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Primitive Paleocene and Eocene Apatemyidae (Mammalia, Insectivora) and the Primate-Insectivore Boundary

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INTRODUCTION

For a number of years the early Tertiary mammalian family Apatemyidae has been considered by various authors to belong to the order Primates. For the most part this conception appears to stem from the early collocation of *Apatemys* with accepted primates, notably *Plesiadapis*, and although all recent workers separate the Apatemyidae from the Plesiadapidae, following Jepsen (1934), there has been a tendency to retain the apatemyids in the primates, doubtless on the authority of Simpson (1940). Hürzeler (1949) has taken exception to primate affinities for the apatemyids, but his evidence has not been presented in detail as yet, and several of the characters he emphasized as apatemyid distinctions actually do occur in *Plesiadapis* (Russell, 1959). The present paper is an attempt to chronicle the history of concepts of apatemyid affinities and to present new illustrations and detailed descriptions of what little is known of the earliest apatemyids. The earliest apatemyids appear to have been derived not from the earliest primates, but rather from a more archaic source.

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ABBREVIATIONS

A.M.N.H., Department of Vertebrate Paleontology, the American Museum of Natural History
C.M., Carnegie Museum
P.U., Princeton University Museum
U.C.M.P., Museum of Paleontology, University of California
U.S.N.M., United States National Museum, Smithsonian Institution

HISTORICAL RÉSUMÉ

Apparently the first apatemyid to be discussed in the literature was *Heterohyus armatus* Gervais (1848–1852). Gervais placed *Heterohyus* among the ungulates, stating (p. 163) that *Heterohyus* was doubtless a relative of the wild boar. Gervais' specimen of *Heterohyus armatus* was refigured by Blainville (1839–1864, atlas, vol. 4, 73d unnumbered plate) and identified merely as "*Arctomys* de Buschweiler [Buchswweiler]." This reference to the Rodentia was not discussed in Blainville's text. Gervais (1859, pp. 201, 202, and pl. 35, fig. 14), in the second edition of his earlier monograph, discussed and rejected Blainville's reference of the Buschweiler specimen to *Arctomys*. *Heterohyus* was returned to the ungulates as the sole member of the "Tribu des Hétérohyins" of the family Suidae. This family-group name was the first to be used for an apatemyid, but its resurrection now would be unfortunate (see Stoll and others, 1961, p. 11, Art. 11, e, iii).

On the opposite side of the Atlantic Ocean, the first apatemyid to be described in North America was *Apatemys* itself, upon which O. C. Marsh published in 1872. Marsh, in his description of *Apatemys* (p. 30), stated that the genus should probably be placed in the insectivores (*sensu* Marsh). Marsh made no mention of either Gervais' or Blainville's figures of European *Heterohyus*. The other mammalian genera discussed near *Apatemys* in Marsh's paper are rodents, "insectivores," and primitive primates.

European references to apatemyids resumed in the closing decade of the nineteenth century, though at that time and until the end of the second decade of the twentieth century Europeans and Americans were unaware of the fact that they were both dealing with members of the

same family. Schlosser (1887–1890, pp. 33, 34), referred *Heterohyus armatus* to his ultra-inclusive and invalid family "Pseudolemuridae," stating that *Heterohyus* was similar to *Microchoerus*, *Microsyoops*, and *Hyopsodus*. Schlosser was much impressed with the resemblance to *Microchoerus* but, in the "Nachträge und Berichtigungen" to his paper (p. 452), adopted the view that the type specimen of *Heterohyus armatus* was an artifact, composed of a jaw of *Adapis* or perhaps *Caenopithecus*, to which a P_2 or perhaps P_4 of some other animal had been added. Meanwhile, another reference to a then unrecognized European apatemyid was provided by Rüttimeyer's description of *Calamodon europaeus* from Egerkingen (1888, pp. 12–17, 1 fig.; 1890, pp. 16–21, 2 figs.; 1891, pp. 126–131, 133, 2 figs., pl. 8, figs. 25–27). *Calamodon* is a synonym of the North American taeniodont genus *Ectoganus*, and Rüttimeyer at first referred *Calamodon europaeus* to the Taeniodonta, but in 1891 he substituted Tillodontia for Taeniodonta in accord with the classification of Flower and Lydekker. Stehlin made the species the type of *Amphichiomys* in 1916. There is some doubt about the exact affinities of *Amphichiomys*, in that it may actually be a plesiadapid in the modern sense, but large true apatemyid teeth of the proper size to belong to *Amphichiomys* are now known from Egerkingen (Stehlin, 1916, p. 1452, figs. 343, 344), and *Amphichiomys* is probably an apatemyid. Another apatemyid was published upon by Rüttimeyer in 1891 (*ibid.*, pp. 11, 12, pl. 8, fig. 23). Rüttimeyer made a single right molar the type of *Phenacodus minor* and referred it to his "Ungulata Trigonodonta," a group that Rüttimeyer himself (p. 7) thought might belong to Cope's Condylarthra. Stehlin (1916, p. 1459) showed that this tooth, too, belongs to what now would be called a European apatemyid. Filhol added still another unrecognized European apatemyid to the literature in 1890 by his description of *Necrosorex quercyi*. Filhol believed *Necrosorex quercyi* to be a shrew and did not compare his fossil specimen with any mammals other than *Sorex*. Stehlin (1916, p. 1494) pointed out the true affinities of the species, and Teilhard (1921 [1916–1921]) made *Necrosorex* a synonym of *Heterohyus*, but Filhol's incorrect reference of *Necrosorex* to the Soricidae persisted as late as Simpson's classification of 1945, in which *Necrosorex* is listed twice: once among the shrews (p. 51) and a second time as a synonym of *Heterohyus* (p. 64).

In America Matthew (1899, p. 39) listed *Apatemys* as an ischyromyid rodent. In this he was followed by Hay (1902, p. 725). There is no evidence that either Matthew or Hay was aware of or influenced by Blainville's reference of the Buchsweiler specimen of *Heterohyus* to *Arctomys*. Palmer (1904, p. 323) placed *Heterohyus* in the primates, questionably in

the Microchoeridae. Evidently Palmer was influenced by Schlosser's comments in the main body of his text (1887–1890, pp. 33, 34) but not by Schlosser's "Nachträge und Berichtigungen."

The family Apatemyidae was proposed by Matthew in 1909 (p. 543) for *Apatemys*, *Uintasorex*, and *Trogolemur*, all of which are American genera. No reference to either *Heterohyus* or *Necrosorex* was made; indeed, reference of European genera to the Apatemyidae did not occur until 1921. *Uintasorex* and *Trogolemur* are, of course, regarded as true primates in all recent work. Matthew placed the Apatemyidae in the Insectivora¹ with a query and similarities to the Mixodectidae were noted,² but Matthew regarded his classification of these forms as provisional. In 1910 Matthew, Gregory, and Mosenthal (1910, p. 522) placed the Apatemyidae with the Mixodectidae (including the Microsyopidae) in Osborn's (1902) suborder Proglires. The Proglires were considered to be a suborder of diprotodont or rodent-like insectivores rather than rodents and were placed on a par with the suborders Lipotyphla, Hyopsodonta, and Menotyphla.

During the interval between 1910 and 1934 apatemyids came to be regarded as plesiadapid-like, principally because of erroneous inclusions of various true primates in the same family with the type genus, *Apatemys*. Matthew continued to associate *Trogolemur* and *Uintasorex* with *Apatemys* (1910, in Matthew, Gregory, and Mosenthal; 1915; and subsequently). with the addition of the primate genera *Phenacolemur* and *Nothodectes* to the family in 1915. None of the European apatemyids was as yet included in the Apatemyidae. The European apatemyids were discussed in some detail by Stehlin in 1916, who considered them (a) primates, (b) related to *Plesiadapis*, and (c) related to *Daubentonia*, the living aye-aye of Madagascar. Stehlin made no mention of *Apatemys* or the family Apatemyidae, although he was thoroughly familiar with Matthew's paper. The fact that both the apatemyids and plesiadapids had been found on two sides of the Atlantic Ocean was only faintly appreciated at that time. A year after the appearance of Stehlin's paper, Matthew (1917) listed *Notho-*

¹ Bowdich (1821) named the Insectivora and based the concept on *Erinaceus*, *Sorex*, *Desmana*, *Scalopus*, *Chrysochloris*, *Talpa*, and a tenrec. The name "Insectivora" is thus virtually synonymous with the name "Lipotyphla" Haeckel, 1866. The ancestors of this still-living group have been traced back to Eocene time and with less certainty as far back as the Cretaceous. The vast majority of early Cenozoic "insectivores" represent another, much earlier radiation, of which the "elephant-shrews" are the only living example still classified within the "insectivores," if the tupaoids are regarded as primates and the colugos are regarded as a separate order.

² The well-known microsyopid primate genera *Microsyops* and *Cynodontomys* were regarded as mixodectids by Matthew in 1909. For an outline of the history of mixodectid and microsyopid classification see McKenna, 1960, pp. 76–79.

dectes, *Plesiadapis*, *Phenacolemur*, *Trogolemur*, *Uintasorex*, *Apatemys*, and *Chiromyoides* as plesiadapids in his key to the genera of the Plesiadapidae (p. 833), but elsewhere in the same paper he placed *Nothodectes*, *Phenacolemur*, *Trogolemur*, *Uintasorex*, and *Apatemys* in his family Apatemyidae. "Apatemyidae" appeared in quotation marks on page 832, but elsewhere in Matthew's paper the name was treated as though Matthew still considered it valid. That Matthew considered the Apatemyidae to be closely related to *Plesiadapis* and *Nothodectes* is not questioned here, but his position in 1917 concerning the validity of the family Apatemyidae is equivocal.¹ Matthew was uncertain of the ordinal affinities of *Nothodectes*, but suggested that it was a primitive primate (p. 838). It follows that the other members of Matthew's Apatemyidae, including *Apatemys*, were also considered to be primates. Though the name of the family ultimately rests on *Apatemys*, the morphology of *Nothodectes*, *Phenacolemur*, *Trogolemur*, and *Uintasorex* served as the real basis for concepts of primate affinity of the Apatemyidae. The morphology of *Apatemys* itself was not emphasized, for at that time knowledge of *Apatemys* was extremely scanty.

