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# A REVIEW OF THE MIDDLE AND UPPER EOCENE PRIMATES OF NORTH AMERICA

(With 14 Plates)

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## INTRODUCTION

One of the more interesting features of life during middle Eocene time in North America was the diversity and relative abundance of primates. A long and interesting history is recorded for them in the earlier Tertiary of this continent, extending back to the middle Paleocene, for which time at least seven distinct genera are known, all older than any recorded from elsewhere in the world. Their diversity even at this early date provides evidence of a very ancient lineage for the order. Following middle Paleocene time primates are recorded as an important part of the successive faunal assemblages; and the Bridgerian interval was characterized by no less than 11 genera, divided between four families and including at least 16 species. Although two families, two highly specialized and evidently monophyletic groups, disappeared, one during and the other at the close of lower Eocene time, the middle Eocene may be looked upon as the time during which primates reached their climax as a significant part of the ever changing fauna, as this is recorded in the Tertiary sediments of the Rocky Mountain region.

In striking contrast, the number and diversity of forms encountered in the upper Eocene beds of the same region are greatly reduced, and in the classic and highly fossiliferous Uinta deposits only two primate forms have been recognized, based on little more than that number of specimens. Several lines of evidence concur to show that this striking depletion was due to marked changes in environment resulting from increasing aridity. Nevertheless, a brief glance at the retreating fauna

is provided by the more recent discoveries of upper Eocene remains in southern California.

The early recorded history of primates outside of North America begins in the upper Paleocene Thanetian of Europe. Unfortunately, no fossiliferous sediments of older Paleocene are known in Europe so that much valuable information on their possible earlier history in the Old World is not available. However, there was evidently an early faunal interchange involving primates between Europe and North America prior to Thanetian or Cernaysian time and also probably near the beginning of the Eocene, but it seems doubtful that they were involved at any later date, such as at the close of Eocene time. In South America primates are not known before Miocene, so it is very doubtful if that continent played a part in the very early history. On the other hand, it is more than probable that the living ceboid primates of Central and South America were derived from some portion of the primate assemblage known from the Eocene of North America. In consequence of this, the present taxonomic arrangement in which both Old and New World monkeys are included under the same suborder, the Anthropoidea, almost certainly derived from different parts of the Eocene Prosimia and hence polyphyletic, is untenable.

Beyond doubt, more has been written on primates than on any other group of animals. Nevertheless, much of this pertains to living and near recent forms with emphasis on man. Discussions regarding the fossil forms have been included in almost every general treatise of this nature, but often these have not involved examination of the fossils themselves, so that many of the earlier errors and much inaccurate information have been perpetuated. During the past 30 years, since Gidley's study of the Fort Union primates, an interval during which considerable fieldwork has been done, the only detailed studies of North American fossil primate materials in which important conclusions regarding relationships have resulted are those of Simpson and of Jepsen. With regard to the Bridger it appears that no study of primate materials from these beds has been made on collections secured later than 50 years ago. The last general review of the Bridger primates was that of Wortman in 1904, based on the Marsh collection, and, as Matthew noted, much in need of revision.

## ACKNOWLEDGMENTS

Investigation of the Bridger middle Eocene primates was undertaken as a part of general study of the Bridger mammalian fauna that

has been underway from time to time since about 1934. The present study, begun in December 1956, was spurred largely by the unusual array of primate specimens, particularly *Notharctus* and *Smilodectes* skulls, encountered by Smithsonian Institution parties during various field seasons in the Bridger Basin in late years, indicating a need for review of the relationships of *Notharctus* and a review and attempt at clarification of relationships of the other, less well known primate genera in the fauna. I am indebted in this study to Peter Robinson (1957) for the groundwork that he so ably covered in setting the taxonomic arrangement within the genus *Notharctus* on a firmer footing, reducing the complex of names to recognizable entities.

Later, upon reviewing the known upper Eocene primate materials, in comparison with those from the Bridger, it became evident that a certain revision in the taxonomy of these was also necessary in order to portray properly their relationships. Because of this the study was expanded to include the upper as well as the middle portion of the North American Eocene.

General revision was not extended to the lower Eocene forms, although certain changes were found necessary and the description of important new genera among these was included in order to facilitate discussion of relationships.

Grateful acknowledgment is made of the kindness extended by Dr. Joseph T. Gregory of Yale Peabody Museum in permitting me to study the surprisingly extensive series of Bridger Eocene primate materials in the Marsh collection. Access to the collections of fossil primate materials in the American Museum and loan of pertinent specimens for further study in Washington was graciously afforded me by Drs. G. G. Simpson, E. H. Colbert, and Bobb Schaeffer; also particular mention may be made of the helpful assistance given me while in the American Museum by Mrs. Rachel H. Nichols. I am indebted to Dr. Glenn L. Jepsen of Princeton University for helpful comments and in allowing me to review earlier primate materials in Guyot Hall. Dr. Horace G. Richards at the Academy of Natural Sciences in Philadelphia aided significantly in lending for study and reillustration two of Leidy's important types. John Clark's Oligocene primate in the Carnegie Museum collections was kindly lent for comparative study by the Museum's director, Dr. M. Graham Netting. Dr. Netting also permitted me to go over in detail the primate materials included in the extensive, undescribed mammal collection obtained by Dr. J. LeRoy Kay in the Green River beds of the Uinta Basin. The entire series of upper Eocene primate materials, formerly

in the California Institute of Technology collections, described by Chester Stock were made available to me for further study and comparison in Washington, through the courtesy of Drs. Theodore Downs and Hildegard Howard of the Los Angeles County Museum. I am particularly indebted to Lawrence B. Isham, scientific illustrator for the Department of Geology in the United States National Museum, for the exquisite pencil drawings comprising the plates illustrating this study, and for preparation of the chart.

## HISTORY OF INVESTIGATION

An excellent history of discovery and investigation was given by W. K. Gregory in 1921, but inasmuch as his review was directed essentially toward *Notharctus,* a more comprehensive account is indicated. In the following, attempt is made to expand consideration to the history of study of all North American fossil primate materials to date, and, as a consequence, that pertaining to *Notharctus* is covered much more briefly than by W. K. Gregory. Consideration, moreover, is limited for the most part to North American finds.

The first fossil primate to be described from the Tertiary of the Western Hemisphere was Leidy's (1869a) *Omomys carteri.* The material, consisting of a lower jaw and associated skull fragments, was found by Dr. J. Van A. Carter of Fort Bridger, evidently in the nearby Grizzly Buttes. Later in the same year (1869b), the jaw, but not the skull fragments, was figured. The material was presented to the Academy of Natural Sciences in Philadelphia. Leidy did not recognize the true relationships of the form, comparing it to various insectivores that he regarded as most nearly related. In 1870, he named the second primate *Notharctus tenebrosus,* from a lower jaw collected by Hayden in beds along Black's Fork in the Bridger Basin. At first he regarded *Notharctus* as a carnivore, possibly related to the raccoon; however, upon seeing upper teeth (for which the name *Hipposyus formosus* [1872b] was proposed, but regarded as possibly representing *Notharctus*) he concluded (1872d) that a closer relationship to the "odd-toed pachyderms" or Perissodactyla was indicated, although "probably one of a carnivorous habit." In the same paper (1872d) a second and larger species of *Notharctus, N. robustior,* was described from a lower jaw portion found by Hayden's party in upper Bridger beds on Henry's Fork.

In 1871, the year following Leidy's diagnosis of *Notharctus tenebrosus,* Marsh described as new the form *Limnotherium tyrannus,* based essentially on portions of both rami of the mandible found on

"Dry Creek" in the Bridger Basin. Leidy (1872b) recognized that the genus *Limnotherium* was a synonym of *Notharctus,* while suspecting that his own *Hipposyus* was likewise invalid. A second species referred to *Limnotherium* by Marsh in 1871, *L. elegans,* was later discovered by Leidy (1873, p. 84) to represent his *Microsyops.* Marsh's *Hyopsodus gracilis* [1] in his 1871 paper was recognized almost immediately by Cope (1872a) as related or belonging to Leidy's *Notharctus.* Cope's observation was generally overlooked or disregarded, and the species was retained in *Hyopsodus* by Matthew as late as 1899. It was placed in both *?Sarcolemur* and *Notharctus* by Osborn (1902), but Wortman (1903) proposed for it the generic name *Smilodectes,* an assignment followed by Matthew in 1909. Troxell (1926) and later Robinson (1957) retained it in *Notharctus* because very little of generic importance could be detected in the characters of the teeth.

Several more primates, also from the Bridger formation, were described by Marsh in 1872(a). Of the 10 new species named, 7 were regarded as representing new genera. This multiplicity of names remained essentially undisturbed until the revisions of Osborn in 1902 and Wortman in 1903. Of Marsh's 1872(a) names only *Hemiacodon gracilis* and the two species of *Apatemys* now remain valid. Marsh made little comment on the possible affinities of these except that *Limnotherium* he regarded as a pachyderm and *Thinolestes* was referred to as a carnivorous mammal. *Hemiacodon* and *Apatemys* were described as small insectivores.

Also in 1872(a), Cope described a primate from near Black's Fork in the Bridger Basin which he named *Tomitherium rostratum.* He discussed its relationship to *Notharctus* but regarded it as distinct. It was placed in synonymy with *Limnotherium affine* by Marsh, and properly with *Notharctus tenebrosus* by Matthew in 1899. Later in 1872(b) Cope described *Anaptomorphus aemulus,* comparing it in dental formula with *Simia* and *Homo.* This would appear to have been tacit recognition of the possible primate affinities of certain of the Bridger forms, but evidently not the first, as the Palaeontological Bulletin (No. 8) in which this appears bears the date Oct. 12, 1872, whereas Marsh, in a separate dated Oct. 8,[2] 1872, from the November

[1] Not to be confused with Leidy's *Microsyops gracilis,* although Leidy himself, upon describing it later, based on different specimens, tentatively held the view that they might be the same.

[2] These dates are but four days apart, and recalling the polemics of 1872 between Cope and Marsh regarding dates of publication, one cannot be certain where credit for discovery should be given.

issue of the American Journal of Science, called attention to the "Discovery of Fossil Quadrumana in the Eocene of Wyoming." The material referred to by Marsh comprised that which he had described earlier in the year under the generic names *Limnotherium, Thinolestes,* and *Telmatolestes.* These he discovered had a lemurlike skeleton. All, of course, are synonyms of *Notharctus.* In 1873(a and b) Cope also recognized the primate affinities of his *Tomitherium,* still mistaken, however, as to the characteristic features of Leidy's *Notharctus,* as he (1873a) referred *Pantolestes longicaudus* to it. *Anaptomorphus* was also further discussed and regarded as more nearly related to the existing Malagasian forms than was *"Tomitherium."*

Marsh added nothing of significance to our information on early primates after 1872, but in 1874 Cope described the first lower Eocene form, *"Prototomus" jarrovii,* from the Wasatchian of New Mexico. He considered it at that time a carnivore, but in 1875 proposed the generic name *Pelycodus* for it and was reasonably certain that it was a primate related to his *"Tomitherium."* Unfortunately, however, in 1876, as a result of some incorrectly associated skeletal material in the New Mexican collections, he concluded that *"Tomitherium,"* with which he now synonymized *Pelycodus,* was after all related somehow to the creodonts. In order to systematize the difficulties that seemed evident, he proposed a new ordinal arrangement with the notharctids in the Mesodonta as a subdivision of the Bunotheria. He had not, however, formulated his ideas as to the relationship that the Prosimiae bore to the Bunotheria, except that, for obvious reasons, he considered his Mesodonta intermediate between the Creodonta and Prosimiae. The composition of the Mesodonta was revealed in 1877 as including such genera as *Omomys, Microsyops, Pantolestes* (retrieved from *Notharctus*), *"Tomitherium," "Sarcolemur"* (=*Antiacodon*), *Hyopsodus, Apheliscus, Anaptomorphus, Notharctus,* and *"Opisthotomus"* (=*Phenacodus*). He further believed that Leidy's *Washakius* was a synonym of *Anaptomorphus.*

The major features of Cope's classification were little modified by him subsequent to 1877, except that in 1882(a) he included the Prosimiae in the Bunotheria, and described under it the genus *Cynodontomys.* With the discovery at this time of the skull from the lower Eocene of the Bighorn Basin, which he described as *Anaptomorphus homunculus* (now included under *Tetonius*), he transferred *Anaptomorphus* to the Prosimiae, calling attention to the tarsiid appearance of this important specimen and including comparisons also with the European Eocene genus *Necrolemur.* In 1883(a) he named the fami-

lies Anaptomorphidae and Mixodectidae, including them with the tarsiers and lemurs in the Prosimiae. At this time he apparently had misgivings as to the status of Mesodonta and did not distinguish it from Insectivora. Mesodonta, however, was revived in "Tertiary Vertebrata" (1884b) with a content arrangement rather similar to that of 1877, although with certain mixodectids and adapids confused between Mesodonta and Prosimiae, *Pelycodus* returned to generic status, and *Anaptomorphus,* as in 1882(a), transferred to the Prosimiae.

Following Schlosser's important 1887 review of the apes, lemurs, etc., of the European Tertiary, which contains discussions of the North American Eocene forms, a general restudy of the Eocene primates of the Rocky Mountain region, working with original materials, was undertaken by Osborn in 1902 and Wortman in 1903-4.

Osborn's work was helpful in furnishing in chronological order a table of species that had been referred to primates, and in straightening much of the taxonomic confusion that prevailed so far as genera are concerned, although the groundwork for this had evidently been prepared for him by Matthew in the latter's 1899 list for the "Fresh-water Tertiary of the West." Significant differences from current interpretation are inclusion of *Hyopsodus* and *"Sarcolemur"* (=*Antiacodon*), now referred to the Condylarthra and Artiodactyla respectively. Missing is consideration of the primate genera *Omomys, Washakius, Hemiacodon,* and *Apatemys.* It is interesting to note that Osborn, in line with Cope's suggestion of 1888, preserved the Mesodonta as an order distinct from the primates, much as the Condylarthra is maintained as an order ancestral to various ungulate orders.

Wortman's (1903-4) scholarly work on the primates in the Marsh collection, while involving a classification not generally followed by later workers, is clearly the most thought-provoking and comprehensive study of the North American fossil materials to date. He disagreed strongly with Osborn for preserving Mesodonta as an order distinct from the primates, placing these early Tertiary forms in the superfamily Paleopithecini as a division of the suborder Anthropoidea. The adapids and *Notharctus,* however, he included in the Anthropoidea, although in the Neopithecini with the higher primates. Other features of Wortman's arrangement include placing together the Microsyopsidae, Metacheiromyidae, and Cheiromyidae in the same suborder, Cheiromyoidea. The Cheiromyidae, or properly the Daubentoniidae, are evidently to be related to the other lemuroids of the Malagasian region; the metacheiromyids have since been shown to be edentates,

and *Microsyops* and its allies, the Mixodectidae, are presently referred to the Insectivora, although the possibility of their being primates merits serious consideration. Osborn (1902), on the other hand, had included the latter in the Rodentia. Wortman is, moreover, responsible for removing *Hyopsodus* from consideration as a primate, allocating it, though, to the Insectivora. Evidently Wortman's study of the primates was not completed before leaving Peabody Museum, as no detailed study of *Notharctus* was included, and there is no discussion of the apatemyids. Quite likely he regarded the latter as insectivores. Consideration of *Smilodectes* appeared under his treatment of the mixodectids. A more detailed review of Wortman's study does not seem necessary at this point, although it was the background for most of the investigations that followed. Many references are made to its particulars in the following pages.

A short paper by Loomis in 1906 followed essentially the classification outlined by Wortman. In this Loomis reviewed the known Wasatchian primates and described the new materials encountered by an Amherst College party in Wyoming, particularly in the Wind River beds. All the species described as new have since been placed in different genera by Matthew, except for *Anaptomorphus minimus,* which is evidently not a primate.

The first of Matthew's principal contributions to the study of early primates is to be found in his 1909(b) memoir on the Bridger Carnivora and Insectivora. In this he proposed the Apatemyidae, under the Insectivora, for Marsh's *Apatemys* and his own two new genera *Uintasorex* and *Trogolemur.* The latter two, however, bear little resemblance to *Apatemys* except in the marked enlargement of an anterior tooth. Matthew followed Wortman, essentially, in his classification and synonymy of the primates listed as such, and while including the Mixodectidae there, was critical of Wortman for ignoring a surface association of certain foot material with a *Mixodectes* jaw. The association, if valid, was regarded as precluding primate affinity. He was impressed, nevertheless, by the primatelike cheek teeth in the mixodectids, as he was also by those in the apatemyids.

Matthew's 1915 contribution to our understanding of early primates was a part of the general Wasatch and Wind River studies, and although including essentially the lower Eocene primates, also reviewed the middle Eocene genera. While the primate portion is brief in comparison with Wortman's study, it is an important milestone in the development of early primate taxonomy. In it are named the genera *Tetonius, Absarokius,* and *Phenacolemur* from lower Eocene ho-

rizons; *Nothodectes* from the upper Paleocene; and *Uintanius* from the middle Eocene. Confusion in the materials referred to *Anaptomorphus* was straightened out and the first of the phenacolemurids and the first of the North American plesiadapids (as *Nothodectes*) to be discovered were described. *Tetonius* and *Absarokius* derived from materials referred by Cope (1882b) and Loomis (1906) respectively to *Anaptomorphus* were included together with *Uintanius, Omomys,* and Granger's *Shoshonius* as primates in the Tarsiidae, but *Phenacolemur* and *"Nothodectes"* were included with *Trogolemur* as insectivores in the Apatemyidae.

In 1917 Matthew described some excellent new materials of his *"Nothodectes,"* collected by Granger in the Tiffanian Paleocene of southwestern Colorado, and as a result of a study of Stehlin's (1916) illustrations realized that his *"Nothodectes"* was closely related, if not identical, to Gervais' (cited as Lemoine's) *Plesiadapis* from the Cernaysian Paleocene. Because of this he concluded that Apatemyidae was a synonym of Plesiadapidae. He (1918) regarded this family as nearly intermediate between Primates and Insectivora, but held to the idea that they were insectivores because of the form of the anterior teeth, aware at the same time that the cheiromyids (daubentoniids) with enlarged, rodentlike anterior teeth were lemuroids, although not closely related to the plesiadapids and mixodectids. Change, moreover, is noted in his (1918) recognizing full family status for Microsyopidae as distinct from Mixodectidae, which he had earlier separated only on a subfamily level.

Stehlin's magnificent exposition of the mammals of the Swiss Eocene, referred to above, includes two parts of a large volume covering the primates. The first half, devoted entirely to *Adapis* and *Protadapis,* was published in 1912 and the second half comprising the remaining genera, *Caenopithecus, Necrolemur,* etc., is dated 1916. Particularly important to paleontologists abroad are the excellent illustrations, giving a most satisfactory representation of the material, especially of the teeth, of the forms described. Stehlin's text gives, in addition to a detailed morphological treatment, the history of the discovery and description of the materials known from the European early Tertiary, and includes also a discussion of the North American forms and their possible relationships. He clearly did not regard *Notharctus* as an adapid, an interpretation not shared by W. K. Gregory (1915a, b, and 1921).

Granger's contribution to the study of early primates, following his description of the upper Wasatchian *Shoshonius* in 1910, was a

revision, made jointly with Gregory in 1917, of the genus *Notharctus*. This included the Lost Cabin forms and a questionably referred Uintan species, as well as those of the Bridger. The various types were figured and 3 species were added, bringing the total recognized to 11. Added to these was description of the interesting notharctid *Aphanolemur,* now known to be *Smilodectes*.

W. K. Gregory's views on the relationships of *Notharctus* were earlier outlined in 1915(a) and then presented in elaborate detail in his beautifully illustrated memoir in 1921. The entire skeleton, as far as known, was described in detail and compared, part by part, with materials of *Adapis* and various modern primates. His discussion of the relationships of *Notharctus* was directed toward its lemuroid affinities and a lengthy demonstration in support of its reference to the Adapidae. In this he disagreed emphatically with Stehlin. In his discussion of the ramifications of the entocarotid circulation, largely derived from earlier authorities, he took sharp exception to Wortman's analysis and conclusions. Moreover, it may be noted that in 1915, while outlining his reasons for adopting Schlosser's interpretations rather than Stehlin's on the adapid relationship, he was equally emphatic in his conclusion, "that in my judgment there is no justification for associating the Notharctinae with the South American monkeys, as Wortman (1904) has done in placing both *Adapis* and *Notharctus,* along with *Tarsius,* in his major group Neopithecini." Nevertheless, we note that in 1921 (p. 220), "we find, after an extended comparison between *Notharctus* and the Platyrrhini, that further evidence supports Dr. Wortman's conclusion that the 'interval . . . is not greater than one would be reasonably led to anticipate between an ancestor of Upper Eocene time and a living descendant.' " [3] Although one may disagree with W. K. Gregory's conclusions or be tempted to criticize certain of the details of often made generalizations regarding structures, some of which seem beyond the scope of the material at hand, his treatment of *Notharctus* is an outstanding model of exhaustive research.

Later work by Matthew (1921) has included description of *Stehlinella* (*Stehlinius* was preoccupied) as a plesiadapid insectivore, extending into upper Eocene time the record of the apatemyids, and with Granger (1921) the new primates *Labidolemur, Ignacius, Nava-*

[3] This change in viewpoint by Gregory seems somewhat at variance with the general tenor of the memoir and almost as in anticipation of Gidley's later criticism. There seems no doubt from records of correspondence on file in the U. S. National Museum that Gregory was aware of Gidley's predisposition toward certain of Wortman's conclusions.

*jovius,* and *Carpodaptes* in the Tiffany Paleocene fauna of southwestern Colorado. *Labidolemur* and *Ignacius* were referred to the problematic order Menotyphla, *Navajovius* to the tarsiid primates, but *Carpodaptes* was left incertae sedis. These assignments have since been amended so that *Labidolemur* is seen to be an apatemyid, *Ignacius* a synonym of *Phenacolemur, Navajovius* possibly an anaptomorphid, and *Carpodaptes* a member of the unusually specialized Carpolestidae.

Gidley's (1923) outstanding contribution to the fossil primates is significant in extending their record back to middle Paleocene time with definition of the genera *Paromomys, Palaechthon, Elphidotarsius,* and *Pronothodectes.* The first three of these he considered as a separate and new section of the Tarsiidae, as that family was constituted by Matthew. *Pronothodectes* he placed in the Plesiadapidae, but rather strongly disagreed with Matthew on its ordinal position, placing it, on the basis of molar structure, quite logically in the Primates rather than in the Insectivora. In the portion of the paper dealing with the relationships of the Eocene forms he took exception to certain features of Wortman's classification, but supported him in regarding the notharctids as more closely allied to the platyrrhines than to the modern lemurs. He discussed at length details of W. K. Gregory's comparisons between the skeleton of *Notharctus* and those of the Malagasian lemurs, considering that Gregory was "too greatly impressed with the primitive features of the Notharctids and with the many resemblances he found between this group of early primates and the Madagascar lemurs, and did not consider sufficiently, or has failed to interpret properly, the special trends in development indicated in the general skeletal structure of the Notharctids."

In the same year as Gidley's paper, Troxell published a short note, including the original diagnoses of the species of *Apatemys,* adding the large and more highly specialized *A. rodens.* In 1926 he reviewed the status of *Smilodectes* and concluded that from the information available it could not be logically separated from *Notharctus.*

At about this point in our chronology we encounter a later generation of investigators, and beginning about 1927 and extending over 10 years a series of papers by Simpson pertaining to the Paleocene faunas from the Paskapoo in southern Alberta, Bear Creek in southern Montana, the Tiffany deposits in southwestern Colorado, and the Fort Union in Montana, has included descriptions and discussions of various primate remains encountered. Plesiadapids were present in all these faunas and Simpson followed Teilhard de Chardin (1921-1922)

in placing *Nothodectes* in synonymy with *Plesiadapis.* The newer Tiffany material, not fully prepared at the time of Matthew's report on *Nothodectes,* formed the basis of a detailed restudy. In 1928 he described *Carpolestes,* the strange primate with the *Ptilodus*-like lower premolar in the Bear Creek fauna, and in his (1935b) study of the Tiffany primates he proposed the new family Carpolestidae to accommodate Gidley's earlier *Elphidotarsius* and Matthew and Granger's *Carpodaptes,* as well as *Carpolestes,* representing a developmental sequence from middle Paleocene through upper Paleocene. Matthew and Granger's *Labidolemur,* recognized in the Bear Creek fauna, as well as in the Tiffany, was allocated by Simpson first to the Plesiadapidae, but later (1935b), following Jepsen (1934), placed in the Apatemyidae. Tiffanian *Navajovius* of Matthew and Granger was regarded as being most nearly related to the anaptomorphids. In the Fort Union studies he found that one of the species described by Gidley under *Palaechthon* represented a distinct genus, to which he gave the name *Palenochtha,* a form somewhat more remotely related to *Paromomys* than was *Palaechthon.* All these he (1937b) then regarded tentatively as anaptomorphid and made a rather thorough review of the possible relationships of these to various other primate genera.[4]

Jepsen's contributions to the primate studies are included in two 1930 papers concerned with collections obtained from the lower Eocene and Paleocene of the Bighorn Basin, and a 1934 revision of the Apatemyidae. In the first of these he described, in addition to a new species of *Tetonius,* the apatemyid genus *Teilhardella* which he at that time referred to the Plesiadapidae. In the second paper the faunas of the four horizons recognized in the Polecat Bench series are described. In three of these primates were encountered. The Torrejon equivalent produced *Plesiolestes,* which Jepsen regarded tentatively as a plesiadapid, but which Simpson (1937b) considered to be very close to Gidley's *Palaechthon.* In the Tiffanian fauna *Plesiadapis, Phenacolemur,* and *Carpolestes* were recognized, and both *Plesiadapis* and *Carpolestes* in the Clark Fork.

In Jepsen's revision of the Apatemyidae he revived the family name first proposed and then suppressed by Matthew, and outlined the way in which the genera belonging to it are distinguished from those remaining in the Plesiadapidae. The remarkably long range of the Apatemyidae in geologic time is illustrated, beginning with *Labido-*

[4] The *Uintalestes* mentioned (p. 146) is probably intended to be *Uintasorex* of Matthew.

*lemur* in the Bear Creek-Tiffany Paleocene, extending through the Eocene, and apparently terminating in the newly described Oligocene genus, *Sinclairella.*

Much interest attaches to the discoveries by Stock in adding greatly to our meager knowledge of North American upper Eocene primates, as represented in the Sespe formation and Poway conglomerate in southern California. Previous to 1933, the only upper Eocene materials known were the skull fragment and jaw belonging to *Stehlinella* and the jaw of *"Notharctus" uintensis* from the Uinta deposits in northeastern Utah. *Chumashius* (1933) and *Dyseolemur* (1934), from the Duchesnean and Uintan horizons of the Sespe respectively, showed the extension of omomyid lines into the upper Eocene; and the Poway lower Uintan *"Yumanius"* (1938), here divided between *Washakius* and the new genus *Stockia,* furnished further evidence as to the longevity of lines within the Omomyidae.

Later work by Simpson has included investigations involving Eocene primate materials, as well as Paleocene, and in 1940 a collection of short studies included description of some skeletal remains referred to Bridger *Hemiacodon* and a new anaptomorphid, *Loveina,* from the upper Wasatchian. Also named is a Belgian lower Eocene omomyid(?), *Teilhardina.* In addition to naming the genus *Jepsenella,* extending the known apatemyid lineage down to middle Paleocene time, a classification of the Anaptomorphidae is made and an excellent summary of the relations and distribution of Paleocene and Eocene primates is given. The annotated bibliography has been found especially useful.

In 1954 Simpson recorded an apatemyid in the Wasatchian of New Mexico, and in 1955, his latest work at hand, he made a detailed study of *Phenacolemur* and its relationships, showing that the earlier forms, *Paromomys* and *Palaechthon,* were closely related. The new family Phenacolemuridae was erected to care for this grouping and to show its distinctness, particularly from the Plesiadapidae. Included also was a general summary on prosimian relationships and the problems of classification.

A number of other investigators in recent years have contributed significantly to our knowledge of North American primates in the description of new forms and in the recording of new occurrences, extending known geographic or geologic ranges. These arranged in alphabetical order would include Burke's (1935) record of a notharctid and an anaptomorphid in horizons of the Green River formation; John Clark's (1941) description of the new omomyid, *Macro-*

*tarsius,* in the lower Oligocene of Montana; Dorr's (1952) new plesiadapid and carpolestid finds in the Hoback Basin Paleocene; Gazin's (1942, 1952, 1956a-c) description of new as well as previously known notharctid and anaptomorphid materials discovered in the Knight lower Eocene, and various plesiadapids from the Almy, Fossil Basin, and Bison Basin Paleocene occurrences; Kelley and Wood's (1954) record of additional notharctid, omomyid, anaptomorphid, and phenacolemurid remains in the Lysite; Morris' (1954) notharctid and new anaptomorphid occurrences in the Cathedral Bluff member of the Knight; Seton's (1940) recognition of the genus *Paratetonius* among the anaptomorphid materials from the lower Eocene; and White's (1952) record of notharctid, anaptomorphid, and apatemyid remains from the Lost Cabin beds in the Boysen Reservoir area. Special mention has been made of Robinson's recent (1957) revision of the middle Eocene species of *Notharctus,* in which the rather large number of names which have been previously applied were logically reduced to three, an undertaking particularly pertinent to the present study.

Inasmuch as the present undertaking has been limited to North American materials, few references have been made to Old World fossil studies, and these only when discussions have a more or less direct bearing on the investigation at hand, such as those of Schlosser (1887), Stehlin (1912 and 1916), and Teilhard de Chardin (1921-1922 and 1927). To these may be added the more recent work of Hürzeler (1948) on the necrolemurids, particularly commendable for the excellent illustrations of these omomyidlike forms.

Among recent studies of primates which have included reviews of fossil forms may be mentioned Le Gros Clark (1934) and the newly published work of Osman Hill (1953, 1955). Particularly pertinent is the latest part, volume 7, of the Traité de Paléontologie by Piveteau, which is devoted to the primates. It is the most recent (1957) and comprehensive account of the order from the paleontological point of view.

## GEOGRAPHIC AND GEOLOGIC OCCURRENCE

Our North American middle Eocene primates, as is true also of the earlier Eocene and Paleocene forms, are known only from the Rocky Mountain region, represented by remains found in early Tertiary basins of deposition associated with Rocky Mountain orogeny. Moreover, these Bridgerian specimens, while comprising much the best preserved primate materials found in the region, are rather more restricted in their known geographic occurrence. Except for certain

notharctid materials from the upper Huerfano beds of lower Bridgerian age in southwestern Colorado, and fragmentary remains of several forms recently secured by J. LeRoy Kay from nearby Green River beds of Bridger age in northeastern Utah, the bulk of the known middle Eocene primate materials are from the Bridger formation in southwestern Wyoming. Undoubtedly the known middle Eocene forms actually had a much wider distribution on the continent, and it is entirely justifiable to assume that there were a number of other forms not represented in the Bridger area. Nevertheless, the Bridger formation has been exceedingly productive in revealing the fauna of this age.

The Bridger formation was divided by Matthew (1909b) into about five stratigraphic units, lettered from A to E; however, only B to D inclusive are essentially productive of mammalian remains. It has been customary to divide the Bridger into upper and lower portions with the division falling between B and C, at the bottom of a conspicuous and widespread ash bed designated by Matthew as the Sage Creek White Layer. Bridger B or the mammal-producing portion of the lower Bridger is extensively exposed in the western part of the Bridger Basin and best seen in the Grizzly Buttes south of Lyman, Wyoming, along Cottonwood Creek and Smith's Fork and along Black's Fork between "Millersville" and Church Buttes. To the east of Little America, on Highway U. S. 30, Bridger B interfingers with the Green River lake beds and is represented largely but not entirely by Green River formation beneath Twin Buttes in the eastern part of the basin. The upper Bridger horizons C and D are best represented along an easterly fork of Sage Creek in the vicinity of Sage Creek Mountain, around Henry's Fork Table and to the north, and the slopes of Twin Buttes, except the lowest, in the eastern part of the basin.

The several seasons' collecting in the Bridger Basin has demonstrated that certain of the genera of primates, i.e., *Notharctus, Smilodectes, Omomys, Washakius,* and apparently *Uintanius,* are represented in both lower and upper Bridger levels, whereas *Hemiacodon* is characteristic of the upper beds. *Uintasorex* and *Apatemys,* insofar as the Bridger formation is concerned, have been found only in the upper beds, but are now known in what may be a lower Bridger equivalent of the Green River beds of Utah. *Trogolemur* and *Anaptomorphus* on the other hand, previously known only from single specimens of lower Bridger age, are now known to be represented by additional materials in the Marsh collection, but the latter are not precisely recorded as to horizon in the Bridger, so that their range cannot be further determined.

The Huerfano beds in the Huerfano Basin in southwestern Colorado are generally divided into "A," a lower portion equivalent in time to Lost Cabin or upper Wasatchian, and an upper portion "B," of lower Bridgerian time. There would appear to be some evidence, based on titanothere remains, that upper Huerfano is roughly equivalent to Bridger A, although the evidence is rather inconclusive, inasmuch as very few fossils of stratigraphic significance have been discovered in the "A" horizon of the Bridger formation. Nevertheless, I would not be inclined to regard Huerfano B as equivalent to Cathedral Bluff because the fauna of this horizon, as represented by materials from the New Fork beds, above the Tipton tongue in the northern part of the Green River Basin, is distinctly less advanced than that from Huerfano B. The Huerfano faunas are currently under study by Peter Robinson and, as would be expected, the Bridger equivalent of these beds has yielded notharctid remains.

The Green River beds in northeastern Utah were deposited during a rather lengthy portion of Eocene time. Presumably beginning in the Paleocene, deposition of lake deposits is known to have extended well into the upper Eocene. Faunal evidence has been shown by Burke (1935) to demonstrate the presence of both Wasatchian and Bridgerian horizons. The upper of the two zones described by him was tentatively regarded as being in the Evacuation Creek member, although this seems very doubtful. Of the primates only *Smilodectes* (*"Notharctus matthewi"*) was listed by Burke, but subsequent collections from the "Powder Springs" locality by Kay include *Omomys, Utahia, Uintasorex,* and *Apatemys* as well.

In upper Eocene time a rather different geographic distribution is presented and most of the known materials are from marginal continental deposits or sandy lenses in coarse near-shore deposits in southern California. The genera *Dyseolemur* and *Apatemys* are recorded from the upper Uintan (Tapo Ranch) horizon in the Sespe formation, and *Chumashius* was described from the Duchesnean (Pearson Ranch) horizon of the Sespe. The material originally described by Stock (1938) as *Yumanius* was found in sandy lenses in the Poway conglomerate of San Diego County. The latter specimens are in this study divided between *Washakius* and the new genus *Stockia.*

Of the two forms represented in collections from the upper Eocene of the Rocky Mountain region, the supposed primate *Stehlinella* and the new genus *Ourayia* are known from remains found in the Uinta formation of northwestern Utah. *Stehlinella* was described by Mat-

thew as coming from "White River, Utah," hence is not recorded as to precise horizon. *Ourayia* is based on *Microsyops uintensis* Osborn, later referred to *Notharctus* which it does not represent. It is recorded as coming from White River pocket, hence is lower Uintan in age.

