

THE PHENACOLEMURIDAE, NEW FAMILY OF EARLY PRIMATES



GEORGE GAYLORD SIMPSON

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CONTENTS

INTRODUCTION	417
TAXONOMY	419
Phenacolemuridae, New Family	419
<i>Palaechthon</i> Gidley, 1923	419
<i>Palaechthon alticuspis</i> Gidley, 1923	419
<i>Paromomys</i> Gidley, 1923	420
<i>Paromomys maturus</i> Gidley, 1923	420
<i>Paromomys depressidens</i> Gidley, 1923	420
<i>Phenacolemur</i> Matthew, 1915	420
Tiffanian Forms	421
<i>Phenacolemur frugivorus</i> (Matthew and Granger, 1921)	421
<i>Phenacolemur pagei</i> Jepsen, 1930	422
Sand Coulee-Gray Bull Forms	423
<i>Phenacolemur praecox</i> Matthew, 1915	423
<i>Phenacolemur praecox praecox</i> Matthew, New Name as Subspecies	426
<i>Phenacolemur praecox citatus</i> Matthew, New Name as Subspecies	426
The San José Form	426
<i>Phenacolemur jepseni</i> , New Species	426
Lysite and Lost Cabin Forms	428
<i>Phenacolemur</i> cf. <i>jepseni</i>	428
<i>Phenacolemur</i> sp.	428
MORPHOLOGY OF <i>Phenacolemur</i>	429
Dentition	429
Upper Teeth	429
Lower Teeth	430
Skull	431
Lower Jaw	431
AFFINITIES	432
The Species of <i>Phenacolemur</i>	432
Generic and Family Relationships	432
Broader Affinities and Comment on Prosimian Classification	436
SUMMARY	440
REFERENCES	440

INTRODUCTION

THE KNOWN PRIMATES and primate-like animals from the Paleocene and Eocene of North America and Europe are extraordinarily diverse. All are distinctly pre-anthropoid in structural grade and are therefore considered in a somewhat general sense to be Prosimii or, in some cases, primate-like Insectivora. There has been a tendency to compare them either with *Tarsius* or with *Lemur* and to place them in the categories Tarsiiformes and Lemuriformes. Most of the supposed early Tarsiiformes have been classified as Anaptomorphidae, and most of the considerably less varied supposed early Lemuriformes have been called Adapidae. A few other families, notably the Plesiadapidae, were also early recognized, although not well defined until more recently.

Over the years it has become evident that the early Cenozoic complex of primates and primate-like insectivores (almost a distinction without a difference) is far more complex than the usual classifications have recognized. It is also increasingly clear that the placing of many or, perhaps, of any of them in the essentially Recent categories Tarsiiformes and Lemuriformes is arbitrary and is not a clear expression of their real affinities. A more recent tendency has been to pick out from the mass smaller groups of genera and species that are really related among themselves, whatever may be their relationships to their contemporaries or to Recent prosimians, with which, indeed, most of them seem to have no special relationships. Such, for instance, was the delimitation by Jepsen (1930) of the Plesiadapidae and Apatemyidae or the clear definition of the Necrolemuridae by Hürzeler (1948).

Phenacolemur, a member of this early complex known since 1915 when it was named by Matthew, is a highly distinctive, primate-like animal. It was at first confused with the distinctly different Plesiadapidae and Apatemyidae and recently has been considered simply as a primate, or perhaps insectivore, *incertae sedis*. Knowledge of the genus has increased, and there are now numerous specimens, described and undescribed, in collections from the late Paleocene (Tiffanian) and early Eocene (Wasatchian) of the Rocky

Mountain region. Among recent discoveries is a specimen with associated upper and lower jaws (not previously known in certain association) and a skull. With this and other extensive undescribed material, it is now possible to give a much fuller account of the genus than any in the scattered literature and to consider its affinities on a far better basis. A fairly well-defined group, here designated as the Phenacolemuridae, emerges as a further contribution to the clarification of the heterogeneous mass of early Cenozoic primate-like mammals.

The new specimen mentioned above, much the best known of this genus, is from a quarry found by Dr. Anne Roe and worked by George O. Whitaker, Carl Sorensen, Henry F. Henriques, Jr., and me. Mr. Whitaker prepared the specimen. The drawings for this paper were made by Chester Tarka. Dr. David B. Kitts calculated the statistics on *P. pagei*.

I am especially and deeply indebted to Dr. G. L. Jepsen, who with great generosity turned over to me for study and publication the large quarry sample of *P. pagei*, of which only three lower jaws had been partially described in naming that species, and also the considerable number of Willwood formation specimens in the Princeton collection, none of which had previously been described. Dr. C. L. Gazin lent four specimens from the United States National Museum, and Dr. A. E. Wood lent one (a particularly rare Lysite specimen) from the Amherst College collection.

The plan of this paper is to give first a formal taxonomic review of the family and all included taxa, then a detailed morphological description of *Phenacolemur*, and finally a discussion of the affinities of the genera and family.

All measurements are in millimeters. The following abbreviations are used throughout:

L, length

M, mean (also molar when with subscript or superscript)

N, number of specimens

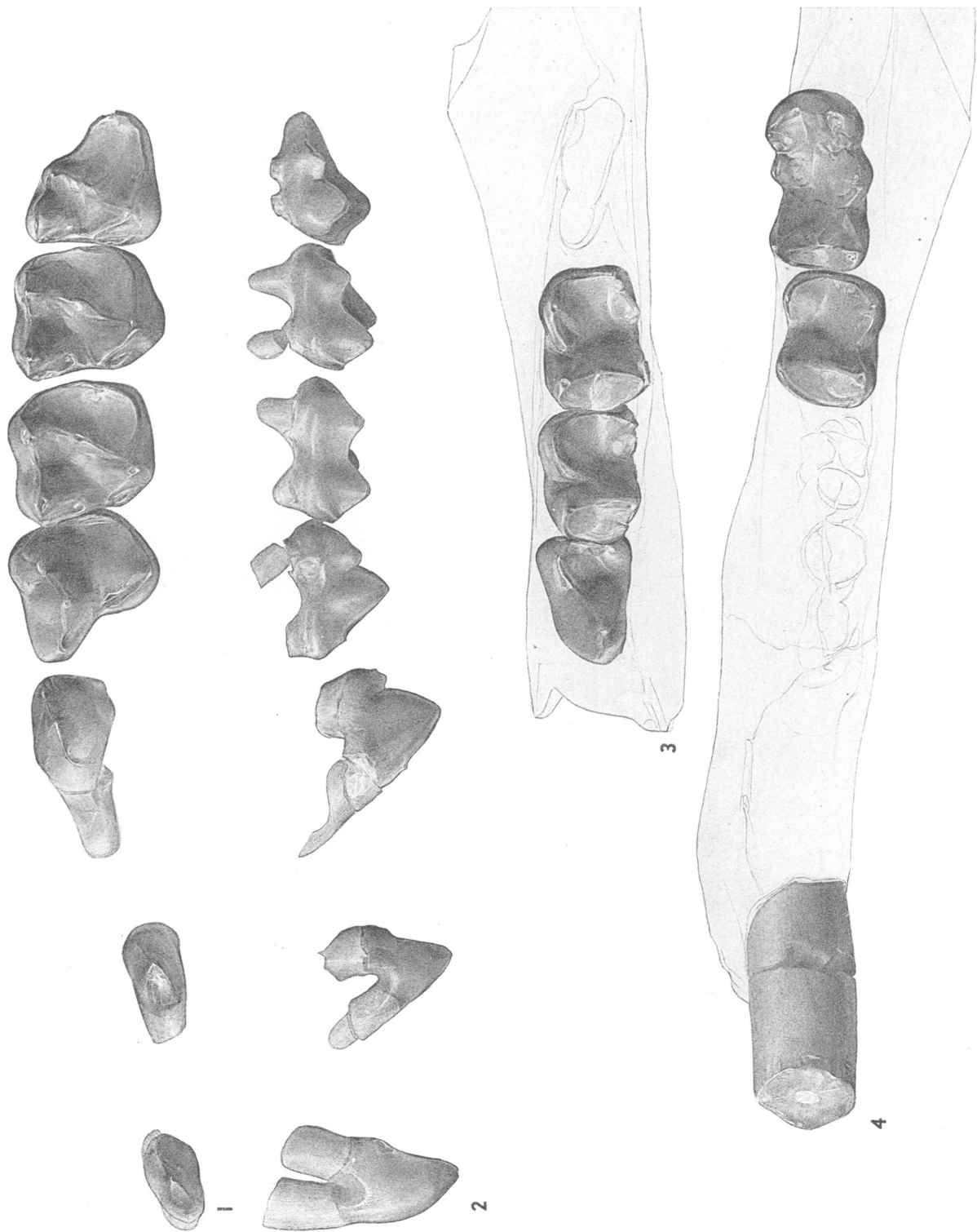
OR, observed range

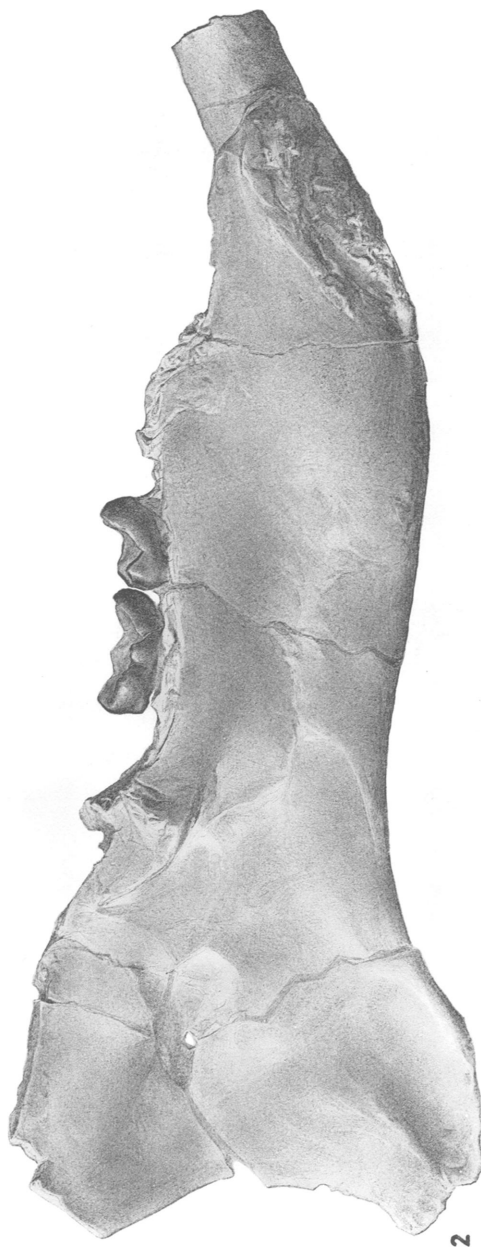
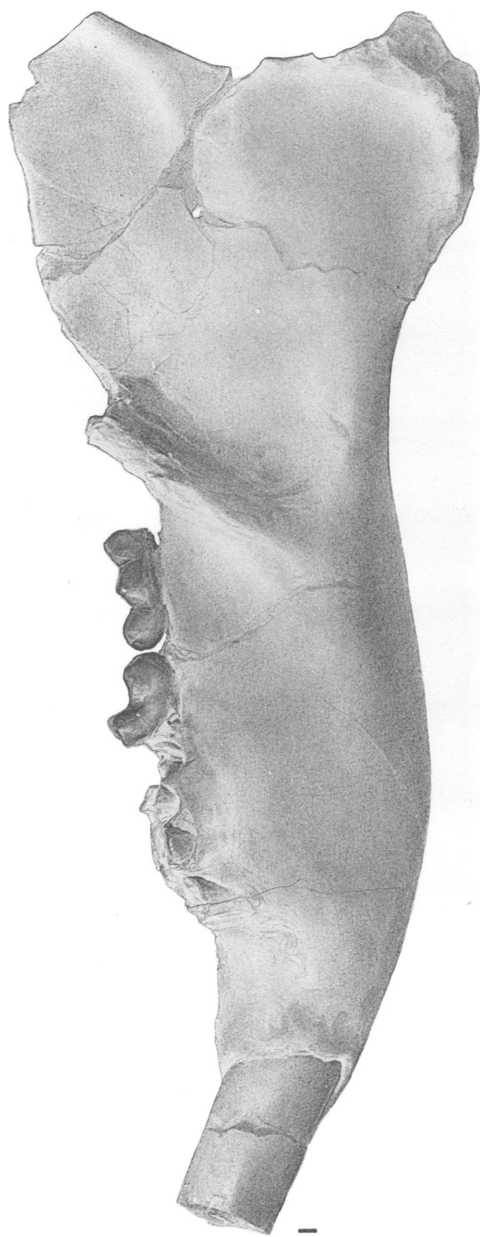
P, probability by statistical test (also pre-

molar when with subscript or superscript)	of which the specimens used in this study belong are abbreviated as follows:
S, standard deviation	A.M.N.H., the American Museum of Natural History
SR, standard range (span, calculated from standard deviation)	A.C., Amherst College
V, coefficient of variation	P.U., Princeton University
W, width	U.S.N.M., United States National Museum
The names of institutions in the collections	

PLATE 30

Phenacolemur jepseni, new species. Type, A.M.N.H. No. 48005. 1. Left C or P¹ and P²-M³, crown view. 2. Left C or P¹ and P²-M³, external view. 3. Right P₄-M₂, crown view. 4. Left I (broken) and M₂₋₃, crown view. All nine times natural size.