Winge (1917 [1941], pp. 219–221) considered the apatemyids and plesiadapids to be doubtfully insectivores. Winge was the first European to mention Matthew's Apatemyidae in a publication, but his book was in Danish. Schlosser (1918, pp. 610–633) listed the Chiromyidae (including at that time the aye-aye plus European apatemyids) and the Plesiadapidae under a "tribe" Chiromyiformes. The Chiromyiformes were placed among what amount to the prosimian primates.

In America, Matthew (1918, p. 569) explicitly stated that the Apatemyidae were synonymous with the previously named Plesiadapidae. This union was not dissolved until Jepsen's revision of the Apatemyidae in 1934. The work of Stehlin (1916) on *Plesiadapis* caused Matthew to refer both *Phenacolemur* and *Nothodectes* to the Plesiadapidae. The other genera previously placed in the Apatemyidae, notably the type genus *Apatemys*, were not discussed. *Nothodectes* was not yet regarded as a synonym of *Plesiadapis*. The affinities of the American *Nothodectes* were discussed, and the Plesiadapidae were tentatively referred to the Insectivora.

Matthew and Granger (1921), in their description of *Labidolemur sorioides*, considered *Labidolemur* to be close to *Phenacolemur*. *Labidolemur* was placed in the Plesiadapidae and the latter in turn in the Menotyphla (considered to be an order). *Apatemys* was not mentioned, nor, curiously

¹ Simpson (1940, p. 203) stated that in 1917 Matthew united the families Plesiadapidae and Apatemyidae under the former name. Such action was not explicitly stated by Matthew, but only implied by Matthew's key.

enough, was the apatemyid genus *Stehlinella*, on which Matthew published one day after the appearance of his joint paper with Granger. Clearly, Matthew and Granger were not aware of the close similarity of *Labidolemur* and *Apatemys*.

Matthew, in his description of the *Apatemys*-like Uintan genus *Stehlinella* in 1921, regarded that genus as a plesiadapid, the Plesiadapidae as tupaoid, and the tupaoids as insectivores (Menotyphla). *Stehlinella* was regarded as possibly related to *Necrosorex*, an advanced European apatemyid which tentatively had been transferred from the Soricidae to the Plesiadapidae by Stehlin (1916, p. 1494), and which in 1921 (1916–1921) Teilhard regarded as a synonym of *Heterohyus*. *Stehlinella* was also compared with *Apatemys*, but, as pointed out by Jepsen (1934, p. 302), P_3 was mistaken for P_4 and the anterior root of M_1 had been placed in the alveolus of P_4 , which resulted in a puzzling arrangement not compatible with that of *Apatemys*. Truly close affinity with *Necrosorex* was denied by Matthew (p. 4) because of a supposed difference in cheek-tooth formula arising from the same misconceptions. Teilhard accepted the supposed difference in premolar morphology (1916–1921, p. 94) but noted that *Stehlinella* and *Heterohyus* were otherwise closely similar. Teilhard (*ibid.*, pp. 24, 48, 62), in his monograph on the early Eocene mammals of France, continued to regard *Plesiadapis* (to which he now referred *Nothodectes*), *Apatemys*, and *Heterohyus* as chiromyid lemuroid primates in the first part of his paper, but in the last chapter (pp. 89–96) he removed the chiromyids from the primates, stating, however, that the chiromyids and primates originated from the same stem. Teilhard's Chiromyidae consisted of *Mixodectes*, *Cynodontomys*, *Plesiadapis* (including *Nothodectes* and *Chiromyoides*), *Phenacolemur*, *Trogolemur*, *Uintasorex*, *Heterohyus* (including *Necrosorex*, *Heterochiromys*, and ?*Amphichiromys*), *Apatemys*, *Stehlinella*,¹ and *Chiromys* (= *Cheiromys*, = *Daubentonia*).

Schlosser (1923, pp. 642–643) united *Plesiadapis*, *Nothodectes*, *Labidolemur*, *Phenacolemur*, *Trogolemur*, *Uintasorex*, *Apatemys*, and *Chiromyoides* in the Plesiadapidae and *Chiromys*, *Amphichiromys*, *Heterohyus* (including *Necrosorex* and *Heterochiromys*), and *Stehlinella* in the Chiromyidae. Both families were placed in a "tribe" Chiromyiformes, as in Schlosser, 1918.

Troxell (1923, p. 506), in his description of the Bridgerian species *Apatemys rodens*, stated that the animal was probably an insectivore, but the assignment was clearly provisional (p. 503). Teilhard (1927, pp. 13–16) placed *Heterohyus*, *Eochiromys*, and others with *Plesiadapis* and the

¹ Matthew's original name "*Stehlinius*" was later found to be preoccupied and was replaced by *Stehlinella* Matthew, 1929.

aye-aye in the chiromyid primates. Certain isolated teeth (pl. 2, figs. 20, 21, possibly fig. 24), which may belong to apatemyids, were referred by Teilhard to the insectivores.

Simpson (1929b, pp. 119–120) described *Apatemys kayi* from the late Paleocene of Montana, but referred the species to *Labidolemur*, a genus that Matthew and Granger (1921) had placed in the Plesiadapidae, that family in turn being placed in the Menotyphla (considered as an order). Matthew and Granger had placed *Labidolemur* in the Plesiadapidae because of similarities to *Phenacolemur* and *Plesiadapis* (i.e., “*Ignacius*” and “*Nothodectes*,” respectively). Furthermore, several specimens of *Phenacolemur* had been doubtfully referred to *Labidolemur*, heightening the supposed similarity to the plesiadapids. There was no mention of similarity to *Apatemys* or *Stehlinella*. Simpson placed *Labidolemur soricoides* and *Apatemys kayi*, which he considered to represent a single genus, in the Plesiadapidae, but contrasted them with *Plesiadapis*. The Plesiadapidae in turn were regarded as either insectivores or primates. Like Matthew and Granger, Simpson did not compare *Apatemys kayi* with any of the Eocene true apatemyids. In a second paper¹ Simpson (1929a) referred *Apatemys kayi* to the Plesiadapidae with a query and the latter in turn to the Primates, again with a query (p. 1), doubtlessly because of the primate-like rather than insectivore-like nature of A.M.N.H. No. 22195, an upper molar referred by Simpson to cf. *Labidolemur*.²

Heller (1930, p. 34) in his description of *Heterohyus heufelderi* from Geiseltal, referred *Heterohyus* to the chiromyid primates. Heller did not discuss either American literature or specimens in his paper.

Hay (1930, p. 445) placed the Microsyopidae, Mixodectidae, and Plesiadapidae (including the Apatemyidae) in a superfamily Mixodectoidae (Hay's spelling) in Osborn's (1902, p. 203) suborder Proglires. The Proglires were placed in the Insectivora along with the suborders Lipotyphla, Hyopsodonta, and Menotyphla. This classification was a minor modification of the Matthew, Gregory, and Mosenthal classification of 1910.

Jepsen (1930, p. 126), in his description of *Teilhardella chardini*, referred the new genus to the Plesiadapidae, the latter being referred in turn to the Primates with a query. Similarities to *Heterohyus* and *Stehlinella* were discussed. The Apatemyidae were still regarded as synonymous with the Plesiadapidae. Simpson's classification of mammals of 1931 did not list

¹ Written after, but published before, the description of *A. kayi*.

² The tooth in question belongs to *Paramys atavus*, the oldest known rodent (McKenna, 1961).

the Apatemyidae, but did list the Plesiadapidae among the lemuroid primates. The Apatemyidae were evidently still regarded as synonymous with the Plesiadapidae. Abel (1931, pp. 262–292) considered the Apatemyidae synonymous with the Plesiadapidae, in which he, too, united *Trogolemur*, *Uintasorex*, and *Phenacolemur*.

Jepsen (1934) brought to a close the practice of placing all small, early Cenozoic, primate-like animals with enlarged procumbent incisors in the Plesiadapidae, pointing out that, as redefined, “the Apatemyidae have a unique and clearly delineated cluster of family characters which separates them from the also delimited Plesiadapidae” (p. 288). Jepsen added the American genera *Stehlinella* and *Sinclairiella* to the Apatemyidae and (p. 305) provisionally returned the apatemyids to the Insectivora, but suggested that apatemyids might eventually prove to deserve ordinal rank. Simpson (1935a), in a discussion of the structure and relationships of *Plesiadapis*, followed Jepsen (1934) in separating the Plesiadapidae from the Apatemyidae. The Plesiadapidae were placed (p. 30) among the lemuroid primates, as in Simpson’s classification of 1931, but the Apatemyidae were not listed as lemuroid primates, even though Simpson in 1935 considered the family to be valid. In a subsequent paper Simpson (1935b) placed the Apatemyidae in the Primates without committing himself as to special affinities within the order.

In 1936 Scott and Jepsen (p. 26) regarded the Apatemyidae as *incertae sedis* among the Insectivora, but continued to regard the family as possibly deserving of ordinal rank. The name “Apatotheria” was suggested, should fuller knowledge of the group require the erection of a new order.

Camp and VanderHoof (1940, p. 499) listed the Apatemyidae as Insectivora, *incertae sedis*. The plesiadapids were placed among the lemuroids.

Simpson (1940) described the Torrejonian apatemyid *Jepsenella praepropera* (pp. 186–187), stating (p. 185) that “the Apatemyidae may not be primates at all, but there is at present no other less doubtful place to put them.” In another section of the same paper (p. 204) Simpson cited the “consensus” that apatemyids were primates and suggested that the late W. D. Matthew would have agreed with this conclusion, because tupaioids were considered to be primates by Le Gros Clark and other authorities. Matthew, however, had referred various true apatemyid genera to the primates mainly because these were erroneously placed in the Plesiadapidae or because various true primates had originally been placed by him in the Apatemyidae. Since 1909 the morphology of various primate genera placed either in the Apatemyidae or the Plesiadapidae (when the apatemyids were considered synonymous with that family)

contributed far more to concepts of apatemyid affinities than did the little-known morphology of the true apatemyids themselves. After noting the paucity of relevant factual data, Simpson (1940, p. 204) went on to conclude that "there is now little more to do with the apatemyids than to call them ?Primates *incertae sedis*. If it were necessary to frame a more definite hypothesis, mine would be, purely as a hypothesis, that the apatemyids might be an aberrant, sterile offshoot of the undifferentiated and probably formally protolemuroid primate ancestry. Such a stock seems to have existed in the Paleocene and to have been differentiating rapidly into many different lines of which only a few were destined to survive into the later Tertiary and Recent. On the other hand, the apatemyids may prove to have nothing to do with the primates."

