

---

*Studies on the Earliest Primates*

BY GEORGE GAYLORD SIMPSON

---

BULLETIN  
OF  
THE AMERICAN MUSEUM OF NATURAL HISTORY

VOL. LXXVII, ART. IV, pp. 185-212

*New York*

*Issued July 31, 1940*

---





## Article IV.—STUDIES ON THE EARLIEST PRIMATES

BY GEORGE GAYLORD SIMPSON

FIGURES 1 TO 8

### CONTENTS

	PAGE
ABSTRACT.....	185
INTRODUCTION.....	185
I.—A NEW APATEMYID.....	186
II.—A NEW AMERICAN LOWER EOCENE ANAPTOMORPHID.....	187
III.—NEW DESIGNATION FOR A EUROPEAN ANAPTOMORPHID.....	189
IV.—SKELETAL REMAINS REFERRED TO <i>Hemiacodon</i> .....	190
V.—CLASSIFICATION OF THE ANAPTOMORPHIDAE.....	197
VI.—RELATIONSHIPS OF PALEOCENE AND EOCENE PRIMATES.....	199
VII.—DISTRIBUTION OF PALEOCENE AND EOCENE PRIMATES.....	206
VIII.—INDEXED BIBLIOGRAPHY OF PALEOCENE AND EOCENE PRIMATES.....	209

### ABSTRACT

This paper consists of a series of eight brief studies on Paleocene and Eocene fossil primates. The first describes *Jepsenella*, new genus, type *J. praepropera*, new species, from the Middle Paleocene of Montana, referred to the Apatemyidae, of which it is the oldest known member. The second describes *Loveina*, new genus, type *L. zephyri*, new species, from the Lower Eocene of Wyoming, an anaptomorphid allied to *Omomys* and *Washakius*. The third proposes and defines the new genus *Teilhardina* for *Omomys belgicus* Teilhard, 1927, from the Lower Eocene of Belgium, pointing out that this is quite distinct from, although allied to, *Omomys* and that it appears to be the most generalized known tarsiod. In the fourth study, a partial skeleton referred to *Hemiacodon* from the Middle Eocene of Wyoming is described and discussed. The skeleton of this supposed tarsiod is found to be unique in several respects and to resemble the lemurioids at least as much as the true tarsiods, and the possible bearings of this unexpected fact on primate history are discussed. The fifth divides the large family Anaptomorphidae into five subfamilies, Omomyinae, Paromomyinae, Anaptomorphinae, Necrolemurinae and Pseudolorisinae, defining

each and discussing them briefly. The sixth study is devoted to the relationships of the five families of Paleocene and Eocene primates to each other and to the Primates in general. *Pronycticebus*, *Caenopithecus* and *Anchomomys* are referred to the lemuriiform family Adapidae in addition to the genera commonly placed there. The Plesiadapidae are held to be definitely lemurioid and not specially related to *Daubentonina*. The Apatemyidae may not be primates at all, but there is at present no other less doubtful place to put them. The Carpolestidae appear to be a peculiarly aberrant offshoot of the proto-primate and probably prototarsioid stock. The usual view that the Anaptomorphidae are tarsiods is accepted, but the contents of the family are somewhat modified and it is pointed out that it is heterogeneous and may now include some non-tarsioid genera. In the seventh study knowledge of early primate distribution is summarized and the occurrences of each of the 55 genera tentatively accepted as valid are given in tabular form. The last, eighth, section gives a selected bibliography of the subject and an alphabetical list of valid genera with references by which the important literature on each can readily be found.

### INTRODUCTION

In the past fifteen years I have had occasion to study most of the known early mammalian faunas and also to identify several large new collections of them. In

the course of this work, original specimens of 38 of the 55 recognized genera of Paleocene and Eocene primates have been examined, and the literature on all has been

studied. Incidentally to this, several new primates were recognized, some important undescribed specimens of known forms were studied, a synthesis of the whole complex was envisioned and opinions, in some part at variance with previous ideas, were formed as to the affinities and interrelationships of these obscure animals. Some of these observations and conclusions were involved in various faunal studies, with which they were published, but others were

accumulated in the form of briefer notes and manuscripts. The purpose of the present publication is to bring out some of these accumulated data, which is done in the form of eight short papers, independent except that all relate to the general subject of early primates. References to the literature cited are gathered together in the bibliography (VIII). The accompanying illustrations were drawn by John C. Germann.

### I.—A NEW APATEMYID

The Third Scarritt Expedition, under my direction, found in 1935 a single specimen in the Gidley Quarry in central Montana that adds to the ranks of the oldest known primates (if such they are) and that carries the peculiar apatemyid line back into the Middle Paleocene. It represents a new genus and species, here described. The delicate specimen was prepared by Mr. Albert Thomson.

#### TAXONOMY

##### *JEPSENELLA*,<sup>1</sup> NEW GENUS

TYPE.—*Jepsenella praepropera*, new species.

DISTRIBUTION.—Middle Paleocene, Montana.

DIAGNOSIS.—An apatemyid with lower molar trigonids elevated far above talonids, protoconids and metaconids high and subequal, paraconids lower but strong and distinct, that of  $M_3$  smallest and median in position, squaring of antero-external trigonid rim less pronounced than in later forms, hardly noticeable on  $M_3$ , talonid of  $M_3$  short.

##### *Jepsenella praepropera*,<sup>2</sup> new species

TYPE.—Amer. Mus. No. 35292, right lower jaw with  $M_{1-3}$ .

HORIZON AND LOCALITY.—Gidley Quarry, Upper Lebo, Middle Paleocene, Fort Union Group, Sweetgrass County, Montana.

DIAGNOSIS.—Sole known species of genus.

#### DESCRIPTION

On  $M_1$  the paraconid ledge is broken, but harmony with  $M_{2-3}$  demands a large paraconid on this tooth and the broken base shows that this cusp was not fully internal, probably less

so than in *Labidolemur*, but probably more so than on  $M_2$  of *Jepsenella*. There is a very minute anteroexternal cusp on the trigonid of  $M_1$ , relatively smaller than in *Labidolemur*, and the trigonid as a whole is less sharply square and less anteroposterior than in *Labidolemur* or later genera. The most marked difference, however, is the greater elevation of the trigonids of all three molars in *Jepsenella*. There is some suggestion of progressive decrease in trigonid height in later forms, *Labidolemur* to *Sin-*

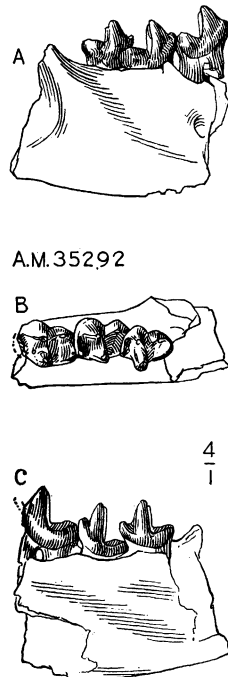


Fig. 1. *Jepsenella praepropera*, new genus and species. Type, Amer. Mus. No. 35292. Fragment of right ramus with molars. A, outer, B, crown and C, inner views. Four times natural size.

<sup>1</sup> For Dr. G. L. Jepsen, in recognition of his outstanding contributions to knowledge of the Apatemyidae and in analogy with *Teilhardella*, *Stehlinella* and *Sinclairiella*, names of allied genera.

<sup>2</sup> *Praepropera*, impetuous, precipitate, premature in allusion to the extraordinarily advanced specialization of this very early animal.



*clairella*, but the difference in this respect between these two, upper Paleocene to Lower Oligocene, is less than between *Jepsenella* and *Labidolemur*, Middle to Upper Paleocene.

Protoconid and metaconid are about equal on  $M_1$  while on  $M_2$  and still more on  $M_3$  the metaconid is somewhat the larger. The talonid is very slightly wider than the trigonid on  $M_1$ . On  $M_2$  it is slightly and on  $M_3$  decidedly narrower than the trigonid. The trigonid of  $M_1$  is a broad, shallow basin with a continuous, sharp, closed rim on which separate cusps are only indistinctly visible. The hypoconid is the highest and most distinct talonid cusp and is subrescenscent in form. There is a very vague cuspule on its anterior wing, which abuts against the base of the trigonid below the notch between protoconid and metaconid. There are vague but distinguishable hypoconulid and entoconid. On the inner side the sharp talonid rim runs into the base of the trigonid at its most internal point, below the metaconid.

On  $M_2$  the paraconid is about halfway between an internal (lingual) and a median position, the anteroexternal cuspule is represented by the faintest rudiment and the squaring of the trigonid is barely incipient, the outline being almost triangular rather than approximately square as in later forms. This squaring seems also to be progressive in the later genera, but again the difference between *Jepsenella* and *Labidolemur* is somewhat more than would be expected from their age difference. The talonid of  $M_2$  has the hypoconid crescent shorter and more angular than on  $M_1$ .

On  $M_3$  the paraconid is smaller than on  $M_2$  and is strictly median. The trigonid is triangular, and only the angulation of the protoconid-paraconid crest suggests incipient development of the more typical apatemyid quadrate outline. Except for being smaller and especially narrower, the talonid of  $M_3$  is essentially similar to that of  $M_2$ . It becomes elongated in later apatemyids, but here there seems to be little difference between *Jepsenella* and *Labidolemur*.

#### MEASUREMENTS

$M_1$		$M_2$		$M_3$	
Width	Length	Width	Length	Width	
1.2	1.6	1.4	1.5	1.1	

As in all apatemyids, the lower jaw is very deep and stout in proportion to the molars. The incisor root is gone, but part of its great alveolus, extending far back beneath the molars, can be

seen. The posterior mental foramen, beneath the posterior end of  $M_1$  and anterior of  $M_2$ , is almost exactly like that of *Labidolemur*.

The length of  $M_1$  is unobtainable because of breakage and those of  $M_{2-3}$  are only approximate because the structure prohibits accurate placing of caliper points.

Depth of jaw on internal side below  $M_2$  : 4.0.

The species is about as large as *Teilhardella chardini* and intermediate between *Labidolemur soricoides* and *L. kayi* in size. It is rather less than half as large as *Sinclairiella dakotensis*, the latest and largest known member of the family.

#### AFFINITIES

Although so sharply different in general aspect from the later genera, there can be little or no doubt that this form is an apatemyid, as that term has been revised and redefined by Jepsen (1934). It has all the essential apatemyid characters such as the large incisor root extending beneath  $M_2$ , the peculiarly placed and constructed posterior mental foramen, the (here incipient) quadrate trigonids, the shallow-basined, sharp-rimmed talonids and the short talonid on  $M_3$  (typical of early apatemyids). Moreover, its distinctions from later forms are on the whole and in varying intensity in line with the evolutionary trends shown by the later genera. It will not be supposed that the few species of these rare animals so fortuitously discovered represent an exact phylogeny—four of the six American genera are monotypic and seven of the nine American species are known essentially from only one specimen each. Yet with some fluctuation these known forms do represent a single structural sequence, the long, almost continuous record of which is very remarkable in view of the extreme rarity of known individual specimens, numbering only a dozen or fifteen in all and yet representing at least six and possibly seven distinct ages, from Middle Paleocene (Upper Lebo) to Lower Oligocene (Chadron).

#### II.—A NEW AMERICAN LOWER EOCENE ANAPTOMORPHID

In a small collection of early Tertiary fossils made by Mr. J. D. Love in western central Wyoming and referred to us for identification, Dr. Walter Granger and I recognized an interesting primate evidently

allied to *Omomys*. Mr. Love generously presented this specimen to The American Museum of Natural History in order that it might be more carefully compared with and included in the largest collection of

early primates. Detailed comparisons have now been made and the specimen proves to represent a new genus, which is described in this paper.

### TAXONOMY

#### LOVEINA,<sup>1</sup> NEW GENUS

TYPE.—*Loveina zephyri*, new species.

DISTRIBUTION.—Lost Cabin Formation, Wyoming, possibly also Gray Bull and Lysite, Wyoming, and Almagre, New Mexico. Lower Eocene of North America.

DIAGNOSIS.—An anaptomorphid with dental formula \_\_\_\_\_ . Jaw relatively short, sym-

2.1.3.3

physis deep, dental series closely crowded. Two lower incisors small and subequal, much smaller than canine, nearly erect. Lower canine not reduced, alveolus about as large as that for P<sub>2</sub>. P<sub>1</sub> absent, P<sub>2</sub> with one large vertical root. P<sub>3</sub> slightly smaller than P<sub>4</sub> and secondary cusps less distinct, otherwise almost identical. P<sub>4</sub> relatively transverse, compressed and rounded triangular in plan, slightly higher than M<sub>1</sub>, with distinct paraconid and metaconid. M<sub>1</sub> almost as in *Omomys*, but paraconid more internal, nearer to but still quite distinct from metaconid, marginal enamel nearly smooth but enamel wrinkled in talonid basin.

#### *Loveina zephyri*,<sup>2</sup> new species

TYPE.—Amer. Mus. No. 32517, left lower jaw with P<sub>3</sub>–M<sub>1</sub>, all anterior alveoli, and root of M<sub>2</sub>. Collected by Mr. J. D. Love.

