Mytonomeryx*, LEPTOMERYCIDAE, AGRIOCHOERIDAE, OROMERYCIDAE, and CAMELIDAE.

Upper molars with mesostyle very weak: *Hylomeryx* and *Antiacodon*.

Upper molars without mesostyle: *Homacodon*, *Mesomeryx*, *Microsus*, DIACODEXINAE, HELOHYINAE, and HYPERTRAGULIDAE.

Upper molars with hypocone on  $M^1$  and  $M^2$ : *Homacodon*, *Microsus*, *Antiacodon*, *Hylomeryx*, *Mytonomeryx*, and *Bunophorus*?

Upper molars with hypocone on  $M^1$  only (vestige or absent on  $M^2$ ): *Bunomeryx*.

Upper molars without hypocone (vestige or absent on  $M^1$ ): *Mesomeryx*, *Pentacemylus*, HELOHYINAE (very small cingular cusp in *Helohyus*), *Diacodexis*,

CAMELIDAE, AGRIOCHOERIDAE, OROMERYCIDAE, HYPERTRAGULIDAE, and LEPTOMERYCIDAE.

Upper molars with distinct protoconule: *Homacodon*, *Microsus*, *Antiacodon*, *Bunomeryx*, *Pentacemylus*, *Mytonomeryx*, *Helohyus*, *Diacodexis*, *Wasatchia?*, *Bunophorus?*, *Protoreodon* (except one species), and *Diplobunops*.

Upper molars with weak protoconule, nearly lost in loph with protocone: *Mesomeryx?*, *Hylomeryx*, *Simimeryx*, and *Protoreodon* (one species).

Upper molars without protoconule: *Achaenodon?*, CAMELIDAE, OROMERYCIDAE, and LEPTOMERYCIDAE.

P<sub>4</sub> with metaconid distinct: *Bunomeryx*, *Hylomeryx* (late), *Pentacemylus*, *Mytonomeryx*, *Microsus*, *Hexacodus* (in part), *Antiacodon*, *Protoreodon*, *Diplobunops*, and *Leptoreodon*.

P<sub>4</sub> with metaconid weak: *Hexacodus* (part), *Hylomeryx* (early), and *Poebromylus*.

P<sub>4</sub> with posterointernal crest instead of metaconid: *Protylopus* and *Leptotragulus*.

P<sub>4</sub> without metaconid: *Homacodon*, HELOHYINAE, DIACODEXINAE, and *Simimeryx*.

Lower molars with emphasized styles lingually on metaconid and entoconid: AGRIOCHOERIDAE.

Lower molars with moderate styles on metaconid but subdued or absent from entoconid: OROMERYCIDAE, *Simimeryx*, and LEPTOTRAGULINAE.

Lower molars without or with but feebly developed lingual styles: HOMACODONTINAE, HELOHYINAE, DIACODEXINAE, and POEBROTHERIINAE.

Lower molars with parastylid on anterior crest of metaconid: *Protylopus* (early stages), *Oromeryx?*, *Camelodon?*, AGRIOCHOERIDAE, and LEPTOTRAGULINAE.

Lower molars with parastylid from anterior crest of protoconid: *Protylopus* (later stages).

Lower molars with paraconid placed close to metaconid, possibly developed by twinning: *Microsus* (M<sub>1</sub> and possibly other molars), *Hexacodus*, *Antiacodon*, *Diacodexis*, *Wasatchia*, *Helohyus*, *Lophiohyus*, and *Parahyus* (M<sub>1</sub>).

Lower molars without paraconid or parastylid: *Homacodon* (possibly on M<sub>2</sub>?), *Bunomeryx*, *Hylomeryx*, *Pentacemylus*, *Mytonomeryx*, and *Poebrodon*.

Lower molars with crescentic outer cusps, but distinct median pocket developed by forward direction of anterior crest of hypoconid. Entoconid united forward with crest only to metaconid: AGRIOCHOERIDAE and *Simimeryx*.

Lower molars with crescentic outer cusps, but distinct median pocket opens lingually posterior to the metastylid. Entoconid isolated forward: OROMERYCIDAE.

Lower molars with crescentic outer cusps, but anterior crest of hypoconid as well as posterior crest of protoconid directed lingually. Entoconid united forward by crest only with metaconid: LEPTOTRAGULINAE.

Lower molars with crescentic outer cusps, but anterior crest of hypoconid as well as posterior crest of protoconid directed lingually and united separately with entoconid and metaconid, respectively. Entoconid united forward by crest to metaconid as well as to hypoconid: POEBROTHERIINAE.

Lower molars essentially bunodont with no significant crest between metaconid and entoconid: HOMACODONTINAE, HELOHYINAE, and DIACODEXINAE.

M<sub>1</sub> and M<sub>2</sub> with pronounced hypoconulid developed from cingulum and posterior to saddle between hypoconid and entoconid: HOMACODONTINAE.

- M<sub>1</sub> and M<sub>2</sub> with pronounced hypoconulid developed on crest or saddle between hypoconid and entoconid: DIACODEXINAE (generally weak in *Bunophorus*).
- M<sub>1</sub> and M<sub>2</sub> with weak hypoconulid often on both cingulum posteriorly and in saddle between hypoconid and entoconid, very close to hypoconid: *Helohyus*.
- M<sub>1</sub> and M<sub>2</sub> of forms having crescentic lower molars with hypoconulid often though not invariably developed as a posteriorly directed spur from posterior crest of hypoconid: AGRIOCHOERIDAE and OROMERYCIDAE.
- M<sub>1</sub> and M<sub>2</sub> of forms having crescentic lower molars with hypoconulid often though not invariably developed as an enlarged or emphasized postero-internal extremity of the crest of the hypoconid: LEPTOTRAGULINAE.
- M<sub>1</sub> and M<sub>2</sub> essentially without hypoconulid: *Parahyus*, *Achaenodon*, and Poë-BROTHERIINAE; sometimes AGRIOCHOERIDAE and LEPTOTRAGULINAE.

### SYSTEMATIC REVISION

#### Family DICHOBUNIDAE Gill, 1872

As arranged by Simpson (1945) this family includes the two subfamilies Dichobuninae and Homacodontinae. Within the Dichobuninae he has included, along with the various European genera, the three North American lower Eocene forms, *Diacodexis*, *Wassatchia*, and *Bunophorus*. Structurally these three are similar to one another and are properly grouped together, but basically they are less like the dichobunes, as represented by such genera as *Dichobune*, *Meniscodon* and *Mouillacitherium*, than are the homacodonts. I am convinced that their degree of relationship is best indicated by separating them into a separate subfamily within the Dichobunidae and designated, as shown in the accompanying chart, by the name of Diacodexinae.

Among the middle Eocene forms, Simpson, as tentatively suggested by Matthew and Granger (1925), has included *Helohyus* in the Choeropotamidae. I am rather inclined to believe, as Stehlin (1906) has indicated and as followed by Sinclair (1914), that *Helohyus* has affinities with the Dichobunidae. The degree of relationship, however, I again regard as best represented by a subfamily separation, including the end product *Achaenodon*, an arrangement anticipated by Matthew and Granger (1925) as an alternate possibility. Nevertheless, their indication that under such an arrangement the forms included would comprise the family Helohyidae is followed only to a degree, because, referring to Matthew's (1910, p. 41) earlier thinking in connection with *Eotylopus*: "If we adopt the 'linear' system and ignore the more important and obvious structural differences between animals, on the plea that they are merely stages in specialization, if we scatter apart a closely related group of ancestral forms among widely divergent types to which they have given rise,

we involve ourselves in a very doubtful and changeable arrangement, dependent upon hypotheses of relationship instead of facts of structural affinity." As explained later, the name Helohyinae is used rather than Zittel's name Achaenodontinae.

#### Subfamily HOMACODONTINAE Peterson, 1919

Two of the dichobunids listed by Simpson (1945) as uncertain in position, *Microsus* and *Antiacodon*, would both appear to be homacodonts. *Microsus*, the oldest of the North American dichobunid names, is clearly to be placed among the homacodonts. Comparison of the type of *Microsus cuspidatus* Leidy with the lower jaw belonging to the type of *Homacodon vagans* Marsh reveals little to distinguish these forms but size. The *Microsus cuspidatus* type has teeth approximately 20 percent smaller and, in addition, the cusps appear to be relatively high and more acute, with the hypoconid and entoconid better separated. However, the teeth in the *M. cuspidatus* type are less worn than in *H. vagans*, and referred material of *M. cuspidatus* has the hypoconid and entoconid less well separated. Moreover, *Microsus* shows greater tendency to retain the paraconid. It is usually distinct on  $M^1$ , variable on  $M_2$ , and usually absent from  $M_3$ . *Homacodon* is in all probability a genus distinct from *Microsus* but there is rather little to show this in posterior lower molars. In referred material of *M. cuspidatus* it should be noted that  $P_4$  exhibits a metaconid not seen in *H. vagans*, suggesting that the later homacodonts may be more closely allied to *Microsus* than to *Homacodon*. Certain undescribed upper molars in the Bridger collections of the American Museum (Nos. 12146 and 12696), cataloged as questionably *Homacodon*, are almost certainly of *Microsus*. They agree structurally in almost all details with *Homacodon vagans* but are distinctly smaller and the cusps are more delicate and acute, as they would be in *Microsus*.

The genus *Antiacodon* was based on the species *A. venustus* Marsh, but careful comparison of type materials shows this species to be a synonym of *Sarcolemur pygmaeus* (Cope) (= *S. furcatus* Cope), likewise a genotype. Nevertheless, the generic name *Antiacodon* has priority so that the type species becomes *Antiacodon pygmaeus*. Recently (Gazin, 1952, p. 73) the record of the *Antiacodon* stem has been extended down into the lower Eocene by the discovery there of *Hexacodus*. The trigonid of the lower molars in *Hexacodus* shows *Antiacodon* peculiarities in an incipient stage but with less difference from the structure of this part seen in *Microsus*. The talonid of the lower molars, with particular attention to the hypoconulid, is very

much as in *Microsus* and *Homacodon*, and rather like *Protodichobune* as well. *Hexacodus*, and hence *Antiacodon*, are regarded as homacodonts but in a sequence somewhat divergent. Although the end product, *Antiacodon*, would appear to be significantly different and markedly divergent from *Microsus* and *Homacodon*, I have not felt that full subfamily recognition was justified, particularly since *Hexacodus* so closely resembles *Microsus*.

The remaining known genera of homacodonts, i.e., *Bunomeryx*, *Hylomeryx*, *Sphenomeryx*, *Mesomeryx*, and *Pentacemylus*, are all peculiar to the upper Eocene and herein discussed at greater length. One of these, *Sphenomeryx*, is regarded as a synonym of *Hylomeryx*, and the new genus, *Mytonomeryx*, is described. Remains representing species of these have been found so far only in the Uinta formation, except for *Pentacemylus progressus* Peterson, which was originally named from a Duchesne River specimen. *Pentacemylus* is now much better represented by Uinta C material.

#### Genus BUNOMERYX Wortman, 1898

*Type*.—*Bunomeryx montanus* Wortman, 1898.

*Discussion*.—The genus *Bunomeryx* was described by Wortman as a part of his study of the Camelidae, and he recognized its relationship to earlier *Homacodon* while suggesting tentatively that the camels may likewise have so originated. *Bunomeryx* is clearly related to *Homacodon* but is advanced over the Bridger genus in several respects. The outer cusps of the upper molar teeth, with the styles much more emphasized, appear somewhat crescentic in comparison. The presence of a prominent mesostyle is in marked contrast to the older form. The talon of the upper molars shows a progressive development of the protoconule, more noticeable in  $M^2$  and  $M^3$ , and a reduction of the hypocone in  $M^2$ .  $P^4$  shows a somewhat more crescentic outer wall and the deuterocone in  $P^3$  is more pronounced.

The outer cusps of the lower molars are perhaps a little more crescentic than in *Homacodon*, and the hypoconid joins the trigonid more conspicuously. The premolars are lower crowned, but the most striking difference lies in the well-developed metaconid of  $P_4$  in *Bunomeryx*, possibly indicating a closer relationship to *Microsus*.

#### BUNOMERYX MONTANUS<sup>5</sup> Wortman, 1895

*Type*.—Rostral portion of a skull with  $P^2$ - $M^3$  on left side and right canine, and left ramus of mandible with  $P_4$ - $M_3$ , A.M. No. 2071.

<sup>5</sup> Illustrated in Peterson, 1919, pl. 36, figs. 3-4.



*Horizon and locality.*—Uinta C, White River, Uinta Basin, Utah.

*Discussion.*—*Bunomeryx montanus* is the type species and is characterized by having its lower premolar teeth in a continuous sequence, without a diastema between  $P_2$  and  $P_3$ .

There is no indication in Wortman's paper as to the locality within the Uinta Basin from which the type was obtained, but specimen labels bear the information "White River" and "Level C." Three referred specimens in the collections of the U. S. National Museum were found in the White River pocket to the south of the White River near its junction with the Green River. This would indicate a level in the upper part of Uinta B, showing that the vertical range is not restricted to "C." Moreover, it seems probable that if the type is actually from Uinta C the level represented is low.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Bunomeryx montanus*, A.M. NO. 2071

Length of upper cheek tooth series, anterior margin of canine alveolus to posterior margin of $M^3$ .....	36.6a
Length of upper cheek tooth series, anterior margin of alveolus for $P^1$ to posterior margin of $M^3$ .....	32.1
Premolar series, anterior margin of alveolus for $P^1$ to posterior margin of $P^4$ .....	17.8
Molar series, $M^1$ - $M^3$ , inclusive.....	14.7
$P^3$ , anteroposterior diameter: transverse diameter*.....	4.9: 3.9
$P^4$ , anteroposterior diameter: transverse diameter.....	4.0: 5.1
$M^1$ , anteroposterior diameter: transverse diameter*.....	5.2: 6.1
$M^2$ , anteroposterior diameter: transverse diameter.....	5.1: 6.9
$M^3$ , anteroposterior diameter: transverse diameter.....	5.1: 7.0
Lower cheek teeth, $P_4$ - $M_3$ , inclusive.....	21.9
Lower molar series, $M_1$ - $M_3$ , inclusive.....	16.9
$P_4$ , anteroposterior length: greatest transverse width.....	5.2: 3.0
$M_1$ , anteroposterior diameter: transverse diameter of talonid.....	4.8: 3.3
$M_2$ , anteroposterior diameter: transverse diameter of talonid.....	5.4: 4.1
$M_3$ , anteroposterior diameter: transverse diameter of trigonid.....	6.8: 3.9

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

**BUNOMERYX ELEGANS** <sup>6</sup> Wortman, 1898

*Type.*—Palatal portion of skull with  $P^2$ - $M^3$  of right and part of left series, and both rami of mandible, right with  $P_2$ - $M_3$ , A.M. No. 2066A.

*Horizon and locality.*—Uinta, White River, Uinta Basin, Utah.

<sup>6</sup> Illustrated in Wortman, 1895, fig. 2.

*Discussion.*—*Bunomeryx elegans* was the second of the two species described by Wortman. The principal justification given for separate recognition is in the short diastema between  $P_2$  and  $P_3$ . Also, Wortman stated that all the teeth in *B. elegans* are smaller, and particularly  $P_4$ , which is considerably narrower and has a less-developed internal cusp. Moreover, it is stated that  $M^2$  has a better-developed hypocone. Doubt may be entertained as to the validity of this species, as some of the characters cited cannot be well defended. The length of the diastema between  $P_2$  and  $P_3$  in *B. elegans* is about 2.5 mm. In a Carnegie Museum specimen (No. 2951), that was referred to by Peterson (1919, p. 67) and otherwise corresponds to *B. elegans*, there is a diastema of 1.3 mm. On the other hand, a U.S.N.M. specimen (No. 20394) of *B. montanus*, that has this portion preserved, has a diastema of 1.1 mm., so that Wortman's "most important" difference appears to be a variable character. Moreover, not all the teeth of *B. elegans* are smaller, as  $M^2$  and probably  $M^3$  are equally as large as in the type of *B. montanus*. The lower teeth, however, are narrower and  $P_4$  is shorter, and although these differences are not great it is on

MEASUREMENTS IN MILLEMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Bunomeryx elegans*, A.M. NO. 2066

Length of upper cheek tooth series, $P^2$ - $M^3$ , inclusive.....	28.7a
Length of upper molar series, $M^1$ - $M^3$ , inclusive.....	15.5a
$P^2$ , anteroposterior diameter: transverse diameter*.....	4.3: 1.7
$P^3$ , anteroposterior diameter: transverse diameter.....	4.6: 3.6
$P^4$ , anteroposterior diameter: transverse diameter.....	3.7: 4.7
$M^1$ , anteroposterior diameter: transverse diameter*.....	5.0: 5.8
$M^2$ , anteroposterior diameter: transverse diameter.....	5.4: 6.8
$M^3$ , anteroposterior diameter: transverse diameter.....	5.4:...
Length of lower cheek tooth series, anterior margin of canine alveolus to posterior margin of $M_3$ .....	38.4a
Length of cheek tooth series, anterior margin of alveolus for $P_1$ to pos- terior margin of $M_3$ .....	35.5a
Length of premolar series, anterior margin of alveolus for $P_1$ to pos- terior margin of $P_4$ .....	18.8a
Length of molar series, $M_1$ - $M_3$ , inclusive.....	16.7
$P_2$ , anteroposterior diameter: greatest transverse diameter.....	4.6a: 1.7
$P_3$ , anteroposterior diameter: greatest transverse diameter.....	4.7: 2.1
$P_4$ , anteroposterior diameter: greatest transverse diameter.....	4.7: 2.8
$M_1$ , anteroposterior diameter: transverse diameter of talonid.....	5.2: 3.6
$M_2$ , anteroposterior diameter: transverse diameter of talonid.....	5.2: 3.9
$M_3$ , anteroposterior diameter: transverse diameter of trigonid.....	6.9: 3.5

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

the basis of them that a tentative separation may be made. The greater development of the vestigial hypocone on  $M^2$  and the lesser development of the metaconid on  $P_4$  are not significant.

There is no certain indication on the specimen label of the type of *B. elegans* as to the horizon of the Uinta in which it was found, except that it came from near the White River. Carnegie Museum No. 2951, referred to *B. elegans*, has the information "Uinta B, Wagonhound, White River, near Ouray, Utah," on the label accompanying it, so that so far only Uinta B has been demonstrated for this species.

#### Genus *HYLOMERYX* Peterson, 1919

*Synonym?*.—*Sphenomeryx* Peterson, 1919.

*Type*.—*Hylomeryx annectens* Peterson, 1919.

*Discussion*.—The genus *Hylomeryx*, the second dichobunid to be named from the Uinta, appears to be clearly distinct from *Bunomeryx* and, although contemporary with the latter, it is more like *Homacodon* in many respects. The outer cusps of the upper molars are, for the most part, rather more conically bunodont than in *Bunomeryx*, resembling *Homacodon*. Also, as in *Homacodon*, the hypocone is a well-developed, circular cone on  $M^1$  and  $M^2$  and but a very slight expression of the cingulum on  $M^3$ . The mesostyle is very weak or in an incipient stage, intermediate between *Homacodon* and *Bunomeryx*. The protoconule, however, is rather different from both in that it seems scarcely defined on the protoloph of  $M^2$  and  $M^3$ . It is more distinctive on  $M^1$ .

The premolar teeth, both upper and lower, are relatively large and robust in comparison with those in species of *Bunomeryx*. Moreover, small diastemata may separate  $P^1$  and  $P_2$  from the adjacent premolars. In the lower premolar series,  $P_4$  has a parastylid and metaconid, but the latter may be weak or blunt in the Uinta B stage to somewhat inflated in the Uinta C stage.

The lower molar teeth are not readily distinguished from those of *Bunomeryx*, although in the type of *Hylomeryx annectens* the protoconid and hypoconid would appear to be a little less crescentic.

*Sphenomeryx* was defined by Peterson as distinct from *Hylomeryx* principally on the absence of a hypocone (posterointernal cusp) on  $M^1$  and the weakness of the deuterocone on  $P^3$ . As far as  $M^1$  is concerned, this appears to have been a misinterpretation.  $M^1$  is rather well worn but under the microscope it is clear, from the enamel construction midway on the metaloph, lingual to the metaconule, that the

hypocone was a well-developed cusp and not just a cingular shelf or prominence. The character of the deuterocone on  $P^3$  is scarcely more than specific in importance when taken with the many similarities. Resemblances allying *Sphenomeryx* to *Hylomeryx* are the very weak or incipient mesostyles; conical paracone, metacone, and (evidently) hypocone; and weak protoconule which nearly loses its identity in a protoloph. As a consequence, *Sphenomeryx* is regarded as a synonym of *Hylomeryx*; however, the single species "*S.*" *quadricuspis* is reported from a later stage of the Uintan and on the basis of small differences noted is retained as a species distinct from *H. annectens*.

#### HYLOMERYX ANNECTENS <sup>7</sup> Peterson, 1919

*Type*.—Anterior portion of a skull and lower jaws, C.M. No. 2335.

*Horizon and locality*.—Uinta B, Red Bluff wash between White and Green Rivers, Uinta County, Utah.

*Discussion*.—*Hylomeryx annectens* is a little larger, particularly in the premolars, than *Bunomeryx montanus*.  $P^3$  in the type specimen shows a prominent deuterocone much as in *B. montanus*, but  $P^4$  as exposed on the right side appears abnormal. The outer wall is

#### MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF *Hylomeryx annectens*, C.M. NO. 2335

Length of upper cheek series, anterior margin of alveolus for $P^1$ to posterior margin of $M^3$ .....	38.5
Upper premolar series, anterior margin of alveolus for $P^1$ to posterior margin of $P^4$ .....	22.1
Upper molar series, $M^1$ - $M^3$ , inclusive.....	16.5
$P^2$ , anteroposterior diameter: greatest transverse diameter.....	5.4: 2.1
$P^3$ , anteroposterior diameter: transverse diameter*.....	5.8: 4.5
$P^4$ , anteroposterior diameter: transverse diameter.....	4.8: 5.1
$M^1$ , anteroposterior diameter: transverse diameter*.....	5.7: 6.5
$M^2$ , anteroposterior diameter: transverse diameter.....	5.7: 6.9a
$M^3$ , anteroposterior diameter: transverse diameter.....	5.4: 6.7
Lower cheek tooth series, anterior margin of alveolus for $P_2$ to posterior margin of root portion of $M_3$ .....	37.8a
Lower molar series, $M_1$ to posterior margin of root portion of $M_3$ ....	18.5a
$P_4$ , anteroposterior diameter: greatest transverse diameter.....	5.9: 3.3
$M_1$ , anteroposterior diameter: transverse diameter of talonid.....	5.8: 3.7
$M_2$ , anteroposterior diameter: transverse diameter of talonid.....	5.8a: 4.1
$M_3$ , anteroposterior diameter: transverse diameter of trigonid.....	7.0a: 4.0

a. Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

<sup>7</sup> Illustrated in Peterson, 1919, figs. 8-10, pl. 36, figs. 5-6.

strikingly convex, anteroposteriorly, and the primary cusp and deuterocone seem pinched together, not at all like other Uintan dichobunids. The occlusal surface of this tooth on the left side is not exposed, but the external wall appears comparatively normal; as a consequence, characters exhibited by the right  $P^4$  probably should not be stressed. If  $P_4$ , the corresponding tooth below and on the same side, can be regarded as normal, the metaconid is very weak. It represents a stage of development advanced over *Homacodon vagans*, but apparently less progressive in this respect than in *Microsus cuspidatus*, as observed in referred specimens of these Bridger forms.

#### HYLOMERYX QUADRICUSPIS<sup>8</sup> (Peterson), 1919

Plate 3, figure 4

*Type*.—Portions of right and left maxillae and rami of the mandible, C.M. No. 2346.

*Horizon and locality*.—Uinta C, south of Kennedy's hole, west of Dragon-Vernal road, Uinta County, Utah.

*Discussion*.—*Hylomeryx quadricuspis* is the type of the genus *Sphenomeryx* which is regarded as a synonym of *Hylomeryx*. The species *H. quadricuspis* is apparently distinct but very close in size to *H. annectens*. The anteroposterior dimensions of the upper and lower teeth are about the same in the types of the two species; however, the upper molars measure a trifle less and the lowers a trifle greater in transverse width than in *H. annectens*. The principal differences noted include a weaker deuterocone on  $P^3$  and a transversely

#### MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF

##### *Hylomeryx quadricuspis*, C.M. NO. 2346

$P^3$ , anteroposterior diameter : transverse diameter*.....	5.9 : 4.1
$P^4$ , anteroposterior diameter : transverse diameter.....	4.9 : 6.1a
$M^1$ , anteroposterior diameter : transverse diameter*.....	5.4 : 6.2
Lower cheek teeth, anterior margin of alveolus for $P_3$ to posterior margin (estimated) of $M_3$ .....	32.0a
Lower molar series, $M_1$ - $M_3$ (estimated), inclusive.....	19.2a
$P_3$ , anteroposterior diameter.....	6.1a
$P_4$ , anteroposterior diameter : greatest transverse diameter.....	5.9 : 3.5
$M_1$ , anteroposterior diameter : transverse diameter of talonid.....	5.9 : 3.9
$M_2$ , anteroposterior diameter : transverse diameter of talonid.....	5.8 : 4.4
$M_3$ , anteroposterior diameter : transverse diameter of trigonid.....	7.5a : 4.0

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

<sup>8</sup> Also illustrated in Peterson, 1919, pl. 37, figs. 15-16.

much broader  $P^4$  in *H. quadricuspis*, although as noted in the discussion of the preceding species,  $P_4$  in *H. annectens* may not be normal. In the lower series  $P_4$  has a better-developed and rather inflated appearing metaconid. Also, the lower molars may be just a little more crescentic.

*Hylomeryx quadricuspis* is recorded as coming from a higher horizon in the Uinta formation than *H. annectens* and may well be descendent from it.

#### Genus MESOMERYX Peterson, 1919

*Type*.—*Mesomeryx grangeri* Peterson.