## ENVIRONMENT

To discuss the environment of a group of animals known to be so closely adapted to, or dependent upon, a particular habitat has perhaps less significance in reaffirming their particular life setting than in furnishing interesting information as to the conditions under which a large number of forms belonging to other mammalian orders may be found. While some of the latter may likewise be restricted to a similar environment, in certain cases absence of living representatives renders interpretation dependent on anatomical and dental analogy or demonstrated faunal association, as in this situation. A rather large number of forms, however, such as the ungulates, will be found to have a rather greater environmental range than monkeys, and others will be found associated because of a combination of environmental factors. For example, in the present instance food-bearing trees as well as an equitable climate have furnished the setting for primates, whereas certain other animals may owe their presence to bodies of water, as has been suspected of *Patriofelis*.

There is included below a list of the genera recognized in the Bridger middle Eocene (including *Utahia* from the Green River) in comparison with a composite list from the various upper Eocene formations, such as the Uinta, Duchesne River, Hendry Ranch member of the Tepee Trail, Swift Current Creek, lower Sespe and Poway conglomerate:

| MIDDLE EOCENE MAMMALIA | UPPER EOCENE MAMMALIA |
|---|---|
| MARSUPIALIA | MARSUPIALIA |
| Didelphidae | Didelphidae |
| *Peratherium* | *Peratherium* |
| INSECTIVORA | INSECTIVORA |
| Deltatheridiidae | |
| *Phenacops* | |
| Leptictidae | Leptictidae |
| *Hypictops* | *Protictops* |
| | Leptictidae? |
| | *Sespedectes* * |

* Found in the upper Eocene of southern California, but not in this horizon of the Rocky Mountain area.

| MIDDLE EOCENE MAMMALIA (Cont.) | UPPER EOCENE MAMMALIA (Cont.) |
|---|---|
| INSECTIVORA (Cont.) | INSECTIVORA (Cont.) |
| Erinaceidae | Erinaceidae |
| *Entomolestes* | *Proterixoides* * |
| Nyctitheriidae | |
| *Nyctitherium* | |
| *Centetodon* | |
| *Myolestes* | |
| Pantolestidae | |
| *Pantolestes* | |
| Mixodectidae | Mixodectidae |
| *Microsyops* | *Microsyops* * |
| | *Craseops* * |
| PRIMATES | PRIMATES |
| Notharctidae | |
| *Notharctus* | |
| *Smilodectes* | |
| Omomyidae | Omomyidae |
| *Omomys* | *Chumashius* * |
| *Hemiacodon* | *Ourayia* |
| *Washakius* | *Washakius* * |
| *Utahia* | *Dyseolemur* * |
| | *Stockia* * |
| Anaptomorphidae | |
| *Anaptomorphus* | |
| *Uintanius* | |
| *Uintasorex* | |
| *Trogolemur* | |
| PRIMATES? | PRIMATES? |
| Apatemyidae | Apatemyidae |
| *Apatemys* | *Apatemys* * |
| | *Stehlinella* |
| TILLODONTIA | |
| Esthonychidae | |
| *Trogosus* | |
| *Tillodon* | |
| TAENIODONTA | TAENIODONTA |
| Stylinodontidae | Stylinodontidae |
| *Stylinodon* | *Stylinodon* |
| EDENTATA | |
| Metacheiromyidae | |
| *Metacheiromys* | |
| | LAGOMORPHA |
| | Leporidae |
| | *Mytonolagus* |

* Found in the upper Eocene of southern California, but not in this horizon of the Rocky Mountain area.

| MIDDLE EOCENE MAMMALIA (Cont.) | UPPER EOCENE MAMMALIA (Cont.) |
|---|---|
| RODENTIA | RODENTIA |
| Paramyidae | Paramyidae |
| *Paramys* | *Paramys* |
| *Reithroparamys* | *Ischyrotomus* |
| *Pseudotomus* | *Leptotomus* |
| | *Rapamys* |
| | *Mytonomys* |
| Sciuravidae | Sciuravidae |
| *Sciuravus* | *Sciuravus* |
| *Tillomys* | |
| *Taxymys* | |
| Cylindrodontidae | Cylindrodontidae |
| *Mysops* | *Pareumys* |
| | *Presbymys* * |
| | Aplodontidae |
| | *Eohaplomys* * |
| | Protoptychidae |
| | *Protoptychus* |
| | Adjidaumidae |
| | *Protadjidaumo* |
| | Geomyidae? |
| | *Griphomys* * |
| Incertae sedis | Incertae sedis |
| *Pauromys* | *Simimys* * |
| CARNIVORA | CARNIVORA |
| Mesonychidae | Mesonychidae |
| *Synoplotherium* | *Mesonyx?* |
| *Mesonyx* | *Harpagolestes* |
| *Harpagolestes* | *Hessolestes* |
| Oxyaenidae | |
| *Patriofelis* | |
| Limnocyonidae | Limnocyonidae |
| *Limnocyon* | *Limnocyon* |
| *Thinocyon* | *Oxyacnodon* |
| *Machaeroides* | *Apataelurus* |
| Hyaenodontidae | Hyaenodontidae |
| *Sinopa* | *Pterodon* * |
| *Tritemnodon* | *Hyaenodon* |
| Miacidae | Miacidae |
| *Viverravus* | *Plesiomiacis* * |
| *Uintacyon* | *Uintacyon* |
| *Miacis* | *Miacis* |
| *Vulpavus* | *Tapocyon* * |
| *Oödectes* | *Pleurocyon* |
| *Palaearctonyx* | |

* Found in the upper Eocene of southern California, but not in this horizon of the Rocky Mountain area.

| MIDDLE EOCENE MAMMALIA (Cont.) | UPPER EOCENE MAMMALIA (Cont.) |
|---|---|
| | CARNIVORA (Cont.) |
| | Canidae |
| | *Procynodictis* |
| | Felidae? |
| | *Eosictis* |
| CONDYLARTHRA | CONDYLARTHRA |
| Hyopsodontidae | Hyopsodontidae |
| *Hyopsodus* | *Hyopsodus* |
| DINOCERATA | DINOCERATA |
| Uintatheriidae | Uintatheriidae |
| *Elachoceras* | *Eobasileus* |
| *Uintatherium* | |
| *Eobasileus* | |
| PERISSODACTYLA | PERISSODACTYLA |
| Equidae | Equidae |
| *Orohippus* | *Epihippus* |
| Brontotheriidae | Brontotheriidae |
| *Limnohyops* | *Metarhinus* |
| *Palaeosyops* | *Mesatirhinus* |
| *Eometarhinus* | *Rhadinorhinus* |
| *Metarhinus* | *Sphenocoelus* |
| *Mesatirhinus* | *Dolichorhinus* |
| *Telmatherium* | *Sthenodectes* |
| *Manteoceras* | *Manteoceras* |
| | *Protitanotherium* |
| | *Teleodus* |
| | *Notiotitanops* |
| | *Diplacodon* |
| | *Eotitanotherium* |
| | Chalicotheriidae |
| | *Eomoropus* |
| Isectolophidae | Isectolophidae |
| *Parisectolophus* | *Isectolophus* |
| *Isectolophus?* | *Schizolophodon* |
| Helaletidae | Helaletidae |
| *Helaletes* | *Dilophodon* |
| | *Desmatotherium* |
| Hyrachyidae | Hyrachyidae |
| *Hyrachyus* | *Hyrachyus* |
| *Colonoceras* | |
| *Metahyrachyus* | |
| *Ephyrachyus* | |
| Hyracodontidae | Hyracodontidae |
| *Triplopus* | *Triplopus* |
| | *Epitriplopus* |
| | *Prothyracodon* |
| | *Mesamynodon* |

MIDDLE EOCENE MAMMALIA (Cont.)

PERISSODACTYLA (Cont.)

Incertae sedis
*Chasmotheroides*

ARTIODACTYLA
Dichobunidae
*Microsus*
*Homacodon*
*Helohyus*
*Lophiohyus*
*Antiacodon*

UPPER EOCENE MAMMALIA (Cont.)

PERISSODACTYLA (Cont.)

Amynodontidae
*Amynodon*
*Amynodontopsis*
*Megalamynodon*
Rhinocerotidae
*Eotrigonias*
Incertae sedis
*Schizotheriodes*

ARTIODACTYLA
Dichobunidae
*Bunomeryx*
*Hylomeryx*
*Mesomeryx*
*Pentacemylus*
*Apriculus*
*Parahyus*
*Achaenodon*
*Auxontodon*
Entelodontidae?
*Dyscritochoerus*
Hypertragulidae
*Simimeryx*
Agriochoeridae
*Protoredon*
*Diplobunops*
Oromerycidae
*Oromeryx*
*Protylopus*
*Camelodon*
*Malaquiferus*
Camelidae
*Poëbrodon*
Leptomerycidae
*Leptotragulus*
*Leptoreodon*
*Poabromylus*

Various observations may be made in a comparison of these lists, in addition to those made in a study of the upper Eocene artiodactyls (Gazin, 1955, p. 9), but overall there is a striking decrease in the representation of insectivores, as well as primates, in the Uinta. The emphasis on these has apparently shifted to the southern California occurrences. This would not seem to be due to collecting methods, because remains of a rather interesting diversity of rodents have been

recorded. No significant differences, other than stage of development, are noted between groups of carnivores, except for the disappearance of the Oxyaenidae and the possible appearance of more modern fissiped families. Striking differences in ungulate groups have been previously noted (1955), particularly in the shift to more-selenodont artiodactyls.

For the environmental conditions which prevailed during the Eocene of the Bridger and Uinta basins, as earlier outlined (Gazin, 1953 and 1955), we have an unusually vivid picture, resulting principally from the limnological investigations of Bradley (1926, 1929, 1931, and 1936) and the paleobotanical studies of Brown (1929 and 1934) relative to the Green River formation. The Green River formation includes, of course, the lacustral facies of the Bridger formation in Wyoming and the later Eocene Uinta formation in Utah. Regarding environmental conditions associated with Wyoming's ancient Lake Gosiute, in which were deposited the Green River beds of the Bridger Basin, I would like to quote again the very pertinent conclusions of Bradley (1929, p. 87):

> A climate is postulated which was characterized by cool, moist winters and relatively long, warm summers. Presumably the temperature fluctuated rather widely from a mean annual temperature that was of the order of 65° F. The rainfall varied with the seasons and probably also fluctuated rather widely from a mean annual precipitation between 30 and 43 inches.

Bradley further concluded (p. 89)—

> . . . that the mountain ranges and high divides that form the rim of the Gosiute drainage basin were probably somewhat higher with respect to the floor of the basin during Eocene time than at present. The floor of the basin, however, in common with the general level of that part of the continent, was probably less than 1000 feet above sea level.

Brown has furnished a detailed review of the Green River flora and in his earlier (1929) paper the following statement, in addition to that quoted in 1953, regarding the climate appears (p. 281):

> Such a preponderance of subtropical mesophytes and especially the presence of many forms like palms, *Planera,* and *Acrostichum,* which require an abundance of rainfall and a warm climate, but the presence also of temperate forms such as *Quercus, Populus, Betula, Juglans,* and *Liquidambar,* point to the conclusion that this flora grew in a warm temperate region, a part of which, at least, received a plentiful supply of rain.

Looking now to the upper Eocene of the Uinta basin, presumably during the earlier part of Uintan time, the conditions may not have been greatly different than in later Bridgerian time in Wyoming, but as suggested by the faunal evidence outlined above and in 1955

(pp. 8-9), there were definite signs of increasing aridity. The geologic relations show a transition from the lake deposits to the lacustral sediments of the Uinta and Duchesne River formations. The transition is not abrupt but there is an interfingering between fluviatile or flood-plain sediments with the deltaic and lacustrine sediments, denoting periodic retreat of the lake with an overall reduction and eventual disappearance. Bradley's limnological study of Lake Uinta, just as in the case of Lake Gosiute, has furnished invaluable information on the life conditions that prevailed, and the changes that took place during that time. His popular summary (1936) of these investigations is particularly pertinent to a "visual" appreciation of environmental reasons for the evident faunal change. His word picture of the change following earlier lush conditions—

> Lake Uinta and the surrounding countryside did not always present a picture of smiling beauty, with forests and green meadows. Instead during the later half of its existence death and starvation laid heavy hands upon the community. From time to time pallid blankets of volcanic ash descended upon it and snuffed out the life. Animals and plants alike were smothered, and the streams were clogged with the harsh mud. Gradually, as rains washed off the slopes, the forest renewed its growth and animals again sought its shelter. But it was to no purpose, for again and yet again at long intervals the volcanoes in the neighboring mountain chains belched forth devastating clouds of pumiceous ash.
>
> As if these recurrent disasters were not enough, the rains came less frequently: the very life-giving source of moisture began gradually but surely to dry up. Under the pitiless summer sun the more lush plants withered and finally gave up, weary of waiting for the rain. Animals wandered away in search of water.
>
> The lake, too, suffered. For a long time it overflowed only during the cooler rainy season, but as the years passed the thirsty air drew more and more greedily from its surface until finally at the highest stage the water could not reach the outlet.

Following this evident change to an arid condition there is further evidence, as Bradley has pointed out, of a temporary return to conditions more like those earlier prevailing, but this was attended by stream overloading, water turbulence, and eventual disappearance of the lake, not to be further juvenated by downwarping of the basin.

As a consequence of the foregoing the dearth of primate remains in the Uinta formation may be explained. *Ourayia* is recorded from the earlier or Uinta B level, and although there is no information in the literature regarding the level for *Stehlinella,* it may likewise have come from the "White River pocket."

Clearly, the primates retreated from the regions of increasing aridity following the pattern of forest distribution and warm or warm-temperate climate, so that except for a possibly limited or relict Oligocene

distribution noted for Montana and South Dakota, the retreat or shrinking distribution would likely have been to the peripheral regions away from the more arid and rising interior of the continent and rather generally southward so that their occurrence in the upper Eocene of southern California is reasonable but also temporary, as favorable climatic conditions there evidently did not persist after Eocene times. I do not believe that primates became extinct on the northern continent but that their more southerly distribution has not been recorded because of the absence of reasonably fossiliferous deposits showing a sylvan association in more southerly portions of the continent. It seems inescapable that they persisted in the more tropical, forested areas of the continent to the present time. That they were not entirely restrained by the narrow water barrier between the northern and southern continents seems also evident, with pre-Pleistocene, but very sparse, occurrences in Argentina and Colombia. Such an interpretation, though not at the present time satisfactorily demonstrable may be more logical than to assume extinction and a reintroduction from the southern continent. I suspect also that southerly retreat or shrinking perimeter of the primates may have been effective enough to isolate their distribution from evident land bridges between the New and Old Worlds in the northerly reaches or extremities of the continents, preventing their involvement in the faunal interchange for which there seems some evidence at about the close of Eocene time.

## REVISION OF CERTAIN LOWER EOCENE PRIMATES AND DESCRIPTION OF THREE NEW UPPER WASATCHIAN GENERA

While not intending to expand this study to include lower Eocene primates in general, examination of the various specimens of Wasatchian omomyids and anaptomorphids for a better understanding of relationships of the later genera indicated that revision of certain of these earlier forms was imperative. At the same time it was found advisable to place on record new genera evident in the later Wasatchian materials of the Knight and Green River.

In the first place, careful examination of the type of Seton's (1940) *Paratetonius steini* has convinced me that this form is not actually distinct from *Tetonius homunculus*. The characters of the lower teeth cited were evidently derived largely from Matthew's *Tetonius musculus,* which Seton considered as representing *Paratetonius*. Certain of these as outlined led me (1952) to believe that the Knight specimen that I described as *Paratetonius? sublettensis* belonged to this genus.

It is now clear that the material of *P.? sublettensis* does not correspond to that described by Seton. The new generic name *Anemorhysis* is proposed, as outlined below, for the Knight anaptomorphid *Anemorhysis sublettensis.*

It was also noted that the upper dentition described by Seton (1940) as *Tetonius barbeyi* probably does not belong to that genus. The form of these teeth seems decidedly different from that characterizing *Tetonius,* particularly the outer portion of the upper molars. Also, the relative proportions of $M^3$ are distinctive. Certain characteristics or features not readily described, such as the so-called "cut" of the teeth, or cusps, as well as the very close correspondence in size, leads me to believe that the maxilla described as *Tetonius barbeyi* belongs to the omomyid *Loveina zephyri,* although there is no proof for this at present. Seton's specimen, moreover, was found in the same beds, although some distance away from the locality for *Loveina.*

New forms encountered include an interesting omomyid from the Knight, exhibiting a resemblance to *Loveina* on the one hand, and possibly to the new middle Eocene form, *Utahia,* from the upper Green River zone on the other, which is described under the new name *Chlororhysis knightensis.* Also, the anaptomorphid listed by Burke (1935) from the lower fossiliferous zone of the Green River, but also Lost Cabin in age, is found to be a new form, possibly related to *Anemorysis* and *Trogolemur.* It has been named *Uintalacus nettingi* in one of the descriptions to follow.

### ANEMORHYSIS,[5] new genus

*Type.—Paratetonius? sublettensis* Gazin, 1952.

*Generic characters.*—Anterior incisor enlarged. $P_4$ not enlarged, exhibiting a well-defined paraconid, a weak but distinct metaconid, a moderately long and broadly basined talonid with a weak posterointernal cusp or entoconid and a somewhat better-defined posteroexternal cusp or hypoconid. Molar cusps less inflated and more marginally placed than in *Tetonius.* Paraconid lingual in position, and in $M_2$ clearly defined and close to the metaconid.

*Discussion.*—The characters of the anaptomorphid *Anemorhysis* are essentially those earlier (Gazin, 1952) thought to characterize *Paratetonius* of Seton. From the Knight material of *Anemorhysis* it is evident that $P_3$ may be two rooted as well as $P_4$. There are

[5] From Greek, *anemos,* wind, and *rhysis,* stream or river; with reference to the Wind River mountains (use of a single letter *r* in the combined form is intentional).

alveoli for three single-rooted teeth anterior to those for $P_3$. These include an enlarged incisor and a small, long-rooted second tooth partially lateral to it. The third alveolus, presumably for C, is intermediate in diameter between the second just ahead and that for the anterior root of $P_3$. $P_4$ is characterized by an anteroposteriorly short trigonid with a distinct paraconid and a weaker metaconid. The talonid of this tooth is distinctly long in comparison with other anaptomorphids, except for *Uintasorex*. It shows a broad basin with a small hypoconid and a somewhat weaker entoconid.

The molar trigonids are distinctly broad and developed much as in *Trogolemur*. In $M_2$ the paraconid is decidedly lingual and close to the metaconid. A low transverse anterior crest joins the anterior slope of the protoconid and of the paraconid. This crest is lower than the more rounded spurs which extend mediad from the paraconid and protoconid. A third, slender crest extends from the protoconid to the metaconid. The talonid crest and basin of $M_1$ and $M_2$ are distinctly *anaptomorphus*-like but the basin appears relatively a little larger than in *Trogolemur,* however its relative size is not as great as in *Omomys*.

*Anemorhysis sublettensis* was originally described as being smaller than *"Paratetonius?" tenuiculus* (Jepsen) and much smaller than *"Paratetonius" musculus* (Matthew). I am uncertain, however, as to whether Jepsen's Gray Bull species should be referred to *Anemorhysis* or returned to *Tetonius*. With regard to Matthew's Lysite species, *"Tetonius" musculus,* however, I was in error in stating that *"P.?" sublettensis* was much smaller. Direct comparison of the two has demonstrated that *"T." musculus* is scarcely at all larger than *A. sublettensis*. Moreover, there would seem to be no doubt but that *"T." musculus* also represents *Anemorhysis*. The minute details of the trigonid of $M_3$, as well as its general form, are surprisingly like those of $M_2$ in *A. sublettensis*. There would appear to be two species represented, however, because not only do they represent different geologic horizons, but $P_3$ in *Anemorhysis sublettensis* must have been a more elongate tooth, as the two separate roots occupy much more space longitudinally than the labially fused roots of this tooth in *Anemorhysis muscula*. The Gray Bull specimen, A.M. No. 15066, that Matthew tentatively referred to *"T." musculus,* has relatively broader molars and slightly narrower trigonid apices than in *A. sublettensis*. Also, $P_4$ has a better developed metaconid and the talonid of this tooth is much shorter. I am inclined to regard No. 15066 as a lower jaw of Jepsen's *Tetonius?* (or *Anemorhysis?*) *tenuiculus*.

### CHLORORHYSIS,[6] new genus

*Type.—Chlororhysis knightensis,* new species.

*Generic characters.*—Close to *Loveina,* but $P_2$ relatively a little smaller with respect to the canine, and $P_3$ more slender and completely lacking the posterointernal crest from the primary cusp and with better development of posterointernal cingulum. Also, $P_4$ slightly more expanded posteroexternally, but posterointernal crest from primary cusp much weaker and metaconid lower in position as well as less prominent.

*Discussion.*—The omomyid *Chlororhysis* had two small, erect lower incisors, much as in *Washakius* and *Loveina.* The canine has a premolarlike crown, but higher and with a larger root than $P_2$. In *Loveina* the alveoli for these teeth are about the same size. There is a prominent internal cingulum on the canine extending back from the anterior crest, and in $P_2$ the internal cingulum is developed into a conspicuous, shelflike posterointernal projection. $P_3$ also shows a prominent lingual cingulum, but there is no posterointernal crest from the apex of the primary cusp as there is in *Loveina.* The posterointernal crest is weakly developed in $P_4$ and the metaconid is lower and much less conspicuous than in *Loveina.* Nevertheless, a pair of small accessory ridges on the posterior slope of the primary cusp are developed quite as in *Loveina.*

*Chlororhysis* may prove to be a synonym of *Loveina,* but I am inclined to regard the differences noted, particularly in $P_3$, as probably of generic importance. The lower molars of *Chlororhysis* are not known, but I predict that eventual discovery will show them to be omomyid rather than anaptomorphid, and like those of *Loveina,* or possibly those of *Utahia.*

### CHLORORHYSIS KNIGHTENSIS,[7] new species

Plate 14, figure 7

*Type.*—Left ramus of mandible with C-$P_4$, inclusive, U.S.N.M. No. 21901.

*Horizon and locality.*—Upper Knight beds, La Barge fauna, south side of Milleson Draw, east side of Green River, NW¼ sec. 4, T. 28 N., R. 111 W., Sublette County, Wyoming.

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[6] From Greek, *chloros,* green, and *rhysis,* stream or river; with reference to the Green River proper.

[7] Named for the Knight formation of the upper Green River Basin.

*Specific characters.*—Size close to that of *Loveina zephyri.* Specific characters not otherwise distinguished from those cited as characterizing the genus.

MEASUREMENTS IN MILLIMETERS OF LOWER JAW AND TEETH IN TYPE SPECIMEN OF *Chlororhysis knightensis,* U.S.N.M. NO. 21901

| | |
|---|---|
| Depth of jaw beneath $P_4$, internally | 3.5 |
| C, transverse diameter at cingulum | 1.1 |
| $P_2$, anteroposterior diameter : transverse diameter | 1.3 : 1.0 |
| $P_3$, anteroposterior diameter : transverse diameter | 1.8 : 1.4 |
| $P_4$, anteroposterior diameter : transverse diameter | 2.0 : 1.7 |

### UINTALACUS,[8] new genus

*Type.—Uintalacus nettingi,* new species.

*Generic characters.*—Lower molars resembling *Tetonius* but with less inflated basal portion, cusps more marginal in position with broader trigonid, somewhat as in *Anemorhysis.* $P_4$ unlike *Anemorhysis,* but resembles that in *Anaptomorphus* and *Tetonius,* although relatively smaller and less inflated appearing.

*Discussion.*—The lower teeth of *Uintalacus,* as far as known, are decidedly anaptomorphid. $P_4$ is a simple tooth with a short, relatively blunt anterior crest, without a paraconid. There is a weak posterointernal crest which lacks any evidence of a metaconid. The talonid is short and exhibits a short median crest that blends anteriorly into the posterior wall of the primary cusp. $P_4$ is much less inflated than in either *Tetonius* or *Anaptomorphus.* This tooth differs strikingly from $P_4$ in *Anemorhysis* which exhibits a short, three-cusped trigonid portion and a longer and basined talonid. In *Trogolemur* this tooth is more compressed anteroposteriorly but shows better evidence for a paraconid and a distinct metaconid.

The lower molars rather resemble *Tetonius* but are distinctly less inflated across the basal portion, and the buccal wall is not nearly so elongate vertically. The trigonid portion appears, however, somewhat more elevated than in *Trogolemur.* The cusps on both the trigonid and talonid have a more marginal position as in *Anemorhysis* and *Trogolemur.* In $M_2$ the top of the trigonid is a little less broad than in *Anemorhysis* and the paraconid is slightly more forward, on the anterior crest rather than posterior to its lingual extremity. This may not be important, however, as *Trogolemur* appears intermediate be-

[8] From *Uinta,* and *lacus* (L.), body of standing water; with reference to ancient Lake Uinta.

tween the two in position of the paraconid, but has the relatively broad trigonid of *Anemorhysis.*

The anterior portion of the jaw in the only known specimen is not preserved so that there is no evidence as to whether the incisors were small, equal, and erect as in *Anaptomorphus,* or unequal, with the anterior incisor large and procumbent, as in *Trogolemur* and *Anemorhysis.*

### UINTALACUS NETTINGI,[9] new species

Plate 14, figure 5

*Type.*—Left ramus of mandible with $P_4$-$M_2$ and part of $M_3$, C.M. No. 9426.

*Horizon and locality.*—Lost Cabin equivalent of Green River formation, "Lower Fossiliferous Zone," 1½ miles northeast of Powder Springs, Uintah County, Utah.

*Specific characters.*—About the same size as *Anemorhysis sublettensis.* Specific characters not otherwise distinguished from those cited for the genus.

*Discussion.*—*Uintalacus nettingi* cannot be compared directly with *Tetonius? tenuiculus,* except to note a slightly smaller size, as lower teeth of this form are not certainly known. Lower teeth in the jaw, A.M. No. 15066, which Matthew referred to *"T." musculus* and here considered as possibly belonging to *T.? tenuiculus,* are a little more inflated basally, and $P_4$ has three cusps forming a true trigonid, unlike *Uintalacus nettingi.*

No other material of *Uintalacus nettingi* was found in the collection and it seems likely that the type specimen is that referred to as "anaptomorphid" by Burke (1935) in listing the forms recognized from the lower Green River zone. It was later identified as *Tetonius?* in the Carnegie Museum catalog.

MEASUREMENTS IN MILLIMETERS OF LOWER TEETH IN TYPE SPECIMEN OF *Uintalacus nettingi,* C.M. NO. 9426

| | |
|---|---|
| Length of lower molar series, $M_1$-$M_3$, inclusive | 5.4 |
| $P_4$, anteroposterior diameter : transverse diameter | 1.6 : 1.25 |
| $M_1$, anteroposterior diameter : transverse diameter | 1.9 : 1.4 |
| $M_2$, anteroposterior diameter : transverse diameter | 2.0 : 1.5 |

[9] Named for Dr. M. Graham Netting, Director of the Carnegie Museum, who graciously permitted me to study the Green River primates.

## CLASSIFICATION OF MIDDLE AND UPPER EOCENE FORMS

NOTHARCTIDAE Trouessart,[10] 1879

*Notharctus* Leidy, 1870

Synonyms—*Limnotherium* Marsh, 1871
*Hipposyus* Leidy, 1872
*Tomitherium* Cope, 1872
*Thinolestes* Marsh, 1872
*Telmalestes* Marsh, 1872
*Telmatolestes* Marsh, 1872

*Notharctus tenebrosus* Leidy, 1870

Synonyms—*Limnotherium tyrannus* Marsh, 1871
*Hipposyus formosus* Leidy, 1872
*Tomitherium rostratum* Cope, 1872
*Thinolestes anceps* Marsh, 1872
*Limnotherium affine* Marsh, 1872
*Notharctus osborni* Granger and Gregory, 1917
*Notharctus pugnax* Granger and Gregory, 1917

*Notharctus robustior* Leidy, 1872

Synonym—*Telmalestes crassus* Marsh, 1872

*Smilodectes* Wortman, 1903

Synonym—*Aphanolemur* Granger and Gregory, 1917

*Smilodectes gracilis* (Marsh), 1871

Synonyms—*Pelycodus relictus* Gregory, 1917
*Notharctus matthewi* Granger and Gregory, 1917
*Aphanolemur gibbosus* Granger and Gregory, 1917

OMOMYIDAE, new name (from Omomyinae of Wortman, 1904)

*Omomys* Leidy, 1869

Synonyms—*Euryacodon* Marsh, 1872
*Palaeacodon* Marsh (not Leidy), 1872

*Omomys carteri* Leidy, 1869

Synonyms—*Hemiacodon nanus* Marsh, 1872
*Hemiacodon pucillus* Marsh, 1872
*Euryacodon lepidus* Marsh, 1872
*Palaeacodon vagus* Marsh, 1872

*Omomys lloydi*, new species

*Hemiacodon* Marsh, 1872

*Hemiacodon gracilis* Marsh, 1872

*Washakius* Leidy, 1873

Synonym—*Yumanius* Stock, 1938

*Washakius insignis* Leidy, 1873

Synonym—*Hemiacodon pygmaeus* Wortman, 1904

*Washakius woodringi* (Stock), 1938

*Chumashius* Stock, 1933

*Chumashius balchi* Stock, 1933

*Dyseolemur* Stock, 1934

*Dyseolemur pacificus* Stock, 1934

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[10] Not Osborn as credited by both Osborn (1902) and Gregory (1915a).

*Utahia,* new genus
*Utahia kayi,* new species
*Stockia,* new genus
*Stockia powayensis,* new species
*Ourayia,* new genus
*Ourayia uintensis* (Osborn), 1895
ANAPTOMORPHIDAE Cope, 1883
*Anaptomorphus* Cope, 1872
*Anaptomorphus aemulus* Cope, 1872
*Anaptomorphus wortmani,* new species
*Uintasorex* Matthew, 1909
*Uintasorex parvulus* Matthew, 1909
*Trogolemur* Matthew, 1909
*Trogolemur myodes* Matthew, 1909
*Uintanius* Matthew, 1915
*Uintanius ameghini* (Wortman), 1904
Synonym—*Uintanius turriculorum* Matthew, 1915
APATEMYIDAE Matthew, 1909
*Apatemys* Marsh, 1872
*Apatemys bellus* Marsh, 1872
*Apatemys bellulus* Marsh, 1872
*Apatemys rodens* Troxell, 1923
*Apatemys downsi,* new species
*Stehlinella* Matthew, 1929
*Stehlinella uintensis* (Matthew), 1921

## SYSTEMATIC REVISION OF MIDDLE AND UPPER EOCENE PRIMATES

### Family NOTHARCTIDAE Trouessart, 1879

The family Notharctidae is revived to care for the genera *Notharctus, Smilodectes,* and *Pelycodus;* to comprise the genera which might otherwise be included in the subfamily Notharctinae, removing them from the implication of any particularly close relationship to the Adapidae. Except for their primitive lemuroid appearance and the presence of a full complement of premolars, there is little to associate them with *Adapis.* With only teeth to compare, I find certain resemblances to other North American fossil primates, such as the omomyids, although I would not want to include these in the Notharctidae. Strangely enough, the lower molars of *Adapis* combine still other characters seen in omomyids, such as the *Omomys*-like talonid and *Washakius*-like metastylid, but with great reduction of the paraconid.

A feature on which I find no comment by W. K. Gregory, but obvious from illustrations he has shown of skeletal material of *Notharctus* and *Adapis,* is the relative length of the fore and hind limbs

in these two genera. In *Notharctus* the humerus, for example, is only about three-fifths as long as the femur. Approximately this ratio also characterizes *Smilodectes,* but within the material of *Adapis parisienses* figured, these elements are seen to be very nearly the same length. *Adapis* in consequence would appear to have possessed relatively very much longer fore limbs than the notharctids.

In consideration of the skeleton as a whole and the skull in particular, I find that the differences between notharctids and adapids, except in their possessing the same primitive dental formula $I\frac{2}{2}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$, seem fully as great as between the Lemuridae and Indriidae. To quote Gregory (1921, p. 194), ". . . a sufficient reason for regarding the animals as divergent representatives of a single family is *not* that they resemble each other in any one character or in several characters taken independently, but that in all views of the skull and skeleton a common general stamp or underlying 'family resemblance' is revealed beneath many conspicuous differences in detail." While not subscribing to this without reservations, because of the marked overall resemblances which can be brought about by similar adaptations, it should be noted that much of the "family resemblance" that has been attributed to *Notharctus* was based on a poorly reconstructed skull which, as in Gregory's figure 30, has a more lemurlike look than it should.

Gregory's family resemblances are cited as [1] "a striking agreement in general proportions of the face and brain case, [2] in the gentle inclination of the face to the basicranial axis, [3] in the relatively slight expansion of the brain case, [4] in the sharp constriction of the skull behind the orbits, [5] in the powerful build of the zygomata, and [6] in the prominence of the sagittal and lambdoidal crests." In No. 1 (my numbering) the general proportions of the face and brain case are relatively very different from those in *Adapis,* as comparison of Stehlin's (1912) figures with those of less distorted skulls of *Smilodectes* and *Notharctus* shows in plates 1 to 4 of this report. (2) The inclination of the face to the basicranial axis is much greater in less crushed skulls, particularly in *Smilodectes.* (3) The relatively slight expansion of the brain case would seem general in early mammals, but even so, the brain case is shorter and relatively broader in notharctids. (4) The skull of *Notharctus* is much less constricted behind the orbits than in most of the adapid skulls figured by Stehlin. (5) The zygoma is powerfully built in *Smilodectes,* but in *Notharctus* it appears much more slender posterior to the orbits than in *Adapis.*

(6) The sagittal and lambdoidal crests, of course, tend to become stronger in more mature individuals, but are certainly less developed in the *Notharctus* material examined than in the *Adapis* material figured. A source of error in the restoration of the *N. "osborni"* skull was the insertion of a portion of the lambdoidal crest in the sagittal line. These crests are particularly weak or undeveloped in mature *Smilodectes.*

*Smilodectes,* an undoubted notharctid, quite independently cancels out the "underlying family resemblances" and shows the extent to which those outlined must be adaptive. Details of the characteristic features of *Smilodectes* are covered below in a comparison of its skull and that of *Notharctus.*

### COMPARISON OF THE SKULLS OF *Notharctus* AND *Smilodectes*

In view of the excellent new material of the Bridger notharctids which has come to light since Gregory's admirable memoir on the genus *Notharctus*—a series of relatively uncrushed skulls, which serve, moreover, to demonstrate the presence of a second genus, *Smilodectes,* among the known species—it seems pertinent at this time to review the characters of *Notharctus* and to call attention to the various features that distinguish *Smilodectes.*

In the dorsal view in general, in a comparison with *Adapis,* one is immediately impressed by the relatively much shorter and broader skull of *Notharctus,* and particularly of *Smilodectes.* The nasals, nevertheless, are distinctly more slender in the notharctids and in none of the material examined do they widen anteriorly as in some of the skulls of *Adapis.* In transverse profile they are sharply convex, forming a narrow elongate bridge on the rostrum, slightly constricted along contact between them and the maxillae. They penetrate a short distance between the frontals but their posterior termination is rather abrupt and they show a slight expansion in width at about the frontomaxillary suture, not greatly different in this latter respect, however, from *Adapis.*

The frontals are relatively much more broadly expanded in the notharctids and occupy a much greater anteroposterior portion of the skull's dorsal surface. In *Notharctus* the frontals appear flattened with possibly a certain tendency toward eversion of the supraorbital margin. *Smilodectes,* on the other hand, shows between the orbits strongly protruding or inflated frontals, as had been indicated in Granger and Gregory's characterization of *Aphanolemur,* now recognized as a synonym of *Smilodectes.* It should be noted, however, that

more or less inflation of the frontals has been noted between species and to a certain extent between individuals of the same species in modern lemurs and indriids.