HORIZON AND LOCALITY.—Near head of Badlands Gulch at the south end of Table Mountain, Kirwin Quadrangle, 6 miles east of Dubois, Fremont County, Wyoming.<sup>3</sup> In the Wind River Group, associated with a small but distinctive fauna almost surely of Lost Cabin age.

DIAGNOSIS.—Very slightly smaller than ?*Loveina vespertina*, horizontal ramus less deep, M<sub>1</sub> with paraconid more internal, coronal enamel more distinctly furrowed, external cingulum weaker.

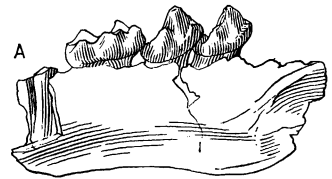
### DESCRIPTION

The incisive alveoli are imperfectly preserved, but it is hardly possible that there were more than two incisors, which had small and subequal roots, that of the first perhaps slightly the larger. Both are procumbent, the second less so, but only in slight degree, the roots being, in fact,

<sup>1</sup> Mr. J. D. Love, who collected the type.

<sup>2</sup> *Zephyri*, of the west wind, in allusion to the western locality, in analogy to the trivial name of its probable ally ?*L. vespertina*, and in suggestion of its occurrence in the Wind River Series.

<sup>3</sup> The locality is designated "XX" in Love's field notes and will be exactly shown by him in forthcoming studies.



A.M. 32517



$\frac{4}{1}$

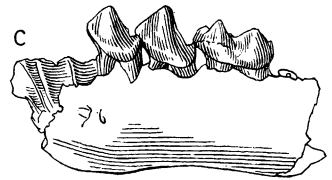


Fig. 2. *Loveina zephyri*, new genus and species. Type, Amer. Mus. No. 32517. Fragment of left ramus with P<sub>3</sub>–M<sub>1</sub>. A, inner, B, crown and C, outer views. Four times natural size.

remarkably erect in comparison with those of presumably allied genera. The canine alveolus is about as procumbent as that for the more posterior incisor, and the alveolus for P<sub>2</sub> is almost vertical.

P<sub>4</sub>, the most characteristic single tooth, is almost as broad as long and has a compressed, rounded-triangular outline quite distinct from that of the homologous tooth in typical *Omomys*. There is a well-differentiated metaconid and a paraconid fully differentiated and only slightly smaller than the metaconid. The talonid is much as in *Omomys*, but is relatively smaller and extends less toward the external side. P<sub>3</sub> is closely similar to P<sub>4</sub> but smaller and with paraconid and metaconid less distinct, although both are visible. These features make it still less like such allied genera as *Omomys* than is P<sub>4</sub>.

M<sub>1</sub> is of the familiar anaptomorphid type and very close to that of *Omomys* except for the small (but possibly important) details mentioned in the diagnoses: paraconid slightly nearer the metaconid, coronal enamel furrowed, external cingulum barely indicated.

#### MEASUREMENTS

P <sub>3</sub>		P <sub>4</sub>		M <sub>1</sub>	
Length	Width	Length	Width	Length	Width
1.6	1.4	1.8	1.7	2.2	1.8



## AFFINITIES

Among previously named genera, the closest resemblance to this form is shown by *Omomys*, *Hemiacodon*, *Washakius*, *Shoshonius* and *Navajovius*, all from the American Lower or Middle Eocene. The antemolar dentition of *Navajovius* is so different that special relationship seems to be excluded. *Hemiacodon* has the anterior incisor relatively much larger,  $P_2$  more reduced,  $P_{3-4}$  without distinct paraconids and with larger heels. The molar enamel is also more rugose, and in general the structure is not very close to *Loveina*. *Washakius* shows a much closer agreement in the relative sizes and structure of the antemolar teeth but  $P_{3-4}$  are less aberrant or advanced (although *Washakius* is the later of the two genera).  $M_1$  has a prominent metastylid that is much less strong or wholly absent in *Loveina*, and the enamel appears to be more wrinkled. The small subequal and nearly vertical incisors, the relatively unreduced canine and  $P_2$ , the crowding of the dental series, the outlines of the premolars, and some lesser features make for a special resemblance between *Washakius* and *Loveina*, and suggest that they are very closely related. *Loveina* might be supposed ancestral to the later form except for the probably slightly more aberrant  $P_{3-4}$ . In *Shoshonius*, only  $M_1$  can be compared and this is very like  $M_1$  of *Washakius*. It is impossible to say whether a closer or more distant relationship to *Loveina* is indicated.

*Omomys*, the best known genus of this group and in a sense its type, has the incisors more differentiated and more procumbent than in *Loveina*,  $P_2$  more reduced, the premolars less crowded and more elongate, paraconids barely rudimentary on  $P_{3-4}$ , and other lesser distinctions in part already mentioned. *Loveina* is clearly related in some degree to *Omomys*, which it

resembles more than it does *Hemiacodon*, for instance, but rather less than it does *Washakius*.

The question arises whether the Lower Eocene species previously tentatively referred to *Omomys* (a Middle Eocene genus) do not belong rather to *Loveina*. These species are ?*Omomys vespertinus* Matthew, 1915, and ?*Omomys minutus* (Loomis, 1906). In neither of these are antemolar teeth known and without these the generic assignment is highly uncertain. It is unlikely that either really belongs in *Omomys*. ?*Omomys minutus*<sup>1</sup> is surely a different species from the other two in question. Its more elongate alveoli for  $P_{3-4}$  suggest that these teeth were unlike those of *Loveina zephyri* and make common generic assignment uncertain. Loomis' species is still *incertae sedis* and may be left questionably in ?*Omomys* pending discovery of better material.

Only  $M_1$  can be compared in ?*Omomys vespertinus* and *Loveina zephyri*. On this slender basis the species might be synonymous, although they probably are not, or they might belong in different genera. Only discovery of the lower antemolar dentition of ?*O. vespertinus* could settle this problem. In defining *L. zephyri* as distinct, I am influenced not only by the probability that this is correct but also, as I think proper, by the fact that *L. zephyri* is surely definable generically and represents a new genus to which ?*O. vespertinus*, the type of which is not generically identifiable, may or may not belong. To define this new genus on a specimen dubiously referred to ?*O. vespertinus* would inevitably lead to serious confusion. There is, however, at least as much chance that *vespertinus* belongs to *Loveina* as to *Omomys* and it might tentatively be called ?*Loveina vespertina*.

## III.—NEW DESIGNATION FOR A EUROPEAN ANAPTOMORPHID

In 1927 Father Teilhard de Chardin described a primate from the Lower Eocene of Belgium, referring it tentatively to the American Middle Eocene genus *Omomys*.

He recognized that this would probably prove to be generically distinct, but he

<sup>1</sup> Placed by Loomis in *Notharctus* and transferred by Matthew (1915) to *Omomys*, to which it is clearly more nearly related.

has not had occasion to make the comparisons involved in checking this point. Upon making these comparisons for myself some years ago I observed that the European form is certainly generically distinct and extremely important. This occasion is therefore taken to give the genus a name, and the circumstances fortunately and appropriately permit that it be named for its discoverer.

#### TEILHARDINA,<sup>1</sup> NEW GENUS

TYPE.—*Omomys belgicus* Teilhard, 1927.

DISTRIBUTION.—Lower Eocene of Belgium.

DIAGNOSIS.—Dental formula  $\frac{1.1.3-4.3}{1.1.3-4.3}$ . At

least two and possibly three small lower incisors, moderately procumbent. Canine root larger than incisors or P<sub>2</sub>. Vestigial P<sub>1</sub> sometimes present. P<sub>2</sub> definitely smaller than canine but not much reduced. P<sub>3-4</sub> of elongate oval outline, not transverse or compressed, with low, rudimentary paraconid. Distinct metaconid on P<sub>4</sub>, none on P<sub>3</sub>. P<sub>4</sub> talonid simpler than in *Omomys*, trenchant, with small basin strictly on internal side of tooth. Lower molars with paraconids distinct, not completely internal but more so than in *Omomys*, proper. M<sub>3</sub> with slender, sharply differentiated, simple third lobe. No metastylids. Enamel nearly smooth. Tooth series continuous but not crowded.

As Teilhard (1927, pp. 16-18) pointed out, the closest known ally of this form is

*Omomys*. He foresaw that generic separation was probable, but did not take this step, largely because not certain that the Belgian species did have three incisors. After review of the various allied American genera and the discovery that some of the American Lower Eocene "*Omomys*" do not belong in that genus and that probably none of them do, it is clear that the Belgian species is also a representative of a distinct genus.

*Teilhardina* is of extraordinary interest not only as the oldest European anaptomorphid but also because it is, in the known parts, the most nearly generalized and the most primitive of all known tarsoids, or even of all known primates (if the tupaoids be excluded from the Order, contrary to my present opinion). Despite its close resemblance to *Omomys*, it differs from that likewise primitive genus in numerous slight particulars throughout the dentition, and every difference seems to stamp *Teilhardina* as less distant from truly prototypal primate morphology.

*Teilhardina* is distinctly more like *Omomys* than like *Loveina*. It could be structurally ancestral to *Loveina*, but has no special indication of the peculiarities of the latter.

#### IV.—SKELETAL REMAINS REFERRED TO *HEMIACODON*

Matthew (1915, p. 451) has mentioned but did not describe, a partial skeleton which he believed to belong to *Hemiacodon*. Skeletal elements of early primates are exceedingly rare and this specimen is of outstanding interest.

The specimen is Amer. Mus. No. 12613, found by Dr. Walter Granger in 1905 in the Upper Bridger, C<sub>6</sub>, on Henry's Fork, Bridger Basin, Wyoming. It includes a considerable part of the hind limbs of one individual, as detailed below, two or more elements of another individual of the same species, and some fragments found at the same spot but certainly not part of the same individual or of the same genus.

These extraneous fragments include M<sub>3</sub> and a symphyseal fragment of *Hyopsodus* and M<sup>2</sup> and a calcaneum of *Notharctus*.

Neither of these genera could possibly include the other skeletal elements found with them. There is also an isolated ophidian vertebra.

#### GENERIC REFERENCE

Wortman (1903, p. 359 [209 of the separate]) figured a calcaneum like that included in the present lot and referred it questionably to *Microsyops*. The basis for the reference was that the calcaneum is evidently of a primate, that Wortman believed *Microsyops* to be a primate, and that he considered no other Bridger primate to be of appropriate size for association with the calcaneum. Matthew (1915, *loc. cit.*) maintained that this sort of calcaneum and the other elements associated with it in the present specimen probably belong to *Hemiacodon*, the evidence being as follows.

1.—Calcanea of similar kind and size are

<sup>1</sup> Father P. Teilhard de Chardin.



confined to the Upper Bridger, and *Hemiacodon* is likewise confined to that level.

2.—Bones of similar type occur more rarely in the Lower Bridger, these are significantly smaller, and *Omomyx*, a smaller genus related to *Hemiacodon*, occurs at that level.

3.—On the other hand, *Microsyops* is more abundant in the Lower than in the Upper Bridger and the species only slightly smaller.

4.—*Cynodontomys*, a close ally of *Microsyops*, is fairly common in the Wind River and Bighorn Basins, but no skeletal material of the sort under discussion has been found there.

In short, 1-4 show that the distribution of this type of skeletal material coincides

## VERTEBRAE

There are parts of eight vertebrae possibly of this individual, but all are poorly preserved and there may be some admixture (as suggested by the fact that an ophidian vertebra is included in the same lot). Two are posterior dorsals, perhaps the last two, four probably lumbar (although at least one may be an anterior caudal), one a medial or distal caudal, and one a centrum of doubtful position. The best preserved dorsal has the prezygapophyses, neural spine and anapophyses broken off, but otherwise agrees closely with the last dorsal of *Tarsius* except for being relatively deeper, absolutely larger, and with corresponding greater production of the proc-

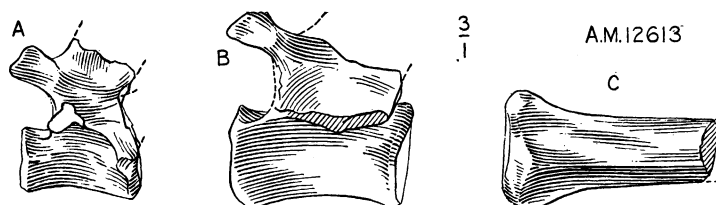


Fig. 3. *Hemiacodon*. Amer. Mus. No. 12613. Side views of three vertebrae; A, dorsal, B, proximal caudal and C, median caudal. Three times natural size.

with that of *Hemiacodon* and its allies, and not with that of *Microsyops* and its.

5.—The size is more appropriate for *Hemiacodon* than for *Microsyops*.

6.—Skeletal elements of very different type and of more appropriate size for *Microsyops* are occasionally found in dubious association with that genus.

7.—The occurrence together of bones of this general type and teeth of the *Omomyx-Hemiacodon* group is repeated in the Lower Eocene of Belgium, where members of the *Microsyops* group have never been found.