*Discussion*.—*Mesomeryx* is a genus clearly distinct from the foregoing, having comparatively simple, bunodont teeth. It is distinguished primarily by the absence of both the mesostyle and hypocone of the upper molars. The outer walls of the upper teeth are more like *Homacodon* than are the corresponding teeth of *Hylomeryx*, as the latter exhibits an incipient mesostyle. The outer portion of the upper molars of *Mesomeryx*, and *Homacodon* as well, are surprisingly like *Hyopsodus*. *Mesomeryx* differs from both *Hylomeryx* and *Homacodon* in lacking the hypocone in both  $M^1$  and  $M^2$ . It should be noted, however, that  $M^1$  in *Mesomeryx* exhibits a definite flexure of the cingulum at the position of the hypocone, but this is in no way comparable to the development of this cusp in either *Homacodon* or *Hylomeryx*. In *Bunomeryx* the cusp, though feeble in  $M^2$ , is robust on  $M^1$ ; moreover, upper molars of *Bunomeryx* further differ in the prominent development of a mesostyle. The extent to which the protoconule is defined in *Mesomeryx* molars cannot be surely determined owing to the degree of wear in the type and only known specimen of the genotype, *M. grangeri*. This portion of the upper molars would appear to be developed as a protoloph, but in all probability the protoconule was distinct in less-advanced wear. The triangular shape of the metaconule in advanced wear would suggest that this cusp tended to be somewhat crescentic in *Mesomeryx*.

The upper premolars in *Mesomeryx* appear to be unspecialized, with  $P^4$  rather like that in *Bunomeryx*.  $P^3$ , however, is somewhat shortened anteroposteriorly, particularly in the anterior portion, giving the deutocone the appearance of having a more forward position on the tooth.

The lower teeth of *Mesomeryx* are not known.

*Mesomeryx* appears to be the only Uintan artiodactyl known which possesses a combination of characters suggesting an ancestral posi-

tion with respect to *Simimeryx* and *Hypertragulus*. This has been considered by Stock (1934) and is further discussed in the portion of this paper treating with the hypertragulids. The possible ancestry of *Mesomeryx* may likely be in a middle Eocene homacodont rather like *Homacodon*, but having a reduced or no hypocone on the upper molars. *Mesomeryx* is rather like *Microsus*, but here again the difference lies in the absence of a hypocone.

#### MESOMERYX GRANGERI<sup>9</sup> Peterson, 1919

*Type*.—Left maxilla with P<sup>3</sup> to M<sup>2</sup>, inclusive, C.M. No. 3189.

*Horizon and locality*.—The horizon and locality are given as Uinta, lower C, 2 miles east of Dragon-Vernal stage road, Uinta Basin, Utah, by Peterson (1919, p. 73); however, the specimen label gives the information "Uinta B" and "N. E. of Well No. 2." It was collected by Douglass in 1908.

*Discussion*.—*Mesomeryx grangeri* is much the smallest of the upper Eocene artiodactyls, and almost as small as the middle Eocene *Microsus cuspidatus*. Other characters of specific importance cannot be determined as there is but one species known.

#### MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF *Mesomeryx grangeri*, C.M. NO. 3189

P <sup>3</sup> , anteroposterior diameter : transverse diameter*	4.4 : 3.3
P <sup>4</sup> , anteroposterior diameter : transverse diameter	3.4 : 4.7
M <sup>1</sup> , anteroposterior diameter : transverse diameter*	4.6 : 5.4
M <sup>2</sup> , anteroposterior diameter : transverse diameter	4.8 : 6.5

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

#### Genus PENTACEMYLUS Peterson, 1931

*Type*.—*Pentacemylus progressus* Peterson.

*Discussion*.—*Pentacemylus* is clearly related to *Bunomeryx* but distinctly more progressive. It is different than the earlier *Bunomeryx*, principally in exhibiting noticeably more crescentic cusps on the upper molars and in the loss of the hypocone on M<sup>1</sup>. *Bunomeryx* has a well-developed hypocone on M<sup>1</sup> and a vestige on M<sup>2</sup>, whereas *Pentacemylus* may have only a slight vestige of this cusp on the cingulum of M<sup>1</sup> and no evidence of it on M<sup>2</sup>. The upper premolars appear to be only slightly more crescentic than in *Bunomeryx*, as noted principally in the deuterocones.

<sup>9</sup> Illustrated in Peterson, 1919, pl. 36, fig. 17.

The lower molars may be a little more hypsodont and possibly more crescentic than in *Bunomeryx*. In the lower premolar series, the paraconid of  $P_3$  in *Pentacemylus* is more clearly defined and that in  $P_4$  is distinctly larger.

*Pentacemylus* very likely evolved from *Bunomeryx*, and the differences between the two are of no great magnitude. These differences, however, appear to be definitive and rather significant considering the shortness of the interval of time separating the known materials of the species of each.

#### PENTACEMYLUS PROGRESSUS<sup>10</sup> Peterson, 1931

Plates 2 (above) and 3, figures 2, 3

*Type*.—Upper molars  $M^2$  and  $M^3$  and lower teeth, including  $M_1$ ,  $M_2$ , and part of  $P_4$ , C.M. No. 11865.

*Horizon and locality*.—Randlett horizon of Duchesne River formation (upper Uintan), 3 miles north of Leota Ranch and 1 mile west of Green River, Uinta County, Utah.

*Discussion*.—The species *Pentacemylus progressus* is much larger than *Bunomeryx montanus* and only a little larger than *Hylomeryx annectens*. *P. progressus* and the new form herein described as *Mytonomeryx scotti* are the largest known homacodonts.

*P. progressus* was originally described, as noted above, from the Randlett or lower member of the Duchesne River formation, but collections obtained by the U. S. National Museum from a quarry in Myton pocket show that it is also represented in the Uinta C fauna, and by considerably more material.

#### MEASUREMENTS IN MILLIMETERS OF DENTITION IN SPECIMENS OF *Pentacemylus progressus*

	C.M. No. 11865 Type	U.S.N.M. No. 20440	U.S.N.M. No. 20435
Length of upper cheek tooth series, C- $M^3$ , inclusive .....	....	45.6	....
Length of upper cheek tooth series, anterior margin of alveolus for $P^1$ to posterior margin of $M^3$ .....	....	40.7 <sup>a</sup>	....
Upper premolar series, anterior margin of alveolus for $P^1$ to posterior margin of $P^4$ .....	....	23.0 <sup>a</sup>	....
Upper molar series, $M^1$ - $M^3$ , inclusive.....	....	18.6	18.9
C, anteroposterior diameter: transverse diameter..	....	4.0: 2.5	....
$P^3$ , anteroposterior diameter: transverse diameter*	....	6.4: 5.0	6.0: 4.4
$P^4$ , anteroposterior diameter: transverse diameter.	....	5.0: 6.4	4.8: 5.7

<sup>10</sup> Also illustrated in Peterson, 1931b, fig. 9; and Scott, 1945, pl. 1, figs. 5-6.



	C.M. No. 11865 Type	U.S.N.M. No. 20440	U.S.N.M. No. 20435
M <sup>1</sup> , anteroposterior diameter: transverse diameter*	....	6.3:7.7	6.3:7.7
M <sup>2</sup> , anteroposterior diameter: transverse diameter.	6.6:8.7 <sup>a</sup>	6.7:8.6	6.7:8.3
M <sup>3</sup> , anteroposterior diameter: transverse diameter.	....:8.5	6.3:8.2	6.5:8.2
		U.S.N.M. No. 20438	U.S.N.M. No. 20437
Length of lower cheek tooth series, C-M <sub>3</sub> , inclusive .....	....	48.0 <sup>a</sup>	49.0 <sup>a</sup>
Length of lower cheek tooth series, P <sub>1</sub> -M <sub>3</sub> , inclusive .....	....	43.4 <sup>a</sup>	44.0 <sup>a</sup>
Lower premolar series, P <sub>1</sub> -P <sub>4</sub> , inclusive.....	....	22.5	23.0 <sup>a</sup>
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	....	20.8 <sup>a</sup>	21.0
C, anteroposterior diameter: greatest transverse diameter .....	....	4.1 <sup>a</sup> :2.4	....
P <sub>1</sub> , anteroposterior diameter: greatest transverse diameter .....	....	4.2 <sup>a</sup> :2.4	....
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter .....	....	5.5:2.1	6.1:2.2
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter .....	....	6.3:2.6	6.8:2.7
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter .....	6.2:...	6.0:3.9	6.1:3.6
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid .....	6.2 <sup>a</sup> :4.4	6.3:4.7	6.3:4.9
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid .....	6.7 <sup>a</sup> :4.7	6.5:5.0	6.2:...
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid .....	....	...:4.7	8.7:...

<sup>a</sup>, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

#### PENTACEMYLUS LEOTENSIS,<sup>11</sup> new species

*Type*.—Rostral portion of skull and left ramus of mandible, P.U. No. 16310.

*Horizon and locality*.—Upper Uinta C, Leota Ranch artiodactyl quarry, Uinta Basin, Utah.

*Specific characters*.—Size distinctly smaller than *Pentacemylus progressus*. Premolars relatively small and separated by short diastemata anterior to P<sup>3</sup> and P<sub>4</sub>.

*Discussion*.—So far, all the known material of *Pentacemylus leotensis*, which consists of approximately a couple of dozen jaws and maxillae, was obtained by Princeton University from a quarry at the old Leota Ranch on the west side of the Green River several miles

<sup>11</sup> Named from the Leota Ranch.

above Ouray. Although there were three specimens from this quarry tentatively referred to *Pentacemylus progressus*, all those referred to *P. leotensis* are characterized by generally smaller and narrower molars. The premolar series may be about as long as in *P. progressus*, but these teeth are significantly smaller and separated from one another anteriorly by more noticeable diastemata.  $P_4$  is decidedly small in *P. leotensis*.

An interesting comparison may be made of the artiodactyl elements in the two above-mentioned quarries. The Leota Ranch quarry, which Dr. John Clark informs me is stratigraphically higher in the

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Pentacemylus leotensis*

	P.U. No. 16310 Type	P.U. No. 16351
Length of upper cheek tooth series, C (at alveolus)- $M^3$ , inclusive .....	43.0a	43.8
Length of upper cheek tooth series, $P^1$ - $M^3$ , inclusive.....	37.0	38.5
Upper premolar series, $P^1$ - $P^4$ , inclusive.....	20.5	21.8
Upper molar series, $M^1$ - $M^3$ , inclusive.....	16.8	17.0a
C, anteroposterior diameter (at margin of enamel): greatest transverse diameter.....	.....	3.0:2.1
$P^1$ , anteroposterior diameter: greatest transverse diameter..	4.0:1.8	4.1:1.4
$P^2$ , anteroposterior diameter: greatest transverse diameter..	4.9:2.3	4.5:1.9
$P^3$ , anteroposterior diameter: transverse diameter*.....	5.4:4.0	5.5:4.2
$P^4$ , anteroposterior diameter: transverse diameter.....	4.0:5.4	4.2:5.5
$M^1$ , anteroposterior diameter: transverse diameter*.....	5.4:6.9	5.3:...
$M^2$ , anteroposterior diameter: transverse diameter.....	5.8:...	6.0:7.7
$M^3$ , anteroposterior diameter: transverse diameter.....	6.0:7.2a	.....
Length of lower cheek tooth series, C (at alveolus)- $M_3$ , inclusive .....	48.5	43.5
Length of lower cheek tooth series, $P_1$ (at alveolus)- $M_3$ , inclusive .....	44.8	39.3
Lower premolar series, $P_1$ (at alveolus)- $P_4$ , inclusive.....	24.2	21.2
Lower molar series, $M_1$ - $M_3$ , inclusive.....	20.7	18.3
C, anteroposterior diameter (at margin of enamel): greatest transverse diameter.....	2.2a:...	2.7:1.6
$P_1$ , anteroposterior diameter: greatest transverse diameter..	3.0:1.8	.....
$P_2$ , anteroposterior diameter: greatest transverse diameter..	5.0a:1.7a	.....
$P_3$ , anteroposterior diameter: greatest transverse diameter..	...:2.3	5.4:2.0
$P_4$ , anteroposterior diameter: greatest transverse diameter..	5.9a:3.1	5.4:2.9
$M_1$ , anteroposterior diameter: transverse diameter of talonid.	6.0a:3.7	5.3:3.8a
$M_2$ , anteroposterior diameter: transverse diameter of talonid.	6.3:4.3	5.7:4.6
$M_3$ , anteroposterior diameter: transverse diameter of trigonid	8.2:4.0	7.7:4.3

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

Uinta C sequence than the *Protylopus annectens* quarry in Myton pocket, has produced, if not always smaller-, essentially narrower-toothed forms. About 90 percent of the *Pentacemylus* material from Leota quarry is *P. leotensis*, perhaps all the *Protoreodon* material is *P. primus*, and all the *Leptotragulus* specimens appear to be *L. clarki*. At Myton pocket all the pentacemylids are *P. progressus*, the equivalent large protoreodont is *P. pumilus annectens*, and about 85 percent of the *Leptotragulus* specimens are *L. medius*. It is highly improbable that the difference in each case is to be accounted for by dimorphism within a species. Moreover, the localities are less than 20 miles apart, and both *P. progressus* and *P. pumilus annectens* noted above in the Myton locality are recorded from the Randlett horizon, still later than the Leota quarry.

#### MYTONOMERYX,<sup>12</sup> new genus

*Type*.—*Mytonomeryx scotti*, new species.

*Generic characters*.—Elongate rostrum with marked diastemata separating the first and second premolars, above and below, from adjacent teeth. M<sup>1</sup> and M<sup>2</sup> noticeably quadrate and both with a well-developed hypocone. Upper molars moderately selenodont with prominent mesostyle.

*Discussion*.—*Mytonomeryx* resembles closely contemporary *Pentacemylus* in the progressiveness of its selenodont tooth structure over that of earlier *Bunomeryx*, but differs strikingly from *Pentacemylus* in retention of a prominent hypocone on both M<sup>1</sup> and M<sup>2</sup>. In this respect it differs also from *Bunomeryx*, which has nearly or quite lost this cusp on M<sup>2</sup>. Retention of the hypocone is suggestive of *Hylomeryx*, but in this stem there is a tendency toward the development of a protoloph and the external styles are weak, with the mesostyle weak or absent. *Mytonomeryx* would appear to have derived from the *Pentacemylus* line but separating from it earlier than the *Bunomeryx* stage.

#### MYTONOMERYX SCOTTI,<sup>13</sup> new species

Plates 1, 2 (below), and 3, figure 1

*Type*.—Skull, jaws, and other skeletal portions, U.S.N.M. No. 20401.

*Horizon and locality*.—Uinta C, Myton pocket, 7 miles east of Myton, Duchesne County, Utah.

<sup>12</sup> From Myton, locality; and Greek μῆρυξ, ruminant.

<sup>13</sup> Named for Prof. W. B. Scott.

*Specific characters.*—Comparable in size with contemporary *Pentacemylus progressus*, but with cheek teeth slightly smaller. Other characters not distinguished from those cited for the genus.

*Discussion.*—In addition to the particular characters of the upper molars distinguishing *Mytonomeryx*, it was noticed that the type of *M. scotti* exhibits a strikingly elongate snout with marked spacing of the premolars between the canine and P3 above and below. From the molar region forward the elongation is somewhat greater than in the larger-toothed *Pentacemylus progressus*, and relatively greater than in the smaller *Pentacemylus leotensis*. Some difficulty has been experienced in distinguishing between lower jaws of *Mytonomeryx scotti* and *Pentacemylus leotensis*, as the latter likewise shows a spacing of the premolars. Differences were noted between the two, such as broader molars, somewhat less reduced size of premolars, possibly better-developed parastylid of lower premolars, somewhat greater length of premolar series, and the absence of a diastema between P<sub>3</sub>

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Mytonomeryx scotti*, U.S.N.M. NO. 20401

Length of upper cheek tooth series, C-M <sup>3</sup> , inclusive.....	49.7 <sub>a</sub>
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive.....	43.1 <sub>a</sub>
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive.....	25.8 <sub>a</sub>
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	17.9
C, anteroposterior diameter (at alveolus) : greatest transverse diameter.	3.8 : 2.8
P <sup>1</sup> , anteroposterior diameter : greatest transverse diameter.....	4.3 : 1.8
P <sup>2</sup> , anteroposterior diameter : transverse diameter*.....	6.0 : 4.6
P <sup>3</sup> , anteroposterior diameter : transverse diameter.....	4.7 : 5.8
M <sup>1</sup> , anteroposterior diameter : transverse diameter*.....	5.9 : 7.3
M <sup>2</sup> , anteroposterior diameter : transverse diameter.....	6.3 : 7.8
M <sup>3</sup> , anteroposterior diameter : transverse diameter.....	6.2 : 7.5
Length of lower cheek tooth series, C (at alveolus)-M <sub>3</sub> , inclusive.....	50.1
Length of lower cheek tooth series, P <sub>1</sub> -M <sub>3</sub> , inclusive.....	46.0
Lower premolars, P <sub>1</sub> -P <sub>4</sub> , inclusive.....	26.4
Lower molars, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	19.7
C, anteroposterior diameter (at alveolus) : greatest transverse diameter.	2.7 : 2.1
P <sub>1</sub> , anteroposterior diameter : greatest transverse diameter.....	3.6 : 2.2
P <sub>2</sub> , anteroposterior diameter : greatest transverse diameter.....	5.0 : 2.1
P <sub>3</sub> , anteroposterior diameter : greatest transverse diameter.....	5.7 : 2.6
P <sub>4</sub> , anteroposterior diameter : greatest transverse diameter.....	5.9 : 3.6
M <sub>1</sub> , anteroposterior diameter : transverse diameter of talonid.....	5.7 : 4.3
M <sub>2</sub> , anteroposterior diameter : transverse diameter of talonid.....	6.0 : 4.6
M <sub>3</sub> , anteroposterior diameter : transverse diameter of trigonid.....	8.5 : 4.6

<sub>a</sub>, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

and  $P_4$  in *M. scotti*, but these are not on a generic level and some, such as the size of teeth and relative size of premolars with respect to molars, are only intermediate between *Pentacemylus progressus* and *P. leotensis*. Nevertheless, the lower premolar spacing is greater and characterizes only the forward part of the series in *M. scotti*, whereas in *P. leotensis* the diastemata are short and nearly the same between all lower premolars.

#### Subfamily HELOHYINAE (from HELOHYIDAE Marsh, 1877)

With regard to the suprageneric arrangement suggested in the chart, *Helohyus*, though not regarded by all as an homacodont, seems closely allied to the genus *Homacodon*, so that separation of this short-lived but rapidly evolving stem with full family recognition, I believe, is unwarranted. As a subfamily its relationships are better demonstrated, and at the same time its direction and its distinctness are given recognition. I prefer also to include this subfamily along with Homacodontinae, under the Dichobunidae, because of the more clearly demonstrable relationship, as indicated in the chart, rather than with the chronologically more remote and distinctive entelodonts. The name Helohyinae is selected rather than Achaenodontinae (Zittel, 1893) as it is based on the older familial designation Helohyidae (Marsh, 1877). Moreover, this name does not carry the implication of including the entelodonts as originally defined, or of being a subfamily of the Entelodontidae as later assigned, as does Zittel's Achaenodontinae.

#### Genus ACHAENODON Cope, 1873

*Synonym.*—*Protelotherium* Osborn, 1895.

*Type.*—*Achaenodon insolens* Cope, 1873.

*Discussion.*—*Achaenodon* was described by Cope on the basis of the species *A. insolens*, from Washakie beds, which he regarded as an arctocyonid creodont. Osborn in 1883 demonstrated its true position to be in the Artiodactyla and, while believing it near the entelodonts, regarded it as belonging in the "ancestral Suidae." Zittel in 1893 placed the entelodonts and achaenodonts together in the subfamily Achaenodontinae under the Suidae. Matthew in 1899 proposed full family recognition, Achaenodontidae, distinct from both Suidae and Entelodontidae (Elotheriidae). He was followed in this interpretation by Peterson (1919). More recently Colbert (1938), in his study of *Brachyhyops*, considered the Achaenodontinae as a subfamily of the Entelodontidae.

Critical examination of the known *Achaenodon* material leads me to

the conclusion that *Achaenodon* and *Archaeotherium*, though both possibly somewhat similarly adapted as large bunodont, piglike animals, in many details of dental structure followed divergent lines. *Achaenodon* is almost surely derived from the Bridger *Helohyus*, and *Parahyus* is an admirable link between the two. There appear to be no important obstacles to such an interpretation, and the resemblance in the dentition is striking. *Achaenodon* achieved considerable size during the interval between Bridger D and Uinta B (or Washakie B) time and developed a somewhat shortened snout, apparently with the loss of a premolar, but the remaining premolars appear to have become robust, though closely placed or crowded. The increased size of the premolars is foreshadowed in *Helohyus* lower-jaw material from Bridger D referred to *H. lentus*. In details of the teeth the *Achaenodon* premolars retain their simple carnivorelike form, and there is little change in the lower molars except size and a somewhat more inflated appearance of the cusps. In the upper molars, however, there has been a trend toward simplification. The rather weak hypocone, which is little more than a prominence of the cingulum in *Helohyus*, is apparently lost in *Achaenodon*, and the protoconule has been much reduced or is absent so that the upper molars have become essentially four cusped.

*Archaeotherium*, which is first known in the Oligocene, may have evolved from *Helohyus* or quite possibly *Lophiohyus*, but this is uncertain. In contrast to *Achaenodon*, *Archaeotherium* developed an elongate snout and retained all its premolars in a well-spaced arrangement. It further developed various bony protuberances on the jaw and arch, and the postorbital processes of the parietal and jugal joined. In details of the teeth, P<sub>3</sub>, rather than P<sub>4</sub>, above and below, became the more prominent or highest crowned of the premolars. The upper molars, rather than becoming more simplified in their structures, gave increasing prominence to the hypocone and protoconule so that the *Archaeotherium* upper molar has essentially six nearly equal cusps and has further given rather marked prominence to the anterior and posterior cingula. Retention of cusps in the lower molars is noted in the rather distinct paraconid and prominent hypoconulid, except that in M<sub>3</sub> the hypoconulid is strikingly reduced (for this tooth) from the primitive structure exemplified in *Helohyus* and in even greater contrast to the development of this cusp in *Achaenodon* and *Parahyus*.

ACHAENODON INSOLENS<sup>14</sup> Cope, 1873

*Type*.—Right and left rami of the mandible with the canine, P<sub>3</sub>, and the last two molars represented, A.M. No. 5143.

*Horizon and locality*.—Washakie B, "Mammoth Buttes," Washakie Basin, Wyoming.

*Discussion*.—*Achaenodon insolens*, the first described species, would appear to be a slender- or shallow-jawed form with relatively elongate molars. The type, according to Granger's listing (1909), is from the upper or B horizon of the Washakie beds, but lower-jaw material from the Uinta B was referred by both Osborn (1895) and Peterson (1919, fig. 11) to this species.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Achaenodon insolens*, A.M. NO. 5143

Length of lower cheek tooth series, C (at alveolus)-M <sub>3</sub> , inclusive...	210.0a
Length of lower cheek tooth series, anterior margin of alveolus for P <sub>2</sub> to posterior margin of M <sub>3</sub> .....	180.0a
Lower molar series, anterior margin of alveolus for M <sub>1</sub> to posterior margin of M <sub>3</sub> .....	92.0a
P <sub>3</sub> , anteroposterior diameter: transverse diameter.....	24.0:17.5
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	26.7:22.5
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	40.0:....

a, Approximate.

ACHAENODON ROBUSTUS<sup>15</sup> Osborn, 1883

*Type*.—Greater portion of the skull and the right ramus of the mandible, P.U. No. 10033.

*Horizon and locality*.—Washakie B, near Haystack Mountain, Washakie Basin, Wyoming.

*Discussion*.—Peterson (1919) regarded this species as distinct from *A. insolens* largely on the basis of the deeper jaw with somewhat shorter molars and relatively larger premolars, particularly P<sub>4</sub>. Shallowness of the jaw in the type of *A. insolens* might have been regarded as immaturity, but the referred specimen figured by Peterson certainly exhibits well-worn teeth. The differences outlined may be no more than might possibly be accounted for in individual variation; however, it would appear that *A. robustus* is somewhat more advanced along the line of development followed in the achaenodonts and somewhat farther removed from *Parahyus* than *A. insolens*.

<sup>14</sup> Illustrated in Cope, 1884, pls. 57 and 57a.

<sup>15</sup> Illustrated in Osborn, 1883, pl. 6; and Peterson, 1919, pl. 39, figs. 1-3.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Achaenodon robustus*, P.U. NO. 10033

Length of upper cheek tooth series, C-M <sup>3</sup> , inclusive.....	185.0
Length of upper cheek tooth series, anterior margin of alveolus for P <sup>2</sup> to posterior margin of M <sup>3</sup> .....	147.0
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	70.0
C, anteroposterior diameter (at alveolus): greatest transverse diameter .....	31.5: 26.5
P <sup>3</sup> , anteroposterior diameter: greatest transverse diameter.....	29.0: 16.5
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	23.0: 27.5
M <sup>1</sup> , anteroposterior diameter: transverse diameter.....	21.8: 25.8
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	24.5: 31.8
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	26.7: 30.0
Length of lower cheek tooth series, C-M <sub>3</sub> , inclusive.....	210.0
Length of lower cheek tooth series, anterior margin of alveolus for P <sub>2</sub> to posterior margin of M <sub>3</sub> .....	172.0
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter.....	24.4: 14.3
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	30.0: 17.5
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	22.5: 17.5
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	24.2: 19.5
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	36.8: 23.0

ACHAENODON UINTENSIS<sup>16</sup> Osborn, 1895

*Type*.—Skull with shattered teeth, A.M. No. 1822.

*Horizon and locality*.—Uinta B, eastern portion of Uinta Basin, Utah.

*Discussion*.—*Achaenodon uintensis* was originally described by Osborn as *Elotherium uintense* and provisionally given the new generic name *Protelotherium*. Peterson, in his monograph on the entelodonts, placed this genus in synonymy with *Achaenodon* and in 1919 outlined his reasons. There appears to be little doubt but that *Protelotherium* is a synonym, and Peterson's critical examination of the distortions affecting the *A. robustus* skull resulted in leaving little of significance to distinguish the species *A. uintensis* other than somewhat greater size. Peterson has also noted the somewhat broader premolars in *A. uintensis* and the presence of an accessory cuspule on M<sup>3</sup>. Much of Peterson's study of this form was based on two referred skulls in the Carnegie Museum stated to be from the same horizon and locality as the type. In reexamining these specimens, as well as material in the American Museum referred to this species, I find differences in proportions between them, particularly in the measurements of teeth, fully as great as there is between the smaller of these and the *A. robustus* type. I am much inclined to regard the species *A.*

<sup>16</sup> Illustrated in Osborn, 1895, figs. 16-17; and Peterson, 1919, pl. 47, figs. 1-4.