The orbits of *Notharctus* and *Smilodectes* are relatively larger than in *Adapis,* and posterior to the orbits the skulls are less constricted than appears in much of the *Adapis* material figured by Stehlin. In none of the Bridger material is the posterior border of the postorbital process of the frontal, in its course toward the sagittal crest, turned so abruptly medial or forward as in *Adapis.* Although Gregory has indicated that the frontals did not extend far back over the brain case in *Notharctus,* it was evident that they did to a noticeably greater extent than in *Adapis.*

While the anteroposterior extent and development of a sagittal crest is in many forms a matter of age or maturity, it is relatively shorter and much less prominent in *Notharctus* and but poorly defined in *Smilodectes.* Although the sagittal crest appears higher in *Notharctus* than *Smilodectes,* it is not as high in A.M. No. 11466 (described as *Notharctus osborni* by Granger and Gregory), as indicated by Gregory in his figure 49, because during restoration of this skull a segment of the left side of the lambdoidal crest was inadvertently inserted into the sagittal line, giving a somewhat erroneous impression of height. At the posterior extremity of the sagittal crest in U.S.N.M. No. 21864 of *Notharctus tenebrosus* a small dorsal exposure of the supraoccipital is seen, and in the skulls of *Smilodectes,* which have practically no sagittal crest, the exposure of the supraoccipital dorsally is somewhat larger.

The zygomatic arch in the Bridger notharctids is not nearly as long as in *Adapis,* but has an anteroposteriorly elongate root of attachment to the side of the cranium posteriorly. Nevertheless, the root of the zygomatic process of the squamosal is conspicuously less extended anteroposterior than in *Adapis.*

In the lateral view neither of the two comparatively good skulls of *Notharctus* show an undistorted profile; nevertheless it would appear that the dorsal surface is gently convex through the combined rostral and cranial portions, inasmuch as the relatively short cranium has but a low and comparatively weak sagittal crest. In better represented *Smilodectes* the gentle convexity of the superior profile is noticeably interrupted by the inflated frontals and there is almost no sagittal crest. In *Adapis,* however, the sagittal crest is strikingly high and decidedly convex in profile, rising much above the alignment given by the superior margin of the face.

The face of the notharctids in lateral view shows the premaxilla as a somewhat sinuous but vertically elongate bar on the anterior margin of the maxilla. It carries two small but nearly equal incisors on the lower margin and above extends dorsoposteriorly a short distance as a wedge between the maxilla and nasal. Although Gregory has indicated that the premaxilla is strikingly like that of *Adapis,* it appears, however, that it did not extend nearly so far backward between the nasal and maxilla, as for example in certain specimens of *Adapis magnus* illustrated by Stehlin.

The greater length of the maxilla anteroposteriorly, which Gregory described as characterizing *Notharctus* in comparison with *Adapis,* is apparently in a large measure due to distortion in the skull of *N. "osborni"* (*N. tenebrosus*) which he described, although this bone is somewhat more elongate than in *Smilodectes.* The shallow fossa ahead of the lachrymal, attributed to the orbicularis palpebrarum muscle by Stehlin, is very weak and shallow in *Smilodectes* and scarcely discernible in the U.S.N.M. *Notharctus* skull. The infraorbital foramen is directly above the anteroexternal root of $P^4$ and about midway between this tooth and the margin of the orbit above. In none of the notharctid materials at hand is this foramen double as it is in certain specimens of *Adapis.*

The lachrymal, though evident in the face of *Notharctus,* is ill defined because of damage or incompleteness of the material at hand, and although Gregory has indicated that there is no pars facialis of the lachrymal in *Notharctus,* this bone is not actually preserved in A.M. No. 11466. In *Smilodectes* it is seen to extend a very short distance forward from the margin of the orbit as a small triangular wedge between the frontal and maxilla, and evidently in contact or closely approaching the jugal below. Contact between the lachrymal and jugal is rather general in lemurs and does not indicate any special affinity between notharctids and *Adapis.* The extent of the lachrymal bone anterior to the orbital rim in *Adapis* appears more restricted. In modern lemurs the lachrymal has a marked facial distribution and the lachrymal foramen is anterior to the orbital rim. The large lachrymal foramen in the Bridger notharctids is on the orbital margin, interrupting the margin anteromedially. The anteroventral margin of the foramen would appear to be the maxilla and it is clearly separated from the jugal by a narrow constricted portion of the maxilla in contact with the lachrymal. The jugal is deep and robust beneath the orbit in notharctids, though less so than in *Adapis.*[11] It carries a strong

[11] It should be noted in this connection that the slender bone shown in this position on the left side of A.M. No. 11466 is not correctly placed.

postorbital process which meets the frontal about halfway, overlapping the latter a short distance along its posterior border, completely closing the orbit behind. There is, however, no evidence of a partition behind the orbit as there is in the anthropoids. Almost immediately behind the postorbital process the jugal makes contact with the zygomatic process of the squamosal and, although Gregory has suggested otherwise, extends beneath it to about the glenoid surface. As a consequence the roughened lower margin of the zygomatic process is not, as Gregory suggests, for the masseter muscle but clearly the sutural surface for the posterior portion of the jugal. The combination of these bones gives considerable depth to the zygoma in *Adapis* and in *Smilodectes,* though much shorter in the latter, but appears noticeably more slender in *Notharctus.* This portion of the zygomatic arch is very slender in modern lemurs, but a more nearly comparable depth to that in *Notharctus* is seen in the indriid *Propithecus.* The superior margin of the zygomatic process of the squamosal in notharctids extends backward and upward into the lambdoidal crest as indicated by Gregory; however, the posterior views of the *Adapis* skulls figured by Stehlin (figures 257 and 258) would indicate that this is not quite the case in *Adapis,* as there is a distinct separation shown.

The better preserved skulls of *Smilodectes* show that the suture bounding the parietal forward rises along the side of the cranium just back of the postorbital constriction, extends forward and outward beneath the posterior margin of the postorbital process of the frontal, then swings back along the superior surface to a position much farther back before crossing to the opposite side of the skull. The effect of this is that a long splinter of the parietal extends forward and outward, forming a lengthy portion of the posterior margin of the postorbital process. This is not evident or is less clearly defined in the *Notharctus* material. The extent of this deviation of the frontoparietal suture is much more restricted in *Adapis.*

The contact of the orbital lamina of the frontal with the orbital plates of the palatine, orbitosphenoid, and "probably also with the alisphenoid," and the "apparent" exclusion of contact between frontals and squamosal by a parieto-alisphenoid contact, though speculative in part, is probable, as many primates show this arrangement, and hence, of course, is not particularly meaningful in indicating any special affinity with *Adapis.* Moreover, the contacts made by the vertical plate of the palatine with other elements of the skull as described by Gregory are probable from consideration of recent lemur material, but since these were not actually visible in the material at hand, the statement should be regarded as conjectural in nature.

The disposition and development of foramina in the deeper part of the orbital fossa cannot be clearly determined in the skulls of *Notharctus;* nevertheless, these are readily seen in material of *Smilodectes.* The foramen lacerum anterius or sphenoidal fissure has a nearly triangular, forward-facing aperture, well concealed by the inflated outer pterygoidal wing or lamella of the alisphenoid. Anteromedial to the sphenoidal fissure and separated from it by a thin partition is the optic foramen, evidently entirely within the orbitosphenoid. What must be the foramen rotundum in the alisphenoid is immediately beneath the sphenoidal fissure and like the optic foramen is about equal to it in size. Foramina about half the size of these are seen, one anterodorsal to the optic foramen in the position of an ethmoidal foramen, evidently on the suture between the orbitosphenoid and frontal; and a second, dorsolateral to the sphenoidal fissure, evidently the cranio-orbital foramen, which may carry a part of the stapedial artery, as well as connect with the venous system internally as in the lemurs. The latter, as in the case of the sphenoidal fissure, appears to be on the suture between the orbitosphenoid and alisphenoid. One or two other vascular foramina, evidently representing the parietosquamosal foramen, are well developed along the posterior portion of this suture between the parietal and squamosal, about directly above the external auditory meatus.

The occiput of *Notharctus* and *Smilodectes* is much narrower than in *Adapis* and the surface distribution of the mastoid is very much less, being limited to a narrow, dorsoventrally elongate and curved wedge. The inion noted by Gregory for A.M. No. 11466 of *Notharctus* is much less developed in U.S.N.M. No. 21864 and is quite lacking in mature skulls of *Smilodectes,* in contrast to the striking development seen in *Adapis.* The foramen above the exoccipital, medial to the dorsal apex of the mastoid, at the bottom of the deep fossa, which Gregory compared with a similarly located foramen in *Adapis,* is in all probability the mastoid foramen, as its position with respect to the mastoid is about the same as in modern lemurs where it communicates interiorly with the channel for the lateral sinus of the vascular system. Apparently the foramen Gregory referred to as the mastoid foramen, located medially on the posterior surface of the mastoid, likely communicates only with the interior of the bone, as in various indriids examined. It is clearly defined in the skull, U.S.N.M. No. 21864, of *N. tenebrosus* but not invariably present on both sides in skulls of *Smilodectes* and may be replaced by a network of very small foramina.

The occipital condyles are for the most part dorsoventrally oriented as described by Gregory; however, ventrally they curve more forward in U.S.N.M. No. 21864 than they do in A.M. No. 11466, so that the motion of the head was evidently not so restricted.

Particularly noteworthy in the ventral view is the angle that the axis of the basicranium makes with the basifacial axis. It is noticeably acute in *Smilodectes,* but somewhat less so in *Notharctus.* While not so acute as in *Tarsius,* the angle between these axes is not so obtuse as in modern lemurs, or as seems evident in *Adapis.* In the crushed *Notharctus* skull illustrated by Gregory the alignment of these axes is distorted so that they appear nearly parallel.

Although the palate of A.M. No. 11466 is described by Gregory as narrow in comparison with *Adapis,* this does not hold true in less crushed and distorted material of *Notharctus* or in *Smilodectes.* The long and narrow palatal shelves of the maxillae described as characterizing *Notharctus* are made to appear so rather largely by transverse crushing which has caused portions of the palate to be overlapping and their length extended by fracturing. The palate of *Notharctus* is seen to be relatively less elongate than in *Adapis,* and resembling *Propithecus* rather than *Lemur* among modern forms.

There are two or more posterior palatine foramina on each side and the larger, anterior one is located opposite the anterior portion of $M^2$ and at the posterior extremity of a conspicuous groove which extends nearly the length of the palate on each side. The suture between the maxilla and palatine in its course forward from the incisura for the posterior palatine artery passes ahead of the posterior palatine foramina and swings medially, crossing the median suture about opposite the middle of $M^1$. The posterior margin of the palate in *Notharctus* is extended forward as the anterior margin of the posterior narial aperture to a line between about the midpoints of the third molars, nearer the anterior margin for these teeth in *Smilodectes.* This is a little farther forward than in *Adapis* and the medial portion of the posterior margin of the palate in the notharctids does not project posteriorly so markedly as in *Adapis.*

The palatine continues to form the lateral wall of the posterior narial aperture for a short distance, approximately a centimeter, to near the point where the wall bifurcates and the medial of the two lamellae is the pterygoid proper and the outer wall a part of the alisphenoid. The pterygoid extends upward as a slender bar along the posterior margin of the palatine where it merges with the roof of the mesopterygoid fossa, and the posterior margin of this is continued

back as a low ridge toward the tympanic bulla, bounding the mesopterygoid fossa laterally. The pterygoid extends downward and posteriorly forming a prominent scimitarlike hamular process.

The outer lamella of the pterygoidal plates, composed of the alisphenoid, is deflected markedly outward and extends as a dorsoventrally deep plate almost or quite to a process on the entoglenoid portion of the squamosal in *Notharctus,* but possibly to the bulla in *Smilodectes,* evidently leaving, in this event, a foramen pterygospinosum for a part of the internal maxillary artery. Posterodorsally the root of the lamella of the alisphenoid bifurcates, sending a low ridge a short distance medially along the posterior margin of the alisphenoid at its union with the anterior margin of the bulla. The outer bifurcation tends to effect a partial separation of the apertures of the foramen ovale on the outside from the Eustachian foramen medially.

The basisphenoid in the mesopterygoid fossa of *Notharctus* is characterized by a gently convex median ridge which tapers forward from the basioccipital and then bifurcates, sending a branch to each of the vertical wings of the palatines. In *Smilodectes* this median ridge is much more sharply compressed and the basisphenoid is deeply pocketed on each side, and exhibits a sharper, better defined ridge or crest separating the pterygoid fossa from the mesopterygoid.

In *Notharctus* the pterygoid fossa formed between the lamellae shows a broad roof about on the level with the mesopterygoid fossa. In *Smilodectes,* however, the pterygoid fossa is surprisingly better developed. Between the lamellae it shows a deep pocketing, distinctly separate from the mesopterygoid fossa, with the ridge extending posteriorly from the root of the pterygoid proper, as noted above, which sharply sets off the deeper pterygoid fossa. The pterygoid lamella of the alisphenoid, defining the pterygoid fossa laterally in *Smilodectes,* sweeps much more widely outward from its union with the palatine so that at the outward extent of its convexity it extends smoothly downward from the side of the brain case. In the broad roof of the fossa a prominent convexity or lobe protrudes from the brain case. Gregory has suggested that the temporal, masseter, and internal pterygoid muscles were better developed in *Adapis* than *Notharctus,* but the internal pterygoid was probably much better developed in *Smilodectes.*

Posteriorly the sphenoidal segment is defined by a suture which extends across the basicranium in a nearly straight line between the glenoid surfaces in both *Notharctus* and *Smilodectes.* In *Adapis* and in much of the recent material the bullae protrude forward of the suture between the basisphenoid and basioccipital. The anterior mar-

gin of the bullae in *Notharctus* are described by Gregory as "closely appressed to the hinder edges of the basisphenoid and true pterygoids." There is no evidence to show that the pterygoids are actually represented so far posteriorly. It is probable that only the alisphenoids are represented in contact with the bullae between the basisphenoid and squamosals.

There is no foramen lacerum medius in the notharctids and the Eustachian foramen is located in a lateral portion of the anterior margin of the bulla, median to and within a bifurcation, mentioned above, of the posterior extremity of the alisphenoid lamella bounding the pterygoid fossa. The foramen ovale lies immediately adjacent and anterolateral to the Eustachian foramen, just at the posterior margin of the root of the alisphenoid lamella in *Notharctus*. The more forward position of the foramen ovale with respect to the Eustachian foramen was noted by Gregory in comparison with *Adapis,* and seems clearly indicated in the U.S.N.M. skull of *Notharctus tenebrosus,* but in *Smilodectes* the spreading out of the pterygoid fossa and the outsweep of the pterygoid lamella of the alisphenoid has forced the foramen ovale outward and backward, about even with the Eustachian foramen, so that communication with the foramen ovale is more laterally directed than in *Notharctus*.

The bullae in *Notharctus* are of moderate size and rather lemurlike in external form, but do not extend so far forward as in *Lemur* or *Adapis*. They are relatively and actually much larger in *Smilodectes*. Their greater size much restricts the width of the basiocciptal between them in *Smilodectes* and tends to conceal from direct ventral view the Eustachian foramen and foramen ovale. Also in *Smilodectes* the anterior surface of the bulla is broadly channeled for the downward and medial course of the Eustachian tube.

Between the bullae in *Notharctus,* the basioccipital is of moderate breadth and shows a median keel which extends forward from the foramen magnum almost to the anterior margin of the basioccipital but is distinct from that on the basisphenoid. Also in *Notharctus* the lateral margin of the basioccipital laps downward to a certain extent on the side of the bulla. The basioccipital evidently does not extend down the medial wall of the bulla in *Adapis,* but in *Smilodectes* this condition is very much emphasized, and the inferior surface of the narrower basioccipital is scarcely more than a deep groove between the inflated bullae, and the median keel noted in *Notharctus* is reduced to a very short spur forward from the foramen magnum. The depth of the overlap increases posteriorly to the posteromedial portion of the

bulla where it rapidly retreats to the posteroexternal margin of the basioccipital above, to the groove between the bulla and the condyle at the point where a foramen enters forward between the bulla and margin of the basioccipital. This foramen is in a position normally occupied by the internal carotid in carnivores and certain other groups; the foramen designated "Fx" by Hürzeler (1948, fig. 28). Gregory was in complete disagreement with Wortman as to the use of this foramen, but his categorical rejection of Wortman's suggestion without constructive evidence as to its use may not have been entirely warranted. Immediately posteromedial to this in *Notharctus,* but not confluent, is the condylar or hypoglossal foramen, posterolateral to the foregoing in *Smilodectes* and deep in the narrower groove separating the bulla from the condyle. More lateral to these, almost midway across the posterior margin of the bulla, is a transversely elongate slitlike aperture, the foramen lacerum posterius. Somewhat lower on the posterolateral surface of the bulla is the principal or greater aperture for the internal carotid, much larger than in the lemurs. Ventral to this opening, a broad shallow groove extends medially and ventrally along the back of the bulla. The internal carotid here extends, as described by Gregory, through the chamber of the bulla, passing lateral to the promontorium of the periotic where it sends a branch, the stapedial artery, through the stapes and evidently into the periotic, the arteria promontorii continuing forward through the anterior wall into the cranial cavity. Immediately posterolateral to the external aperture (for this portion?) of the internal carotid is a clearly defined pedicle for the stylohyal, and just posteroexternal to this and evidently entirely surrounded by the mastoid is a small stylomastoid foramen. Posterior to this the prominent mastoid process is deeply excavated below in both *Notharctus* and *Smilodectes.* As in the lemurs in general, there is no bony audital tube and the external auditory meatus in a recess behind the postglenoid process faces outward and slightly downward. The general form of the bulla, as well as the absence of a bony audital tube, or any other outward evidence, adds credence to the suggestion by Gregory that the tympanic annulus was internal to the bulla as in lemurs and indriids.

The postglenoid process of the squamosal projects downward prominently and is sharply separated from the bulla by a deep notch. Just anterior to the notch, about on the suture between the squamosal and alisphenoid, is a small foramen in *Smilodectes,* but not in *Notharctus.* It is suggested, but there is no assurance, that this might have carried the chorda tympani. The postglenoid foramen is promi-

nently displayed posterior to the medial margin of the postglenoid process.

The sharp horizontal ridge which Gregory described as continuous with the anterior edge of the glenoid region, the pterygoid ridge, appears much emphasized in the skull of A.M. No. 11466, but this may be in part due to crushing farther forward, as it is more subdued in U.S.N.M. No. 21864. It is obscured in *Smilodectes,* where the outflaring or inflation of the pterygoid lamella of the alisphenoid almost or quite eliminates any horizontal portion of the area for attachment of the external pterygoid muscle. The development of the pterygoid ridge is noticeably greater in *Adapis* and seems variable between genera of modern primates. Gregory has noted the more concave character of the glenoid surface in *Notharctus* than in *Adapis. Smilodectes* is very much like *Notharctus* in this respect.

In a part of an endocranial cast of *Smilodectes* in which the posterodorsal portion is exposed, only the vermis and two paramedian lobes of the cerebellum are seen, apparently a little more dorsal in position than on modern lemurs. Also, the transverse fissura prima cerebelli separating the two lobes of the vermis is evident. These lobes and a forward depression (over the mesencephalon) are small in comparison with the size of the brain case.

The systematic treatment of the genera and species is resumed below.

### Genus NOTHARCTUS Leidy, 1870

*Synonyms.—Limnotherium* Marsh, 1871.
*Hipposyus* Leidy, 1872.
*Tomitherium* Cope, 1872.
*Thinolestes* Marsh, 1872.
*Telmalestes* Marsh, 1872.
*Telmatolestes* Marsh, 1872.

*Type.—Notharctus tenebrosus* Leidy, 1870.

*Discussion.*—The characters of the genus *Notharctus* have been discussed by Osborn (1902), Granger and Gregory (1917), Gregory (1921), and Robinson (1957). Characters of the teeth regarded as diagnostic remain the same, but changes in those relating to other details of the skull follow discovery of better material and include many of the features outlined in the comparison of the skulls of *Notharctus* and *Smilodectes.* These may be summarized as follows:

In comparison with *Pelycodus,* in the absence of better skull material of this earlier form, diagnostic features of *Notharctus* include

development of a hypocone (or pseudohypocone) on the posterior crest (*Nannopithex*-fold) extending posteriorly from the apex of the protocone, prominent development of a mesostyle of the upper molars, and partial or incipient twinning of the primary outer cusp of $P^4$. In the lower cheek teeth there is noted a marked reduction or loss of the paraconid on $M_2$ and $M_3$, with often scarcely more than a short spur extending anteromedially from the protoconid, but the entoconid in these two teeth is somewhat more emphasized by its greater isolation from the crest which carries the hypoconulid in *Notharctus*. There is a tendency, moreover, in some material, for the protoconid-metaconid crest to become more oblique than usual in *Pelycodus*. This analysis is, of course, highly arbitrary as these two genera are believed to form a nearly continuous sequence. As a consequence certain later Wasatchian species will be assigned arbitrarily.

Better skull material of *Notharctus* has shown that there is a gentle convexity to the superior, anteroposterior profile, and the facial and cranial portions are not elongate. The frontals are broad but show little or no inflation. There is a moderate development of the sagittal and lambdoidal crests, not nearly so emphasized as in *Adapis*. The zygoma is weak posterior to the orbits. The bullae and pterygoid fossae are not so developed as in *Smilodectes* but the summary of details regarding its comparison with that genus is deferred to consideration of the diagnostic features of *Smilodectes*.

### NOTHARCTUS TENEBROSUS Leidy, 1870

Plate 1, figure 4; plate 2, figure 4; plate 3, figure 3; plate 4, figures 1-3; plate 5, figures 2, 5

*Synonyms.*—*Limnotherium tyrannus* Marsh, 1871.
*Hipposyus formosus* Leidy, 1872.
*Tomitherium rostratum* Cope, 1872.
*Thinolestes anceps* Marsh, 1872.
*Limnotherium affine* Marsh, 1872.
*Notharctus osborni* Granger and Gregory, 1917.
*Notharctus pugnax* Granger and Gregory, 1917.

*Type.*—Right ramus of mandible, with C and $P_2$-$M_3$ inclusive, U.S.N.M. No. 3752.

*Horizon and locality.*—Lower Bridger (B), middle Eocene, Black's Fork, Bridger Basin, Wyoming.

*Discussion.*—A form intermediate in size of teeth between *Smilodectes gracilis* and *Notharctus robustior*. Robinson (1957) has worked out the synonomy of this species and shown that it exhibits consid-

erable range in size with the length of the lower molar series varying from 16.1 to 22.2 millimeters. Because this species grades upward into larger *Notharctus robustior,* it has been arbitrarily limited to the materials from the lower Bridger.

The most nearly complete skull and jaws known, U.S.N.M. No. 21864, collected in 1957, are shown in plate 4. The review of the morphology of the skull of *Notharctus* and revision of our understanding of the characteristics of the genus are based largely on this material, supplemented by the more distorted and incomplete specimen (*N. "osborni"*) described by Gregory. Details of this study are included in the comparison of the skulls of *Notharctus* and *Smilodectes.* It should be noted, however, that U.S.N.M. No. 21864 is somewhat compressed dorsoventrally, and in the view of the left side of the skull the forward portion of the left half of the face has been turned up slightly with respect to the right so that in the view shown the basifacial axis appears less deflected from the basicranial axis and the superior profile rather less convex than it should.

### NOTHARCTUS ROBUSTIOR Leidy, 1872

Plate 5, figures 3, 6, 7

*Synonym.—Telmalestes crassus* Marsh, 1872.

*Type.*—Portion of left ramus of mandible, with $M_2$, U.S.N.M. No. 3750.

*Horizon and locality.*—Upper Bridger (C and D), middle Eocene, Henry's Fork, Bridger Basin, Wyoming.

*Discussion.*—This is the larger species of *Notharctus,* overlapping in size its forerunner, *N. tenebrosus,* hence limited by definition to materials from the upper part of the Bridger formation. The range in length of lower molar series is given by Robinson (1957) as 20.9 to 23.6 millimeters. The known skull material of this species is limited to fragmentary portions, which, so far as I can determine, are characterized principally by increase in size over known material of *N. tenebrosus.* There is, however, as shown in A.M. No. 12567, indication of greater development of the sagittal and lambdoidal crests than in *N. tenebrosus,* and I suspect that the supraorbital margin may be heavier and more turned-up. Moreover, in the upper cheek teeth, the primary outer cusp of $P^4$ is more distinctly divided and the hypocone of $M^1$ and $M^2$ seems relatively better developed. Also, the paraconid, metaconid, and hypoconid of $P_4$ are increasingly more emphasized in upper Bridger material.

Adequate statistical analysis has been made of the size of teeth in *N. robustior* so that, except for the type, no measurements will be given here. $M_2$ in the type specimen measures 7.6 mm. anteroposteriorly by 5.7 mm. transversely across the talonid.

### NOTHARCTUS, species

A *Notharctus* jaw from the upper Huerfano beds in southwestern Colorado was mentioned by Granger and Gregory (1917, pp. 846-847). It was believed by them to represent *Notharctus* rather than *Pelycodus* because of its age and the development of $P_4$ and the talonid of $M_3$. It is not known whether this specimen represents *Notharctus* or *Smilodectes,* although the character of $M_3$ in certain other specimens in later collections suggests the latter genus. The Huerfano fauna is currently under study by Robinson.

Granger (1909) cited the occurrence in the Washakie beds of a species of *Notharctus.* This was not seen by me, but may well be the material referred to by Robinson (p. 14) in giving the range of *Notharctus robustior* as including the Washakie formation (Washakie A) of southwestern Wyoming.

### Genus SMILODECTES Wortman, 1903

*Synonym.—Aphanolemur* Granger and Gregory, 1917.

*Type.—Hyopsodus gracilis* Marsh, 1871.

*Discussion.—Smilodectes* was originally named by Wortman because of a misunderstanding as to the identity of certain of the anterior teeth. Troxell (1926) and Robinson (1957) have concluded that on the basis of the teeth it could not be distinguished generically from *Notharctus.* Several excellent skulls of *Smilodectes gracilis* obtained by Smithsonian Institution parties in the Bridger Basin show clearly that not only is *Smilodectes* a valid genus, but that it is the same as the form described by Granger and Gregory (1917) as *Aphanolemur.* The characteristics of the *Smilodectes* skull have been given in detail in a comparison with *Notharctus* but may be summarized as follows:

The frontals in *Smilodectes* are broad and much inflated and the superior profile in lateral view is evidently more convex than in *Notharctus.* There is little or no sagittal crest and the lambdoidal crest is comparatively weak. The orbits may be a little farther apart in *Smilodectes* and the zygoma is much deeper and heavier posterior to the orbits than in *Notharctus.* The pterygoid fossae are more widely in-

flated and more deeply pocketed and the median ridge on the basisphenoid is more sharply keeled. The audital bullae are distinctly larger and more downwardly protruding than in *Notharctus* and the basioccipital between is narrower and laps down on the bullae to a greater extent.

The teeth are relatively smaller in proportion to the size of skull than in the *Notharctus* material where this relation can be seen, and, as noted by Robinson, the outer cusp of $P^4$ is not twinned and $M^3$ is more rectangular in appearance. The latter feature also more or less characterizes $M^1$ and $M^2$. A particular feature of the lower dentition noted by Robinson is that in $M_3$ of *Smilodectes* the crista obliqua running forward joins the crest between the metaconid and protoconid at a point about midway, or extends actually to the metaconid. This is much as in $M_2$. However, in *Notharctus* the crista obliqua in $M_3$, after a sharp flexure, turns outward and joins the protoconid instead. I have examined all the Lost Cabin *Notharctus* material to which I have had access and found that apparently none shows the *Smilodectes* condition. Almost none of the *Pelycodus* specimens in the National Museum, Princeton, or American Museum is suggestive of *Smilodectes* except certain specimens where it is suspected that stage of wear has created the illusion by the eroding away of the portion of the hypoconid crest nearest the protoconid.

### SMILODECTES GRACILIS (Marsh), 1871

Plate 1, figures 1-3, 5, 6; plate 2, figures 1-3, 5; plate 3, figures 1, 2; plate 5, figures 1, 4

*Synonyms.*—*Pelycodus relictus* Gregory, 1917 (see Robinson, 1957).

*Notharctus matthewi* Granger and Gregory, 1917.

*Aphanolemur gibbosus* Granger and Gregory, 1917.

*Type.*—Left ramus of mandible with $P_4$, $M_1$, and part of $P_3$, Y.P.M. No. 11800.

*Horizon and locality.*—Lower Bridger (B), middle Eocene, Grizzly Buttes, Bridger Basin, Wyoming.

*Discussion.*—The synonymy of species under *Smilodectes gracilis* is essentially as indicated by Troxell (1926) and Robinson (1957), except for the addition of *Aphanolemur gibbosus*. The identity of *Aphanolemur gibbosus* to *Smilodectes gracilis* could not, of course, be determined until sufficiently complete material was discovered to demonstrate, as in plates 1 and 2, that the skull of *"Aphanolemur gibbosus"* had the teeth of *Smilodectes gracilis*. Inasmuch as but one

species is known, no attempt is made to distinguish between generic and specific characters except to note that *Smilodectes gracilis,* though having a skull with proportions as large as or larger than some mature specimens of *Notharctus tenebrosus,* has teeth rather consistently smaller. Moreover, Robinson (1957) has indicated that this species is apparently not confined to the lower Bridger but ranges through Bridger B, C, and D. Its presence in the upper Bridger has not been verified in the extensive Bridger collections of the National Museum. It is well represented by jaw fragments and isolated teeth in the Green River collection from the Bridger equivalent near Powder Springs in the Uinta Basin.

## Family OMOMYIDAE, new name

The family Omomyidae is proposed to include a group of closely related genera composed approximately as intended by Wortman (1903) for the subfamily Omomyinae, with important differences, however, from Wortman's definition. It includes various phyletic lines and a now imposing number of known genera. In addition to *Omomys, Hemiacodon* and *Washakius* of the Bridger, and the new genus *Utahia* from the upper fossiliferous zone of the Green River, embraced in this family, are the earlier forms *Shoshonius, Loveina,* and the new genus *Chlororhysis* from the upper part of the lower Eocene, and possibly *Navajovius* from the upper or Tiffanian Paleocene, although I am more inclined to regard the latter as an anaptomorphid. The later genera include *Chumashius, Dyseolemur,* and the two new genera *Ourayia* and *Stockia* of the upper Eocene, and the lower Oligocene *Macrotarsius.*

The genera are somewhat more primitive or generalized than the anaptomorphids, and in this way occupy a position away from the anaptomorphids toward the notharctids. The dental formula, as far as can be determined or surmised, is probably $I\frac{2}{2}$, $C\frac{1}{1}$, $P\frac{3}{3}$, $M\frac{3}{3}$, although there is very little known in the case of certain of the genera. In *Navajovius* the number of teeth is almost certainly less.

The upper dentition for several genera is not known but in the more abundantly represented Bridger forms, particularly *Hemiacodon,* maxillary portions are not uncommon. The canine, as interpreted, has a moderately large root, but apparently a low crown (*Hemiacodon*). Only the third and fourth of the premolar series have three roots. $P^4$, and to a more limited extent, $P^3$, in the middle Eocene genera show a tendency toward development of a posterointernal

basin. The molars show in general a simple three-cusped arrangement transversely elongate and with a large protocone. The protocone may be essentially conical as in *Washakius* and *Hemiacodon* to more decidedly crescentic as in *Omomys*. Accessory cuspules, protoconule and metaconule, are weak (*Omomys*) to conspicuously developed (*Hemiacodon*), and the metaconule may be double (*Washakius*) or ridgelike (*Dyseolemur*). A cingulum is generally prominent lingually with a tendency toward the development of anterointernal and posterointernal cuspules. There is no external mesostyle in most forms, but it is present in *Shoshonius* and may be incipient in some material of *Washakius*.

In the lower dentition there is a tendency in some of the genera toward moderate enlargement of an anterior tooth, here interpreted as the anterior of two incisors, at the expense of the posterior or more lateral of the two. The incisor in these cases evidently does not grow from persistent pulp and has the enamel restricted to a crown portion. The lower canine is present and generally has a somewhat larger and more rounded root than $P_2$. The crown of the canine, as shown in *Hemiacodon,* and as seems probable in *Omomys* and unlike *Notharctus,* may be moderately low and rather premolarlike in form and, as in the case of $P_2$, lap forward partially over the position of the preceding tooth. Only the third and fourth lower premolars are two rooted and $P_4$, and to a less extent $P_3$, shows a tendency, as in the notharctids, toward increasing importance of the primary cusps of the trigonid and talonid. In the anaptomorphids, on the other hand, the tendencies are toward simplification, crowding and sometimes enlargement of $P_4$. The omomyid lower molars generally show a primitive tricuspid arrangement on the trigonid, although the paraconid in some forms may be reduced or obscure. The talonids are broadly basined. The anaptomorphid molar structure, as these genera are retained together, is rather diversified, but in more typical forms shows somewhat more inflated cusps, unreduced trigonids, and shallower, less expanded talonid basins.

### Genus OMOMYS Leidy, 1869

*Synonyms.—Euryacodon* Marsh, 1872.
*Palaeacodon* Marsh (not Leidy), 1872.

*Type.—Omomys carteri* Leidy, 1869.

*Discussion.*—Wortman (1904) has shown that the upper teeth described by Marsh as *Palaeacodon* are actually those of *Omomys;* there now seems no doubt of this. Wortman, however, considered

*Euryacodon* as a valid genus, characterized by a small cingular cuspule lingual to the protocone of the upper molars. Among the rather numerous partial dentitions of *Omomys* available to me in the National Museum, Yale, and Carnegie Museum collections, several are uppers which show that the development of an anterolingual cuspule on the molars is quite variable (see pl. 6) and that no systematic separation can be made. There seem, moreover, to be no other characters that might be used to separate the *Euryacodon* from the *Palaeacodon* type teeth, so that there can be little doubt but that *Euryacodon* as well as *Palaeacodon* is a synonym of *Omomys*. It should be noted, also, that Wortman tentatively referred some lower jaws to *"Euryacodon"* that he realized showed a resemblance to *Anaptomorphus* in molar structure. His suggestion that *Anaptomorphus* might be a synonym of *Euryacodon* was accepted by Matthew (1915, p. 457) and Simpson (1940, p. 198). There seems no doubt that the lower jaws referred by Wortman to *Euryacodon lepidus* are actually of *Anaptomorphus* and their reference to *"Euryacodon"* was unfortunate. As noted by Wortman, the teeth in these jaws are quite unlike *Omomys*.

Among the omomyids, *Omomys* exhibits the least specialized premolars and molars. The upper premolars show a well-defined deuterocone, and through development of the cingulum, a weak posterointernal basin. The upper molars exhibit a continuous cingulum around the lingual portion of the tooth with variable development of a hypocone and an anterolingual cusp. The protoconule and metaconule are weak and there is no mesostyle. The teeth anterior to $P^3$ are not certainly known.