8.—It is not demonstrated, and is rather improbable, that *Microsyops* is a primate, whereas *Hemiacodon* and the animal to which these bones belong certainly are.

This does not amount to rigid proof, but it is adequate evidence to proceed on the theory that these skeletal parts do belong to *Hemiacodon*.

As *Tarsius* hardly differs significantly from *Lemur* or various other primitive primates in this bone, the evidence is not strong. The four lumbar or anterior caudals are so poorly preserved that they show nothing of interest, except that they are very sharply keeled ventrally, more so than in any genus with which I have made comparison although *Tarsius*, *Lemur*, *Galago* and some others have some of the lumbar slightly keeled. This keel makes it improbable that these elements are caudals. The median caudal, of which only one end is preserved, is of the type common to all primitive, long-tailed primates. The vertebrae as a whole cast no real light on affinities, but seem worthy of record.

## PELVIS

Most of the left ilium and ischium and part of the pubis are preserved. The pel-

vis as a whole is strikingly and unexpectedly lemuroid in aspect. From *Lemur* it differs principally as follows:

1.—The (anteroinferior) iliac spine is equally prominent but considerably shorter, a tubercle rather than a crest, and is more lateral than ventral. In both respects it resembles *Galago*, but is somewhat more prominent than in that genus.

2.—The posterior lip of the acetabulum is slightly less produced.

3.—The ischial spine is posterior to the acetabulum, rather than above its posterior rim, and is slightly smaller, although sharp.

distinguish it equally from *Hemiacodon*, and *Tarsius* shares with *Hemiacodon* no other non-lemuroid characters. Aside from characters also seen in living lemurs, there is no special resemblance between *Hemiacodon* and *Notharctus* in the pelvis, and considerably less between *Hemiacodon* and *Plesiadapis*.

#### FEMUR

Proximal and distal ends of both femora are preserved, but slightly crushed and broken. The length cannot be determined. The bone is larger than in *Tarsius spectrum* throughout, but the shaft is only



Fig. 4. *Hemiacodon*. Amer. Mus. No. 12613. Outer view of left side of pelvis. Three times natural size.

4.—The lateral surface of the dorsal bar of the ischium is more sharply crested.

5.—The free part of this bar is slightly shorter (cf. *Galago*), the dorsal end of the descending process distinctly wider antero-posteriorly.

The last point, which seems rather superficial in any case, is the only one in which any special resemblance to *Tarsius* is seen. In *Tarsius* the iliac tubercle is practically absent, but what may be its vestige occupies nearly the position of the strong process in *Hemiacodon*. Otherwise the very distinctive characters differentiating the pelvis of *Tarsius* from that of the lemurs

slightly heavier relative to the size of the ends. The femur closely resembles both *Tarsius* and *Lemur*, which are rather similar in this respect. Special resemblances and distinctions are as follows:

1.—The neck is less definite and constricted than in *Lemur*, the notch between head and greater trochanter shallower, with the articular surface extending onto it, and the fovea is well marked. These are all resemblances to *Tarsius*, but also in equal or greater degree to *Galago*.

2.—The shape and size of the lesser trochanter are as in *Tarsius*, differing very slightly from *Lemur*, but the process is di-



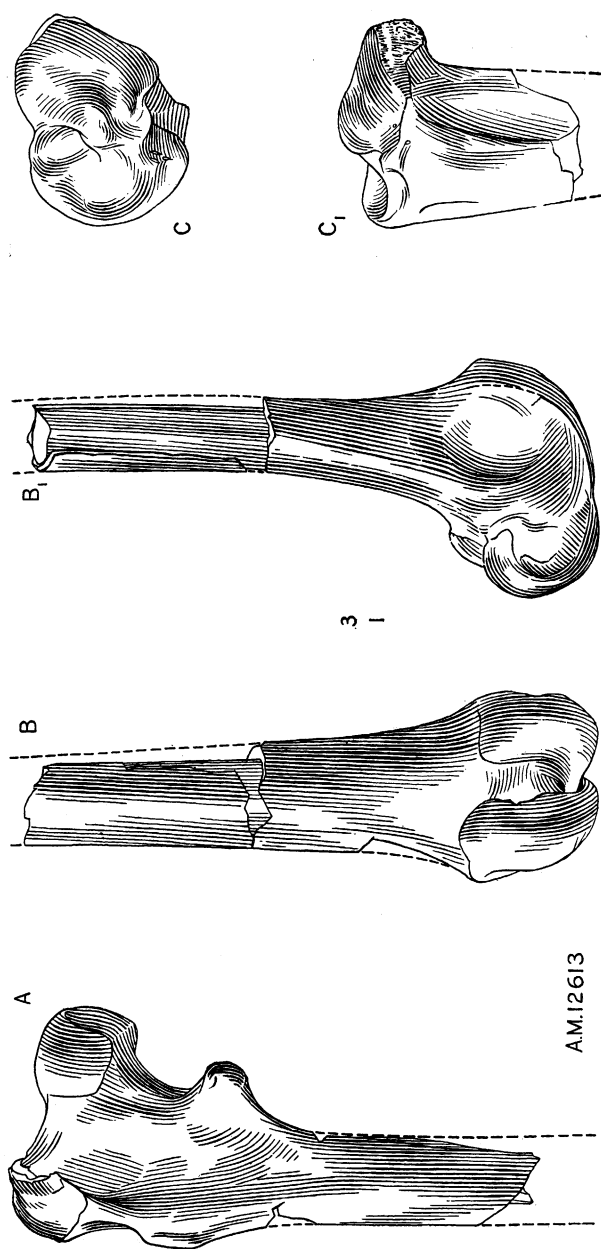


Fig. 5. *Hemiaecodon*. Amer. Mus. No. 12613. Bones of the hind limb: A, proximal end of right femur, anterior view; B, distal end of left femur, posterior view; B<sub>1</sub>, distal end of left femur, inner view; C, proximal view of upper end of left tibia, C<sub>1</sub>, anteroexternal view of upper end of left tibia. All figures three times natural size.

rected more posteriorly than in either recent genus. Here, again, resemblance to *Galago* is rather close.

3.—The third trochanter is slightly more proximal than in *Tarsius* or *Lemur*, and is markedly weaker than in *Tarsius*, more like *Lemur* in this respect, and very like *Galago* in both features.

4.—A fairly prominent ridge runs onto the shaft from the greater trochanter, much as in *Tarsius*, and unlike *Lemur*. *Galago* is intermediate.

5.—Both distal ends are somewhat crushed laterally, but allowing for this they appear to be almost identical in form with this part in *Lemur* or *Tarsius*, which seem to have no significant difference here except that the condyles project further posteriorly in *Lemur* and in the present specimen.

#### TIBIA

Proximal ends of both tibiae are preserved, but no recognizable fragment of the fibula. It is thus impossible to determine whether *Hemiacodon* shared with *Tarsius* the nearly unique fusion of tibia and fibula.<sup>1</sup> The fibula was free proximally, but so is it in *Tarsius*. The parts preserved are not very distinctive from either *Tarsius* or *Lemur*, although the articular surface seems to have been more nearly transverse to the shaft than in either.

#### PES

The right calcaneum, cuboid, navicular, entocuneiform and first metatarsal are preserved. There are also a second right calcaneum and first metatarsal of the same species which of course are not of the same individual.<sup>2</sup> The simplest description of these bones is that they are in every respect close to *Lemur* except that all (except the metatarsal) are more elongate and slender. All are elongate about equally, in proportion to *Lemur*. The cuboid, navicular and entocuneiform are of roughly equal size in *Lemur* and this relationship is preserved in *Hemiacodon* although all are so much more slender. This difference in proportions

<sup>1</sup> This was already typically developed in the European Middle to Upper Eocene *Necrolemur* and *Pseudoloris*.

<sup>2</sup> They may possibly have been placed with the specimen for comparison with it, and not have been found with the rest of the material.

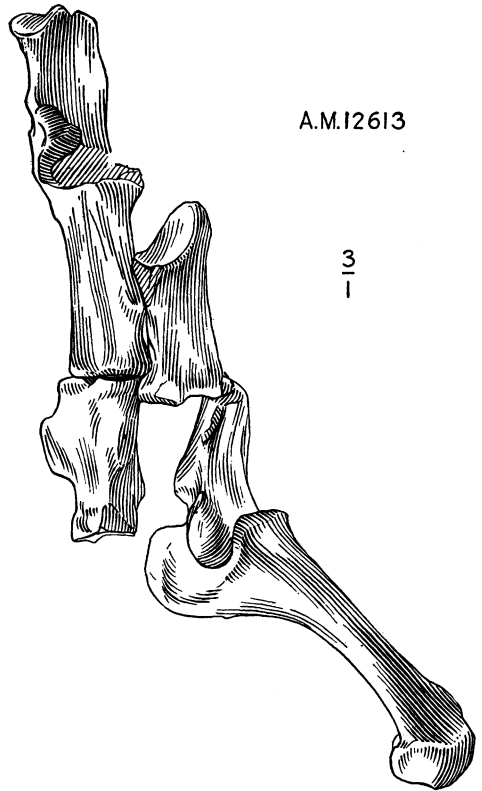


Fig. 6. *Hemiacodon*. Amer. Mus. No. 12613. Calcaneum, cuboid, navicular, entocuneiform and first metatarsal of the right hind foot. Three times natural size.

seems to affect all parts of the bones evenly except that the elongation of the calcaneum is almost entirely distal, the tuberosity being relatively less elongate. Aside from proportions, the structure and articulations of these elements are almost exactly as in *Lemur*, the only noteworthy difference being the presence of a marked tubercle on the posterior surface of the entocuneiform which I do not find so strongly developed in any of the other forms compared.

This elongation of the tarsus is, of course, a gross resemblance to *Tarsius* (and also to *Galago* and some other lemuroids), but *Hemiacodon* is by no means midway between a primitive lemuroid condition and a fully tarsoid stage: it is very much nearer the former. It is still fully lemuroid, with none of the really distinctive features (chiefly in slender bones and their



shafts) seen in the tarsus of *Tarsius*. Furthermore the elongation is not proceeding as in *Tarsius* or *Galago*. In the latter, but in greater degree in *Tarsius*, the navicular is enormously elongated relative to the primitive lemuroid condition and the cuboid very little elongated, while the entocuneiform is the smallest bone of the three and seems actually to have shortened slightly relative to the primitive condition. In *Hemiacodon* all have elongated equally and are of approximately equal size.

The first metatarsal differs from that of *Lemur* in the relatively much greater development of the tubercle for the peroneus longus, and in the almost complete suppression of the more internal of the two grooves on the phalangeal articulation so that the median and internal ridges tend to form a single, large, cylindrical facet, a modification approached by *Tarsius* and by *Galago*.

Among the other fragments present are the distal end of another metatarsal, and several fragmentary (but no complete) phalanges. The distal end of a metatarsal is symmetrical, closely similar to the third or fourth metatarsal of *Lemur*. Some, perhaps all, of the phalanges were distinctly arched, not straight as in *Tarsius*. The distal articulations preserved are all of the simple grooved or pulley type, some shallow and some deeper. An articulation for a terminal phalanx is largely plantar.

#### OTHER SPECIMENS

There are about ten other calcanea of this general type in our Bridger collection, with some variation in size but little in form. There are several fragmentary astragali perhaps referable to *Hemiacodon*, of which I figure the most complete. Its lemuroid aspect, size and (as far as the facets are preserved) articulation with the calcanea suggest this reference which is nevertheless far from certain. This differs from *Lemur* chiefly in the slightly deeper head, more vertical fibular facet and less pronounced flexor hallucis groove. The depth is more lemuroid, but the other two features are minor or slight resemblances to *Tarsius*. The probably more important characters of the inferior face oppose comparison with

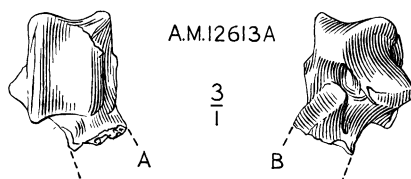


Fig. 7. *Hemiacodon*. Amer. Mus. No. 12613A. Right astragalus, A, dorsal view; B, plantar view. Three times natural size.

*Tarsius*, for the ectal facet is more concave, ectal and sustentacular facets sharply separated by a groove and the pit deeper and stronger—all resemblances to *Lemur*. The astragalus as a whole is strikingly like that of *Galago*.

#### COMPARISONS AND AFFINITIES

The supposed Paleocene and Eocene tarsioids are known chiefly from teeth and jaws, with good skulls of *Tetonius* and *Necrolemur*, poor and partial skulls of two or three other genera, and various other fragments. Comparison of limb material can be made only with *Teilhardina*, to which (as *Omomys*) Teilhard (1927) referred a calcaneum and astragalus, with *Necrolemur*, to which Schlosser (1907) referred a femur, tibia-fibula and calcaneum, with *Pseudoloris*, of which Weigelt (1933) described a fairly complete hind limb, and with *Microtarsioides*, of which there is a poorly preserved partial skeleton (Weigelt, 1933). Comparable parts are also known in several genera, such as *Notharctus* (Gregory, 1910) and *Plesiadapis* (see Simpson, 1935), that are definitely lemuroid and not closely related to *Hemiacodon* if the dental evidence is at all trustworthy.