TAXONOMY

PHENACOLEMURIDAE, NEW FAMILY

TYPE: *Phenacolemur* Matthew, 1915.

INCLUDED GENERA: *Phenacolemur*, *Paromomys*, and *Palaechthon*.

DISTRIBUTION: Torrejonian to Wasatchian, Rocky Mountain region (Montana, Wyoming, Colorado, New Mexico), United States.

DIAGNOSIS: Small, early primates. One pair of greatly enlarged but rooted lower incisors. P_1 absent, P_{2-3} small or absent. P_4 well developed, with postero-internal basined heel, and with simple to only incipiently molariform trigonid. Molar trigonids slightly elevated, subquadrate, short and wide, cusps marginal, paraconids reduced, lingual, near metaconids. Molar talonids broad, with simple closed basins, large hypoconids, distinct but smaller entoconids, and no or very obscure hypoconulids on M_{1-2} . M_3 with large, prominent third lobe, nearly or quite as large as second lobe and with two cusps (or double hypoconulid). P^3 small, not transverse, no distinct protocone. P^4 well developed, with strong protocone, submolariform to almost molariform. Upper molars without hypocones; a ridge running posteriorly and then externally from the protocone enclosing a postero-internal basin. No or indistinct parastyle or mesostyle. Conules well developed in earlier but vague in later forms. No proliferation of secondary cuspules.

The conclusion that *Phenacolemur* represents a distinct family of Primates is supported by the discussion of affinities later in this paper. The inclusion of *Paromomys* in the family is somewhat dubious, and the doubt increases for *Palaechthon*. Their tentative inclusion is, however, defensible on present evidence, as also discussed later, and the family is defined to include them. Other genera that could be placed here but are not now definitely referred to the family are *Palenochtha* and *Plesiolestes*. *Paromomys* and

Palaechthon and their species have been described elsewhere (Simpson, 1937). Modified diagnoses in this different context are now given as well as new and better figures. The taxonomy of *Phenacolemur* has not previously been reviewed as a whole.

PALAECHTHON GIDLEY, 1923

Palaechthon GIDLEY, 1923, p. 6. SIMPSON, 1937, p. 156 (genus redefined and revised).

TYPE: *Palaechthon alticusps* Gidley, 1923.

INCLUDED SPECIES: Type only.

DISTRIBUTION: Torrejonian, Lebo formation (Gidley and Silberling Quarry faunules), Crazy Mountain Field, Montana.

DIAGNOSIS: Lower dental formula, 1.1.3.3. Incisor and canine about as in *Paromomys*. P_4 with small but distinct paraconid and metaconid. Trigonids more elevated than in other genera of the family. Third lobe of M_3 relatively smaller and narrower. Lower molars with external cingula. P^4 - M^3 strongly transverse, postero-internal basin relatively small, especially on P^4 and M^3 . Strong external cingula with distinct metastyles. Metacone small but distinct on P^4 . Conules well developed on molars. M^{1-2} grooved internally but only vaguely bilobed.

Palaechthon alticusps Gidley, 1923

Plate 33, figure 2; plate 34, figure 3

Palaechthon alticusps GIDLEY, 1923, p. 6. SIMPSON, 1937, p. 156.

TYPE: U.S.N.M. No. 9532, right lower jaw with P_2 - M_2 .

HYPODIGM: Two upper and 14 lower jaws in the United States National Museum collection (hypodigm of Simpson, 1937) and four upper and 14 lower jaws in the American Museum collection.

DISTRIBUTION: As for the genus.

DIAGNOSIS: Sole known species of the genus.¹ Measurements and statistical data in

¹ "*Palaechthon*" *minor* Gidley, 1923, was placed in a then new genus, *Palenochtha*, in Simpson, 1935b (see also Simpson, 1937).

PLATE 31

Phenacolemur jepsoni, new species. Type, A.M.N.H. No. 48005. Left lower jaw. 1. External view. 2. Internal view. Both five times natural size.

Simpson (1937, p. 158).

PAROMOMYS GIDLEY, 1923

Paromomys GIDLEY, 1923, p. 3. SIMPSON, 1937, p. 148 (genus redefined and revised).

TYPE: *Paromomys maturus* Gidley, 1923.

INCLUDED SPECIES: *Paromomys maturus* and *P. depressidens*.

DISTRIBUTION: Torrejonian, Lebo formation (Gidley and Silberling Quarry faunules), Crazy Mountain Field, Montana.

DIAGNOSIS: Lower dental formula, 1.1.3.3 (as in *Palaechthon*). Incisor enlarged but not fully procumbent, root extending to about P_3 . Canine little reduced; no noteworthy diastema. P_4 relatively smaller than in *Palaechthon* and with paraconid and metaconid rudimentary or absent. Third lobe of M_3 large and wide. External cingula on lower molars. P_4 - M^3 less transverse than in *Palaechthon*; postero-internal basins large, but less so than in *Phenacolemur* and not projecting more posteriorly than metacone on M^3 . Strong external cingula with metastyles. Metacone very small or indistinct on P_4 . Conules well developed on molars. M^{1-2} bilobed on internal faces.

Paromomys maturus Gidley, 1923

Plate 34, figure 1; plate 35, figure 1

Paromomys maturus GIDLEY, 1923, p. 3. SIMPSON, 1937, p. 149.

TYPE: U.S.N.M. No. 9473, right lower jaw with P_4 - M_3 and anterior alveoli.

HYPODIGM: Seven upper and 32 lower jaws in the United States National Museum (hypodigm of Simpson, 1937) and 13 upper and 44 lower jaws in the American Museum.

DISTRIBUTION: As for the genus.

DIAGNOSIS: Third lobe of M_3 wide. Larger than *P. depressidens*; length of M_1 , 2.9-3.2 mm.; mean, 3.0 mm. (21 specimens).

Paromomys depressidens Gidley, 1923

Plate 35, figure 2

Paromomys depressidens GIDLEY, 1923, p. 4. SIMPSON, 1937, p. 154.

TYPE: U.S.N.M. No. 9546, part of right upper jaw with P_4 - M^3 .

HYPODIGM: Three upper and four lower jaws in the United States National Museum (hypodigm of Simpson, 1937) and two upper

and 10 lower jaws in the American Museum.

DISTRIBUTION: As for the genus, but known from Gidley Quarry only.

DIAGNOSIS: Third lobe of M_3 generally narrower than in *P. maturus*. Smaller than *P. maturus*; length of M_1 , 1.9-2.3 mm.; mean, 2.1 mm. (nine specimens).

PHENACOLEMUR MATTHEW, 1915

Phenacolemur MATTHEW, 1915, p. 479. SIMPSON, 1935a, p. 16 (revised description of genus).

Ignacius MATTHEW AND GRANGER, 1921, p. 5; probably = *Phenacolemur*, Jepsen, 1934, p. 289; = *Phenacolemur*, Simpson, 1935a, p. 16.

TYPE: *Phenacolemur praecox* Matthew, 1915. (Type here selected; this species was the first of two listed under the original designation of the genus.)

INCLUDED SPECIES: *Phenacolemur praecox*, *P. praecox citatus*, *P. frugivorus*, *P. pagei*, and *P. jepseni* (new species, *infra*).

DISTRIBUTION: Tiffanian to Wasatchian, Rocky Mountain region.

DIAGNOSIS: Lower dental formula, 1.0.1.3. Incisor procumbent, root extending beneath M_1 . Canine absent; large diastema. P_4 without distinct paraconid or metaconid. Third lobe of M_3 large and wide. No cingula on lower molars. P_4 - M^3 quadrate; postero-internal basins very large, the basin on M^3 projecting far posteriorly beyond level of metacone. Variable external cingula, without definite metastyles. Metacone distinct on P_4 . Conules feeble on molars. Internal faces of M^{1-2} flattened but not grooved or bilobed.

In the Tiffanian two well-defined species are known, *P. frugivorus* and *P. pagei*, sharply distinct from each other and from the early Wasatchian forms. Two species have also been described from the early Wasatchian (Sand Coulee and Gray Bull) and are here retained as subspecies, but they are not very clearly separable. Another species of the same group is here described from the San José formation. Occurrence of the genus in the later Wasatchian (Wind River equivalents) is confirmed, but clear designation of Lysite or Wind River species is not now possible. The known species (and also specimens of doubtful specific status) are considered in temporal sequence. Summary metrical data on some apparently diag-

TABLE 1

SOME DIAGNOSTIC METRICAL DATA FOR SAMPLES OF *Phenacolemur*(Where a range is given, the mean and, in parentheses, the number of specimens are given below.
Where no range is given, only one specimen is involved.)

Sample	LP ₄	LM ₁	LP ₄ /LM ₁	LM ₁ /WM ₁
Tiffany formation				
<i>P. frugivorus</i>				
Mason pocket	1.6	2.0	0.8	1.25
Melville formation				
<i>P. frugivorus</i>				
Scarritt quarry	1.4-1.6 1.5(2)	1.8-2.0 1.9(3)	0.8-0.8 0.8(3)	1.2-1.4 1.3(3)
Polecat Bench formation				
<i>P. pagei</i>				
Silver Coulee quarry	3.0-3.5 3.31(16)	2.0-2.4 2.25(16)	1.3-1.7 1.48(14)	0.8-1.1 1.01(15)
Willwood formation (A.M.N.H. samples only)				
<i>P. praecox praecox</i>				
Sand Coulee	3.5-3.7 3.6(3)	2.7-3.2 2.9(4)	1.2-1.2 1.2(2)	1.2-1.4 1.3(4)
Lower Gray Bull	3.3-4.0 3.6(4)	2.9-3.0 2.9(3)	1.1-1.4 1.2(3)	1.1-1.3 1.2(3)
Both	3.3-4.0 3.6(7)	2.7-3.2 2.9(7)	1.1-1.4 1.2(5)	1.1-1.4 1.3(7)
<i>P. praecox citatus</i>				
Upper Gray Bull	2.8	2.3-2.6 2.4(4)	1.1	1.2-1.3 1.2(4)
San José formation				
<i>P. jepseni</i>				
Almagre	2.7	2.2	1.2	ca. 1.3

nostic characters for the principal samples are given in table 1.

TIFFANIAN FORMS

All the known Tiffanian specimens can be clearly referred to *P. frugivorus*, from the Tiffany and Melville formations, or to *P. pagei*, from a single quarry in the Polecat Bench formation.

Phenacolemur frugivorus (Matthew and Granger, 1921)

Plate 32, figure 1; plate 33, figure 1

Ignacius frugivorus MATTHEW AND GRANGER, 1921, p. 5. JEPSEN, 1934, p. 289.

Phenacolemur sp., JEPSEN, 1934, p. 289.

Phenacolemur frugivorus (Matthew and Granger), SIMPSON, 1935a, p. 19; 1936, p. 22; 1937, p. 9.

TYPE: A.M.N.H. No. 17368, left maxilla with P² and P⁴-M².

HYPODIGM: Including the type, but specific diagnosis based mainly on A.M.N.H. Nos. 17408 and 17405 from the Tiffany formation (Mason Pocket) and A.M.N.H. Nos. 33988, 33987, and 33896 from the Melville formation (Scarritt Quarry), all lower jaw fragments with cheek teeth.

DISTRIBUTION: Tiffanian age in local quarry (or "pocket") concentrations in the

Tiffany (northern San Juan Basin, La Plata County, Colorado) and Melville (Crazy Mountain Field, Sweetgrass County, Montana) formations.¹

DIAGNOSIS: Smallest known species of the genus. Mean length of M_1 (four specimens), 1.9 mm. P_4 shorter than M_1 ; ratio of length of P_4 to length of M_1 , 0.8 in each of four specimens. (The ratio is greater than 1 in all other known species.) Mean ratio of length of M_1 to width of M_1 (four specimens), 1.3. No diastemata around P^2 , which is very simple in structure. M^{1-2} with simple external cingulum, weak on the metacone.

There can be no doubt whatever that this species is distinct from the two earlier-named Sand Coulee and Gray Bull species and also from the later-named contemporaneous Silver Coulee species (*P. pagei*). It is, on the whole, the most distinctive of the species now placed in the genus. Nevertheless its distinction does not seem sufficient to warrant retention of the separate generic name *Ignacius*.

In their brief preliminary description Matthew and Granger (1921) based *Ignacius frugivorus* on a partial upper jaw and did not compare it with *Phenacolemur*, in which upper teeth were then known but were not of completely certain reference. They also mentioned and summarily described but did not compare two specimens (A.M.N.H. Nos. 17377 and 17408) including lower teeth. Two other specimens now known to belong to "*Ignacius*" *frugivorus* (A.M.N.H. Nos. 17401 and 17405) were referred to *Labidolemur soricoides*, although their resemblance to *Phenacolemur* was noted. Jepsen (1934) referred A.M.N.H. No. 17405 to *Phenacolemur* sp. and noted the probability that *Ignacius* was based on the upper teeth of *Phenacolemur*. I (Simpson, 1935a) accepted and sub-

stantiated this suggestion and placed *Ignacius* in the synonymy of *Phenacolemur*. *Labidolemur*, not at first clearly distinguished from "*Ignacius*" or *Phenacolemur*, is a valid and entirely different genus, a member of the Apatemyidae.