The lower jaw of *Omomys* is long and slender and the anterior teeth show a distinct specialization, more marked than in other Bridger omomyids, in which the anterior tooth, interpreted as the anterior of two incisors, is noticeably enlarged. The enlargement, however, is not comparable to that seen in the apatemyids. The second incisor, as shown by the alveolus for its root, is much reduced and the root is anteroposteriorly compressed. The following alveolus, believed to be that for the canine, is rounded, faces more nearly vertically and is a little larger than that for the small, single-rooted $P_2$. $P_3$ and $P_4$ are two rooted and anteroposteriorly elongate. $P_4$, and sometimes $P_3$, shows a weak anterior crest joining an anterointernal cingulum. $P_3$ lacks a distinct paraconid or metaconid but there is a short talonid that on some specimens exhibits one or two incipient cusps. On $P_4$ the trigonid portion is anteroposteriorly elongate but the paraconid may not

be distinct and there is no cusp midway on the anterior crest as in *Hemiacodon*. The metaconid is usually distinct and well defined, but may be weak. The talonid is short, but a small hypoconid and entoconid are commonly noted, sometimes only a hypoconid. The trigonids of the lower molars show a simple three-cusped arrangement with the paraconid conical and present on all three teeth, more distinctly lingual in $M_1$, but nearly lingual in $M_2$ and $M_3$. The molar talonids are elongate and broadly basined. $M_3$ is a little smaller than $M_2$.

### OMOMYS CARTERI Leidy, 1869

Plate 6, figures 1-7; plate 7, figures 2-6

*Synonyms.*—*Hemiacodon nanus* Marsh, 1872.
*Hemiacodon pucillus* Marsh, 1872.
*Euryacodon lepidus* Marsh, 1872.
*Palaeacodon vagus* Marsh, 1872.

*Type.*—Right ramus of mandible with $P_3$, $P_4$, and $M_2$, A.N.S. No. 10335. Among the original materials described by Leidy as representing *Omomys carteri* are, in addition to the lower jaw, the top portion of a skull and a fragment of an exoccipital. These were sent by Dr. J. Van A. Carter to Dr. Leidy in two lots, the jaw at a later time but from the same locality, and were believed by Leidy to be from one individual. The top of the cranium is of a slender, elongate skull and does not look like a primate. Detailed comparison with skull material of a number of small contemporary Bridger forms shows beyond doubt that the frontoparietal portion, and probably also the exoccipital piece, are of *Hyopsodus*. Although Leidy discussed the cranial fragment first, fortunately no further mention seems to have been made of this specimen by others, so that the lower jaw is clearly the type by subsequent designation.

*Horizon and locality.*—Lower Bridger (B), middle Eocene, vicinity of Fort Bridger, Bridger Basin, Wyoming.

*Discussion.*—*Omomys carteri* is represented by over 90 specimens in Bridger collections (cited in order of abundance) of Yale Peabody Museum, U. S. National Museum, and American Museum. Approximately 15 Green River specimens having more than one tooth were observed in the Carnegie Museum collections, in addition to numerous isolated teeth. It is a small form, compared in size by Leidy with the tree shrew, *Tupaia ferruginea,* of Java and neighboring islands. Wort-

man placed *Hemiacodon nanus* as well as *Palaeacodon vagus* in synonymy with *Omomys carteri,* but in addition to regarding *Euryacodon lepidus* as generically distinct from *Omomys carteri* he considered *Hemiacodon pucillus* as a distinct and valid species of *Omomys.* Moreover, he described as new the species *Omomys ameghini.*

In reviewing the various types involved, I find that *Omomys ameghini* properly belongs with *Uintanius turriculorum* and, as Wortman's is the older name, *ameghini* replaces *turriculorum* as the type of *Uintanius.* Of the species synonymized with *Omomys carteri, Hemiacodon nanus* is a large individual of *O. carteri,* and the species *Euryacodon lepidus* and *Palaeacodon vagus* are clearly the upper teeth of *O. carteri.* There remains *O. pucillus* which Wortman considered valid. Except for size, the characters cited are not distinctive. The form of the trigonid of the only preserved molar in the type of *O. pucillus* clearly shows that it is $M_2$. I have measured all the available Bridger specimens of *Omomys* in which this tooth is preserved and find that no reasonable separation on the basis of size can be made. Listed below are the figures indicating the frequency distribution for the length and width of $M_2$ in 64 Bridger specimens:

| Length | f. | | Width | f. | |
|---|---|---|---|---|---|
| 2.3 | 2 | (*O. pucillus*) | 1.9 | 2 | |
| 2.4 | 8 | | 2.0 | 20 | (*O. pucillus*) |
| 2.5 | 13 | | 2.1 | 12 | |
| 2.6 | 28 | (*O. carteri*) | 2.2 | 17 | (*O. carteri*) |
| 2.7 | 10 | | 2.3 | 6 | (*O. nanus*) |
| 2.8 | 3 | (*O. nanus*) | 2.4 | 3 | |

The three types based on lower jaws are indicated in their respective size groups. The data for length of the second molar would produce a simple curve with but a single node. *O. pucillus* and *O. nanus* fall at the extremes and *O. carteri* near the mean. For width such a curve would appear bimodal but the apices are only .2 mm. apart and certainly of no taxonomic significance.

With length of $M_2$ in the Bridger material as the variate, the following statistical information has been calculated:

| | | |
|---|---|---|
| N = 64 | OR = 2.3-2.8 | M = 2.57 |
| $\sigma$ = .112 | V = 4.35 | |

The coefficient of variability would appear to be a reasonable figure for a single species.

MEASUREMENTS IN MILLIMETERS OF *Omomys carteri* DENTITIONS

| | Y.P.M. No. 13228-1 | A.M. No. 12041 | Y.P.M. No. 11854* |
|---|---|---|---|
| Length of upper cheek tooth series, $P^3$-$M^3$, inclusive | 10.7 | 11.1[e] | |
| Length of upper molar series, $M^1$-$M^3$, inclusive. | 6.7 | 7.0[e] | 7.0 |
| $P^3$, Length along outer wall : width perpendicular to outer wall | 2.3 : 2.2 | 2.4 : 2.6 | |
| $P^4$, Length along outer wall : width perpendicular to outer wall | 2.2 : 2.6 | 2.2 : 3.0 | |
| $M^1$, Length along outer wall : width transversely. | 2.5 : 3.2 | 2.5 : 3.4 | 2.5 : 3.6 |
| $M^2$, Length along outer wall : width transversely. | 2.5 : 3.4 | 2.5 : 3.6 | 2.5 : 3.8 |
| $M^3$, Length along outer wall : width transversely. | 2.0 : | | 2.1 : 3.4 |

| | A.N.S. No. 10335 Type | U.S.N.M. No. 17783 | U.S.N.M. No. 13289 |
|---|---|---|---|
| Length of lower cheek tooth series, $P_3$-$M_3$, inclusive | 12.4[e] | 11.9 | 11.7 |
| Length of lower molar series, $M_1$-$M_3$, inclusive. | 8.0[e] | 7.6 | 7.9 |
| $P_3$, Length : greatest width | 2.6 : 1.7 | 2.4 : 1.6 | 2.2 : 1.5 |
| $P_4$, Length : greatest width | 2.6 : 1.8 | 2.5 : 1.7 | 2.4 : 1.6 |
| $M_1$, Length : greatest width | | 2.6 : 1.9 | 2.7 : 2.0 |
| $M_2$, Length : greatest width | 2.6 : 2.2 | 2.5 : 2.0 | 2.7 : 2.0 |
| $M_3$, Length : greatest width | | 2.7 : 1.8 | 2.8 : 1.7 |

* Type of *Palaeacodon vagus* Marsh.
[e] Estimated.

### OMOMYS LLOYDI,[12] new species

Plate 14, figure 6

*Type.*—Left ramus of mandible with $P_4$-$M_2$, C.M. No. 6417.

*Horizon and locality.*—Lower(?) Bridger equivalent or "Upper Fossiliferous Zone" of the Green River formation, about 2 miles SE. of Powder Springs, sec. 8, T. 7 S., R. 25 E., Uinta Basin, Uintah County, Utah.

*Specific characters.*—Size of teeth smaller than in *Omomys carteri* and $M_3$ relatively smaller.

*Discussion.*—In the Green River collection a somewhat different frequency distribution for size of teeth is noted than in the Bridger materials. There is a noticeable bimodality for the length of $M_2$, as well as for the width. Moreover, the observed range in length of $M_2$ is greater although not nearly so many individuals were measured. The

[12] Named for S. C. Lloyd, Jr., who assisted Dr. J. LeRoy Kay in the collecting of the Green River materials.

frequency distribution for length and width of $M_2$ in *Omomys* of the Green River collection is shown below:

| Length | f. | Width | f. |
|---|---|---|---|
| 2.1 | 1 | 1.7 | 2 |
| 2.2 | 4 | 1.8 | 4 |
| 2.3 | 1 | 1.9 | 3 |
| 2.4 | 0 | 2.0 | 6 |
| 2.5 | 5 | 2.1 | 7 |
| 2.6 | 7 | 2.2 | 3 |
| 2.7 | 6 | | |
| 2.8 | 1 | | |

With length of $M_2$ in the Green River material as the variate, the following statistical information was calculated:

$N = 25$ OR = 2.1-2.8 M = 2.52
$\sigma = .195$ V = 7.73

The coefficient of variability appears rather high in comparison with 4.35 obtained for the Bridger material, suggesting that the sample is not homogeneous even though, unlike the Bridger material, all specimens were obtained from a single quarry. The evidence, while not alone conclusive, when combined with the indication for a relatively shorter talonid of the third molar in the smaller group of specimens, suggests the presence of a second species.[13] It was noted, moreover, that the ratio of width to length of the second molar has a greater average value in the smaller than in the larger specimens. The group of larger specimens is, of course, referred to *Omomys carteri.*

The coefficient of variability calculated for the two size groups separately was found to be 3.36 for the Green River material referred to *O. carteri* and 2.62 for that recognized as *O. lloydi.* That for *O. lloydi* is probably too low.

While the size of $M_2$ in the material of *Omomys lloydi* is only a little less than in the type of *Omomys pucillus,* the latter name cannot logically be used because the type is a specimen which almost certainly represents *O. carteri* in the Bridger population.

MEASUREMENTS IN MILLIMETERS OF LOWER DENTITIONS OF *Omomys lloydi*

| | C.M. No. 6417 Type | C.M. No. 6418 | C.M. No. 6420 |
|---|---|---|---|
| $P_4$, Length : width | 2.1 : 1.6 | | |
| $M_1$, Length : width | 2.2 : 1.7 | | |
| $M_2$, Length : width | 2.3 : 1.8 | 2.2 : 1.8 | 2.1 : 1.7 |
| $M_3$, Length : width | | 2.2 : 1.4 | 2.3 : 1.5 |

[13] Not a subspecies, as this would be untenable, coming from the same horizon and quarry.

### Genus HEMIACODON Marsh, 1872

*Type.—Hemiacodon gracilis* Marsh, 1872.

*Discussion.—Hemiacodon* is without doubt rather closely related to *Omomys* but with specialization somewhat divergent from that genus. The teeth in general have a more rugged or less delicate appearance, with rugose enamel and a distinct tendency toward development of accessory cuspules. The third and fourth upper premolars are like *Omomys,* but with a broader development of a posterointernal basin. In the molars the protocone, in addition to its wrinkled appearance, sometimes shows development of a broad angulation posteriorly, as a blunt *Nannopithex*-fold separated from the cingulum. Anterointernally, a somewhat more acute angulation may join the cingulum, or there may be an anterointernal cuspule arising from the generally serrated cingulum. Just as in *Omomys,* the anterointernal cuspule is not invariable. A hypocone arises from the cingulum posterointernally and is normally present in the first and second molars. Because of the more persistent and relatively greater development of the hypocone these molars have, as do the premolars, a more rectangular appearance than in *Omomys.* $M^3$, however is distinctly triangular, and a little smaller than $M^2$, but does not appear so slender as in *Omomys.* In the absence of a mesostyle *Hemiacodon* resembles *Omomys,* but the paracone and metacone appear more sharply or deeply separated and the protoconule and metaconule are more prominently developed.

In the anterior part of the lower jaw the anterior incisor is enlarged, but relatively a little less so than in *Omomys,* and the second incisor, though smaller than the first, is less reduced than in the latter genus. The canine, if properly identified, has a rounded but larger root than $P_2$ with a distinctly premolarlike crown, perhaps a little more robust, that overlaps the tooth ahead just as does $P_2$. $P_2$, though single rooted, has a crown resembling that of $P_3$, distinctly longer than broad, and exhibits, just as does the canine, a weak transverse talonid crest. $P_3$ is two rooted, the posterior root being the heaviest as in *Omomys,* but the crown is broader and the single cusp is not so high. There is an anterior crest, however, as in *Omomys* which joins an anterolingual cingulum but with a slight or no parastylid. $P_3$ shows no metaconid but the posterior crests extend from the primary cusp to near the posterointernal and posteroexternal angles of the tooth. An anteroposteriorly much-abbreviated talonid shows a sharp transverse crest that may exhibit a very small hypoconid and possibly a minute entoconid. $P_4$ appears relatively a little broader than in

*Omomys* and has a higher, better developed metaconid. The anterior crest is acute and joins the anterointernal cingulum at a point where there may be a slight paraconid. Unlike *Omomys,* part way up this crest, a little above the position of a paraconid, there is a well-developed cuspule, giving the trigonid portion a more molariform appearance. The talonid is anteroposteriorly brief as in *Omomys* but the transverse crest is stronger, with better evidence of the internal and external cusps than in $P_3$. The lower molars have a pattern similar in a general way to that seen in *Omomys,* but they exhibit, in addition to a more wrinkled enamel, cusps that are relatively higher and most distinctly separated from one another, and possibly a heavier external cingulum. In the trigonid there is a more deeply impressed basin and prominent folds of the principal cusps extend into it. The paraconid, moreover, is a little less lingual in position, particularly in $M_3$ where it is almost in the middle of the anterior margin. The talonid basin is deep and perhaps relatively a little shorter and broader, with the hypoconid and entoconid set well back and the crests of the hypoconid forming a more acute angle than in *Omomys.* The hypoconulid, moreover, is well defined in $M_1$ and $M_2$ of *Hemiacodon,* whereas it is scarcely or not at all evident in *Omomys.*

The characters of certain vertebrae and of pelvic, limb, and foot material believed to represent *Hemiacodon* were described by Simpson (1940), with the conclusion that they appeared to be rather more lemuroid than tarsioid. A skull portion, found by me in Bridger C of upper Sage Creek includes almost the entire upper surface of the frontals (see pl. 4, fig. 4) in addition to both maxillae and part of the left ramus of the mandible. The frontal area is very broad between the postorbital processes, and is slightly depressed on both sides of the midline. The orbits are very large and the superior margin is turned up as far forward as the point where the orbital margins most closely approach each other. At this position, near the posterior limit of the nasals, the orbits are separated on the surface of the rostrum by 8.2 mm. Resemblance is seen to the frontal area of *Notharctus* (not *Smilodectes*), but the orbits by comparison seem relatively larger and closer together.

### HEMIACODON GRACILIS Marsh, 1872

Plate 4, figure 4; plate 8

*Type.*—Right ramus of mandible with $P_3$-$M_3$, inclusive, Y.P.M. No. 11806.

*Horizon and locality.*—Upper Bridger (C or D), middle Eocene, Henry's Fork, Bridger Basin, Wyoming.

*Discussion.*—Over 160 specimens of this species are known. Many of them are in the Marsh collection, but nearly half are included in the more recently collected and better documented Bridger materials in the National Museum. All those for which horizon information is available are from the upper Bridger, or horizons C and D. Variation in size is noted, as well as degree of enamel rugosity; nevertheless, I was unable to recognize any criteria by which a second or more species might be defined. Those named by Marsh, i.e., *Hemiacodon nanus* and *Hemiacodon pucillus,* have been found to represent *Omomys carteri,* and Wortman's *Hemiacodon pygmaeus* is a synonym of *Washakius insignis.*

Listed below are the measurements of $M_2$ in millimeters for 85 specimens of *Hemiacodon gracilis*—all those at hand in which this tooth is preserved. These are arranged to show frequency for length and width.

| Length | f. | Width | f. |
|---|---|---|---|
| 3.4 | 1 | 2.8 | 6 |
| 3.5 | 1 | 2.9 | 8 |
| 3.6 | 8 | 3.0 | 29 (type) |
| 3.7 | 16 (type) | 3.1 | 27 |
| 3.8 | 22 | 3.2 | 11 |
| 3.9 | 22 | 3.3 | 3 |
| 4.0 | 12 | 3.4 | 1 |
| 4.1 | 2 | | |
| 4.2 | 1 | | |

The above indications for only one species seem almost too perfect. Nevertheless, measurements were made of the specimens as they were encountered in the collections, with the calipers measuring from the anterior margin of the paraconid to the posterior surface of the tooth lingually for length, and at the cingulum of the talonid for width. Further analysis of the data for length of $M_2$ is given below:

$N = 85$ OR = 3.4-4.2 $M = 3.81$
$\sigma = .142$ $V = 3.75$

MEASUREMENTS IN MILLIMETERS OF *Hemiacodon gracilis* DENTITIONS

| | U.S.N.M. No. 21878 | U.S.N.M. No. 17730 | Y.P.M. No. 12976-2 |
|---|---|---|---|
| Length of upper cheek tooth series, $P^3$-$M^3$, inclusive | 14.8 | | |
| Length of upper molar series, $M^1$-$M^3$, inclusive. | 9.7 | 9.5 | 9.9 |
| C, Anteroposterior diameter at cingulum | 1.8 | | |
| $P^3$, Length along outer wall: width perpendicular to outer wall | 3.5 : 3.4 | | |
| $P^4$, Length along outer wall: width perpendicular to outer wall | 3.0 : 3.8 | 2.9 : 3.7 | 2.9 : 3.7 |
| $M^1$, Length along outer wall: width perpendicular to outer wall | 3.7 : 5.0 | 3.7 : 4.6 | 3.8 : 4.8 |
| $M^2$, Length along outer wall: width perpendicular to outer wall | 3.4 : 5.2 | 3.5 : 4.9 | 3.5 : 5.0 |
| $M^3$, Length along outer wall: width perpendicular to outer wall | 3.0 : 4.2 | 2.8 : 3.9 | 3.0 : 4.3 |

| | Y.P.M. No. 11806 Type | A.M. No. 18991 | U.S.N.M. No. 17778 |
|---|---|---|---|
| Length of lower cheek tooth series, $P_3$-$M_3$, inclusive | 16.4 | 15.7 | 15.3[e] |
| Length of lower molar series, $M_1$-$M_3$, inclusive. | 11.0 | 11.3 | 10.4 |
| $P_3$, Length: greatest width | 2.8 : 2.1 | 2.8 : 2.0 | |
| $P_4$, Length: greatest width | 3.2 : 2.2 | 3.2 : 2.4 | 3.0 : 2.3 |
| $M_1$, Length: greatest width | 3.8 : 3.0 | 4.0 : 3.0 | 3.7 : 2.9 |
| $M_2$, Length: greatest width | 3.7 : 3.0 | 4.0 : 3.0 | 3.6 : 2.8 |
| $M_3$, Length: greatest width | 3.9 : 2.4 | 4.3 : 2.7 | 2.8 : 2.4 |

[e] Estimated.

### Genus WASHAKIUS Leidy, 1873

*Synonym.*—*Yumanius* Stock, 1938.

*Type.*—*Washakius insignis* Leidy, 1873.

*Discussion.*—Although characterized by a rather distinctive molar structure in comparison with *Omomys,* there would appear to be little doubt that *Washakius* is an omomyid. *Washakius,* in the rugosity of the tooth enamel and development of accessory cuspules, resembles *Hemiacodon,* but has developed peculiarities, such as the double metaconule on the upper molars and a metastylid on the lowers, that particularly characterize the genus. On the other hand, the lower incisors are less differentiated from one another than they are in either *Omomys* or *Hemiacodon.*

Wortman believed that there were two upper incisors in *Washakius.* This is probably true, although I have been unable to find material

sufficiently complete to verify it. The specimen described by Wortman (pl. 9, fig. 1) shows evidence of a small incisor, but is not complete enough to include a more anteromedial alveolus. The alveoli for the canine and $P^2$ appear subequal and moderately large; that for $P^2$ is relatively broad transversely. $P^3$ and $P^4$ are three rooted, essentially bicuspid but with a small parastyle anteroexternally and a rather well-developed cingulum posterointernally as well as buccally. On $P^4$ of the material at hand the posterointernal cingulum shows a small tetartocone or hypocone, although the posterointernal basin is not as prominent as in *Hemiacodon*. The upper molars of *Washakius* are transversely elongate as in *Omomys,* but differ in form most noticeably in the more conical protocone. In *Omomys* the protocone is distinctly more crescentic with the cusp less clearly defined. The protoconule and metaconule are better developed than in *Omomys,* but possibly less conspicuously so than in *Hemiacodon*. There is, moreover, the "second metaconule" of somewhat smaller size on the posteroexternal slope of the protocone, slightly crescentic in form, and evidently developed from the enamel rugosity. It corresponds to the position of a weak crest from the protocone in *Hemiacodon*. Anterolingually there may be a slight cuspule, although not always, whereas the small hypocone on the posterolingual portion of the cingulum is evidently present invariably, except in $M^3$. As noted by Wortman, $M^3$ is about the size of $M^1$. It has a posterointernal basin of moderate size, generally very rugose, but with no clearly defined hypocone. This tooth is distinctly less slender than in *Omomys*.

Wortman thought that there was only one lower incisor in *Washakius* but more than one specimen now clearly shows that there were two. They were small, evidently equal, and relatively erect. In this respect *Washakius* is less specialized than either *Omomys* or *Hemiacodon*. The lower canine alveolus has perhaps a little more than twice the diameter of one of the incisor alveoli, and though more circular in outline, may not be much wider than that for $P_2$. As in *Omomys* and *Hemiacodon,* $P_2$ laps forward over the position of the canine, so that the crown of the canine was low and in all probability rather premolarlike in form, as appears in *Hemiacodon*. The lower premolars of *Washakius* are relatively a little shorter and broader than in *Omomys* or even than in *Hemiacodon*. $P_2$ appears relatively less reduced in size, in comparison with $P_3$, than in *Hemiacodon,* so that there is a more uniform increase from $P_2$ to $P_4$. Moreover, $P_2$ has very much the form of the following premolars. $P_2$, $P_3$, and $P_4$ show emphasized anterolingual and posterolingual crests from the primary

cusp, and a bifurcated posteroexternal crest. Only in $P_4$, however, are the paraconid and metaconid clearly defined. The shortness of the premolars is effected in part by the more medially directed anterior crest, in which respect *Hemiacodon* is intermediate between *Omomys* and *Washakius*. The paraconid of $P_4$ is at the anteromedial extremity of this crest and there is no cuspule midway on it as in *Hemiacodon*. The talonid of the premolars is scarcely more than a crest of the posterior cingulum, best developed in $P_4$. A small hypoconid was noted on both $P_3$ and $P_4$ of one specimen, located on the posterior crest at the point where it is joined by the medial of the two bifurcations of the posteroexternal crest. More rarely a very small entoconid may be seen on $P_4$. The most characteristic feature of the lower molars is the presence on all of a metastylid about halfway up the posterolingual slope of the metaconid. The paraconid is placed well forward so that the trigonid is a little longer, anteroposteriorly, and the talonid (except for $M_3$) a little shorter than in *Omomys*. Moreover, the paraconid is a little less lingually placed and the crest between the paraconid and protoconid is more nearly straight, not so convex forward as in *Omomys*. The cusps of the talonid, as in *Hemiacodon,* are more sharply defined than in *Omomys,* but the basin is less broadly excavated than in either and opens lingually between the metaconid and entoconid. The crest extending anteromedially from the hypoconid shows a characteristic flexure, developing a pocket on its medial side near the hypoconid, not seen in other Bridger genera. The hypoconulid, moreover, may in some instances be closer to the entoconid than it is to the hypoconid, but rather sharply separated from it, somewhat reminiscent of mixodectids. $M_3$ is not reduced in size and exhibits a relatively larger and more complex hypoconulid portion than in either *Omomys* or *Hemiacodon*.

I know of no skeletal material other than jaws and maxillary portions; however, it may be noted that the orbit of *Washakius* is relatively large, to judge by the maxillary portion whose teeth are figured in plate 9, figure 1. Also, as Wortman observed in this specimen, the malar did not reach the lachrymal, as it does, for example, in *Smilodectes*. Moreover, the anterior part of the lower jaw shows a greater deflection medially toward the plane of the suture so that the rami, as paired, would show the teeth in a somewhat more U-shaped plan than in *Omomys*. In *Omomys* the dental rows are more V-shaped.

The genus *Yumanius,* I find, is too close to *Washakius* and *Dyseolemur* to be defended as valid. The material representing it came from sandy lenses of lower Uintan age in the Poway conglomerate of

southern California. Unfortunately the specimen designated as the type for *Yumanius woodringi* was the partial upper dentition which Stock compared with *"Euryacodon"* (=*Omomys*) rather than *Washakius*. Possibly he did not see upper teeth of the latter. In any case the lower teeth upon which much of the discussion of relationships was based cannot possibly represent the same genus. Teeth of the lower jaws are in no way comparable either in size or form to that expected for proper occlusion with the uppers. They represent a genus clearly distinct, which in this report has been named *Stockia*. The upper teeth of *Yumanius* are in some ways about intermediate between *Washakius* and *Dyseolemur*. They show a somewhat more elongate lingual slope of the protocone, approaching *Dyseolemur*, but clearly retain the second metaconule, close to the protocone, of *Washakius*. They could be referred with no difficulty to either *Washakius* or *Dyseolemur*, but I prefer *Washakius*, partly on the evidence presented by the second metaconule and the somewhat less elongate appearance of the lingual slope of the protocone, although geographic distribution might weigh somewhat against this solution. They are, nevertheless, intermediate in time and surely a third genus is not warranted.

### WASHAKIUS INSIGNIS Leidy, 1873

Plate 9

*Synonym.*—*Hemiacodon pygmaeus* Wortman, 1904.

*Type.*—Portion of right ramus of mandible with $M_2$ and $M_3$, A.N.S. No. 10332.

*Horizon and locality.*—Bridger formation, middle Eocene, Bridger Basin, Wyoming.

*Discussion.*—Approximately 32 specimens of *Washakius insignis* were examined. The species is clearly not restricted to the upper Bridger, although Matthew (1909b, p. 298) had so indicated. Among the five specimens observed in the American Museum collections, one each were from horizons B and D, and the other three from C. Four of the 14 in the collections of the National Museum are from low in B, not far from the confluence of Black's Fork and Smith's Fork. Specimens in the Marsh collection, so far as locality data are available, came from the Black's Fork, Church Buttes, and Dry Creek, so there can be no doubt of its occurrence in Bridger B. The horizon of the Bridger represented by the type specimen is in doubt. It was given to Dr. Carter by a Shoshone Indian and then sent on to Leidy. I have been able to locate only one specimen, A.M. No. 12039, which appears certain to have come from horizon D.

The upper molar described by Wortman as *Hemiacodon pygmaeus* differs in no way diagnostically that I can see from $M^2$ in the upper dentition of *Washakius insignis* that Wortman figured. It may perhaps be a trifle more slender medially. The high sharp cusps are due to its completely unworn condition. The anterolingual cuspule is variable in *Washakius* but usually suppressed. The tooth measures 2.2 mm. long by 3.4 mm. wide transversely.

The lower teeth of *Washakius insignis* are a little smaller than in *Omomys carteri* but with about the same depth of jaw. A rather noticeable variation in size of teeth was observed, but evidently not more than would be included in a single species. The type specimen, incidentally, has teeth rather near the lower limit of the observed size range. I have been able to obtain measurements of $M_2$ in 21 specimens of *Washakius insignis,* and these are listed below to show frequence of occurrence.

| Length | f. | Width | f. |
|---|---|---|---|
| 2.3 | 1 (type) | 1.8 | 4 (type) |
| 2.4 | 2 | 1.9 | 11 |
| 2.5 | 9 | 2.0 | 4 |
| 2.6 | 5 | 2.1 | 2 |
| 2.7 | 1 | | |
| 2.8 | 2 | | |
| 2.9 | 1 | | |

The following information is derived from the data for length of $M_2$:

$M = 2.56$ $\sigma = .14$ $V = 5.47$

It seems unlikely that more than a single species is represented, where size is the only criterion.

MEASUREMENTS IN MILLIMETERS OF *Washakius insignis* DENTITIONS

| | Y.P.M. No. 13235-4 | U.S.N.M. No. 17795 | Y.P.M. No. 13235-2 |
|---|---|---|---|
| Length of upper cheek tooth series, $P^3$-$M^3$, inclusive | 9.9 | | |
| Length of upper molar series, $M^1$-$M^3$, inclusive. | 6.4 | | |
| $P^3$, Length along outer wall: width perpendicular to outer wall | 2.0 : 2.5 | | |
| $P^4$, Length along outer wall: width perpendicular to outer wall | 2.1 : 2.7 | 2.0 : 2.4 | |
| $M^1$, Length along outer wall: width perpendicular to outer wall | 2.3 : 3.2 | 2.3 : 2.8 | |
| $M^2$, Length along outer wall: width perpendicular to outer wall | 2.2 : 3.5 | 2.2 : 3.1 | 2.1 : 3.2 |
| $M^3$, Length along outer wall: width perpendicular to outer wall | 2.0 : 3.0 | | 2.1 : 2.9 |

| | U.S.N.M. No. 21879 | U.S.N.M. No. 18013 | Y.P.M. No. 13235-2 |
|---|---|---|---|
| Length of lower cheek tooth series, $P_3$-$M_3$, inclusive | | 11.0 | |
| Length of lower premolar series, $P_2$-$P_4$, inclusive | 4.5 | | |
| Length of lower molar series, $M_1$-$M_3$, inclusive. | | 7.9 | 7.6 |
| $P_2$, Length : greatest width | 1.4 : 1.3 | | |
| $P_3$, Length : greatest width | 1.7 : 1.5 | 1.8 : 1.4 | |
| $P_4$, Length : greatest width | 2.1 : 1.7 | 2.0 : 1.6 | 2.0 : 1.8 |
| $M_1$, Length : greatest width | 2.5 : 1.8 | 2.4 : 1.7 | 2.4 : 1.8 |

| | A.N.S. No. 10332 Type | | |
|---|---|---|---|
| $M_2$, Length : greatest width | 2.3 : 1.8 | 2.7 : 2.0 | 2.5 : 1.9 |
| $M_3$, Length : greatest width | 3.2[a] : 1.9 | 3.5 : 2.0 | 3.3 : 1.9 |

[a] Approximate.

### WASHAKIUS WOODRINGI (Stock), 1938

Plate 13, figure 7

*Type.*—Right maxillary fragment with $M^1$ and $M^2$, L.A.C.M. (C.I.T.) No. 2233.

*Horizon and locality.*—White sandstones associated with the Poway conglomerate, lower Uintan upper Eocene, near San Diego Mission, San Diego County, California.

*Discussion.*—The first and second upper molars, the only known material that can be retained in this species, indicate a form a little smaller than earlier *Washakius insignis.* The lingual slope of the protocone in these appears to be relatively a little longer and gentler, whereas the buccal slope is more abrupt, so that the apex of the protocone is somewhat closer to the paracone and metacone than in *W. insignis.* This condition, however, is not so striking as in *Dyseolemur pacificus* where the long lingual slope more or less continues from the root with less interruption by the cingulum. The presence of a second metaconule in the *W. woodringi* molars and the peculiarly rugose enamel are much as in *Washakius insignis. Washakius woodringi* is a little closer in size to *Dyseolemur pacificus* but with the transverse width of upper molars a little less.

The anteroposterior and transverse dimensions of $M_1$ in *Washakius woodringi* are 1.9 and 2.7 mm. respectively. These dimensions for $M_2$ are 1.9 and 3.0 mm.

### Genus CHUMASHIUS Stock, 1933

*Type.—Chumashius balchi* Stock, 1933.

*Discussion.*—The genus *Chumashius* is strikingly close to *Omomys,* so much so that had the material which represents it been found in the Bridger formation instead of the Sespe it would logically have been included in that genus. Nevertheless, the small, persistent differences noted, correlated with the undoubtedly long period of time separating them, probably warrant regarding the morphological change as of generic importance.

In the two known upper molars differences from *Omomys* include relatively a little less transverse width, a somewhat more evenly rounded lingual margin (particularly on $M^3$), a shallower basin, and a weaker cingulum. The absence of lingual cuspules on the cingulum, except for a very slight or vestigial hypocone, is not important considering variability and near absence of these in *Omomys.*

The lower teeth of *Chumashius* are relatively a little shorter and wider than in *Omomys,* and $P_4$ is characterized by a generally weaker metaconid. The paraconid of the lower molars is more reduced and may not be distinguished on the anterior crest of $M_2$ and $M_3$ in most cases. Moreover, the talonid basin, in addition to being a trifle shorter, appears shallower. $M_3$ is a little more reduced than in *Omomys,* and the entoconid of this tooth has almost or quite disappeared.

The lower jaws were described in detail by Stock, but I note that in two of them something of the alveolar arrangement anterior to $P_3$ can be seen. In one of these, the type, there is a suggestion that the first incisor was only slightly enlarged, less so than in *Omomys,* although the second appears noticeably reduced; however, a second jaw, No. 1390, not figured by Stock, shows less disparity in size between these teeth, approaching *Washakius* in this respect, and a slight increase in the size of the canine. This specimen shows none of the molar features of *Washakius.* It would appear, as a consequence, that if *Chumashius* is descendent from *Omomys,* which from other evidence seems logical, in addition to a tendency toward reduction of the cusps of the lower teeth, the anterior incisor became much weaker and the canine a little stronger.

### CHUMASHIUS BALCHI Stock, 1933

Plate 13, figures 1, 2

*Type.*—Left ramus of mandible with $P_3$-$M_3$, inclusive, L.A.C.M. (C.I.T.) No. 1391.

*Horizon and locality.*—Sespe upper Eocene, Duchesnean, C.I.T. locality 150, north of Simi Valley, Ventura County, California.

*Discussion.*—In addition to the type there are three lower jaws and a maxillary portion belonging to *Chumashius balchi.* Photographs of all but one of the lower jaws were included with Stock's (1933, pl. 1) description. In size *C. balchi* is very close to *Omomys carteri.* $M_2$ in the largest of the *C. balchi* dentitions, for example, is near the mean for this tooth in the size range of *O. carteri.*

MEASUREMENTS IN MILLIMETERS OF *Chumashius balchi* DENTITIONS

| | L.A.C.M. (C.I.T.) No. 1394 |
|---|---|
| $M^2$, Length along outer wall: width transversely | 2.2: 3.4 |
| $M^3$, Length along outer wall: greatest transverse width | 2.0: 2.6 |

| | L.A.C.M. (C.I.T.) No. 1391 Type | L.A.C.M. (C.I.T.) No. 1393 |
|---|---|---|
| Length of lower cheek tooth series, $P_3$-$M_3$, inclusive | 11.1 | 11.4 |
| Length of lower molar series, $M_1$-$M_3$, inclusive | 7.2 | 7.5 |
| $P_3$, Length: greatest width | 2.3: 1.6 | 2.2: 1.5 |
| $P_4$, Length: greatest width | 2.4: 1.7 | 2.3: 1.7 |
| $M_1$, Length: greatest width | 2.4: 1.9 | 2.6: 2.0 |
| $M_2$, Length: greatest width | 2.5: 2.0 | 2.7: 2.1 |
| $M_3$, Length: greatest width | 2.6: 1.6 | 2.6: 1.9 |

### Genus DYSEOLEMUR Stock, 1934

*Type.—Dyseolemur pacificus* Stock, 1934.