The calcaneum of *Teilhardina* is similar to that of *Hemiacodon*, but its distal end is relatively less elongate, as might be expected in an earlier form. The astragalus figured by Teilhard is, however, quite unlike that very tentatively referred to *Hemiacodon*, so much so that it is improbable that both the references are correct. The calcanea confirm to a limited extent the dental evidence that *Hemiacodon* and *Teilhardina* belong to a general *Omomys*-like group.

The femur referred to *Necrolemur* by Schlosser resembles that of *Hemiacodon* in the position of the third trochanter, which is, however, still more proximal and somewhat larger in the European form.<sup>1</sup> The imperfect preservation of the tibiae referred to the two genera permits no useful comparison, at least without being able to compare the originals. The tuberosity of the calcaneum referred to *Necrolemur* is very like that referred to *Hemiacodon*, but the distal end is considerably more elongate, slender, simplified and circular in section, specializations in the direction of *Tarsius*, to be expected in a later tarsiid genus. The limb of *Necrolemur* could be derived from one like that of *Hemiacodon*, but the points of comparison are so few and there are so many elements of doubt in the whole subject that this conclusion carries little force.

As far as can be judged from Weigelt's brief description and diagrammatic figures, *Pseudoloris* shows considerable resemblance to *Hemiacodon* in the hind limb. The iliac spine seems to be much as in *Hemiacodon*, but the anterior end of the ilium is less expanded (possibly broken?) and no ischial spine appears in Weigelt's drawing, which includes the region where this occurs in *Hemiacodon*. On the femur, the head, greater trochanter and lesser trochanter seem to be almost as in *Hemiacodon*, but Weigelt does not mention or illustrate a third trochanter. If this is absent, it is an unexpected difference from known allied forms. The distal end of the femur allows of no useful comparison, nor does the tibia. The preservation and publication of the calcaneum and astragalus suggest a general similarity in aspect, without supplying special details bearing on affinity.

*Microtarsioides* is so poorly preserved, despite the discovery of a partial skeleton, that almost no helpful comparison is possible. Weigelt thinks that the calcaneum probably was not elongated, a remarkable difference from any known tarsiid, even in the Eocene. It is not certain that *Microtarsioides* really belongs in this group.

The known limb bones of *Hemiacodon* appear not to have any characters typical of *Notharctus*, *Adapis* or *Plesiadapis*, but only to share with them some characters that mark the lemuroids in general.

Comparison with recent genera, as indicated in the preceding description, shows that *Hemiacodon* is certainly a primate and that it resembles both lemuroids and tarsiods. There appear to be no definitely tarsiid characters that are not either too superficial to be granted any importance or equally or more clearly shown in the long-footed lemuroids typified by *Galago*. The tarsal elongation, which might be taken as a tarsiid character, is less than in the lemuroid *Galago* and is somewhat different in kind from either tarsiods or lemuroids among recent forms. On the whole the tarsus, and indeed all the preserved parts of the skeleton, are more like the lemuroids than like *Tarsius*.

If these bones were judged entirely on their own merits, without reference to allied genera or to the teeth of *Hemiacodon*, probably no one would refer them definitely to the Tarsiodea. They might be assigned with greater or less probability to the Lemuroidea or they might be considered as indicative of an offshoot allied to both groups. The jaws and dentition of *Pseudoloris* give almost indisputable evidence of alliance with *Tarsius*. The skulls of *Necrolemur* and *Tetonius* suggest the same affinity in somewhat less degree. Genera like *Omomys* and *Hemiacodon* have many dental peculiarities in common with these probable tarsiods and are linked to them by various more or less annectent types, yet generally similar dentitions did occur among definite lemuroids, as witness *ProNycticebus*. The skeleton of *Hemiacodon*, as far as known, is at least as lemuroid as tarsiid, probably more. Comparable parts in the almost definitely tarsiid *Necrolemur* and *Pseudoloris* are not at all conclusive but could stand between *Hemiacodon* and *Tarsius* in adaptive type and phyletic indications, probably being nearer the former.

This is a very complex series of resemblances and differences, and not enough facts are known to settle the problems raised. The evidence of *Hemiacodon*, in

<sup>1</sup> The backward extension of the distal condyles, emphasized by Schlosser, does not seem to me to be greater than in most lemuroids.

conjunction with that of its probable and possible allies, suggests the possibility that the tarsioids and lemuroids were not as sharply distinguished in the Eocene as has commonly been supposed, that there were then many divergent lines from a basically lemuroid, tupaoid-like stock, some more and some less *Tarsius*-like, and that *Tarsius* is the sole survivor of one of these lines nearly represented in the Eocene by *Pseudoloris* and more distinctly by *Necrolemur*, etc. In this case it would perhaps be more accurate to think of *Tarsius* as an aberrant and peculiarly specialized lemuroid than to think of it as representing a separate major division of the primates, independent since an indefinitely remote time. The evidence does not conclusively support this as a theory, but it does suggest it as a good working hypothesis. It is still possible, but seems to me improbable, either (1) that *Hemiacodon* and its allies are true and fully differentiated tarsioids resembling the lemuroids only by convergence or in pre- or proto-primate characters, or (2) that they are lemuroids convergent toward

the tarsioids in some respects. In this latter case, it would probably be quite impossible to determine the affinities of an early primate unless it were much better known than any is at present.

The comparative anatomy of the recent forms is also equivocal. Competent and thorough students differ so widely that, for example, one says that "*Tarsius* is a Lemur of the Lemurs" (Woollard, 1925, p. 1182) and another that "A generalized common type which might have given rise to both the Tarsiodea and the Lemuroidea . . . could hardly be distinguished from a generalized eutherian mammal" (Le Gros Clark, 1934, p. 271). On the first view, one could expect, *a priori*, that the early fossil forms would be lemuroid in a general sense probably with a tendency to develop tarsioid-like characters irregularly in various lines. In the second view, the *a priori* presumption would be that the lemuroids and tarsioids were already quite distinct in the Eocene. It is generally stated that the latter is the case, but the actual fossil evidence, dubious as it is, now appears rather to favor the first alternative.

#### V.—CLASSIFICATION OF THE ANAPTOMORPHIDAE

Several relatively small and more or less clearly defined groups of Paleocene and Eocene primates have been defined as families: Adapidae, Plesiadapidae, Apatemyidae, Carpolestidae. There remain some twenty-eight genera most of which are usually referred to the Anaptomorphidae or to the Tarsiidae *sensu latissimo*. Aside from a few very doubtful genera, like *Phenacolemur*, *Trogolemur* and *Uintanorex*, the diversity of these does not exceed that of many single mammalian families and from this point of view there is no strong reason for rejecting their collocation. On the other hand, the reasons for so uniting them are in large part negative. They are enough alike in the known parts, to be related but there is in most cases little or no positive assurance that the affinity is real and special.

On the basis of the known dentitions, these genera may be grouped by a balance of dental resemblances. This evidence is imperfect and the resemblances do not

prove real affinity, but they are the only logical basis for a working arrangement such as is desirable. There is, in my opinion, insufficient reason for family separations, and the groups of genera thus defined may perhaps be best placed at present as provisional subfamilies of Anaptomorphidae. Considering their wide geographic range and enormous span of time covered, the scarcity rather than the abundance of definable genera is surprising and it may be predicted that many more will be discovered. Tentative definitions of the proposed subfamilies follow:

OMOMYINAE.—The more generalized forms. At least two incisors always present as far as known. Canines unreduced.  $P_4$  about as high as  $M_1$  and incipiently molariform, with metaconid and sometimes paraconid, but heel short. Molar paraconids distinct, not fusing with metaconids, generally submedian on  $M_{2-3}$ . Heel of  $M_3$  simple (except in *Washakius*).  $P^3-4$ , where known, not elevated and with strong proto-

cones. Upper molars simple, trigonal, with small hypocones. Included genera: *Omomys*, *Teilhardina*, *Loveina*, *Dyseolemur*, *Washakius*, *Shoshonius*, *Hemiacodon*, *Nava-jovius*, *Chumashius*. *Palenochtha* is near this group in morphology, but it seems to be diverging slightly toward *Paromomys* and so is placed with the latter. *Pseudoloris* is also possibly allied to this group but is sufficiently distinct to warrant placing in a separate subfamily in the absence of annectent types. This subfamily is Wortman's *Omomyinae* with little change.

**PAROMOMYINAE.**—Two large anterior lower teeth, perhaps an incisor and the canine, the first with root extending beneath the second, and teeth between these vestigial or absent.  $P_4$  about as in *Omomyinae* or less molariform. Molar paraconids distinct or nearly fused with metaconids, internal in position. Trigonids subquadrate, short. Talonid of  $M_3$  elongated and with double hypoconulid (except *Palenochtha*).  $P^3$  anteroposterior.  $P^4$  transverse, not elevated, with strong protocone. Upper molars without cuspidate hypocones but with a posterointernal cingulum basin (rudimentary in *Palenochtha*). Genera: *Paromomys*, *Palaechthon*, *Plesiolestes*, *Palenochtha*. *Trogolemur* or the *Necrolemurinae* might be derived from this subfamily and if so could perhaps be included in it, but at present this is largely hypothetical.

**ANAPTOMORPHINAE.**—Anterior teeth highly variable within the group.  $P_4$  not molariform but much enlarged and rising to a single high apex, metaconid rudimentary or absent. Molar paraconids tending to fuse with metaconids.  $M_3$  more or less reduced, heel simple.  $P^{3-4}$  enlarged, each with a single high external cusp and a much lower protocone. Upper molars trigonal, with minute cingulum hypocones. Upper and lower molar cusps less marginal than in other subfamilies. Genera: *Anaptomorphus*, *Euryacodon*,<sup>1</sup> *Uintanius*, *Absarokius*, *Tetonius*. This group is "V" of Matthew's key (1915, p. 448), plus *Uintanius*, which seems to me to belong here, and it is

Abel's "Tetoniidae"<sup>2</sup> (1931), except that he includes in it the surely extraneous carpolestids. It is nominally Wortman's *Anaptomorphinae*, but the concept is radically different. The differences in the anterior teeth are puzzling, but the genera seem to be closely related. No very similar forms are known from Europe.

**NECROLEMURINAE.**—One enlarged anterior lower tooth.  $P_4$  not elevated, becoming nearly molariform but with a short heel. Paraconids of  $M_{2-3}$  fusing with metaconids, trigonids basined and subovate.  $M_3$  formed by three nearly equal lobes.  $P^{3-4}$  low, oval in contour. Upper molars quadrate, large hypocones developed on the border of a posterointernal basin, metaconule duplicated and in the more advanced forms numerous accessory cuspules present. Genera: *Necrolemur*, *Microchoerus*. *Nannopithec* may belong here, but this peculiar and very imperfectly known animal is of uncertain affinities. Most students agree in making this a family, under the name *Necrolemuridae* or *Microchoeridae*, and there is no particular objection to this except that it seems unnecessary. While *Microchoerus* is unusual in the proliferation of secondary cuspules, this is a superficial specialization, not of family rank in itself in comparison with other mammalian families, and one that can be followed by almost complete transitions and in a short span from the quite simple *Necrolemur zitteli* to the complex *Microchoerus ornatus*. Exact relationships to various other anaptomorphids (or to the anaptomorphids) are so dubious and their possible indications so complex that the elevation of these two genera to family rank at present would seem merely to complicate and unbalance taxonomy unnecessarily. As noted, there is a distinct possibility that the *necrolemurines* are especially related to the *paromomyines*, but only a possibility in the absence of any annectent Upper Paleocene and Lower Eocene types.

**PSEUDOLORISINAE.**—Dentition closely similar to that of *Tarsius* throughout. Genus: *Pseudoloris*. So far as the dental

<sup>1</sup> *Euryacodon* is probably synonymous with *Anaptomorphus*, but this is uncertain.

<sup>2</sup> Since he includes *Anaptomorphus* and since his family is simply a restricted conception of the long-established *Anaptomorphidae*, there is no reason for the change of name.



evidence goes, this genus stands considerably closer to *Tarsius* than does any other known from the Paleocene or Eocene, and should perhaps be placed definitely in the Tarsiidae. Its inclusion in the Anaptomorphidae, very provisional and frankly conventional in any case, is justifiable only by the fact that it stands so close to the more typical anaptomorphids, and so far from *Tarsius*, in time and in space.<sup>1</sup>

INCERTAE SEDIS.—*Periconodon*, based on a single specimen with P<sup>3</sup> and M<sup>1-2</sup>, perhaps belongs in or near one of the above groups, but cannot be even provisionally placed at present. *Phenacolemur*, *Trogolemur* and *Uintasorex* cannot be placed in this family with any assurance nor, *a fortiori*, in any subfamily of it. It is possible that they represent two aberrant branches from a *Paromomys*-like ancestry. At present it is difficult to assign them any definite taxonomic rank or position. Their resemblances are so confusing and they are so poorly known that it seems unwarranted to base separate families on them, and yet they are too distinctive to enter with any reasonable probability into one of the established families.