The Scarritt Quarry specimens from central Montana can be compared with those from the Mason Pocket in southwestern Colorado as regards some characters of the mandible and all characters of P_4 - M_2 . They are very closely similar. There is as much difference among specimens from one faunule (and these are small quarry deposits of populations highly unified in space and time) as among those of the two faunules. There is every reason to consider the two samples conspecific, and no reason to anticipate that the populations differed in any significant way. It is an oddity, probably caused by differences in facies, that the two distant faunules in the Tiffany and Melville contain the same species, while a Silver Coulee faunule of nearly if not precisely the same age and geographically between the Tiffany and Melville (nearer the latter) contains a definitely different species of the same genus, *P. pagei*.

Phenacolemur pagei Jepsen, 1930

Plate 32, figure 2; plate 33, figure 2

Phenacolemur pagei JEPSEN, 1930, p. 514.

TYPE: P.U. No. 13286, right lower jaw with P_4 - M_2 and alveoli of I, M_3 .

HYPODIGM: Eighteen partial lower and 11 partial upper jaws and one isolated lower incisor, all in the Princeton collection.

DISTRIBUTION: All known specimens from a single Silver Coulee quarry, Polecat Bench formation, Park County, Wyoming.

DIAGNOSIS: Jaws and teeth larger, over all, than in *P. frugivorus* and approaching, in various dimensions, *P. praecox*. P_4 much larger relatively than in *P. frugivorus*; LP_4/LM_1 range, 1.3-1.7; mean, 1.5 (14 specimens); range slightly overlaps *P. praecox*, but upper limit and mean are significantly higher. P_4 bulbous, notably wide posteriorly, and high. M_1 and M_2 almost equidimensional; LM_1/WM_1 range, 0.8-1.1; mean, 1.0 (15 specimens). M_1 with long external slope. P^{3-4} about as in *P. praecox*. No noteworthy diastemata around P^2 . M^{1-2} with well-devel-

¹ Some recent workers in these regions, specifically the United States Geological Survey, do not recognize either of these formations as such. The Tiffany is traditionally included in the "Wasatch," and I have tentatively designated it as a local fauna in the San José (e.g., Simpson, 1948). I now think that it is a distinct rock, and not only faunal, unit, which was Granger's original opinion when he named it. The Melville is a distinct formational rock unit in the Fort Union group.

TABLE 2
METRICAL DATA ON LOWER TEETH OF *Phenacolemur pagei*

Variate	N	OR	SR	M	S	V
LP ₄	16	3.0-3.5	1.0	3.31 ± .04	.16 ± .03	4.8 ± .8
WP ₄	16	2.3-2.9	1.0	2.57 ± .04	.16 ± .03	6.2 ± 1.1
LM ₁	16	2.0-2.4	.6	2.25 ± .02	.10 ± .02	4.4 ± .8
WM ₁	15	2.0-2.5	.8	2.21 ± .03	.12 ± .02	5.4 ± 1.0
LM ₂	12	1.9-2.3	.8	2.12 ± .03	.12 ± .02	5.7 ± 1.2
WM ₂	12	2.0-2.2	.4	2.12 ± .02	.07 ± .01	3.3 ± .7
LM ₃	6	2.8-3.2	.8	2.95 ± .05	.13 ± .03	4.4 ± 1.3
WM ₃	6	1.6-1.8	.5	1.72 ± .03	.08 ± .02	4.6 ± 1.3
LP ₄ /LM ₁	14	1.3-1.7	.6	1.48 ± .02	.09 ± .02	6.1 ± 1.2
LM ₁ /WM ₁	15	.8-1.1	.5	1.01 ± .02	.08 ± .01	7.9 ± 1.4
LM ₁ /LM ₃	6	.7- .8	.3	.77 ± .02	.05 ± .01	6.5 ± 1.9

oped external cingulum, interrupted and with a spur suggestive of an incipient mesostyle.

This is the best-known species, thanks to the large quarry collection made by Jepsen and his associates. Description of the dentition of *Phenacolemur* in a different section of this paper draws heavily on the specimens of *P. pagei*, and some further distinctions of the species are there mentioned. The quarry collection is unusually homogeneous in origin and provides metrical data for a highly unified population (see tables 2, 3). There is considerable variation. The mean V for 20 linear dental dimensions is 6.1. There is no indication of dimorphism, sexual or other, in the distributions. The upper teeth are strikingly more variable than the lower.

SAND COULEE-GRAY BULL FORMS

Phenacolemur praecox Matthew, 1915

Plate 32, figures 3, 4; plate 33, figure 3

Phenacolemur praecox MATTHEW, 1915, p. 480.

Phenacolemur citatus MATTHEW, 1915, p. 481.
(Tentatively recognized as a subspecies, *infra*.)

TYPE: See the subspecies.

HYPODIGM: Twelve lower and four upper partial jaws in the American Museum, nine lower and three upper partial jaws in the Princeton collection, and two lower and two upper partial jaws in the United States National Museum.

DISTRIBUTION: Sand Coulee and Gray Bull faunas of the Willwood formation, Wyoming.

DIAGNOSIS: The largest species of the

TABLE 3
METRICAL DATA ON UPPER TEETH OF *Phenacolemur pagei*

Variate	N	OR	SR	M	S	V
LP ²	4	2.1-2.5	1.2	2.30 ± .09	.18 ± .06	7.8 ± 2.8
WP ²	4	1.5-1.8	.9	1.60 ± .07	.14 ± .05	8.8 ± 3.1
LP ³	7	2.5-2.8	.6	2.67 ± .04	.10 ± .03	3.8 ± 1.0
WP ³	8	1.8-2.2	.9	2.08 ± .05	.14 ± .03	6.7 ± 1.7
LP ⁴	11	1.7-2.5	1.3	2.12 ± .06	.20 ± .04	9.4 ± 2.0
WP ⁴	11	2.7-3.2	.9	3.00 ± .04	.14 ± .03	4.7 ± 1.0
LM ¹	8	2.0-2.3	.8	2.15 ± .04	.12 ± .03	5.6 ± 1.4
WM ¹	7	3.0-3.5	1.2	3.27 ± .07	.18 ± .05	5.5 ± 1.5
LM ²	7	1.8-2.1	.8	1.97 ± .05	.13 ± .03	6.6 ± 1.8
WM ²	7	2.7-3.3	1.6	3.00 ± .09	.25 ± .07	8.3 ± 2.2
LM ³	5	1.7-2.1	1.0	1.90 ± .07	.16 ± .05	8.4 ± 2.7
WM ³	5	2.0-2.4	1.2	2.28 ± .08	.18 ± .06	7.9 ± 2.5

genus, although in most dimensions the lower end of the range approaches or overlaps *P. pagei* and *P. jepseni*. P_4 averaging relatively smaller than in *P. pagei*; LP_4/LM_1 range, 1.1–1.4; mean, 1.2 (12 specimens). M_1 and M_2 more elongate; LM_1/WM_1 range, 1.1–1.4; mean, 1.2 (16 specimens). P_4 generally lower and less bulbous or expanded posteriorly than in *P. pagei*. M_1 with shorter external slope. P^{3-4} with well-developed metacones and P^3 with small, distinct postero-internal basin. Anterior margin of P^4 nearly straight. M^{1-2} with continuous external cingulum, without median spur.

With a single possible exception (from the San José formation, see below; that specimen may be a little later than the Willwood Gray Bull), all the early Wasatchian specimens of *Phenacolemur* known to me are from the Willwood formation. The specimens are highly diverse and surely must sample a considerable number of different local populations. The range in size and proportions is consistent with the presence of two or even of several species, and the types of Matthew's two species, *P. praecox* and *P. citatus*, are included. The range of LP_4 for all known specimens (15) from the Willwood is 2.7–4.0, the largest tooth is almost 50 per cent longer than the smallest, and the coefficient of variation is 12.6, which is decidedly large (although not altogether impossible) for a single species. The specimens are from a large area, and almost all were found singly. In only one instance do as many as three have the same locality datum, and that is still an area rather than one precise horizon and locality. The range in time is also considerable, from the beginning of the Wasatchian into the latest Gray Bull faunules.

The samples are thus heterogeneous, and there is every reason to suspect that at least two taxonomically distinguishable populations are represented. The American Museum collections, made by parties under Walter Granger, were with a few exceptions recorded by Granger as "Sand Coulee," "Lower Gray Bull," or "Upper Gray Bull," a field sorting largely by levels and in part by geographic area, the Sand Coulee being both lower than Gray Bull, *sensu stricto*, and marginal in position.¹ The taxonomically useful "Sand

Coulee" (or, in early field notes, "Intermediate Beds") specimens are from "3 miles southeast of mouth of Pat O'Hara Creek" (A.M.N.H. Nos. 16101, 16102, 16142) and from "Point of bluff north of Ralston" (No. 16100). The "Lower Gray Bull" specimens are from "3 miles southeast of Otto" (No. 15074), "Elk Creek... Camp 4" (No. 15075), and "Elk Creek... Camp 5" (Nos. 15077, 15078). The "Upper Gray Bull" specimens are from "Head of 10 mile creek" (Nos. 16777, 16833), "Willow Creek" (No. 15695), and "2 miles southwest of St. Joe" (No. 15076).

Granger's Sand Coulee and lower Gray Bull samples, combined, vary rather more than is usual for a single population (see table 4), but they seem to be taxonomically inseparable in size or structure. The upper Gray Bull sample has no consistent difference in structure, but the teeth are smaller in all mean dimensions, and in most cases the ranges do not overlap those of the other two samples (see tables 1 and 4). Statistical comparison (by the *t*-test for small samples) gives for WP_4 and LM_2 P between 0.05 and 0.02 and for LM_1 $P = 0.01$. For LP_4 P is slightly above 0.05. There is reasonable probability that the population represented by the upper Gray Bull sample is different from that represented by the other two samples. There is thus a basis for Matthew's distinction of *P. praecox*, type from the Sand Coulee, and *P. citatus*, type from the upper Gray Bull.

The Princeton Gray Bull specimens are in part fragmentary and not diagnostic as between the two supposed species of Matthew, but they include two relatively good specimens (P.U. Nos. 16220 and 16225) which are intermediate and tend to close the gap between *P. praecox* and *P. citatus* (see table 4). This does not necessarily contradict the evidence that those are different taxa, but it does suggest that their populations intergraded spatially, temporally, or both. A reasonable hypothesis is that the taxa are such as to be best designated subspecies and that

¹ Separation of Sand Coulee and Gray Bull beds or faunas has been disputed, but specimens labeled "Sand Coulee" by Granger do represent a fairly homogeneous fauna within the Willwood and one that can in some respects be definitely distinguished from the (or the other) Gray Bull faunas.

TABLE 4
MEASUREMENTS OF LOWER TEETH OF *Phenacolemur* FROM THE WILLWOOD FORMATION

	P ₄		M ₁		M ₂		M ₃		LP ₄ /LM ₁	LM ₁ /WM ₁
	L	W	L	W	L	W	L	W		
Sand Coulee, Granger										
A.M.N.H. No. 16102										
(type, <i>P. praecox</i>)	3.7	2.5	3.2	2.5	3.1	2.4	—	—	1.2	1.3
A.M.N.H. No. 16142	ca. 3.5	ca. 2.5	2.9	2.2	—	—	—	—	ca. 1.2	1.3
A.M.N.H. No. 16101	3.5	2.3	2.9	2.5	2.8	2.3	—	—	1.2	1.2
A.M.N.H. No. 16100	—	—	2.7	1.9	2.8	2.1	—	—	—	1.4
Sand Coulee, Jepsen										
P.U. No. 13151	3.2	2.1	3.0	2.5	3.0	2.5	—	—	1.1	1.2
P.U. No. 13277	3.0	2.1	2.7	2.2	—	—	—	—	1.1	1.2
P.U. No. 13281	2.7	1.9	2.4	2.2	2.3	2.2	3.5	2.1	1.1	1.1
Lower Gray Bull, Granger										
A.M.N.H. No. 15075	4.0	2.7	2.9	2.4	2.7	2.3	—	2.1	1.4	1.2
A.M.N.H. No. 15074	3.6	2.7	2.9	2.6	3.1	2.6	—	—	1.2	1.1
A.M.N.H. No. 15078	3.3	2.0	3.0	2.3	—	—	—	—	1.1	1.3
Upper Gray Bull, Granger										
A.M.N.H. No. 15695										
(type, <i>P. citatus</i>)	—	—	2.5	2.1	2.5	2.2	3.8	2.0	—	1.2
A.M.N.H. No. 15076	—	—	2.4	2.0	2.3	2.0	3.5	1.9	—	1.2
A.M.N.H. No. 16833	2.8	1.8	2.6	2.0	2.6	2.1	—	—	1.1	1.3
A.M.N.H. No. 16777	—	—	2.3	2.0	—	—	—	—	—	1.2
Gray Bull, Jepsen										
P.U. No. 16220	2.7	2.1	2.5	2.2	—	—	—	—	1.1	1.1
P.U. No. 16219	—	—	—	—	2.6	2.3	—	—	—	—
P.U. No. 16225	2.9	2.0	2.7	2.4	2.7	2.3	—	—	1.1	1.1
P.U. No. 16221	3.4	2.1	—	—	2.6	2.2	—	—	—	—
P.U. No. 16226	—	—	—	—	2.9	2.2	—	—	—	—
P.U. No. 16224	—	—	—	—	2.8	2.3	3.4	1.7	—	—
Gray Bull, Gilmore										
U.S.N.M. No. 19167	3.5	2.3	2.6	2.5	2.6	2.4	—	—	1.4	1.0
U.S.N.M. No. 19168	3.9	2.3	2.8	2.5	2.8	2.5	4.1	2.2	1.4	1.1

there was a tendency for one to replace the other in the Willwood area from earlier to later Gray Bull time either by evolution *in situ* or by geographic spread.