*uintensis* as not distinct from *A. robustus*, but since the two are not from the same beds and there may be some doubt as to their age equivalence, *A. uintensis* is tentatively retained.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN A REFERRED SPECIMEN <sup>17</sup>  
OF *Achaenodon uintensis*, A.M., NO. 2047

Length of upper cheek tooth series, anterior margin of alveolus for C to posterior margin of M <sup>3</sup> .....	210.0a
Length of upper cheek tooth series, anterior margin of alveolus for P <sup>2</sup> to posterior margin of M <sup>3</sup> .....	175.0a
Upper molar series, M <sup>2</sup> -M <sup>3</sup> , inclusive.....	83.5
C, anteroposterior diameter (at alveolus) : greatest transverse diameter .....	35.5 : 35.5
P <sup>3</sup> , anteroposterior diameter : greatest transverse diameter.....	32.0 : 23.5
P <sup>4</sup> , anteroposterior diameter : greatest transverse diameter.....	27.5 : 35.5
M <sup>1</sup> , anteroposterior diameter : transverse diameter anteriorly.....	25.0 : 31.0
M <sup>2</sup> , anteroposterior diameter : transverse diameter anteriorly.....	27.0 : 37.0
M <sup>3</sup> , anteroposterior diameter : transverse diameter anteriorly.....	32.5 : 36.0

a, Approximate.

Genus **PARAHYUS** Marsh, 1876

*Type*.—*Parahyus vagus* Marsh, 1876.

*Discussion*.—The close resemblance of *Parahyus* to *Achaenodon* was observed by Osborn (1895), who did not regard the genera as distinct. Osborn noted, however, that Cope believed them to be different, primarily on the assumption that *Achaenodon* had one more premolar. Although this distinction does not exist, *Parahyus* has been rather generally treated as a separate genus, possibly in part as a result of the doubt regarding its geologic age. *Parahyus*, like *Achaenodon*, is characterized by three large, single-cusped premolars, with P<sub>4</sub> much the largest, and simple bunodont molars. However, the one valid species, in addition to being much smaller than *Achaenodon*, has molars relatively much longer in relation to the depth of the jaw and to the length of the premolar series than in *Achaenodon*, in which respect it is about intermediate between *Helohyus* and *Achaenodon*. Like *Achaenodon* it differs from *Helohyus* essentially in the loss of a premolar (if the latter had four, as suggested by Sinclair in 1914); in the more-inflated appearance of the cusps; and in the reduction or suppression of the paraconid on the lower molars and of the hypoconulid on M<sub>1</sub> and M<sub>2</sub>.

<sup>17</sup> Teeth not preserved in type specimen.

PARAHYUS VAGUS<sup>18</sup> Marsh, 1876

*Type*.—Right ramus of mandible with P<sub>3</sub>-M<sub>3</sub>, Y.P.M. No. 10972.

*Horizon and locality*.—The type was described by Marsh as coming from the lower Eocene of Wyoming. This, however, I cannot believe, as *Parahyus vagus* is clearly and in every respect at a stage of development intermediate between Bridger *Helohyus lentus* and Washakie B or Uinta B *Achaenodon insolens*. Moreover, during an intensive field program involving the lower Eocene of southwestern Wyoming in the past several years, no further evidence has been discovered of such a form in the Wasatchian. With the help of Dr. J. T. Gregory, I have carefully gone over the data which accompanied the material in the Marsh collection and have extracted the following information from the labels: The tray label for the type of *P. vagus* bears the information "Lower Eocene Washakie?, Coryphodon zone, Wyoming Bitter Creek Station"; the old exhibition label—"Eocene (Bridger), Bitter Creek Station, J. Heisey Coll. 1876"; and the shipping label—"Bitter Creek Station, Formation ash color, 200 feet above coal, July 8, 1876, J. Heisey." The information gained here is completely confusing, but the principal evidence is that the specimen was included in a shipment made from Bitter Creek Station. Reference to Washakie in one case and Bridger in another is somewhat reassuring, but that pertaining to "Lower Eocene," "Coryphodon zone," and "200 feet above coal" is rather imperiling. It should be noted that the description of *Parahyus vagus* accompanied that of *Eohippus pernix*, and the latter undoubtedly came from the lower Eocene near Bitter Creek, as did Cope's *Coryphodon armatum*. It seems almost certain that the *P. vagus* specimen was confused with materials collected at Bitter Creek, but actually came from the Washakie beds farther to the southwest of there. Bitter Creek Station was likely the shipping point for much of that general region. It did not, of course, come from Evanston, Wyo., as implied in Matthew's 1899 tabulation.

*Parahyus vagus* is apparently, though not necessarily, too advanced for Bridger D, so that in all probability the occurrence was high in Washakie A or nearly transitional to Washakie B.

*Discussion*.—As noted above, *Parahyus vagus* is about intermediate between *Helohyus lentus* and *Achaenodon insolens* in size. This is the only known valid species, as the upper molar described by Marsh in 1894 as *Parahyus aberrans* belongs to *Helohyus*. Structurally, the *P. aberrans* tooth is entirely like upper molars of *Helohyus plicodon*,

<sup>18</sup> Illustrated in Peterson, 1919, fig. 12.

and in size is quite appropriate to occlude with the known lower molars of *Helohyus lentus*. In consequence of this, *P. aberrans* should be regarded as a synonym of *H. lentus*.

As for *P. vagus*, the locality data for the "*P. aberrans*" tooth are confused but would appear to be Washakie Basin, and in all probability Washakie A.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Parahyus vagus*, Y.P.M. NO. 10972

Length of cheek tooth series, anterior margin of alveolus for P <sub>2</sub> to posterior margin of M <sub>3</sub> .....	135.0a
Premolar series, anterior margin of alveolus for P <sub>2</sub> to posterior margin of P <sub>4</sub> .....	61.0a
Molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	75.0
P <sub>3</sub> , anteroposterior diameter : greatest transverse diameter.....	19.0a : 9.7
P <sub>4</sub> , anteroposterior diameter : greatest transverse diameter.....	26.0 : 12.8
M <sub>1</sub> , anteroposterior diameter : transverse diameter of talonid.....	19.3 : 13.0
M <sub>2</sub> , anteroposterior diameter : transverse diameter of talonid.....	21.1 : 14.8
M <sub>3</sub> , anteroposterior diameter : transverse diameter of trigonid.....	34.8 : 17.0

a, Approximate.

Family HYPERTRAGULIDAE Cope, 1879

Subfamily HYPERTRAGULINAE Matthew, 1908

Consideration of the form *Simimeryx* Stock, which appears rather certainly to be a true hypertragulid, evidently related to the Oligocene genus *Hypertragulus*, suggests possible diverse origins for the groups now united in this family. The antecedents of the Duchesnean *Simimeryx* would appear to be in a dichobunid of the type exemplified by *Mesomeryx*, whereas the leptotragulids, more highly specialized in selenodont development at an earlier date than *Simimeryx*, were likely derived from a separate portion of the dichobunid stock. This may also be true of the leptomerycines. The rather strong implication for a polyphyletic origin introduces problems in the supergeneric arrangement, so that the Hypertragulidae as currently constituted appears unnatural. I do not propose to raise all tribes or subfamilies to full family rank, as I have not been able to determine the extent to which these groups are independent. Perhaps the only forms that should be retained in the Hypertragulidae are the hypertragulids *sensu stricto*, *Simimeryx*, and possibly *Hypisodus* as it seems closer to *Hypertragulus* than to any of the other Oligocene forms. On the other hand, there is a suggestion that the leptotragulids and leptomerycines form a

natural family group separate from the Hypertragulidae. A tentative arrangement is as follows:

- Hypertragulidae Cope, 1879
  - Hypertragulinae Matthew, 1908
    - Simimeryx* Stock, 1934
    - Hypertragulus* Cope, 1873
    - Nanotragulus* Lull, 1922
  - Hypisodontinae Cope, 1887
    - Hypisodus* Cope, 1873
- Leptomerycidae Scott, 1899
  - Leptotragulinae Zittel, 1893
    - Leptotragulus* Scott and Osborn, 1887
    - Leptoreodon* Wortman, 1898
    - Poabromylus?* Peterson, 1931
  - Leptomerycinae Zittel, 1893
    - Leptomeryx* Leidy, 1853
    - Heteromeryx* Matthew, 1905

This does not, however, take into account the Protoceratidae. Scott (1899) was of the opinion that *Protoceras* was derived from *Leptoreodon*. However, he considered that *Stibarus* may have been a connecting link. There is much to be said in favor of an interpretation that places the leptotragulids in an ancestral position to *Protoceras*, but this does not include *Stibarus*, and the Uintan stage is much better represented by *Leptotragulus* as far as the dentition is concerned. This is most interestingly displayed by the lower premolars. There is little to distinguish the leptomerycids, leptotragulids, and protoceratids in the molar structures, but they may be diagnosed by their premolars, and among these the two that are most alike in this respect are *Protoceras* and *Leptotragulus*. The various protoceratids form a natural family group that would be obscured in the Leptotragulinae, and removing *Leptotragulus* from *Leptoreodon*, as an association of primitive and related leptomerycids, tends also to distort the picture. A suggested arrangement is shown in the phylogenetic chart.

#### Genus SIMIMERYX Stock, 1934

*Type*.—*Simimeryx hudsoni* Stock, 1934.

*Discussion*.—Stock's description of this form and estimate of its probable relationships appear quite accurate. The resemblance to *Hypertragulus* is rather close and particularly striking in characters of the premolars, both upper and lower. With these teeth the principal differences to be noted are the somewhat less reduced size anteriorly, the absence of a diastema between  $P_2$  and  $P_3$ , the less-selenodont

deuterocone of  $P^4$ , and the less deeply basined talonid of  $P_4$ . Their general form is, nevertheless, remarkably similar.

The molar teeth of *Simimeryx* are somewhat less progressive than those of *Hypertragulus* in the achievement of selenodonty. The upper molars lack the mesostyle as do those of *Hypertragulus*, but are a little more brachydont, exhibit a slight external cingulum, and the external rib of the metacone is less outstanding. The less-selenodont character is most noticeable in the lingual portion of the upper teeth, in which the stage of development approximates that in *Protoreodon*. A small protoconule is preserved on the anteroexternal crest of the protocone, and the posterior crest of the protocone is directed toward the anterior wall of the metaconule, about as in *Protoreodon*. Also, the anterior crest of the hypoconid of the lower molars is directed toward the posterior crest of the protoconid so as to leave a small pocket or basin anteroexternal to the entoconid, somewhat as in *Protoreodon*, though perhaps less conspicuously. Selenodonty is rather advanced beyond that of the homacodonts. However, as Stock has pointed out, *Simimeryx* most nearly resembles *Mesomeryx* among the various homacodonts. Although differences were noted, some were only of degree, and there is strong indication that a homacodont rather like *Mesomeryx* gave rise to *Simimeryx*. The leptotragulids on the other hand, even as early as Uinta B time, were too highly specialized to be considered as potential ancestors or to have been derived from the same homacodont stock.

#### SIMIMERYX HUDSONI<sup>10</sup> Stock, 1934

*Type*.—Right maxilla with  $P^2$  to  $M^3$ , inclusive, C.I.T. No. 1764.

*Horizon and locality*.—Sespe upper Eocene, C.I.T. loc. 150, Pearson Ranch, north side of Simi Valley, Ventura County, Calif.

#### MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF *Simimeryx hudsoni*

	C.I.T. No. 1764 Type
Length of upper cheek tooth series, $P^2$ - $M^3$ , inclusive.....	28.9
Upper premolar series, $P^2$ - $P^4$ , inclusive.....	13.4
Upper molar series, $M^1$ - $M^3$ , inclusive.....	15.8
$P^2$ , anteroposterior diameter: greatest transverse diameter.....	4.4: 1.7
$P^3$ , anteroposterior diameter.....	5.3
$P^4$ , anteroposterior diameter: transverse diameter*.....	4.2: 4.4
$M^1$ , anteroposterior diameter: transverse diameter*.....	5.4: 5.9
$M^2$ , anteroposterior diameter: transverse diameter.....	6.1: 7.2
$M^3$ , anteroposterior diameter: transverse diameter.....	5.5: 7.2

<sup>10</sup> Illustrated in Stock, 1934, pl. I.

	C.I.T. No. 1244
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive.....	42.3
Lower premolar series, P <sub>1</sub> (at alveolus)-P <sub>4</sub> , inclusive.....	22.8
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	19.7
P <sub>1</sub> , anteroposterior diameter (at alveolus).....	3.1 <sup>a</sup>
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter.....	4.2: 1.8
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter.....	5.5: 2.6
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	5.8: 3.2
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	5.0: 4.1
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	5.9: 4.7
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	8.9: 4.9

<sup>a</sup>, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

*Discussion.*—Included in the material upon which this species was based is also a lower jaw, C.I.T. No. 1244, with P<sub>1</sub>-M<sub>3</sub>, designated as a paratype, and a left maxillary portion exhibiting P<sup>3</sup> and P<sup>4</sup>. In size *S. hudsoni* is rather close to *Leptotragulus clarki*, even to the length of diastema separating P<sub>1</sub> from P<sub>2</sub>. The teeth, however, both upper and lower, are fundamentally different in structure.

#### SIMIMERYX MINUTUS<sup>20</sup> (Peterson), 1934

*Type.*—Portion of right ramus of mandible with P<sub>4</sub>-M<sub>2</sub>, C.M. No. 11913.

*Horizon and locality.*—Lapoint member of Duchesne River formation, north side of "Red Narrows," east of Tridell, Uinta County, Utah.

*Discussion.*—That Peterson should have referred this form, even questionably to *Leptomeryx*, is surprising, inasmuch as the P<sub>4</sub> is quite unlike that in the Oligocene genus. Correspondence to *Simimeryx hudsoni*, not known to Peterson at the time of his writing, is rather marked. Apparently, the only differences to be noted between the types are the much smaller size of *Simimeryx minutus* and the better-

#### MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF *Simimeryx minutus*, C.M. NO. 11913

Length of lower cheek tooth series, P <sub>4</sub> -M <sub>2</sub> , inclusive.....	12.4
P <sub>4</sub> , anteroposterior diameter.....	3.9
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	4.1: 2.8
M <sub>2</sub> , anteroposterior diameter: transverse diameter of trigonid.....	4.6: 3.1 <sup>a</sup>

<sup>a</sup>, Approximate.

<sup>20</sup> Illustrated in Peterson, 1934, fig. 6.

defined metaconid on  $P_4$ . The form of  $P_4$ , like that of *S. hudsoni*, corresponds more closely to that of *Hypertragulus* than it does to *Leptomeryx*. The molars of *S. minutus* are almost identical to those of *S. hudsoni*.

Family AGRIOCHOERIDAE Leidy, 1869

Genus PROTOREODON Scott and Osborn, 1887

*Synonyms*.—*Eomeryx* Marsh, 1894.

*Hyomeryx* Marsh, 1894.

*Agriotherium* Scott, 1898 (not Wagner, 1837).

*Chorootherium* Berg, 1899.

*Protagriochoerus* Scott, 1899.

*Mesagriochoerus* Peterson, 1934.

*Type*.—*Protoreodon parvus* Scott and Osborn, 1887.

*Discussion*.—Much of the taxonomic confusion earlier referred to for upper Eocene artiodactyls relates to the redundancy of generic names that have been applied to these small agriochoerids. Marsh's name *Eomeryx* first appeared in 1877 in the published text of an address, but as it was given without adequate description and without designation of species it remained a nomen nudum until 1894. In the meantime, Scott and Osborn (1887) described the genus and species *Protoreodon parvus* from the Uinta. In 1894 Marsh announced that the type of his *Eomeryx* was the earlier-named species (1875) *Agriochoerus pumilus*, and at the same time named as new, *Hyomeryx breviceps*. The generic name *Agriotherium* (preoccupied) was given by Scott to his new species "*A.*" *paradoxicus* in 1898, which Berg replaced by *Chorootherium*. In Scott's monograph on the selenodont artiodactyls of the Eocene in 1899 he reassigned this species to *Protoreodon* and at the same time named the relatively large *Protagriochoerus amnectens*. More recently (1934) Peterson contributed to the growing list of synonyms by proposing *Mesagriochoerus* for the Duchesne River protoreodont.

From a review of all the types involved and much referred material, I have been led inescapably to the conclusion that *Protoreodon*, as Peterson (1919, p. 82) indicated, was essentially an agriochoerid and not a merycoidodont. It is unfortunate that the name *Protoreodon* should be the one to survive, but there appears to be no doubt of its priority.

*Protoreodon* differs from *Agriochoerus* principally in the less-molarized form of  $P^4$  and  $P_4$ , retention of a protoconule on the upper molars, absence of any appreciable diastema behind the upper canine

and lower  $P_1$ , and the general, though possibly not invariable, retention of the upper incisors. Moreover, the outer walls of the upper molars of *Protoreodon* may be slightly more ribbed at the paracone and metacone. This is somewhat more noticeable in the Uinta B than in the Uinta C material. Also, the mesostyle has a more pinched or constricted appearance ventrally than is customary in *Agriochœrus*.

Resemblances to *Agriochœrus* are seen in the basic structure of both the upper and lower molars, structures that would appear to be more conservative and to show generic relationships. In the upper molars it is particularly significant that the posterior crest of the protocone in *Protoreodon* is directed at about right angles to the anterior crest of the metaconule<sup>21</sup> and terminates abruptly just short of a union, quite as in *Agriochœrus*. In *Merycoidodon* the posterior crest of the protocone, together with the anterior crest of the metaconule, extend parallel and deep into the valley between the paracone and metacone, somewhat as in *Leptoreodon*. In the lower molars a crest arrangement somewhat analogous to that in the upper molars persists through *Protoreodon* and *Agriochœrus*. Here the anterior crest of the hypoconid is directed toward the posterior crest of the protoconid, leaving a conspicuous pocket anteroexternal to the entoconid. In *Merycoidodon* this pocket is not developed inasmuch as the anterior crest of the hypoconid as well as the posterior crest of the protoconid are directed lingually together into the valley between the metaconid and entoconid, again rather as in *Leptoreodon*.

The lachrymal in *Protoreodon* is like that in *Agriochœrus*. It has nowhere near the forward expansion, nor the characteristic depression seen in *Merycoidodon*. The orbits are widely open posteriorly, and the posterior narial aperture extends well forward between the molars. Moreover, in the *Protoreodon* foot the distal phalanges have a somewhat compressed or more-acute dorsal surface than in *Merycoidodon*, resembling in this way, also, the agriochœrid almost clawlike structures.

I find difficulty in visualizing derivation of *Merycoidodon* from any of the better-known species of *Protoreodon*. There seems to be no certain point of origin within the *Protoreodon* complex, but I am inclined to believe that the line represented by *P. minor* and leading to the new Myton species, *Protoreodon petersoni*, is less unlikely than any part of the sequence of larger protoreodonts represented by *P. parvus* and producing the more distinctly *Agriochœrus*-like *P. pumilus annectens*.

<sup>21</sup> Wortman (1898) has shown that this is not the hypocone.



*Leptoreodon*, as noted by Wortman, comes close in the general structural plan of upper dentition, but the anterior extension of the snout as well as other skull characters would seem to preclude this genus, and I particularly note that the lower premolars, especially  $P_4$ , present greater difficulties than *Protoreodon*. The lower premolars of *Leptotragulus*, on the other hand, as exemplified by *L. medius*, would appear potentially close. In both *Leptoreodon* and *Leptotragulus* the lingual portion of the upper molars and the labial portion of the lower molars satisfactorily meet the requirements. The primary cusps, outer above and inner below, however, are decidedly more conical than in *Merycoidodon*; a condition that might be expected in a somewhat more remote ancestry of the highly crescentic pattern of *Merycoidodon*. I believe that the gap is rather significant and that the dental indications are for a closely related common ancestry rather than direct sequence. Clearly a compromise form is needed, exhibiting the parameral form more as in *Protoreodon* and the protomerial structure of *Leptotragulus* or *Leptoreodon*.

PROTOREODON PUMILUS<sup>22</sup> (Marsh), 1875

Plates 4, 5, and 6, figure 2

*Synonyms*.—*Protagriochcerus annectens* Scott, 1899.

*Protoreodon medius* Peterson, 1919.

?*Protoreodon tardus* Scott, 1945.

*Type*.—Lower jaw fragments with  $M_1$  and portions of  $M_2$  and  $M_3$  from right side and  $M_2$  from left, including also various other skeletal fragments of Y.P.M. No. 11890.

*Horizon and locality*.—Vicinity of White River, Uinta Basin, Utah, probably Uinta C according to Thorpe.

*Discussion*.—Although Thorpe lists Y.P.M. No. 11890 as a cotype, I believe it should be regarded as the holotype, and is here so designated, inasmuch as the maxillary portions and upper molars belonging to Y.P.M. No. 11890a were referred to by Marsh (1875) as the "second specimen." It is interesting to note that neither of these specimens was figured and that the skull, Y.P.M. No. 11891, and jaws, Y.P.M. No. 10570, illustrated by Marsh in 1894, among the materials that he obtained "by subsequent researches in the Uinta basin,"<sup>23</sup> may not represent *Protoreodon pumilus* as they appear to be closer to *Protoreodon parvus*.

<sup>22</sup> Illustrated also in Scott, 1899, pl. 4, figs. 26-27; 1945, pl. 2, figs. 1, 1a; pl. 3; Peterson, 1919, fig. 13; pl. 40, figs. 1-16, 19-27, and pl. 41; and Thorpe, 1937, fig. 8; pl. 1, fig. 1.

<sup>23</sup> As an aside on the record of collections, Marsh (1894) claimed that the

*Protoreodon pumilus* is clearly the best represented species of *Protoreodon*, and its remains are by all odds the most frequently encountered in the Myton fauna. Much individual variation is noticed in size, details of the cheek teeth, and development of canines. The extremes in most details are rather well represented by the types of *P. pumilus* and "*Protagriochœrus*" *annectens*, and the latter might well be regarded as a variant, or mutation in time, and would have been recognized as a separate species were it not for the mass of material intervening. *Protagriochœrus* is not a valid genus, as Peterson (1919, p. 88) fully appreciated, and at the same time there appears to be no justification for Peterson's *Protoreodon medius*, which corresponds rather closely to the type of "*Protagriochœrus*" *annectens*. The greater selenodonty of the outer cusps of the upper molars noted by Scott as characterizing *Protagriochœrus* was evidently a comparison made with the type of *Protoreodon parvus*, which must surely be from Uinta B. The significance of this, however, on a generic level, is lost in the intervening material of *P. pumilus*. With regard to the development of the upper premolars of *P. pumilus*, the slightly more basined talon on P<sup>3</sup> of the referred material is rather general throughout and advanced over the condition noted in *Protoreodon parvus*, and particularly *P. paradoxicus*. P<sup>4</sup> shows perhaps less conspicuous difference between *P. pumilus* and *P. parvus*, but in *P. paradoxicus* the talon of P<sup>4</sup> is much more bunodont.

*Protoreodon tardus* is stated to be from the Beaver Divide conglomerate, in which case it is as late as, or later than, *Protoreodon primus*, but the transverse width of the premolars is greater than is regarded as characterizing that species, being more nearly as in *P. pumilus* in this respect, as well as in size and degree of selenodonty; hence, it is tentatively included in the latter species. It may be further noted that the division of the primary cusp and the development of the talon or deuterocone portions of P<sup>3</sup> and P<sup>4</sup> in the type of *Protoreodon tardus* are perhaps a trifle less progressive than in most referred material of *P. pumilus*, suggesting the smaller and even earlier *Protoreodon parvus*.

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material of the three small artiodactyls (*Eomeryx*, *Parameryx*, and *Oromeryx*) was found by himself in 1870. The labels, in Marsh's handwriting, accompanying the material originally described as *Agriochœrus pumilus* read "J. Heisey, White River, Aug. 20th, 1874" and "S. Smith, Lake Fork, Aug. 9th, 1874." All the *Oromeryx* and part of the *Parameryx* material has the field number 1057, which was for the year 1877. The remaining material of *Parameryx* is labeled "M. Forshay, Sept. 5, 1876."

Slight changes noted in the cheek teeth of *P. pumilus* are apparently to be correlated with time. It is interesting to note that most of the *Protoreodon* dentitions from the *Protylopus* quarry and vicinity in Myton pocket tend to resemble the type of "*Protagriocherus*" *annectens* somewhat more closely than that of *P. pumilus*. This is noted in an average larger size and almost imperceptibly more selenodont outer cusps of lower molars as compared with materials obtained from Leland Bench draw. I am convinced that the level from which fossil material was collected along Leland Bench draw is a little earlier in Uinta C time than the quarry in Myton pocket, and that the type of *P. pumilus* which these materials closely resemble is from low in "C," which would be in keeping with the locality designation "White River" on the Marsh specimen.

In view of the average difference between specimens in the collection noted above, I am tentatively designating the more-advanced material, including much of that from Myton pocket, as the subspecies *Protoreodon pumilus annectens*.

The size of the caniniform teeth in *P. pumilus* is clearly not to be correlated with size or other characters of the cheek teeth. Large and small upper canines and lower  $P_1$ 's are to be found in individuals grouped according to size and development of cheek teeth. There does appear, however, to be correlation between caniniform tooth size and the extent to which the angle is expanded posteriorly, together with the somewhat more posterior placement of the condyle, and to a minor degree the depth of the ramus generally. The latter variables are in part, of course, a function of the age of the individual as determined by wear on the cheek teeth. Specimens can be readily divided into two groups where preservation includes the upper canine or  $P_1$ , but I have been unable to make this same separation on the basis of the cheek teeth alone. I cannot regard the differences here cited as of more than dimorphic significance within the species of *P. pumilus*. It may be further noted that in those individuals which I regard as males, a slightly greater diastema developed posterior to the large C.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Protoreodon pumilus*

	A.M. <sup>24</sup> No. 1818	U.S.N.M. No. 20352
Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive .....	81.5	76.0a
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive....	70.7a	69.3
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive.....	36.4a	35.0

<sup>24</sup> Type of "*Protagriocherus*" *annectens*.

	A.M. No. 1818	U.S.N.M. No. 20352
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	36.0a	34.5a
C, anteroposterior diameter (at alveolus): greatest transverse diameter .....	8.5a:7.1a	5.0:4.7
P <sup>1</sup> , anteroposterior diameter: greatest transverse diameter .....		7.7:3.7
P <sup>2</sup> , anteroposterior diameter: transverse diameter*.....	10.0:5.1	9.4:5.0
P <sup>3</sup> , anteroposterior diameter: transverse diameter.....	9.5:10.3	9.7:8.5
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	8.0:10.5	8.2:11.0a
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....		10.7a:1.0
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	13.3:15.8	13.0:14.2
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	13.4:17.4	13.7:16.0
	Y.P.M. No. 11890 Type	U.S.N.M. No. 20352
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive .....		71.0a
Lower premolar series, P <sub>1</sub> (at alveolus)-P <sub>4</sub> , inclusive... ..		32.4
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....		39.0
P <sub>1</sub> , anteroposterior diameter (at alveolus): greatest transverse diameter .....		5.9:4.1
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter .....		8.0:3.8
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter .....		9.9:4.9
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter .....		10.0:6.9
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid .....	9.5:7.1	9.7:7.5
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid .....	10.0:7.8	11.4:8.1
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid .....		17.8:7.8

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

#### PROTOREODON PARVUS<sup>25</sup> Scott and Osborn, 1887

*Synonym.*—*Hyomeryx breviceps* Marsh, 1894.