Since Simpson's paper in 1940, most subsequent authorities have regarded the Apatemyidae as probably a primitive side branch of the early primates, but generally admit that such an allocation may be questioned. Scott and Jepsen (1941, p. xiv) reversed their earlier position, following Simpson (1940). Camp, Taylor, and Welles (1942, pp. 658-659) listed the Apatemyidae under both the lemuroid primates and the Insectivora, *incertae sedis*! Simpson (1944, p. 73) referred to the Apatemyidae as "an unusual extinct family of rodent-like primates." This statement was modified to read "an unusual family of rodent-like insectivores or primates" in the expanded and revised discussion of the same subject published in 1953. Simpson (1945, pp. 64, 184) placed the Apatemyidae in the Prosimii, infraorder uncertain. In the same year Romer (1945, pp. 613-614) placed the apatemyids among the tarsioid primates. The Plesiadapidae were placed among the lemuroids. Camp, Welles, and Green (1949, p. 377) followed Simpson (1945, p. 64) and listed the apatemyids as prosimian primates, *incertae sedis*.

In two nearly identical abstracts, Hürzeler (1949a, 1949b) stated that in contrast to all fossil and Recent primates, including *Tupaia*, *Heterohyus* possesses (1) no bony postorbital bar¹ and (2) no osseous bulla, and (3) the internal carotid artery crosses the intratympanic space not in an enclosed bony carotid canal, but rather in an open groove on the ventral side of the promontorium.² Hürzeler removed the apatemyids from the

¹ *Anagale* and *Anagalopsis* lack a complete bar, but are not primates (McKenna, 1963), and papers by Russell (1959) and myself (in preparation) show that *Plesiadapis* and *Microsyops* as well lack this character. All four genera are regarded here as very primitive descendants of earliest Cenozoic animals on one side or the other of the boundary between primates and non-primates.

² Russell (1959) notes that in *Plesiadapis* the promontory artery crosses the promontory of the petrosal in a furrow.

primates and placed them in the Insectivora, but stated that, "what their position finally is to be among the heterogeneous order Insectivora is still to be made clear." Hürzeler promised an illustrated detailed description, but as yet this has not appeared. Hürzeler's work is especially important, because it deals with crucial details of vascular supply within the ear region, but the only character he listed that differs from the morphology of *Plesiadapis* is the lack of an osseous bulla.

In a phylogeny published by Stirton and Savage (1950, pl. 91) and republished in slightly modified form by Stirton (1951, p. 319, fig. 2), the apatemyids were considered to be primates of uncertain infraordinal reference. The Carpolestidae were placed in the same vague category. This treatment is the same as that of Simpson (1945).

Camp, Welles, and Green (1953, p. 461) continued to classify the apatemyids as Prosimii, *incertae sedis*. Simpson (1953, pp. 126-128), in the expanded and revised version of his earlier book of 1944, referred to the Apatemyidae as "an unusual family of rodent-like insectivores or primates."

Simpson (1954), in his description of *Teilhardella whitakeri*, did not commit himself on relationships but merely stated that the apatemyids have "usually been placed in the Primates, but the assignment has been questionable." Simpson noted Hürzeler's transfer of the family to the Insectivora, but neither agreed nor disagreed with Hürzeler.

Patterson (1954) continued to classify the apatemyids as primates.

Saban (1954) placed the mixodectids (*sensu lato*, including the Microsyopidae) and apatemyids together in an insectivore¹ suborder which he named the Mixodectomorpha. The apatemyids were placed in a superfamily bearing the etymologically incorrect new name Apatemyioidea. Saban believed that the apatemyids were probably derived from the mixodectids after the differentiation of the latter from pantothers, perhaps from the Paurodontidae. Saban would derive other "insectivore" groups from the Docodontidae and Amphitheriidae, so one must conclude that the mixodectomorphs were believed to have a very long and isolated history.

Fiedler (1956) omitted the apatemyids from his classification of the primates. He cited Hürzeler (1949a, 1949b) in his list of references. In another article in the volume that contained Fiedler's paper, Remane (1956) placed the family in the primates but admitted that apatemyid affinities were rather uncertain. Remane cited both of Hürzeler's ab-

¹ Saban cited one of Hürzeler's abstracts in his bibliography, but in the text Saban did not refer to Hürzeler's transfer of the apatemyids to the Insectivora.

stracts in his bibliography but mentioned neither in the text.

Piveteau (1957, pp. 70, 111) regarded the apatemyids as incontestable insectivores but did not discuss the problem further.

Saban (1958, pp. 858–863, 901–903) expanded his classification of 1954 with little change. As before, the apatemyids and mixodectids were placed in a suborder of insectivores, and no close relationship to any other Tertiary or Cretaceous mammals was noted. The Mixodectomorpha were believed to have arisen directly from pantotheres.

Gazin (1958) tentatively placed the apatemyids in the primates, following Simpson rather than Jepsen (1934), Saban, or Hürzeler.

Clark (1959) continued to regard the apatemyids as an aberrant offshoot of the early lemuroid primates.

McKenna (1960) placed the Apatemyoidea (emended from Saban's superfamily Apatemyoidea) with Butler's (1956) Leptictoidea, the Pantolestoidea, and the Mixodectoidea (from which the microsypids were removed) in the order Menotyphla, *faute de mieux*. All these early Tertiary forms have been placed in the Insectivora in the past, but they are more closely related to one another than to true insectivores. The latter appear to represent a separate radiation the members of which were not abundant until middle Tertiary time. McKenna did not propose an ordinal or subordinal name for the early Tertiary forms placed in the Menotyphla, *faute de mieux*. McKenna described and figured (*ibid.*, p. 63, fig. 30; and fig. 4 of the present paper) an unrecognized *Apatemys* M³ which he was unable to allocate at that time other than to place the specimen in the Insectivora or Menotyphla, *incertae sedis*.

Simons (1962, pp. 23, 26) considered the Apatemyidae to be lemuroid primates near the boundary between the orders Primates and Insectivora. Noting Hürzeler's (1949a, 1949b) comments, Simons remarked that the Apatemyidae had no close connection with the Paleocene-Recent primates, though both groups may have arisen from the same eutherian stock. Simons therefore placed the Apatemyidae in a group of "borderline" primates, to which he also referred the Amphilemuridae and Microsypidae.

The preceding historical review is by no means complete, but it demonstrates the confused status of our knowledge of the apatemyids. The origin of this confusion can be traced to early failure to consider foreign specimens or literature, to the incorrect association of *Apatemys* with true primates and the utilization of these as the basis of the apatemyid concept, and to a failure to give adequate taxonomic weight to the earliest apatemyids rather than their superficially primate-like descendants.

SYSTEMATICS

ORDER INSECTIVORA

SUPERFAMILY APATEMYOIDEA SABAN, 1954¹

FAMILY APATEMYIDAE MATTHEW, 1909 (EQUAL TO OR INCLUDING "TRIBU DES HÉTÉROHYINS" GERVAIS, 1859)

Apatemyids are generally reported to be rare in the American early Tertiary (Simpson, 1944, pp. 72, 73; 1953, pp. 126–128), and seem to be rare faunal elements in the early Tertiary of Europe as well. Knowledge of the skull is largely confined to the skulls of *Heterohyus* and *Sinclairiella*, and important features of the cranial anatomy are still not known in any great detail. The most diagnostic feature of the skulls of *Heterohyus* and *Sinclairiella* yet reported is the lack of an ossified auditory bulla. If this feature can be confirmed, it furnishes evidence that apatemyids are more primitive in this regard than even the lowly *Plesiadapis*. Of course primates also had to acquire an ossified bulla at some point, and possibly animals even more primitive than *Plesiadapis*, lacking an ossified bulla, will nevertheless come to be classified as primitive primates. The acquisition of an ossified bulla need not coincide with the origin of the order Primates. As many morphological features as possible should be brought to bear on the question, and a single character should not be overemphasized. For that reason only a provisional diagnosis of the family can be attempted here, pending publication of more complete cranial data by Hürzeler and others. The jaws and teeth must be emphasized at present, for no fragments of apatemyid skulls have been reported from the Paleocene, and the closest Paleocene relatives of the apatemyids are also known principally from jaws and teeth.

The insectivore family Apatemyidae can be diagnosed provisionally

¹ Saban is the author of this concept at this taxonomic rank, but under the current rules Matthew, 1909, must be credited with this coordinate family-group name. But to list Matthew's surname after all coordinate family-group taxonomic names derived from "Apatemyidae" is not only redundant but yields no information about authorship of relative taxonomic rank. The orthography of "Apatemyoidea" dates from McKenna (1960, p. 47). The concept of a family group dates from Gervais (1859), but the name supplied by Gervais has never been used since and should not displace Apatemyidae Matthew, 1909, or coordinate names based on "Apatemyidae." "Heterohyinae" would of course be available should European apatemyids be found to comprise a valid subfamily, but there is no evidence for that and no one has suggested such splitting. The matter is of more interest to bookworms than to bonediggers, but some course must be followed, and what I believe to be the most useful solution is selected here.

as follows: skull lacking postorbital bar and ossified bulla¹; skull shape convergently rodent- and *Dactylopsila*-like; anterior upper incisors reduced to two where known,² of which the anteriormost is enlarged greatly and the posteriormost moderately; upper canine absent; upper premolars reduced to two small, blade-like teeth by late Eocene time; P³ larger than P⁴; M¹ more elongate relative to transverse width than M² or M³, with parastyle projecting forward, metastyle in some cases prominent, conules weak or absent, and with a small conical hypocone present at posterior base of protocone, which may extend far to the rear as a shelf (see especially *Heterohyus*); M² with prominent styles in known American genera, weak conules, and a small conical hypocone as in M¹ (situated on a projecting shelf in *Heterohyus*); M³ with prominent parastyle (except *Heterohyus*), only slightly reduced metacone, and weak conules; M³ hypocone reduced or absent in American genera, but hypocone shelf hypertrophied in *Heterohyus*, in which it is reminiscent of *Phenacolemur*; lower jaw with condyle set lower than dental row; masseteric fossa deep; mental foramen compound and actually a pit into which several passages open, as McDowell (1958, p. 206) has noted in pantolestids; fossa often present labially on dentary, below P₄; lower jaws with single enlarged anterior "incisor,"³ the growth of which is not continuous; "incisors" meeting in front of symphysis to form a spoon- or beak-shaped tool the dorsal enamel surface of which thins and, in some cases, is absent; lateral and ventral "incisor" enamel not extending far along root into alveolus; lower canine absent; by late Paleocene time lower premolars reduced to two where known; P₃ enlarged, procumbent, and with hatchet-like slicing crown projecting forward over posterior end of spoon-like dental beak in advanced forms; P₄ variably reduced, either double-rooted or single-rooted; lower molars progressively smaller from M₁ to M₃ in *Jepsenella*, in which "incisor" does not extend far beneath molar roots, but progressively larger from M₁ to M₃ in other known apatemyids, in which large, unerupted anterior molars would compete with "incisor" root for space; lower molars tending to acquire oblique trigonid with reduced paraconid and anterolabial projection, with metaconid shifted to position well behind level of protoconid; molar trigonids very high in primitive forms, becoming lower in advanced genera.