*Discussion.*—Just as *Chumashius* of the Sespe is related to *Omomys, Dyseolemur* is surely a relative of *Washakius.* This is strongly indicated in the general plan of the teeth and in certain minor features which seem to have carried over and are suggestive of *Washakius.* Differences, however, such as in the relative proportions of the teeth and the degree to which cusps are emphasized warrant generic separation.

The known second and third upper molars, in addition to rugose enamel, show the marked transverse diameter characteristic of *Omomys* and *Washakius,* but the protocone has the conical appearance of *Washakius,* not the smooth, crescentic form seen in *Omomys.* This cusp, however, has a somewhat longer lingual slope, so that the apex of the protocone appears a little nearer the external cusps. Moreover, the second metaconule of *Washakius* seems to have disappeared or to have joined the metaconule to form a short crest (or

elongate cuspule). The hypocone arising from the cingulum of $M^2$ is evidently persistent, but a small anterointernal cuspule is present on only one of the two partial upper dentitions from the Sespe. $M^3$ is relatively a little smaller than in *Washakius* and is slightly less expanded posterointernally.

In the lower series, the teeth are all shorter and broader than in *Washakius.* In $P_4$ the paraconid and metaconid are much subdued or vestigial and the anteromedial crest is rather shortened. The molars, as in *Washakius* and *Shoshonius,* are characterized by a metastylid, but the crest between the paraconid and protoconid is shortened so that the paraconid is actually closer to the protoconid than it is to the metaconid. In the increased relative breadth of the lower teeth the expansion seems to have been largely in the basal part of the crown so that the outer cusp walls are a little more sloping, paralleling the longer slope of the protocone on the upper molars. The talonid basin, as a result, is comparatively small. It still opens lingually, however, through a deep cleft between the entoconid and metastylid. Moreover, the crista obliqua still preserves, though less conspicuously, the peculiar flexure characteristic of *Washakius.* $M_3$, except for the position of the paraconid closer to the protoconid and a relatively smaller hypoconulid region, much resembles $M_3$ in *Washakius,* although reduced in size in comparison with $M_2$. In none of the specimens is the incisor region preserved, but in No. 1395, the type of *D. pacificus,* alveoli for $P_2$ and the canine are seen. That for the canine is a little larger than that for the single-rooted premolar, and is placed slightly anterolateral to the alignment of the cheek teeth. The anterior extremity of the jaw, as in *Washakius,* is more distinctly flexed toward the symphysis than in *Omomys,* indicating a more U-shaped arrangement of the teeth than in the latter genus.

### DYSEOLEMUR PACIFICUS Stock, 1934

Plate 13, figure 3-5

*Type.*—Right ramus of mandible with $P_4$-$M_3$, inclusive, and a part of $P_3$, L.A.C.M. (C.I.T.) No. 1395.

*Horizon and locality.*—Sespe upper Eocene, upper Uintan, C.I.T. locality 180, Tapo Ranch, north of Simi Valley, Ventura County, California.

*Discussion.*—In addition to the type there are seven lower jaw portions and two maxillary fragments, including representation of lower teeth from the posterior portion of $P_3$ (as in the type) to $M_3$, and

of $M^2$ and $M^3$. In size of teeth *Dyseolemur pacificus* runs only slightly smaller than *Washakius insignis*.

MEASUREMENTS IN MILLIMETERS OF *Dyseolemur pacificus* DENTITIONS

| | L.A.C.M. (C.I.T.) No. 1528 | L.A.C.M. (C.I.T.) No. 5191 |
|---|---|---|
| $M^2$, Length along outer wall: width transversely | 2.0: 3.2 | 2.0: 3.3 |
| $M^3$, Length along outer wall: width transversely | 1.8: 2.8 | 1.6: 2.6 |

| | L.A.C.M. (C.I.T.) No. 1395 Type | L.A.C.M. (C.I.T.) No. 5194 | L.A.C.M. (C.I.T.) No. 5192 |
|---|---|---|---|
| Length of lower molar series | 6.3 | 6.8[a] | |
| $P_4$, Length: width | 1.8: 1.6 | 2.0: 1.7 | |
| $M_1$, Length: width | 2.2: 1.8 | 2.3: 1.9 | |
| $M_2$, Length: width | 2.2: 2.0 | 2.5: 2.3 | 2.4: 2.1 |
| $M_3$, Length: width | 2.6: 1.7 | | 2.8: 1.8 |

[a] Approximate.

**UTAHIA,[14] new genus**

*Type.—Utahia kayi,* new species.

*Generic characters.*—$P_4$ comparatively short, with short anterior crest and weak paraconid. Metaconid weak or possibly absent. Talonid of $P_4$ short and broad with little development of cusps although there is a slight median crest. Trigonid of $M_2$ and particularly $M_3$ anteroposteriorly short with paraconid on anterior crest and close to metaconid. Talonids of $M_1$ and $M_2$ slightly rugose, short, broad, and open lingually through sharp notch between metaconid and entoconid. Hypoconulid median on posterior crest and not sharply set off. Basin of $M_3$ talonid shows distinct enamel rugosity, particularly on the hypoconulid portion.

*Discussion.*—The Green River genus *Utahia* appears in many ways intermediate between *Hemiacodon* and *Washakius,* but possibly closer to *Hemiacodon.* $P_4$, except for the primary cusp, shows much more weakly developed cusps than in either *Washakius* or *Hemiacodon.* The metaconid has been worn off in the only specimen exhibiting $P_4$, but the general form of the tooth shows that the cusp was not markedly developed. $P_4$ differs in much the same way from this tooth in *Loveina* and *Chlororhysis,* and in addition is relatively not so broadly expanded as in these two genera. On the other hand, the shortness of the anterior crest of $P_4$ is suggestive of *Loveina* and

[14] Named for Utah, the State in which the Green River fossil mammal localities occur.

*Chlororhysis.* Moreover, there is no evidence of the cuspule developed midway on this crest in *Hemiacodon.*

The trigonid of $M_1$ resembles that seen in *Washakius, Hemiacodon,* and *Loveina,* but is a little less open between the paraconid and metaconid than in *Washakius,* and does not exhibit a metastylid. The summits of the trigonids of $M_2$ and $M_3$ are noticeably compressed anteroposteriorly and the paraconid is a part of the anterior crest. The position of the paraconid is decidedly less forward and not so isolated from the metaconid as in *Washakius,* or referred material of *Loveina,* and is somewhat less distinctly defined than in *Hemiacodon.* The crista obliqua is less complex than in *Washakius,* but joins the posterior wall of the trigonid in a depressed or grooved portion much as in *Washakius.* The talonid is very much shorter than in *Omomys* and its surrounding crest most nearly resembles *Hemiacodon* and *Loveina,* but the basin, unlike these genera, opens lingually through a sharp notch between the metaconid and entoconid, much as in *Washakius.* The cusps of the talonid in $M_1$ and $M_2$, as in *Loveina,* are not so emphasized as in *Hemiacodon,* and much less so than in *Washakius.* The talonid of $M_3$, except for the lingual notch, shows a somewhat closer resemblance to *Hemiacodon* than it does to *Washakius.* $M_3$ is not enlarged as in *Washakius.*

Possibly *Utahia* is ancestral to *Hemiacodon,* but I am rather inclined to think that the shortening of the trigonid of $M_2$ and $M_3$ in *Utahia* is a specialization away from the more primitive appearing structure seen in *Hemiacodon.*

A single isolated upper molar observed in the Green River collection (pl. 14, fig. 4), suspected as representing *Utahia,* shows a simple primate form with a decidedly conical protocone, rather as in *Washakius,* but the hypocone is comparatively weak. The cingulum anteriorly and externally is weak and there is no anterointernal cuspule. The protoconule and metaconule are developed only a little better than in *Omomys.* The tooth, moreover, is less extended transversely than in *Washakius.* There is no certainty as to the identity of the form represented but the size of the tooth is about right and it occludes well with the lower molars of *Utahia.*

### UTAHIA KAYI,[15] new species

Plate 14, figures 3, 4

*Type.*—Right ramus of mandible with $P_4$-$M_3$, inclusive, C.M. No. 6488.

[15] Named for Dr. J. LeRoy Kay, who developed the Green River quarry near Powder Springs in the Uinta Basin.

*Horizon and locality.*—Lower(?) Bridger equivalent or "Upper Fossiliferous Zone" of Green River formation, about 2 miles SE. of Powder Springs, sec. 8, T. 7 S., R. 25 E., Uintah County, Uinta Basin, Utah.

*Specific characters.*—*Utahia kayi* appears to be the smallest of the known omomyids. Its teeth are distinctly smaller than in *Washakius insignis,* but only a little smaller than in *Dyseolemur pacificus.* The depth of the lower jaw, however, is relatively greater than in either *Omomys carteri* or *Washakius insignis.*

*Discussion.*—In addition to the type, there are two, more fragmentary, lower jaws recognized as representing *Utahia kayi,* C.M. Nos. 6411 and 6412. Each exhibits $M_2$ and $M_3$. In one of these, No. 6411, the third molar is a little longer than in the type. In No. 6412 the paraconid of $M_2$ and $M_3$ is a little farther from the metaconid but the general form and size of these teeth are as in the type. Moreover, the talonid basin opens lingually, as in No. 6488, so that there would seem to be no doubt as to identity. The upper molar thought to be of this species, C.M. No. 6413, is either the first or second of the series. This tooth measures 1.7 mm. anteroposteriorly by 2.2 mm. wide.

MEASUREMENTS IN MILLIMETERS OF LOWER JAWS AND TEETH OF *Utahia kayi*

| | C.M. No. 6488 Type | C.M. No. 6411 | C.M. No. 6412 |
|---|---|---|---|
| Depth of lower jaw beneath $M_2$ | 3.7 | | |
| Length of lower molar series, $M_1$-$M_2$, inclusive. | 6.3 | | |
| $P_4$, Length: width | 2.0: 1.5 | | |
| $M_1$, Length: width | 2.0: 1.6 | | |
| $M_2$, Length: width | 2.1: 1.7 | 2.2: 1.8 | 2.1: 1.7 |
| $M_3$, Length: width | 2.5: 1.6 | 2.7: 1.6 | 2.5: 1.6 |

**STOCKIA,[16] new genus**

*Type.*—*Stockia powayensis,* new species.

*Generic characters.*—Trigonid of $M_2$ and $M_3$ relatively broad and anteroposteriorly much compressed, and with talonid basins of $M_1$ and $M_2$ relatively large and deeply excavated. The hypoconid and entoconid are decidedly marginal in position and much compressed. Small, anteroposteriorly compressed hypoconulid on $M_1$ and $M_2$. $M_3$ is narrower than $M_2$ and relatively elongate. Enamel highly rugose.

[16] Named for Chester Stock in recognition of his contributions to the Eocene faunas of southern California.

*Discussion.—Stockia* is readily distinguished from *Hemiacodon,* although there are several characteristics that ally the two genera. Among the differences between the lower molars it is noted that the cusps of the trigonid are relatively a little lower and those of the talonid appear a little higher, so that there is less disparity in the height of the trigonid over that of the talonid cusps, and the talonid portion is relatively larger with a more deeply excavated basin than in *Hemiacodon.* Moreover, the cusps appear more compressed in outline, or a little less conical, and the crest surrounding the talonid basin is a little less angular. Nevertheless, the crista obliqua joins the posterior surface of the protocone in much the same detail, and the transverse compressed ridge extending down the posterior wall of the metaconid and that on the anterior margin of the entoconid approach each other and are separated by a sharp notch at the base quite as in *Hemiacodon,* though not so deep as in *Utahia.* Moreover, although there is a slight tendency toward development of a posterior crest between the protoconid and metaconid, it is much depressed, resembling the distinct separation of these cusps in *Hemiacodon.*

Of the three molars, $M_1$ most closely resembles that in *Hemiacodon,* whereas $M_2$ shows a rather striking anteroposterior shortening of the trigonid. The paraconid of $M_2$, though about midway in position as in *Hemiacodon,* is almost lost on the high anterior crest between the protoconid and metaconid. Weak hypoconulids on $M_1$ and $M_2$ are more reduced or anteroposteriorly compressed than in *Hemiacodon.* $M_3$, as in *Hemiacodon,* is a little narrower than $M_2$ but appears more elongate and the hypoconulid broadly developed, more as in *Washakius,* although this tooth is relatively not so enlarged as in the latter genus. The entoconid, moreover, is a little less emphasized than in either. The trigonid of $M_3$, as in the case of $M_1$'s, more nearly resembles that of *Hemiacodon.* Although somewhat shortened anteroposteriorly, it shows a clearly distinct paraconid midway across the anterior margin, but evidently a little higher on the crown.

The character of the trigonid in $M_2$ and $M_3$ of *Stockia* strongly suggests a close relationship to *Utahia.* The anteroposterior compression of this portion of the tooth and arrangement of the cusps are much alike in the two genera. Possiby *Utahia* is ancestral to *Stockia.* If this is true, the trigonid of $M_2$ has become wider and the talonid basin much more expanded and more rugose. The notch between the metaconid and entoconid characterizing *Utahia,* while present in *Stockia,* is not so deeply impressed and the deeper part of the talonid basin is not adjacent to this notch but nearer the basin center.

### STOCKIA POWAYENSIS,[17] new species

Plate 13, figure 6

*Type.*—Portion of right ramus of mandible with $M_1$-$M_3$, inclusive, L.A.C.M. (C.I.T.) No. 2234.

*Horizon and locality.*—White sandstones associated with the Poway conglomerate, lower Uintan upper Eocene, near San Diego Mission, San Diego County, California.

*Specific characters.*—First and second lower molars of *Stockia powayensis* about intermediate in size between those of *Washakius insignis* and *Hemiacodon gracilis*. $M_3$ near actual size of that in *Washakius insignis*. *S. powayensis* is decidely larger than *Utahia kayi*. Characteristics of species not otherwise distinguished from those of genus.

*Discussion.*—In addition to the type, there is a second jaw fragment, L.A.C.M. (C.I.T.) No. 2235, that has preserved only $M_2$ and $M_3$. An isolated $M_1$ is of interest in that it has the trigonid portion complete. The anterior extremity of this tooth in the type has been damaged. As indicated above, these are the specimens that were described by Stock (1938) as belonging to *Yumanius woodringi*. The possibility that the upper and lower teeth that he described were not of the same genus evidently occurred to him (p. 289), but he placed more weight on their field association than was warranted. Any attempt to occlude the upper and lower teeth shows the association to be meaningless.

MEASUREMENTS IN MILLIMETERS OF *Stockia powayensis* LOWER JAWS

| | L.A.C.M. (C.I.T.) No. 2234 Type | L.A.C.M. (C.I.T.) No. 2235 |
|---|---|---|
| Depth of jaw beneath $M_2$ lingually | 4.3[a] | 4.4 |
| Length of lower molar series, $M_1$-$M_3$, inclusive | 8.7[a] | |
| $M_1$, Length : greatest width | 2.9[a] : 2.2 | |
| $M_2$, Length : greatest width | 2.8 : 2.1[a] | 2.7 : 2.5 |
| $M_3$, Length : greatest width | 3.1 : 1.9 | 3.2 : 2.0 |

[a] Approximate.

### OURAYIA,[18] new genus

*Type.*—*Microsyops uintensis* Osborn, 1895.

*Generic characters.*—Resembles *Hemiacodon* but differs from that

[17] Named from the Poway formation.

[18] Derived from Ouray, the name of the village situated near the confluence of the Duchesne, Green, and White Rivers, to the north of "White River pocket" in the Uinta basin.

genus in the less elevated and anteroposteriorly shortened trigonid of the lower molars, paraconid more or less obscured in anterior crest of trigonid in $M_2$ and talonid basins relatively larger and cusps of crest surrounding basin more subdued.

*Discussion.—Ourayia* is quite unlike *Notharctus* and is clearly more closely related to *Hemiacodon.* The dental formula cannot be determined in the type specimen, but it is likely the same as *Hemiacodon.* The lower premolars $P_3$ and $P_4$ have a brief talonid with a low but transversely elongate crest and a weak hypoconid and entoconid, resembling *Hemiacodon.* In *Notharctus* the emphasis is on a posterior crest or crests extending down from the primary cusp. The metaconid is not present on $P_3$, but on $P_4$ it is well developed and lingual to the primary cusp as in *Hemiacodon,* not posterolingual as in *Notharctus.*

In the lower molars the trigonid is anteroposteriorly shortened and the talonid basin enlarged, more so than in *Hemiacodon.* The trigonid of $M_1$ shows the paraconid at the anterointernal extremity of a more direct crest from the protoconid as in *Hemiacodon,* not nearly so arcuate as in *Notharctus.* In $M_2$ the paraconid is nearly lost, but weakly discernible about midway across the high anterior crest connecting the protoconid and metaconid. It has this position in *Hemiacodon,* but is much better defined and clearly separated from the metaconid. In *Notharctus* the paraconid may not be present on this tooth but the anterior crest from the protoconid arcs prominently forward and decidedly downward and may not then join the apex of the metaconid. The metaconid in both the preserved molars is, as in the case of $P_4$, situated more nearly lingual to the protoconid as in *Hemiacodon,* not nearly so posterolingual as in *Notharctus,* particularly in comparison between the first molars. The posterior or direct crest between the protoconid and metaconid, much emphasized in *Notharctus,* is lacking in *Ourayia* and *Hemiacodon.* These cusps appear deeply separated in the latter two. The talonid basins show the rugose condition of *Hemiacodon,* but are relatively larger and the surrounding crest has more subdued cusps. Moreover, the entoconid is not separated from the posterior part of this crest in $M_2$. It is in *Notharctus.*

Several of the differences which distinguish *Ourayia* from *Hemiacodon* are suggestive of (or parallel those of) *Stockia.* This is noted in the lower trigonid, the relatively larger talonid, and in the relatively less acute angle between the anterior and posterior crests of the hypoconid and entoconid of the anterior lower molars as in *Stockia.* Resemblance is particularly noted in $M_2$, in that the trigonid

is much shortened anteroposteriorly and the paraconid almost lost on the high anterior crest between the protoconid and metaconid. Differences noted, in addition to the great disparity in size of the animals, include a more inflated and less marginal position for the cusps, a relatively narrower trigonid apex that is somewhat less compressed anteroposteriorly in $M_2$, and a less broadly and deeply excavated talonid basin than in *Stockia.*

The possibility of *Ourayia* being closer to the line or lines of *Utahia* and *Stockia* has been considered, but the present evidence does not appear conclusive. Closer relationship to *Utahia* would imply very close parallelism with *Hemiacodon* in development of the premolars, deeper separation of the metaconid from the protoconid in the molars, and in the more expanded and lingual closure of the talonid basins, whereas a closer relationship to *Hemiacodon* would denote parallelism principally in the anteroposterior shortening of the trigonid of $M_2$ (and probably $M_3$). I am rather inclined to believe that a closer relationship to *Hemiacodon* is indicated, and that shortening of the trigonid parallels that of *Utahia* and *Stockia.*

### OURAYIA UINTENSIS (Osborn), 1895

Plate 13, figure 8

*Type.*—Portion of left ramus of mandible with $P_3$-$M_2$ inclusive, A.M. No. 1899.

*Horizon and locality.*—Lower Uinta (B), upper Eocene, White River pocket, Uinta Basin, Utah.

*Discussion.*—Since its description in 1895 this species had been referred to various genera, but probably most frequently, though tentatively, to *Notharctus,* probably because of its size. It bears very little resemblance to that genus. The teeth show *Ourayia uintensis* to be an animal very close in size to *Smilodectes gracilis,* much larger than *Hemiacodon gracilis.* It is interesting to note that Wortman considered it a species of *Omomys.*

Better materials of this form in the collections of Princeton University were shown to me by Dr. Jepsen so that we can be assured of a more adequate treatment of Osborn's Uinta primate in the future.

MEASUREMENTS IN MILLIMETERS OF *Ourayia uintensis* TYPE LOWER JAW, A.M. NO. 1899

| | |
|---|---|
| Depth of jaw beneath $M_2$ lingually | 7.5 |
| $P_3$, Length: greatest width | 3.2 : 2.3 |
| $P_4$, Length: greatest width | 3.7 : 2.6 |
| $M_1$, Length: greatest width | 4.6 : 3.6 |
| $M_2$, Length: greatest width | 4.5 : 3.8 |

## Family ANAPTOMORPHIDAE Cope, 1883

With the removal of the omomyids, the anaptomorphids still appear to be a somewhat unnatural association of genera. There is, nevertheless, a more compact combination of characters involved, in which is seen a greater reduction of the dentition—through rather general loss of a tooth interpreted as $P_2$, or possibly the canine, in most forms —from that characterizing the Omomyidae. With one or two exceptions there is also a basic resemblance in molar structure, which had appeared too broad with the inclusion of the omomyids.

With *Anaptomorphus* as a central or nearly "prototypal" form there remain two rather striking divergent tendencies. In one there is an enlargement of the fourth premolar and in the other an enlargement of a procumbent chisel-like anterior tooth, almost certainly an incisor. In *Tetonius,* which exhibits a strong basically anaptomorphid molar structure, these tendencies are combined, showing that they may be linked in the same family. With *Tetonius* we have *Anemorhysis* and *Trogolemur* showing emphasis on the incisor; and on the other hand, *Absarokius* and similarly constructed *Uintanius* in which $P_4$ is emphasized. *Uintasorex* is perhaps the most difficult to reconcile but is included only because of a certain resemblance to *Anemorhysis* and *Trogolemur,* its reduced dentition, and specialized anterior tooth. Certain characters in the molar structure of *Uintasorex* are rather *Omomys*-like, but separation from the omomyids must have been remote in any case.

The dental formula for the more typical anaptomorphids was previously regarded (Gazin, 1952, p. 24) as including three lower premolars. In the *Absarokius* jaw from the Knight showing replacement of the deciduous premolars (pl. 14, fig. 8), the first of the three permanent cheek teeth in the antemolar series, following the two small and erect incisors, appears to be the first erupting, and for this reason was interpreted as $P_2$. This would be closely followed or nearly coincident in time with $P_4$, and followed later by $P_3$. $P_3$ does not actually show in the illustration but its presence within the jaw (unerupted) has been verified. In examining recent primates for evidence of tooth succession, it is seen that the canine is rather generally the last of the permanent antemolar teeth to erupt, and may even coincide with or follow eruption of the third molar. This might seem rather forceful evidence; however, in the case of the modern tarsiers, while $P_2$ and then $P_4$ follow the permanent incisors, it was not certain that $P_3$ always precedes the canine, and the canine may well be erupting with $P_4$. Omitting from consideration the large and very early erupting

$P_2$ of *Tarsius,* it is at once seen that an approximation is made to the situation evident in the *Absarokius* jaw. As a result, the interpretation suggested, in which the tooth in question is regarded as $P_2$ instead of the canine, cannot be considered as conclusive. Further interpretation might be derived from the supposed not too remote relationship between the anaptomorphids and omomyids. In the latter $P_2$ would appear to be the less sturdy of the two teeth in question and possibly would be the first to be lost in any reduction or crowding of the anterior portion of the dental series. Possibly it should be noted, moreover, that so often in those cases where a premolar becomes large and caniniform, the canine, as in the lemurs and in many artiodactyls, is not actually lost but has moved forward and become incisiform. This surely does not follow in the case of *Absarokius.*

An upper dentition of *Absarokius* from the Knight formation is likewise significant in demonstrating that $P^2$ was a very small, spikelike tooth with a relatively small globular crown, located immediately anterior to the deuterocone of $P^3$, so that the large alveolus anterior to the outer wall of $P^3$ may well have been for an upper canine. This, moreover, seems to provide further evidence as to the identity of the vertically elongate tooth anterior to $P_3$ in the lower jaw. In attempting to occlude a lower jaw of *Absarokius* with the maxilla from the Knight it appears that the lower tooth in question would almost certainly project in front of a normal canine in the upper position, indicative of the opposing canine rather than a premolar.

From the foregoing it is believed that the formula for the more typical of the anaptomorphids might be written, $\frac{?}{2}$, $\frac{1}{1}$, $\frac{2 \text{ or } 3}{2}$, $\frac{3}{3}$, with a further reduction in the number of lower teeth in *Uintasorex,* and possibly some material of *Tetonius,* interpreted as the loss of the second lower incisor.

### Genus ANAPTOMORPHUS Cope, 1872

*Type.—Anaptomorphus aemulus* Cope, 1872.

*Discussion.*—Various forms have been referred to *Anaptomorphus,* but until now only *A. aemulus* was properly included. Much that had been earlier regarded as characterizing this genus was derived from *"Anaptomorphus" homunculus.* Matthew showed that the latter species could not represent *Anaptomorphus* and made it the type of *Tetonius.*

*Anaptomorphus,* known only from lower dentitions, is a rather generalized type, reduced in dental formula from that rather generally

characterizing the omomyids, and has a molar structure in which the talonid basin of the molars is short and not particularly well excavated and the trigonid inflated but with the cusps of the crown comparatively close together. The cusp arrangement on the crown of the trigonid rather resembles that of *Omomys*. The paraconid of $M_2$, however, is rather closer to the metaconid and not always particularly well defined. $P_4$ is not enlarged but relatively short and broad. There is a weak anterior crest from the primary cusp and the metaconid is scarcely more than a flexure of the posterointernal crest. These crests join the terminals of a brief cingulum developed anterolingually. The talonid is extremely abbreviated anteroposteriorly and consists of only the upturned posterior crest with its highest point about midway transversely. Anterior to $P_4$ appear 5 alveoli, all for relatively erect teeth. The third one of these is the largest and assumed to be for a canine. This would leave two small, nearly equal incisors and a two-rooted $P_3$, unless, of course, there are three premolars and no canine. The foregoing would suggest the formula: $\frac{-}{2}, \frac{-}{1}, \frac{-}{2}, \frac{-}{3}$. It is, moreover, interesting to note that the anterior root of $P_4$ is relatively elongate anteroposteriorly and the posterior evidently flattened anteroposteriorly and transversely rather broad.

The relatively shorter jaw of *Anaptomorphus,* in comparison with *Omomys,* shows a rather more definite anterior flexure toward the symphysis, much as in *Washakius,* and is, as a consequence, a little less tarsiidlike than *Omomys.*

### ANAPTOMORPHUS AEMULUS Cope, 1872

Plate 10, figure 1

*Type.*—Left ramus of mandible with $P_4$-$M_2$, inclusive, A.M. No. 5010.

*Horizon and locality.*—Lower Bridger, middle Eocene, Ham's Fork, Bridger Basin, Wyoming.

*Discussion.*—As far as can be determined, this species is represented by only the type specimen. The jaws which Wortman referred to *Euryacodon* are clearly of *Anaptomorphus,* but apparently represent a smaller species. *Anaptomorphus aemulus* is very close in size to *Omomys carteri.* It may be noted, possibly in further characterizing the species, that the cusps of the lower molars are much subdued and the enamel is smooth.

Measurements of teeth are included with those of *A. wortmani.*

### ANAPTOMORPHUS WORTMANI,[19] new species

Plate 10, figure 2

*Type.*—Right ramus of mandible with $M_1$-$M_3$, inclusive, Y.P.M. No. 13233.

*Horizon and locality.*—Bridger middle Eocene, Bridger Basin, Wyoming.

*Specific characters.*—Smaller than *Anaptomorphus aemulus,* closer in size to *Washakius insignis.* Lower molars relatively broader than in *A. aemulus,* cusps of trigonids a little better defined, paraconid more lingual and talonid basins slightly rugose.

*Discussion.*—*Anaptomorphus wortmani* appears to be a valid species, but the difference in size from *A. aemulus* is not particularly great. Nevertheless, the four lower jaws (one more than Wortman saw) in the Marsh collection, all have teeth very close to the same size, distinctly and consistently smaller than in *A. aemulus.* Actually the length of the first two molars in *A. aemulus* is only about 17 percent greater than in the largest of the *A. wortmani* jaws and about 20 percent greater than in the smallest. However, somewhat smaller size, together with the relatively wider molars, somewhat more prominent and lingually placed paracone, and slight rugosity of the talonid basins would appear to warrant recognition of a distinct species. It should be noted, moreover, that the rugosity, so clearly evident in the type, and in the jaw figured by Wortman (Y.P.M. No. 13230-1), is not observed in the talonid basins of the more worn teeth of No. 13232. The horizon of the Bridger represented by the type specimen is not known, but accompanying one of the referred jaws, Y.P.M. No. 13228-2, there is a specimen label that reads "Black's Fork," so that its presence in the lower Bridger is verified.

The frequency distribution for the measurements of $M_2$, combining the very limited materials of both *A. aemulus* and *A. wortmani,* may be listed as follows:

| Length | f. | | Width | f. | |
|---|---|---|---|---|---|
| 2.2 | 1 | | 1.9 | 1 | |
| 2.3 | 3 | | 2.0 | 2 | |
| 2.4 | 0 | | 2.1 | 1 | |
| 2.5 | 0 | | 2.2 | 1 | (*A. aemulus*) |
| 2.6 | 0 | | | | |
| 2.7 | 1 | (*A. aemulus*) | | | |

[19] Named for Jacob L. Wortman in recognition of his work on Eocene primates in the Marsh collection.

For length of $M_2$ the coefficient of variability, though probably not too meaningful for such a small number of specimens, has the relatively large value of 7.4.

COMPARATIVE MEASUREMENTS IN MILLIMETERS OF *Anaptomorphus* LOWER JAWS

| | *A. aemulus* | *Anaptomorphus wortmani* | | | |
|---|---|---|---|---|---|
| | A.M. No. 5010 Type | Y.P.M. No. 13233 Type | Y.P.M. No. 13230-1 | Y.P.M. No. 13228-2 | Y.P.M. No. 13232 |
| Depth of jaw beneath $M_2$... | 4.5 | 3.9 | 3.8 | 4.0 | 3.5 |
| Length of molar series..... | 8.0[e] | 6.8 | 6.5 | | |
| $P_4$, Length ..... | 2.4 | | | | |
| $P_4$, Width ..... | 2.2 | | | | |
| $M_1$, Length ..... | 2.7 | 2.2 | 2.3 | 2.3 | 2.3 |
| $M_1$, Width ..... | 2.1 | 1.8 | 1.9 | 1.9 | 1.8 |
| $M_2$, Length ..... | 2.7 | 2.3 | 2.2 | 2.3 | 2.3 |
| $M_2$, Width ..... | 2.2 | 2.1 | 2.0 | 2.0 | 1.9 |
| $M_3$, Length ..... | | 2.5 | 2.4 | | |
| $M_3$, Width ..... | | 1.7 | 1.6 | | |

[e] Estimated.

### Genus UINTASOREX Matthew, 1909

*Type.—Uintasorex parvulus* Matthew, 1909.

*Discussion.—Uintasorex* would appear to be the least anaptomorphidlike of the various genera which have been retained in this family. Upper molars discovered in the Green River collection are seen to be surprisingly *Omomys*-like. The outer wall and external cusps are quite as in *Omomys*. Relatively, however, these teeth are a little less wide transversely and the protocone is rather more conical and perhaps a little higher. The accessory cuspules at the lateral extremities of the crests from the protocone are formed much as in *Omomys* but are a little more prominent. A cingulum is present on the anterior and posterior margins of the talon, but does not continue around the lingual margin, as it usually does in *Omomys*. Except for the lingual termination of the anterior cingulum there is no evidence of the anterolingual or lingual cuspule variably developed in *Omomys*. The hypocone is scarcely more than a widening of the posterior cingulum at its lingual extremity in $M^1$ and $M^2$. $M^1$ and $M^2$ are probably not much different in size, but $M^1$ may be characterized by a slightly broader posterior portion, whereas $M^2$, if the isolated teeth are properly interpreted, is more nearly symmetrical in this respect. $M^3$ is a smaller tooth with the metacone smaller than the paracone, and the

posterior cingulum weakens lingually without evidence of a hypocone.

$P_4$ is comparatively small, but relatively elongate anteroposteriorly. At the base of the anterior crest there is a small paraconid, and the posterointernal crest shows a weak metaconid about as in *Omomys*. The talonid of this tooth, however, is relatively a little more elongate, much more suggestive of *Anemorhysis*. Anterior to $P_4$ in the type specimen of *U. parvulus* there are two alveoli, preceded by the root portion of a large, procumbent, rodentlike tooth. It is not known whether this large tooth is an incisor or a canine, but since the enlarged anterior tooth in omomyids, as far as known, is certainly an incisor, I am inclined, as did Matthew, to favor this interpretation. The first of the following alveoli is smaller than the second and, in order to be consistent, I prefer to regard it as for the canine. The larger second alveolus would then be for a single-rooted $P_3$. The formula suggested would be: $\frac{?}{1}, \frac{?}{1}, \frac{?}{2}, \frac{3}{3}$.

The trigonid of $M_1$ is much like that of *Omomys,* but a little more shortened anteroposteriorly. In $M_2$ and $M_3$ the trigonid is very much shortened anteroposteriorly and the paraconid is scarcely evident. Unlike *Ourayia* and *Stockia,* where the paraconid is nearly lost midway on the anterior crest, in *Uintasorex* this cusp appears anaptomorphidlike, almost united with the metaconid. The talonid of $M_1$ and $M_2$ strongly resembles that of *Omomys,* except that the hypoconulid is more distinct and lingual in position and separated from the entoconid by a sharp notch, rather as in *Microsyops* and certain material of *Washakius*. The talonid of $M_3$ is more slender and elongate than that of $M_2$ and shows a prominent, nearly conical hypoconulid distinctly set off from both hypoconid and entoconid, again suggestive of certain of the mixodectids. The talonid is, however, relatively less expanded transversely than in the mixodectids, and shows relative proportions more as in *Omomys*. In the latter genus, however, the entoconid and hypoconulid form a scarcely interrupted crest.

*Uintasorex* is surely a primate, but inclusion of it in the Anaptomorphidae is tentative. The lower molar structure, however, though somewhat suggestive of *Trogolemur* as noted by Matthew, seems a little atypical for anaptomorphids. Perhaps it should be included in the Omomyidae, but the reduction of teeth and specialization of the front part of the series are more as in *Trogolemur* and *Anemorhysis,* which in turn have perhaps a more *Anaptomorphus*-like molar structure. Possibly *Uintasorex* will prove in time to represent a distinctive family, but too little of it is now known. The molar structure is, of course, very different from that of the apatemyids.

### UINTASOREX PARVULUS Matthew, 1909

Plate 11, figures 3, 4; plate 14, figures 1, 2

*Type.*—Right ramus of the mandible with $P_4$-$M_1$ and the root portion of the enlarged, rodentlike anterior tooth, A.M. No. 12052.

*Horizon and locality.*—Upper Bridger (D), middle Eocene, Henry's Fork, Bridger Basin, Wyoming.

*Discussion.*—The type of *Uintasorex parvulus* includes but two cheek teeth; however, a better specimen has been found in the Marsh collection at Yale. It is a right mandibular ramus, Y.P.M. No. 13519, and includes $P_3$-$M_3$. Unfortunately the anterior extremity is damaged, so shows a little less of the alveolar arrangement ahead of $P_3$. In size *Uintasorex parvulus* is very minute, evidently the smallest primate known from the North American early Tertiary, as its teeth have dimensions a little less than in *Palenochtha minor* from the middle Paleocene.

Upper teeth of *Uintasorex* were not previously known, but approximately 20 isolated upper molars, as well as a number of isolated lower teeth and jaw fragments, were discovered in the Carnegie Museum Green River collection made by Kay in the "Upper Fossiliferous Zone" of Burke (1935). These upper teeth were selected from among numerous insectivore and other small mammalian upper molars because of their typically primate form. Their exceedingly small size suggested *Uintasorex,* and a direct comparison with lower molars of *Uintasorex* from the same locality revealed an occlusion that left no doubt as to their identity. A composite upper molar series is shown in plate 14, figure 2.