Two of the Princeton Sand Coulee specimens (P.U. Nos. 13151 and 13277) of course differ in detail from any in Granger's Sand Coulee sample but could well represent the same population, *P. praecox* (*sensu stricto*) or *P. praecox praecox*. Another specimen (P.U. No. 13281), although labeled "Sand Coulee," is decidedly different and cannot be distinguished from the upper Gray Bull *P. citatus* or *P. praecox citatus*. It is, then, possible after all that only one extremely variable group is present throughout and that the apparent distinction of the latest forms is illusory.

Nevertheless the variation is extreme, and there are good reasons to think that at least two taxa are present, whether or not all specimens can be clearly assigned to one or the other. The apparently anomalous Sand Coulee specimen could represent either an extreme variant in the direction of the later taxon or a stray from a geographically adjacent taxon which resembled or in fact was the group later predominant in this area. It is perhaps also possible that the specimen is actually from later beds.

Any solution of these problems is necessarily dubious. The important point is that the indicated populations are all very closely related but probably are heterogeneous. The arrangement here proposed is tentatively to

TABLE 5
MEASUREMENTS OF TEETH OF TYPE OF
Phenacolemur jepseni

	Length	Width
P ₄	2.7	1.7
M ₁	2.2	ca. 1.7
M ₂	2.3	1.9
M ₃	3.2	1.8
P ²	1.6	0.9
P ³	2.2	1.4
P ⁴	2.3	2.6
M ¹	2.3	2.7
M ²	2.2	2.7
M ³	2.4	2.4

recognize Matthew's two species as subspecies, making them definable by using Granger's samples as hypodigms.

Phenacolemur praecox praecox Matthew, new name as subspecies

Plate 32, figure 3

Phenacolemur praecox MATTHEW, 1915, p. 480.

TYPE: A.M.N.H. No. 16102, right mandible with broken incisor and P₄-M₂.

HYPODIGM: Granger's Sand Coulee and lower Gray Bull specimens, listed in text above.

DISTRIBUTION: Early Wasatchian, Sand Coulee, and early Gray Bull faunules, Willwood formation, Bighorn Basin, Wyoming.

DIAGNOSIS: The largest animals referred

to this genus. Mean, LP₄ (seven specimens), 3.5. (See metrical data in tables 1 and 4.)

Phenacolemur praecox citatus Matthew, new name as subspecies

Plate 32, figure 4

Phenacolemur citatus MATTHEW, 1915, p. 481.

TYPE: A.M.N.H. No. 15695, part of right mandible with M₁-M₃.

HYPODIGM: Granger's upper Gray Bull sample, listed in text above.

DISTRIBUTION: Early Wasatchian, late Gray Bull faunules (possibly also earlier) in the Willwood formation, Bighorn Basin, Wyoming.

DIAGNOSIS: Smaller than *P. praecox praecox*. LP₄ (one specimen), 2.8. (See metrical data in tables 1 and 4.)

Matthew defined *P. citatus* as also having the anterior molars narrower and more elongate than in *P. praecox*, but measured ratios do not substantiate this impression.

THE SAN JOSÉ FORM

Phenacolemur jepseni,¹ new species

Plate 30, figures 1-4; plate 31, figures 1, 2; plate 32, figure 5; plate 33, figure 4

¹ For G. L. Jepsen, outstanding student of Paleocene and Eocene faunas and collector of many specimens of *Phenacolemur*.

PLATE 32

Phenacolemur Matthew. Comparative series of lower teeth of known taxa.

1. *Phenacolemur frugivorus* (Matthew and Granger). A.M.N.H. No. 33987, right P₄-M₂, Scarritt Quarry, Melville formation, Tiffanian.

2. *Phenacolemur pagei* Jepsen. P.U. No. 14030, right I and P₄-M₃, Silver Coulee quarry, Polecat Bench formation, Tiffanian.

3. *Phenacolemur praecox praecox* Matthew. A.M.N.H. No. 16102, type, right I (broken) and P₄-M₂, Sand Coulee faunule, Willwood formation, early Wasatchian.

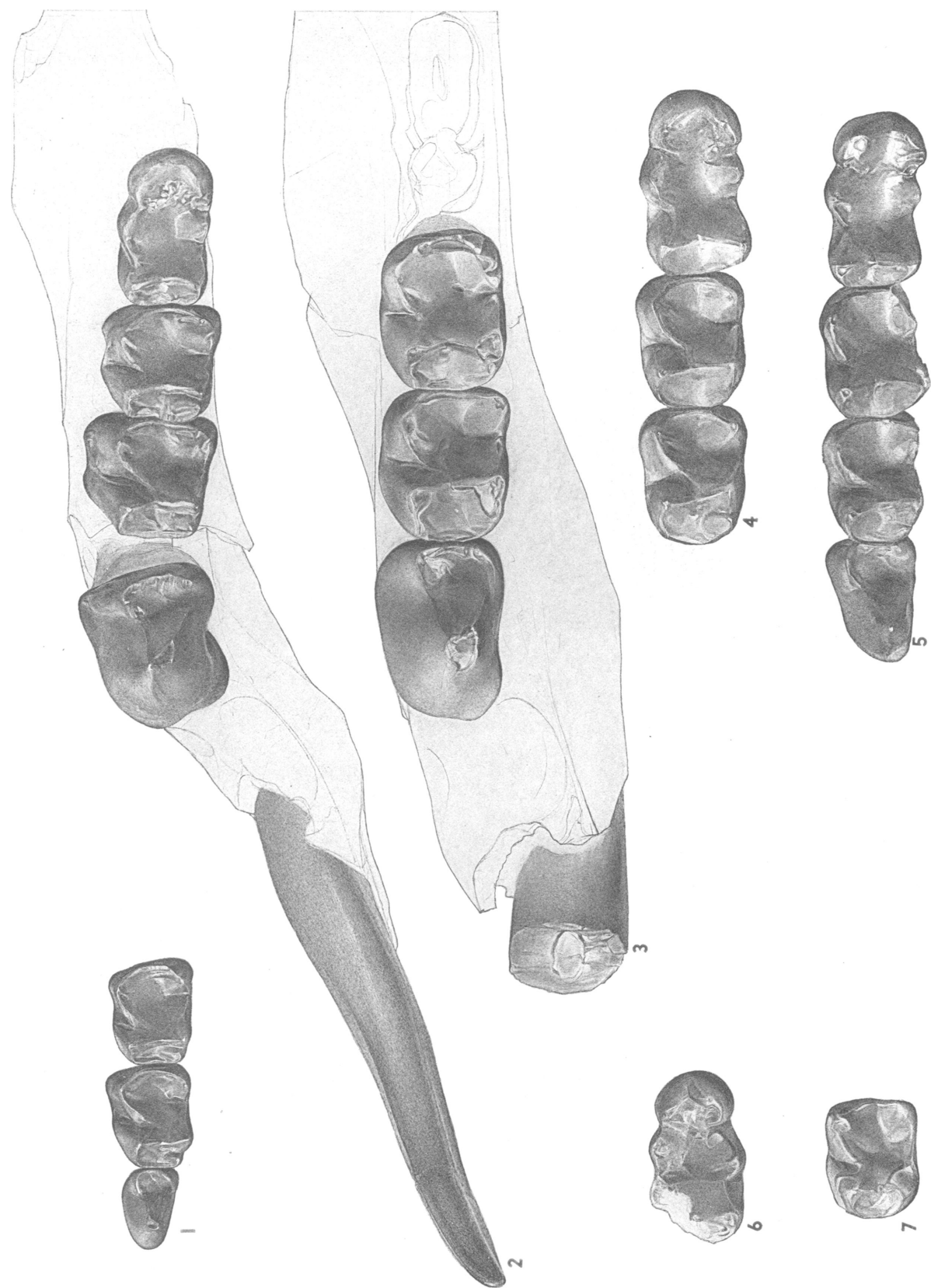
4. *Phenacolemur praecox citatus* Matthew. A.M.N.H. No. 15076, right M₁₋₃, upper Gray Bull faunule, Willwood formation, early Wasatchian.

5. *Phenacolemur jepseni*, new species. A.M.N.H. No. 48005, type, right P₄-M₂ and M₃ drawn in reverse from left side, San José formation, Wasatchian.

6. *Phenacolemur* cf. *jepseni*. P.U. No. 13841, incomplete left M₃, Lysite member, Wind River formation, middle Wasatchian.

7. *Phenacolemur* cf. *jepseni*. A.C. No. 3463, right M₂, Lysite member, Wind River formation, middle Wasatchian.

All crown views, nine times natural size.



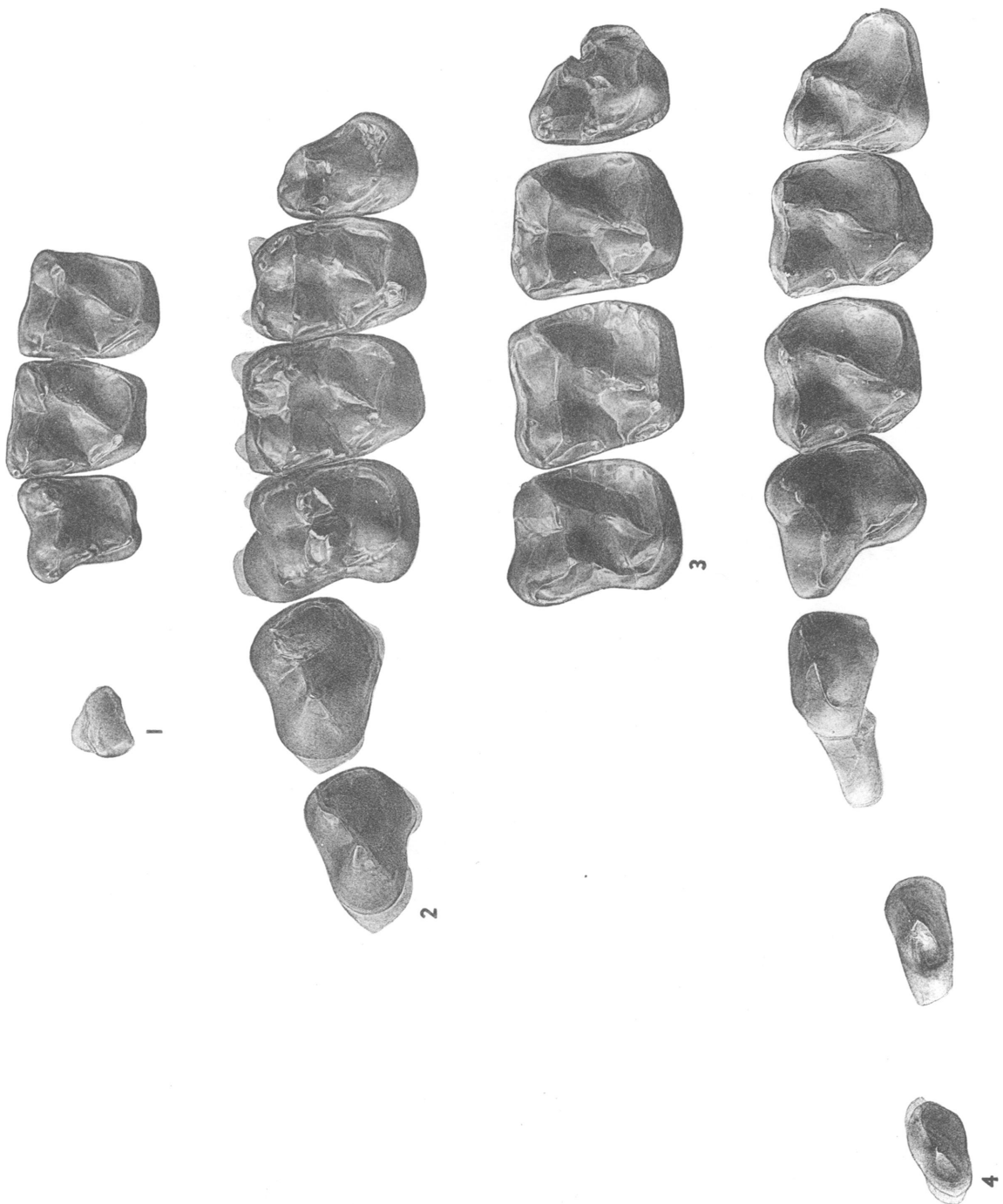


TABLE 6
COMPARISON OF TYPE OF *Phenacolemur jepseni* WITH *Phenacolemur praecox citatus*

		Hypodigm of <i>P. praecox citatus</i>			<i>P. jepseni</i>
		N	R	M	
P ₄	L	1	—	2.8	2.7
	W	1	—	1.8	1.7
M ₁	L	4	2.3–2.6	2.4	2.2
	W	4	2.0–2.1	2.0	ca. 1.7
M ₂	L	3	2.3–2.6	2.5	2.3
	W	3	2.0–2.2	2.1	1.9
M ₃	L	2	3.5–3.8	3.6	3.2
	W	2	1.9–2.0	2.0	1.8

TYPE: A.M.N.H. No. 48005, skull with most of cheek teeth and associated lower jaws with left I, M₂₋₃, and right P₄–M₂.