¹ It should be borne in mind that the entotympanic ossification, if it was present in the living animal, may have become detached as is often the case in leptictid skulls. Only about one leptictid skull in 10 retains the bulla.

² *Stehlinella* included. See Jepsen (1934, p. 302).

³ I am not sure that this tooth is an incisor rather than a canine, though it is probably the former. Quotation marks are used where certainty is lacking.

JEPSANELLA SIMPSON, 1940

TYPE LOCALITY, DISTRIBUTION, AND DESCRIPTION: As for the monotypic species.

DIAGNOSIS: Apatemyids with molars decreasing in size from M_1 to M_3 ; large lower "incisor" present, but not extending so far back beneath lower molars as in later apatemyids; molar trigonids high, possibly somewhat recurved; anterior cingulum absent on lower molars; M_1 trigonid wider than talonid (also seen in *Labidolemur soricoides*); fourth (anterolabial) trigonid cusp indicated only on M_1 ; notches between protoconids and metaconids of molars more acute than in later genera.

Jepsenella praepropera Simpson, 1940

Figure 1

TYPE: A.M.N.H. No. 35292, a fragmentary right lower jaw, with M_1 - M_3 .

TYPE LOCALITY: Gidley Quarry, upper Lebo Formation, Fort Union group, Crazy Mountain Field, Sweetgrass County, Montana. Torrejonian.

DISTRIBUTION: Type locality only.

DESCRIPTION: (Slightly revised and expanded from the original description). When in place, the "incisor" root extended under M_1 , probably reaching a point below the middle of M_2 . The alveolus ends at that point. The "incisor" root occupied approximately the lower half of the jaw beneath M_1 and was not particularly compressed, judged from the imperfect remains of the alveolus. As in other apatemyids, the "incisor" alveolus was situated near the lingual wall of the dentary, allowing the cheek-tooth roots to extend ventrad for a distance on its labial side. The "incisor" did not yet crowd the molars as much as in later apatemyids, which adjusted by making an increase in molar size from M_1 to M_3 . In *Jepsenella* the reverse is the case. *Apatemys kayi* represents an intermediate grade in this shift.

M_1 is implanted by two roots, of which the posterior is considerably the larger. The trigonid is very high and apparently tilted backward over the talonid basin. As noted in the original description, the paraconid (now destroyed) was not so lingually placed as that on M_2 . The anterior base of the trigonid slopes steeply upward anterior to the anterior root. A very faint trace of the fourth trigonid cusp of more advanced apatemyids can be seen at the anterior base of the protoconid, but there is no trace of a cingulum connecting to it. The protoconid apex has four

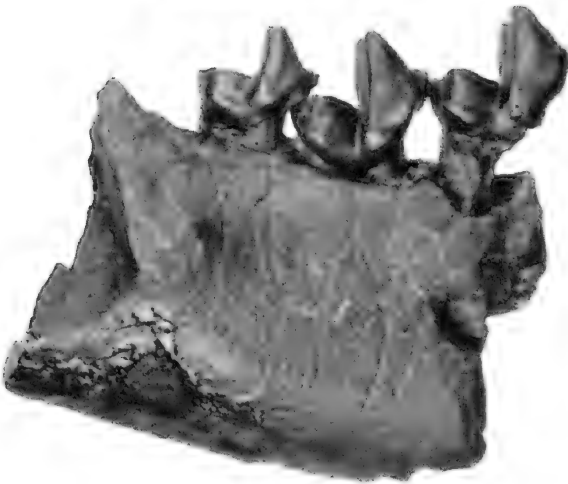
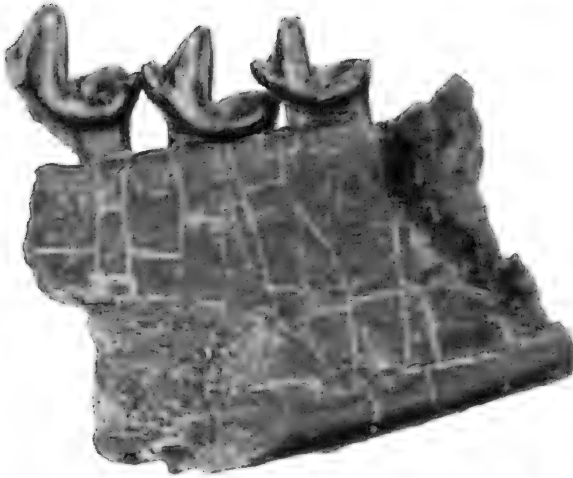


FIG. 1. *Jepsenella praepropera*, A.M.N.H. No. 35292, fragmentary right lower jaw, with M_1 - M_3 , type specimen. Gidley Quarry, Upper Lebo Formation, Sweetgrass County, Montana. Torrejonian. *Above*: Occlusal view. *Center*: Lingual view. *Below*: Buccal view. All $\times 10$.

sides: the smallest is concave and faces the metaconid; the next largest is planoconvex and faces anterolingual; the third surface extends to the rear from the anterior crest, forming the curved labial wall of the trigonid; and the fourth surface is the planoconcave labial part of the M-shaped, posterior, trigonid wall. A feature of the protoconid which is progressively reduced on M_2 and M_3 is the sharp anterior crest from the apex to the trace of the fourth trigonid crest. The metaconid is as large as the protoconid but possesses only three faces: the posterior face is continuous with that of the protoconid; the lingual face curves forward to the blunt anterior crest; and a small third surface faces the protoconid. A blunt anterior crest is present on the metaconid, and this feature is also progressively reduced on M_2 and M_3 . The talonid is as broad as the trigonid and is deeply basined. The basin floor is not bowl-shaped but "funnels" to a deep pit just posterior to the base of the metaconid. The crista obliqua connects to the posterior trigonid wall slightly labial from its midpoint and extends posterolabial to the hypoconid. A small cuspule halfway along the crista obliqua may have been present, but the details are obscured by wear. The hypoconid apex rises slightly above the posterolabial end of the crista obliqua. The hypoconulid is set lower than the hypoconid. It consists of a transversely elongate blade which lodges against the labial end of the anterior surface of the paraconid base of M_2 . From the hypoconulid the raised lingual rim of the talonid basin curves forward to join the trigonid at the extreme lingual margin of the posterior trigonid wall. The entoconid apex can be seen projecting a little distance above the rim. No cingula are present anywhere on M_1 .

M_2 possesses a high trigonid, with a steeply sloping anterior base, as in M_1 . The paraconid is more conical than blade-like, but a crest runs from its apex to the anterior base of the protoconid, where the crest turns, becoming the anterior protoconid crest. No fourth trigonid cusp is present at that point; consequently the anterolabial corner of the trigonid does not project so far forward as does the paraconid. The paraconid is more lingually placed than was evidently the case on M_1 . The protoconid and metaconid are high and subequal but otherwise are similar to the same cusps on M_1 . The anterior protoconid crest is weaker than that of M_1 , but is not absent. The talonid is somewhat narrowed at its anterior end, because the crista obliqua joins the center of the posterior trigonid wall at a greater angle than on M_1 . The crista obliqua does not bear an accessory cuspule, and the hypoconid apex does not rise above the crest, possibly partly because of wear. The hypoconulid cannot be clearly seen but must be low and little differentiated from the talonid rim. The entoconid apex is only barely perceivable. As in M_1 , there are no cingula,

but swellings along the base of the hypoconid and up the anterolabial edge of the protoconid suggest that cingula at these sites were present in apatemyid ancestors.

M_3 is smaller than M_1 or M_2 and has a relatively narrower talonid. The protoconid and metaconid are large and high cusps, with precipitous walls, particularly the metaconid, but the paraconid is low. Although definitely a separate cusp, the paraconid is to a large extent incorporated in a shelf. This shelf is widest at the lingual side of the trigonid and disappears anterior to the base of the protoconid. It is not to be confused with a true cingulum. There is no trace of a fourth trigonid cusp, nor is there an anterior crest on the protoconid. The talonid is short and relatively narrower with respect to the trigonid than that on M_1 or that on M_2 . The principal cusps are all submerged in a nearly continuous rim, but the apices would probably be distinguishable if the tooth were less worn. As in M_1 and M_2 , the talonid basin "funnels" to a pit just posterior to the base of the metaconid instead of presenting a bowl-shaped floor. The talonid rim is broken lingual to the deepest part of the floor, just posterior to the juncture of the rim with the posterolingual corner of the metaconid base. Whether this break is normal is uncertain, but it does "drain" the talonid basin to some extent.

As in more advanced apatemyids, the molars present a highly characteristic lingual curvature which sweeps smoothly from the paraconid to the rear of the talonid. If the specimen is viewed with the vertical plane of the dentary perpendicular to the focal plane of the microscope, the metaconid apices progressively project beyond the curve more and more linguad from M_1 to M_3 . Apatemyid molar crowns are, however, set at an angle from the roots and plane of the dentary. If the molars are viewed with the focal plane parallel to what would normally be considered the occlusal plane, then only the metaconid of M_3 projects lingual to the curved base of the tooth.