## VI.—RELATIONSHIPS OF PALEOCENE AND EOCENE PRIMATES

There are now about 50 or 55 known valid genera of Paleocene and Eocene primates. Of these, the skeleton is well known only in *Notharctus*. Much of the skeleton is known in *Megachiromyoides*, *Microtarsioides* and *Ceciliolemur*, but preserved in such a way as to leave obscure many of the most desirable details. Important parts of the skeleton are also known in *Plesiadapis*, *Adapis*, *Hemiacodon*, *Necrolemur* and *Pseudoloris*, and a few relatively unimportant fragments in other genera. Good skulls are known only in

*Hoanghoniuss*, from a horizon in China now considered Oligocene by the Chinese Survey, is perhaps a tarsioid, but is too uncertain for reference to the Anaptomorphidae or any other definitely established family. The European *Anchomomys*, *Pronycticebus* and *Caenopithecus* have some resemblance to the Anaptomorphidae or Tarsioida, to which they have usually been referred, but it is more probable that they are lemuroids allied to or belonging in the Adapidae. *Megatarsius*, from the German Middle Eocene, does not appear to be an anaptomorphid and is *incertae sedis*, although a primate and more or less tarsioid in aspect. *Microtarsioides*, from the same deposit, is also tarsioid in general impression, but of quite uncertain affinities.

*Yumanius* was considered by Stock to belong with the "*Euryacodon*-*Anaptomorphus* stock," hence in the Anaptomorphinae of my arrangement, but its method of paracoid reduction is different, the heel of M<sub>3</sub> is likewise very different, and the distinctive premolars and more anterior teeth are unknown. It seems necessary, therefore, to consider it as an anaptomorphid *incertae sedis* until more completely known.

*Notharctus*, *Adapis*, *Tetonius*, *Pronycticebus* and *Necrolemur*, as well as the Oligocene *Sinclairiella*, which belongs to an Eocene group. Considerable but imperfect parts of the skull are also known in *Aphanolemur* (but its teeth are unknown), *Europolemur*, *Megatarsius*, *Microtarsioides*, *Pseudoloris* and *Ceciliolemur*. Knowledge of the other genera is mostly confined to the dentition, jaws and in a few instances (e.g., *Stehlinella*) inconsiderable parts of the skull adjacent to the upper jaw.

In view of the general rarity and fragility of these small and ancient animals, this is a good showing, but it is clear that knowledge sufficient for really well-founded opinion as to affinities is available for only a few genera, especially:

*Adapis*  
*Notharctus*  
*Pronycticebus*  
*Necrolemur*  
*Tetonius*

<sup>1</sup> *Pseudoloris* and *Necrolemur* show considerable resemblance which may represent special phyletic connection or may be merely of somewhat generalized anaptomorphid character. The latter is true if, as seems possible, *Necrolemur* is from a paromomyine and *Pseudoloris* from an omomyine ancestry. If, however, *Pseudoloris abderhaldeni* and *Necrolemur raabi* from the Geiseltal (see Weigelt, 1933) are correctly placed, these two genera became differentiated only at the end of the Middle Eocene, and subfamily distinction is not warranted. But it seems almost certain that these two species belong to one genus, which is *Pseudoloris* or a very close ally and not *Necrolemur*. Indeed their specific separation is questionable.

With less secure but still fairly good data for:

*Plesiadapis*  
*Pseudoloris*  
*Hemiacodon*  
 (*Sinclairiella*)

How confusing the evidence is, even when data are available, is well shown by the case of *Pronycticebus*, which was until recently generally agreed to be a tarsoid nearly allied to *Omomys*, but which has now been found (by Le Gros Clark, 1934) to be a lemuroid related to *Adapis*. If a genus known from the nearly complete skull and dentition is thus difficult to place, it is obvious that no opinion can carry much weight regarding the great majority of established genera. If they have a very marked dental resemblance, approaching identity, with a genus that is classified on strong grounds, they can be placed with considerable probability, but otherwise they must remain of very doubtful affinities.

Some genera have such generalized or such apparently synthetic or eclectic dentitions that it is practically impossible to place them at all, or even to be quite certain that they are primates. There are, however, certain more specialized dental types that characterize groups of genera, and it is possible to use these to form entities of varying size, each including a number of forms that are probably related to each other. It is thus possible to form a working system for most of the Eocene primates, among themselves. The determination of the relationships of these groups to larger categories, however, or to Recent primates, and their insertion in a general, formal, Linnaean taxonomy are much more difficult and much less reliable.

For example, it can hardly be doubted that the genera *Elphidotarsius*, *Carpodactes* and *Carpolestes* are closely related to each other and form a closed and natural group. But their superfamily position is a problem to which there is now no wholly satisfactory solution.

Faced by these serious difficulties and the certainty of falling into error in attempting to overcome them, it might seem better simply to leave all the early primates, with the possible exceptions of the few better known genera listed above, as *incertae sedis*

and to wait indefinitely for better material. I believe, however, that it is preferable for each student acquainted with any considerable part of the data to attempt some systematic grouping at frequent intervals. Many errors are inevitably involved, but surely it is better to interpret the evidence actually available as best one can, accepting correction with good grace when it comes, than simply to discard as inadequate these priceless earliest records of that part of mammalian history of most immediate interest to our species. The accretence of interpretation and theory is as essential to the achievement of knowledge as is the accumulation of the raw materials from which these arise, and isolated observations of fact have little value until some progress has been made toward their integration.

Possible groupings among Paleocene and Eocene genera are of two general sorts. In some cases there appear to be approximate phyletic or structural lines of successive related genera, such as the *Labidolemur* - *Teilhardella* - *Apatemys* - *Stehlinella* - *Sinclairiella* line so well worked out by Jepsen. In other cases the grouping can only be of a number of contemporaneous or nearly contemporaneous genera that are divergent but that suggest origin from a common ancestor, such as the *Omomys* - *Teilhardina* - *Loveina* - *Hemiacodon* - *Washakius* - *Shoshonius* - *Navajovius* group. This is, of course, the familiar distinction between vertical and horizontal classification. The early primates cannot now be classified consistently by either method alone, but necessarily involve a compromise and combination between the two.

### Adapidae

By far the best known, although not the most clearly defined, group of Eocene primates is that including at least the genera *Protoadapis*, *Pronycticebus* and *Adapis* in Europe and *Pelycodus*, *Notharctus* and *Aphanolemur* in North America. *Notharctus* has been studied by Gregory (especially 1920) in such careful detail that it is among the best known of all fossil mammals and Stehlin (especially 1912) has rendered a similar service with regard to the less com-

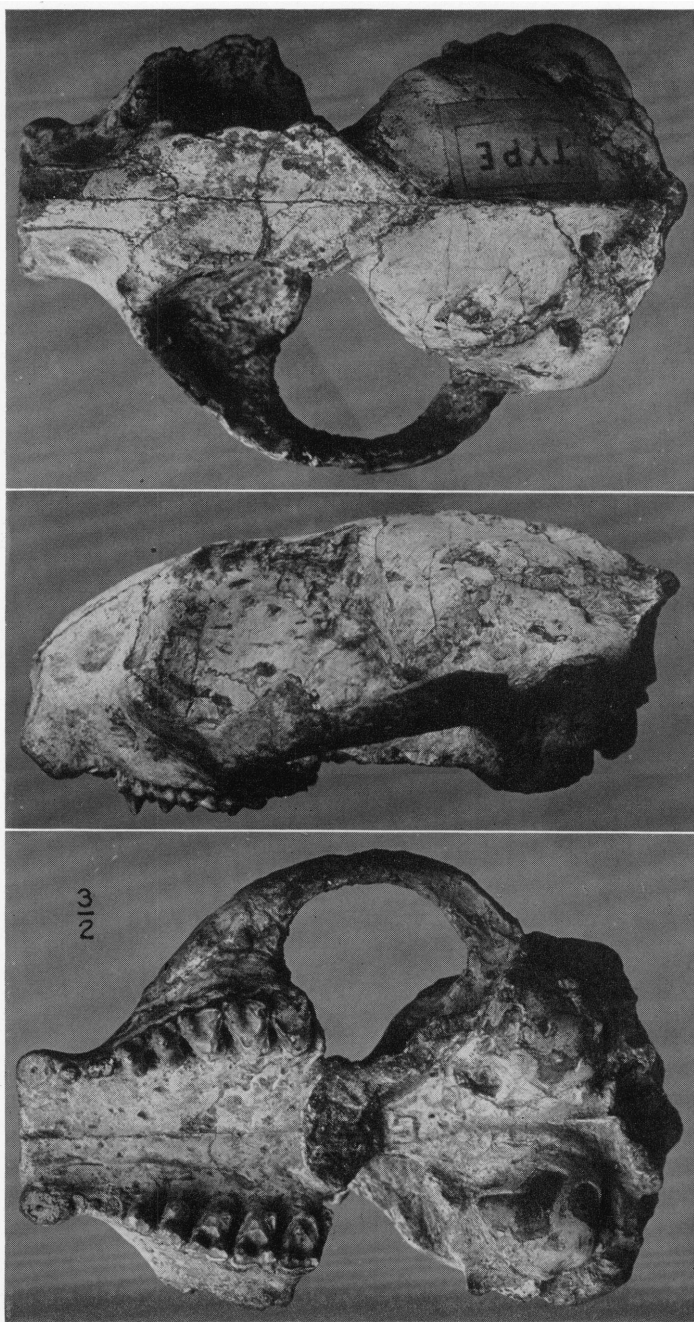


Fig. 8. *Pronycticebus gaudryi*. Type skull in Muséum d'Histoire Naturelle, Paris. Superior, left lateral and palatal views. One and one-half times natural size. (Opportunity to insert the first published photographs of this important and unique type is due to the kindness of Dr. J. Piveteau, who sent them to Dr. W. E. Le Gros Clark for publication, and to Dr. Le Gros Clark, who was unable to include them in his study of the genus and has sent them on for inclusion in this paper.)

pletely preserved remains of *Adapis*. As they have shown, *Notharctus* and *Adapis* are both basically lemuroid in structure and typify two lines that must have diverged in the Paleocene, although their common ancestry has not been discovered.

*Pelycodus* is closely related and probably ancestral to *Notharctus*. *Aphanolemur*, known only from a toothless skull fragment, is evidently an adapid but of uncertain closer affinities. *Protoadapis*, although not well known, seems to be closer to *Notharctus* than to *Adapis*, despite its European provenience. *Pronycticebus* is clearly closer to *Adapis*, although aberrant in some respects and in others conservative as compared with the latter (Le Gros Clark, 1934).

*Caenopithecus* is usually classified as a tarsioid, in the Anaptomorphidae or Tarsiidae, but I would associate it provisionally with the Adapidae. Stehlin (1916) has shown that its anterior dentition is divergent from that of *Adapis* but that the molar structure shows, on the whole, close analogies with *Adapis* or the Adapidae in general. The dental formula suggests comparison only with *Tarsius*, but Stehlin goes on to say, and all must agree, that this by no means signifies necessarily close relationship to the Eocene forerunners of *Tarsius* and he also emphasizes the presence of distinctly non-tarsioid characters. *Caenopithecus* is very distinctive, wherever it be placed, but it is less anomalous as an adapid than as a tarsioid. It has, for instance, the open trigonids, and the peculiar mode of paraconid reduction so characteristic of *Adapis* and its close allies and unknown among any forms of really probable tarsioid affinities. As always, such dental evidence may be misleading, but it is all we have and it does favor reference to the Adapidae.

*Anchomomys* has also been referred, almost without question, to the tarsioid group, but this was done largely because of its resemblance to *Pronycticebus*.<sup>1</sup> Now that Le Gros Clark has shown, in a manner entirely convincing to me, that *Pronycticebus*

is really an adapid, it becomes probable that *Anchomomys* is too. Le Gros Clark suggests (1934, p. 26) that the adapine skull structure of *Pronycticebus* contradicts the evidence of tarsioid affinities provided by the dental resemblance to *Anchomomys*, but I do not feel that this is a contradiction. On the contrary, reference of both genera to the Adapidae clears up several anomalies. The dentition of *Anchomomys* is not convincingly tarsioid. Like *Caenopithecus* and *Pronycticebus*, it has dental characters that would be unique among tarsioids but that are normal or even diagnostic for adapids.

Although Stehlin and some others tend to class *Adapis* and *Notharctus* in two families, Gregory has suggested that they might better be held as typical of two subfamilies of Adapidae. The difficulty of assignment of some related genera to one group rather than the other is a further practical reason for preferring this arrangement. The best provisional classification of these genera at present thus seems to be:

#### Adapidae

Adapinae: *Adapis*, *Pronycticebus*, *Anchomomys*.

Perhaps *Aphanolemur* and *Caenopithecus*, which are otherwise Adapidae *incertae sedis*.