HYPODIGM: Type only.

DISTRIBUTION: Known only from American Museum Quarry 88, Wasatchian, high in Almagre facies of the San José formation, head of Arroyo Blanco, Rio Arriba County, New Mexico. (The locality is shown on the map in Simpson, 1948, fig. 3.)

DIAGNOSIS: Dental dimensions near or below lower limit of known range of Willwood *Phenacolemur* and well below mean for any indicated population there. (Measurements in table 5.) LP₄ in type, 2.7. LP₄/LM₁, 1.2. LM₁/WM₁, ca. 1.3. P₄ with laterally expanded heel, about as in *P. pagei*. P₃₋₄ with minute metacones, distinctly smaller than in

known specimens of *P. praecox* or *P. pagei* and P₃ little basined postero-internally. P₄ emarginate anteriorly. Large diastemata anterior and posterior to P₂. M₁₋₂ without sharp external cingula.

This specimen is certainly closely related to the Willwood complex and is especially similar to the smaller specimens tentatively separated as *P. praecox citatus*. The difference in size is far less than occurs within the Willwood samples (table 6). There is therefore some doubt in recognizing the San José specimen as taxonomically distinct. However, its over-all size is below the observed range in the rather large total Willwood collection, and there are some apparently distinct

PLATE 33

Phenacolemur Matthew. Comparative series of upper teeth of known species.

1. *Phenacolemur frugivorus* (Matthew and Granger). A.M.N.H. No. 17368, type, left P₂ and P₄–M₂, Mason Pocket, Tiffany formation, Tiffanian.

2. *Phenacolemur pagei* Jepsen. P.U. No. 16216, left P₂–M₂, Silver Coulee quarry, Polecat Bench formation, Tiffanian.

3. *Phenacolemur praecox* Matthew. P.U. No. 13028, left P₄–M₃ (M₃ slightly broken postero-internally and not restored), protocone of M₁ restored from other side, Gray Bull fauna, Willwood formation, early Wasatchian.

4. *Phenacolemur jepseni*, new species. A.M.N.H. No. 48005, type, left C or P₁ and P₂–M₃, San José formation, Wasatchian.

All crown views, nine times natural size.

morphological differences as noted in the diagnosis. The locality is widely different, and the faunal facies somewhat different. It thus does seem sufficiently probable that the San José (Almagre facies) *Phenacolemur* population was taxonomically distinct from either of the two tentatively recognized Willwood populations. It is not altogether clear whether the taxon so distinguished is best considered a subspecies or a species, but tentative designation as a species is more convenient and is probable.

LYSITE AND LOST CABIN FORMS

Phenacolemur also occurs in the Lysite and in a Lost Cabin equivalent in Wyoming.

Phenacolemur cf. *jepseni*

Plate 32, figures 6, 7

Jepsen (1934, p. 289) reported but did not discuss "*Phenacolemur* (undescribed species)" from the Lysite. The specimen is P.U. No. 13841, a fragment of left lower jaw with slightly broken M_3 , from the type Lysite in the Wind River formation on Cottonwood Creek 3 miles northeast of Lysite, Wyoming, collected by L. Cook in 1928. M_3 measures 3.1 by 1.8 and is almost exactly like the type of *P. jepseni* except that the third lobe is slightly narrower and more rounded. A second Lysite specimen is A.C. No. 3463, right lower jaw with M_2 and the alveoli of the other cheek teeth, with the field label "Locality Bridger Creek, Wyo. Horizon Wind River. Field No. 463. Collector T. C. B." M_2 measures 2.3 by 1.8 and is also very like the type of *P. jepseni* although slightly more slender. Kelley and Wood (1954) have described and figured this tooth as *Phenacolemur* sp.

These specimens could be small variants of *P. praecox citatus*,¹ but both of them are even

¹ With the Amherst specimen is a label "*Phenacolemur citatus* gen. et sp. indesc." in W. D. Matthew's handwriting and evidently written while his 1915 paper was in press.

nearer to *P. jepseni*. They do not suffice for positive identification, but they do suggest that something near the San José form occurs in the Lysite.

It is interesting that in the sequence of known, clearly related specimens of *Phenacolemur* from Sand Coulee through lower Gray Bull and upper Gray Bull to Lysite the mean size decreases.

Phenacolemur sp.

Nace (1936, p. 175) quoted from an unpublished manuscript by S. H. Knight the presence of "*Phenacolemur* sp. nov." in a collection from Bates Hole.² The identification was by Walter Granger, who was quoted by Nace from Knight as follows: "The *Phenacolemur* has not been previously recorded from the Wind River and the single lower molar in your collection represents a somewhat more advanced form than is found in the Wasatch." There are no further remarks on the specimen in Granger's original letter to Knight, and no notes on it by Granger have been found. There is no sure way of knowing what characters were judged to be more advanced.³ The specimen itself was recently sought by Paul O. McGrew in the University of Wyoming collection, to which it was apparently returned by Granger, but was not found. Granger's identification of the genus is authoritative, however, and may be accepted as extending the range to the Lost Cabin, end of the Wasatchian.

² Van Houten (1945, p. 451) repeated the record from Nace but ascribed it to the Wind River Basin.

³ There may, however, be some suspicion that larger size was considered a more advanced character because no clear structural trend was or is known within the genus, and increase in size was generally considered progressive by Granger and commonly is so. Nevertheless, as noted above, it now appears that there may possibly have been an exceptional but not unparalleled trend towards reduction of size in the Sand Coulee to Lysite populations of the genus.

MORPHOLOGY OF *PHENACOLEMUR*

DENTITION

THE DENTAL FORMULA IS

$$\frac{? . 1 . 3 . 3}{1 . 0 . 1 . 3}$$

The number of upper incisors is unknown. The tooth tentatively identified as a canine might be P^1 , in which case the upper formula would be ? . 0 . 4 . 3.

UPPER TEETH: Isolated teeth from faunules containing *Phenacolemur* probably include representatives of its presumably enlarged upper incisors, but the association is too uncertain to warrant definite ascription. The anterior maxillary tooth is preserved only in the type of *P. jepseni* and one specimen of *P. pagei*, although obscure alveolar traces indicate its presence also in *P. frugivorus*, and it was doubtless constant in the genus. In *P. jepseni* that tooth is small but two-rooted, with a slightly recurved, simple crown, more convex on the outer face, with secant edges, the posterior edge sharper. In *pagei* the homologous tooth is larger, both absolutely and relatively, and has a minute posterior cuspule, hardly incipient in *jepseni*.

P^2 of *jepseni* is much lower than the first maxillary tooth and has a distinct but tiny posterior cuspule. Diastemata anterior and posterior to P^2 are about equal to it in length. In *pagei* there are no diastemata around P^2 , and that tooth is larger than in *jepseni*, plumper, widened posteriorly, with a distinct posterior cuspule and incipient postero-internal basin. In *frugivorus* diastemata are also absent, and the tooth, although somewhat higher relatively, is simple as in *jepseni*. P^2 is unknown in the *praecox* group, but U.S.N.M. No. 19169 has its roots, which show that it was large and was not followed by a significant diastema.

P^3 of *jepseni* is almost exactly like P^2 of *pagei*: a fairly large tooth, somewhat expanded posteriorly, with a posterior cuspule and an incipient postero-internal basin. In A.M.N.H. No. 16938, *P. praecox* (probably *citatus*), the tendency is carried further: posterior cusp and basin are more developed. P^3 of U.S.N.M. No. 19169 (probably *P. p. praecox*) is larger. It was otherwise probably

similar, but it is badly broken. In *pagei* the posterior cusp and basin are still more distinct, and the whole tooth is plumper.

P^4 is abruptly different from P^3 , being a transverse tooth with a protocone (wholly absent on P^3) as large as and opposite to the main outer cusp, descriptively the paracone. A ridge descends the posterior slope of the protocone to the postero-internal corner of the quadrate tooth, then runs externally, enclosing a large basin with somewhat crenulated enamel. There is a small parastyle from which an anterior cingulum runs internally for about half of the width of the tooth. In *jepseni* the anterior margin of P^4 is sharply notched in the middle; the metacone is distinct but small. In all specimens (four) of the *praecox* group the anterior margin is nearly straight, and the metacone is relatively larger. In *pagei* P^4 is about as in *praecox* but has the plump look characteristic of most of the premolars of this species and has a prominent bulbous anterosuperior expansion suggested but much less prominent in *praecox* and vaguer still in *jepseni*. The basal expansion is not even incipient in *frugivorus*, which otherwise is nearly like *praecox* in P^4 except for its smaller size. The metacone is relatively a little smaller.

On M^1 the three primary trigon cusps are subequal. From the tip of the protocone three crests descend: one antero-externally to the anterior border of the tooth near the midline, one postero-externally to the metacone, and one posteriorly or a little postero-internally to the postero-internal corner of the crown, where it turns and runs externally to the posterior side of the metacone. The latter crest encloses a prominent basin and does not bear a distinct hypocone. From the paracone a crest runs internally and somewhat anteriorly to the same point on the anterior border reached by the antero-external crest from the protocone. On the end of the paracone crest at the point of junction there is a slight cuspule on completely unworn teeth, presumably a vestigial protoconule. The protocone-metacone crest on completely unworn teeth may also have a slight suggestion of a median metaconule swelling or papilla, but this is vague at best. The inner face of the

tooth is flattened and has no cingulum. In most specimens there is a cingulum along the whole anterior face, rising to connect medially with the protoconule vestige, and variably papillated. In *P. frugivorus* (type only) the internal half of the anterior cingulum seems to have been particularly feeble, but it is somewhat affected by wear.

The only noteworthy specific differences in M^1 involve the external cingulum. In all material of the *praecox* complex (six specimens) there is a sharp, continuous, variably papillated cingulum from a minute parastylar projection to the postero-external face of the metacone, where it dies out. The type of *frugivorus* is similar. In *pagei* there is a slight median interruption of the external cingulum, and a small, sharp spur projects towards the paracone-metacone notch from the anterior end of the posterior half of the cingulum. The prominence of this peculiar feature varies, but it is present on all eight specimens of M^1 . The type of *jepseni* is unique in lacking any sharp external cingulum on the upper molars, with only a rounded bulge in its place.

M^2 is similar to M^1 but is beyond the antical axis of the molariforms and tends to be a little narrowed posteriorly, with the metacone slightly reduced. The external cingulum on the metacone is not so sharp as on M^1 , or is only a rounded bulge, and in *pagei* it lacks the spur characteristic on M^1 of that species.

As regards the trigon, M^3 simply continues the sort of serial field differentiation visible as between M^1 and M^2 . That is, M^3 has the trigon smaller, metacone more reduced, external cingulum less distinct. The talon (or posterior basin) of M^3 is, however, extraordinary: it projects far posteriorly as a sort of ear-like tab. The projection is slightly but definitely more prominent in *praecox* (one specimen) and *jepseni* (only specimen) than on the earlier *pagei* (five specimens). M^3 is unknown in *frugivorus*.

LOWER TEETH: The single, procumbent, large lower incisor has a relatively enormous, closed root the alveolus and canal for which extend backward beneath the whole cheek tooth series, although the root itself ends beneath M_1 or M_2 . The crown, fully enameled, is simple, without cingulum or cuspules, and curves forward and upward to its single apical point. A smoothly convex externo-

inferior face is separated by low longitudinal crests and accompanying grooves from a smaller, also convex, mediosuperior face.

P_4 differs in relative size and proportions in the various species (as suggested in the diagnoses) but is fundamentally the same in all, and so are the lower molars. P_4 is a large tooth, extending above the molar level (least so in *frugivorus*, with the relatively smallest P_4). There is no trace of paraconid or metaconid. Vague crests fall from the protoconid apex anteriorly and postero-externally and a more distinct crest drops postero-internally. The talonid has a well-developed hypoconid and a basin, sloping somewhat towards the inner side and open through the notch between the base of the protocone and the relatively small entoconid. There is no hypoconulid.

M_1 has a moderately elevated trigonid extending upward and forward. Protoconid and metaconid have low, plump apices and are approximately equal in size. The metaconid is postero-internal to the protoconid, and the two are connected by a sharp low crest. The paraconid is smaller and is nearly internal, near the metaconid. It seems to be relatively smallest and least fully internal in *P. jepseni*. On nearly unworn teeth there is a rounded and vague yet definitely present crest directly between protoconid and paraconid. A sharp crest runs straight anteriorly from the protoconid, then turns at a right angle and runs straight internally along the anterior margin of the trigonid and ends on the anterior face of the paraconid. The whole trigonid pattern is highly distinctive: transversely quadrate and with two definite and one vague transverse crests. The talonid is low and large, wider than the trigonid. The large crescentic hypoconid has one crest running antero-internally to the middle of the base of the trigonid and the other postero-internally and around the posterior rim of the tooth to the entoconid, which is smaller than the hypoconid. There is no hypoconulid. The basin is broad and is closed, but there is a sharp notch between the entoconid and the trigonid. On the least worn teeth there is visible a tendency to develop an extremely minute cuspule anterior to and on the slope of the entoconid (nominally an entostylid).

M_2 resembles M_1 , but the trigonid is lower and is shorter antero-posteriorly, although

equally wide. The paraconid is closer to the metaconid and somewhat smaller. On the type of *jepseni* the paraconid cannot be distinguished on M_2 . That is partly due to wear, but the cusp was surely minute. The talonid of M_2 resembles that of M_1 but is somewhat larger, especially longer.