The dentary is not so deep relative to molar-crown height as in more advanced apatemyids, but, of course, the crown height is relatively higher in *Jepsenella* than in such forms. The ratio of the length of M_2 to the depth of the ramus beneath that tooth is similar to that of Eocene apatemyid species such as *Apatemys bellus* (1/2.2 versus 1/2-2.4). The "incisor" alveolus terminates under the anterior end of M_2 , whereas it extends beneath M_3 in later apatemyids. The masseteric fossa is deep, but does not extend beneath M_3 . The anterior ridge of the ascending ramus extends halfway down the labial surface of the jaw, opposite the rear of M_3 , but does not obscure any of that tooth in a labial view. A broad, curved shelf posterolabial to the talonid of M_3 is present, as in

more advanced apatemyids. A large, slit-like, mental foramen is present about halfway up the labial side of the dentary, below the posterior root of M_1 . The slit is about twice as wide as it is long and is oriented in a posterodorsal-anteroventral direction. The jaw is broken at the anterior end of the foramen, but evidently a groove in the labial surface of the dentary led forward from the foramen. Excavation of the foramen has revealed that the principal passage within the dentary runs postero-ventromedial in the progressively thicker and thicker labial wall of the jaw, next to the tapering tip of the "incisor" root. At least one and perhaps two minor passages lead forward in the labial wall of the "incisor" alveolus.

LABIDOLEMUR MATTHEW AND GRANGER, 1921

TYPE LOCALITY, DISTRIBUTION, AND DESCRIPTION: As for the monotypic species.

DIAGNOSIS: Apatemyids advanced beyond *Jepsenella* in that molar trigonids are lower and molars probably increase in size from M_1 to M_2 and perhaps M_3 , but trigonid of M_1 wider than talonid as in *Jepsenella*; sides of notch between protoconid and metaconid of M_1 making angle of about 100 degrees, in contrast to *Apatemys kayi* (about 120°) and *Jepsenella praepropera* (about 80°); P_3 , if correctly identified, small and relatively simple compared to P_3 of *Stehlinella*, *Sinclairiella*, and *Apatemys rodens*, but comparison with other Eocene species not yet possible; dorsal edge of labial enamel face of "incisor" with one large and several small serrations; "incisor" root terminating under M_3 .

COMMENTS: The diagnosis given here suffices to distinguish *Labidolemur* from *Jepsenella* at the generic level but is almost certainly not adequate to separate *Labidolemur* from *Apatemys* and some of its Eocene allies that may themselves be referable to *Apatemys*. *Labidolemur soricoides* is distinguishable from other known apatemyids at the specific level, but it may be necessary to merge *Labidolemur* with *Apatemys* when Eocene apatemyids are next revised.

Labidolemur soricoides Matthew and Granger, 1921

Figure 2

TYPE: A.M.N.H. No. 17400, associated right and left lower jaws, with "incisor" and M_1 on each side and doubtfully associated lower premolar.

REFERRED SPECIMEN: A.M.N.H. No. 17402, a lower left "incisor."

TYPE LOCALITY: Mason Pocket, Tiffany beds, southern Colorado. Tiffanian.



FIG. 2. *Labidolemur soricoides*, A.M.N.H. No. 17400 (in part), right "incisor" and M_1 in a fragment of the jaw, part of the type specimen. Mason Pocket, Tiffany beds, southern Colorado. Tiffanian. *Above*: Occlusal view. *Center*: Lingual view. *Below*: Buccal view. All $\times 6$.

DISTRIBUTION: Type locality only.

REVISED DESCRIPTION: The "incisor" root extends beneath the molars, terminating under M_3 . The root is nearly straight, in contrast to the curved crown. The pulp cavity is constricted at the rear of the root. Faint transverse wrinkles such as those on the root of an *Eochiromys* "incisor" observed by Teilhard¹ (1927, p. 15) are present on the ventral surface of the root, near the tip. They almost certainly represent growth bands. The crown is completely enamel-covered and strikingly similar to the "incisor" in certain shrews, e.g., *Blarina*. It is not possible to say whether the enamel begins exactly at the point where the tooth emerges from the alveolus, as in shrews, or whether the enamel begins anterior

¹ "La couronne est entièrement émaillée, et séparée de la racine par un sillon bien distinct. Cependant la face inférieure de cette racine est brillante, et se couvre, vers l'extrémité proximale, de petits plis transversaux, comme se elle tendait à se revêtir, elle aussi, d'une couche d'émail."

to that point. The anterior walls of the alveolus have been lost. Even though the exact extent of the dentary is not known, it is doubtful that the enamel crown could have extended within the alveolus in the adult. That it did so in more advanced apatemyids is well known, but in at least one other apatemyid, *Eochiromys landenensis*, the enamel crown of the "incisor" does not extend into the alveolus. In general, the posterior border of the enamel is not raised into any sort of fold or buttress like that in some shrews, but simply thins and terminates. The posterodorsal border of the enamel is slightly thickened, however, on the type (A.M.N.H. No. 17400).

The crown is crudely triangular in cross section. The lingual face was appressed to the opposite "incisor" for slightly more than the anterior third of its length. That part of the lingual face is nearly flat (partly from wear). The face abuts against the opposite "incisor" both dorsally and ventrally, but there is a furrow in the enamel which extends from near the crown tip to the point where the lingual enamel divides. The furrow then broadens and is continued in the lingual wall of the root. The posterior part of the lingual enamel divides into two sections, one dorsal and continuous with the spatulate-dorsal surface of the crown, the other ventral and continuous with the curved labial face. The surface of the dorsal section curves gently labiad and loses its contact with the opposite "incisor." As its upper edge curves posterodorsad, the enamel decreases in ventral extent until it becomes merely the lingual edge of the curved dorsal surface of the crown. The ventral section does not extend so far to the rear on the lingual face as does the dorsal, because its upper edge, after descending to the ventral border of the root, passes across the root to continue as the posterior border of the labial enamel face.

The labial face of the crown curves upward in a 90-degree arc from the ventral border of the lingual face; there is therefore no ventral face as such. The enamel is rugose, with considerable anteroposterior alignment of irregularities on the enamel surface. On the type specimen, individual irregularities are pointed in front and seem to overlap more anteriorly placed ones. On the referred specimen the reverse is true. The posterior edge of the labial enamel face is really the curved continuation of the upper edge of the ventral section of the lingual face. After running anterodorsally a short distance up the curved ventrolateral surface of the root, the thin posterior border of the labial enamel face curves anterodorsad and then runs dorsolingual across the side and top of the root to meet the posterior part of the labial edge of the dorsal enamel surface of the crown. The dorsal edge of the labial enamel face consists of a serrate cutting edge which arises as a ridge diverging from the upper part of the

posterior enamel border before the latter meets the edge of the spatulate dorsal surface of the crown. The ridge runs forward, meets the edge of the dorsal surface of the crown as the latter curves forward, and then runs to the tip of the crown. Both incisors of the type specimen possess a small serration at the junction of the ridge and the dorsal surface of the crown and have a large compound serration anterior to that, but the referred specimen possesses only one large serration in this region. Evidently these characters are rather variable. In front of the notch anterior to the steep front of the large serration a number of tiny serrations are present, but wear has dulled their apices, and their presence can be deduced only from fairly regular variations in the thickness of the cutting edge. Teilhard (1927, p. 15) has observed similar tiny serrations on an "incisor" referred to *Eochiromys landenensis*, but the large posterior serration or serrations are not present on Teilhard's specimen.

The dorsal face of the crown is concave anteroposteriorly, convex and continuous with the lingual face lingually, and concave labially. Labially the dorsal face is continuous with the serrate ridge. On the right incisor of the type specimen the rear of the dorsal face is broken in such a way as to suggest the presence of several cuspules (cf. some specimens of *Plesiadapis*), but the referred specimen and the left incisor of the type show that such cuspules are lacking. At the tip of the crown the dorsal face curves away from the midline slightly. A short lingual shelf is present in this area, below the level of the dorsal surface of the crown. This shelf probably represents all that remains of the original anterior crest of the "incisor." Similar shelves are present on the "incisors" of such genera as *Plesiadapis* and *Microsyops* and on the canines of *Notharctus* and *Adapis*. The crowns of the incisors and canines of various more pertinent genera are either unknown or undescribed.

The left P_3 seems almost certainly represented by an isolated tooth which is present in the same box as the jaws of the type specimen. Simpson (1935b, p. 8) suggested, probably correctly, that the tooth was found in the same matrix as the type, but the original degree of association is now unknown. Matthew and Granger (1921, p. 4) originally stated that *Labidolemur soricoides* had only one premolar, P_4 , but this conclusion was based on alveoli in the jaws. They did not describe an actual premolar. P_3 undoubtedly was recovered in the course of additional preparation of the type material between 1921 and 1935.

The root of P_3 was implanted at an angle, but not enough of the alveolus is present for the angle to be determined exactly. The root is forced into its cramped position by the enlarged "incisor." The root is not only tilted but curved, presumably to fit over the dorsolabial curva-

ture of the "incisor" root and to bring the vertical blade of the crown to a more lingual position than that of the alveolus. The crown consists of an elongate blade supported by the root only at the posterior end. The anterior half of the crown probably rested on the dentary somewhat as in *Apatemys rodens* (Gazin, 1958, pl. 12, fig. 6, U.S.N.M. No. 13277), but support from this source could not have been very great. The crown does not project so far forward as in *Stehlinella* or *Sinclairiella*. A low posterior cusplule rises above the "rear" edge of the root. The crest of the main blade of the tooth begins at the front of the posterior cusplule, runs anterolabially a short distance, and then climbs gently to the apex. From the apex the crest plunges steeply to the anterior base of the crown. A rather poorly differentiated cingulum extends from the anterior base of the crown posterolingual and then to the rear, along the lingual base of the crown, finally connecting to the base of the posterior cusplule. The posterior part of the lingual cingulum is broad. The labial wall of the blade is smooth, extends more ventrally than the lingual wall, and lacks a cingulum at the base. The ventrolingual surface of the projecting part of the crown is covered with enamel nearly to the root. Of the known third lower premolars of American apatemyids, if it be assumed that the present specimen is correctly identified, *Labidolemur soricoides* possesses the most primitive crown.

P₄ apparently possessed two roots. The tooth itself is missing, but the crushed alveoli of the jaws permit the interpretation. Matthew and Granger (*ibid.*) also believed that P₄ possessed two roots, but their belief was based on the alveolus of P₃ and only one of the alveoli here attributed to P₄. Simpson (1935, p. 7) also believed that P₄ was probably double-rooted, but did not state his reasons. If evidence from both lower jaws is combined, three alveoli for premolars can be seen. On the right lower jaw the anterior alveolus is obscure, and on the left lower jaw the posterior alveolus is also, but the middle of the three alveoli is well shown on both jaws. All the alveoli are somewhat crushed, a very common condition in specimens of many genera from the same locality. If the tooth identified in this paper as P₃ is correctly identified and a single-rooted P₂ was not present, two of the three premolar alveoli are for P₄. A double-rooted P₄ is primitive for the family, but if *Unuchinia* is a Tiffanian apatemyid, single-rooted fourth lower premolars were present in at least one other late Paleocene genus.