Notharetinae: *Pelycodus*, *Notharctus*, *Protoadapis*.

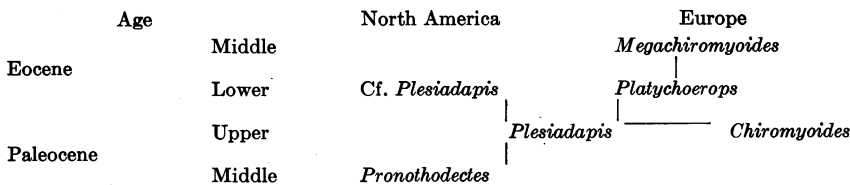
Both subfamilies appear to be polyphyletic in detail, but their divergent phyla are not yet adequately traced. The family as a whole is surely lemuroid and probably includes, or at least is very near, the actual ancestry of the modern lemurs in a strict sense. It may not be very distant from the ancestry of all lemuroids or even of the higher primates.

#### Plesiadapidae

The plesiadapids and apatemyids have often been confused, but Jepsen (1934) has now clearly shown that the two groups are quite distinct. The genera referable to the Plesiadapidae are *Pronothodectes*, *Plesiadapis*, *Chiromyoides*, *Platychoerops*, and *Megachiromyoides*. The morphological, temporal and spatial relationships of these genera are summed up in the following diagram, which roughly approximates a phylogeny but cannot be claimed as such in detail:

<sup>1</sup> In fact the argument has been used both ways in most illogical fashion: *Anchomomys* is a tarsioid because it resembles *Pronycticebus* and *Pronycticebus* is a tarsioid because it resembles *Anchomomys*. Yet neither convincingly resembles any genera known surely to be tarsioids.





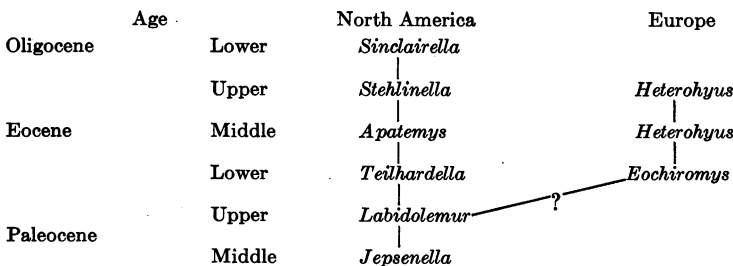
The recent discovery (Weigelt, 1933) of *Megachiromyoides*, based on a very poor skull, good lower jaws, forelimbs, and much of the vertebral column, has greatly added to knowledge of this family.<sup>1</sup>

The affinities of this family have long been disputed. It has been referred to the Insectivora and to the Rodentia, but its primate affinities are now indisputable. Within the Primates, Stehlin (who did not differentiate it from the Apatemyidae), believed that it was closely related to *Daubentonia*, and this opinion was widely accepted. On the basis of the dentition and much of the skeleton of *Plesiadapis*, I have, however, shown (1935) that there is no valid evidence of special relationship to *Daubentonia* but that the family is probably an early offshoot of a definitely lemuroid stock, not leading clearly to any known later forms.

Although Weigelt accepted Stehlin's general view as to daubentonioid affinities, *Megachiromyoides* seems to me to agree with and to reënforce my previous opinion. It is a remarkably specialized genus suggestive of the termination of a strongly aberrant lemuroid phylum. It does not, as the alternative theory would expect or demand, show any definite trend in a direction from *Plesiadapis* toward *Daubentonia*, but only an intensification of characters not or manifestly only superficially daubentonioid.

### Apatemyidae

Stehlin (1916) pointed out the similarity between *Plesiadapis* (and *Chiromyoides*) and *Heterohyus* (with its allies or synonyms) but did not definitely unite them in one family. When Matthew (1915) described "*Nothodectes*" he did not immediately recognize its European affinities and referred it to his family Apatemyidae, described a few years before (1909). Later Matthew (1917) recognized the close similarity (identity according to subsequent students) of "*Nothodectes*" and *Plesiadapis*, and he united the families Plesiadapidae and Apatemyidae under the former name, but excluded *Heterohyus* (etc.). Teilhard (1921) united *Heterohyus* (and also the mixodectids) with these and included all in the recent family "*Chiromyidae*" (*Daubentoniidae*). It was, however, suspected by most students that two or more distinct phyla were confused in these various groupings. Knowledge of the group was significantly increased by the discovery of *Stehlinella* (Matthew, 1921), *Labidolemur* (Matthew and Granger, 1921, Simpson, 1929, 1935), *Teilhardella* (Jepsen, 1930) and *Sinclairiella* (Jepsen, 1934), and on this basis Jepsen (1934) was able to separate the Apatemyidae clearly from the Plesiadapidae. As thus redefined, the Apatemyidae form an undoubtedly natural



<sup>1</sup> Copies of Weigelt's publication did not reach us until after Jepsen had written his important study of the Apatemyidae (1934) and I my discussion of *Plesiadapis* (1935) so that *Megachiromyoides* is not considered in those papers.

group, which may be retained as of family rank, with the structural sequence shown in the diagram.

The two geographic groups are not as distinct as might be suggested by this arrangement, and are not now distinctly definable as separate phyla.

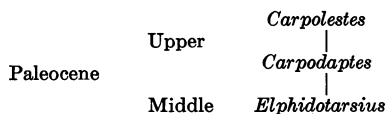
These eight genera show many differences, chiefly in the way of evolutionary advances from Paleocene to Oligocene, but they are clearly related to each other. Their relationships to other mammals are dubious in the extreme. No skeletal parts are known, but the snout of *Stehlinella* and most of the skull of *Sinclairiella* have been found. Unfortunately these are the two most specialized genera. Matthew (1921) said of *Stehlinella* that it "has no especial suggestion of primate about it; but that is of little significance." He referred it to the Plesiadapidae, which he believed, on grounds not affected by *Stehlinella*, to include tupaoid insectivores near the boundary line of the primates. Jepsen (1934) placed *Stehlinella* and *Sinclairiella* in the Apatemyidae, where they clearly belong, and said that they "have few characters to justify placing the family in any known order of mammals. Those structures which indicate Primate relationships are contradicted by others, equally convincing, to place the family elsewhere." He provisionally followed Matthew in referring the family to the Insectivora as an artifice subject to revision. He did not make detailed comparisons with other mammals except to contrast the dentition with that of the Plesiadapidae. The consensus is that these strange animals are primates—such would be Matthew's opinion, also, if he agreed to draw the insectivore-primate boundary below rather than above the tupaoids as Le Gros Clark and some other more recent authorities do. The factual basis for reference of the apatemyids to the Primates is, indeed, slight and faulty, but it is at least as good as any basis for referring them to the Insectivora and better than for reference to any other order. The subject requires further study and, especially, discovery.

Within the Primates, there are really no grounds at present for suggesting the closer affinities of the Apatemyidae. If Stehlin's widely quoted theory that the Plesiadapidae plus Apatemyidae are near the

ancestry of *Daubentonina* is true, it is probably true only of the Apatemyidae and not of the Plesiadapidae. Even as regards the Apatemyidae it seems at present almost entirely hypothetical. Jepsen says that *Sinclairiella* has no structures to link it with *Daubentonina*, but does not compare the two in explicit detail. 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 proto-lemuroid 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.

### Carpolestidae

This small but highly distinctive family is known at present only by three genera, all American, in the Middle and Upper Paleocene:



*Carpodaptes* and *Carpolestes* are closely similar and nearly contemporaneous, probably partly overlapping in distribution, but *Carpolestes* is slightly more specialized. Only jaws and teeth are known.

Despite their extraordinary premolar specialization, the teeth of these genera have many characters common in early primates and not definitely known to occur in any other order, and they have no characters typical of any other order. This is not rigid proof that they are primates, but leaves no reasonable alternative to so classifying them unless contrary evidence is later discovered. With differences of detail, the molars are suggestive of those of various anaptomorphids, and there is no theoretical difficulty in deriving the pre-

molars also from those of anaptomorphids although there is no conclusive evidence that this really happened. On this basis Abel (1931, p. 199) united the carpolestids with some of the anaptomorphids, including *Anaptomorphus* itself, under the name "Tetoniidae" (= Anaptomorphidae, a name with almost fifty years' priority). This collocation is not clearly invalid, but it does not seem to me sufficiently well grounded at present for acceptance. The family as so constituted is defined only by the presence of enlarged  $P_4$ , but this is an adaptive character requiring coördination with stronger, more numerous and more particular other resemblances before it can be considered as significant in this sense. The mere enlargement is not accompanied by true and exclusive structural similarity. *Elphidotarsius*, along with other evidence, indicates almost certainly that a common ancestor of *Carpolestes* and *Tetonius* would have  $P_4$  much as in *Paromomys* or indeed almost any very primitive primate and I cannot agree that any special affinity is indicated, as opposed to possible generally tarsiod affinities for all these genera.

Even this degree of affinity is not strongly supported by the known facts, although they do not more definitely suggest any other. There is a remarkably close resemblance in the lower molars between carpolestids and plesiadapids, but it does not extend to all parts of the dentition and may indicate nothing more than that all are early primates. The same is true of a somewhat more distant resemblance to the adapids. On the whole it is suggested that the carpolestids may be another sterile offshoot of the poorly differentiated more or less broadly lemuroid proto-primate stock, probably somewhat nearer to the tarsiods than to the lemuroids in a strict sense.

### Anaptomorphidae

The tentative contents and proposed subdivision of the Anaptomorphidae have been discussed in a previous section of these studies. Here some remarks on the nature and affinities of the family as a whole may be added.

There is little or no doubt that all the genera now referred to this family are true

primates. A few of them, particularly *Necrolemur*, *Pseudoloris* and *Tetonius*, show definite and almost conclusive evidence of special relationship to *Tarsius*. Even these genera, however, have some characters making a closer approach to the true lemuroids than is seen in the living form. *Hemiacodon* in its skeleton shows a curious blend of lemuroid, tarsiod and aberrant characters, with the balance inclining rather toward the lemuroids. Most of the genera referred to the Anaptomorphidae have been considered to be tarsiods principally because of dental resemblances or linking by apparently annectent types to the three genera known to be tarsiod. Even in the dentition, however, some genera, such as *Paromomys*, have some evidently lemuroid characters, although the balance here favors closer alliance with known tarsiods.

The family as now constituted is clearly heterogeneous although it could be natural in having arisen from one origin. It includes many different minor phyla. As far as these can be definitely placed, they show affinities with the tarsiods. It is, however, quite possible that some of the less well-known phyla now placed here will later demand separation and some may prove not to be truly tarsiod in affinities.

### Primates incertae sedis

The three American genera *Phenacolemur*, *Trogolemur* and *Uintasorex* are probably primates, but are of wholly uncertain position within that order. Because of some adaptive characters, they are sometimes referred to the Plesiadapidae, or to the Apatemyidae, but as Jepsen and others have suggested this cannot be accepted if those families are bounded in any way at all likely to be natural. All three of these genera might be derived from a more or less *Paromomys*-like ancestry, which in turn might or might not warrant their inclusion in the Anaptomorphidae (to which they would add two or three very distinctive phyla), but all this is too uncertain now to be of any real use.

In addition to several definitely classifiable and important forms, Weigelt (1933) has described four *Primates incertae sedis* from the German Middle Eocene: *Europo-*

*lemur*, *Megatarsius*, *Microtarsioides* and *Ceciliolemur*. All of these are based on relatively complete material, but preserved in such a way as to leave many essential details obscure.

*Europolemur* is based on a badly crushed skull with complete upper dentition. As Weigelt has shown, it seems to be definitely lemuroid, but does not compare very closely with *Adapis*. Common ancestry with the Adapidae would probably have to be remote, somewhere in the Paleocene, and definite reference to that family is not probable. In some respects *Europolemur* seems to be closer to the living lemuroids than are the adapids.

*Megatarsius* is also based on a skull, but in still worse preservation and with only the canine and  $M^{1-3}$  clearly preserved. There is some resemblance to *Periconodon*, but not identity, and *Periconodon* is not wholly certain as to position. The general aspect is rather tarsioid, but not clearly enough to make reference to that group clear.

*Microtarsioides* is represented by a skull and much of a skeleton, but all so poorly preserved that few important details stand out. The crown patterns of the teeth are not shown. The aspect is only vaguely tarsioid. It is probable that the calcaneum is not elongated as it is in all true tarsioids,

as far as known. The systematic position of the genus is wholly uncertain.

*Ceciliolemur* is represented by a nearly complete skeleton, with fairly good limb gross structure but the skull very poor and the dental patterns almost unknown. Weigelt erects for the genus a new family and a new group Ceciliolemuroidea. This is defined essentially as including primitive primates with no primate characters. There are, however, a few suggestions of primate affinities, as Weigelt shows, although none warranting positive reference to that order. Truly diagnostic features are in part vague and in part unknown, and the proposed Ceciliolemuroidea can hardly be clearly recognized at present as against various groups of very primitive primates or of insectivores. The anterior dentition seems to be less modified than in most lemurs or tupaoids, but probably only two incisors are present. The skeleton is very primitive and insectivore-like, but the observed details refer more to matters of proportion and other superficial features than to characters that give much insight as to broader affinities. The genus may be a tupaoid in a broad sense, despite a few observed differences from *Tupaia*, or it may indeed belong to some distinct but as yet really undefinable ancient primate or primate-like group, or it may be an insectivore of some sort.