*Type.*—Portions of skull and left ramus of mandible, P.U. No. 10398.

*Horizon and locality.*—Uinta B (according to Thorpe), Uinta County, Utah.

*Discussion.*—*Protoreodon parvus* is distinguished from *Protoreodon*

<sup>25</sup> Illustrated in Scott and Osborn, 1887, p. 257; Scott, 1889, pl. 7, figs. 1-2; Marsh, 1894, figs. 18, 19, and 22; and Thorpe, 1937, figs. 12-17; pl. 1, fig. 3.

*pumilus* primarily by its significantly smaller size. In addition to this there are slight differences in the structure of the teeth that may be regarded as representing a stage somewhat more primitive than is evident in the *P. pumilus* dentitions. In P<sup>4</sup> the primary cusp is twinned but less markedly so than in much of the *P. pumilus* material, and the talon portions of both P<sup>3</sup> and P<sup>4</sup> are slightly more constricted anteroposteriorly. It is also noted that the cheek teeth, both upper and lower, are perceptibly less selenodont. The cusps are just a little more bunodont, and the outer wall of the upper molars has slightly better-developed ribs on the paracone and metacone. *Protoreodon parvus* would appear to be ancestral in every way to *Protoreodon pumilus* and is somewhat closer to the type material of *P. pumilus* than it is to the referred material of Myton pocket, indicating a gradational sequence in which an arbitrary separation might be made corresponding about to the transition between Uinta B and Uinta C time. It should be noted, however, that a few of the larger protoreodont specimens from White River pocket (Uinta B) seem difficult to distinguish from *P. pumilus* and might also be confused with *Diplobunops vanhouteni*.

The type of *Hyomeryx breviceps* Marsh is almost indistinguishable in the upper cheek teeth from *Protoreodon parvus*. The only possibly significant character brought forth in defense of *Hyomeryx breviceps* was absence of upper incisors. I was unable to find this portion of the specimen in the collections at Yale, but there appears to be some doubt as to Marsh's interpretation, inasmuch as Thorpe noted that this portion of the premaxilla was broken down and that there may have been a small incisor. In all the *Protoreodon* material that I have examined where the alveolar portion of the premaxilla was well preserved, the three incisors were present, increasing in size from a very small I<sup>1</sup> to a moderate I<sup>3</sup>. Only in certain damaged specimens was there any doubt as to the presence of all. However, inasmuch as the anterior incisors are relatively small, it would not be surprising if they were occasionally missing, possibly in some instances through damage and loss during the life of the individual. This portion is apparently not preserved in the type of *P. parvus*. Among other characters attributed to *Hyomeryx breviceps*, the absence or weakness of the internal cingulum is probably of doubtful significance, but in any case does not differ in this respect from the type of *P. parvus*. The character of the styles noted by Thorpe for the upper molars of *H. breviceps* is in part surmise, as all but the parastyle on M<sup>1</sup> are broken off. Marsh's illustration (1894, fig. 19) of these teeth gives the wrong impression, inasmuch as the damage is not indicated and

no restoration was made. This error was corrected in Thorpe's illustrations (1937, figs. 16 and 17).

Marsh stated that the horizon for "*H. breviceps*" was nearly the same as that for *Eomeryx* (*P. pumilus*), which may mean little more than near the White River. This would suggest lower "C" or upper "B." Although Thorpe gives the horizon as "C," I suspect that it is very low in this level, or to judge by the development of the dentition I would be inclined to regard it as more likely from Uinta B.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Protoreodon parvus*

	P.U. No. 10398 Type	Y.P.M. No. 11891
Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive .....	.....	67.0
Length of upper cheek tooth series, P <sup>1</sup> (at alveolus)-M <sup>3</sup> , inclusive .....	.....	56.0
Upper premolar series, P <sup>1</sup> (at alveolus)-P <sup>4</sup> , inclusive...	26.8a	29.5
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	26.4	27.7
C, anteroposterior diameter (at alveolus): greatest transverse diameter .....	.....	8.0: 7.0
P <sup>3</sup> , anteroposterior diameter: transverse diameter*.....	7.3: 7.4a	7.8: 7.5
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	6.7: 8.8	6.5: 8.8
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	8.0: 10.2	8.8: 10.0
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	8.8: 11.4	9.4: 12.0
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	10.0: 12.8	10.0: 13.0
	U.S.N.M. No. 20383	
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive .....	.....	60.0a
Lower premolar series, P <sub>1</sub> (at alveolus)-P <sub>4</sub> , inclusive...	.....	30.0a
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	.....	30.5
P <sub>1</sub> , anteroposterior diameter (at alveolus): greatest transverse diameter .....	.....	8.0a: 5.2a
P <sub>2</sub> , anteroposterior diameter.....	.....	6.0a
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter .....	8.9: 4.3	.....
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter .....	8.6a: 5.7	8.0: 4.7
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid .....	8.2: 6.5	8.1: 6.2
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid .....	8.8: 7.5	8.5: 6.8
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid .....	...: 7.5	13.8: 6.8

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

**PROTOREODON PARADOXICUS** <sup>26</sup> (Scott), 1898

*Type*.—Skull, jaws, a few vertebrae, limb and foot bones, P.U. No. 11234.

*Horizon and locality*.—Upper Uinta B or lower Uinta C, mouth of White River, Utah, according to Thorpe.

*Discussion*.—The dentition in the type of *Protoreodon paradoxicus* is only a little smaller than that of *Protoreodon parvus*. It exhibits, however, distinctly more primitive appearing premolars. P<sup>3</sup>, for example, is three rooted but shows scarcely more than a robust cingulum at the position of the deuterocoene, and in P<sup>4</sup> the deuterocoene is decidedly conical in comparison with that in *P. parvus*. Moreover the primary cusp in P<sup>4</sup> of *P. paradoxicus*, though somewhat worn, is almost certainly not twinned. The molars show noticeable wear but are perhaps more conical than in *P. parvus*; also, the parastyles are rather more outstanding. The canines in the type specimen are particularly large so that I suspect this is a male individual. I<sup>3</sup> is present on one side, but beyond this the premaxillae are not sufficiently complete to warrant further conclusions regarding the number of incisors.

Beyond doubt *Protoreodon paradoxicus* possesses the most primi-

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Protoreodon paradoxicus*, P.U. NO. 11234

Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive....	59.6
Upper premolar series, P <sup>2</sup> -P <sup>4</sup> , inclusive.....	19.5
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	23.4
C, anteroposterior diameter.....	7.0
P <sup>2</sup> , anteroposterior diameter : transverse diameter*.....	6.7a : 3.5a
P <sup>3</sup> , anteroposterior diameter : transverse diameter.....	6.7 : 5.6
P <sup>4</sup> , anteroposterior diameter : transverse diameter.....	6.4 : 8.7
M <sup>1</sup> , anteroposterior diameter : transverse diameter*.....	7.3 : 8.8
M <sup>2</sup> , anteroposterior diameter : transverse diameter.....	8.2 : 8.7
M <sup>3</sup> , anteroposterior diameter : transverse diameter.....	8.8 : 12.1
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	27.1
P <sub>3</sub> , anteroposterior diameter.....	7.5
P <sub>4</sub> , anteroposterior diameter : greatest transverse diameter.....	8.0 : 4.4
M <sub>1</sub> , anteroposterior diameter : transverse diameter of talonid.....	7.1 : 5.5
M <sub>2</sub> , anteroposterior diameter : transverse diameter of talonid.....	8.0 : 6.0a
M <sub>3</sub> , anteroposterior diameter : transverse diameter of trigonid.....	12.5 : 6.3

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

<sup>26</sup> Illustrated in Scott, 1899, pl. 4, figs. 24-25; and Thorpe, 1937, fig. 11; pl. 1, fig. 2.

tive dentition of any form now included in *Protoreodon*. Separate generic recognition was considered by Scott in 1898 but abandoned the following year. I am inclined to agree that basically *P. paradoxicus* belongs to *Protoreodon*, and that the differences from other species are only those of degree, representing less-advanced development along observed trends. It should, moreover, be noted that in the illustration of the type given by both Scott (1899, pl. 4, fig. 24) and Thorpe (1937, pl. 1, fig. 2) the flattening of the skull is due to crushing and that the unusual depth of the jaw anteriorly does not take into consideration a certain amount of faulty plaster restoration.

PROTOREODON MINOR<sup>27</sup> Scott, 1899

Plate 6, figure 1

*Type*.—Right and left maxillary portions with the left side exhibiting C and P<sup>2</sup> to M<sup>3</sup>, but M<sup>1</sup> and M<sup>3</sup> only partially preserved, P.U. No. 11339.

*Horizon and locality*.—Uinta C, Kennedy's Hole (according to Thorpe), Uinta Basin, Utah.

*Discussion*.—*Protoreodon minor* is only a little smaller than *Protoreodon paradoxicus* and on this character alone would not have been separable specifically from *P. paradoxicus*; however, the more-advanced condition of the upper premolars in *P. minor*, together with the fact that a distinctly later horizon is represented, causes me to regard *P. minor* as a separate species. P<sup>3</sup> in *P. minor* has a distinct deuterocone, and a slight basin is developed posterior to it by the extension of the posterior cingulum. In P<sup>4</sup> the deuterocone has better-developed crests, giving the tooth a more-selenodont appearance than in *P. paradoxicus*. On the other hand, like *P. paradoxicus*, there is no evidence for twinning of the primary cusp of P<sup>4</sup> in the *P. minor* type, although in a referred specimen from the Devil's Playground a slight indication of this is seen on one side only. The molars of *P. minor*, as in *P. paradoxicus*, have distinctly conical paracones and metacones, exhibiting likewise heavily ribbed outer walls. Also, the protoconule is sharply defined.

I have not seen lower teeth that belong without doubt to the *P. minor* stage, as the lower teeth associated with the type specimen are leptotraguline, probably *Leptoreodon* but not *Protoreodon*. Lower teeth of *P. paradoxicus* show distinctly conical metaconids and entoconids with a peculiarly prominent styler development. Those of *P. minor* may have been similar.

<sup>27</sup> Also illustrated in Scott, 1899, pl. 3, fig. 23; and Thorpe, 1937, fig. 10.



It is entirely possible that *P. minor* is no more than a variant in time of *P. paradoxicus* and that *P. minor* in turn gave rise to the form described as a new species, *Protoreodon petersoni*, in the Myton pocket and Leland Bench draw collections.

## MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF

*Protoreodon minor*

	P.U. No. 11339 Type	U.S.N.M. No. 20674
Length of upper cheek tooth series, C-M <sup>3</sup> , inclusive, measured at alveoli.....	55.0	.....
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive, measured at alveoli.....	46.9	.....
Upper premolar series, P <sup>1</sup> (at alveolus)-P <sup>4</sup> , inclusive.....	25.2	.....
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive, measured at alveoli..	22.0	22.0a
C, anteroposterior diameter (at alveolus): greatest transverse diameter .....	5.5:4.8	.....
P <sup>2</sup> , anteroposterior diameter: greatest transverse diameter.	6.0:3.8	.....
P <sup>3</sup> , anteroposterior diameter: transverse diameter*.....	6.5:6.0a	6.4:6.5
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	6.0:7.5	6.0:7.3
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	.....	7.2:8.8
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	8.1:11.7	8.2:10.4
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	8.0a:12.0	8.5:11.6

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

PROTOREODON PRIMUS<sup>28</sup> (Peterson), 1934

*Type*.—Portion of skull and jaws, C.M. No. 11893.

*Horizon and locality*.—Randlett member of Duchesne River formation, Randlett Point, Uinta County, Utah.

*Discussion*.—The specimen that Peterson designated as the type of *Mesagriochcerus primus* from Randlett horizon and that (C.M. No. 11904) from the Halfway, which he regarded as the paratype, appear to represent a distinct species. The slenderness of the premolars noted by Peterson is distinctive. Most of the characters, however, that he cited as indicating a separate genus, and certainly those in particular that he regarded as more closely foreshadowing *Agriochcerus*, are not significant in comparison with material of *Protoreodon pumilus annectens* from Myton pocket. The twinning of the primary cusp in P<sup>4</sup> is no further advanced than in much of the Myton material, and the crescentic deuterocone is somewhat more like that noted in *Protoreodon petersoni* than in *Agriochcerus*, as for

<sup>28</sup> Illustrated in Peterson, 1934, figs. 3-5.

example, *A. minimus*. The tetartocone is actually more advanced and rather more *Agriochoerus*-like in certain specimens of *P. pumilus*. A particularly advanced tetartocone on P<sup>4</sup> was noted in a specimen from the Uinta C of Leland Bench draw (U.S.N.M. No. 20449).

Not all the protoreodont specimens from the Duchesne River beds, or attributed to the Beaver Divide conglomerate, are to be referred to *P. primus*, as the specimen (C.M. No. 12080) from near Baser Bend in the Uinta Basin, which Scott (1945, p. 233) referred to this species is, I believe, closer to *Protoreodon pumilus annectens* in the premolars. The specimen (A.M. No. 22558) purported to be from the Beaver Divide conglomerate, which Scott also included in this species, is rather immature and exhibits no permanent premolars. The molars in this are typically protoreodont with distinctly selenodont cusps, very distinct protoconules, and a size close to *P. pumilus*. The species represented is not clearly evident. The type of *Protoreodon tardus* is also stated to be from the Beaver Divide conglomerate. The differences between molars of it and A.M. No. 22558 are slight, but the *P. tardus* type strangely enough would appear to be closer to *Protoreodon pumilus* ss. than to *P. primus*.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Protoreodon primus*, C.M. NO. 11893

Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive...	73.8a
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive.....	64.3a
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive.....	32.8
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	33.0a
C, anteroposterior diameter.....	6.0a
P <sup>1</sup> , anteroposterior diameter: greatest transverse diameter.....	6.8: 3.0a
P <sup>2</sup> , anteroposterior diameter: greatest transverse diameter.....	8.8: 3.9
P <sup>3</sup> , anteroposterior diameter: transverse diameter*.....	8.3: 6.2
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	7.5: 8.8
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	9.4a: 9.6a
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	10.6: 12.5a
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive..	70.0a
Lower premolar series, P <sub>1</sub> (at alveolus)-P <sub>4</sub> , inclusive.....	34.4
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	35.5a
P <sub>1</sub> , anteroposterior diameter: greatest transverse diameter.....	7.0: 4.5
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter.....	7.9: 3.2
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter.....	8.5: 3.7
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	9.2: 4.7
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	8.3: 6.2
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	10.6a: ...
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	16.0a: 7.8a

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

The rather interesting collection of artiodactyl remains obtained by Princeton at the Leota Ranch quarry includes several protoreodont specimens. These are of a form about as large as *P. p. annectens*, but the teeth, particularly those of the lower series, are distinctly narrower than in the Myton pocket series and are hence tentatively referred to *Protoreodon primus*. As previously noted, the Leota Ranch quarry horizon is regarded as later than that at Myton pocket, but earlier than Randlett.

**PROTOREODON PETERSONI,<sup>29</sup> new species**

Plate 7

*Type*.—Skull and jaws with complete dentition, and other skeletal portions, P.U. No. 14404.

*Horizon and locality*.—Uinta C, Myton pocket, Uinta Basin, Utah.

*Specific characters*.—A little smaller than *Protoreodon minor* but decidedly more progressive in the achievement of a selenodont dentition. P<sup>2</sup> and P<sup>3</sup> both with deuterocone posterior in position and with a small posterointernal basin. P<sup>4</sup> has a single primary cusp and highly selenodont deuterocone. The outer cusps of upper molars are more crescentic than in *P. minor*, having their outer walls smoothly concave with the ribs weak or indistinct. Parastyle of each is perhaps less outstanding laterally, mesostyle compressed, and the lateral cingulum less shelflike. Protoconule is weak on M<sup>1</sup>, weak or absent on M<sup>2</sup>, and usually absent on M<sup>3</sup>. On some upper molars there is a spur extending anteriorly from about midway along anterior crest of the metaconule which may, particularly on M<sup>3</sup>, join the posterior crest of the protocone. P<sub>4</sub> is much as in *Protoreodon pumilus* but in one specimen exhibits a small spur extending anterolingually into the talonid basin from about midway across the posterior wall. Inner cusps of the lower molars are less conical than in *P. paradoxicus*, with the outer walls more flattened and the stylids somewhat less pocketed or shelflike than in the larger protoreodonts.

*Discussion*.—In addition to the type there are three skulls, two of which are immature but remarkably complete with jaws and other skeletal portions, in the Princeton collections, Nos. 14401, 14402, and 14403, and four partial dentitions in the collections of the U. S. National Museum. All but one of the specimens are from Myton pocket. One of these, U.S.N.M. No. 20386, including the right maxilla and portions of both lower jaws, is from Leland Bench draw. In all instances the material is clearly separable from the *P. minor* material

<sup>29</sup> Named for O. A. Peterson. Illustrated also in Scott, 1937, fig. 232.

of Kennedy's Hole and Devil's Playground. Kennedy's Hole type specimen of *P. minor* would appear to be from a distinctly earlier horizon than the Myton pocket material. I have no doubt but that *P. petersoni* was derived from *P. minor* and that when more material of these small protoreodonts is found, presumably at intervening horizons, no clear-cut separation will be feasible and that, as in the sequence of large protoreodonts (*P. pumilus* and *P. pumilus annectens*), *P. petersoni* may come to be regarded as an advanced variant of *P. minor*. At present, however, it would appear that *P. petersoni* has actually progressed somewhat farther from its antecedent, *P. minor*, than its contemporary *P. pumilus annectens* has from *P. pumilus* (sensu stricto).

In general, the skull of *Protoreodon petersoni* is like that of *P. pumilus*. Other than size, there is little in their form to distinguish them. It is noted, however, that the postorbital processes are better developed in *P. petersoni*, although they do not close behind the orbit

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Protoreodon petersoni*, P.U. NO. I4404

Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive....	50.5
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive.....	42.0
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive.....	21.8
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	21.5
C, anteroposterior diameter (at alveolus): greatest transverse diameter .....	4.9:4.7
P <sup>1</sup> , anteroposterior diameter: greatest transverse diameter.....	5.5:2.8
P <sup>2</sup> , anteroposterior diameter: transverse diameter*.....	5.5:3.9
P <sup>3</sup> , anteroposterior diameter: transverse diameter.....	5.6:5.0
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	5.3:6.7
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	6.5:7.9
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	7.9:9.8
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	8.3:10.4
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive....	46.4
Lower premolar series, P <sub>1</sub> , (at alveolus)-P <sub>4</sub> , inclusive.....	22.4
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	24.3
P <sub>1</sub> , anteroposterior diameter (at alveolus): greatest transverse diameter .....	4.8:3.8
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter.....	5.3:2.3
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter.....	6.2:3.0
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	6.5:4.6
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	6.2:5.0
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	7.3:5.8
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	11.4:5.9

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

as in *Merycoiodon*. I am unable to determine whether or not there was a preorbital fossa. The slight depression in this area on the type specimen may be due to crushing on one side, and there has been some restoration in plaster on the other. Of the remaining two skulls, one is too crushed at this point and the other suggests that if there was a preorbital fossa it was scarcely more than a very shallow depression.

*Protoreodon petersoni* comes nearer to being a possible ancestor of *Merycoiodon* than any members of the *P. parvus*-*P. pumilus* line. The modification of the paramere in molars of *P. petersoni*, unlike the *P. pumilus* line, is not so distinctly in the direction of *Agriochoerus* with rather small differences suggestive of *Merycoiodon*. P<sup>4</sup>, moreover, has no triticocone, and the deuterococone tends to form a single crescent. Nevertheless, the lingual portion of the upper molars and the buccal portion of the lower molars are still agriochoerid in appearance. The posterior crest of the protocone is directed toward and not parallel with the anterior crest of the metaconule, and the anterior crest of the hypoconid is directed toward the posterior crest of the protoconid so as to leave a distinct basin external or buccal to the metastylid, quite unlike *Merycoiodon*.

#### Genus DIPLOBUNOPS Peterson, 1919

*Type.*—*Diplobunops matthewi* Peterson, 1919.

*Discussion.*—*Diplobunops* appears to be a distinctive and valid genus, although close to *Protoreodon*. It is characterized most noticeably by the somewhat lengthened rostrum, enlarged canines, and the widely expanded anterior extremity in comparison with *Protoreodon*. The premaxillae appear blunted forward with the third incisor alveolus distinctly more median to the enlarged canine than in *Protoreodon*. The rostrum is constricted posterior to the lateral expansion of the maxillae over the roots of the canines, and P<sup>1</sup> (in Uinta C and later forms) is isolated by diastemata from the canine and P<sup>2</sup>. P<sup>3</sup> has a simple conical deuterococone with little or no tendency toward the development of a posterointernal basin. In P<sup>4</sup> the primary cusp in an unworn state does not appear to be twinned, but two generally prominent ridges on the lingual side of this cusp converge toward the apex so that moderate wear may produce the illusion of twinning. The deuterococone on P<sup>4</sup> is comparatively conical although the anterolaterally and posterolaterally directed crests are well defined. The lower premolars, and the molars in both the upper and lower series, are very much like those in *Protoreodon*; however, the molars are distinctly less selenodont, buccally above and lingually below, than in

such advanced types as *Protoreodon p. annectens* or the small *Protoreodon petersoni*. The mesostyles, as noted by Peterson, may be divided and project anteroposteriorly, but do not project buccally nearly so much as in the more-selenodont forms of *Protoreodon*. Moreover, the molars are relatively wider transversely than in the *Protoreodon* material I have examined.

*Diplobunops*, like *Protoreodon*, is, of course, not closely related to the bothriodonts although there is some resemblance in molar form. The specialization of  $P_1$  rather than C as the functional caniniform tooth, as well as other differences, indicates agriochoerid affinities. Neither is *Diplobunops* the ancestor of *Agriochoerus*, as certain of its specializations, such as the transversely expanded rostrum anteriorly, more nearly enclosed orbit, etc., together with its retention of a more-primitive cheek tooth dentition even in the Duchesne River beds, suggest aberrance.

**DIPLOBUNOPS MATTHEWI**<sup>30</sup> Peterson, 1919

Plates 10, 11, and 12

*Synonyms*.—*Diplobunops uintensis* Peterson, 1931.

*Diplobunops ultimus* Peterson, 1931.

*Type*.—Much fragmentary skeletal material, C.M. No. 2974, also including portions of maxillae and jaws with the upper teeth broken or missing, but with  $P_3$ ,  $P_4$ ,  $M_2$ , and  $M_3$  represented in the lower series (originally designated as a paratype, C.M. No. 3394, but later recognized by Peterson as a part of the type).

*Horizon and locality*.—Near base of Uinta C, 6 miles east of Myton, Uinta County, Utah.

*Discussion*.—Peterson (1931a, p. 344) indicated that teeth in *Diplobunops matthewi* were approximately equal in size to those in the type of "*Protagriocherus annectens*." Actually, the former are about 15 percent larger in such dimensions as may be compared. The preserved lower teeth are relatively much wider transversely than in referred *Protoreodon p. annectens* material in both the premolar and molar portions, and the lower jaws are conspicuously thicker. The type of *D. matthewi* exhibits the very large canine and isolation of  $P^1$  by diastemata characterizing the genus.

I find nothing in the type skull of *Diplobunops uintensis* in comparison with the limited material of *D. matthewi* which would serve to distinguish the second species. Peterson apparently looked forward to the finding of additional material of *D. matthewi* in beds of lower

<sup>30</sup> Also illustrated in Peterson, 1919, pl. 38, and 1931a, figs. 1-9, pls. 19, 20.

Uinta C to justify his belief that *D. uintensis* from the middle part of Uinta C would turn out to be a distinct and more-advanced species. So far only a time interval represented by about 250 feet of Uinta sediments separates them, and until more useful evidence is forthcoming, I do not think *D. uintensis* should be recognized.

The skull belonging to the portion of a skeleton that Peterson named *Diplobunops ultimus* came from about 400 feet above the base of Uinta C and hence about 150 feet above the type of *D. uintensis*. The skull of *D. ultimus* is rather crushed transversely, and proportions relative to those of the type of *D. uintensis* are difficult to determine. As Peterson noted, the molars appear to be a little narrower transversely. The primary cusp of P<sup>4</sup> has a prominent anterolingual ridge, but this seems characteristic of *Diplobunops* and is certainly present in the *D. uintensis* type, *D. crassus*, and the Badwater *Diplobunops* specimens. Peterson noted the smaller size of the canines in *D. ultimus* and suggested that this, together with the smaller size of the skull, may be no more than a sexual character. Such differences as noted do not appear to be due to any transition or development in time, leading, for example, to *D. crassus*, so I am inclined to regard *D. ultimus*, as well as *D. uintensis*, as a synonym of *D. matthewi*. The nomen nudum, *Diplobunops leotensis* Peterson (1931b, p. 74), evidently refers to the type of *Diplobunops ultimus*, as the latter was found in the "Leota Ranch" area.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Diplobunops matthewi*

	C.M. <sup>31</sup> No. 3394 Type	C.M. <sup>32</sup> No. 11769	C.M. <sup>33</sup> No. 11801A
Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive . . . . .	100.0a	102.3	105.0a
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive . . . . .	85.0a	86.0	....
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive..	45.2a	48.7a	48.0
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive....	39.3a	38.5a	39.5
C, anteroposterior diameter (at alveolus) : greatest transverse diameter... 10.1a : 9.9a	10.0a : 11.7a	10.0a : ....	....
P <sup>2</sup> , anteroposterior diameter : greatest transverse diameter . . . . .	.....	10.2a : ....	9.2 : 5.7
P <sup>3</sup> , anteroposterior diameter : transverse diameter* . . . . .	.....	10.0a : 10.0a	9.8 : 9.5

<sup>31</sup> Overall measurements on teeth of *D. matthewi* type taken at or interpreted from alveoli.

<sup>32</sup> Type of *D. uintensis*.

<sup>33</sup> Type of *D. ultimus*.