M₁ possesses a low trigonid and a widely basined heel. There is a large posterior root beneath the talonid and a small anterior root beneath the rear of the trigonid. Most of the trigonid projects far forward, as in other apatemyids and in various primitive primates. The trigonid is propor-

tioned differently from that of M_1 of *Apatemys kayi*, a species formerly placed in *Labidolemur*. The protoconid and metaconid are quite widely separated, resulting in a posterior trigonid wall wider than the talonid, in agreement with M_1 of *Jepsenella*, and probably representing the primitive condition. In Eocene and Oligocene American apatemyids the trigonid of M_1 became narrowed. In *L. soricoides* the notch between the protoconid and metaconid is deeper than in *A. kayi*, and the angle between the sides is about 100 degrees, in contrast to about 120 degrees in *A. kayi*. In the earlier and more primitive species *Jepsenella praepropera*, the notch was even more acute (about 80°) than in *L. soricoides*. The protoconid apex is slightly less massive than that of the metaconid, and its labial surface is more curved than in *A. kayi*, though not so convex as in the primitive genus *Jepsenella*. A crest runs from the apex anteroventrad to connect with a low cuspule that is the predecessor of the fourth trigonid cusp of some of the more advanced apatemyids. The cuspule is quite weak on the right M_1 but is stronger on the left M_1 , though not so distinct as in *A. kayi*. Its presence, however, transforms the primitive triangular trigonid into a crude parallelogram. A low ridge or paralophid runs from the apex of the cuspule across the front of the trigonid to connect with the anterolabial corner of the tiny paraconid, thereby nearly enclosing a narrow transverse basin between itself, the anterior slope of the protoconid, the paraconid, and the fourth trigonid cuspule. On the left M_1 a minute cuspule is present on the mid-section of the paralophid, but this has either been worn off or was originally absent on the right M_1 . The metaconid is relatively more massive than that of M_1 of *A. kayi* and has a more convex lingual face. The posterior face of the metaconid is flat and continuous with the posterior face of the protoconid, as in all apatemyids. The talonid consists of a broad bowl with a smooth floor and an even rim. Only the most minute traces of cusp apices remain. The lowest point in the bowl is just behind the base of the metaconid, but the curvature is more shallow than in *Jepsenella*. The rim of the bowl-like talonid begins on the posterolingual base of the metaconid and curves gently around to the position of the hypoconid, where the curvature becomes sharper as the rim swings around to join the posterior trigonid wall below and slightly labial to the deepest point in the notch between the protoconid and metaconid. There are no traces of cingula anywhere on the tooth. The enamel is smooth.

The lower jaws of *Labidolemur soricoides* have suffered considerable post-mortem damage. Both jaws have been laterally crushed to an unknown extent, accounting in part or wholly for the thinness of the horizontal ramus in comparison with that of other apatemyids. It is not

possible to say how far forward the dentary extended, but there are no marks on the "incisor" root to indicate the limit of the alveolus. The dentary may well have extended to the posterior limits of the "incisor" enamel, with a slender median projection lying in the furrow separating the two sections of lingual enamel of each "incisor." Such is the condition in shrews.

Enough of the dentary below P_4 and M_1 is preserved to show that a fossa was not present in that region. The right lower jaw shows two small vertical depressions, but these are caused by crushing of the dentary against the roots of M_1 . Most small mammal jaws from the same locality are similarly crushed. Possibly a fossa could have existed farther forward, in the region of P_3 where the dentary is no longer preserved, but it seems very unlikely.

But one mental foramen is visible, and this lies ventral to the anterior alveolus of M_2 . The foramen is large and oval in outline. The major axis of the oval is anteroventral-posterodorsal. The principal passage from the foramen leads almost directly to the rear, with perhaps a small ventral component. No minor passage has been seen to lead forward from the anterior wall of the foramen, though a small pit exists at the proper site. It is possible that a minor passage exists but is unobservable by present techniques. The dentary is somewhat grooved anterior to the foramen, possibly because the root of M_1 ends just dorsal to the groove. Crushing of the dentary below the root probably accounts for the groove. In any event, the groove does not lead to another foramen. No minor foramina anterodorsal to the mental foramen are present.

APATEMYS MARSH, 1872

DISTRIBUTION: North America only, but closely similar species of *Eochiromys* and *Heterohyus* are known from the early Eocene of Europe and indicate dispersal between North America and Europe by an unknown route at about the end of the Paleocene.

CHRONOLOGIC RANGE: Tiffanian late Paleocene (Bear Creek) to Uintan late Eocene (Tapo Ranch).

DIAGNOSIS: It is not practical to give a diagnosis for this predominantly Eocene apatemyid at the present time. *Labidolemur*, *Teilhardella*, *Eochiromys*, and *Stehlinella* may all be synonyms of it, but the known specimens of these forms are not often adequate for comparison. A revision of *Apatemys* and the other Eocene apatemyids is greatly needed but must await the collection of more material. Only *Apatemys kayi* is discussed here, because of its Paleocene occurrence.

Apatemys kayi (Simpson, 1929b)

Figure 3

TYPE: C.M. No. 11703, a fragmentary left lower jaw bearing the "incisor" root and P_4-M_3 .

TYPE LOCALITY: A layer of carbonaceous clay above coal vein No. 3, in the Eagle Mine, Bear Creek, Carbon County, Montana. The age of this locality is generally regarded as Tiffanian.

DISTRIBUTION: Type locality and possibly the Four Mile fauna, earliest Wasatchian of Moffat County, northwest Colorado (see McKenna, 1960, pp. 47-51).

REVISED DESCRIPTION: The "incisor" extends for a considerable distance below the cheek teeth and terminates under the anterior root of M_3 , according to a skiagram made by Jepsen (1934, p. 296, fig. 4). The cross section of this tooth beneath P_4 and M_1 is oval. The "incisor" at this point occupies only the lower half of the dentary and does not come near the pit beneath P_4 as in the Four Mile form, cf. *Apatemys kayi*. Such differences of position could be functions of age of the individuals involved or represent real differences in "incisor" size and placement, but the question cannot be settled at present. Inspection of the "incisor" cross section under ultraviolet light indicates that enamel is not present so far back on the root.

A worn and broken "incisor" undoubtedly referable to *Apatemys kayi* is present in the Princeton Bear Creek collection (P.U. No. 17176). This tooth shows considerable similarity to A.M.N.H. No. 17402, an "incisor" referred to *Labidolemur soricoides*. The root is deeper and thicker, however, and the enamel generally thinner, even when wear is taken into account. The enamel of the dorsal face of the crown has worn completely through on the lingual side, as in a Wasatchian apatemyid incisor (P.U. No. 17177) from the early Gray Bull fauna. Faint traces of a tiny posterior and a somewhat larger anterior serration exist at the same place on the posterolabial edge of the dorsal surface of the crown as in *Labidolemur soricoides*, but wear has nearly obliterated them. Even when unworn, however, the serrations could not have been so large as the large serration possessed by *Labidolemur soricoides*.

The alveolus of P_3 is indicated in Jepsen's illustration (1934, p. 296, fig. 4), but only the tiniest pit is present ventrolingual to the bottom of the root of P_4 on the broken cross section of the jaw, and this is not in the proper position to house the root of P_3 , which would have been labial to that point. *Apatemys kayi* undoubtedly had a procumbent P_3 but this feature is not demonstrated by known material.

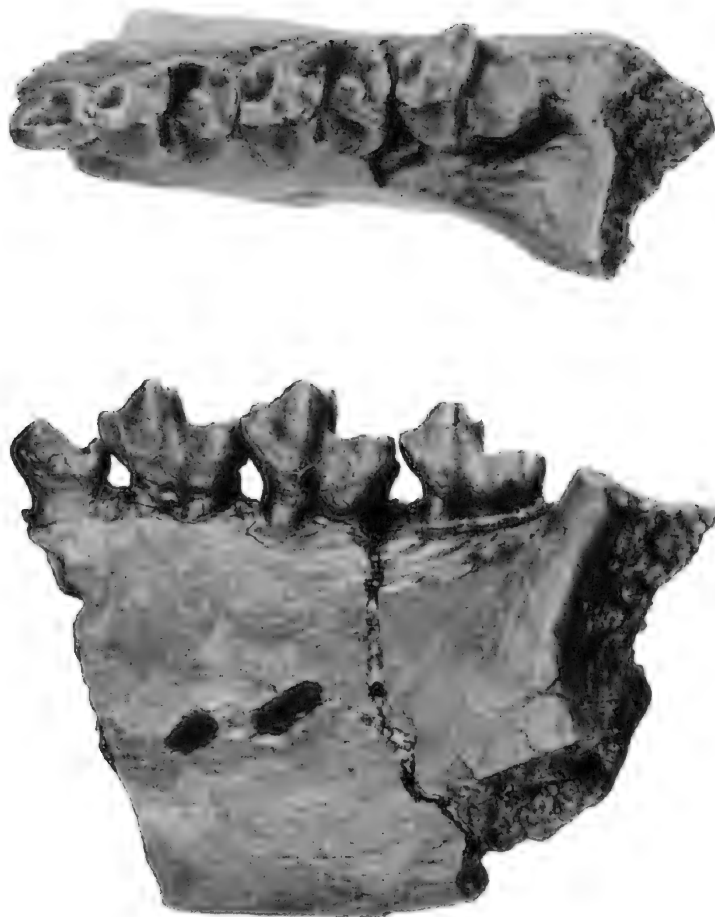


FIG. 3. *Apatemys kayi*, C.M. No. 11703, fragmentary left lower jaw, with P_4 - M_3 , type specimen. Eagle Mine, Bear Creek, Carbon County, Montana. Tiffanian. *Above*: Occlusal view. *Below*: Buccal view. $\times 10$.