## VII.—DISTRIBUTION OF PALEOCENE AND EOCENE PRIMATES

From the geographic and phyletic relationships of the European and American forms, it is inferred with considerable probability that Asia was an important early Tertiary center of evolution for the primates, perhaps even their place of origin and primary differentiation. At present this is entirely theoretical, however, because no Paleocene or Eocene primates have yet surely been identified from Asia. The earliest possible Asiatic primates are *Hoanghoniuss*, *Adapidium* and *Anagale*. *Hoanghoniuss*, very imperfectly known, is probably a primate and has some resemblance to early tarsioids, but is really of unknown affinities. It is from the "River Section" of the Yuanchu Series in the

Middle Huangho Valley, a horizon now regarded as uppermost Eocene or lowest Oligocene. *Hoanghoniuss*, based on a jaw fragment with  $M_{2-3}$ , is from the same horizon and locality. Its affinities are wholly uncertain and I am inclined to doubt its being a primate. *Anagale*, a genus based on excellent knowledge of skull, jaws and part of the skeleton, is a tupaoid from the Ulan Gochu, Lower Oligocene, of Mongolia. Its reference to the Primates depends on that of the Tupaioidea. I would now follow Le Gros Clark in referring all the tupaoids, including *Anagale*, to the Lemuroidea, but in any case *Anagale* is well off the main line of primate descent and is not clearly related in any special way to known



Eocene forms. Aside from these three records, the oldest known Asiatic primates are from the Miocene and already belonged to specialized modern groups.

In Africa the first known primates occur in the Oligocene. They are primitive within their groups, but they belong to higher types still extant and are quite unlike the Paleocene and Eocene forms. Lack of early Tertiary records makes it impossible to judge when the lemuroids, now so characteristic of Africa, entered that continent and whether it played any other rôle in their history than that of an asylum for relicts and a scene of secondary radiation. Africa certainly has had an important part in the deployment of some of the higher primates, but its connection with Paleocene and Eocene primate history cannot even be inferred reasonably until fossils of those ages are found.

In South America the oldest known primates occur in the late Oligocene or early Miocene, supposed older records having been shown to be probably erroneous as to identification or as to assigned age. These first records are of primates already of typically South American type and combined with later and Recent forms they indicate that South America's rôle in primate history has been a simple one. As far as known, that area received some primitive, more or less unified stock of primates which radiated over the isolated continent and had no further connection with primate history in general. Gregory has shown that it is probable that this original stock was adapid (notharcine) or something closely allied to those ancient lemuroids. It is not impossible but is unlikely that primates were present in what is now Patagonia during the Paleocene and Eocene. It seems to me probable that they did then occur in central or northern South America, but Paleocene and Eocene mammals have yet to be discovered in those regions. There is a long gap both in time and in morphology between possible ceboid ancestors in the North American early Tertiary and true ceboids in the Patagonian middle Tertiary, and I suspect, as almost pure speculation, that the time was occupied and the morphologic changes ac-

quired in the course of slow infiltration southward along the length of Central and South America.

In North America primates first appear in the Middle Paleocene, where they are already differentiated into Anaptomorphidae (Paromomyinae), Plesiadapidae, Carpolestidae, Apatemyidae. The Adapidae appear in the Lower Eocene, completing the roster of known families. Anaptomorphids and adapids were relatively abundant and the former were highly differentiated in the Lower and Middle Eocene, but they are rare in the Upper Eocene in America. In the American Lower Oligocene an apatemyid and a possible anaptomorphid are known from one specimen each.<sup>1</sup> No later North American primates are known until the coming of man.

The European Paleocene is very poorly known, and only plesiadapids have been found. In the lower Eocene, however, there are all the families known in the American Lower Eocene, Plesiadapidae, Apatemyidae, Anaptomorphidae and Adapidae. All of these still occurred in the European Middle Eocene and all but the Plesiadapidae in the Upper Eocene. On present evidence it appears that Plesiadapidae and Adapidae survived longer in Europe than in America and the Apatemyidae almost (perhaps quite) as long. Carpolestidae are not yet known from Europe, perhaps only because of inadequate knowledge of the Paleocene there. Like other mammals, the primates show close connection between America and Europe in the Lower Eocene and increasing divergence in the later part of the epoch. There is a sharp break in European primate history at the end of the Eocene and none of the groups then present can be traced with any clarity into known later forms.

The distribution of the recognized families and subfamilies and of all the genera considered valid is shown in the accompanying table, in which A represents known occurrence in North America and E in Europe. Similar tabulations have recently

<sup>1</sup> After this paper had been submitted for publication, the discovery of an American Oligocene anaptomorphid, was announced, without any published details (Clark in Bull. Geol. Soc. Amer., L, p. 1963, December, 1939).

been published by several authors, especially Abel (1931) and Weigelt (1933), but they do not follow the classification here suggested, do not include the results of

some still more recent work and discovery, and involve some errors here corrected, especially regarding the ages of American genera.<sup>1</sup>

	Paleocene		Eocene		
	Middle	Upper	Lower	Middle	Upper
Adapidae			AE	AE	E
Adapinae				E	E
Adapis				E	E
Pronycticebus					E
Anchomomys				E	E
Notharctinae			AE	A	
Pelycodus			A		
Notharctus			A	A	
Protoadapis			E		
Adapidae inc. sed.					
Caenopithecus				E	
Aphanolemur				A	
Plesiadapidae	A	AE	AE	E	
Pronothodectes	A				
Plesiadapis		AE	?A		
Chiromyoides		E			
Platychoerops			E		
Megachiromyoides				E	
Apatemyidae <sup>2</sup>	A	A	AE	AE	AE
Jepsenella	A				
Labidolemur		A			
Teilhardella			A		
Eochiromys			E		
Apatemys				A	
Heterohyus <sup>3</sup>				E	E
Stehlinella					A
Carpolestidae	A	A			
Elphidotarsius	A				
Carpodaptes		A			
Carpolestes		A			
Anaptomorphidae <sup>4</sup>	A	A	AE	AE	E
Paromomyinae	A	?A			
Palenochtha	A				
Palaechthon	A				
Plesiolestes	A				
Paromomys	A	?A			

<sup>1</sup> For instance, Abel gives *Plesiolestes* as Lower Paleocene and *Pronothodectes*, *Palaechthon*, *Elphidotarsius* and *Paromomys* as Upper Paleocene—all are really from the Middle Paleocene. Weigelt lists the European genus *Protoadapis* as North American and gives Paleocene to Upper Eocene for the distribution of the Notharctinae (really Lower to Middle Eocene). It is almost impossible to eliminate such errors entirely from a tabulation and perhaps mine still includes some despite the advantage of having Abel's, Weigelt's and others' work as a point of departure.

	Paleocene		Eocene		
	Middle	Upper	Lower	Middle	Upper
Omomyinae		A	AE	A	
Navajovius		A			
Teilhardina			E		
Loveina			A		
Shoshonius			A		
Omomys			?A	A	
Hemiacodon				A	
Washakius				A	
Chumashius					A
Dyseolemur					A
Anaptomorphinae			A	A	
Absarokius			A		
Tetonius <sup>5</sup>			A		
Anaptomorphus			?A	A	
Euryacodon <sup>6</sup>				A	
Uintanius				A	
Necrolemurinae				E	E
Necrolemur				E	E
Microchoerus					E
Pseudolorisinae				E	E
Pseudoloris				E	E
Anaptomorphidae inc. sed.					
Periconodon				E	
Nannopithec				E	
Yumanius					A
Family uncertain					
Phenacolemur <sup>7</sup>		A	A		
Trogolemur				A	
Uintasorex				A	
Europolemur				E	
Megatarsius				E	
Microtarsioides				E	
Ceciliollemur				E	

<sup>2</sup> Also in the Lower Oligocene of North America, *Sinclairiella*.

<sup>3</sup> *Amphichiromys*, *Heterochiromys* and *Necrosorex* are synonymous with or very close to *Heterohyus* and are not listed separately.

<sup>4</sup> Also in the Lower Oligocene of North America (Clark).

<sup>5</sup> The Upper Paleocene specimen referred to *Tetonius* belongs to *Plesiadapis*.

<sup>6</sup> *Euryacodon* is probably the upper dentition of *Anaptomorphus* but is tentatively listed.

<sup>7</sup> *Ignacius* is a synonym of *Phenacolemur*.

## VIII.—INDEXED BIBLIOGRAPHY OF PALEOCENE AND EOCENE PRIMATES

The references given here include all those explicitly cited in the preceding notes and also a selected bibliography of the subject. The bibliography is brief, yet the titles chosen include most of the important recent literature and give access to essentially all original work on these early primates. The most recent and best illustrated accounts of each genus are cited, and

these in turn refer back to all the older literature. Search for original information on each genus here recognized as valid is facilitated by the following index, in which the genera are listed alphabetically, with author and date for each name, followed in parentheses by references to those titles in the bibliography that are of special importance for the given genus.

## BIBLIOGRAPHY

- ABEL, O.  
1931. "Die Stellung des Menschen im Rahmen der Wirbeltiere." Jena. [Review of all fossil primates then known.]
- CLARK, W. E. LE GROS.  
1934a. "Early forerunners of man." Bailiere, Tindall and Cox: London.  
1934b. "On the skull structure of *Pronycticebus gaudryi*." Proc. Zool. Soc. London, 1934, pp. 19-27.
- GIDLEY, J. W.  
1923. "Paleocene primates of the Fort Union, with discussion of relationships of Eocene primates." Proc. U. S. Nat. Mus., LXIII, pp. 1-38. [*Paromomys*, *Palaechthon* (includes *Palenochtha*), *Elphidotarsius*, *Pronothodectes*.]
- GRANGER, W.  
1910. "Tertiary faunal horizons in the Wind River Basin, Wyoming, with descriptions of new Eocene mammals." Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 235-251. [*Shoshonius*, pp. 249-250.]
- GRANGER, W., AND GREGORY, W. K.  
1917. "A revision of the Eocene primates of the genus *Notharctus*." Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 841-859. [*Notharctus*, *Aphanolemur*.]
- GREGORY, W. K.  
1920. "On the structure and relations of *Notharctus*, an American Eocene primate." Mem. Amer. Mus. Nat. Hist. (N.S.) III, Pt. II, pp. 49-243. [*Pelycodus*, *Notharctus*, *Adapis* and allied genera.]  
1922. "The origin and evolution of the human dentition." Baltimore. [Reviews all genera then known; new figures of *Necrolemur*.]
- HELLER, F.  
1930. "Die Säugetierfauna der mitteleozänen Braunkohle des Geiseltals bei Halle a.S." Jahrb. Hall. Verb. (N.F.) IX, pp. 13-41. [*Heterohyus*, *Adapis*, "*Necrolemur*" *raabi* (*Pseudoloris*?), *Periconodon*.]
- JEPSEN, G. L.  
1930a. "Stratigraphy and paleontology of the Paleocene of northeastern Park County, Wyoming." Proc. Amer. Phil. Soc., LXIX, pp. 463-528. [*Plesiolestes* pp. 505-506, *Phenacolemur* pp. 514-515, *Plesiadapis* pp. 515-517 and 525-528, *Carpolestes* pp. 520-524.]  
1930b. "New vertebrate fossils from the Lower Eocene of the Bighorn Basin, Wyoming." Proc. Amer. Phil. Soc., LXIX, pp. 117-131. [*Teilhardella*, pp. 126-127.]  
1934. "A revision of the American Apatemyidae and the description of a new genus, *Sinclairiella*, from the White River Oligocene of South Dakota." Proc. Amer. Phil. Soc., LXXIV, pp. 287-305. [*Sinclairiella*, also notes on all apatemyids then known.]
- LOOMIS, F. B.  
1906. "Wasatch and Wind River Primates." Amer. Jour. Sci., (4), XXI, pp. 276-285. [*Anaptomorphus*, *Pelycodus*; note that none of the specimens placed in *Notharctus* belong there: "*N.*" *minutus* is? *Omomys minutus* and the others are not primates; *Anaptomorphus abbotti* was later made type of *Absarokius* by Matthew.]
- MATTHEW, W. D.  
1909. "The Carnivora and Insectivora of the Bridger Basin, Middle Eocene." Mem. Amer. Mus. Nat. Hist., IX, Pt. VI, pp. 291-567. [?Primates, pp. 543-546; *Apatemys*, *Uintasorex*, *Trogolemur*.]  
1915. "A revision of the Lower Eocene Wasatch and Wind River faunas. Part IV.—Entelonychia, Primates, Insectivora (part)." Bull. Amer. Mus. Nat. Hist., XXXIV, pp. 429-483. [Lower and Middle Eocene Primates, pp. 433-465, 477-483; *Pelycodus*, *Notharctus*, *Omomys*, *Hemia-codon*, *Washakius*, *Shoshonius*, *Uin-*