	C.M. No. 3394 Type	C.M. No. 11769	C.M. No. 11801A
P <sup>4</sup> , anteroposterior diameter: transverse diameter .....	8.3a: 11.8a	9.0a: 12.4a	9.9: 12.2
M <sup>1</sup> , anteroposterior diameter: transverse diameter* .....	.....	.....	12.2: 14.0
M <sup>2</sup> , anteroposterior diameter: transverse diameter .....	.....	13.5: 19.0a	14.4: 16.8
M <sup>3</sup> , anteroposterior diameter: transverse diameter .....	.....	14.3: 21.0	15.3: 17.7
		U.S.N.M. No. 20390	
Length of lower cheek tooth series, P <sub>1</sub> -M <sub>3</sub> , measured at alveoli.....	.....	84.5	95.0a
Lower premolar series, P <sub>1</sub> -P <sub>4</sub> , measured at alveoli .....	.....	41.5	51.0a
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , measured at alveoli .....	45.7	43.3	43.4a
P <sub>1</sub> , anteroposterior diameter (at alveolus): greatest transverse diameter...	.....	10.7: 8.0	.....
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter .....	.....	.....	8.3: 5.2
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter .....	10.4: 6.6	11.7: 7.3	10.0a: 6.3
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter .....	11.5a: .....	.....	10.0a: 7.8a
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	.....	.....	.....
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	13.8: 9.9	12.8: 10.2	12.6: 10.0a
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	21.4: 9.7	20.2: 9.9	21.0: 10.0a

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

#### DIPLOBUNOPS CRASSUS<sup>34</sup> Scott, 1945

*Type*.—Nearly complete skull, C.M. No. 2967.

*Horizon and locality*.—Randlett member of Duchesne River formation, 1 mile south of Baser Bend and ½ mile west of Green River in Utah.

*Discussion*.—This is evidently a valid and recognizable species. The skull of *Diplobunops crassus* is more massive and broader than those referred to *Diplobunops matthewi*. Also, the molar teeth and P<sup>4</sup> are appreciably larger, although in the anterior premolars this is

<sup>34</sup> Illustrated in Scott, 1945, pl. 4, fig. 3, and pl. 5, figs. 1, 1b.



not so evident. I do not, however, find that the deuterocone on  $P^3$  is particularly small as noted by Scott. It seems better defined than in the specimen Peterson designated as the type of *Diplobunops uintensis*. The distinctly less-selenodont character of the teeth in comparison with the more-advanced forms among *Protoreodon* species is well shown in the type of *Diplobunops crassus*.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Diplobunops crassus*, C.M. NO. 2967

Length of upper cheek tooth series, C (at alveolus)- $M^3$ , inclusive...	110.0
Length of upper cheek tooth series, $P^1$ - $M^3$ , inclusive.....	94.3
Upper premolar series, $P^1$ - $P^4$ , inclusive.....	59.6
Upper molar series, $M^1$ - $M^3$ , inclusive.....	46.7
C, anteroposterior diameter (at alveolus): greatest transverse diameter .....	9.5 <sup>a</sup> : 8.5 <sup>a</sup>
$P^1$ , anteroposterior diameter: greatest transverse diameter.....	8.8: 4.0
$P^2$ , anteroposterior diameter: greatest transverse diameter.....	10.6: 5.6
$P^3$ , anteroposterior diameter: transverse diameter*.....	12.0: 10.0
$P^4$ , anteroposterior diameter: transverse diameter.....	11.0: 13.8
$M^1$ , anteroposterior diameter: transverse diameter*.....	13.6: 16.8
$M^2$ , anteroposterior diameter: transverse diameter.....	15.7: 19.7
$M^3$ , anteroposterior diameter: transverse diameter.....	17.5: 22.3

<sup>a</sup>, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

**DIPLOBUNOPS VANHOUTENI**,<sup>35</sup> new species

Plates 8 and 9

*Type*.—Skull, mandible, and other associated skeletal portions, P.U. No. 14251.

*Horizon and locality*.—Uinta B, White River pocket, Uinta Basin, Uinta County, Utah.

*Specific characters*.—Size much smaller than *Diplobunops matthewi*. Upper canine and  $P_1$  almost as large as in *D. matthewi*. No diastema between  $P^1$  and  $P^2$ .  $P^4$  with ridges on lingual wall of single primary cusp much subdued. Deuterocone of  $P^4$  subcrescentic. Upper molars low crowned and transversely very broad, with well-developed styles and moderate ribs. Molar cusps somewhat conical appearing and but weakly crescentic. Lower jaw shallow and lower premolars relatively large and crowded, with  $P_3$  and  $P_4$  rather distinctly pocketed anterolingually. Lower molars with comparatively conical lingual cusps, and lingual styles moderately developed only on the metaconid.

<sup>35</sup> Named for Dr. Franklyn B. Van Houten.

*Discussion.*—*Diplobunops vanhouteni* would appear to fulfill in all respects the requirements for a stage ancestral to the upper Uintan species of *Diplobunops*. Moreover, it more closely resembles contemporary forms of *Protoreodon* than do the later representatives of *Diplobunops*. The skull is nearly the size of later materials referred to *Protoreodon pumilus*, distinctly smaller than *Diplobunops matthewi*. The teeth are in a stage of development comparable to that of *Protoreodon parvus*, though possibly somewhat more primitive in being perhaps lower crowned and more weakly crescentic. Its assignment to *Diplobunops*, however, is based on the large size of the caniniform teeth and their broad separation, although it should be noted that the procumbent appearance of anterior cheek teeth in the lower jaw, as seen in plate 9, may be largely due to crushing. Moreover, the upper molars are, as in *Diplobunops*, significantly broad transversely, and the low cusps are rather widely spaced across the crown. This is not fully evident in plate 8 as there is marked foreshortening of the trans-

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Diplobunops vanhouteni*, P.U. NO. 14251

Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive....	78.5a
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive.....	65.0a
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive.....	34.0a
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	31.9
C, anteroposterior diameter (at alveolus): greatest transverse diameter .....	9.0a: 8.5a
P <sup>1</sup> , anteroposterior diameter.....	8.0a
P <sup>2</sup> , anteroposterior diameter.....	10.0
P <sup>3</sup> , anteroposterior diameter.....	9.0
P <sup>4</sup> , anteroposterior diameter: transverse diameter*.....	8.0: 11.9
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	9.4: 12.2
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	10.9: 14.4
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	12.1: 16.0
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive...	70.9
Lower premolar series, P <sub>1</sub> (at alveolus)-P <sub>4</sub> , inclusive.....	35.4
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	36.1
P <sub>1</sub> , anteroposterior diameter: greatest transverse diameter (at alveolus) .....	9.2: 6.5
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter.....	9.5: 3.7
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter.....	10.1: 5.1
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	10.5: 6.2
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	9.4: 7.8
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	10.3: 8.4
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	17.1: 8.3

a. Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

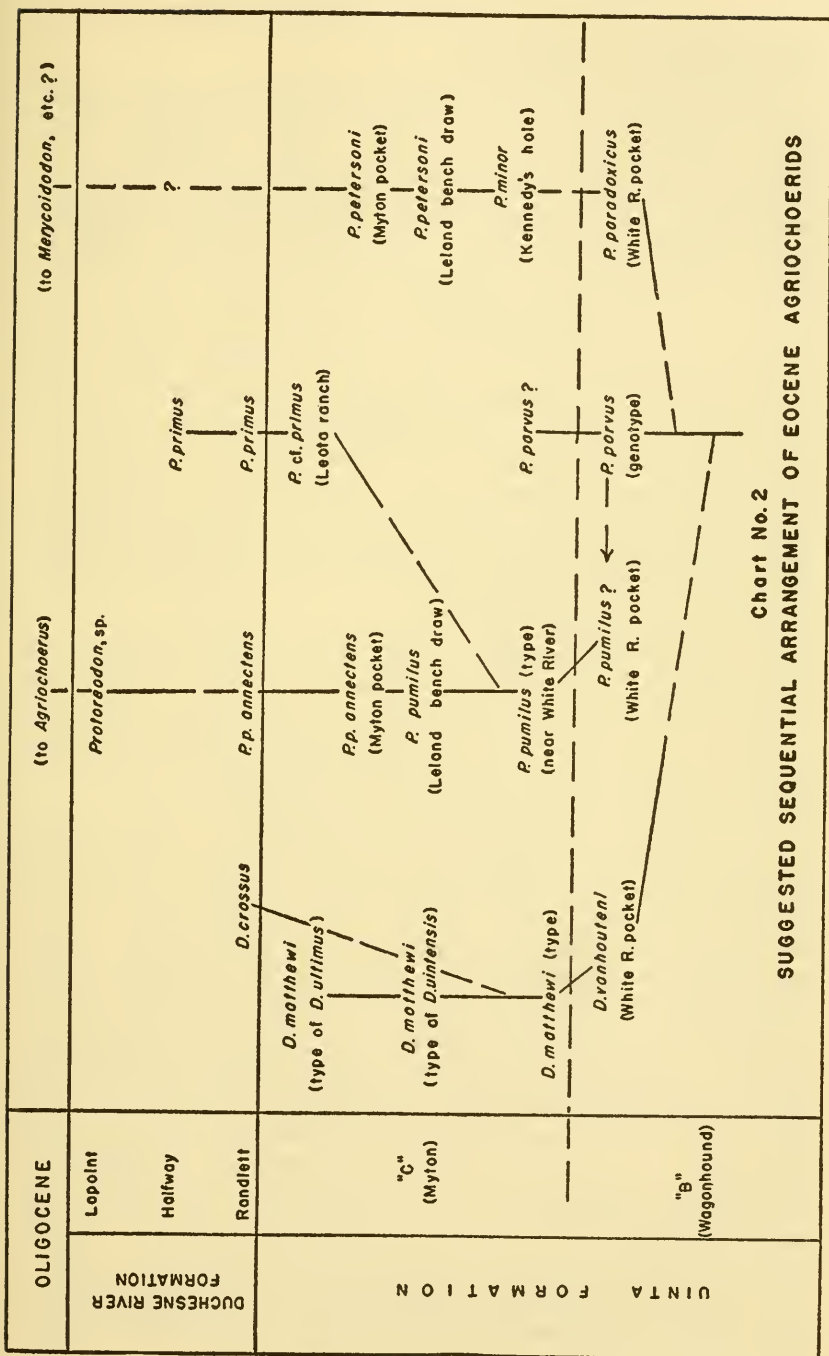


Chart No. 2  
SUGGESTED SEQUENTIAL ARRANGEMENT OF EOCENE AGRIOCHŒRIDS

verse diameter of these teeth as a consequence of the angle they are turned to the plane of the palate.

A feature not so evident in either *Protoreodon* or other *Diplobunops* material is the more noticeable pocketing or distinct basining of the anterolingual portion of the posterior lower premolars. In  $P_3$  this may be largely due to crushing although it seems clear that there was a lingual rim along this portion of the tooth. In  $P_4$ , though likewise distorted by crushing, the basin appears more clearly defined.

#### OROMERYCIDAE, new family

The genera grouped in this very distinctive family include *Oromeryx*, *Protylopus*, *Camelodon*, *Malaquiferus*, and *Eotylopus*. It is characterized as distinct from the Camelidae in comprising comparatively short-snouted forms in which the teeth are more brachydont. The upper molars exhibit a protocone which bifurcates posteriorly, and the external ribs and mesostyle are strongly developed. The lower molars are peculiar in that the conical entoconid is distinctly isolated from the metaconid by a deep pocket which opens through a notch in the lingual wall of the tooth.

The name Oromerycidae is selected rather than one derived from *Protylopus* or *Eotylopus*, although these forms are better known, because *Oromeryx* is the oldest available name and there is a strong probability that *Protylopus* may eventually prove to be a synonym. Moreover, both *Protylopus* and *Eotylopus* give unwarranted and undesired suggestion of a relationship to the camelids.

The oromerycids would appear to be camelids in certain respects, particularly in the character of the lower premolars, the scarcely emphasized canines, and the procumbent lower incisors. In the premolars there are points of resemblance to the leptotragulids as well, but the first premolar below is not caniniform. The molars, usually considered to be the more-conservative structures, are highly distinctive and raise considerable doubt as to camelid as well as leptotragulid affinities of this group. Although Scott (1940) called attention to the many noncamelid-like structures and appearances of the *Eotylopus* skull and skeleton, he, unlike Matthew (1910), placed it in the Camelidae. Actually, *Eotylopus* is superficially more camel-like than *Protylopus*, but the resemblance is in characters which may be of no more than adaptive significance. It seems clearly evident that certain of the similarities are to be accounted for by convergence, and the basic relationship of the oromerycids is not so close to the camelids as the adaptive parallelism shown in the later form tends to suggest.

For example, I<sup>3</sup> in *Eotylopus* has become the caniniform tooth as in *Poëbrotherium*, whereas in *Protilyopus* I<sup>3</sup> has not yet surpassed the canine in importance.

Matthew, with specific reference to *Eotylopus*, was inclined to stress lateral relationships in these primitive groups, but grouping *Eotylopus* and its allies with the leptotragulids with their more advanced selenodont dentition seems less clearly indicated. One could perhaps make a better case for a not too remote relationship between the poëbrotherines and the leptotragulids, or between the oromerycids and the agriochoerids.

#### Genus OROMERYX Marsh, 1894

*Type*.—*Oromeryx plicatus* Marsh, 1894.

*Discussion*.—*Oromeryx* was the third of the Uintan artiodactyls that Marsh named in 1877 but which remained nomina nuda until their description and type designation in 1894. Marsh regarded *Oromeryx* as a cervid, but in subsequent references it has been considered as a hypertragulid. Peterson (1919) included *Oromeryx* with *Leptoreodon* and *Leptotragulus* in the Hypertragulidae, but noted certain resemblances to *Protilyopus*. Direct comparison of the type materials of *Oromeryx* and *Protilyopus* reveals that there is very little of significance distinguishing them.

Marsh's illustration (1894, fig. 23) of the type specimen of *Oromeryx plicatus* is, as Peterson noted, a composite of the two sides, and there are a number of inaccuracies in the drawing. The position of P<sup>3</sup> is shown as two alveoli. This tooth is actually broken off level with the palate, and the root portion is a single three-lobed structure, which clearly divided into at least a fore-and-aft root within the maxilla. The third lobe in a position supporting the deuterocone portion of the tooth may well have had a separate root, but if not the posterior root was evidently very broad and bilobed. P<sup>4</sup> is shown as a simple bicuspid tooth whereas, in fact, the crest of the deuterocone posteriorly divides the basin of the talon, leaving a deep and prominent pocket posteriorly closed by the raised cingulum, quite as in the *Protilyopus petersoni* type specimen. Moreover, there are strong plications on the posterior portion of the external surface of this tooth (probably also on the anterior extremity of this surface as well), variously developed in *Protilyopus petersoni*. The external styles and ribs of the upper molars are much more strongly developed, as Peterson noted, than the illustration shows, and the posterior portion of the protocone is strongly bifurcate, extending a crest

toward the metaconule and a rounded lobe toward the cleft between paracone and metacone. There is no indication of the latter character in Marsh's illustration.

The highly rugose or plicate character of the enamel in *Oromeryx* is well shown in the median valleys, and somewhat better on the lingual than on the labial surfaces. The crests, where unworn, are serrate, and the portions of a lingual cingulum exhibited are highly cusped, particularly between the protocone and metaconule and as it is carried part way around the metaconule. The plicate character of the enamel is not peculiar to *Oromeryx* but is likewise highly developed on most *Protylepus* material of the Uinta B stage and on teeth of the Badwater form, *Malaquiferus*.

Perhaps the significant features of *Oromeryx*, if *Protylepus* is to be regarded as distinct, lie in the relative elongation of the teeth, anteroposteriorly, along the outer surface and the distinctly narrower posterior portion in comparison with the anterior width of the upper molars. The latter character was noted by both Scott and Peterson, but their comparisons were made with various leptomerycids. This distinction is somewhat emphasized by the incompleteness of the teeth in the *Oromeryx plicatus* type and, moreover, is less noticeable when viewed with materials of *Protylepus petersoni*.

#### OROMERYX PLICATUS<sup>86</sup> Marsh, 1894

Plate 15, figures 1-2

*Type*.—Right maxillary fragment with P<sup>4</sup> and the lingual portions of M<sup>1</sup>-M<sup>3</sup>; left maxillary fragment with M<sup>3</sup> and the labial portion of M<sup>2</sup>, Y.P.M. No. 14571.

*Horizon and locality*.—Uinta B, mouth of White River (determined from Marsh's notes pertaining to collection No. 1057), Uinta Basin, Utah.

#### MEASUREMENTS IN MILLIMETERS OF DENTITION IN SPECIMENS OF *Oromeryx plicatus*

	Y.P.M. No. 14571 Type
Length of upper cheek tooth series, anterior margin of alveolus for P <sup>3</sup> to posterior margin of M <sup>3</sup> .....	34.8
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	23.5
P <sup>4</sup> , anteroposterior diameter: transverse diameter*.....	...: 5.7
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	7.4a:...
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	8.3:...
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	8.8: 9.3

<sup>86</sup> Also illustrated in Marsh, 1894, fig. 23.

	U.S.N.M. No. 20391
Length of lower cheek tooth series, anterior margin of alveolus for $P_3$ to posterior margin of $M_3$ .....	40.3 <sup>a</sup>
Lower molar series, $M_1$ - $M_3$ , inclusive.....	26.1 <sup>a</sup>
$M_1$ , anteroposterior diameter: transverse diameter of talonid.....	7.0: 4.7
$M_2$ , anteroposterior diameter: transverse diameter of talonid.....	7.9: 5.6
$M_3$ , anteroposterior diameter: transverse diameter of trigonid.....	11.2: 5.7 <sup>a</sup>

<sup>a</sup>, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

*Discussion.*—The specific characters of *O. plicatus* are not readily separated from those that have been cited as characterizing the genus, but in size the cheek teeth are slightly larger than in specimens referred to the better-known *Protylopus petersoni*.

#### Genus PROTYLOPUS Wortman, 1898

*Type.*—*Protylopus petersoni* Wortman, 1898.

*Discussion.*—*Protylopus* received marked attention by Wortman (1898) in his diagnosis of the genus and particularly by Scott (1899) in his study of the Uinta selenodonts. The skull, dentition, and other portions of the skeleton of *Protylopus petersoni*, as far as known, were compared in detail with the Oligocene *Poebrotherium*. Except in Peterson's 1919 study of the Uinta fauna, however, I find no mention of comparisons made with Marsh's *Oromeryx plicatus*. Nevertheless, the similarity between the two in almost all details of the teeth is rather striking. The oversight may be due to the fact that the upper molars in all or nearly all the previously known *Protylopus petersoni* specimens were so badly worn or obscured that details of the pattern could not be readily discerned. Camelid affinities were diagnosed largely from the snout and anterior cheek teeth. It is important to note that the crown view of the upper cheek teeth shown by Scott (1899, pl. 2, fig. 6) is largely incorrect, or does not represent *Protylopus*. That of the lower teeth (fig. 7) may represent *Protylopus*, but  $M_3$  is peculiar and  $M_2$  is surely incorrect. Wortman's illustration (1898, fig. 4) of the lower teeth would appear to be more accurate.

*Protylopus* may well be a synonym of *Oromeryx*, as I suspect that additional material from Uinta B will demonstrate, but is tentatively retained as distinct on the basis of the more nearly rectangular appearance of the upper molars and their relatively shorter length anteroposteriorly. Serious doubt may be entertained as to the importance of these proportional differences, as material referred to *Protylopus petersoni* shows rather distinctive variations.

**PROTYLOPUS PETERSONI**<sup>37</sup> Wortman, 1898

*Type*.—Anterior portion of skull, right ramus of mandible, ulna and radius, A.M. No. 2076.

*Horizon and locality*.—Uinta C (according to Amer. Mus. labels, but probably low in C, or possibly Uinta B to judge by other collections), Uinta Basin, Utah.

*Discussion*.—In size *Protylopus petersoni* is only slightly smaller than *Oromeryx plicatus*, to judge by the limited amount of material known of each. P<sup>3</sup> is three rooted in the type, as appears to be true also in *O. plicatus*; however, the deuterococone is very weak and com-

MEASUREMENTS IN MILLIMETERS OF DENTITION IN SPECIMENS OF  
*Protylopus petersoni*

	A.M. No. 2076 Type	P.U. No. 14647
Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive .....	45.0a	47.0a
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive.....	41.0a	43.1a
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive.....	22.0a	21.7
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	21.0a	22.0a
C, anteroposterior diameter: greatest transverse diameter..	2.7 : ...	2.9a : ...
P <sup>1</sup> , anteroposterior diameter: greatest transverse diameter..	4.6 : ...	5.1 : 1.7
P <sup>2</sup> , anteroposterior diameter: greatest transverse diameter..	6.0 : ...	6.0a : ...
P <sup>3</sup> , anteroposterior diameter: transverse diameter*.....	5.8 : 3.8	6.5 : 2.7
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	5.6a : 5.7a	5.6 : 5.5
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	6.5a : ...	6.6a : 7.0a
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	7.2 : 8.5	7.8 : 8.8
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	8.3a : 9.0	8.8 : 9.4
Length of lower cheek tooth series, C (at alveolus)-M <sub>3</sub> , inclusive .....	50.5a	49.1a
Length of lower cheek tooth series, P <sub>1</sub> -M <sub>3</sub> , inclusive.....	.....	46.2
Lower premolar series, P <sub>1</sub> -P <sub>4</sub> , inclusive.....	.....	21.9
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	24.3	25.3
C, anteroposterior diameter: greatest transverse diameter..	3.7a : ...	3.7 : 2.0
P <sub>1</sub> , anteroposterior diameter: greatest transverse diameter..	.....	3.7a : 2.0
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter..	.....	5.9 : 2.0
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter..	.....	6.2 : 2.3
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter..	.....	6.7 : 2.8
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid	6.0a : ...	5.9 : 4.6
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid	7.2 : ...	7.0 : 5.8
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid .....	11.8 : 5.8	12.5 : 6.0

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

<sup>37</sup> Illustrated in Wortman, 1898, figs. 3-6; and Scott, 1899, pl. 2, figs. 5, 8, 9.



prises scarcely more than one of the several plications noted on the posterointernal wall of this tooth. In referred specimens of *P. peter-soni* in the Princeton collection, from in or near the White River pocket, P<sup>3</sup> is clearly two rooted. One of these, P.U. No. 11222, is the excellent skull and jaws figured by Scott (1899, pl. 2, fig. 5). The teeth in this specimen are not fully exposed, as the jaws have not been separated from the skull, but enough can be seen of the upper molars on the left side to indicate that the protocone is noticeably bilobate posteriorly only on M<sup>3</sup>. Moreover, the parastyle and mesostyle are surprisingly prominent and so deflected on M<sup>2</sup> and M<sup>3</sup> as to form conspicuous pockets with the paracone and metacone, respectively. Evidence of such a prominent styler development is seen also on the rather well worn molars of P.U. No. 14647. The latter specimen likewise has a two-rooted P<sup>3</sup> but may have more strongly crenulated enamel as indicated by the highly serrate cingulum lingual to the metaconulid of M<sup>3</sup>. These two specimens may represent a species or possibly a genus distinct from *Protylopus peter-soni*, but too little is known of the dental characters of this species, and I suspect that the above Princeton specimens are no more than variants. The outline of the molars in occlusal view resembles *Protylopus* more closely than *Oromeryx*.

#### PROTYLOPUS? ANNECTENS<sup>38</sup> Peterson, 1919

Plates 13 and 14

*Type*.—Portions of the skull, lower jaws, and other parts of the skeleton, C.M. No. 2932.

*Horizon and locality*.—Uinta C, Myton pocket, Uinta Basin, Utah.

*Discussion*.—The type of *Protylopus? annectens* was not available for examination at Carnegie Museum, as it has been temporarily removed from the collections, or possibly lost. It is, however, represented by a magnificent array of nearly 200 skulls, maxillae, and jaws in the National Museum collection from a single quarry in Myton pocket. From Peterson's description, measurements, and information as to horizon and general locality, there appears to be no doubt as to the species represented by these specimens, but the generic reference is questioned as it is not certain as to whether this species should be referred to *Protylopus* or to *Oromeryx*. So long as *Protylopus* is regarded as distinct, it may be preferable to retain the species in that genus, as the outline of the upper molars more nearly corresponds to *P. peter-soni*. However, the bifurcate character of the posterior crest of the protocone, so well developed in the Myton pocket

<sup>38</sup> Also illustrated in Peterson, 1919, fig. 15; pl. 37, fig. 14.

material, as it is also in *Eotylopus*, is certainly recognized only in *Oromeryx plicatus* of the earlier forms. In *Protylopus petersoni* this character, though suggested, is not clearly determined because of advanced wear in teeth of critical material.

*Protylopus? annectens* is further characterized by much greater size than either *P. petersoni* or *O. plicatus*, and the tooth enamel is comparatively smoother. P<sup>3</sup> has three distinct roots, but the deuterocone varies from weak to nearly as prominent as in P<sup>4</sup>. The cingulum may be absent from the lingual margin of the upper molars but, if present, is usually developed around the protocone rather than the metaconule. However, a cusp (or cusps) is present lingually between the protocone and metaconule as in the earlier forms.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN REFERRED SPECIMENS OF  
*Protylopus? annectens*

	U.S.N.M. No. 20290	U.S.N.M. No. 20285
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive.....	53.9	55.6
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive.....	26.3	27.3
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	28.5	28.8
C, anteroposterior diameter: greatest transverse diameter. ....		4.0: 3.2
P <sup>1</sup> , anteroposterior diameter: greatest transverse diameter. ....	5.7: 2.5	6.2: 2.4
P <sup>2</sup> , anteroposterior diameter: greatest transverse diameter. ....	7.7a: 2.8	7.8: 2.5
P <sup>3</sup> , anteroposterior diameter: transverse diameter*.....	7.3: 6.0	7.8: 4.7
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	6.7: 7.2	6.9: 7.1
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	9.0: 9.3	8.8: 8.9
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	9.9: 10.8	10.2: 10.7
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	11.0: 12.0	11.0: 12.0
	U.S.N.M. No. 20149	U.S.N.M. No. 20190
Length of lower cheek tooth series, C (at alveolus)-M <sub>3</sub> , inclusive .....	69.0	64.3
Length of lower cheek tooth series, P <sub>1</sub> -M <sub>3</sub> , inclusive.....	63.0	60.2
Lower premolar series, P <sub>1</sub> -P <sub>4</sub> , inclusive.....	31.1	28.8
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	32.2	32.0
C, anteroposterior diameter: greatest transverse diameter. ....	4.0: 2.8	4.3: 2.8
P <sub>1</sub> , anteroposterior diameter: greatest transverse diameter. ....	4.8: 2.5	5.3: 2.5
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter. ....	8.0: 2.5	6.6: 2.3
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter. ....	8.5: 3.0	7.8: 2.5
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter. ....	8.1: 4.2	7.7: 3.5
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid	8.4: 5.6	8.5: 5.6
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid	9.8: 6.1	9.9: 6.3
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trig- onid .....	14.8: 6.8	14.5: 6.8

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

The lower dentition of *Protylopus?* *annectens* is characterized by a small but distinct metaconid on the posterointernal crest of  $P^4$ . The entoconid of the lower molars is conical as in *Protylopus petersoni*, and likewise the valley between the entoconid and hypoconid is open lingually through a small pocket formed by the anterior crest of hypoconid and a metastylid crest on the posterior surface of the metaconid. However, the anterior surface of the metaconid is different in that it is smoothly conical and lacks the anterior spur or crest which joins the anterior wing of the protoconid in the earlier form. In *P.?* *annectens* the parastylid or anterior wing of the protoconid swings widely forward around the metaconid so that the valley between the metaconid and protoconid is also open lingually. In *P. petersoni* and in lower molars believed to represent *Oromeryx plicatus*, this valley is closed forward and an anterior cingulum is carried around the tooth, rising on the lingual side of the metaconid so as to form a small pocket on the anterolingual surface of this cusp. It is further noted that a marked hypoconulid is developed on the posterior extremity of the crest from the hypoconid in  $M_1$  and  $M_2$ , perhaps better defined than in the earlier forms, and the lingual cusp on the hypoconulid of  $M_3$  has nearly or entirely lost its identity in the horseshoe-shaped crest of the hypoconulid lobe.