The Green River *Uintasorex* material may well represent a distinct species, as all the measured lower teeth are smaller than in either of the two Bridger jaws. The length of $M_2$, for example, ranges from 1.0 to 1.2 mm. in the Green River collection, whereas $M_2$ in the only Bridger specimen in which this tooth is preserved measures 1.3 mm. Also, a disparity is seen in the length of $M_3$. In the three examples of this tooth encountered among the sorted materials, each was found to be only 1.2 mm. long. The difference from 1.4 mm. in the Bridger jaw is effected by a less projecting hypoconulid. Although the range of measurements appears slight, it is relatively great considering the magnitude of each. The data secured for the length of $M_2$ in six specimens with an observed range of 1.0 to 1.3 give a coefficient of variability of 8.3. Measurements at this scale, however, are so difficult to obtain without a rather large percentage of error that the results may not be satisfactory. I am rather inclined to believe that

the Green River material represents a form that should, on the present evidence, be regarded as a variant in time, of probably no more than subspecific importance.

MEASUREMENTS IN MILLIMETERS OF *Uintasorex parvulus* LOWER JAWS

| | A.M. No. 12052 Type | Y.P.M. No. 13519 | C.M. No. 6414 |
|---|---|---|---|
| Depth of lower jaw beneath $M_2$ | 2.4 | 2.5 | 2.2 |
| Length of molar series | | 3.6 | |
| I, Depth : width | 1.2 : 0.75 | | |
| $P_4$, Length : width | 1.2 : 0.7 | 1.2 : 0.8 | 1.1 : 0.8 |
| $M_1$, Length : width at talonid | 1.4 : 1.0 | 1.4 : 1.1 | 1.2 : 0.9 |
| | | | C.M. No. 6415 |
| $M_2$, Length : width at talonid | | 1.3 : 1.1 | 1.2 : 0.9 |
| $M_3$, Length : width at talonid | | 1.4 : 0.9 | 1.2 : 0.9 |

### Genus TROGOLEMUR Matthew, 1909

*Type.—Trogolemur myodes* Matthew, 1909.

*Discussion.*—The molar structure of *Trogolemur* appears rather clearly to be of the general anaptomorphid type, but in greater detail a surprisingly close resemblance is seen to Wasatchian *Anemorhysis* and *Uintalacus*. It exhibits the short, broad molars with the short, in comparison with *Omomys,* and moderately shallow talonid basin of the anaptomorphids. It differs from such forms as *Anaptomorphus* and *Tetonius,* as do *Anemorhysis* and *Uintalacus,* in the somewhat less inflated basal portion of the molar crown and the more marginal position of the cusps.

As in *Anaptomorphus, Anemorhysis, Absarokius,* and *Uintanius,* there are five teeth anterior to the lower molars, one less than in omomyids, as far as known, and one more than in *Uintasorex* and possibly some material of *Tetonius*. It is reasonable to assume that the lower teeth of *Trogolemur,* as suggested for *Anaptomorphus,* include two incisors, a canine and two premolars; or the formula again might be written $\frac{-}{2}, \frac{-}{1}, \frac{-}{2}, \frac{-}{3}$.

The anterior lower tooth in *Trogolemur* is procumbent and enlarged as in *Tetonius* and *Anemorhysis*. Immediately behind or posterolateral to it, with the root much flattened and paralleling that of the anterior incisor, is an evidently very small tooth regarded as the second or lateral incisor, the crown of which, however, is not known. The following three antemolar teeth are simple, premolarlike teeth

increasing in size to $P_4$. All appear to be single rooted, with the anterior portion of the tooth projecting forward and lapping over the heel of the preceding tooth. The first of these has the lowest crown, unlike *Absarokius* in which this tooth is a little higher than the following, but could, nevertheless, be a canine. Its premolarlike form is not inconsistent with that seen in some the omomyids, although it is of relatively smaller size. $P_3$ shows a slight anterior crest and an anteroposteriorly very brief but broad talonid, hidden beneath the anterior part of $P_4$. $P_4$ has an anterior crest which is deflected medially at its anterior extremity but no distinct paraconid. There is, however, a weak metaconid and the transverse talonid crest is better defined than on $P_3$.

The lower molars, in keeping with the less inflated basal portion, show less convergence upward of the outer and inner walls. As a consequence the cusps are more marginal in position with the protoconid more widely separated from the metaconid and paraconid, so that the top of the trigonid is broader and relatively shorter appearing. In these respects *Trogolemur* almost exactly corresponds to *Anemorhysis*.

The jaw of *Trogolemur* shows a striking increase in depth forward from below the molars, indicating considerable emphasis on the enlarged anterior tooth which originates well back in the jaw, at least as far back as beneath $M_2$. Three mental foramina were observed, spaced below the root of $P_4$ to below the posterior root of $M_1$.

In all probability the Wasatchian ancestor of Bridgerian *Trogolemur* is a form close to *Anemorhysis,* possibly *Uintalacus,* and the changes which may be noted are essentially those accompanying a shortening and deepening of the anterior portion of the jaw. In consequence of this we see that both $P_3$ and $P_4$ appear to be reduced to single-rooted teeth. The anterior and posterior roots of both $P_3$ and $P_4$ in *Anemorhysis,* and evidently of $P_4$ in *Uintalacus,* are close together, but in *Trogolemur* it would seem that they have become fused. Moreover, the paraconid and talonid seen in $P_4$ of *Anemorhysis* are more reduced in *Trogolemur.* It is not certain, of course, but probably the difference noted between these forms is not too great for the time interval involved. In southwestern Wyoming this would be represented by the time required for deposition of the Green River formation as it is included in the western part of the Bridger Basin. On the other hand, $P_4$ of *Uintalacus* is much closer in form to that of *Trogolemur* but, unfortunately, nothing is known of the more anterior portion of the jaw in the Green River specimen.

### TROGOLEMUR MYODES Matthew, 1909

Plate 11, figures 1, 2

*Type.*—Right ramus of mandible with C(?)-$M_3$, inclusive, A.M. No. 12599.

*Horizon and locality.*—Lower Bridger (B), middle Eocene, 6 miles south of Granger, Bridger Basin, Wyoming.

*Discussion.*—In addition to the type specimen, which is an unusually well preserved jaw with all but two teeth complete, there is a posterior portion of the left ramus of a mandible in the Marsh collection, Y.P.M. No. 13523, that includes $M_2$, $M_3$, and the talonid portion of $M_1$. These teeth differ in no important way from those in the type, although it was noted that the trigonid of $M_3$ is a trifle more shortened anteroposteriorly. Beneath the teeth, moreover, the jaw, though very incomplete, shows an indication of the increase in depth forward.

In size *Trogolemur myodes* is a little larger than *Anemorhysis sublettensis* or than *T.? tenuiculus,* but smaller than *Tetonius homunculus* and much smaller than *Anaptomorphus aemulus.*

MEASUREMENTS IN MILLIMETERS OF *Trogolemur myodes* LOWER JAWS

| | A.M. No. 12599 Type | Y.P.M. No. 13523 |
|---|---|---|
| Depth of jaw (least) beneath $M_3$, lingually | 3.5 | 3.2 |
| Length of cheek tooth series, C-$M_3$, inclusive | 8.0 | |
| Length of antemolar series, C-$P_4$, inclusive | 2.8 | |
| Length of molar series, $M_1$-$M_3$, inclusive | 5.5 | |
| C, Length : greatest width | 0.8 : 0.75 | |
| $P_3$, Length : greatest width | 1.3 : 1.0 | |
| $P_4$, Length : greatest width | 1.6 : 1.3 | |
| $M_1$, Length : greatest width | 1.9 : 1.4 | : 1.3 |
| $M_2$, Length : greatest width | 1.9 : 1.6 | 1.8 : 1.5 |
| $M_3$, Length : greatest width | 2.3 : 1.4 | 2.1 : 1.3 |

### Genus UINTANIUS Matthew, 1915

*Type.—Uintanius ameghini* (Wortman), 1904.

*Discussion.—Uintanius,* as noted by Matthew, rather closely parallels *Absarokius,* but cannot be derived from that genus as there are certain rather basic differences in the structure of both the premolars and molars which preclude such a relationship. Matthew suggested a dental formula $\frac{?}{?}, \frac{?}{1}, \frac{3}{3}, \frac{3}{3}$, which may be correct, but this presupposes one more premolar than in more typical anaptomorphids.

The third and fourth upper premolars of *Uintanius* are known and these are relatively large with a high primary cusp and a small but distinct parastyle. The latter is better defined on $P^3$. A distinct but relatively small deuterocone is present on the lingual margin of a rather abbreviated talon on each. These teeth resemble those in *Absarokius,* but in the latter genus $P^3$, though comparatively large and inflated appearing, does not have nearly so high a primary cusp, and the talon with its deuterocone is much better developed. $P^4$ of *Absarokius* has a high primary cusp as in *Uintanius,* but here again the talon and deuterocone are much better developed, and the talon shows a posterolingual expansion not seen in *Uintanius.* Anterior to $P^3$ in the known maxilla there is alveolar evidence for a large root which may be for a canine, or possibly $P^2$ as Matthew believed. As has been noted, the maxilla of *Absarokius* from the Knight shows a minute, single-rooted, spikelike tooth immediately anterior to the deuterocone of $P^3$, as well as the single large alveolus placed as in *Uintanius.* Interpretation of this small tooth as a vestigial $P^2$ lends support to the suggestion that the large alveolus in both forms is for the canine. Since these forms are not actually close relatives, however, the homology suggested may not be valid.

The upper molars of *Uintanius* are essentially similar to those of *Absarokius,* exhibiting, as in the latter genus, a simple transversely broad arrangement of the paracone, metacone, and protocone, and with a small but distinct protoconule and metaconule. There is no hypocone but, as on the lingually somewhat broader talons of *Absarokius,* there is a posterior cingulum. The crests from the protocone to the two accessory cuspules are perhaps slightly better defined, although there is less evidence of rugosity about the protocone. $M^3$ in *Uintanius* is not so reduced as in *Absarokius.*

The third and fourth lower premolars have a high primary cusp and $P_4$ is enlarged much as in *Absarokius.* However, in *Uintanius* the anterior crest of these teeth is very much shortened so that the anterior cingulum rises nearly to the top of the primary cusp and the small paraconid is nearly at the level of the primary cusp. Moreover, there is no evidence of a metaconid on $P_4$ of *Uintanius,* whereas this cusp, though of rather small size, can usually be observed on $P_4$ in *Absarokius.*

The anterior portion of the lower jaw offers an interesting problem in identification of alveoli. It is possible that these should be interpreted somewhat at variance with the suggestion of identity derived from the more typical anaptomorphids. Anterior to $P_3$ in *Uintanius*

are three alveoli for comparatively erect anterior teeth. The second of these is appreciably larger than the others and might logically be for a canine, as interpreted by Matthew. This leaves smaller alveoli for a single-rooted $P_2$, and an incisor, about as in *Tarsius*. It should be noted, however, that the anterior extremity of the lower jaw is not complete, so that the presence of two lower incisors by this interpretation is not precluded. In this case the formula would be like that in the omomyids. It is certain, nevertheless, that there was no large, procumbent anterior incisor, such as in *Tetonius, Anemorhysis,* and *Trogolemur*.

The lower molars are rather distinctive in comparison with those of more typical anaptomorphids, particularly in the character of the trigonid. In $M_1$ of *Uintanius,* except for the less inflated appearance of the cusps and crests, the trigonid is not appreciably different. In $M_2$ and $M_3$, however, the distinctive paraconid is median in position and well separated from the metaconid. The talonids of $M_1$ and $M_2$ are simple and *Anaptomorphus*-like but appear a little more deeply basined or better excavated. The talonid of $M_3$, on the other hand, shows a narrower hypoconulid portion that is more distinctly set off from the hypoconid. In general the lower molars, particularly the trigonids, are reminiscent of *Palenochtha*. Torrejonian *Palenochtha,* however, could scarcely be considered ancestral, as it has a more specialized incisor and fewer antemolar teeth.

There is suggestion in the form of the outer wall of the maxillary portion that, as noted in better preserved material of *Washakius* and *Hemiacodon,* the orbit was of comparatively large size. Also, the lower jaw, A.M. No. 12598, shows a gentle convexity to the longitudinal profile of the lower margin and the alignment of the lower cheek teeth is distinctly arcuate in comparison with such forms as, for example, *Omomys*. Two mental foramina of good size were noted, the larger about beneath the alveolus just ahead of $P_3$, and the other beneath the posterior root of $P_3$.

### UINTANIUS AMEGHINI (Wortman), 1904

Plate 10, figures 3-6

*Synonym.—Uintanius turriculorum* Matthew, 1915.

*Type.*—Left ramus of mandible with $M_2$ and $M_3$, Y.P.M. No. 13241.

*Horizon and locality.*—Bridger middle Eocene, Bridger Basin, Wyoming.

*Discussion.*—It is unfortunate that Wortman's type of *Omomys ameghini* should prove to be the same as Matthew's *Uintanius turriculorum,* as Matthew's type specimen is much superior. The very close correspondence of the preserved molars, however, leaves little doubt as to the synonymy of the two. Certain of the special features characterizing the genus, nevertheless, are exhibited only in the dentitions described by Matthew.

No information is available as to the horizon represented by the Marsh specimen Wortman described; however, that which Matthew made the type of *Uintanius turriculorum,* A.M. No. 12598, came from the lower Bridger at Grizzly Buttes, and the referred upper dentition, A.M. No. 13039, was from low in Bridger C at the mouth of "Summers' Dry Creek." A second lower jaw in the American Museum collection, No. 12376, is recorded from Bridger D on Henry's Fork, so that the range certainly includes both upper and lower Bridger.

*Uintanius ameghini* is a species much smaller than *Anaptomorphus aemulus* or *Absarokius noctivagus.* In size of molar teeth it is perhaps closest to *Trogolemur myodes,* which it does not otherwise closely resemble.

MEASUREMENTS IN MILLIMETERS OF *Uintanius ameghini* DENTITIONS

| | A.M. No. 13039 |
|---|---|
| Length of upper cheek tooth series, $P^3$-$M^3$, inclusive | 8.2 |
| Length of upper molar series, $M^1$-$M^3$, inclusive | 4.6 |
| $P^3$, Length: transverse width at cingulum | 2.0: 2.1 |
| $P^4$, Length: transverse width at cingulum | 2.0: 2.3 |
| $M^1$, Length along outer wall: transverse width | 1.8: 2.2 |
| $M^2$, Length along outer wall: transverse width | 1.7: 2.5 |
| $M^3$, Length along outer wall: greatest transverse width | 1.4: 2.2 |

| | A.M. No. 12598 * | A.M. No. 12376 | Y.P.M. No. 13241 Type |
|---|---|---|---|
| Length of lower cheek tooth series, $P_3$-$M_3$, inclusive | 8.8[e] | | |
| Length of lower molar series, $M_1$-$M_3$, inclusive | 6.0[e] | 5.7 | 5.6[e] |
| $P_3$, Length: width across cingulum | 1.3[a]: 1.8 | | |
| $P_4$, Length: width across cingulum | 2.0[a]: 2.0 | | |
| $M_1$, Length: greatest width | 2.1: 1.6 | 2.0: 1.5 | |
| $M_2$, Length: greatest width | 2.0: 1.6 | 1.9: 1.6 | 1.8: 1.4 |
| $M_3$, Length: greatest width | | 2.2: 1.3[a] | 2.0: 1.3 |

* Type of *Uintanius turriculorum.*
[a] Approximate.
[e] Estimated.

## Family APATEMYIDAE Matthew, 1909

The apatemyids are a very distinctive group of mammals, questionably regarded as primates, and have a remarkably long and nearly continuous record in North America from middle Paleocene to lower Oligocene time. Their European range, however, was apparently limited to the Eocene. The Bridger middle Eocene apatemyids, the first of the American forms to be described (Gervais' *Heterohyus* from the European Eocene was known much earlier), together with the newly described *Uintasorex* and *Trogolemur,* were the genera on which Matthew based his family classification. He later included *"Nothodectes"* and *Pronothodectes,* but upon discovering the relationship of the latter two to *Plesiadapis* believed Apatemyidae to be synonymous with Plesiadapidae. The confusion of genera was straightened out by Jepsen (1934) and his revival and redefinition of the family is here followed, except that the family is very tentatively included with the Primates, as suggested but not followed by Matthew and as allocated by Simpson. The North American genera now grouped together in the Apatemyidae from oldest to latest are *Jepsenella, Labidolemur, Teilhardella, Apatemys, Stehlinella,* and *Sinclairella.* Only *Apatemys* is recognized in the Bridger middle Eocene but this genus apparently extends into the upper Eocene where it is a contemporary of *Stehlinella.*

The apatemyids are characterized by a combination of characters which include the strikingly shrewlike development of the lower incisor; a reduced dental formula, probably $\frac{2}{1}, \frac{0}{0}, \frac{2}{2}, \frac{3}{3}$, as suggested by Jepsen (1934) and Simpson (1935b); and a distinctive molar structure. The upper molars are relatively elongate anteroposteriorly and broadly expanded posterointernally with a very well developed hypocone. The lower molars, except for $M_3$, show a simple talonid, but the trigonid, particularly in $M_2$ and $M_3$, shows a distinctive parallelogram arrangement of the cusps and crests. This is effected by the sharp anteroexternal angle made by the crest between the protoconid and paraconid.

### Genus APATEMYS Marsh, 1872

*Type.—Apatemys bellus* Marsh, 1872.

*Discussion.*—No skull or upper teeth are known of *Apatemys;* however, the various lower teeth are represented in partial dentitions of at least a dozen jaws, comprising about four species. As in other apatemyid genera, *Apatemys* exhibits an enlarged, procumbent, shrew-

like lower incisor, much as in *Phenacolemur*. This is followed by a peculiar single-rooted tooth, believed to be $P_3$, that projects forward over the incisor, the same as the tooth in *Stehlinella* that Matthew thought was $P_4$. $P_3$ has a single small cuspule for a talonid and a very extended and bluntly crested anterior portion, as observed in material of *Apatemys rodens*. $P_4$ is much reduced in size and may be single or double rooted.

The lower molars, as indicated by Matthew (1909b), are more like those of primates than those of insectivores. As mentioned above, the trigonids of $M_2$ and $M_3$ show, not a rectangular, but a parallelogram pattern in the direction of the crests and positions of the cusps. The protoconid and metaconid form a high, slightly oblique crest that forms an obtuse angle with the crest extending forward and downward from the protoconid. An anterior crest extends across the front of the trigonid, rising to the paraconid and paralleling the protoconid-metaconid crest. The paraconid is prominent and anterolingual in position. In $M_1$ the trigonid is different in that it narrows forward and the anterolingually placed cusp, assumed to be the paraconid by analogy with the posterior molars, is generally reduced and there may be a small cuspule at the anterior extremity of the crest that extends forward from the protoconid, at the anterior extremity of the tooth. The talonids of $M_1$ and $M_2$ are basined rather as in anaptomorphids, but with the surrounding crest possibly smoother and only the hypoconid clearly defined. The talonid of $M_3$ is, of course, more elongate with a constricted but posteriorly projecting hypoconulid.

### APATEMYS BELLUS Marsh, 1872

Plate 11, figure 5; plate 12, figures 3, 4

*Type*.—Fragment of left ramus of mandible with $M_2$, Y.P.M. No. 13512.

*Horizon and locality*.—Upper Bridger, middle Eocene, near Henry's Fork, Bridger Basin, Wyoming.

*Discussion*.—In addition to the type there are about five Bridger jaw portions at hand that may be referred to this species. A lower jaw, including the basal portion of the incisor but lacking cheek teeth, encountered in the Green River collection may also be of this species. *Apatemys bellus* is a comparatively small form, smaller in size of molar teeth than *Washakius insignis* and larger in this respect than *Uintanius ameghini*. $P_4$, though small and simple, has a slender, more or less elongate crown with two roots generally close together or nearly

fused. The large, procumbent incisor extends back beneath the molars at least as far as the anterior portion of $M_3$. The mental foramen is beneath about the middle of $M_2$.

Measurements of teeth are included with those of *A. rodens.*

### APATEMYS BELLULUS Marsh, 1872

Plate 12, figures 1, 2

*Type.*—Portion of right ramus of mandible with $M_1$-$M_3$, Y.P.M. No. 13513.

*Horizon and locality.*—Upper Bridger, middle Eocene, near Henry's Fork, Bridger Basin, Wyoming.

*Discussion.*—Two lower jaw portions in the American Museum collection may be referred to this species. It is characterized by distinctly smaller teeth than *A. bellus,* and in particular, $P_4$ is relatively more reduced in size and has but a single root. It would appear that the shortening of the crown of this tooth took place essentially through the anterior portion, as there is preserved a small talonid only slightly reduced, relatively, from that in *A. bellus.* The enlarged incisor extends back beneath the teeth as far as below the posterior root of $M_3$, although this may not be distinctive in comparison with *A. bellus.* The mental foramen is beneath about the middle of $M_2$ as in *A. bellus* and may be divided. There is also an unexplained pit or depression higher on the jaw between the root of $P_4$ and the anterior root of $M_1$, much better defined than in *A. bellus.*

Measurements of teeth are included with those of *A. rodens.*

### APATEMYS RODENS Troxell, 1923

Plate 12, figures 5, 6

*Type.*—Left ramus of mandible with the basal part of I, the posterior portion of $M_2$, and $M_3$, Y.P.M. No. 12973.

*Horizon and locality.*—Bridger middle Eocene, Bridger Basin, Wyoming.

*Discussion.*—In addition to the type, described by Troxell from the Marsh collection, there are two jaws in the National Museum collections which undoubtedly represent this species. One of these (pl. 12, fig. 6) is a jaw portion in which most of the third premolar is present, and the other is of an immature individual showing the lower incisor almost complete but only the alveoli for the cheek teeth.

*Apatemys rodens* is a relatively robust form with a deep and massive jaw and a very powerful incisor. Troxell described the species

as having small molars. This is true relative to the size of the jaw and incisor but the molars are actually distinctly larger than in *Apatemys bellus*. The referred material shows that $P_4$ had a moderately large but single and transversely flattened root in one individual and a smaller single and rounded root in the other. $M_3$ in the type shows a relatively shorter talonid with the hypoconulid portion less extended than in referred material of *A. bellus*. In one of the referred specimens of *A. rodens*, U.S.N.M. No. 13277, the very large lower incisor is seen to extend backward beneath the molars at least as far as the posterior margin of $M_3$. The mental foramen may be divided and is below a position between $M_1$ and $M_2$. In the immature jaw there are two foramina slightly farther forward, about beneath $M_1$.

COMPARATIVE MEASUREMENTS IN MILLIMETERS OF BRIDGER *Apatemys* JAWS

| | *A. bellulus* | | *A. bellus* | | | *A. rodens* | |
|---|---|---|---|---|---|---|---|
| | Y.P.M. No. 13513 Type | A.M. No. 12048 | Y.P.M. No. 13512 Type | U.S.N.M. No. 13276 | A.M. No. 12047 | Y.P.M. No. 12973 Type | U.S.N.M. No. 13277 |
| Depth of jaw beneath $M_2$ | | 4.8 | 5.6 | 5.3 | | 9.6 | |
| I, Depth | | 2.5[a] | 3.0[a] | 3.1 | | 5.4 | 6.0[a] |
| I, Width | | 1.3[a] | 1.5[a] | 1.6[a] | | 2.9 | 2.9 |
| $P_3$, Length | | | | | | | 5.0[e] |
| $P_3$, Width | | | | | | | 2.1 |
| $P_4$, Length | 1.1[e] | 1.1 | | 1.5[e] | | | 1.5[e] |
| $P_4$, Width | | 0.8 | | | | | |
| Length of molar series | 5.7 | | | 7.3[e] | 6.5 | 8.0[e] | 8.5[e] |
| $M_1$, Length | 1.8 | 1.7 | | | 2.0 | | |
| $M_1$, Width, overall. | 1.2 | 1.2 | | | 1.4 | | |
| $M_2$, Length | 1.9 | 1.9 | 2.3 | 2.4 | 2.1 | | |
| $M_2$, Width, overall. | 1.5 | 1.4 | 1.6 | 1.7 | 1.4 | | |
| $M_3$, Length | 2.2 | | | 2.9 | 2.7 | 3.0 | |
| $M_3$, Width, overall. | 1.4 | | | 1.8 | 1.6 | 1.9 | |

[a] Approximate.
[e] Estimated.

### APATEMYS DOWNSI,[20] new species

Plate 13, figure 9

*Type*.—Fragment of right ramus of mandible with $P_4$-$M_2$, L.A.C.M. (C.I.T.) No. 5202.

[20] Named for Dr. Theodore Downs, to whose care the Sespe collections are now entrusted.

*Horizon and locality.*—Sespe upper Eocene, upper Uintan, C.I.T. locality 180, Tapo Ranch, north side of Simi Valley, Ventura, County, California.

*Specific characters.*—The type and only known specimen of this species was apparently overlooked by Stock in his study of the Tapo Ranch or locality 180 materials, although the cork to the vial in which the specimen was discovered carries the information "Primate?." The species represented has molars a little larger than in *Apatemys rodens,* and the small $P_4$ has a sturdy single root much as in U.S.N.M. No. 13277 of *A. rodens.* The form and structure of the two anterior molars is essentially as in *A. bellus,* or the smaller *A. bellulus,* except for a weaker paraconid. As a consequence, I believe that *A. downsi* is properly referred to *Apatemys.*

*Apatemys downsi* is very much larger than *Stehlinella uintensis* and $P_4$ has a root very much larger than that suggested by the alveolus in *S. uintensis.* Detailed comparison of $M_1$ shows that the trigonid portion in *A. downsi* is relatively broader anteriorly and has both an anterointernal and anteroexternal cusp. In *Stehlinella* the anterointernal cusp or paraconid is absent. Talonids of both $M_1$ and $M_2$ of *A. downsi* appear relatively shorter and broader, and with a more distinctive hypoconid than in the Uinta type.

Measurements of the teeth are included with those of *Stehlinella uintensis.*

### Genus STEHLINELLA Matthew, 1929

*Type.*—*Stehlinella uintensis* (Matthew), 1921.

*Discussion.*—Matthew described *Stehlinella* as distinct from *Apatemys* under the mistaken impression that the large premolar that laps over the base of the lower incisor in the Uinta specimen was homologous with the small $P_4$ in *Apatemys,* and that there was a reduction in the cheek teeth further than in *Apatemys.* It is now known that these conditions do not hold, and that *Stehlinella* is scarcely, if at all, distinct from *Apatemys.* Justification for retaining the genus, however, may be seen in small differences in the pattern of the lower molars, such as the more reduced trigonid of $M_1$ and the more elongate talonids of $M_1$ and $M_2$, noted in comparison with Bridger apatemyids. The small size of $P_4$ noted by Jepsen may be a valid difference or character, but close examination of the alveolus leads me to suspect that the tooth was lost during life and that subsequent bone deposition has partially closed the alveolus. The probability that the genera are distinct is, nevertheless, strengthened by the sig-

nificant difference in age. It is hoped that future collecting in the Bridger may yield better apatemyid materials so that relationships may be more clearly demonstrated.

### STEHLINELLA UINTENSIS (Matthew), 1921

*Type.*—Anterior portion of skull with part of the upper dentition, and the right ramus of the mandible with all teeth except $P_4$, A.M. No. 1903.

*Horizon and locality.*—"Upper Eocene (Uinta) of White River," Uinta Basin, Utah.

*Discussion.*—*Stehlinella uintensis* is a comparatively small form, close in size to *Apatemys bellus,* but with more slender lower molars. The type skull portion and jaw are the only known materials. The specimen is currently on exhibition at the American Museum and, of course, could not be removed for any extended time so that new illustrations of it were not prepared for this review.

COMPARATIVE MEASUREMENTS IN MILLIMETERS OF TEETH IN UPPER EOCENE *Apatemys* AND *Stehlinella* JAWS

| | *Apatemys downsi* L.A.C.M. (C.I.T.) No. 5202 Type | *Stehlinella uintensis* A.M. No. 1903 Type |
|---|---|---|
| $P_4$, Length : width | 1.2 : 0.8 | |
| $M_1$, Length : width, overall | 2.5 : 1.8 | 2.1 : 1.4 |
| $M_2$, Length : width, overall | 2.8 : 2.0 | 2.3 : 1.4[a] |
| $M_3$, Length : width, overall | | 2.6 : 1.5 |

[a] Approximate.

## SUMMARY OF RELATIONSHIPS OF NORTH AMERICAN FOSSIL PRIMATES

*Notharctidae.*—Although, as I have elsewhere discussed, the notharctids must surely represent a family separate from the adapids, because of the many, rather basic structural differences, both, nevertheless, are distinctly lemuroid in character. On this basis alone, possibly within the superfamily arrangement of Simpson, they may be considered as related. The fact, however, should not be lost sight of that there is a rather strong resemblance between families of Eocene primates that ties them more together than to remote groups of living descendants. Separation between them, moreover, into superfamily or subordinal groups to show relationships to various modern families tends to overemphasize these differences.

The modern lemurs may well have been derived from some member of the Adapidae, but evidently not from *Adapis* itself. All considered, however, there is a certain futility involved in discussing relationships of the Malagasian fauna without some information on the earlier Tertiary of either Madagascar or Africa. It is evident, nevertheless, that neither *Notharctus* nor *Smilodectes* were involved in the descent of modern lemurs.

Much thought has been given by paleontologists to the possibility that the notharctids gave rise to the ceboid primates. The possibility persists, but I am rather more inclined to regard the omomyids in this relationship and to consider the notharctids as having become extinct, possibly at the end of Bridgerian time.

Neither the Notharctidae nor the Adapidae are known prior to Eocene time, so that speculation as to their origin is futile. With the development of our knowledge of North American Paleocene faunas, however, it is becoming increasingly probable that they did not originate in this area. For this reason we should regard notharctids as immigrants, arriving here about the beginning of Eocene time, presumably from some other continent.

Within the Notharctidae there seems no doubt but that *Notharctus* was derived from *Pelycodus*. *Smilodectes,* however, though clearly a notharctid, exhibiting rather numerous resemblances to *Notharctus* and *Pelycodus,* may not certainly be derived from known *Pelycodus*. This situation is further discussed in the systematic portion of this paper, that is, the peculiar course of the crista obliqua of $M_3$ in *Smilodectes* was not certainly detected in any *Pelycodus* material. Although the hiatus represented by Bridger A time may be entirely adequate for such a change, a slight change in tooth pattern that is actually of no great moment, it seems preferable to consider that isolation was involved in protecting the divergent specializations observed. *Smilodectes,* for this reason, possibly did not evolve from *Pelycodus* of the Rocky Mountain region.

*Omomyidae.*—The relationships of the Omomyidae would appear to be closest to the anaptomorphids among the contemporary North American forms. A somewhat closer tie, however, may exist with the European Necrolemuridae, although the latter for the most part appear to have a more reduced dental formula. The closest relationship between these groups may well be between *Omomys* and *Teilhardina,* evidently the more primitive of the European assemblage, although there is a suggestion of parallelism between *Hemiacodon* and such forms as *Nannopithex* in molar structure. Nevertheless,

| PALEOCENE | | | EOCENE | | | | | | | OLIGOCENE |
|---|---|---|---|---|---|---|---|---|---|---|
| Torrejonian | Tiffanian | Clarkforkian | Wasatchian | | Bridgerian | | Uintan | | Duchesnean | Chadronian |
| Torrejon & Lebo | Tiffany & Melville | Clark Fork & Almy | Gray Bull & Lysite | Last Cabin & Knight | L.Bridger(incl. Huerfano B) | U.Bridger | L. Uinta & Poway | U. Uinta & Sespe (Tapo) | Duchesne River Sespe(Pearson) | Chadron |
| | | | | | | *Notharctus* | | | | |

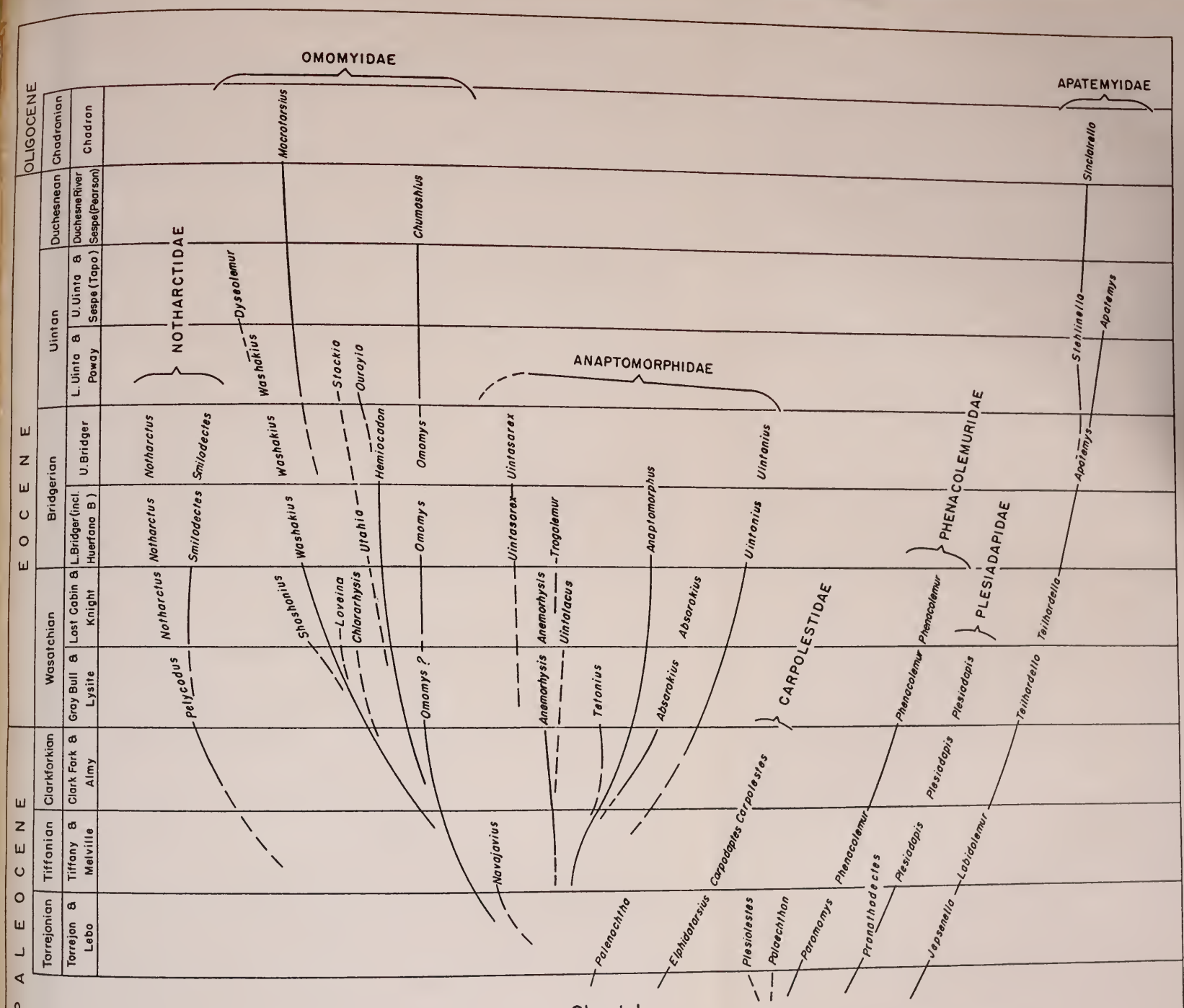


Chart I

Diagrammatic arrangement of North American early Tertiary primates, showing their stratigraphic succession and a tentative interpretation of relationships.