The trigonid of M_3 continues the field gradient: it is still lower and still shorter than on M_2 and has the paraconid so small and so nearly fused with the metaconid that it cannot be distinguished at all except when practically unworn. The comparatively tremendous talonid consists of two lobes, approximately equal to each other and each longer than the trigonid and about as wide; in some specimens the posterior lobe (third lobe of the tooth as a whole) is a little narrower. The second lobe has a large, open-crescentic hypoconid the anterior wing of which abuts against the trigonid more externally than on M_2 . The entoconid, on the opposite side, is a more slender, discrete cusp usually well separated by anterior and posterior notches, although the posterior notch is not always prominent.¹ The posterior lobe, even when nearly unworn, has no really distinct cusps but has an elevated, bulging or rolled rim that tends to be a little more elevated at the external and internal ends. The internal part of this elevated rim is narrower, more elevated, and sharper and does end in an approximation of a cusp. There are wrinkled enamel folds and valleys in the talonid basin, mainly on the posterior lobe, evidently highly variable in pattern.

SKULL

Several specimens show that the anterior root of the zygoma is above the molars, mainly M_1^{1-2} , and has a broad, sloping anterior face forward to the relatively large infra-orbital foramen above the posterior end of P^3 . Other information about the skull comes mostly from A.M.N.H. No. 48005, type of *P. jepseni*. That specimen includes virtually the whole skull except the premaxillae, but it is so fragmented and crushed that reliable information from it is disappointingly mea-

¹ I have no strong conviction that this cusp is "really" an entoconid in phylogenetic origin rather than, say, an entostylid, but the point seems of little importance and "entoconid" is as good a label as any.

ger. (P.U. No. 13028, mentioned but not described by Jepsen, 1934, p. 289, footnote, apparently includes the cranium, but is so crushed and concretionary that literally nothing of the structure can be made out.)

Despite the crushing that has accentuated these features, it is fairly clear that the skull was broad and low and had the post-palatal length not longer and probably shorter than the palatal. Those features and the established presence of a low medial sagittal crest imply that the brain case was broad, short, low, and relatively small. The palate was unusually broad and only gently concave. This is confirmed by P.U. No. 16216, which also shows more clearly that the palatine bone extended forward to about the level of the anterior end of M^1 and that the choanae were wide, but less so than the posterior palatal width, and had their rim about opposite the posterior end of the molar series.

A short ossified external auditory meatus and adjacent lateral part of an ossified bulla are clearly visible. The inner parts of the bulla are broken down into an inchoate mass of fragments, but the bulla was probably rather large and fully ossified. I can make out nothing of the crucial features of the carotid circulation. Immediately anterior to the meatus is a small but sharply distinct, almost styliform postglenoid process, and the foramen lies posteromedial to this, squeezed between it and the meatus or anterolateral part of the bulla.

The specimen neither establishes nor makes improbable the presence of a postorbital bar.

LOWER JAW

The lower jaw, known from many fragments but most completely in the type of *P. jepseni*, is clear enough as to general form in the figures (pl. 31, figs. 1, 2). Noteworthy are the expansion downward of the flat angular region and its excavation on the inner side; the rise of the coronoid process posterior and only slightly external to the last molar; the position of the dental foramen far posterior to and slightly below the alveolar rim; the unfused symphysis, and the (main) mental foramen below the posterior end of the diastema. (Some specimens also have a smaller foramen,¹ and some even two minute foramina, beneath M_1 , but in other specimens this may be absent.)

AFFINITIES

THE SPECIES OF *Phenacolemur*

THE PRECEDING TAXONOMIC REVIEW has established the existence of three obviously distinct, clear-cut species: *Phenacolemur frugivorus*, *pagei*, and *praecox*. Samples referred to *praecox* represent heterogeneous, but evidently closely related, populations with at least two taxa, tentatively labeled as subspecies. *Phenacolemur jepseni* is clearly a distinct taxon and seems to be a species, but may be more nearly related to *praecox* than to *frugivorus* or *pagei*.

The Tiffanian *P. frugivorus* could be taken as the most primitive species: P_4 is relatively small; there is no upper diastema; P^2 is very simple, and P^3 (although unknown) doubtless was also; the metacone is moderate on P^4 ; and the external cingulum of the upper molars is simple. But on most of these criteria the contemporaneous *P. pagei* is the most specialized species: P_4 is very large; the upper premolars are relatively advanced in development of cuspules and of a metacone on P^4 ; all premolars are bulbous, a peculiarity doubtless specialized and not primitive; and the upper molar cingulum tends to form a mesostyle rudiment. And *P. jepseni*, one of the latest if not the latest species, would appear about as primitive as *frugivorus*, if not more so in some aspects such as the small metacone on P^4 . Only in the absence of upper diastemata in *P. pagei* and their presence in *P. jepseni* could the later of those two species be considered probably more specialized. The size sequence also is erratic. *Phenacolemur frugivorus* is smallest, but its contemporary *pagei* is, over all, about as large as the late *P. jepseni*, and the largest forms of all are of intermediate age, early *P. praecox*.

In the known forms there is, then, no evident progressive trend. The time involved is (in extremely loose approximation) on the order of five to 10 million years. Some associated groups do show definitely progressive trends through comparable spans of time, for instance, the plesiadapids from middle Paleocene to earliest Eocene or the notharcines from earliest to middle Eocene. By the beginning of late Paleocene *Phenacolemur* had acquired all the fundamentals of a specialized adaptive type. As is indicated below, *Paromomys* and some other forms hint, although they do not clearly demonstrate,

that the special structural level was reached rather rapidly during the middle Paleocene. Once the adaptive level or zone was reached, species differentiated within it, but they remained within it. The speciation was a confined deployment, not a progression.

There is here a speculative and yet suggestive bearing on some concepts of systematics. A genus (or other supraspecific group) is often considered a subjective or purely arbitrary bundling together of as many divergent species as it may be convenient to include. Or, again, it may be considered, by paleontologists especially, as an arbitrarily separated stage in a continuously evolving sequence. Undoubtedly both sorts of entities occur among those labeled "genus." *Phenacolemur* seems to exemplify a third kind of genus, which also undoubtedly exists: one in which the taxon labeled "genus" corresponds with a real and definite evolutionary entity no more arbitrary (in any but the most narrowly genetical view) than the species. It is an adaptive relationship, reflected in the structure of the genus, which once achieved does not tend to change but only to be overlain by fluctuating local speciation.

GENERIC AND FAMILY RELATIONSHIPS

Phenacolemur is a strikingly distinctive genus that could not possibly be confused with any other yet known. Matthew (1915) appreciated the peculiarity of his "singular little genus." He referred it to the Apatemyidae but found more differences from than resemblances to *Apatemys* or *Trogolemur*, the only other supposedly (it is now believed erroneously) apatemyid genus that he explicitly mentioned. Matthew noted some resemblance to the early rodent *Paramys* and even speculated that *Phenacolemur* might represent a (structural but not genetical) "ancestral stage in the evolution of the simplicidentate rodents."¹ Nevertheless Matthew

¹ This passing remark by Matthew was somewhat unfortunate. It was picked up and even emphasized by Schlosser and hence passed into what might be called the folk-lore of the genus, if the "folk" aware of it were more numerous. In fact the resemblance to rodents is remote and obviously of no significance. The incisor is not at all a gnawing tooth but is more analogous to the pinching teeth of shrews. The jaw and musculature are not at all adapted to true gnawing, either, nor do the molars have more than a general and highly superficial resemblance to those of any rodents.

considered the Apatemyidae, and *Phenacolemur* among them, as either Insectivora or Primates.

Schlosser (1923) referred all Matthew's Apatemyidae, including *Phenacolemur*, to the Plesiadapidae and considered the whole group as ancestral or nearly related to the recent *Daubentonia* (or *Chiromys*, as it was usually called in the literature of that period). Abel (1931) accepted the essentials of Schlosser's arrangement, as did several other reviewers of early primates up to 1934 or later. (There are no first-hand publications on *Phenacolemur* except Matthew's original paper, Kelley and Wood, 1954, and the present paper.)

Jepsen (1934) showed that the Apatemyidae and Plesiadapidae are two quite different families and expressed the opinion that *Phenacolemur* does not belong to either one of them: "*Phenacolemur* itself presents a cluster of what may be regarded as family characters which exclude it from close relationship with either the Apatemyids or the Plesiadapids as defined above." Since then the few who have mentioned *Phenacolemur* at all and were not simply copying from Schlosser or Abel have generally been content to leave it as more or less *incertae sedis*. I (1945) listed it as doubtfully prosimian of otherwise unknown position, and Romer (1945) listed it with a question mark among the Anaptomorphidae.

Phenacolemur is certainly quite distinct from the Apatemyidae. Both groups have enlarged incisors and quadrate trigonids on M_{2-3} , but these are evidently convergent adaptations, and there are no other special

resemblances. The directions of specialization are so different and appear so early that a common ancestor would have to be an extremely primitive (or, in that sense, generalized) insectivore. The most radical specializations of the apatemyids are all absent in *Phenacolemur*, notably the very peculiar, blade-like P_3 and the reduction of P_4 . On the other hand the most obvious peculiarities of *Phenacolemur*, such as the enlargement of P_4 and the enlarged, basined upper molar talons, are quite opposite to the diagnostic trends of the apatemyids.

Phenacolemur resembles the middle Paleocene (Torrejonian) *Paromomys* more nearly than it does any other genus known to me. Resemblances include:

Enlarged pair of incisors

Teeth between large incisors and P_4 simple and in process of reduction

P_4 large but not molariform, with basined heel

Molar trigonids transverse and quadrate, especially on M_{2-3} which have the paraconid internal and twinned with the metaconid

Broad, basined talonids without hypoconulids

Large, bicuspid third lobe on M_3

P_4 large, submolariform but with barely rudimentary to small metacone

Upper molars quadrate but without hypocones, with talon basin enclosed by crest from protocone turning at a right angle in the usual place for a hypocone

These characters are so distinctive and so similar in the two genera that the conclusion that they are related is almost inescapable. On the other hand, the genera are decidedly distinct:

Paromomys

Teeth probably $\frac{?1.1.3.3}{1.1.1.3}$

Lower incisor root short

No lower diastema

Basin of P_4 narrow, on inner side of tooth only

Molar trigonids less compressed anteroposteriorly and with larger paraconids

Third lobe of M_3 with cleft distinctly dividing two cusps

Metacone indistinct on P_4

Talon basins on P_4 - M^3 small; not projecting posteriorly on M^3

Molar conules well defined

Upper molars grooved or bilobed on inner side

Phenacolemur

Teeth probably $\frac{?1.1.3.3}{1.0.1.3}$

Long

Long lower diastema

Wide, nearly or quite across greatest width of tooth

Strongly compressed; paraconids minute

Bicuspid, but separation of cusps obscure

Distinct, although very small in some species

Prominent talon basins on P_4 - M^3 , projecting far posteriorly on M^3

Ill defined

Flattened but not distinctly grooved or bilobed

In almost every one of these characters *Paromomys* is more primitive than *Phenacolemur*, that is, it is nearer the inferable ancestral primate or insectivore condition. With only minor possible exceptions (such as the last character listed), all the special characters of *Paromomys* are advances in the direction of *Phenacolemur*. *Paromomys* must in fact be rather closely related to *Phenacolemur* or must be paralleling the ancestry of the latter genus with extraordinary fidelity. There are few or no "crossing specializations" that would exclude *Paromomys* from the direct ancestry of *Phenacolemur*, and *Paromomys* (Torrejonian) is older than the earliest *Phenacolemur* (Tiffanian). It is, however, somewhat improbable that *Paromomys* is the literal and direct ancestor of *Phenacolemur*. The change may be too great for the relatively short lapse of time involved. It is, at any rate, somewhat greater than in more probably established ancestral-descendent Torrejonian-Tiffanian lines, such as *Elphidotarsius-Carpodaptes*, *Pronothodectes-Plesiadapis*, or *Jep-senella-Labidolemur*.