Genus CAMELONDON Granger, 1910

*Type*.—*Camelodon arapahovius* Granger, 1910.

*Discussion*.—The teeth in this form, as far as can be determined considering the advanced wear exhibited in the only known specimen, are rather like those in *Protylopus*, but with smoother enamel. The principal character distinguishing *Camelodon* is the marked diastema between  $P_2$  and  $P_3$ . *Camelodon* would appear to represent an aberrant stem within the Oromerycidae, not ancestral to *Eotylopus*. It should be noted, moreover, that the diastema in the lower premolar series of *Poëbrotherium* is anterior to  $P_2$ .

CAMELONDON ARAPAHOVIUS<sup>39</sup> Granger, 1910

*Type*.—Left ramus of mandible with  $P_2$ - $M_3$ , A.M. No. 14604.

*Horizon and locality*.—Uintan equivalent of the Wagonbed deposits on Beaver Divide, Fremont County, Wyo.

*Discussion*.—In size *Camelodon arapahovius* is about intermediate between *Protylopus petersoni* and *Protylopus?* *annectens*. Neither of

<sup>39</sup> Illustrated in Granger, 1910, fig. 4; and Scott, 1945, pl. 2, fig. 2.

these forms, however, shows any tendency toward a diastema in the premolar series as long as that in *C. arapahovius*. The jaw, moreover, appears to be relatively slender, taking into consideration its maturity as evidenced by tooth wear.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Camelodon arapahovius*, A.M. NO. 14604

Length of lower cheek tooth series, P <sub>2</sub> -M <sub>3</sub> , inclusive.....	51.0
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	27.1
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter.....	6.4: 2.0
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter.....	6.7: 2.3
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	7.0: 2.9
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	6.8:...
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	8.3: 5.7
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	12.8: 5.3

**MALAKUIFERUS**,<sup>40</sup> new genus

*Type*.—*Malaquiferus tourteloti*, new species.

*Generic characters*.—Orbit large and cranial portion of skull elongate. Enamel of cheek teeth highly rugose. P<sup>4</sup> without labially directed styles. External styles of upper molars weak but ribs outstanding. Upper molars nearly rectangular, transversely elongate, and not oblique. M<sup>2</sup> and M<sup>3</sup> of equal size. Protocone strongly bilobate posteriorly, at least in M<sup>3</sup>.

*Discussion*.—*Malaquiferus* is clearly related to *Oromeryx* and *Protylopus*, but differs rather noticeably in the striking shift in emphasis from styles to ribs in the upper molars. These teeth are nearly rectangular, transversely elongate, and not so oblique as in *Oromeryx*. There is much less disparity in size between succeeding molars in *Malaquiferus* so that M<sup>3</sup> is relatively much smaller than in *Oromeryx* or *Protylopus*, being scarcely distinguished from M<sup>2</sup> in size and form. There appears to be no cingulum around the lingual margin of the protocone and metacone in any of the molars, although there is a prominent style or pillar lingually between these cusps in each. An additional feature noted is the comparatively large orbit and more elongate cranial portion of the skull than in *Protylopus*. *Malaquiferus* bears a strong resemblance to *Oromeryx*, and evidently to *Protylopus*, in the distinctly rugose tooth enamel and in the bilobate character of the posterior portion of the protocone in the upper molars.

<sup>40</sup> From Latin *malus*, bad; *aqua*, water; and *ferus*, wild animal. In allusion to its occurrence in the Badwater region.

MALAQUIFERUS TOURTELOTI,<sup>41</sup> new species

Plate 16

*Type*.—Greater part of skull with P<sup>4</sup>-M<sup>3</sup>, inclusive, U.S.N.M. No. 20588.

*Horizon and locality*.—Uintan deposits in sec. 11, T. 39N., R. 92 W., 1½ miles northeast of east fork of Dry Creek, Fremont County, Wyo.

*Specific characters*.—*Malaquiferus tourteloti* is comparable to *Protorcodon petersoni* in size of teeth, although the cranial proportions indicate a form somewhat greater in size. Other specific characters are not distinguished from those of the genus. The lower teeth are not known.

*Discussion*.—The type specimen of this rather unusual oromerycid was found by Harry A. Tourtelot, of the U. S. Geological Survey, in upper Eocene deposits exposed along the northern margin of the Wind River Basin, not far from and possibly equivalent in age to the fossiliferous exposures along the south side of Badwater Creek west of Badwater P. O. Further search of the exposures in the vicinity of the *Malaquiferus* occurrence for confirming evidence as to the age of the beds has produced remains of *Eomoropus*, cf. *amarorum*.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Malaquiferus tourteloti*, U.S.N.M. NO. 20588

Length of preserved portion of upper cheek tooth series, P <sup>4</sup> -M <sup>3</sup> , inclusive .....	27.1
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	21.7
P <sup>4</sup> , anteroposterior diameter: transverse diameter*.....	5.8:6.5
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	6.8:7.8
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	7.4:8.8
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	7.5:9.0

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

Family CAMELIDAE Gray, 1821

Subfamily POËBROTHERIINAE Zittel, 1893

Attention was early directed to the possibility of camelids occurring in the Eocene of North America when Scott in 1889 suggested that *Leptotragulus* was closely allied to *Poëbrotherium* and belonged in the Tylopoda. This genus, however, is now regarded as a leptomerycid. Some time later (1898), Wortman described *Protylopus*,

<sup>41</sup> Named for Harry A. Tourtelot.

which was generally accepted as camelid, along with certain other Eocene forms now also included in other families. Subsequent studies have included description of *Camelodon* by Granger in 1910, here assigned along with *Protylopus* to the Oromerycidae, and description of the Duchesnean *Poabromylus* by Peterson in 1931, which I believe should be regarded as a leptomerycid, closely related to *Leptoreodon*. The new form *Poëbrodon*, the description of which follows, thus would seem significant as perhaps the first true camelid to be known from the Eocene.

Discovery of the rather limited material representing *Poëbrodon* has given new evidence as to the phylogenetic arrangement of certain of the Eocene selenodonts and has further emphasized the necessity for designating the new family Oromerycidae. *Protylopus* was early looked upon, particularly by Wortman (1898) and Scott (1899), as being in an ancestral position within the Poëbrotheriinae, although Matthew (1910) suggested that this relationship applied only to the descent of *Eotylopus*. Matthew went still further and excluded *Protylopus* and *Eotylopus* from the Camelidae and suggested that *Poëbrotherium* was derived from "an advanced contemporary (to *Protylopus*) genus of more northern habit." Peterson, like Scott, retained *Protylopus* in the Camelidae but agreed with Matthew that the ancestry of *Poëbrotherium* was to be sought "in some more advanced contemporary genus." It was evident, however, that he thought this would be found in the Uinta Basin; a prediction that has been made good. Scott (1945), however, remained convinced that *Protylopus* gave rise to *Poëbrotherium* as well as to *Eotylopus*.

Discovery of *Poëbrodon*, distinctly precocious, now furnishes the form, in support of Matthew's and Peterson's views, that completely anticipates *Poëbrotherium* in its combination of characters, as far as known. It likewise gives further evidence of the separateness of the oromerycids from the camelids.

#### POËBRODON,<sup>42</sup> new genus

*Type*.—*Poëbrodon kayi*, new species.

*Generic characters*.—Teeth like *Poëbrotherium* but shorter crowned. Anteroposteriorly much-compressed styles of upper molars slightly more outstanding. Weak metastylid flexure on lingual wall of lower molars, and lingual surface of metaconid and entoconid slightly more convex than in *Poëbrotherium*. Hypoconulid lobe of M<sub>3</sub> with lingual portion less reduced than in *Poëbrotherium*.

<sup>42</sup> From Greek πότη (πόα), grass; βρώω, to eat; and ὀδών, tooth.

*Discussion.*—As has been noted in the previous discussion, discovery of such a form as *Poëbrodon* has been long anticipated. The most significant information to come from this find, however, is the demonstration that the Uintan stage of development is strikingly *Poëbrotherium*-like. Except for the more-brachydont teeth and only slightly more-noticeable styles of the molars, *Poëbrodon* is scarcely more than a very small *Poëbrotherium*. The upper molars of *Poëbrodon* do resemble *Leptomeryx*, but the parastyles and mesostyles are more compressed, the ribs flatter, and the transverse width of the teeth, particularly of  $M^1$ , is very much less. Moreover, there is evidence for a very strong posteriorly directed style from the metacone of  $M^3$ .

The poëbrotherine character of the lower molars is possibly even more striking. The lingual wall of these teeth, however, is somewhat less flattened, as noted in the slight flexure in early wear at about the position of a metastylid, and in the somewhat more emphasized bilobate appearance resulting from convexities about the metaconid and entoconid, respectively. Nevertheless, the anterior and posterior columns of these teeth, as in *Poëbrotherium*, are more distinctly separate from one another than, for example, in the leptomerycids. This effect of separate columns results from the early union of the flattened metaconid with the anterior and posterior crests of the protoconid, and similarly the union of the hypoconid crests with the entoconid. The important poëbrotherine distinction lies in the deflection of the anterior crest of the hypoconid inward and away from the posterior crest of the protoconid and its joining instead with the entoconid. The two columns are thus joined only along the lingual wall. In these respects the Poëbrotheriinae are distinct from the leptomerycids and differ fundamentally from the oromerycids.

#### POËBRODON KAYI,<sup>43</sup> new species

Plate 15, figure 3

*Type.*—Left maxillary fragment with  $M^1$ ,  $M^2$ , and most of  $M^3$ , U.S.N.M. No. 20393.

*Horizon and locality.*—Uinta C, Myton pocket, Uinta Basin, Duchesne County, Utah.

*Specific characters.*—Teeth a little less than one-half the size of those in *Poëbrotherium wilsoni*.

*Discussion.*—In addition to the type upper dentition there are in the collection two portions of a left mandibular ramus, U.S.N.M. No. 20392, including  $M_3$ ,  $M_2$  with entoconid portion broken away,

<sup>43</sup> Named for Dr. J. LeRoy Kay.

and the posterior half of  $M_1$ . The lower jaw is from the same general locality as the type but is evidently not from the same individual, as the upper teeth show somewhat greater wear. It is rather surprising that two specimens of this rare form should show up about the same time, and fortunate that they complement one another in furnishing information on both the upper and lower molars. The anterior cheek teeth are not known, and no other skeletal portions in the collections have been recognized as pertaining to this form.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Poëbrodon kayi*

	U.S.N.M. No. 20393 Type
Length of upper molar series, $M^1$ - $M^3$ (posterior margin of root), inclusive .....	20.2
$M^1$ , anteroposterior diameter : transverse diameter* .....	6.3 : 5.3
$M^2$ , anteroposterior diameter : transverse diameter .....	7.0 : 6.7
$M^3$ , anteroposterior diameter : transverse diameter .....	7.7a : 6.8a
	U.S.N.M. No. 20392
$M_1$ , transverse diameter of talonid .....	4.4
$M_2$ , anteroposterior diameter : transverse diameter of talonid .....	7.0a : 4.8a
$M_3$ , anteroposterior diameter : transverse diameter of trigonid .....	10.7 : 5.0

a. Approximate.

\* Measurements of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

Family LEPTOMERYCIDAE Scott, 1899

Subfamily LEPTOTRAGULINAE Zittel, 1893

The reasons for separating the leptotragulines from Hypertragulidae and including them tentatively with the leptomerycines in a separate family have been discussed above under the Hypertragulinae. Such an arrangement seems preferable to including the leptotragulids in the Camelidae, as Wortman (1898), Matthew (1903, p. 224), and Scott (1899) were inclined to do.

Attention is also again directed to the conclusion that *Oromeryx*, generally included with the leptotragulids, does not represent this subfamily but belongs in a distinct family. *Oromeryx* is clearly related to *Protylepus* and should not be grouped either with the hypertragulids or the leptotragulids. Moreover, *Poabromylus*, which Peterson described as a camelid, does not appear to present characters of significance other than size, suggesting the Camelidae, and seems to be more closely related to the leptotragulines. Its premolars, though large,



rather suggest *Leptoreodon* and the molars, though relatively high crowned, are of a *Leptoreodon-Leptotragulus* type.

The leptotragulids appear, with one exception, to be the only Eocene artiodactyls to have early developed a simple and nearly complete selenodont structure in the protomerous portion of the molars. The protocone and metaconule of the upper molars and the protoconid and hypoconid of the lower molars in the Uintan leptotragulines are simple crescentic structures without important bifurcations, and free, except in advanced wear, from the paramere, although the posterior crest of the hypoconid joins or forms a lingually placed hypoconulid. It is noteworthy that the posterior crest of the protocone and the anterior crest of the metaconule are directed more toward the saddle midway in the paramere rather than as *Protoreodon*. The exception noted above is in the precocious *Poëbrotherium*-like molars of *Poëbrodon*. Here the selenodontology is advanced but of a different character, in which an early union is established between the crests of the inner and outer cusps.

Genus **LEPTOTRAGULUS** Scott and Osborn, 1887

*Synonym.*—*Parameryx* Marsh, 1894.

*Type.*—*Leptotragulus proavus* Scott and Osborn, 1887.

*Discussion.*—*Parameryx* and *Leptotragulus* have been considered synonymous since 1894 when Marsh furnished a description of *Parameryx*. Later, when Wortman (1898) reviewed the characters, he concluded that the form represented was a tylopod, but in citing the name gave priority to *Parameryx*. *Parameryx*, like *Eomeryx* and *Oromeryx*, was named by Marsh in an address published in 1877; however, these were without adequate description and no types were named at that time. They remained nomina nuda until 1894. Therefore, if *Parameryx* and *Leptotragulus* are identical, *Leptotragulus*, of course, has priority. It should be noted, however, that since the molars of *Leptotragulus* and *Leptoreodon* are so much alike, and the teeth belonging to the type material of *Parameryx laevis* consist only of a few molars, there is perhaps a possibility, not too remote, that the synonymy adopted here is incorrect and that *Parameryx* and *Leptoreodon* are synonymous, in which case *Parameryx* would be the older term. The nature of the *Parameryx laevis* material is highly unsatisfactory so that preservation of the status quo is much to be desired.

The genus *Leptotragulus* is distinguished from *Leptoreodon* principally on the basis of the premolars. The difference is perhaps less noticeable in the upper premolars although P<sup>2</sup> and P<sup>3</sup> show evidence

of a better-developed tritocone than in *Leptoreodon*. In the lower jaws both  $P_3$  and  $P_4$  have an anterolingually directed crest from the protoconid, but in *Leptotragulus* the anterior extremity is more sharply flexed with a better-defined parastyliid. A posteroexternal crest extends from the protocone, then swings inward forming the posterior crest of the heel. A posterointernal crest extends posteriorly and only slightly inward from the apex of the protoconid but terminates before reaching the posterior crest, leaving the talonid basin broadly open lingually. In some material of *Leptotragulus* this talonid basin of  $P_4$  may be partially constricted medially by a slight plication from the posterointernal crest. In *Leptoreodon* there is a prominent metaconid posterointernal to the protoconid in  $P_4$  and apparently also in  $P_3$ . Moreover,  $P_4$  of *Leptoreodon* exhibits a usually distinctive, though variably developed, entoconid. In *Leptomeryx* the entoconid is well developed, and in  $P_4$  joins the metaconid in early wear, but in  $P_3$  joins the external crest well back of the protoconid. It may be further noted that the upper molars in *Leptomeryx* have a noticeably more oblique appearance than in the Eocene forms.

**LEPTOTRAGULUS PROAVUS** <sup>44</sup> Scott and Osborn, 1887

Plate 18, figure 1

*Synonyms.*—*Parameryx laevis* Marsh, 1894.

?*Parameryx sulcatus* Marsh, 1894.

*Type.*—Anterior portion of the left ramus of a mandible with  $P_4$  and  $M_1$ , P.U. No. 11501.

*Horizon and locality.*—Uinta upper Eocene, "White River," Uinta Basin, Utah.

*Discussion.*—The gentyope, *Leptotragulus proavus*, is much the larger of the three Eocene species now recognized and is represented in collections by a relatively small amount of material. The premolars are relatively elongate and  $P_4$  has a distinctive, lingually placed, nearly conical parastyliid. The posterolingual crest swings slightly inward with a weak suggestion of a metaconid nearly halfway down its slope, and there is a slight plication from this crest directed toward the middle of the talonid basin.  $M_1$  shows a prominent accessory cusp or pillar between the protoconid and hypoconid.

The cotype lower jaw material of *Parameryx laevis*, which exhibits part of  $M_1$  and  $M_2$ , corresponds in all details to the  $M_1$  in *L. proavus*.

The Chadron form *Leptotragulus profectus* Matthew, from Pipe-

<sup>44</sup> Also illustrated in Scott, 1889, pl. 7, figs. 10, 10a.

stone Springs, is much larger than *L. proavus* but is surprisingly similar. It also bears a striking resemblance to *Protoceras*. I believe that a closer affinity is indicated here than with the camelids. *L. profectus* may be a connecting link between the Eocene *Leptotragulus* and later *Protoceras*. Possibly Cook's form *Pseudoprotoceras longinaris* is the same as Matthew's *L. profectus*. As yet only the upper dentition of one and the lower of the other have been described or illustrated.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Leptotragulus proavus*

	C.M. No. 10199
Length of upper cheek tooth series, P <sup>3</sup> -M <sup>1</sup> , inclusive.....	22.0
P <sup>3</sup> , anteroposterior diameter: transverse diameter.....	8.0: 6.0
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	7.0: 7.3
M <sup>1</sup> , anteroposterior diameter: transverse diameter.....	7.4: 10.1
	P.U. No. 11501 Type
Length of lower cheek tooth series, P <sub>2</sub> -M <sub>1</sub> , inclusive.....	27.7
P <sub>2</sub> , anteroposterior diameter (at alveoli).....	6.4
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	7.3: 3.5
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	7.4: 5.5

LEPTOTRAGULUS MEDIUS<sup>45</sup> Peterson, 1919

Plate 17, figures 2, 3

*Type*.—Rostral portion of skull with upper dentition P<sup>3</sup>-M<sup>3</sup>, C.M. No. 2986.

*Horizon and locality*.—Uinta C, 6 miles east of Myton, Uinta Basin, Utah.

*Discussion*.—Peterson listed a lower-jaw portion with M<sub>3</sub> and certain limb fragments as belonging to the type. However, in the lower jaw the preserved tooth (probably M<sub>2</sub> but not M<sub>3</sub>) is at the point of erupting and hence does not belong to the same individual as the rostrum. For this reason there may be some doubt as to which individual the limb fragments belong.

This species is represented in the collections of the U. S. National Museum by about 27 jaws and maxillae with teeth. All these are from Myton pocket and all but four from the *Protylopus* quarry.

The *Leptotragulus medius* material is a little less than four-fifths the size of *L. proavus*. The lower premolars are relatively less slender, and in P<sub>4</sub> the parastyle, though distinct, is not so nearly conical.

<sup>45</sup> Also illustrated in Peterson, 1919, pl. 37, figs. 1-4.

## MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF

*Leptotragulus medius*

	C.M. No. 2986 Type	U.S.N.M. No. 16549
Length of upper cheek tooth series, P <sup>2</sup> -M <sup>3</sup> , inclusive.....	.....	34.5
Length of upper cheek tooth series, P <sup>3</sup> -M <sup>3</sup> , inclusive.....	31.0	29.3
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	20.4	19.5
P <sup>2</sup> , anteroposterior diameter: transverse diameter*.....	.....	5.5: 3.4a
P <sup>3</sup> , anteroposterior diameter: transverse diameter.....	5.8: 4.6	5.8: ...
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	5.2: 5.8	5.3: 5.5
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	5.9: 7.3	6.2: 7.2
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	7.2: 8.7b	7.2: 8.9b
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	7.3: 9.2b	7.3: 8.9b
	U.S.N.M. No. 20361	U.S.N.M. No. 20365
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive .....	.....	48.0a
Length of lower cheek tooth series, P <sub>2</sub> -M <sub>3</sub> , inclusive.....	38.3	38.6a
Lower premolar series, P <sub>1</sub> (at alveolus)-P <sub>4</sub> , inclusive.....	.....	25.0a
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	23.0	23.4
P <sub>1</sub> , anteroposterior diameter (at alveolus): greatest transverse diameter .....	.....	4.7: 3.6
P <sub>2</sub> , anteroposterior diameter.....	5.0	.....
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter..	5.9: ...	5.8: 3.2
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter..	5.8: ...	6.2: 4.1
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid .....	6.1: ...	6.1: 5.2
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid .....	6.7: ...	6.9: 5.8
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid .....	10.6: ...	10.7: 6.2

a, Approximate.

b, Margin of enamel lingually.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

LEPTOTRAGULUS CLARKI,<sup>46</sup> new species

## Plate 17, figure 1

*Type*.—Right ramus of mandible with P<sub>1</sub> and P<sub>3</sub>-M<sub>3</sub>, U.S.N.M. No. 20378.

*Horizon and locality*.—*Protylopus* quarry, Myton pocket, 6 miles east of Myton, Uinta Basin, Utah.

*Specific characters*.—Size only a little smaller than *Leptotragulus medius* but with teeth relatively much more slender. P<sub>3</sub> and P<sub>4</sub> with posterior crests from protoconid less divergent.

<sup>46</sup> Named for Dr. John Clark.

*Discussion.*—In addition to the type, there were three other lower jaws and possibly a maxilla found representing this species in association with the bulk of the *Leptotragulus medius* material in the *Protylopus* quarry. Two of the lower jaws are immature and retain milk premolars along with the permanent molars. The referred maxilla has but three molariform teeth preserved.

The difference between *Leptotragulus clarki* and *L. medius* was not at first evident, but when measurements were taken of a series of lower dentitions, two size groups were clearly indicated. Upon more detailed examination further differences observed included relatively narrower teeth, particularly in the premolar region, and the fact that the two crests extending posteriorly from the apex of the protoconid in  $P_3$  and  $P_4$  were in consequence much less divergent than in *L. medius*. The single upper dentition, U.S.N.M. No. 20373, preserved shows that  $M^1$  to  $M^3$ , if these teeth are correctly identified, though only a little shorter anteroposteriorly than in *L. medius*, are conspicuously narrower transversely. There is a possibility, however, that the first of these is  $Dp^4$  rather than  $M^1$ , as suggested by advanced wear, in which case the specimen would represent a moderately large *L. medius*. Nevertheless, I have been unable to find evidence of a replacing  $P^4$  beneath the position of the first tooth. It may be noted that  $Dp^4$  in *Leptotragulus* material would appear to be an exact replica of  $M^1$ , though smaller, and the wear would be relatively more advanced in comparison with the tooth next posterior.

The *Leptotragulus* material in the Princeton collections, found associated with specimens of *Pentacemylus leotensis* and *Protoreodon*,

MEASUREMENTS IN MILLIMETERS OF DENTITION IN SPECIMENS OF  
*Leptotragulus clarki*

	U.S.N.M. No. 20378 Type	U.S.N.M. No. 20380
Length of lower cheek tooth series, $P_1$ (at alveolus)- $M_3$ , inclusive .....	43.0a	.....
Lower premolar series, $P_1$ (at alveolus)- $P_4$ , inclusive.....	23.0a	.....
Lower molar series, $M_1$ - $M_3$ , inclusive.....	20.3	20.1
$P_1$ , anteroposterior diameter (at alveolus) : greatest transverse diameter .....	3.8 : 2.5	4.0a : 2.4
$P_3$ , anteroposterior diameter : greatest transverse diameter..	5.2 : 2.3	.....
$P_4$ , anteroposterior diameter : greatest transverse diameter..	5.3 : 3.4	5.4 : 3.0
$M_1$ , anteroposterior diameter : transverse diameter of talonid.	5.6 : ...	5.5 : 4.4
$M_2$ , anteroposterior diameter : transverse diameter of talonid.	6.5 : ...	6.3 : 5.1
$M_3$ , anteroposterior diameter : transverse diameter of trigonid .....	9.0 : 5.0	8.7 : 5.2

a, Approximate.

cf. *primus* at the Leota Ranch quarry, all appears to represent a smaller, more slender toothed species than *Leptotragulus medius* and may well represent *Leptotragulus clarki*.

Genus **LEPTOREODON** Wortman, 1898

*Synonyms*.—*Merycodesmus* Scott, 1898.

*Camelomeryx* Scott, 1898.

*Type*.—*Leptoreodon marshi* Wortman, 1898.

*Discussion*.—*Merycodesmus* and *Camelomeryx* were named by Scott in a paper presented before the Philosophical Society in March, 1898, but not published until April 15, 6 days after Wortman's paper that included the description of *Leptoreodon*. Careful comparison of the materials representing these three convinces me that only one form is represented.

The principal characters defining *Leptoreodon* have been discussed above in comparison with *Leptotragulus*. It has been noted that *Leptoreodon* is characterized as distinct from *Leptotragulus* essentially in the different development of the lower premolars. In these, notably  $P_3$  and  $P_4$ , there is only a single crest immediately posterior to the apex of the protoconid, but in both these there is a distinct metaconid which is joined by a spur to the principal posterior crest at some position behind the protoconid. This arrangement generally leaves a prominent forward- and inward-facing groove between these cusps, particularly in  $P_4$ , which is rather unlike *Leptotragulus*. Moreover, there is generally a well-defined cusp at the posterointernal extremity of the posterior crest in the position of an entoconid in  $P_4$  and possibly, though not clearly observed, in  $P_3$ . Also, the parastyloid of these two teeth is not clearly distinguished on the anterior crest in *Leptoreodon*. In *Leptomeryx* the metaconid and entoconid are well developed, but in  $P_4$  the metaconid is nearly opposite and joins the protoconid, and the large entoconid nearly or quite joins the metaconid. In  $P_3$  the metaconid is weak and takes the form of a crest extending posteriorly from the protoconid. The entoconid usually does not join it but unites with the principal posterior crest about midway of its length. *Leptomeryx*, moreover, exhibits a well-developed parastyloid on  $P_2$  to  $P_4$ .