Inclusion of the Apatemyidae in this schematic is very tentative.

these family groups apparently have evolved quite independently from possibly common Paleocene antecedents. The relationships of the Omomyidae to the Anaptomorphidae may not be as close as would seem implied by the earlier classification in which these were regarded as parts of the same family. The reduced dental formula coupled with important differences in molar structure suggests somewhat more than subfamily separation, and likewise warrants recognition of the Omomyidae as distinct from the Necrolemuridae. There remains, moreover, the possibility that the reduction in number of lower teeth in the Anaptomorphidae, assumed to be loss of $P_2$, may be loss of the lower canine, a tooth usually of significant development in the omomyids.

Within the Omomyidae, *Omomys* is seen to be a long-lived stem first recognized in *Omomys vespertinus* and *Omomys minutus* of the lower Eocene, culminating, as far as known, in Duchesnean *Chumashius*. Simpson has suggested that *Omomys vespertinus* may be *Loveina* but the root portions of the lower premolars of *O. vespertinus* show that these teeth were not shortened as in *Loveina*. *Loveina,* though differing in important respects from *Shoshonius,* such as in the absence of a metastylid on the lower molars and the better closure of the talonid basin lingually, bears a strong resemblance to this genus. *Shoshonius* might well be regarded as an ancestor of *Washakius,* were it not for the mesostyle of the upper molars. It should be noted, moreover, that a lower jaw of *Shoshonius* in the collections of the University of Wyoming shows that the lower premolars in this genus, as might be expected, very closely resemble those in both *Lovcina* and *Washakius*. For these reasons both *Loveina* and *Shoshonius* are shown nearer the line of *Washakius,* but evidently neither were ancestral to it.

*Washakius* is perhaps the most peculiarly specialized of the omomyids. The general or overall tooth pattern seems comparatively primitive but there is a strong tendency toward development of accessory cuspules (suggestive of *Microchoerus*), as well as a marked rugosity. Although the premolars are short and perhaps more crowded than in *Omomys,* the lower incisors are small and of equal size. *Washakius* is first recognized in the lower Bridger but continues into lower Uintan time. Sespe *Dyseolemur* is surely a descendant though noticeably modified, particularly in the shortening and broadening of the cheek teeth.

*Hemiacodon* would appear to be somewhat more closely related to *Omomys* than is *Washakius*. Possibly it would not have been clearly

distinguished from *Omomys* in earlier Wasatchian time, although I suspect that their convergence was somewhat farther back. It resembles *Washakius* in rugosity of the tooth enamel but has developed its own tooth pattern in which the width of the talonid and shortness of the molar trigonids characterize the lower teeth.

*Utahia* apparently preceeds *Hemiacodon* in time and would seem closely related, although I do not believe it is ancestral to *Hemiacodon*. The anteroposterior compression of the trigonid in $M_2$ and $M_3$ would appear rather advanced for *Hemiacodon* at this stage (lower(?) Bridger). This is a condition more suggestive of an ancestral relationship to *Stockia*.

*Ourayia* is structurally a good successor to *Hemiacodon* but the modification, particularly of $M_2$, seems a little abrupt, so that it may possibly have originated a little lower on the *Hemiacodon* stem. *Stockia* rather markedly parallels *Ourayia* but with its own distinctive features and may well be derived from the *Hemiacodon* stem somewhat earlier than *Ourayia,* possibly through *Utahia*. These four, *Hemiacodon, Utahia, Ourayia,* and *Stockia,* seem to me to be a general group within the Omomyidae which may well have given rise to the ceboids. Nevertheless, earlier *Loveina* and *Chlororhysis* might also be considered as potentially in this relationship. Although *Omomys* appears favorably characterized by its molar structure, the greater disparity in size of the two incisors presents difficulties. *Washakius,* on the other hand, is potentially better in this respect and may well have been the focal point; the molars, however, show a rather aberrant trend. Possibly more than one group of Eocene omomyids was involved.

Oligocene *Macrotarsius* has been compared by Clark (1941) with *Hemiacodon,* but the strong V-shaped arrangement of the trigonid cusps and crests of the lower molars does not appear to be the *Hemiacodon* trend. Although rather more suggestive of *Washakius* in this one respect, even greater difficulties are involved in attempting to derive *Macrotarsius* directly from *Washakius*. I have indicated *Macrotarsius* in the chart as somewhat intermediate between these two stems and find that the only form which possesses most of the necessary characteristics, as far as known, is much earlier *Loveina*.

Simpson (1940) has suggested including *Navajovius* among the omomyids. While this may seem justified from certain aspects of the molar structure, the trigonid of the lower molars is unusual and almost apatemyidlike. The absence from the lower series of a tooth believed to be the canine and the presence of only one incisor, together

with a large $P_2$, make family allocation questionable. In any case the reduced dental formula precludes derivation from it of any of the better known omomyids.

*Anaptomorphidae.*—It is clear that the anaptomorphids, as here limited, could not have been involved in the descent of the tropical American primates. Their reduced dentition and aberrant specializations preclude such a possibility. It is probable, moreover, that they did not survive after Bridgerian time, although this cannot be demonstrated. Their origin is uncertain but it would seem probable that they were derived during Paleocene time from the less specialized omomyids. No true anaptomorphids of the type here included in the restricted family arrangement are known in the European early Tertiary; on the other hand, such forms as *Palenochtha,* and possibly *Navajovius,* in the Rocky Mountain Paleocene might indicate that the anaptomorphids were of North American origin.

Among the Eocene forms *Anaptomorphus* would appear to be the least specialized, and closely related but earlier *Tetonius* and *Absarokius* show somewhat divergent tendencies. *Anemorhysis* and *Uintalacus* exhibit a molar structure which seems closely related to that of *Tetonius,* but the premolars are less or differently specialized. *Trogolemur* is evidently closely related to *Anemorhysis* and *Uintalacus,* and almost certainly derived from near these. *Uintanius* shows a specialization which rather parallels that of *Absarokius* but is clearly not a descendant. In its molar pattern, the trigonids of the lower series are rather strikingly reminiscent of *Palenochtha.* I suspect that the resemblance is more than casual, although *Palenochtha* apparently had a rather large procumbent lower incisor, precluding a direct ancestral relationship. *Uintasorex* is the least easily reconciled of those included in the family. Its specialization in the anterior part of the lower dentition quite parallels that of *Anemorhysis* and *Trogolemur,* but the molars, upper and lower, though not too different from those of other anaptomorphids, exhibit a structure which seems rather suggestive of omomyids.

*Carpolestidae, Phenacolemuridae, and Plesiadapidae.*—While these families are not represented in the Bridgerian, Uintan, or Duchesnean faunas, they are shown in the general chart for the North American sequence and hence require a word of explanation.

The Carpolestidae are strangely specialized primates with an almost *Ptilodus*-like fourth lower premolar, exhibiting an incipient stage in middle Paleocene *Elphidotarsius,* but reaching full development in upper Paleocene *Carpodaptes* and *Carpolestes.* A lower-molar struc-

ture is exhibited that suggests in some ways that they may not be far removed from the Anaptomorphidae. Indeed the lower premolar specialization would seem to foreshadow that seen to a much lesser degree and at a much later time in *Absarokius* and *Uintanius*. $P^4$, however, is very differently developed than in these and appears incipiently "multituberculate." The special features and relationships of this family have been rather thoroughly considered by Simpson (1935b and 1940). They are peculiar to North America and not known after Paleocene time.

The phenacolemurids, as well as the carpolestids, are peculiarly North American, as far as the record is known. Their lower Eocene representation would appear to be late survival in one line of a rather diversified group of related middle Paleocene forms. While having developed a very shrewlike lower incisor, much as in the apatemyids, the molar structures are rather distinctive and clearly primate, perhaps closest to those of the plesiadapids. The Phenacolemuridae was recently proposed by Simpson (1955) to include essentially those forms which he had originally allocated to the Paromomyinae but with the addition of *Phenacolemur*. Possibly Jepsen's *Plesiolestes* belongs here, as Simpson (1937b) believed that it was very close to *Palaechthon*. *Palenochtha,* which he later regarded as probably not a phenacolemurid, I have shown as tentatively included with the anaptomorphids.

The Plesiadapidae is the only Primate family known in the Paleocene of Europe, at a level corresponding to our Tiffanian. There is no question, however, as to the ancestral position of *Pronothodectes* in the middle Paleocene of North America. From the presently known distribution it would seem that following *Pronothodectes, Plesiadapis* became widely dispersed in the Northern Hemisphere during upper Paleocene time but lived only into the earliest part of the Eocene in North America. In Europe the family survived into lower and middle Eocene time represented by the succeeding genera *Platychoerops* and *Megachiromyoides*. Plesiadapids are by all odds the most abundantly represented of the Paleocene primates in North America. In some Tiffanian faunas plesiadapids may actually outnumber other mammalian forms in remains encountered. The confused relationship between the plesiadapids and apatemyids was clarified by Jepsen (1934), whereas the most detailed description of *Plesiadapis* proper was made by Simpson (1935a).

In the accompanying chart it may be noted that *Pronothodectes* is shown in part contemporaneous with *Plesiadapis*. This situation was

observed (Gazin, 1956a) in the earliest of the Tiffanian horizons represented in the Bison Basin sequence.

*Apatemyidae.*—It is not generally agreed that the apatemyids are primates and although Matthew (1909b) in proposing the family designation regarded them as belonging to the Insectivora, essentially because of the shrewlike anterior lower tooth, he was impressed by the primatelike appearance of the molars. Jepsen (1934), in his revision of the apatemyids, preferred to retain them in the Insectivora, as does Hürzeler, with apparently good reason. However, I have followed Simpson in retaining them tentatively in the Primates because of their molar form, and partly because I suspect that they were basically of remote primate origin and may very early have become adapted to a shrewlike habitat that was possibly not arboreal. Such a view is, of course, highly speculative, and is advanced only in an attempt to account for certain paradoxical features.

The record of the apatemyids is first revealed in the middle Paleocene genus *Jepsenella* from the upper Lebo of Montana. The sequence is then represented by Tiffanian *Labidolemur,* Wasatchian *Teilhardella* to Bridgerian *Apatemys.* Quite possibly the North American sequence then divided and the later *Stehlinella* to Oligocene *Sinclairella* line may well have arisen from the smaller *Apatemys bellulus* with the more reduced $P_4$. The large apatemyid in the upper Eocene of southern California represents survival from possibly the larger form, *A. bellus,* or perhaps *A. rodens.*

Presumably at about the end of Paleocene time the family became widely distributed and is represented in the lower Eocene of Europe by the genus *Eochiromys* followed by *Heterohyus* and related forms in the middle and upper Eocene. It is not certain that the daubentoniids are to be derived from the apatemyids. It has been suggested, no doubt correctly, that they originated closer to the Malagasian lemurs. In any case, the Eocene and later North American forms were not involved in this problem. It is particularly noted that the anterior lower tooth in the American sequence was, as far as known, extremely procumbent, with an almost horizontal root beneath the cheek teeth and with little or no curvature (except for a slightly arcuate crown). The later forms of the European Eocene, as illustrated by Stehlin, show a more arcuate condition with the crown more erect, much more rodentlike than in the American sequence, approaching in form (evidently an instance of parallelism) the extremely rodentlike conditions seen in *Daubentonia* where the tooth grows continuously from persistent pulp. *Daubentonia* is an arboreal primate, and though exhibiting unusual dental features, has a basically lemuroid skull.

*Mixodectidae.*—This family is currently allocated to the Insectivora, although it was earlier regarded as more properly primate in its affinities. It was considered primate by Wortman, but Matthew objected on the grounds that certain Paleocene foot material believed to be associated with a mixodectid jaw precluded a primate relationship. Wortman, however, did not regard the association as valid. Inasmuch as a study of this family has apparently been undertaken elsewhere, its affinities have not been investigated for this report.

## DISCUSSION OF PLATYRRHINE RELATIONSHIPS

One of the most impressive lessons learned from a study of primates is the very deep-seated effect that an arboreal adaptation has on the morphology of the animal. It is possibly exceeded only by the effect resulting from adaptation to flight and to that of an aquatic life. The various specializations acquired through adaptations to a variety of ground-living conditions or habits are much less distinctive. Much has been written regarding the modifications of the foot for an arboreal existence, but emphasis should also be placed on the modification or morphological change related to the forward position of the eyes that must surely be related to this habitat. Undoubtedly the advantages of binocular vision are keenly appreciated where depth of vision is so important as it is among branches of trees, and especially with the more nocturnal forms. The effect of such greatly modifying adaptive factors in both the skull and feet would be to bring about marked convergence in forms of unrelated or remotely related origins, and to result in strikingly parallel development in related groups distinguished or separated in an early dispersion.

As a result of the first of these conditions, it should be very difficult after an extended period of geologic time to distinguish between different origins where possibly more than one kind of animal has taken to the trees. This, of course, leads to the suggestion that the primate order may be polyphyletic, and such indications as may exist can probably be verified only through a more adequate paleontological record. For example, in reviewing the various groups included among the primates, perhaps the most questionable are the tupaiids. These show a number of primate characters, but their teeth do not appear to be of primate origin. The molars seem surprisingly marsupial-like. Might not this be an instance in which a group from a different order, by later adaptation, has had impressed upon it several characteristics resulting from an arboreal life? This would seem to me to be a question which goes beyond a simple matter of definition. The lorisids,

moreover, though more than likely primate in origin, show rather fundamental structural differences in comparison with both tarsiids and lemurs, particularly in the basicranium, that are contrasted with striking adaptive similarities.

The second of the above conditions cited, that of parallel development, is surely exemplified in the similarity between the platyrrhine and catarrhine monkeys. They undoubtedly resemble each other superficially or in gross detail more than they do their remote ancestors. Moreover, I am strongly convinced, in agreement with Patterson (1954), that they have evolved quite separately from distinct Eocene families. These families, moreover, may have been somewhat more "tarsiidlike" than the descendants. Deep-seated differences that evidently go back to Eocene time include, in addition to a more reduced dental formula, development of the annulus into a long audital tube in the Old World forms. Such features, on the other hand, as those related to the more forward position of the eyes are believed to be adaptive, so that the partition between the temporal and orbital fossae suggesting a close relationship between the lines, was probably, as in the tarsiers, quite independently developed. Separate origin of this partition in the platyrrhines and catarrhines, as well as in the tarsiers, seems evident in the different arrangement and relative development of the bones participating. Moreover, aside from very cogent geographic indications, discussed under environment, the North American Eocene fauna is not without potential ancestry for the western or platyrrhine group. Also, the catarrhines are almost certainly to be derived from one of the Old World Eocene groups and not from the Omomyidae or the platyrrhine monkeys. Recognition of this, of course, rather weakens the ordinal arrangement currently subscribed to in which both the Old and New World monkeys are included in the same suborder, different from that of the Eocene forms.

With regard to the tarsiers, quite aside from the determinations of Le Gros Clark, Osman Hill, and others, I see no escape from the conclusion that these highly specialized forms represent, nevertheless, relictlike survival in decidedly peripheral areas of the Old World of one of the Eocene forms in or near the Necrolemuridae, possibly more closely related to the Old World anthropoids than they are to the lemurs. There seems to be some support for this latter possibility in the embryological work of J. P. Hill (1932) in which "anthropoid" derivation from a "tarsioid" stage is suggested, but I would make the further suggestion that the "pithecoid" stage must have been divided at least as far back as the Eocene "tarsioid" forms and to have evolved in parallel lines.

Reviewing the North American groups for possible platyrrhine ancestry, we may dismiss without further consideration the Apatemyidae, Phenacolemuridae, Plesiadapidae, Carpolestidae, and evidently the Anaptomorphidae as here constituted. This leaves only the Notharctidae and Omomyidae fulfilling one rather basic requirement, that of having a sufficient number of teeth. Much has been said by Wortman, Gregory, Gidley, and others regarding the possibility of *Notharctus* filling this role.[21] However, detailed study of the dentitions of western omomyids, leading me to distinguish them as a separate family, has indicated that they possess greater potentiality than the notharctids for a direct platyrrhine relationship. Wortman (1904) greatly stressed the probability of this relationship in the case of *Omomys*. For this reason, I fail to see the necessity for attempting to derive the platyrrhines from a possible primate with three premolars in the Eocene of Burma. The skull structure of the lorisids would seem to remove their line from serious consideration, although the latter idea has not lacked proponents.

In conclusion I may add that while I do not propose to add a new version to the growing list of primate classifications, I feel there is a certain absurdity in attempting to force the complex of early Tertiary forms of both the Eastern and Western Hemispheres into a subordinal arrangement based essentially on the present terminal forms of the few surviving lines; a classification, moreover, that I believe does not take full cognizance of the extent to which parallelism seems to have taken place.

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## EXPLANATION OF PLATES

### Plate 1

*Notharctus* and *Smilodectes* from the Bridger middle Eocene

Figs. 1, 2, 3, 5, 6. *Smilodectes gracilis* (Marsh): 1, Skull (Y.P.M. No. 12152), type of *Aphanolemur gibbosus* Granger and Gregory. 2, Skull (U.S.N.M. No. 21815). 3, Skull (U.S.N.M. No. 17994). 5, Skull (U.S.N.M. No. 17995). 6, Skull (U.S.N.M. No. 17996). Dorsal views. Two-thirds natural size. Bridger Basin, Wyoming.

Fig. 4. *Notharctus tenebrosus* Leidy: Skull (A.M. No. 11466), type of *Notharctus osborni* Granger and Gregory, dorsal view. Two-thirds natural size. Bridger Basin, Wyoming.

### Plate 2

*Notharctus* and *Smilodectes* from the Bridger middle Eocene

Figs. 1, 2, 3, 5. *Smilodectes gracilis* (Marsh): 1, Skull (Y.P.M. No. 12152), type of *Aphanolemur gibbosus* Granger and Gregory. 2, Skull (U.S.N.M. No. 21815). 3, Skull (U.S.N.M. No. 17794). 5, Skull (U.S.N.M. No. 17995). Lateral views. Two-thirds natural size. Bridger Basin, Wyoming.

Fig. 4. *Notharctus tenebrosus* Leidy: Skull (A.M. No. 11466), type of *Notharctus osborni* Granger and Gregory, lateral view. Two-thirds natural size. Bridger Basin, Wyoming.

### Plate 3

*Notharctus* and *Smilodectes* from the Bridger middle Eocene

Figs. 1, 2. *Smilodectes gracilis* (Marsh): 1, Skull (U.S.N.M. No. 17996). 2, Skull (U.S.N.M. No. 17994). Ventral views. Natural size. Bridger Basin, Wyoming.

Fig. 3. *Notharctus tenebrosus* Leidy: Skull (A.M. No. 11466), type of *Notharctus osborni* Granger and Gregory, ventral view. Natural size. Bridger Basin, Wyoming.

### Plate 4

*Notharctus* and *Hemiacodon* from the Bridger middle Eocene

Figs. 1-3. *Notharctus tenebrosus* Leidy: 1, Skull (U.S.N.M. No. 21864), dorsal view. 2, Skull and mandible (U.S.N.M. No. 21864), lateral view. 3, Skull (U.S.N.M. No. 21864), ventral view. Natural size. Bridger Basin, Wyoming.

Fig. 4. *Hemiacodon gracilis* Marsh: Frontal portion of skull (U.S.N.M. No. 21878), dorsal view. Natural size. Bridger Basin, Wyoming.

## Plate 5

*Notharctus* and *Smilodectes* from the Bridger middle Eocene

Figs. 1, 4. *Smilodectes gracilis* (Marsh): 1, Right upper cheek teeth (U.S.N.M. No. 21862), occlusal view, twice natural size. 4, Left ramus of mandible (Y.P.M. No. 11800), type specimen; lateral view, natural size; occlusal view, nearly twice natural size (7/4). Bridger Basin, Wyoming.

Figs. 2, 5. *Notharctus tenebrosus* Leidy: 2, Right upper cheek teeth (U.S.N.M. No. 13230), occlusal view, twice natural size. 5, Right ramus of mandible (U.S.N.M. No. 3752), type specimen; lateral view, natural size; occlusal view, twice natural size. Bridger Basin, Wyoming.

Figs. 3, 6, 7. *Notharctus robustior* Leidy: 3, Left upper cheek teeth (U.S.N.M. No. 12014), occlusal view, twice natural size. 6, Right ramus of mandible (U.S.N.M. No. 13238); lateral view, natural size; occlusal view, twice natural size. 7, Left ramus of mandible (U.S.N.M. No. 3750), type specimen; lateral view, natural size; occlusal view of $M_2$, nearly twice natural size (9/5). Bridger Basin, Wyoming.

## Plate 6

*Omomys* from the middle and lower Eocene

Figs. 1-7. *Omomys carteri* Leidy: 1, Right and left maxillae (Y.P.M. No. 13228-1), occlusal view of cheek teeth. 2, Right maxilla (Y.P.M. No. 13225-3), occlusal view of molars. 3, Left maxilla (Y.P.M. No. 11813), type of *Euryacodon lepidus* Marsh, occlusal view of teeth. 4, Right maxilla (A.M. No. 12041), occlusal view of cheek teeth. 5, Left maxilla (Y.P.M. No. 11854), type of *Palaeacodon vagus* Marsh, occlusal view of molars. 6, Left maxilla (U.S.N.M. No. 17797), occlusal view of teeth. 7, Right maxilla (Y.P.M. No. 13229-2), occlusal view of teeth. Four times natural size. Middle Eocene, Bridger Basin, Wyoming.

Fig. 8. *Omomys vespertinus?* Matthew: Left maxilla (A.M. No. 16213), occlusal view of teeth. Four times natural size. Lower Eocene, San Juan Basin, New Mexico.

## Plate 7

*Omomys* from the middle and lower Eocene

Fig. 1. *Omomys vespertinus* Matthew: Left lower molars (A.M. No. 16835), type specimen, occlusal view. Four times natural size. Lower Eocene, Big Horn Basin, Wyoming.

Figs. 2-6. *Omomys carteri* Leidy: 2, Right lower cheek teeth (U.S.N.M. No. 13290), occlusal view. 3, Right ramus of mandible (Y.P.M. No. 11804), type of *Omomys pucillus* (Marsh), lateral and occlusal views. 4, Right ramus of mandible (Y.P.M. No. 11805), type of *Hemiacodon nanus* Marsh, lateral and occlusal views. 5, Right ramus of mandible (A.N.S. No. 10335), type specimen, lateral and occlusal views. 6, Left ramus of mandible (U.S.N.M. No. 13289), lateral and occlusal views. All four times natural size. Middle Eocene, Bridger Basin, Wyoming.

## Plate 8

*Hemiacodon* from the Bridger middle Eocene

Figs. 1-5. *Hemiacodon gracilis* Marsh: 1, Right maxilla (Y.P.M. No. 12976-2), occlusal view of cheek teeth. 2, Left ramus of mandible (Y.P.M. No. 13204-1, showing C to $P_4$), lateral view. 3, Right maxilla (U.S.N.M. No. 17730), occlusal view of teeth. 4, Right ramus of mandible (Y.P.M. No. 11806), type specimen, lateral and occlusal views. 5, Right ramus of mandible (A.M. No. 18991), lateral and occlusal views. All four times natural size. Bridger Basin, Wyoming.

## Plate 9

*Washakius* from the Bridger middle Eocene

Figs. 1-8. *Washakius insignis* Leidy: 1, Left maxilla (Y.P.M. No. 13235-5), occlusal view of teeth. 2, Left maxilla (U.S.N.M. No. 17795), occlusal view of teeth. 3, Right maxilla (Y.P.M. No. 13235-2), occlusal view of teeth. 4, Left ramus of mandible (Y.P.M. No. 13235-2), lateral and occlusal views. 5, Left $M^2$ (Y.P.M. No. 13238), type of *Hemiacodon pygmaeus* Wortman, occlusal view. 6, Right $M_2$ and $M_3$ (A.N.S. No. 10332), type specimen, occlusal view. 7, Left ramus of mandible (Y.P.M. No. 13236-1), lateral and occlusal views. 8, Right ramus of mandible (U.S.N.M. No. 18013), lateral and occlusal views. All four times natural size. Bridger Basin, Wyoming.

## Plate 10

*Anaptomorphus* and *Uintanius* from the Bridger middle Eocene

Fig. 1. *Anaptomorphus aemulus* Cope: Left ramus of mandible (A.M. No. 5010), type specimen, lateral and occlusal views. Three times natural size. Bridger Basin, Wyoming.

Fig. 2. *Anaptomorphus wortmani,* new species: Right ramus of mandible (Y.P.M. No. 13233), lateral and occlusal views. Three times natural size. Bridger Basin, Wyoming.

Figs. 3-6. *Uintanius ameghini* (Wortman): 3, Right ramus of mandible (A.M. No. 12598), type of *Uintanius turriculorum* Matthew, lateral and occlusal views. 4, Left ramus of mandible (Y.P.M. No. 13241), type specimen, lateral and occlusal views. 5, Left maxilla (A.M. No. 12598), occlusal view of upper cheek teeth. 6, Right ramus of mandible (A.M. No. 12376), lateral and occlusal views. Four times natural size. Bridger Basin, Wyoming.

## Plate 11

*Trogolemur, Uintasorex,* and *Apatemys* from the Bridger middle Eocene

Figs. 1, 2. *Trogolemur myodes* Matthew: 1, Right ramus of mandible (A.M. No. 12599), type specimen, lateral and occlusal views. 2, Left ramus of mandible (Y.P.M. No. 13523), lateral and occlusal views. Five times natural size. Bridger Basin, Wyoming.

Figs. 3, 4. *Uintasorex parvulus* Matthew: 3, Right ramus of mandible (A.M. No. 12052), type specimen, lateral and occlusal views. 4, Right ramus of mandible (Y.P.M. No. 13519), lateral and occlusal views. Six times natural size. Bridger Basin, Wyoming.

Fig. 5. *Apatemys bellus* Marsh: Left ramus of mandible (A.M. No. 12047), lateral and occlusal views. Five times natural size. Bridger Basin, Wyoming.

## Plate 12

*Apatemys* from the Bridger middle Eocene

Figs. 1, 2. *Apatemys bellulus* Marsh: 1, Right ramus of mandible (Y.P.M. No. 13513), type specimen, lateral and occlusal views. 2, Left ramus of mandible (A.M. No. 12048), lateral and occlusal views. Five times natural size. Bridger Basin, Wyoming.

Figs. 3, 4. *Apatemys bellus* Marsh: 3, Left ramus of mandible (U.S.N.M. No. 13276), lateral and occlusal views. 4, Left ramus of mandible (Y.P.M. No. 13512), type specimen, lateral and occlusal views. Five times natural size. Bridger Basin, Wyoming.

Figs. 5, 6. *Apatemys rodens* Troxell: 5, Left ramus of mandible (Y.P.M. No. 12973), type specimen, lateral and occlusal views. 6, Left ramus of mandible (U.S.N.M. No. 13277), lateral and occlusal views. Twice natural size. Bridger Basin, Wyoming.

## Plate 13

Upper Eocene primates from California and Utah

Figs. 1, 2. *Chumashius balchi* Stock: 1, Left ramus of mandible (L.A.C.M. [C.I.T.] No. 1391), type specimen, lateral and occlusal views. 2, Left $M^2$ and $M^3$ (L.A.C.M. [C.I.T.] No. 1394), occlusal view. Four times natural size. Sespe (Pearson Ranch), California.

Figs. 3, 4, 5. *Dyseolemur pacificus* Stock: 3, Right ramus of mandible (L.A.C.M. [C.I.T.] No. 1395), type specimen, lateral and occlusal views. 4, Left $M^2$ and $M^3$ (L.A.C.M. [C.I.T.] No. 1528), occlusal view. 5, Left $M^2$ and $M^3$ (L.A.C.M. [C.I.T.] No 5191), occlusal view. Four times natural size. Sespe (Tapo Ranch), California.

Fig. 6. *Stockia powayensis,* new genus and species: Right ramus of mandible (L.A.C.M. [C.I.T.] No. 2234), type specimen, lateral and occlusal views. Four times natural size. Poway conglomerate, California.

Fig. 7. *Washakius woodringi* (Stock): Right $M^1$ and $M^2$ (L.A.C.M. [C.I.T.] No. 2233), type specimen, occlusal view. Four times natural size. Poway conglomerate, California.

Fig. 8. *Ourayia uintensis* (Osborn), new genus: Left ramus of mandible (A.M. No. 1899), type specimen, lateral and occlusal views. Three times natural size. Uinta Basin, Utah.

Fig. 9. *Apatemys downsi,* new species: Right ramus of mandible (L.A.C.M. [C.I.T.] No. 5202), type specimen, lateral and occlusal views. Five times natural size. Sespe (Tapo Ranch), California.

## Plate 14

Green River and Knight primates

Figs. 1, 2. *Uintasorex parvulus* Matthew: 1, Composite of left ramus of mandible including $P_4$ and $M_1$ (C.M. No. 6414) and left $M_2$ and $M_3$ (C.M. No. 6415), lateral and occlusal views. 2, Composite left upper molar series (C.M. No. 6419), occlusal view. Six times natural size. Upper fossiliferous zone, Green River formation, middle Eocene, Uinta Basin, Utah.

Fig. 3. *Utahia kayi,* new genus and species: Right ramus of mandible (C.M. No. 6488), type specimen, lateral and occlusal views. Four times natural size. Upper fossiliferous zone, Green River formation, middle Eocene, Uinta Basin, Utah.

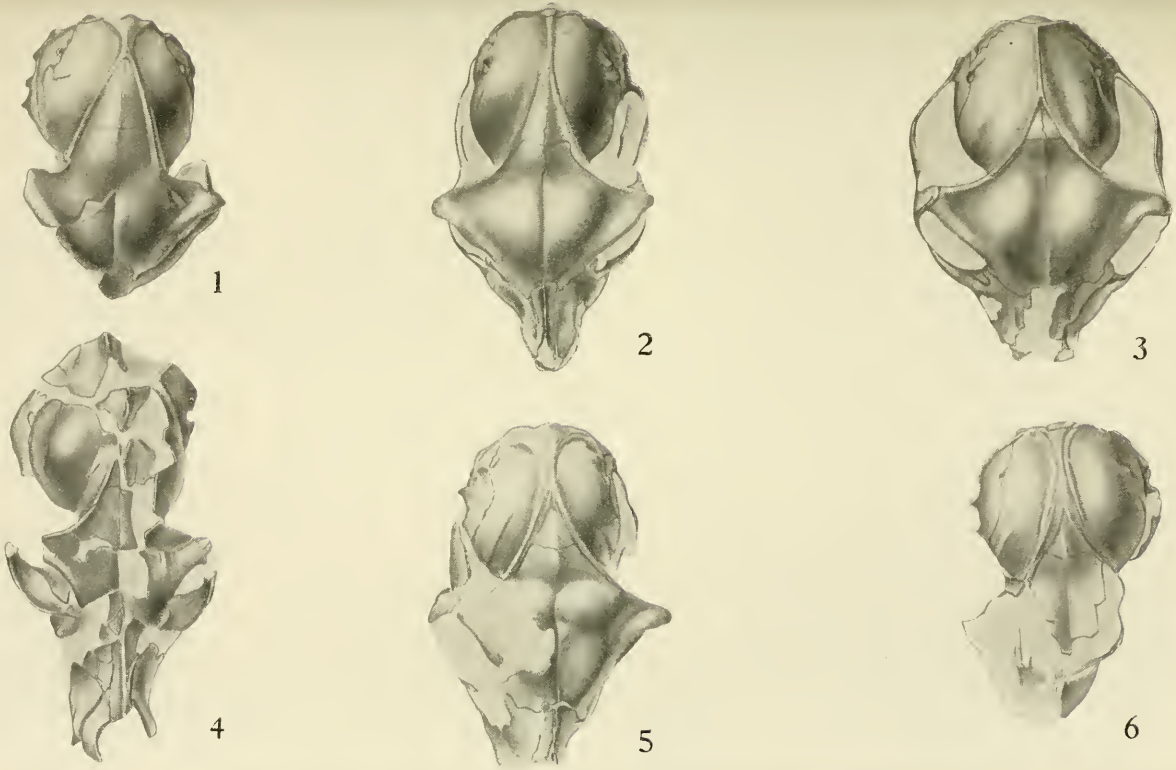
Fig. 4. Cf. *Utahia kayi,* new genus and species: Left upper molar (C.M. No. 6416), occlusal view. Four times natural size. Upper fossiliferous zone, Green River formation, middle Eocene, Uinta Basin, Utah.

Fig. 5. *Uintalacus nettingi,* new genus and species: Left ramus of mandible (C. M. No. 9426), type specimen, lateral and occlusal views. Five times natural size. Lower fossiliferous zone, Green River formation, lower Eocene, Uinta Basin, Utah.

Fig. 6. *Omomys lloydi,* new species: Left ramus of mandible (C.M. No. 6417), occlusal view of $M_3$ drawn from C.M. No. 6418), lateral and occlusal views. Four times natural size. Upper fossiliferous zone, Green River formation, lower Eocene, Uinta Basin, Utah.

Fig. 7. *Chlororhysis knightensis,* new genus and species: Left ramus of mandible (U.S.N.M. No. 21901), type specimen, lateral and occlusal views. Four times natural size. Knight lower Eocene, upper Green River Basin, Wyoming.

Fig. 8. *Absarokius noctivagus* Matthew: Left ramus of mandible (U.S.N.M. No. 19198, showing eruption of permanent cheek teeth), lateral and occlusal views. Four times natural size. Knight lower Eocene, upper Green River Basin, Wyoming.