As elsewhere discussed (Simpson, 1937), the Torrejonian species *Paromomys maurus*, *Paromomys depressidens*, *Palaechthon alticuspis*, and *Palenochiha minor*, although they all occur in a single quarry, form a graded evolutionary series in many respects. The stated sequence is the order of decreasing size and, for many characters, of decreasing specialization. (See comparative figures, pls. 34 and 35.) There are minor exceptions, such as the presence of distinct paraconid and metaconid on P_4 of *Palaechthon*, which is presumably a more specialized condition than the simpler P_4 of *Paromomys* (and *Phenacolemur*). The generally most specialized or aberrant member of the sequence, *Paromomys maurus*, is the most like *Phenacolemur*. *Palaechthon* is less advanced in the direction of *Phenacolemur* and somewhat aberrant (espe-

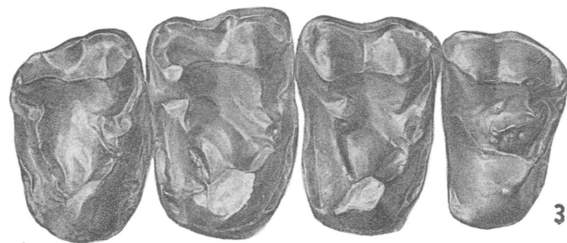
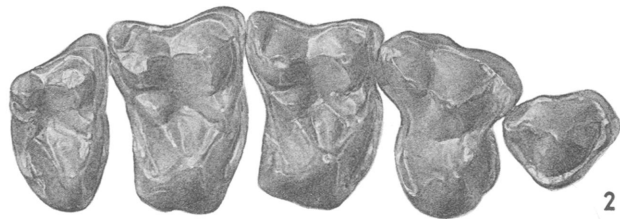
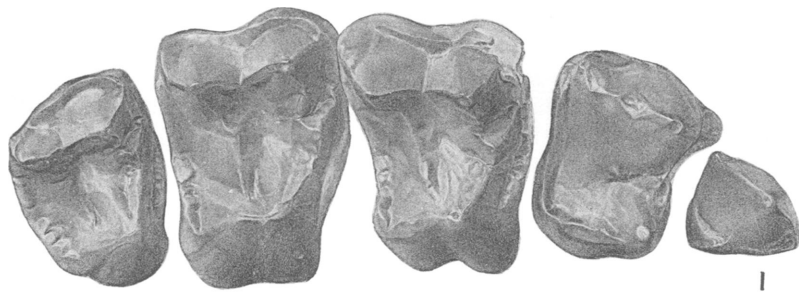
cially in P_4) with respect to that direction, yet it does seem to be a fairly close relative of *Paromomys* and does have some special *Phenacolemur*-like characters. *Palenochiha*, at the other end of the structural series, also seems to be tied in somehow by relationship to *Palaechthon*, but *Palenochiha* is almost devoid of really distinctive *Phenacolemur*-like specialization. Even though close to the ancestral structure of *Phenacolemur*, it could be about equally close to the ancestry of some other groups such as the Necrolemuridae or some of the Omomyinae. Those considerations underlie the entirely tentative and somewhat arbitrary inclusion of *Paromomys* and *Palaechthon* in the Phenacolemuridae and the exclusion of *Palenochiha*. Another possibly pertinent Torrejonian genus is *Plesiolestes* Jepsen, 1930, in which the lower teeth closely resemble *Palaechthon* but are perhaps a little less like *Paromomys* or *Phenacolemur* than is *Palaechthon*. Upper teeth of *Plesiolestes* are unknown.

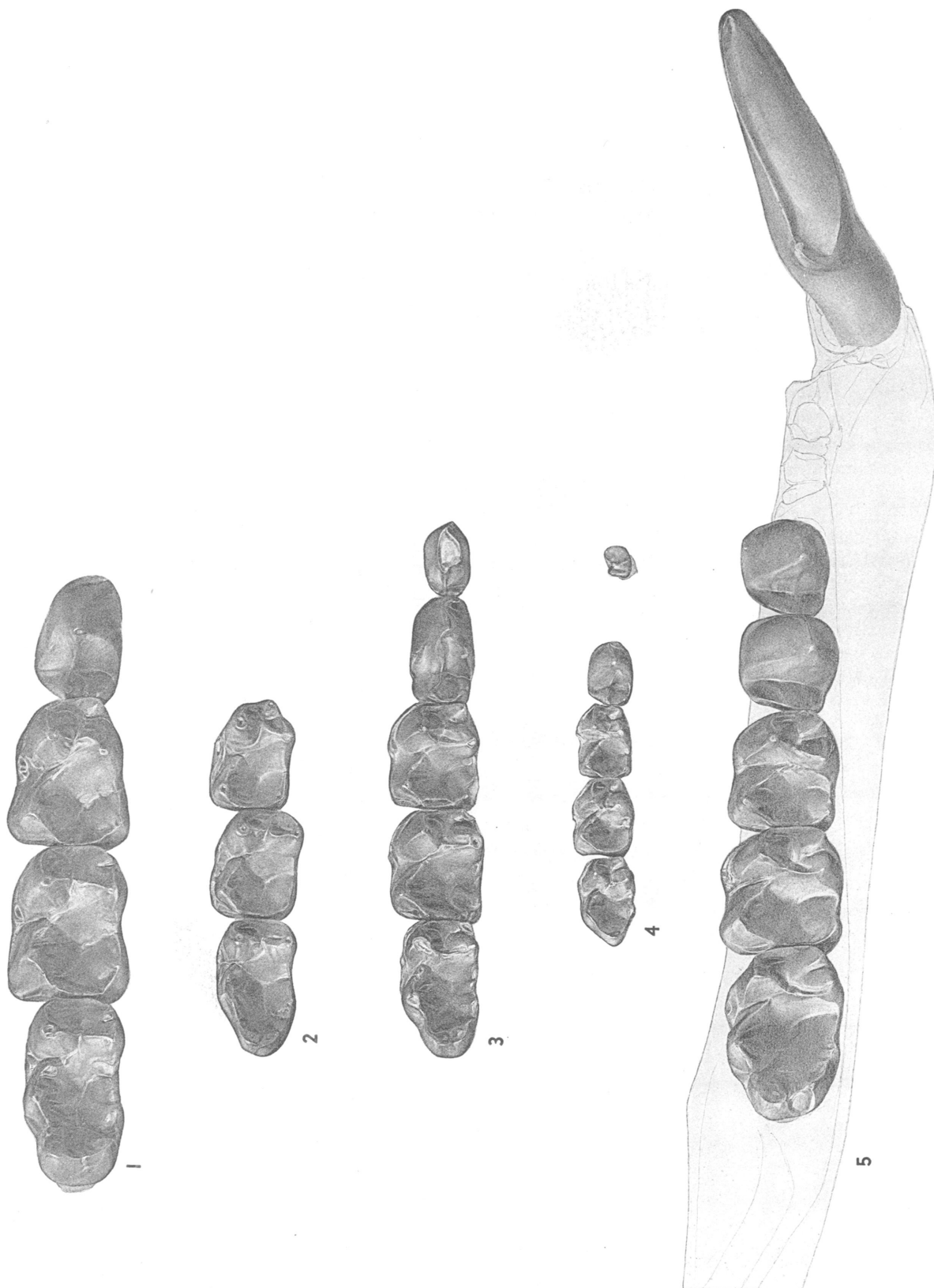
The Torrejonian structural series, although obviously not a phyletic sequence, shows how the generic peculiarities of *Phenacolemur* could have been derived from a more primitive and general, more or less omomyine-like middle Paleocene or earlier ancestry. The differences among, say, *Palenochiha*, *Paromomys*, and *Phenacolemur* definitely represent structural progression although, as earlier remarked, the differences known within the genus *Phenacolemur* do not. *Phenacolemur* is a specialized and (as far as known) terminal member of a progression that probably did depart from the same ancestry as the highly heterogeneous genera currently lumped in the Anaptomorphidae. If so, that ancestry could not yet have developed any of the special characters of *Paromomys* or *Phenacolemur*, on one hand, or of the Eocene omomyines and anaptomorphines on the other. It is on that basis

PLATE 34

Comparative series of upper teeth of middle Paleocene, Torrejonian, primates from the Lebo formation.

1. *Paromomys maurus* Gidley. A.M.N.H. No. 35574, right P^3-M^3 .
 2. *Palaechthon alticuspis* Gidley. A.M.N.H. No. 35483, right P^3-M^3 .
 3. *Pronothodectes matthewi* Gidley. A.M.N.H. No. 35463, P^4-M^3 , left in actual specimen, drawn in mirror image as if from right side for comparison.
- All crown views, nine times natural size.





that family status for the Phenacolemuridae seems justified and most convenient.

At least two other lines deriving from the basic prosimian complex evolved with some parallelism to the Phenacolemuridae: the Necrolemuridae and the Plesiadapidae. As is clear by comparison with Hürzeler's (1948) careful figures and descriptions of the Necrolemuridae, although there is considerable parallelism with the Phenacolemuridae, there can be no serious question of immediate phyletic relationship. For instance: the Necrolemuridae developed no diastemata; the third lobe of M_3 remained much smaller than in the Phenacolemuridae; the talon basin remained small and was bounded by a cingulum that was distinct from the "Nannopithecus-fold," which corresponds more or less with the crest bounding the talon basin in the Phenacolemuridae; and there was a tendency to emphasize and reduplicate, rather than to reduce, conules and secondary cusps. Parallelism of the Phenacolemuridae with the Plesiadapidae was also rather close, but it clearly was parallelism and not a more intimate genetic relationship. The earliest plesiadapid, *Pronothodectes*, already had characters that were unlike those of *Paromomys* or *Phenacolemur* and that were destined to continue to distinguish the families, such as the strong conules (including one on P_4) and the small talon basin with incipient hypocone.¹ (See pl. 34, fig. 3, and pl. 35, fig. 5.)

¹ Some point has been made (by Stehlin, Gregory, and Hürzeler, among others) of a belief that in some primates (e.g., Adapinae, Necrolemuridae) a "true" hypocone arises from a cingulum, while in others (e.g., Notharctinae, Plesiadapidae) a "pseudohypocone" or "pseudypocone" arises from the protocone or the "Nannopithecus-fold." The precise way in which a postero-internal cusp arises undoubtedly may have a bearing on

The Phenacolemuridae show other, eclectic resemblances in single characters to diverse Eocene prosimians. The structure of P_4 is much as in *Omomys*. M_3 is more or less like that of *Washakius*. The upper molars and M_2 have suggestive resemblances to those of *Absarokius*. Furthermore, the molar dentition of *Paromomys* and also that of *Phenacolemur* (if its more aberrant specialization be discounted) has considerable and even detailed similarity to that of the most primitive Notharctinae such as *Pelycodus ralstoni* or *trigonodus*. The latter species may even have the upper external molar cingulum as in *Phenacolemur pagei*. In *Pelycodus* the spur on the cingulum is a presage of a mesostyle developed in more advanced species and in *Notharctus*. In *Phenacolemur* it is a specific character of *pagei*, absent in other known species and apparently leading nowhere. There is, in any case, no possibility of really close

the affinities of a group. I strongly question, however, whether independent origin of the cusp from, say, a cingulum in two different groups makes it in an objective sense any more the "same" cusp than if it arose in the same place but not from a cingulum. I further question whether there is a clear-cut and always significant difference between a hypocone and a pseudypocone, as defined. In *Pronothodectes* the "Nannopithecus-fold," which is poorly developed, runs straight posteriorly and dorsally from the protocone apex and meets a horizontal posterior cingulum at right angles. The fold and cingulum may be continuous with each other and so may be considered nominally one crest, approximating the condition in *Phenacolemur* or, more closely, *Paromomys*. There may, however (cf. M^2 of A.M.N.H. No. 35463), be a cusplike bulge or apparent continuation of the cingulum internal to its juncture with the "Nannopithecus-fold." It is in the region of that juncture that the postero-internal cusp of more advanced *Plesiadapis* arises. Whether the cusp originates from the "Nannopithecus-fold" and is a "pseudypocone" or from the cingulum and is a "hypocone" seems to me a distinction without a difference.

PLATE 35

Comparative series of lower teeth of middle Paleocene, Torrejonian, primates from the Lebo formation.

1. *Paromomys maturus* Gidley. A.M.N.H. No. 35609, left P_4 - M_3 .
 2. *Paromomys depressidens* Gidley. A.M.N.H. No. 35552, left M_{1-3} .
 3. *Palaechthon alticuspis* Gidley. A.M.N.H. No. 35484, left P_3 - M_3 .
 4. *Palenochtha minor* (Gidley). A.M.N.H. No. 35451, P_2 (trigonid broken off to base) and P_4 - M_3 , right in actual specimen but drawn in mirror image as if from left side for comparison.
 5. *Pronothodectes matthewi* Gidley. A.M.N.H. No. 35462, left I and P_3 - M_3 .
- All crown views, nine times natural size.

relationship between Notharctinae and Phenacolemuridae because of the totally different trends in the antemolar region. Nevertheless the general resemblances and even such manifestly independent developments as the cingulum spur or incipient mesostyle in *Pelycodus* and in *Phenacolemur pagei* suggest the sharing of elements from a common genetic source.

BROADER AFFINITIES AND COMMENT ON PROSIMIAN CLASSIFICATION

The evidence strongly suggests that *Phenacolemur* is the terminal member of a rapidly specialized offshoot from the same basic stock that gave rise to the Omomyinae, Necrolemuridae, Plesiadapidae, Notharctinae, and probably also the Anaptomorphinae, Adapinae, and a variety of genera of even less clearly established supergeneric position. Adaptive resemblance to the Apatemyidae is considerable, but genetic affinity is probably more distant. There is little special resemblance either adaptive or putatively genetic to the Carpolestidae.

The separate questions of the affinities of the Apatemyidae and Carpolestidae may be set aside. On present evidence, the Phenacolemuridae should be broadly grouped with the other families and subfamilies named above. All are usually considered Primates, but for the more aberrant of them, at least, the question arises whether they are "really" Primates, and the question has more insistently arisen for the particularly aberrant *Phenacolemur*. In fact, the question whether or not the various more or less primate-like Paleocene-Eocene groups were "really" primates, or even whether or not certain recent groups are, does not make sense when put in just that way. Some orders have key characters or a basic adaptive pattern sufficiently distinctive that the fixation of that character or pattern constitutes the origin of the order and gives (except for a possible few rapidly transitional forms) a definite criterion as to whether a given animal did or did not belong to the order. It does make sense, for instance, to ask whether *Zanycteris* was really a bat or *Phenacodaptes* was really an artiodactyl. *Zanycteris* was really a bat if it had a wing (a point on which there is at present no real evidence), and *Phenacodaptes* was really an

artiodactyl if it had a double-pulley astragalus (a point on which there is no direct evidence but which indirect evidence opposes). No such criterion exists for the rise of Primates from Insectivora. The differentiation of the two orders was gradual, among a multitude of lineages which display a sort of continuous spectrum of resemblances and differences in diverse characters and no threshold or marked and definable shift of adaptive type.