In the upper premolar series less of significance was observed, but  $P^4$  in *Leptoreodon* appears broader transversely and the deuterocone preserves somewhat more of its identity as a cusp. In *Leptotragulus* the deuterocone is perhaps more selenodont, and  $P^2$  and  $P^3$  exhibit a better-developed tritocone.

*Leptomeryx* does not appear to have originated in either *Leptotragulus* or *Leptoreodon* but in some intermediate form possessing a combination of characters in part resembling one and in part the other. The upper dentition of *Leptomeryx* most nearly resembles that of *Leptotragulus* but the posterior portions of the lower premolars are not readily reconciled. Likewise, the lower premolars of *Leptoreodon* present an arrangement which is perhaps too differently specialized.

**LEPTOREODON MARSHI** <sup>47</sup> Wortman, 1898

Plate 18, figure 2

*Synonyms.*—*Merycodesmus gracilis* Scott, 1898.

*Camelomeryx longiceps* Scott, 1898.

*Type.*—Skull and both rami of mandible, A.M. No. 2064.

*Horizon and locality.*—Uinta formation, near White River, Uinta Basin, Utah.

*Discussion.*—*Leptoreodon marshi* corresponds rather closely in size to *Leptotragulus proavus*. The essential characteristics of the premolars have been described above in comparisons on a generic level. The molars may not be distinguishable from those in the larger species of *Leptotragulus*. In general, they are relatively broad and highly selenodont, lingually above and buccally below. The outer wall of the upper teeth has prominent ribs and styles and a cingulum is well developed. Internally, the cingulum may be heavy around the metaconule but is weaker or not defined lingual to the protocone. Between these cusps lingually there is a distinct pillar or accessory cuspule which, though variably developed, appears to be persistent. An equivalent cuspule is present between protoconid and hypoconid below. The lower molars, however, show less evidence of a cingulum, except on the anterior and posterior faces.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Leptoreodon marshi*

	A.M. No. 2064 Type	P.U. <sup>48</sup> No. 11225	P.U. <sup>49</sup> No. 11226
Length of upper cheek tooth series, C (at alveolus)-M <sup>3</sup> , inclusive .....	58.0	64.0a	57.5
Length of upper cheek tooth series, P <sup>1</sup> -M <sup>3</sup> , inclusive .....	50.8	55.2a	51.5a
Upper premolar series, P <sup>1</sup> -P <sup>4</sup> , inclusive..	29.5	33.5a	31.0a

<sup>47</sup> Also illustrated in Wortman, 1898, fig. 1; and Scott, 1899, pl. 2, figs. 10-14; pl. 3, figs. 15, 16.

<sup>48</sup> Type of *Merycodesmus gracilis*.

<sup>49</sup> Type of *Camelomeryx longiceps*.

	A.M. No. 2064 Type	P.U. No. 11225	P.U. No. 11226
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive....	23.0	22.5	21.9
C, anteroposterior diameter (at alveolus): greatest transverse diameter...	4.5:...	5.4:3.2a	4.5:3.0
P <sup>1</sup> , anteroposterior diameter: greatest transverse diameter .....	4.5:...	5.0:...	3.5:...
P <sup>2</sup> , anteroposterior diameter: greatest transverse diameter .....	6.5:...	7.0a:...	6.9:2.5
P <sup>3</sup> , anteroposterior diameter: transverse diameter* .....	7.3a:...	7.0a:5.0a	7.0:6.0a
P <sup>4</sup> , anteroposterior diameter: transverse diameter .....	6.2:...	5.3a:7.0	...:6.5a
M <sup>1</sup> , anteroposterior diameter: transverse diameter* .....	7.0a:8.5a	6.6a:8.9	6.2:7.7
M <sup>2</sup> , anteroposterior diameter: transverse diameter .....	8.0a:10.0a	8.4a:10.5	7.3:10.3
M <sup>3</sup> , anteroposterior diameter: transverse diameter .....	8.6a:11.0a	8.9:11.5	8.4:11.6
			U.S.N.M. No. 20397
Length of lower cheek tooth series, P <sub>1</sub> (at alveolus)-M <sub>3</sub> , inclusive.....	58.0a	58.1	.....
Lower premolar series, P <sub>1</sub> (at alveolus)-P <sub>4</sub> , inclusive .....	31.5	32.3	.....
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive....	26.5	26.0	.....
P <sub>1</sub> , anteroposterior diameter (at alveolus) .....	4.5a	4.4	.....
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter .....	5.5a:2.2a	5.0a:...	.....
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter .....	7.2:2.5a	7.0:3.0	7.0a:...
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter .....	7.5:...	6.8:4.0	7.1:3.9
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	7.0:...	6.6a:...	6.8a:5.4
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	8.0:...	7.8:6.0	8.2:6.4
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	11.6:...	12.0a:6.3	...:6.8

a, Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

#### LEPTOREODON (HESPEROMERYX) EDWARDSI<sup>50</sup> Stock, 1936

Type.—An upper cheek tooth series, P<sup>2</sup> to M<sup>3</sup>, inclusive, C.I.T. No. 1839.

<sup>50</sup> Illustrated in Stock, 1936, pl. 1.



*Horizon and locality.*—Upper Uintan, Sespe formation, Tapo Ranch or C.I.T. loc. 180, north side of Simi Valley, Ventura County, Calif.

*Discussion.*—*Leptoreodon* (*H.*) *edwardsi* is a little smaller than *Leptoreodon marshi*, but clearly belongs to *Leptoreodon* rather than *Leptotragulus* as Stock has shown. P<sup>2</sup> and P<sup>3</sup>, though worn, show no evidence of a triticocone as in *Leptotragulus*. P<sup>4</sup> is transversely broad as in *Leptoreodon* but the deuterococone would appear to be perhaps somewhat less crescentic than in *L. marshi*, certainly less so than in *Leptotragulus*. The lower dentition belonging to C.I.T. No. 1840, designated as a paratype, shows advanced wear, but P<sub>4</sub> has a prominent, rounded metaconid. The bifurcation of the posterior crest posterointernally has also been noted in *P. marshi* material. The anterior crest, however, shows a somewhat more sharply flexed anterior extremity suggesting a distinct parastylid cusp as in *Leptotragulus*, although this is clearly not present in P<sub>2</sub> and P<sub>3</sub>. The latter two teeth are slender, and P<sub>2</sub> as well as P<sub>3</sub> has a weak posterointernal crest rather than a distinct metaconid which joins the outer crest nearer the apex of the protoconid than is noted in *L. marshi* material.

MEASUREMENTS IN MILLIMETERS OF DENTITIONS IN SPECIMENS OF  
*Leptoreodon (Hesperomeryx) edwardsi*

	C.I.T. No. 1839 Type
Length of upper cheek tooth series, P <sup>2</sup> -M <sup>3</sup> , inclusive.....	37.7 <sup>a</sup>
Upper molar series, M <sup>1</sup> -M <sup>3</sup> , inclusive.....	21.3
P <sup>2</sup> , anteroposterior diameter: transverse diameter*.....	6.3: 3.1
P <sup>3</sup> , anteroposterior diameter: transverse diameter.....	6.5: 3.6
P <sup>4</sup> , anteroposterior diameter: transverse diameter.....	5.7: 6.3
M <sup>1</sup> , anteroposterior diameter: transverse diameter*.....	6.3: 8.2
M <sup>2</sup> , anteroposterior diameter: transverse diameter.....	7.7: 9.8
M <sup>3</sup> , anteroposterior diameter: transverse diameter.....	8.0: 10.0

	C.I.T. No. 1840
Length of lower cheek tooth series, P <sub>2</sub> -M <sub>3</sub> , inclusive.....	41.1
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	35.0
P <sub>2</sub> , anteroposterior diameter: greatest transverse diameter.....	5.5: 2.0
P <sub>3</sub> , anteroposterior diameter: greatest transverse diameter.....	6.4: 2.9
P <sub>4</sub> , anteroposterior diameter: greatest transverse diameter.....	6.4: 3.6
M <sub>1</sub> , anteroposterior diameter: transverse diameter of talonid.....	6.3: 5.2
M <sub>2</sub> , anteroposterior diameter: transverse diameter of talonid.....	7.3: 6.1
M <sub>3</sub> , anteroposterior diameter: transverse diameter of trigonid.....	10.2: 5.9

<sup>a</sup>. Approximate.

\* Measurements of posterior upper premolars are taken anteroposteriorly across outer portion and transversely perpendicular to outer margin. Those of upper molars are taken anteroposteriorly perpendicular to anterior margin and transversely across anterior portion of tooth.

The upper molars of *L. (H.) edwardsi* show a somewhat less sharply flexed outer wall with less-prominent styles and ribs than observed in *L. marshi*. In the lower molars the lingual median cuspule is well developed and the cingulum appears to encroach somewhat farther lingually on the principal inner cusps, but this would not appear to be significant.

As Stock has indicated in his description of *Hesperomeryx*, the differences in the premolars between *Leptoreodon (H.) edwardsi* and *Leptoreodon marshi* are rather significant but probably not of full generic importance.

#### Genus POABROMYLUS Peterson, 1931

*Type*.—*Poabromylus kayi* Peterson.

*Discussion*.—*Poabromylus* was described by Peterson as a camelid and regarded as such by Scott (1945). I am convinced, however, regardless of its large size, that it is a leptotragulid. In the structure of the lower molars it more closely resembles the leptomerycids in general than it does either the oromerycids or Poëbrotheriinae.  $P_4$  has a metaconid developed similarly but relatively not so large as in *Leptoreodon*, and the anterior crest in both  $P_3$  and  $P_4$  extends forward and inward as in *Leptoreodon* without the separate parastylid cusp noticed in the camelids. The heel of  $P_4$  has a basin somewhat resembling that in *Protylopus*, but this portion of the tooth is much broader, as it is in *Leptoreodon*. The talonid portion of  $P_3$  is slightly damaged posterointernally, but the posterior half of this tooth is not unlike the camelids; neither is it unlike *Leptotragulus* or even the Sespe subgenus *Hesperomeryx*.

Of more fundamental significance would appear to be the structure of the molars. In the lower series the inner wall is continuous as in both the leptotragulids and poëbrotherines, not deeply interrupted as it is in the oromerycids. On the other hand, the highly crescentic outer cusps have the leptotragulid pattern, not the oromerycid arrangement where the entoconid remains relatively isolated except in advanced wear, or the poëbrotherine arrangement where the separation of the two outer crests from each other is very distinct and a union is made primarily with the opposite inner cusp to form an irregular ellipse in both the trigonid and talonid portion. Moreover, the heel or hypoconulid portion of  $M_3$  is quite like that characterizing *Leptoreodon* and *Leptotragulus* rather than the camelids.

The *Poëbrotherium*-like slenderness of the lower jaw attributed to *Poabromylus* cannot be verified, as the lower margin of the jaw of

the type of *P. kayi* is nowhere preserved; hence the profile given in Peterson's illustration may be misleading.

*Poabromylus* appears to be a valid genus most nearly resembling *Leptoreodon* but with premolars somewhat distinctive and both premolars and molars a little more hypsodont.

**POABROMYLUS KAYI**<sup>51</sup> Peterson, 1931

*Type*.—Left ramus of mandible with P<sub>3</sub> to M<sub>3</sub>, inclusive, C.M. No. 11753.

*Horizon and locality*.—Lapoint member of Duchesne River formation, near *Teleodus* quarry, 11 miles west of Vernal, Uinta County, Utah.

*Discussion*.—The specific characters of *Poabromylus kayi* are not distinguished from those on a generic level, except that in size it is much larger than other known leptotragulids. So far this is the only Duchesnean artiodactyl which may be allocated to the Leptomerycidae.

MEASUREMENTS IN MILLIMETERS OF DENTITION IN TYPE SPECIMEN OF  
*Poabromylus kayi*, C.M. NO. 11753

Length of lower cheek tooth series, P <sub>3</sub> -M <sub>3</sub> , inclusive.....	51.9
Lower molar series, M <sub>1</sub> -M <sub>3</sub> , inclusive.....	35.5
P <sub>3</sub> , anteroposterior diameter : greatest transverse diameter.....	8.8 : 4.0
P <sub>4</sub> , anteroposterior diameter : greatest transverse diameter.....	8.8 : 5.1
M <sub>1</sub> , anteroposterior diameter : transverse diameter of talonid.....	8.9 : 6.7a
M <sub>2</sub> , anteroposterior diameter.....	10.7
M <sub>3</sub> , anteroposterior diameter : transverse diameter of trigonid.....	16.5 : 8.8

a, Approximate.

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<sup>51</sup> Illustrated in Peterson, 1931b, fig. 12; and Scott, 1945, pl. 1, figs. 4, 4a.

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## EXPLANATION OF PLATES

### PLATE I

*Mytonomeryx scotti*, new genus and species: Dorsal, lateral, and ventral views of skull and lateral view of left ramus mandible (U.S.N.M. No. 20401), type specimen. Natural size. Myton pocket, Uinta Basin, Utah.

### PLATE 2

Above, *Pentacemylus progressus* Peterson: Left maxilla (U.S.N.M. No. 20435), occlusal view of teeth. Approximately three times natural size. Myton pocket, Uinta Basin, Utah.

Below, *Mytonomeryx scotti*, new genus and species: Skull (U.S.N.M. No. 20401), type specimen, occlusal view of teeth. Approximately three times natural size. Myton pocket, Uinta Basin, Utah.

### PLATE 3

Fig. 1. *Mytonomeryx scotti*, new genus and species: Left ramus of mandible (U.S.N.M. No. 20401), type specimen, occlusal view of teeth. Approximately one and one-half times natural size. Myton pocket, Uinta Basin, Utah.

Figs. 2, 3. *Pentacemylus progressus* Peterson: 2, Left ramus of mandible (U.S.N.M. No. 20437), occlusal view of teeth; 3, left ramus of mandible (U.S.N.M. No. 20438), lateral view. Approximately one and one-half times natural size. Myton pocket, Uinta Basin, Utah.

Fig. 4. *Hylomeryx quadricuspis* (Peterson): Right ramus of mandible (C.M. No. 2346), type specimen, occlusal and lateral views. Approximately three lateral view. Natural size. Leland Bench draw, Uinta Basin, Utah.

## PLATE 4

*Protoreodon pumilus* (Marsh): Skull and mandible (U.S.N.M. No. 20590), lateral view. Natural size. Leland Bench draw, Uinta Basin, Utah.

## PLATE 5

*Protoreodon pumilus* (Marsh): Above, skull and mandible (U.S.N.M. No. 20590), dorsal and lateral views. Approximately two-thirds natural size. Leland Bench draw, Uinta Basin, Utah. Below, upper and lower dentitions (U.S.N.M. No. 20352), occlusal view. Natural size. Myton pocket, Uinta Basin, Utah.

## PLATE 6

Fig. 1. *Protoreodon minor* Scott: Right upper cheek tooth series (U.S.N.M. No. 20674), occlusal view. Approximately two times natural size. Devil's Playground, Uinta Basin, Utah.

Fig. 2. *Protoreodon pumilus* (Marsh): Right lower molars and left  $M_2$  (Y.P.M. No. 11890), type specimen, occlusal view. Approximately three times natural size. Near White River, Uinta Basin, Utah.

Fig. 3. *Protoreodon parvus* Scott: Left ramus of mandible (U.S.N.M. No. 20383), occlusal and lateral views. Approximately two times natural size. Uinta Basin, Utah.

## PLATE 7

*Protoreodon petersoni*, new species: Above, lateral view of skull and mandible (P.U. No. 14404), type specimen. Below, ventral view of skull and dorsal view of mandible (P.U. No. 14404), type specimen. Natural size. Myton pocket, Uinta Basin, Utah.

## PLATE 8

*Diplobunops vanhouteni*, new species: Skull (P.U. No. 14251), type specimen, ventral view. Natural size. White River pocket, Uinta Basin, Utah.

## PLATE 9

*Diplobunops vanhouteni*, new species: Mandible (P.U. No. 14251), type specimen, occlusal view. Natural size. White River pocket, Uinta Basin, Utah.

## PLATE 10

*Diplobunops*, cf. *matthewi* Peterson: Skull (U.S.N.M. No. 20303), dorsal view. Natural size. Badwater upper Eocene, Wind River Basin, Wyoming.

## PLATE 11

*Diplobunops*, cf. *matthewi* Peterson: Skull (U.S.N.M. No. 20303), lateral view. Natural size. Badwater upper Eocene, Wind River Basin, Wyoming.

## PLATE 12

*Diplobunops*, cf. *matthewi* Peterson: Skull (U.S.N.M. No. 20303), ventral view. Natural size. Badwater upper Eocene, Wind River Basin, Wyoming.

## PLATE 13

*Protylopus? annectens* Peterson: 1, 2, Skull (U.S.N.M. No. 20263), lateral and ventral views. 3, Skull (U.S.N.M. No. 20261), ventral view. Natural size. Myton pocket, Uinta Basin, Utah.

## PLATE 14

*Protylopus? annectens* Peterson: 1, Right maxilla (U.S.N.M. No. 20290), occlusal view. Approximately one and one-half times natural size. 2, Left maxilla (U.S.N.M. No. 20275), occlusal view. Approximately one and one-half times natural size. 3, Left ramus of mandible (U.S.N.M. No. 20149), occlusal and lateral views. Natural size. Myton pocket, Uinta Basin, Utah.

## PLATE 15

Figs. 1, 2. *Oromeryx plicatus* Marsh: 1, Right upper molars and P<sup>4</sup> (Y.P.M. No. 14571), type specimen, occlusal view. Approximately three times natural size. 2, Left M<sup>2</sup> and M<sup>3</sup> (Y.P.M. No. 14571), type specimen, occlusal view. Approximately two times natural size. Uinta Basin, Utah.

Fig. 3. *Poëbrodon kayi*, new genus and species: Left maxilla (U.S.N.M. No. 20393), type specimen, occlusal view. Approximately three times natural size. Myton pocket, Uinta Basin, Utah.

Figs. 4, 5. Cf. *Oromeryx plicatus* Marsh: 4, Left ramus of mandible (U.S.N.M. No. 20391), occlusal and lateral views. 5, Right ramus of mandible (U.S.N.M. No. 20391), occlusal view. Approximately two times natural size. White River pocket, Uinta Basin, Utah.

## PLATE 16

*Malaquiferus tourteloti*, new genus and species: Skull (U.S.N.M. No. 20558), type specimen, ventral view. Approximately two times natural size. Upper Eocene of Dry Creek, Wind River Basin, Wyoming.

## PLATE 17

Fig. 1. *Leptotragulus clarki*, new species: Right ramus of mandible (U.S.N.M. No. 20378), type specimen, occlusal and lateral views. Approximately one and one-half times natural size. Myton pocket, Uinta Basin, Utah.

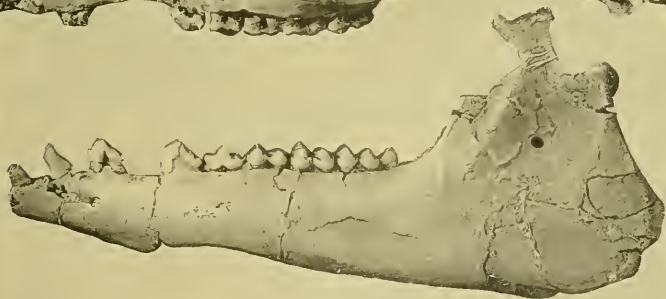
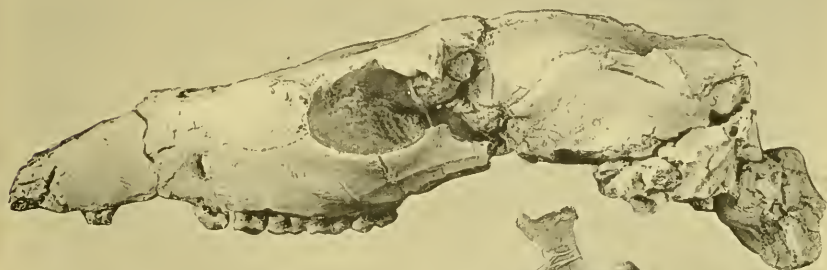
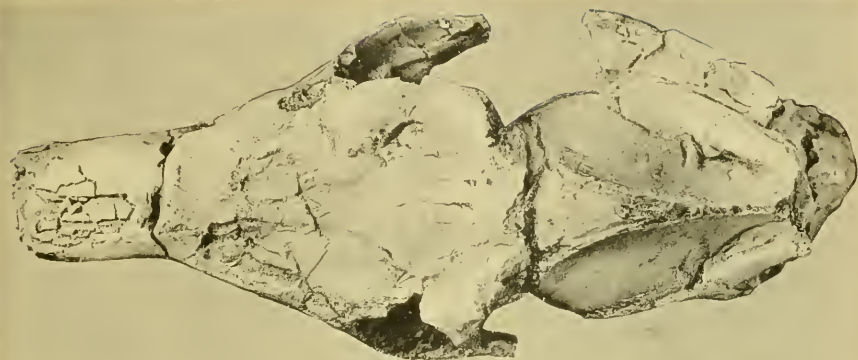
Figs. 2, 3. *Leptotragulus medius* Peterson: 2, Left maxilla (U.S.N.M. No. 16549), occlusal view. Approximately three times natural size. Myton pocket, Uinta Basin, Utah. 3, Right ramus of mandible (U.S.N.M. No. 20361), occlusal and lateral views. Approximately two times natural size. Myton pocket, Uinta Basin, Utah.

## PLATE 18

Fig. 1. *Leptotragulus proavus* Scott and Osborn: Left ramus of mandible (P.U. No. 11501), type specimen, occlusal and lateral views. Approximately three times natural size. Uinta Basin, Utah.

Fig. 2. *Leptoreodon marshi* Wortman: Left ramus of mandible (U.S.N.M. No. 20397), occlusal and lateral views. Approximately three times natural size. White River pocket, Uinta Basin, Utah.





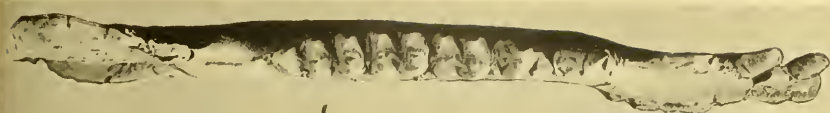
MYTONOMERYX FROM THE UINTA UPPER EOCENE

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HOMACODONTS FROM THE UINTA UPPER EOCENE

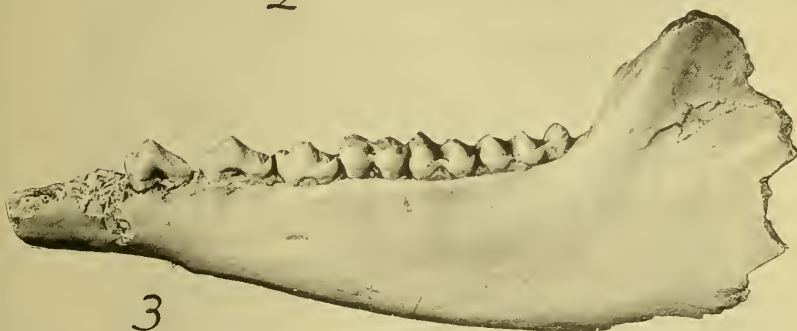
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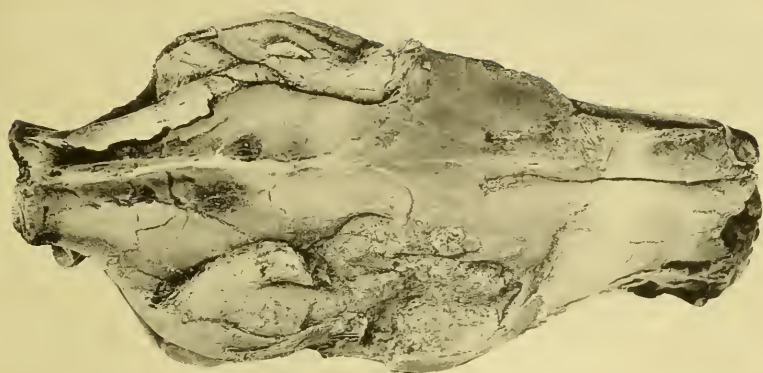


HOMACODONTS FROM THE UINTA UPPER EOCENE

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PROTOREODON FROM THE UJINTA UPPER EOCENE  
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PROTOREODON FROM THE UINTA UPPER EOCENE