NOTHARCTUS AND SMILODECTES FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)

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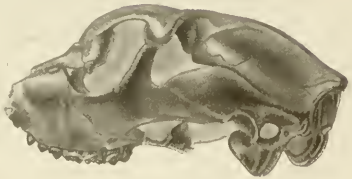

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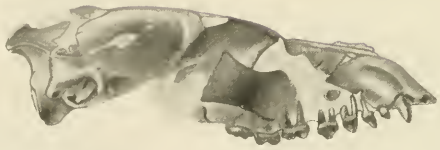

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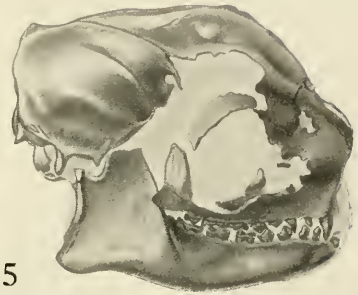

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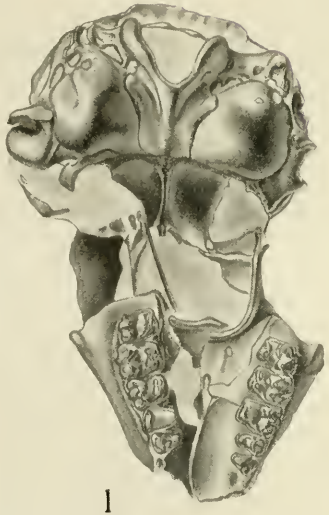
NOTHARCTUS AND SMILODECTES FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)



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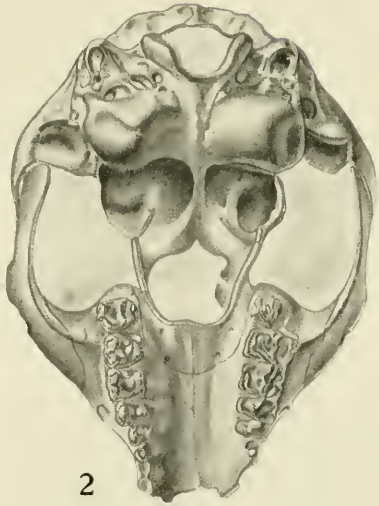

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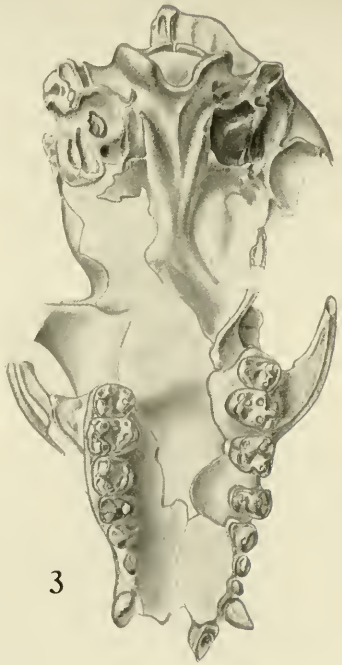


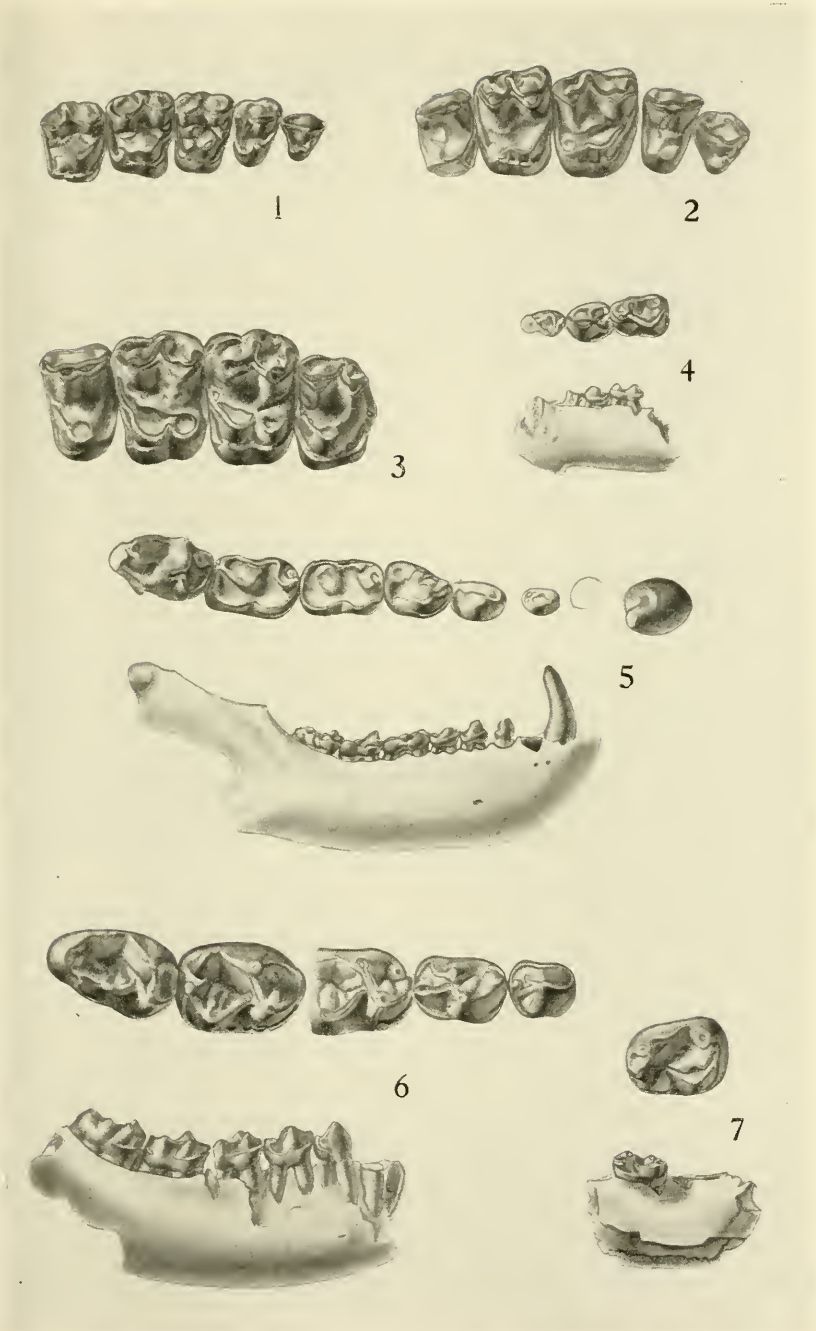
3

NOTHARCTUS AND SMILODECTES FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)

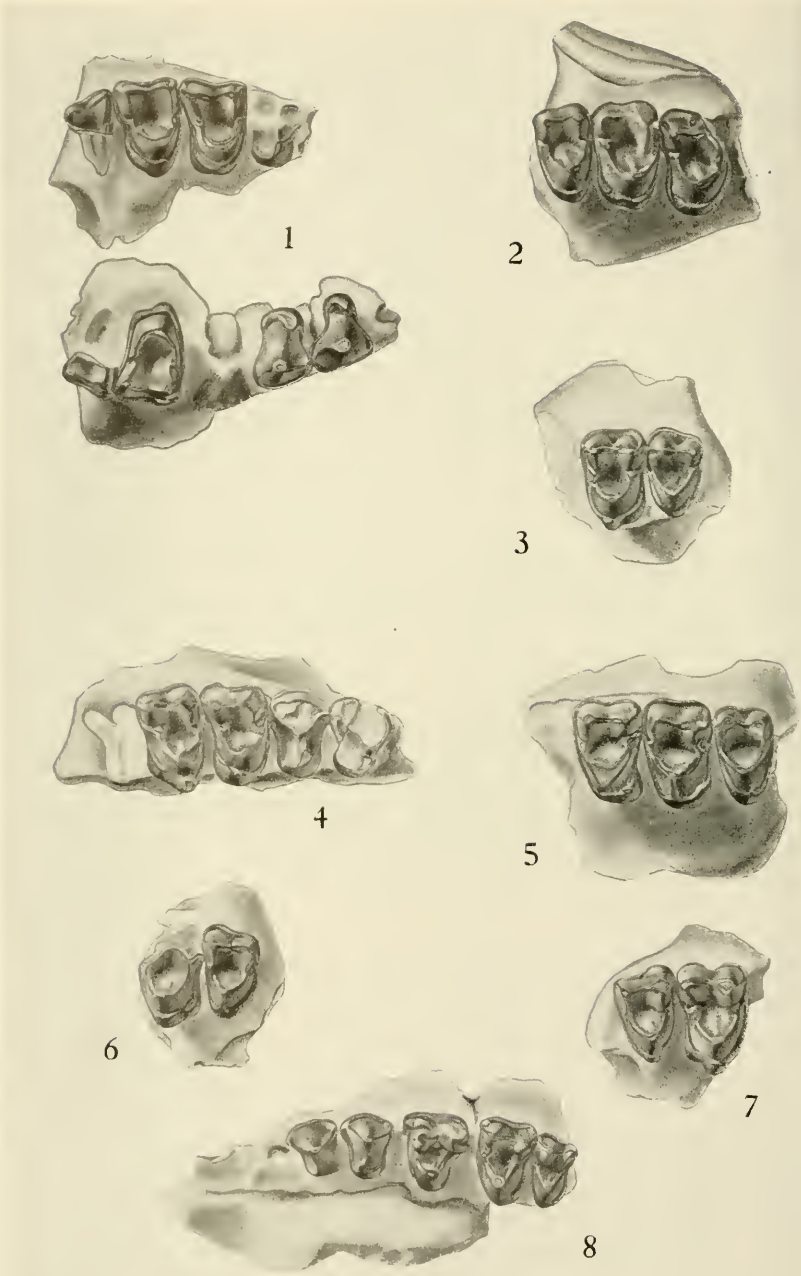
NOTHARCTUS AND HEMIACODON FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)



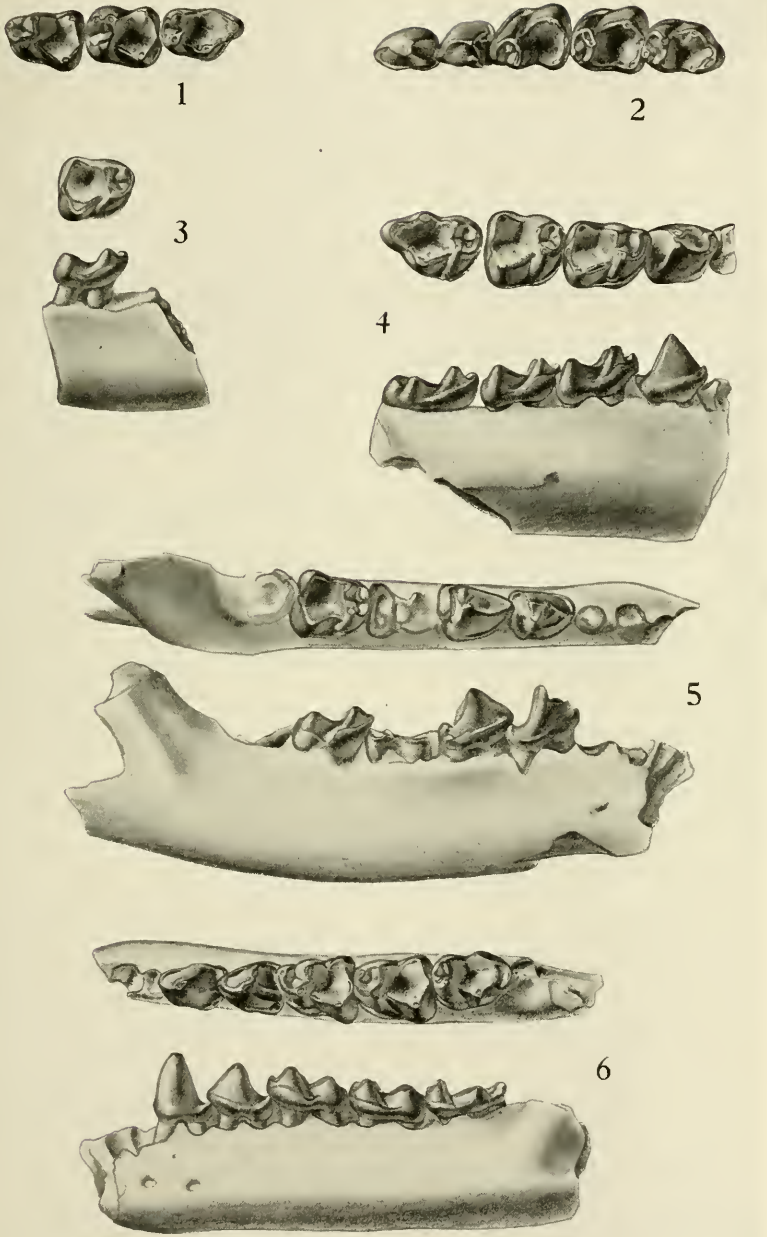

NOTHARCTUS AND SMILODECTES FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)



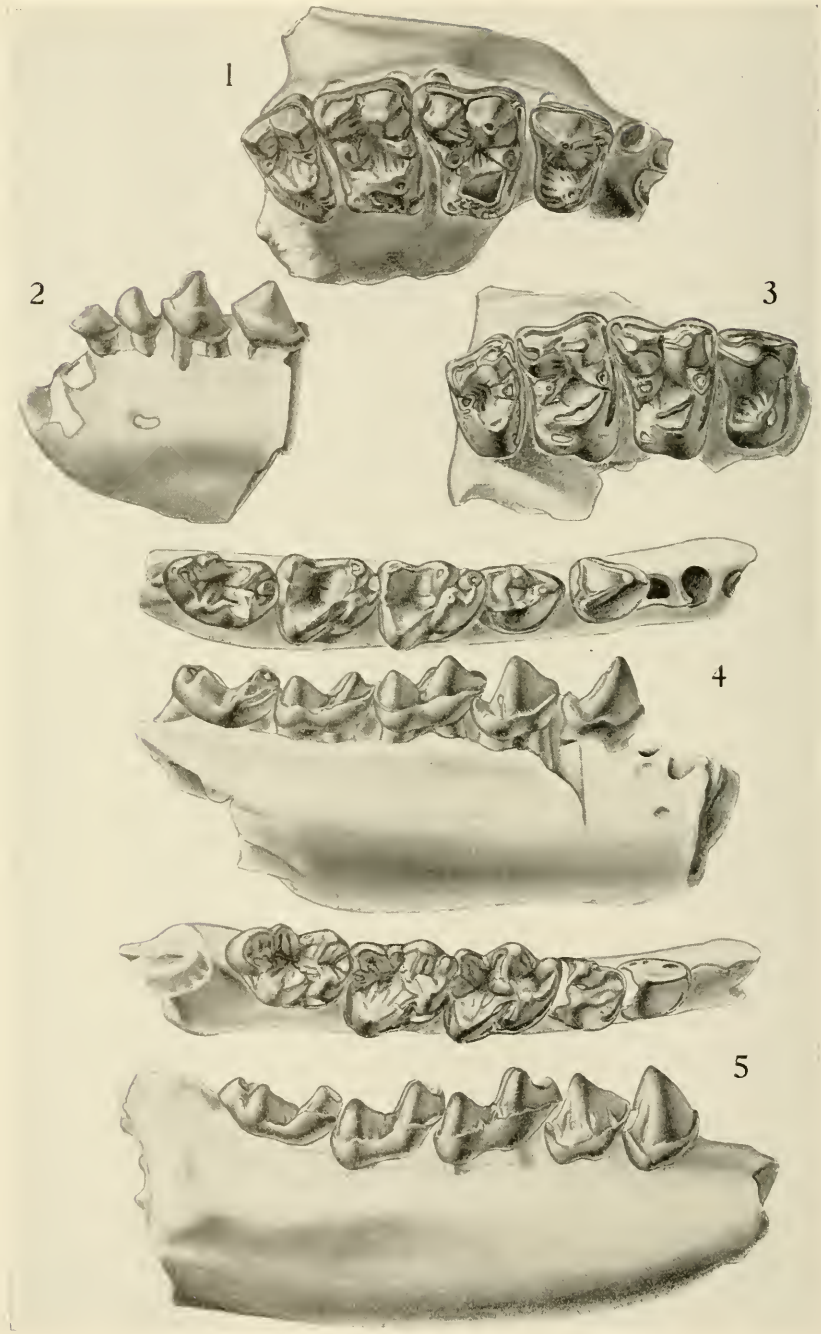

OMOMYS FROM THE MIDDLE AND LOWER EOCENE

(See explanation at end of text.)



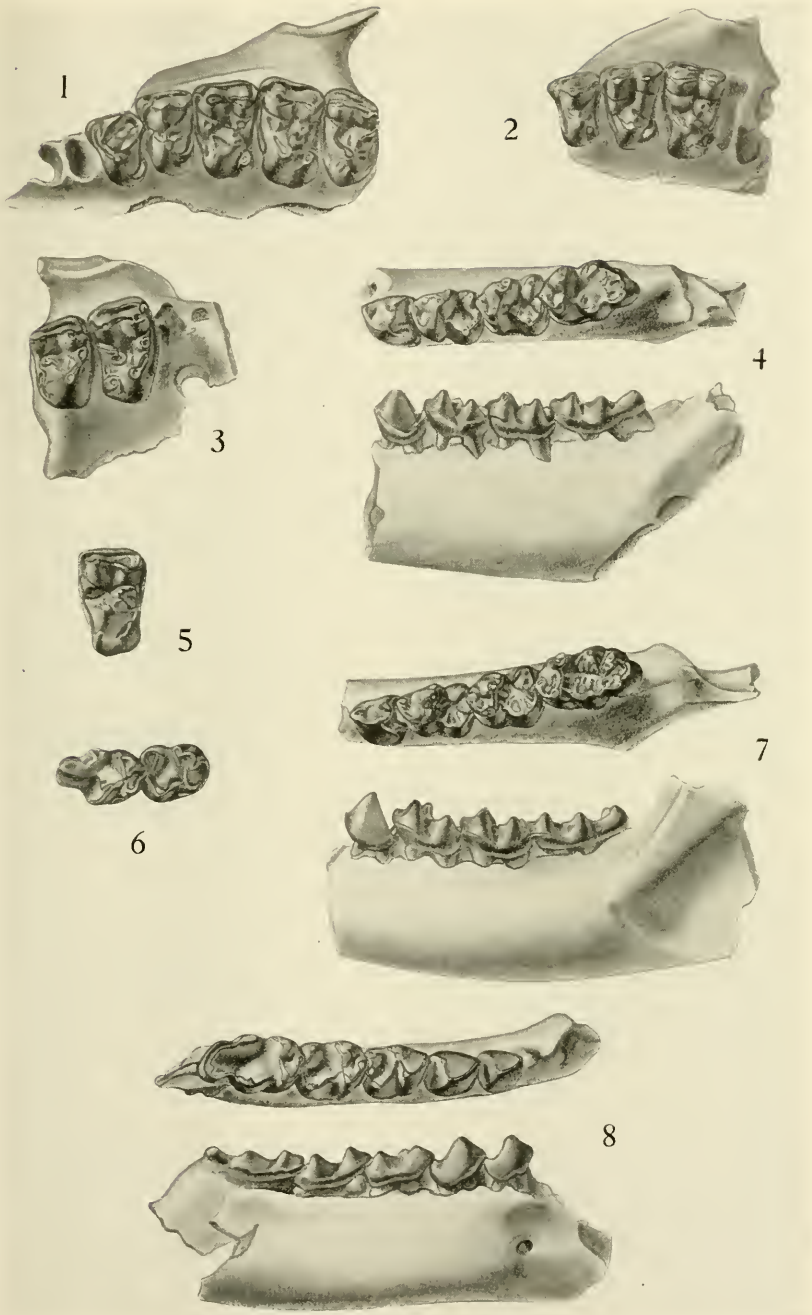

OMOMYS FROM THE MIDDLE AND LOWER EOCENE

(See explanation at end of text.)



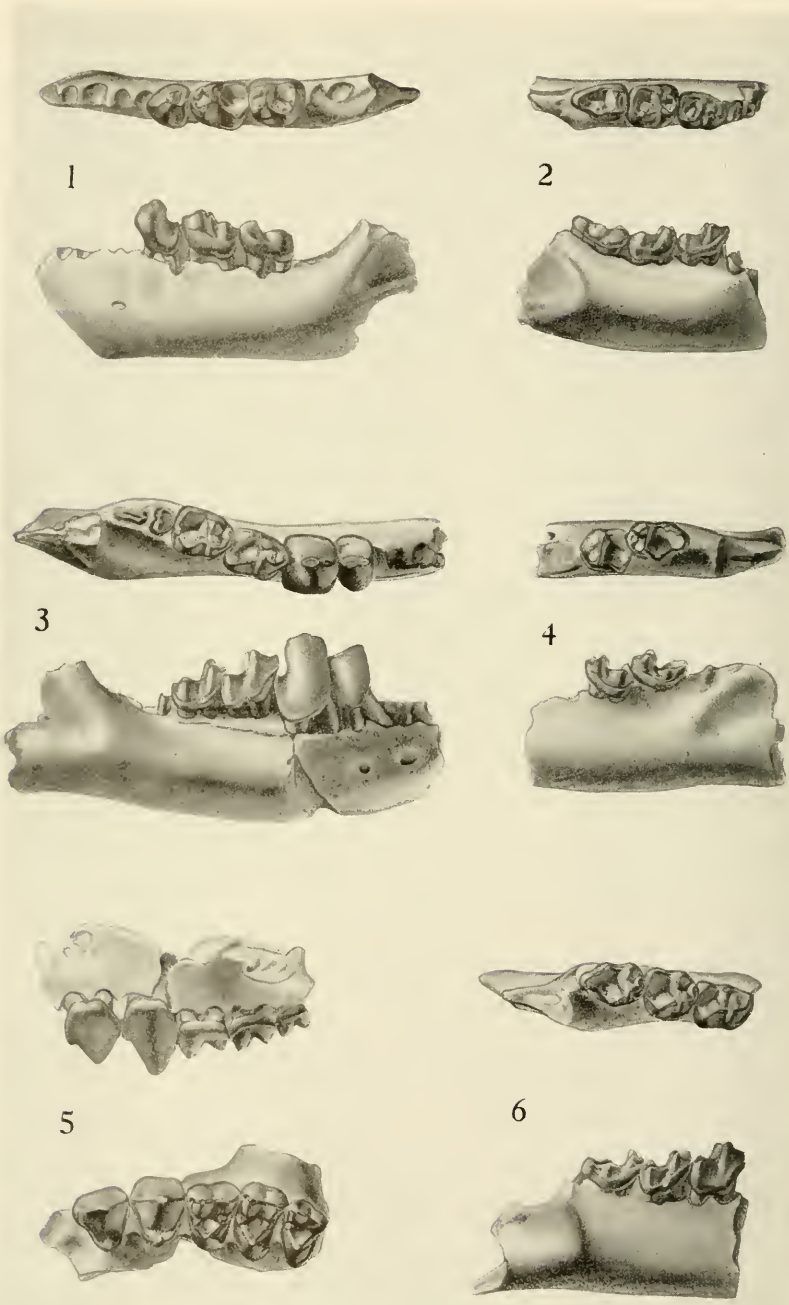

HEMIACODON FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)



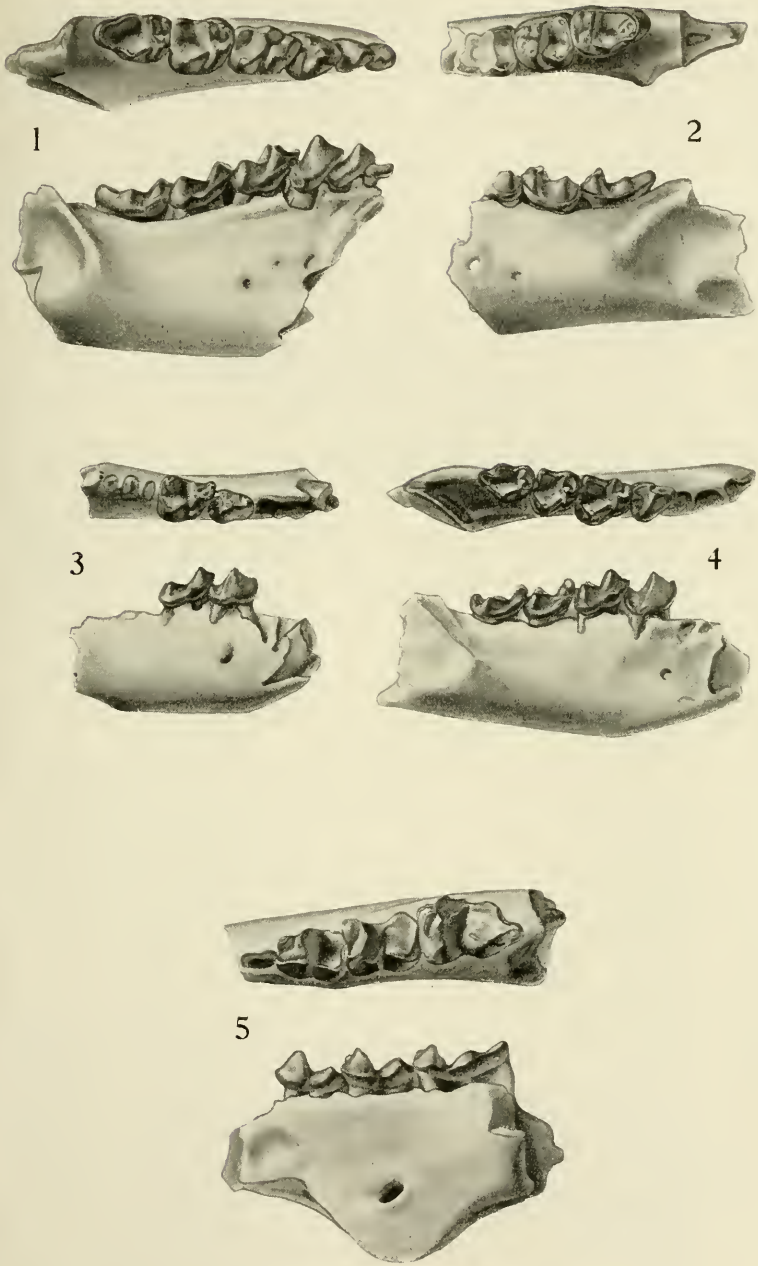

WASHAKIUS FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)



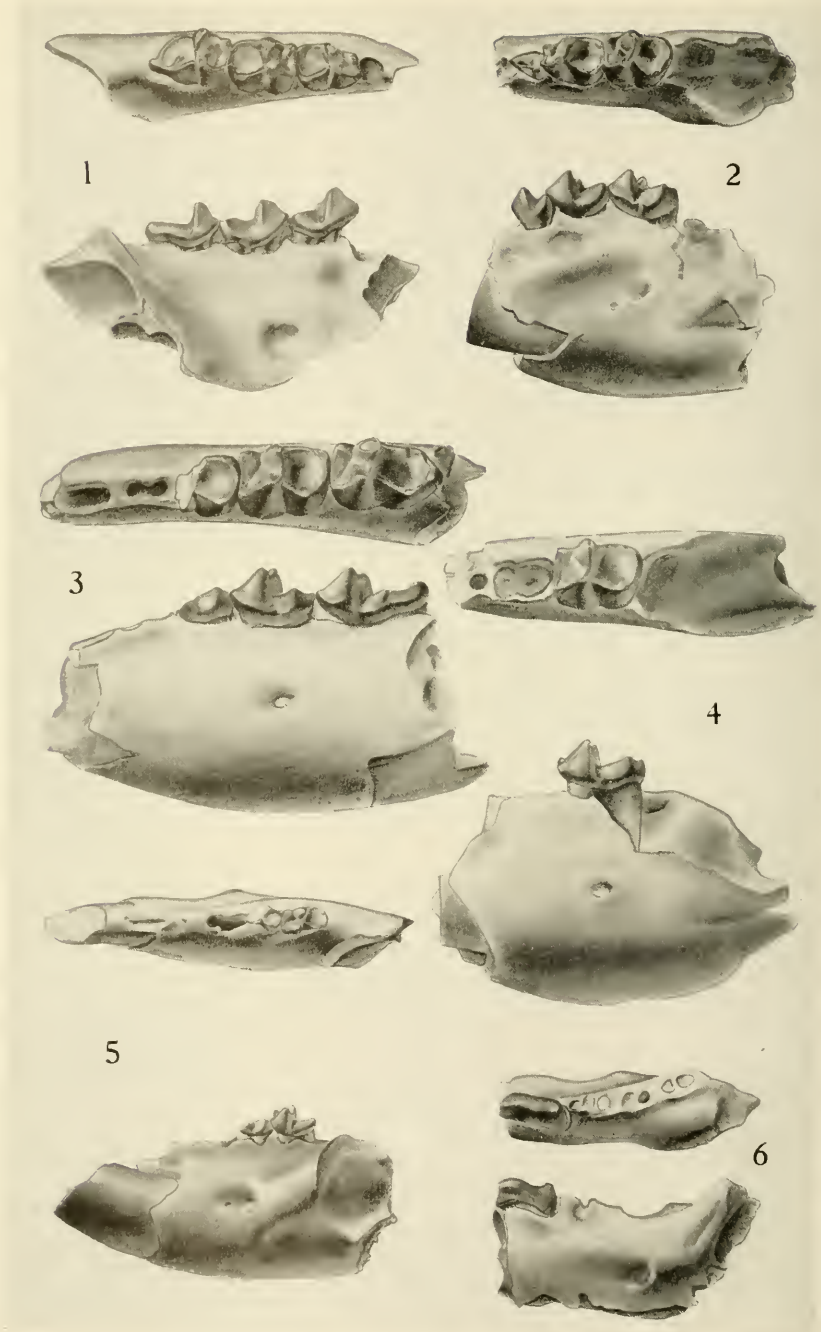

ANAPTOMORPHUS AND UINTANIUS FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)



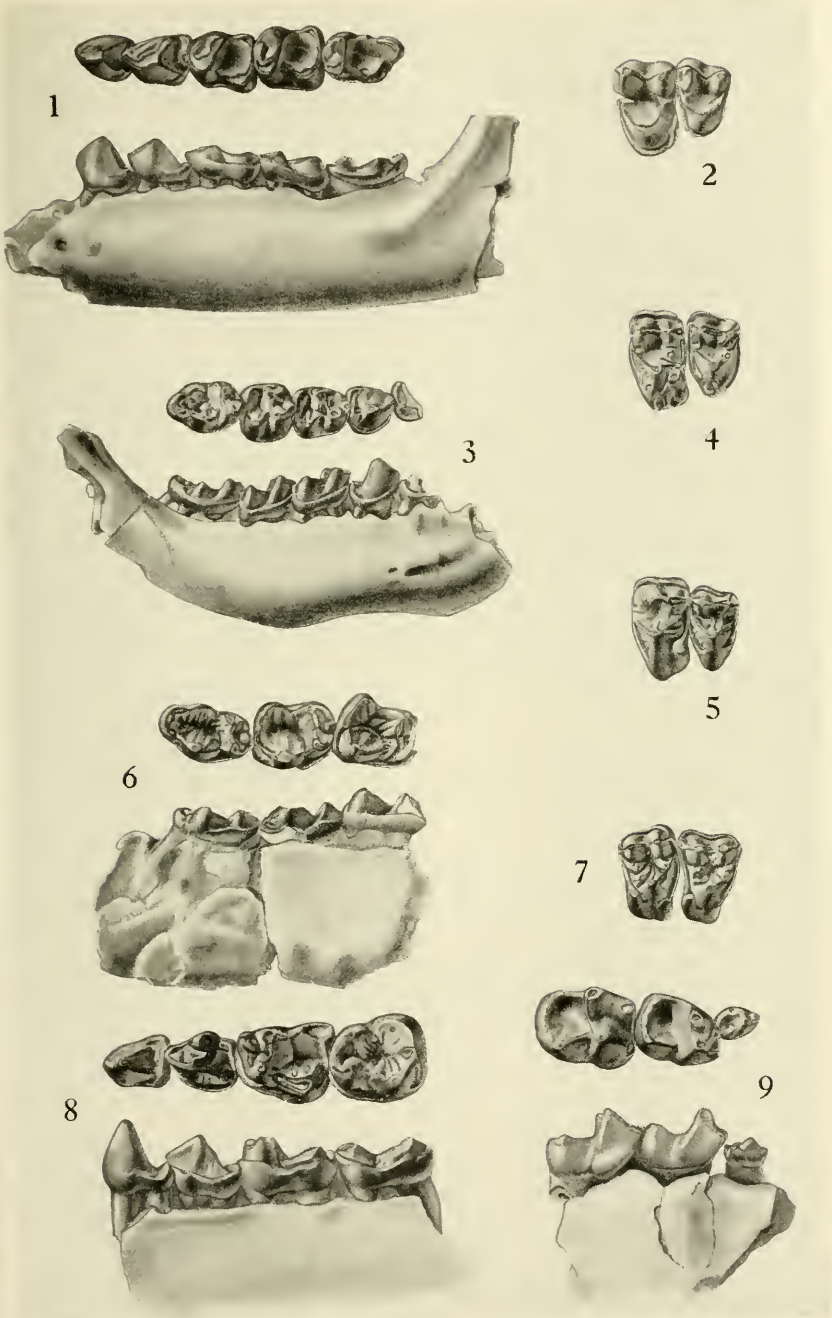

TROGOLEMUR, UINTASOREX, AND APATEMYS FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)



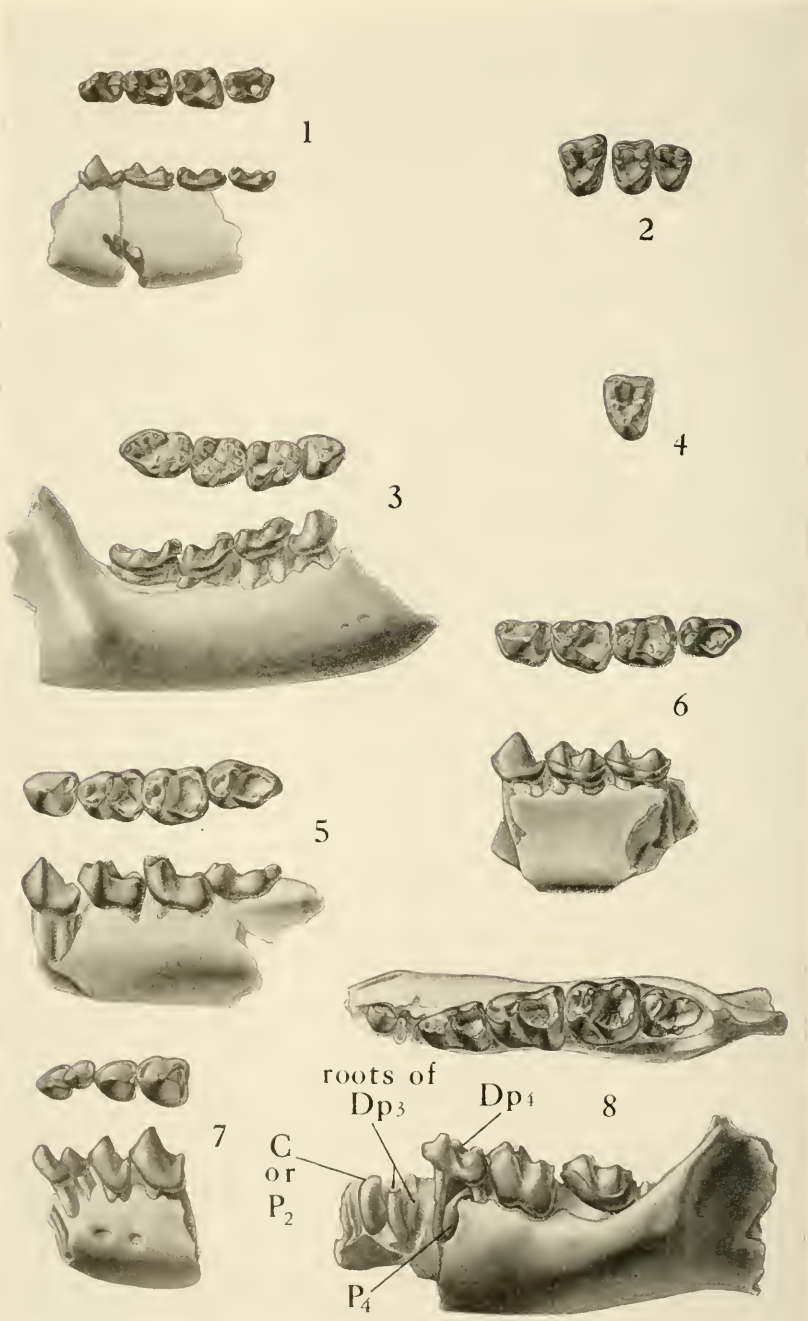

APATEMYS FROM THE BRIDGER MIDDLE EOCENE

(See explanation at end of text.)




UPPER EOCENE PRIMATES FROM CALIFORNIA AND UTAH

(See explanation at end of text.)




GREEN RIVER AND KNIGHT PRIMATES

(See explanation at end of text.)