P_4 is single-rooted. The root may have extended somewhat deeper, on the labial side of the "incisor," than is indicated by Jepsen's skiagram. A faint crease exists below the crown on the lingual side of the root, but the root does not divide in the alveolus. The crown of P_4 is secondarily simplified. It resembles the crown of *Teilhardella chardini* and is not so reduced as the crown of *T. whitakeri*. The crown is small, but traces of formerly important cusps remain. The principal cusp is the protoconid. It is set well forward and possesses an anterior crest, which plunges to the former site of the paraconid, and a posterior crest, which connects

on the labial side of the tooth to the anterior base of the hypoconid. A faint swelling on the posterolingual base of the protoconid is all that remains of the metaconid. From its faint apex a crest curves ventrolingually and then posteriorly to delimit the talonid basin. The heel possesses but one high cusp, evidently the hypoconid, which is closely appressed to the ventral wall of the jutting trigonid of M_1 and probably was not of functional importance in occlusion. The heel is of the type that is called crested by one author and basined by another. The hypoconid and posterior protoconid crests are higher than the lingual talonid rim, but the heel is best described as basined.

M_1 possesses a low trigonid and a widely basined heel. There are two roots, of which the anterior is the smaller. The trigonid projects anterodorsally from the anterior root, overtopping the heel of P_4 . This part of the tooth is relatively more elongate and narrow than the corresponding structure in *Labidolemur soricoides*. The protoconid is the most massive and highest trigonid cusp, but it does not greatly exceed the metaconid in these features. Its labial and posterior faces are nearly flat, but the remaining wall is curved. From the protoconid apex a crest runs anteroventrad to join the posterolabial base of a small cusp which is characteristically present in several apatemyids. The cusp is present at the position where the paralophid once joined the anterior protoconid crest, but this part of the trigonid in most apatemyids has been extended forward, even farther than the paraconid, giving the trigonid a peculiar aspect, like a parallelogram when seen in occlusal view. The trigonid actually has four main cusps. The paraconid is isolated, but a faint labial crest from its anterior edge indicates the former extent of the paralophid. The metaconid is set posterolingual to the protoconid. Its flat posterior face is continuous with that of the protoconid, forming a sheer wall considerably lower than that of *Jepsenella* but similar to that of *Labidolemur soricoides* and some Eocene apatemyids. The talonid is wider than the trigonid. The apex of the hypoconid is not a truly distinct cusp, for it actually is merely the posterolabial end of the crista obliqua. The hypoconid apex exists at the end of this crest, but it is overshadowed by the hypoconulid. The base of the talonid in this region widely overhangs the labial side of the posterior root. The entoconid and hypoconulid are blade-like cusps that rise above a curving ridge which runs from the indistinct apex of the hypoconid around the posterior border of the talonid basin. The hypoconulid is the highest talonid cusp. Its apex is transversely elongate, but the highest point lies immediately in front of and closely appressed to the indistinct fourth trigonid cusp of M_2 . The entoconid is a much smaller blade-like rise situated just labial to the posterolingual corner of

the talonid. Anterior to the entoconid the talonid basin is not well closed. The floor of the talonid basin is quite rounded or bowl-shaped. There are no cingula at all, even below the fourth trigonid cusp. The characteristic sweeping lingual "apatemyid curve" of the tooth is broken at its anterior end by the paraconid, which lingually juts out relatively more than in M_2 .

M_2 is the largest cheek tooth. The trigonid is relatively much wider than that of M_1 and is swollen at the labial base, partly because of the presence of a remnant of the anterior and anterolabial cingulum. The cusps are similar to those of M_1 , but are set more widely apart, are larger, and the anterior crest from the protoconid apex does not terminate at so large a fourth trigonid cusp as in M_1 . The anterolabial (or fourth) trigonid cusp is situated at the anterodorsolingual end of the remnant of the anterior cingulum. That it arose from the cingulum is possible but not proved. *Jepsenella* lacks all but the faintest trace of a cingulum, and the cingulum of *Unuchinia* does not reach the notch between the parolophid and anterior protoconid crest, where the fourth cusp is situated in the more advanced forms that possess it. The talonid of M_2 is essentially like that of M_1 but is slightly wider, and its basin is more spacious. The crista obliqua joins the posterior trigonid wall at a slightly more labial position than in M_1 . The cusps are virtually the same as those of M_1 . The characteristic apatemyid lingual curve of the tooth crown is present and is not broken by either the paraconid or the metaconid.

M_3 is approximately the size of M_1 . The trigonid of M_3 possesses cusps in about the same positions as on M_2 , but the fourth cusp is minute. As on M_2 , the tiny fourth cusp is situated at the anterodorsolingual end of the remnant of the anterior cingulum. As in the other molars, it is the most anterior area of the crown and lies just posterior to the labial end of the hypoconulid blade of M_2 . A cingulum rises to the cusp along the anterolabial base of the protoconid, as in M_2 , but the anterior end of the trigonid does not jut forward and upward at so great an angle as does the trigonid of M_2 . Although M_3 may not be seated perfectly in its two alveoli, nevertheless the metaconid has a more nearly vertical lingual wall than does that of M_1 or that of M_2 ; in occlusal view the cusp projects lingual to the curving lingual base of the crown. The talonid is slightly reduced and in occlusal view is almost semicircular in outline. None of the usual talonid cusps is raised very far above the basin rim. The latter consists of a straight crista obliqua which begins at a point on the posterior trigonid wall almost beneath the protoconid apex, turns sharply at the weak hypocone apex, and from there sweeps around the posterior and lingual borders of the talonid basin to rejoin the posterior trigonid wall

at the posterolingual base of the metaconid. The hypoconulid and perhaps the entoconid are present as faint swellings on this rim. The smooth talonid basin is broad and relatively longer than that of M_2 , though is not so elongate as that of most other apatemyids.

The enamel of all the teeth present in the specimen is somewhat rugose and covered with tiny grooves, notably on the lingual sides of the teeth. The jaw is covered with the same grooves. Evidently the jaw was enveloped in a system of plant rootlets before fossilization. Although it is certain that some of the enamel has been dissolved away the amount is surely not important enough to modify significantly the preceding description of the dentition.

The lower jaw is very incompletely preserved, but certain crucial features not discussed or illustrated in the original description may be noted. The jaw is deep with respect to the height of the molars. The anterior ridge of the ascending ramus arises labially from the dorsal third of the horizontal ramus under the rear of M_3 , creating a sloping shelf labial to M_3 and sharply delimiting the masseteric fossa. The masseteric fossa extends forward to a point beneath the posterior border of the talonid of M_3 . The fossa was deep and evidently supported powerful musculature.

Beneath P_4 and the foremost part of the trigonid of M_1 the dentary possesses a deep pit the purpose of which is unknown. The anterior part of the pit has been destroyed. At its deepest preserved point the pit nearly reaches the root of P_4 ; only a thin wall of bone covers the root. No foramen enters the preserved part of the pit. Two large mental foramina are present and are interconnected on the surface of the dentary by a trough. Careful excavation has failed to show the direction of entry of either passage into the dentary, or whether the posterior foramen is compound, but at least one can state that the anterior one could not have opened very far anteroventrally, for the broken cross section of the dentary shows that there was no large passage in that direction. The passage could have passed forward in the dentary labial to the dorsal part of the "incisor," or it may have led to the rear. The posterior mental foramen almost certainly led mainly to the rear, but whether posterodorsad, posteroventrad, or directly posteriad is unknown. It is not possible to say whether the posterior foramen was compound, with a small passage leading forward, but such a condition probably prevailed, judged from the closely related Four Mile form. The anterior mental foramen lies beneath the posterior root of M_1 ; the posterior one lies beneath the middle of M_2 . Both lie at the top of the lower half of the dentary, the anterior foramen being placed somewhat more ventrally than the posterior one, resulting in a postero-

dorsal orientation of their interconnecting trough. No subsidiary foramina have been noted, in contrast to a Four Mile specimen (U.C.M.P. No. 44784) which I have (1960) called cf. *Apatemys kayi*.

MEASUREMENTS (IN MM.) OF TYPE: Length of P_4 - M_3 , 6.7; length of M_1 - M_3 , 5.6; length of P_4 , 1.3; width of P_4 , 0.8; length of M_1 , 1.9; width of M_1 talonid, 1.3; length of M_2 , 2.1; width of M_2 trigonid, 1.6; width of M_2 talonid, 1.4; length of M_3 , 1.9; width of M_3 trigonid, 1.8; width of M_3 talonid, 1.2; depth of jaw under M_2 , 5.2.

IS *UNUCHINIA* SIMPSON, 1937, AN APATEMYID?

In 1936 Simpson described a small lower jaw fragment from Scarritt Quarry in the late Paleocene of the Crazy Mountain Field, Montana, naming it *Apator asaphes*. The name "*Apator*" was later (1937) found to be preoccupied and was replaced by "*Unuchinia*." *Unuchinia* was referred to the Insectivora with a query and placed in that order, *incertae sedis*, because Simpson believed that the teeth were those of an insectivore, even if they should prove to be P_3 - M_1 rather than P_4 - M_2 . No comparisons with apatemyids were made. The crushed alveolus for the "incisor" was not discussed or figured and presumably was not recognized.

If *Unuchinia* is an apatemyid, as seems possible to me, it represents a distinctive lineage within the family, derived from the very earliest apatemyids at a stage even more insectivore-like than *Jepsenella* from the Torrejonian. There is no resemblance to early primate dentitions other than the enlarged "incisor." Nevertheless, enough doubt as to the placement of *Unuchinia* in the Apatemyidae remains so that restraint is called for, either in erecting a new apatemyid subfamily for reception of the genus or in utilizing *Unuchinia* as convincing evidence that primitive apatemyids are insectivore-like.

UNUCHINIA SIMPSON, 1937 (= *APATOR* SIMPSON, 1936,
NOT SEMENOW, 1898)

TYPE LOCALITY, DISTRIBUTION, AND DESCRIPTION: As for the monotypic species.

DIAGNOSIS: (?) Primitive apatemyids; P_4 high and single-rooted; molars possessing high trigonids with distinct, anterolingually directed, blade-like paraconid, metaconid approximately as high as protoconid, and distinct anterior cingulum cusps beneath notch separating protoconid and paraconid; no incorporation of this cusps into squared anterolabial corner of trigonid; molar talonid cusps distinct and basin less rounded than in undoubted apatemyids; large mental foramen lying

beneath diastema between P_3 and P_4 ; no fossa in labial wall of jaw below P_4 or M_1 .