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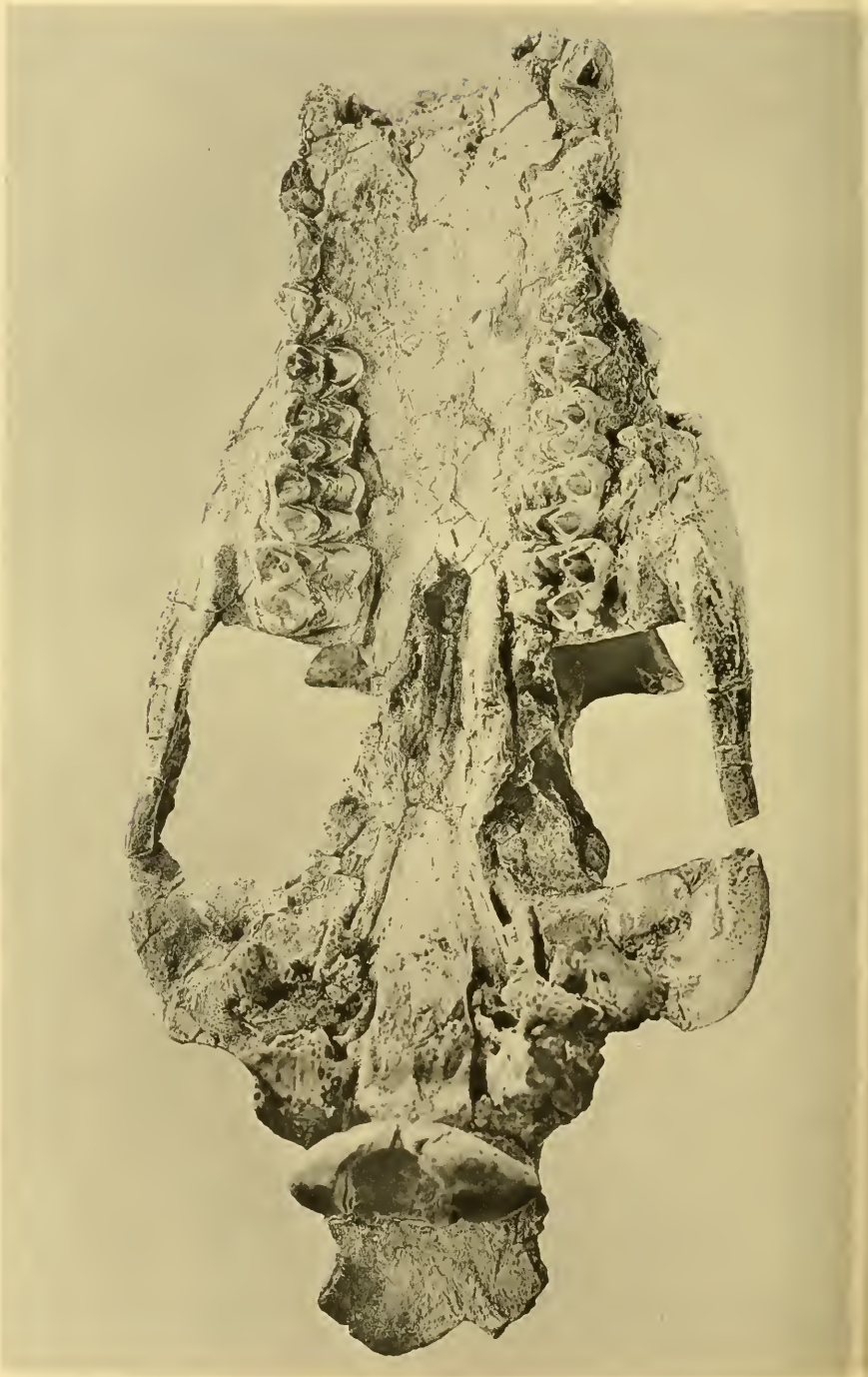


PROTOREODON FROM THE UINTA UPPER EOCENE  
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PROTOREODON FROM THE UINTA UPPER EOCENE

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DIPLOBUNOPS FROM THE UINTA UPPER EOCENE

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DIPLOBUNOPS FROM THE UINTA UPPER EOCENE  
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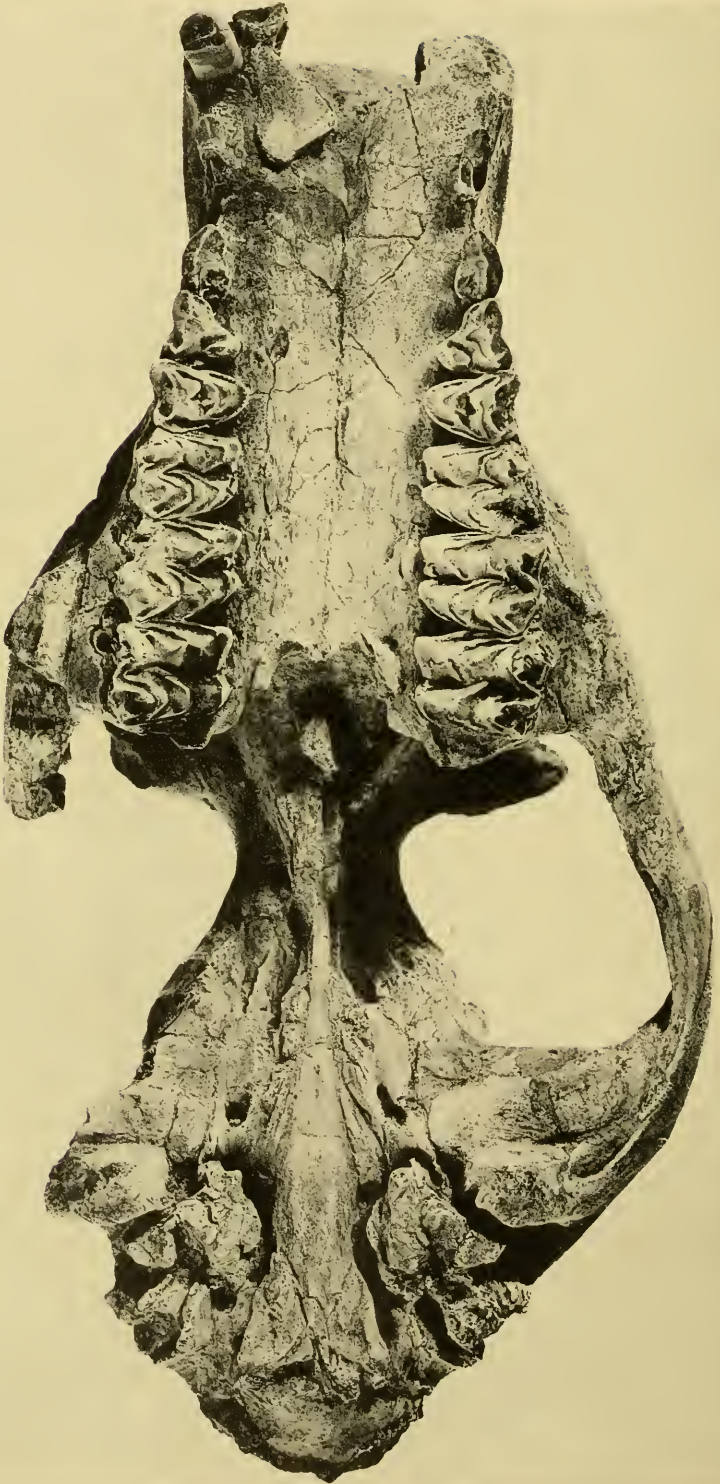


DIPLOBUNOPS FROM THE BADWATER UPPER EOCENE

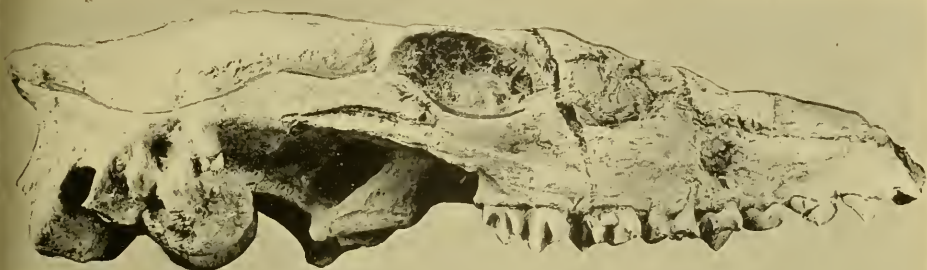


DIPLOBUNOPS FROM THE BADWATER UPPER EOCENE

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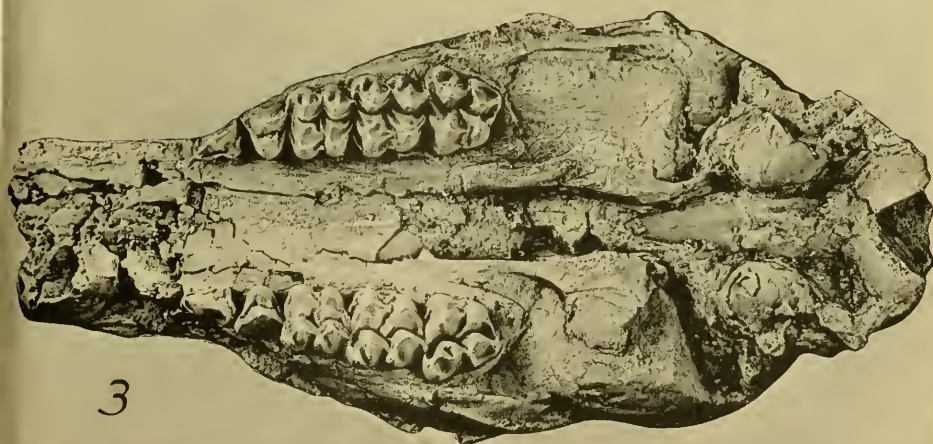
DIPLOBUNOPS FROM THE BADWATER UPPER EOCENE



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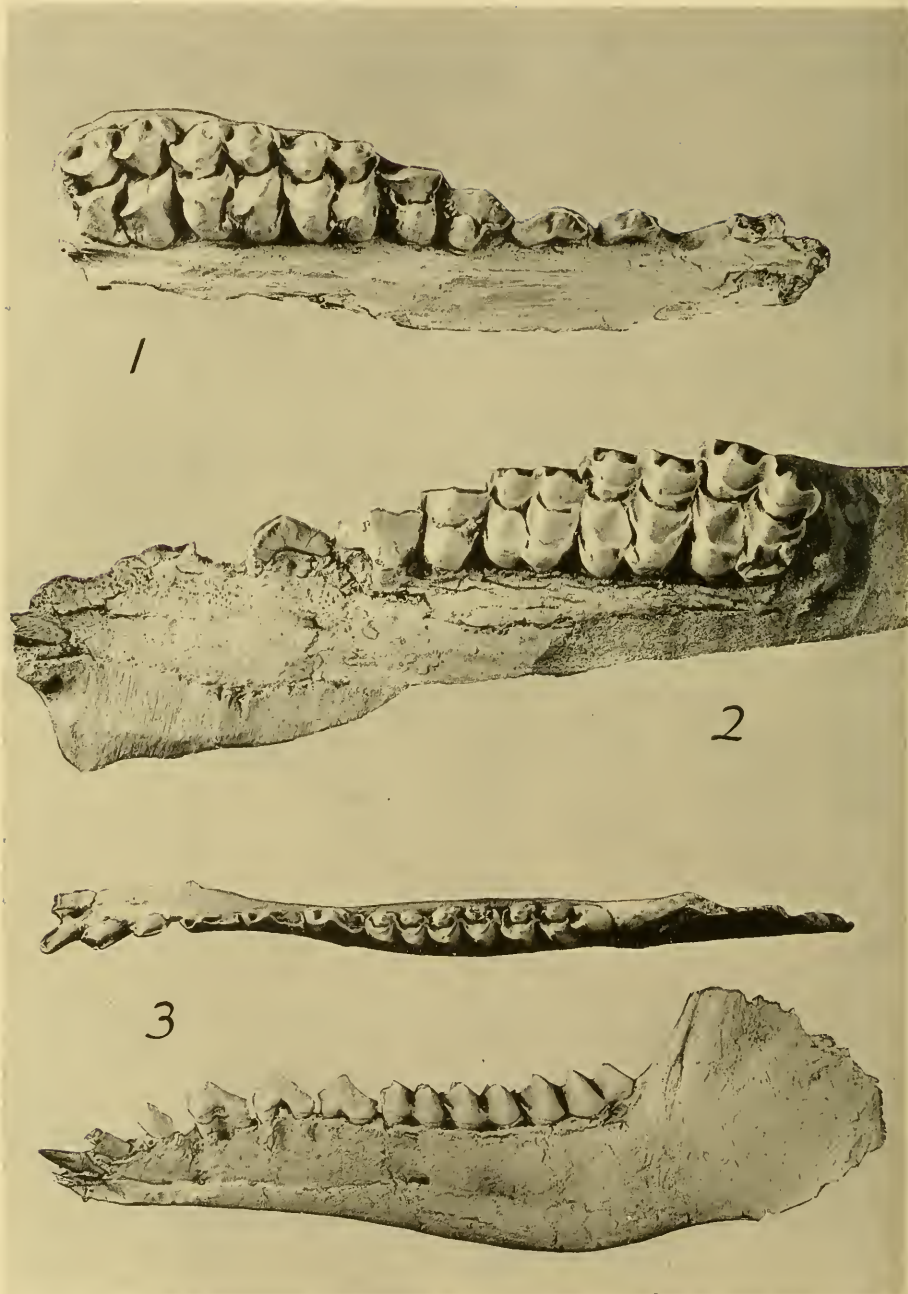
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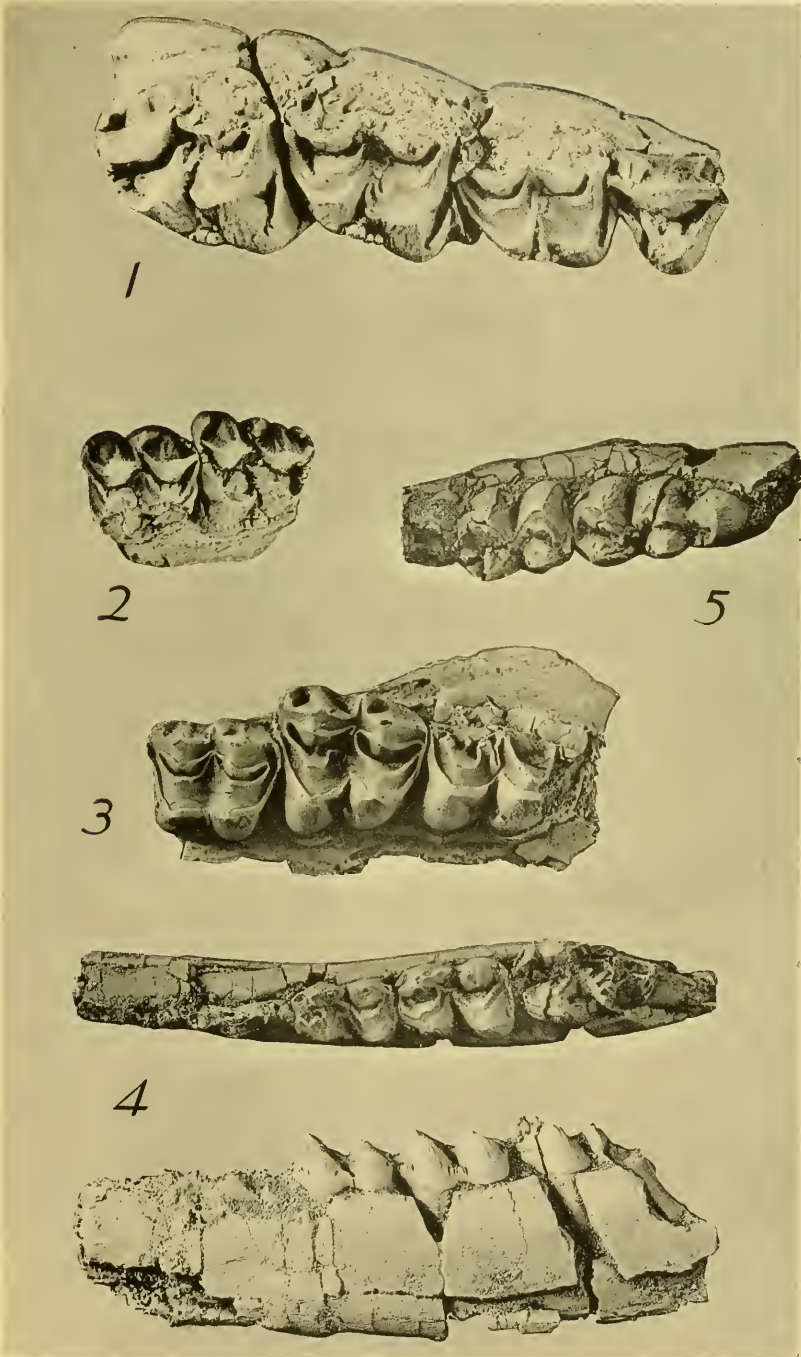
PROTYLOPUS? FROM THE UINTA UPPER EOCENE

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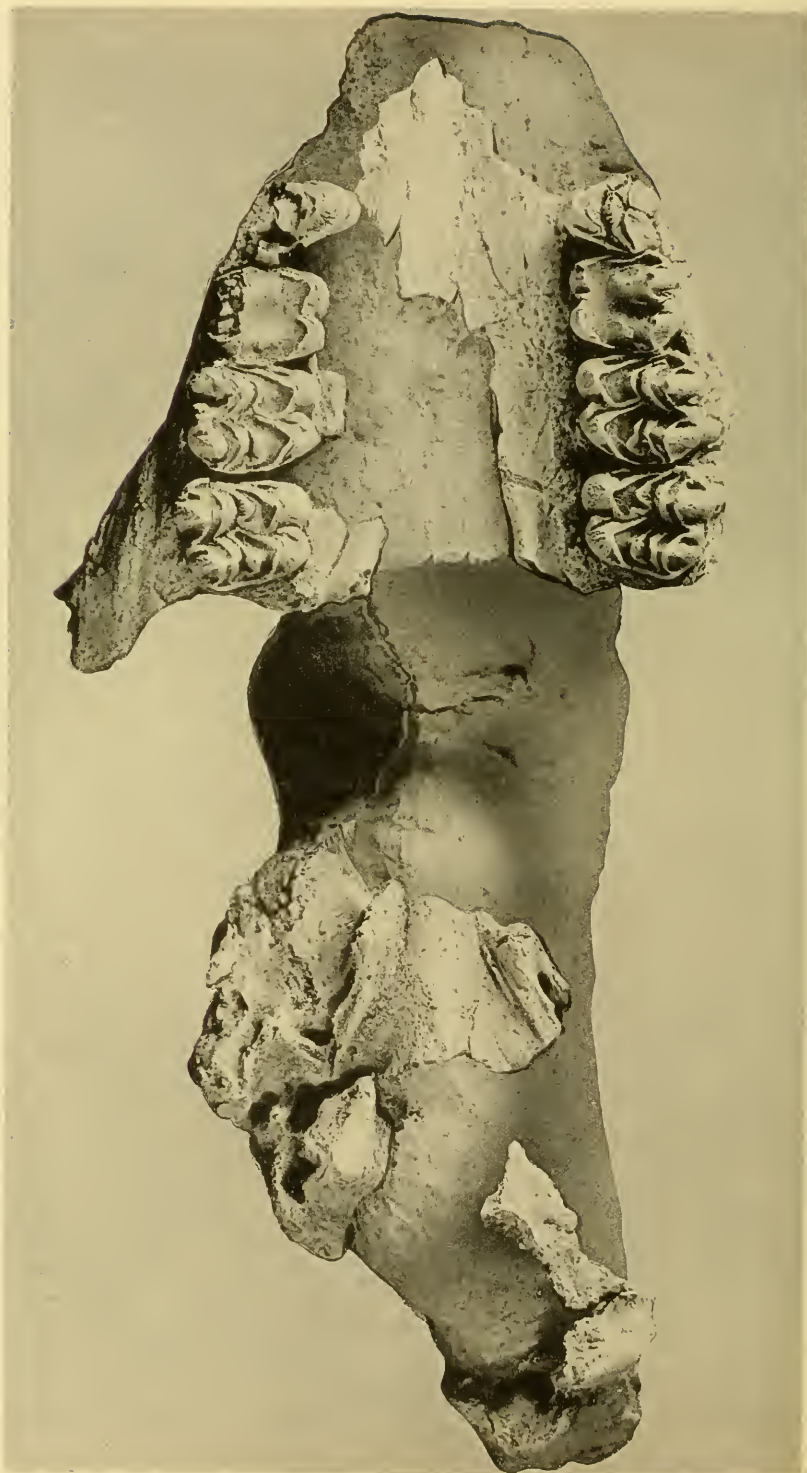


PROTYLOPUS? FROM THE UINTA UPPER EOCENE

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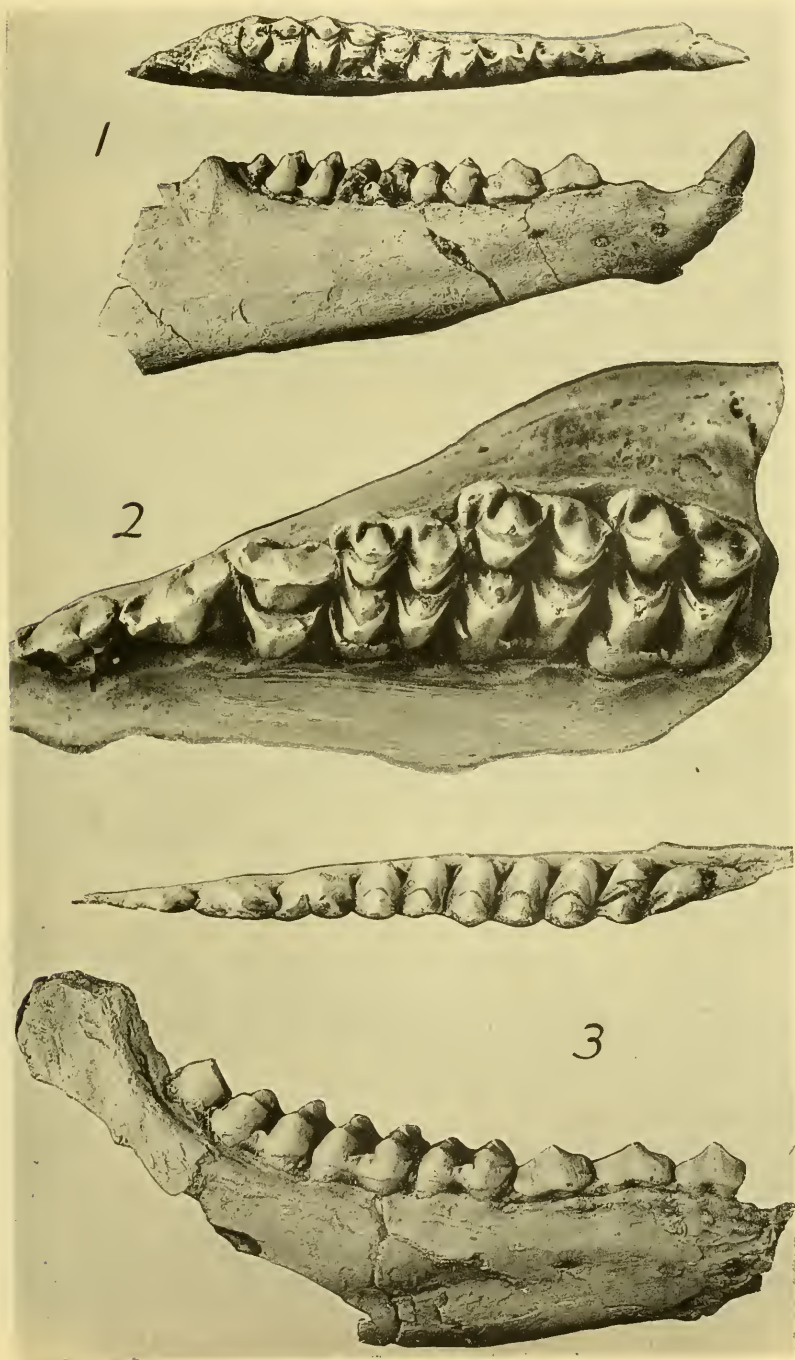
OROMERYX AND POËBRODON FROM THE UINTA UPPER EOCENE  
(SEE EXPLANATION OF PLATES AT END OF TEXT.)



MALAQUIFERUS FROM THE UPPER EOCENE OF THE WIND RIVER BASIN

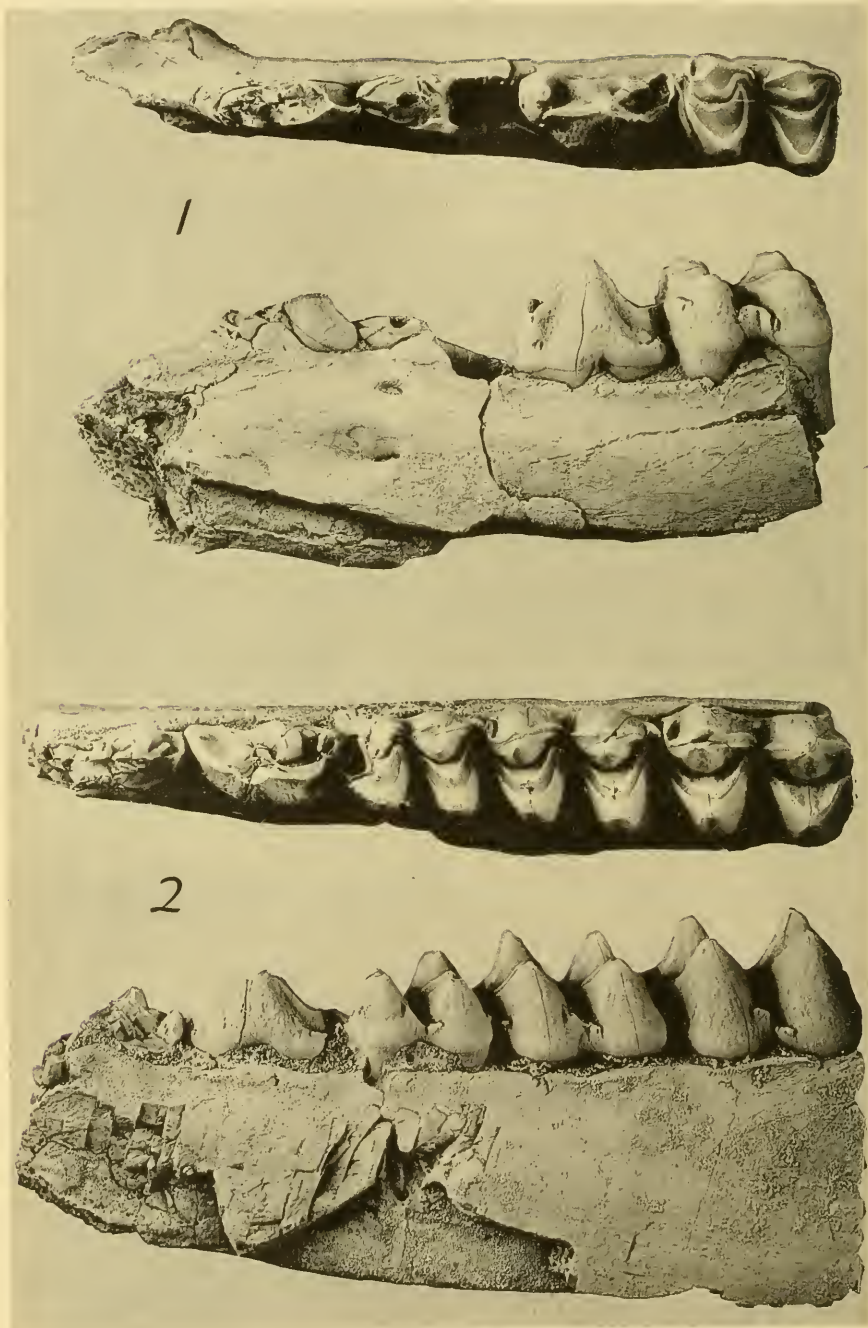
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LEPTOTRAGULUS FROM THE UINTA UPPER EOCENE

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LEPTOTRAGULUS AND LEPTOREODON FROM THE UINTA UPPER EOCENE  
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