- tanius*, *Anaptomorphus*, *Tetoni*, *Ab-sarokius*, *Trogolemur*, *Phenacolemur*, *Nothodectes* (= *Plesiadapis*).]
1917. "The dentition of *Nothodectes*." Bull. Amer. Mus. Nat. Hist., XXXVII, pp. 831-839. [*Plesiadapis*.]
1921. "*Stehlinius*, a new Eocene insectivore." Amer. Mus. Novitates, No. 14, pp. 1-5. [*"Stehlinius"* = *Stehlinella*.]
- MATTHEW, W. D., AND GRANGER, W.
1921. "New genera of Paleocene mammals." Amer. Mus. Novitates, No. 13, pp. 1-7. [Primates, pp. 4-6; *Labidolemur*, *Ignacius* (= *Phenacolemur*), *Navajovius*, *Carpodaptes*; brief diagnoses only, for descriptions see Simpson, 1935.]
- SCHLOSSER, M.
1907. "Beitrag zur Osteologie und systematischen Stellung der Gattung *Necrolemur*, sowie zur Stammesgeschichte der Primaten überhaupt." N. Jahrb. Min. Geol. Pal., Festband 1907, pp. 197-226. [*Necrolemur* and allies.]
- SCOTT, W. B., AND JEPSEN, G. L.
1936. "The mammalian fauna of The White River Oligocene—Part I. Insectivora and Carnivora." Trans. Amer. Phil. Soc. (N.S.) XXVIII, Pt. I, pp. 1-153. [*Sinclairiella*, pp. 26-29.]
- SIMPSON, G. G.
1928. "A new mammalian fauna from the Fort Union, of southern Montana." Amer. Mus. Novitates, No. 297, pp. 1-15. [*Carpolestes*, pp. 7-10.]
- 1929a. "A collection of Paleocene mammals from Bear Creek, Montana." Ann. Carnegie Mus., XIX, pp. 115-122. [*Labidolemur*, pp. 119-120.]
- 1929b. "Paleocene and Lower Eocene Mammals of Europe." Amer. Mus. Novitates, No. 354, pp. 1-17. [*Platychoerops*, pp. 11-12; *Eochiromys*, pp. 12-13.]
1931. "A new insectivore from the Oligocene, Ulan Gochu horizon, of Mongolia." Amer. Mus. Novitates, No. 505, pp. 1-22. [*Anagale*.]
- 1935a. "The Tiffany fauna, Upper Paleocene II.—Structure and relationships of *Plesiadapis*." Amer. Mus. Novitates, No. 816, pp. 1-30.
- 1935b. "The Tiffany fauna, Upper Paleocene. III.—Primates, Carnivora, Condylarthra, and Amblypoda." Amer. Mus. Novitates, No. 817, pp. 1-28. [*Plesiadapis*, *Labidolemur*, *Carpodaptes*, *Navajovius*, *Phenacolemur*; pp. 1-19.]
1936. "A new fauna from the Fort Union of Montana." Amer. Mus. Novitates, No. 873, pp. 1-27. [*Plesiadapis*, *Carpodaptes*, *Phenacolemur*; pp. 19-23.]
- 1937a. "The Fort Union of the Crazy Mountain Field, Montana, and its mammalian faunas." U. S. Nat. Mus., Bull. 169, pp. i-x, 1-287. [*Paromomys*, *Palaechthon*, *Palenochtha*, *Elphidotarsius*, *Pronothodectes*, *Plesiadapis*; pp. 141-169.]
- 1937b. "Additions to the Upper Paleocene fauna of the Crazy Mountain Field." Amer. Mus. Novitates, No. 940, pp. 1-15. [*Carpodaptes*, pp. 5-9.]
- STEHLIN, H. G.
1912. "Die Säugetiere des schweizerischen Eozäns, 7. Teil, 1. Hälfte. *Adapis*." Abh. Schweiz. Pal. Ges., XXXVIII, pp. 1165-1298. [*Adapis*, *Protoadapis*.]
1916. "Die Säugetiere des schweizerischen Eozäns, 7. Teil, 2. Hälfte. *Caenopithecus* — *Necrolemur* — *Microchoerus* — *Nannopithecus* — *Anchomomys* — *Periconodon* — *Amphichiromys* — *Heterochiromys*—Nachträge zu *Adapis*—Schlussbetrachtungen zu den Primaten." Abh. Schweiz. Pal. Ges., XLI, pp. 1299-1552. [Besides the genera named in title, *Pseudoloris*, *Plesiadapis*, *Chiromyoides* and *Necrosorex* which, as well as *Amphichiromys* and *Heterochiromys*, is now believed to equal *Heterohyus*.]
- STOCK, C.
1933. "An Eocene primate from California." Proc. Nat. Acad. Sci., XIX, pp. 954-959. [*Chumashius*.]
1934. "A second Eocene primate from California." Proc. Nat. Acad. Sci., XX, pp. 150-154. [*Dyseolemur*.]
1938. "A tarsiid primate and a mixodectid from the Poway Eocene, California." Proc. Nat. Acad. Sci., XXIV, pp. 288-293. [*Yumanius*.]
- TROXELL, E. L.
1923. "The Apatemyidae." Amer. Jour. Sci., V, pp. 503-506. [*Apatemy* only.]
- TEILHARD DE CHARDIN, P.
- 1916-1921a. "Sur quelques primates des phosphorites de Quercy." Annales Paleont., X, pp. 3-20. [*Pseudoloris*, *Anchomomys*, *Microchoerus*, *Necrolemur*.]
- 1916-1921b. "Les mammifères de l'éocène inférieur français et leurs gisements." Annales Paleont., X, pp. 171-176, XI, pp. 1-108. [*Plesiadapis*, pp. 12-17, 43-44, 51-55 (= *Platychoerops*); *Protoadapis*, pp. 58-59, 88-90; *Heterohyus*, pp. 81-88.]
1927. "Les mammifères de l'éocène inférieur de la Belgique." Mem. Mus. Roy. Hist. Nat. Belgique, No. 36. [*"Omomys"* *belgicus* (*Teilhardina*), pp. 16-18; *Plesiadapis*, pp. 13-14; *Eochiromys*, pp. 14-16.]

WEIGELT, J.

1933. "Neue Primaten aus der mitteleozänen (oberlutetischen) Braunkohle des Geiseltals." *Nova Acta Leopoldina* (N. F.), I, pp. 97-156. [*Megachiromyoides*, *Europolemur*, *Pseudoloris*, *Megatarsius*, *Microtarsioides*, *Ceciliolemur*.]

WOOLLARD, H. H.

1925. "The anatomy of *Tarsius spectrum*." *Proc. Zool. Soc. London*, 1925, II, pp. 1071-1184.

WORTMAN, J. L.

- 1903-1904. "Studies of Eocene Mammalia in The Marsh Collection, Peabody Museum. Part II. Primates." *Amer. Jour. Sci.*, XV (1903), pp. 163-176, 399-414, 419-436; XVI (1903), pp. 345-368; XVII (1904), pp. 23-33, 133-140, 203-214. [*Omomys*, *Hemiacodon*, *Euryacodon*, *Washakius*, *Anaptomorphus*.]

## INDEX

- Absarokius* Matthew, 1915  
*Adapis* Cuvier, 1823  
*Anaptomorphus* Cope, 1872  
*Anchomomys* Stehlin, 1916  
*Apatemys* Marsh, 1872  
*Aphanolemur* Granger and Gregory, 1917  
*Caenopithecus* Rüttimeyer, 1862  
*Carpodaptes* Matthew and Granger, 1921  
*Carpolestes* Simpson, 1928  
*Ceciliolemur* Weigelt, 1933  
*Chiromyoides* Stehlin, 1916  
*Chumashius* Stock, 1933  
*Dyseolemur* Stock, 1934  
*Elphidotarsius* Gidley, 1923  
*Eochiromys* Teilhard, 1927  
*Europolemur* Weigelt, 1933  
*Euryacodon* Marsh, 1872  
*Hemiacodon* Marsh, 1872  
*Heterohyus* Gervais, 1848  
*Jepsenella* Simpson, 1940  
*Labidolemur* Matthew and Granger, 1921  
*Loveina* Simpson, 1940  
*Megachiromyoides* Weigelt, 1933  
*Megatarsius* Weigelt, 1933  
*Microchoerus* Wood, 1846  
*Microtarsioides* Weigelt, 1933  
*Nannopithecus* Stehlin, 1916  
*Navajovius* Matthew and Granger, 1921  
*Neurolemur* Filhol, 1873  
*Notharctus* Leidy, 1870  
*Omomys* Leidy, 1869  
*Palaeochthon* Gidley, 1923  
*Palenochtha* Simpson, 1935  
*Paromomys* Gidley, 1923  
*Pelycodus* Cope, 1875  
*Periconodon* Stehlin, 1916  
*Phenacolemur* Matthew, 1915  
*Platychoerops* Charlesworth, 1854  
*Plesiadapis* Gervais, 1876  
*Plesiolestes* Jepsen, 1930  
*Pronothodectes* Gidley, 1923  
*Pronycticebus* Grandidier, 1904  
*Protoadapis* Lemoine, 1878  
(Loomis, 1906; Matthew, 1915)  
(Gregory, 1920; Heller, 1930; Stehlin, 1912, 1916)  
(Matthew, 1915; Wortman, 1904)  
(STehlin, 1916; Teilhard, 1916-1921a)  
(Jepsen, 1934; Matthew, 1909; Troxell, 1923)  
(Granger and Gregory, 1917)  
(STehlin, 1916)  
(Matthew and Granger, 1921; Simpson, 1935b, 1936, 1937b)  
(Jepsen, 1930a; Simpson, 1928)  
(Weigelt, 1933)  
(STehlin, 1916)  
(Stock, 1933)  
(Stock, 1934)  
(Gidley, 1923; Simpson, 1937b)  
(Simpson, 1929b; Teilhard, 1927)  
(Weigelt, 1933)  
(Matthew, 1915; Wortman, 1904)  
(Matthew, 1915; Wortman, 1904)  
(Heller, 1930; Stehlin, 1916; Teilhard, 1916-1921b)  
(This paper)  
(Jepsen, 1934; Matthew and Granger, 1921; Simpson, 1929a, 1935b)  
(This paper)  
(Weigelt, 1933)  
(Weigelt, 1933)  
(STehlin, 1916; Teilhard, 1916-1921a)  
(Weigelt, 1933)  
(STehlin, 1916)  
(Matthew and Granger, 1921; Simpson, 1938)  
(Gregory, 1922; Schlosser, 1907; Stehlin, 1916; Teilhard, 1916-1921a)  
(Granger and Gregory, 1917; Gregory, 1920; Matthew, 1915)  
(Matthew, 1915; Wortman, 1904)  
(Gidley, 1923; Simpson, 1937a)  
(Gidley, 1923; Simpson, 1937a)  
(Gidley, 1923; Simpson, 1937a)  
(Gregory, 1920; Matthew, 1915)  
(Heller, 1930; Stehlin, 1916)  
(Jepsen, 1930a; Matthew, 1915; Matthew and Granger, 1921; Simpson, 1935b, 1936)  
(Simpson, 1929b; Teilhard, 1916-1921b)  
(Jepsen, 1930a; Matthew, 1915, 1917; Simpson, 1935a, 1935b, 1936, 1937a; Stehlin, 1916; Teilhard, 1916-1921b, 1927)  
(Jepsen, 1930a; Simpson, 1937a)  
(Gidley, 1923; Simpson, 1937a)  
(Le Gros Clark, 1934b)  
(Gregory, 1920; Stehlin, 1912, 1916; Teilhard, 1916-1921b)



*Pseudoloris* Stehlin, 1916

(Stehlin, 1916; Teilhard, 1916-1921a; Weigelt, 1933)

*Shoshonius* Granger, 1910

(Granger, 1910; Matthew, 1915)

*Sinclairiella* Jepsen, 1934<sup>1</sup>

(Jepsen, 1934; Scott and Jepsen, 1936)

*Stehlinella* Matthew, 1929

(Jepsen, 1934; Matthew, 1921)

*Teilhardella* Jepsen, 1930

(Jepsen, 1930b, 1934)

*Teilhardina* Simpson, 1940

(This paper; Teilhard, 1927)

*Tetonijs* Matthew, 1915

(Gregory, 1922; Matthew, 1915)

*Trogolemur* Matthew, 1909

(Matthew, 1909, 1915)

*Uintanijs* Matthew, 1915

(Matthew, 1915)

*Uintasorex* Matthew, 1909

(Matthew, 1909)

*Washakius* Leidy, 1873

(Matthew, 1915; Wortman, 1904)

*Yumanijs* Stock, 1938

(Stock, 1938)

---

<sup>1</sup> Lower Oligocene, but included because it has wholly Paleocene and Eocene affinities.