Whether a given group of animals is to be called primate or insectivore depends on how we choose to evaluate a balance of resemblances and differences. To the extent that the evaluation can be phylogenetic, it depends on how far back into the multiple basic branching of the protoprimates or preprimates we care to go. A slight broadening of the balance or deeper delving into the ancestry led Le Gros Clark (1934) to include the Tupaiidae in the Primates. Further extension could well bring in such groups as the Macroscelididae, the Leptictidae, and even the Erinaceidae.

Various solutions of the problem of giving a clearly differential definition of the Primates have been suggested, but they are all arbitrary and not really diagnostic or are equally unsatisfactory on other grounds. One suggestion is to put the groups that are usually called insectivores but that could be called primates in a third order, which can be designated Menotyphla. The result is simply that no useful and significant diagnosis can distinguish between any two of the three orders. Another suggestion is to cut off the Order Primates where there is, indeed, a fairly definite shift of structural and adaptive level, at the base of the Anthroipoidea (as a group including true monkeys, apes, and men). Then, however, the Primates = Anthroipoidea are almost certainly polyphyletic, derived from at least two and possibly three or more different lines of prosimians that are not Primates by that definition. That is not too bad a practical solution, because the various ancestral lines were doubtless rather closely related, and completely monophyletic origin for each unit is frequently an unobtainable ideal in classification. But it provides no solution to the original problem, which was the distinction of the prosimians from the

insectivores. If only the Anthropeidea are called Primates, then the prosimians must be included in the insectivores, an arrangement that would surely be unsatisfactory to almost all students of the subject, or they must form an Order Prosimii, which still cannot be clearly defined as against Insectivora.

The entity Prosimii (whatever its taxonomic rank) is "real": it represents a broadly genetic and adaptive group of animals markedly different from, say, the shrews and moles and distinctly related, both genetically and adaptively, to the monkeys, apes, and man. It is not, however, clear cut, and it is merely futile to attempt a sharp diagnosis where no sharp distinction has ever existed in nature.

To return to the Phenacolemuridae, it has been indicated above that they seem to be Prosimii on the evidence of fairly immediate common ancestry with better known lineages that are, at present, always included in the Primates and Prosimii on an impressive balance of genetic characters. In the Phenacolemuridae themselves, non-dental characters that weigh most heavily in balancing between Insectivora and Primates are mostly unknown, notably the carotid circulation, ectotympanic, and postorbital bar. It can at least be said that no character mainly prosimian at a basic level is known to be *absent* in *Phenacolemur*. It is known that the genus had an ossified bulla, which of course is not diagnostic but is rather more suggestive of the prosimians than not. Further, established resemblances are closer to groups quite definitely considered Prosimii than to groups of more seriously questioned position such as the Tupaiidae, Apatemyidae, or Carpolestidae, or to any generally referred to the Insectivora such as the Macroscelididae, Mixodectidae, or Leptictidae.

An attempt to place the Phenacolemuridae more precisely within the Prosimii runs up against the fact (it is increasingly evident that it is a fact) that the current classifications are all impractical and unrealistic when early forms are taken into account. On the basis of the living prosimians, the Prosimii have long been and are now universally divided into at least two main groups: Tarsiiformes and Lemuriformes, under those or

other names such as Tarsiioidea and Lemurioidea. A third group, Lorisiformes, is frequently included in the Lemuriformes but also frequently given coordinate rank, the fact being that in ear structure, which involves some of the most striking differences between Tarsiiformes and Lemuriformes, the Lorisiformes are markedly distinct from the Lemuriformes and also, but less, different from the Tarsiiformes. Many taxonomists have recognized a fourth major group that is sometimes called "Chiromyiformes" but would more properly be "Daubentonii-formes" if distinguished at all at this level. That group was based on the aberrant, rodent-like habitus of *Daubentonia* and on the belief that separation of its lineage had already occurred in the Paleocene among the Plesiadapidae (*sensu lato*).

It is now beyond reasonable doubt that the Plesiadapidae and the various other early groups formerly confused with that family were not ancestral or particularly related to *Daubentonia*. They represent merely the independent acquisition of a general habitus rather common among early primates and more or less primate-like insectivores but, as it happens, absent among recent primates except *Daubentonia*.¹ Except for its special adaptive characters, *Daubentonia* fundamentally and specially resembles the Lemuridae, and there is little doubt that it had a common origin with the other Malagasy prosimians and in all probability in Madagascar. *Phenacolemur*, which was also formerly confused with the Plesiadapidae, is probably really more closely related to them than to *Daubentonia* and in any event had no more than they to do with the ancestry of *Daubentonia*. The "Chiromyiformes" are thus rejected as a major subdivision of Prosimii and would not, even if accepted, be the

¹ It is a reasonable speculation to relate these facts to the evolution of early rodent-like primates and insectivores at a time before or during the earliest deployment of the true rodents. In normal later faunas the niches are occupied, or lethally overlapped, by the rodents. The Malagasy fauna is not normal and is notably deficient in rodents, with only 14 recent species (some of which may be subspecies) covering a limited, mostly rat-like, adaptive range. It is not surprising that the abundant and plastic Malagasy prosimians should again evolve a rodent-like form in the absence of serious rodent competition.

phylogenetically proper place for the Phenacolemuridae.

The Tarsiiformes, Lorisiformes, and Lemuriformes seem to me to be valid and approximately coordinate phylogenetic units among the recent prosimians. The usual assumption has been that the Lorisiformes either belong among or were derived from the Lemuriformes, and it has been the usual or indeed universal practice to distribute the Paleocene-Eocene primates in the Tarsiiformes and Lemuriformes. Although I have expressed misgivings (e.g., Simpson, 1940, p. 197), I also have previously followed that usual practice (e.g., Simpson, 1945). I now think it must be abandoned.

The majority of Eocene genera have at one time or another been considered "tarsioid." Restudy of some, especially those represented by skulls or other relatively good material, has resulted in their transfer to the "lemuroids." *Caenopithecus* (see Stehlin, 1916), *Pronycticebus* (see Le Gros Clark, 1934), *Anchomomys* (see Simpson, 1940), *Nannopithecus*, *Necrolemur*, and *Microchoerus* (see Hürzeler, 1948) are examples particularly to the point.¹ Still the mass of "Anaptomorphidae" (probably not a natural family even after recent removals) has continued to be labeled "tarsioid." The fact is that there is no convincing evidence that any early primate is more "tarsioid" than "lemuroid" in natural affinities. The mooted "tarsioid" characters are some features of the cheek dentition, characters for the most part merely primitive for prosimians and now known (as in the genera just named) to be of possible association with "lemuroid" skulls; enlargement of the orbits (e.g., in *Tetonius*), which does not reach the *Tarsius* extreme or resemble it in detailed anatomy and which has certainly occurred independently in many primates, especially those that became nocturnal; and in a few cases elongation of the tarsus, which again is not demonstrably like *Tarsius* in extent or detail, which also occurs among "lemuroids" (or, notably, Lorisiformes, and also among nominal insectivores), and which in some instances at least (e.g., *Hemiacodon*)

is different from the truly tarsioid trend and quite surely independent.

Classifications of Paleocene-Eocene primates (including those by me) have largely merited the stricture by Hürzeler (1948): "Wer diese neuere Literatur [Depéret, Teilhard, Gregory, Ossenkopp, Abel, Simpson] über die fossilen Primaten erfolgt, kann sich des peinlichen Eindrucks nicht erwehren, dass gelegentlich nicht so sehr sachliche Erwägungen, sondern eigentliche Modeströmungen für die systematische Einreihung der verschiedenen Formen massgebend waren." Hürzeler further truly remarks that "Das Beispiel der Necrolemuriden zeigt, wie unheilvoll das Hineinzwängen von fossilen Genera in das System der rezenten Primaten sein kann." The point would have been more fully made if Hürzeler had made that as a flat statement, without adding "wenn wichtige Teile der Organisation noch nicht genügend bekannt sind," and if he had not himself still inserted the Necrolemuridae "in das System der rezenten Primaten," only transferring them from Tarsiiformes to Lemuriformes. In fact their "lemuroid" characters are probably merely primitive for all prosimians and not diagnostic features relating them in a special and phylogenetic way to recent lemuroids. (Indeed, the tympanic is "lemuroid," the carotid circulation is "tupaoid," and the dentition is *sui generis*.)

Many or most of the Paleocene-Eocene primates may have more nearly resembled the recent lemuroids than the recent tarsioids, but probably just to the extent that the living lemuroids are on the whole less aberrantly specialized than is *Tarsius*, or at least include genera less specialized in one feature or another. To call Paleocene-Eocene groups Lemuriformes, even in the cases of the most *Lemur*-like forms such as *Adapis*, may well be simply to extend the concept of Lemuriformes to include not only the diagnostically specialized recent lemuroids and their ancestry and specially phylogenetic specialized relatives but also virtually all primitive prosimians. The usage is defensible if so understood, but becomes confusing where it is necessary to include groups like the Necrolemuridae (or the Phenacolemuridae, for that matter) that were specializing in their own way

¹ All the genera named are, for instance, "Tarsiioidea" in Abel, 1931.

and certainly have no particular connection with any recent or true lemurs.

At present the most likely tentative conclusion from the admittedly very incomplete knowledge of Paleocene-Eocene primates is that they include a large number of lines all radiating from an unspecialized basic stock, each line becoming specialized in its own way. The complex is not meaningfully to be classified into two or a few larger groups, because there is little or no special relationship among different lines except through the undifferentiated ancestry of all of them. The later Cenozoic lemuroids, lorisoids, and tarsiods represent further specialization and (for the first two named) diversification from three (probably, or possibly one or two more) of the Paleocene-Eocene radiating lines. To label any but those actually ancestral lines either "lemuroid" or "tarsioid" is probably quite meaningless. That conclusion applies forcefully to the Phenacolemuridae, a divergent group not conceivably ancestral to any in the later Cenozoic.

This opinion regarding the Paleocene-Eocene primates of course bears on the long discussion of whether the ancestors of the higher primates were tarsiod, lemuroid, or something else. It seems probable or is, at

least, a good hypothesis on present evidence that the ancestors of the Anthroidea were not in any meaningful sense either tarsiods or lemuroids but were two or three of the numerous diverging Paleocene-Eocene lineages distinct from an early (say, middle Paleocene) date. In other words, the Order Primates does not seem to have split into two (or a few) suborders, infraorders, or other major subdivisions from one or another of which the late forms arose. It seems, rather, to have split into a large number of divergent, progressing lineages, symbolizable especially as families or subfamilies, among which some five or six survived and separately gave rise to the later Cenozoic (Oligocene-Recent) Primates. Not a single one of those ancestral lineages has been surely identified in the Paleocene or Eocene. (They may well have lived in regions now tropical, from which Eocene mammals are virtually unknown.) The known Paleocene-Eocene groups do, nevertheless, cast light on the origins of higher primates. Some may, indeed, prove to be ancestral groups or closely related to such. In any event they do, in sum, indicate the generally primitive characters for Primates and the levels of progression reached in the Paleocene and Eocene.

SUMMARY

THE TIFFANIAN through Wasatchian North American genus *Phenacolemur* represents a highly distinctive group here defined as a family: Phenacolemuridae. The Torrejonian genus *Paromomys*, although more primitive than *Phenacolemur*, foreshadows most of its peculiarities and is tentatively placed in the same family. The likewise Torrejonian *Palaeochthon*, although less like *Phenacolemur*, seems to be related to *Paromomys* and is still more tentatively referred to the family. *Palenochtha* and *Plesiolestes* may possibly also belong in this general group, but are not now referred to it.

Phenacolemur, as now known, includes four species: Tiffanian *P. frugivorus* and *P. pagei* and Wasatchian *P. praecox* and *P. jepseni*. *Phenacolemur praecox* is heterogeneous, but included taxa cannot be sharply distinguished by available samples. There is some suggestion of distinguishable early populations of larger and later of smaller individuals in the Willwood formation, and these are tentatively redefined as subspecies.

There is no evident progressive tendency among the species of *Phenacolemur*. They

represent non-progressive deployment within an early established and specialized generic pattern. The generic pattern of the dentition is characterized especially by a nipping pair of incisors, reduction of other teeth anterior to P_4^4 , retention and enlargement of P_4^4 , short, transversely quadrate molar trigonids, great development of a third lobe on M_3 , and development of a talon basin but no hypoconid on M_1^{1-2} .

The Phenacolemuridae represent a sharply distinct special group or line, extinct without issue, and with eclectic resemblances suggesting origin from the same unspecialized ancestry as the Omomyinae, Notharctinae, Plesiadapidae, Necrolemuridae, and others. On this basis, the Phenacolemuridae are considered Primates and Prosimii. The advisability or, indeed, possibility of dividing Paleocene-Eocene Prosimii into Tarsiiformes (or Tarsiioidea) and Lemuriformes (or Lemuroidea) is strongly questioned. The Phenacolemuridae are considered one of many divergent, extinct early families that do not properly belong in either of those later Cenozoic groups.

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