Unuchinia asaphes (Simpson, 1936)

TYPE: A.M.N.H. No. 33894, left lower jaw fragment, with P_4 - M_2 and alveoli for P_3 and M_3 . The alveolus for the enlarged "incisor" has collapsed because of crushing.

TYPE LOCALITY: Scarritt Quarry, Melville Formation, Fort Union group, Tiffanian of the Crazy Mountain Field, Montana.

DISTRIBUTION: Type locality only.

DESCRIPTION: The jaw is deep with respect to the molar height, even though the molars themselves are high. The "incisor" is missing but was enlarged and extended an unknown but probably short distance beneath the molars. There is a large, probably compound mental foramen beneath the diastema between P_3 and P_4 . The mental foramen opens to the labial surface of the jaw in what may be regarded as an elongate fossa, the anterior end of which narrows and passes forward into a groove in the surface of the dentary for an unknown length at the broken anterior edge of the specimen. Whether this groove contained another foramen anterior to the break is of course unknown. McDowell (1958, p. 206) has noted that this type of compound mental foramen is not restricted to apatemyids but also occurs in pantolestids. The large foramen in the deepest part of the fossa is directed posteroventromedially, suggesting that the "incisor" root terminated a short distance behind the foramen as in "*Teilhardella*" *whitakeri* (A.M.N.H. No. 48004; this detail is visible on the specimen but not on the published figure of it: Simpson, 1954, p. 2, fig. 1). No minor foramina have been noted anterodorsal to the major mental foramen beneath the diastema, nor is there any evidence for any more posteriorly placed mental foramina. Tiny foramina could be present but masked by the poor preservation but this appears to be unlikely.

Anterior to P_4 there is one definite alveolus and just possibly a trace of a second. Probably P_3 was single-rooted, like P_4 , but possibly it was not. Judged from the vertical orientation of the alveolus, it is probable that P_3 did not tilt forward to any appreciable extent. Following P_3 there is a short diastema, approximately 0.8 mm. in length, between the roots of P_3 and P_4 .

P_4 is supported by a single stout, vertically implanted root. The crown is very high, and its apex is in line with the paraconid of M_1 . On the principal cusp, presumably the protoconid, a raised cutting edge is present on the anterior face, running anteroventrolingually in a curve

to a slight swelling at the anterolingual base of the enamel. A similar raised cutting edge is present medially on the posterior face of the principal cusp, but the edge was not functional and is worn by wear against the paraconid of M_1 . The posterior cutting edge terminates at a deep notch that separates the principal cusp from the heel. At the posterior base of the principal cusp a tiny, partially basined heel is present. The heel is slightly damaged but possesses a high labial cusp which is probably the hypoconid. The dorsal surface of the heel tilts linguad and was either flat or somewhat basined. The heel is beneath the paraconid of M_1 and was non-functional.

M_1 is implanted by two roots, of which the posterior is considerably the larger. No interradicular crest is present. The trigonid is high for an apatemyid, relatively about as high as that of M_1 of *Jepsenella*. The posterior face of the trigonid consists of a single, nearly vertical, M-shaped, plane surface, the dorsal apices of which, the protoconid and metaconid, are of equal height (depending on the orientation of the jaw and the observer; Simpson's illustration depicts the protoconid as the higher of the two cusps). The protoconid apex is directly over the center of the anterior root. From the apex of the protoconid a sharp anterior ridge runs down the cusp to the base of a notch at the raised rim of the anterolabially trending trigonid valley. On the other side of the notch the cutting edge curves linguad and rises to the medially placed paraconid apex just posterior to the apex of P_4 . The trigonid is not squared or projecting at the anterolabial notched corner of the cutting edge and in this regard is more like the trigonid of *Jepsenella*, leptictids, and pantolestids than like that of the later apatemyids, all of which are greatly modified in this region of the trigonid. Below the notch between the paraconid and protoconid blades a trace of an anterior cingulum is present. The cingulum broadens and bears a minute ridged cuspule at its abrupt termination anteroventral to the above-mentioned notch. This type of structure is present in a good many small Paleocene mammals but is absent in *Jepsenella* and other previously known apatemyids. The metaconid is as high as the protoconid. It does not possess an anterior cutting edge. A "hollow-ground" labial cutting edge meets the lingual cutting edge of the protoconid at the base of a deep notch in the posterior trigonid wall. The talonid possesses the usual three major cusps, of which the hypocone is the largest. The hypocone is pyramidal rather than rounded and forms the sharp posterolabial corner of the talonid. A straight crista obliqua runs from the hypoconid apex to the posterior trigonid wall, joining it well below the notch that separates the protoconid from the metaconid. The crista obliqua does not bear an accessory cusp. The entoconid is a

small, anteroposteriorly oriented, blade-like cusp at the squared posterolingual corner of the talonid. Its anterior crest joins the posterolingual corner of the metaconid at the lingual base of the posterior trigonid wall. The hypoconulid is the smallest talonid cusp. It is medially situated and projects slightly to the rear, beneath the anterior cingulum cusp of M_2 . No definite posterior cingulum rises to join the hypoconulid, though there is a faint swelling along the posterior face of the hypoconid. The talonid basin floor is nearly flat rather than bowl-shaped and is shaped like a parallelogram of which the acute angles are posterolabial and anterolingual, respectively. The deepest point is a pit just posterior to the base of the metaconid. There are no lingual or labial cingula. The whole lingual side of the tooth follows an unbroken curve from entoconid to paraconid, as in apatemyids. The apex of the metaconid lies lingual to this curve in the occlusal view, but the base of the cusp conforms to the curve.

M_2 is larger than M_1 but agrees in most essential details. The paraconid is placed somewhat more lingually, and the notched cutting crest that runs from its apex to that of the protoconid does not make so great an angle in the horizontal plane at the notch as does the homologous crest of M_1 . The paraconid is not an isolated cone nor is it so reduced as is that of later apatemyids. The crista obliqua is placed somewhat more medially on the tooth crown than is that of M_1 , and the talonid basin is therefore relatively somewhat narrower and has a curved floor. The tip of the metaconid has been lost subsequent to the publication of the original illustration (Simpson, 1936, p. 17, fig. 7).

M_3 is missing. The anterior alveolus is approximately the same size as the anterior alveolus of M_1 and M_2 and is wider than long. The posterior alveolus is not completely preserved but is narrower than the anterior one and is elongate. Presumably M_3 possessed a relatively elongated talonid.

MEASUREMENTS: P_4 width, 0.9 mm.; P_4 length, 1.4 mm. M_1 , width of trigonid, 1.5 mm. at base, wider if measured between projected protoconid base and metaconid apex; length of tooth crown, 2.3 mm. M_2 , width of trigonid, 1.6 mm. at base, wider if measured between projected protoconid base and metaconid apex; length of tooth crown, 2.4 mm.

EOCENE APATEMYIDS

Figures 4, 5

No revision of the post-Paleocene apatemyids is attempted here, but two Wasatchian and Bridgerian specimens that show the upper molar

morphology of American apatemyids are figured for reference, because no Paleocene upper molars are known. The apatemyid upper dentition is fairly well known in the late Eocene European *Heterohyus quercyi* and American *Stehlinella uintensis*, and in the Oligocene genus *Sinclairiella*, but the more primitive early and middle Eocene species on both sides of the Atlantic Ocean are still known from very incomplete material. Recently a large number of fragmentary specimens of middle Eocene American

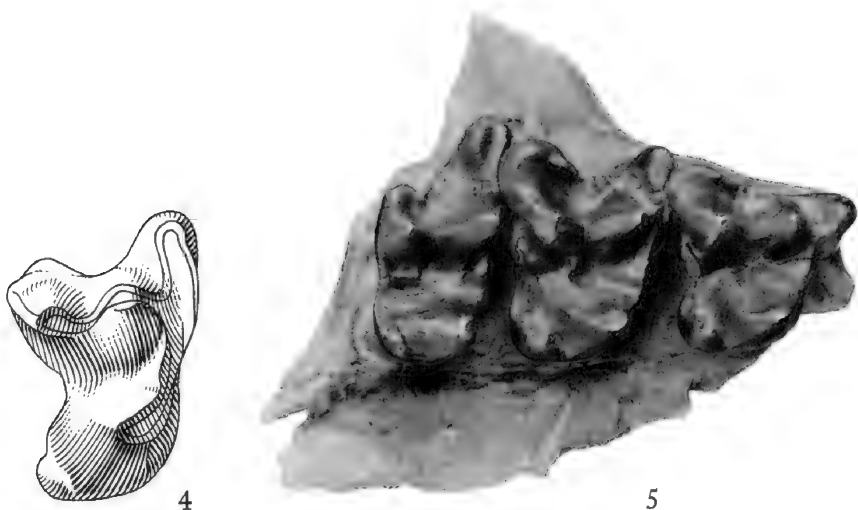


FIG. 4. *Apatemys* cf. *A. kayi* (Simpson, 1929b), U.C.M.P. No. 46873, right M³, U.C.M.P. V-5346, Four Mile fauna, earliest Wasatchian, Moffat County, Colorado. This specimen was referred to the Insectivora or Menotyphla, *incertae sedis*, by McKenna (1960a, p. 63, fig. 30). Occlusal view. $\times 10$.

FIG. 5. *Apatemys* sp., U.S.N.M. No. 17765, fragmentary right maxillary, with M¹-M³, NW. 1/4, sect. 23, T. 15 N., R. 111 W., Bridger C, Bridger Basin, Wyoming. Occlusal view. $\times 10$.

apatemyids were found by Robinson in the Marsh Collection at the Peabody Museum of Natural History, Yale University, but it has not been possible to describe these remains here. What little is known of the early and middle Eocene apatemyid upper dentition, however, does not demonstrate an approach to primate molar morphology as would be expected if apatemyids and primates were diverging from a close common ancestor, but instead suggests affinities with the Insectivora. The earliest known apatemyid lower dentition, that of *Jepsenella* from the middle Paleocene, suggests the same conclusion. Both the upper and lower dentitions appear to have converged with primate dental mor-

phology, having become superficially quite similar to those of some primates by the late Eocene, just as they have converged with the living Australasian phalangerid marsupial *Dactylopsila*, but there is no significant similarity to the earliest primate dentitions now known. Instead, the transverse upper molars and wide styles of *Apatemys* and the high trigonids of the lower molars of *Jepsenella* suggest affinities with insectivores such as the leptictoids and erinaceoids.

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