SYSTEMATICS, PHYLOGENY, AND EVOLUTION OF EARLY EOCENE ADAPIDAE (MAMMALIA, PRIMATES) IN NORTH AMERICA

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Abstract.– Several large new collections of early Eocene Adapidae have been made in recent years from stratified sediments in the Big Horn Basin of Wyoming. These collections permit a much more detailed reconstruction of the evolutionary history of the genus *Pelycodus* than was previously possible. Restudy of the described collections of early Eocene Adapidae indicates the following taxonomic modifications: *"Pelycodus" tutus* Cope is made the type of a new genus *Copelemur*, which includes also *C. praetutus, C. feretutus* (nov.), and *C. consortutus* (nov.). Restudy of New Mexico fossils from the Largo and Almagre facies indicates that *Pelycodus jarrovii* and *Pelycodus frugivorus* are senior synonyms having priority over *P. venticolis* and *P. nunienus*, respectively, from the Lost Cabin beds of Wyoming. Four additional North American species of *Pelycodus* are recognized: *P. ralstoni, P. mckennai* (nov.), *P. trigonodus,* and *P. abditus* (nov.).

A single lineage of *Pelycodus* is known from Sand Coulee, Graybull, and Lysite beds, but in Lost Cabin beds two lineages are known that were both almost certainly derived from the Lysite species *Pelycodus abditus*. Samples of species from successively higher stratigraphic horizons are progressively larger, until the second lineage of *Pelycodus* appears, after which one lineage begins to decrease in size while the other continues to increase. This is interpreted as a probable result of character divergence in body size to minimize competition between the two sympatric species. The mesostyle and hypocone become progressively larger through time in *Pelycodus*. The evolution of *Pelycodus* appears to be continuous and gradual from the earliest to the latest species.

Pelycodus jarrovii is perfectly intermediate between earlier *Pelycodus* and later *Notharctus*, showing that the generic transition from one to the other was also both continuous and gradual. The fossil record is now sufficiently complete that the boundary between *Pelycodus* and *Notharctus* is necessarily arbitrary. One morphological characteristic, acquisition of symphyseal fusion, appears to coincide approximately with the Wasatchian-Bridgerian (early Eocene-middle Eocene) boundary. The evolution of early Eocene *Copelemur* appears to have paralleled that of *Pelycodus*, but detailed evidence is not yet available. The origin of middle Eocene *Smilodectes* is not yet clear, but an origin from *Pelycodus frugivorus* or *Pelycodus jarrovii* appears likely.

INTRODUCTION

Pelycodus is the earliest member of the primate family Adapidae. It is known from North America and from Europe. *Pelycodus* appeared on both continents at about the same time – early in the Ypresian in Europe, and at the beginning of the Wasatchian in North America. On the basis largely of the presumed relationship of Adapidae to Lemuroidea and Lorisoidea, it has been suggested that Adapidae possibly originated in Africa (McKenna, 1967, *et al.*). However, the primate fossil record of Africa is still very limited. In Eurasia, all of the Eocene Adapidae appear possibly to have been derived from *Pelycodus* (Gingerich, 1977a,b), and the same can be said of the Adapidae found in North America. The North American adapid subfamily Notharctinae evolved independently of the European subfamily Adapinae, but both can be traced back to the common ancestral genus *Pely-codus*. Opening of the North Atlantic Ocean in the early Eocene (McKenna, 1975) appears to have been responsible for this geographic separation and independent evolution.

Pelycodus is important for another reason. It has one of the best stratigraphic records of any mammal yet studied, and it thus provides additional perspective on evolutionary patterns in mammals. To understand the evolution of a mammalian lineage through a significant amount of geological time requires (1) a sound stratigraphical framework based ultimately on measured stratigraphic sections, (2) a detailed study of the distribution of variation of morphological characteristics within each fossil sample, and (3) integration of all fossil samples into the given stratigraphic framework. This "stratophenetic" approach to the study of phylogeny and evolution is discussed at greater length in Gingerich (1976b). Without going into details of the method, we shall employ it here and amply demonstrate its utility – where the fossil record is as dense and continuous as it is for North American *Pelycodus*, a stratophenetic approach yields an almost direct reading of genealogical relationships and the evolution of morphological adaptations.

We first outline the stratigraphic and geographic framework for this study, describe dental variation in *Pelycodus*, review and revise the systematic nomenclature of early Eocene Adapidae, and in the final section consider evolutionary patterns in the evolution of North American *Pelycodus* and *Copelemur* with a brief consideration of the origin of middle Eocene *Smilodectes* and *Notharctus*.

Abbreviations used herein are as follows: ACM, Pratt Museum of Geology, Amherst College (Amherst, Mass.); AMNH, American Museum of Natural History (New York); KU, University of Kansas Museum of Natural History (Lawrence); PU, Princeton University Museum of Natural History (Princeton, N. J.); UCM, University of Colorado Museum (Boulder); UM, University of Michigan Museum of Paleontology (Ann Arbor); USNM, National Museum of Natural History, Smithsonian Institution (Washington); UW, University of Wyoming Geological Museum (Laramie); and YPM, Yale Peabody Museum (New Haven, Ct.).

STRATIGRAPHIC AND GEOGRAPHIC FRAMEWORK

The stratigraphic framework for this study was outlined in Gingerich (1976a, p. 4-9). To review and bring that summary up to date, in 1962 one of us (E. L. S.) began an intensive annual summer program to collect fossil mammals in the lower Eocene Willwood Formation of the central Big Horn Basin in northwestern Wyoming. Most of these collections came from a geographic area some 40 km by 50 km on a side. All mammals collected up to, and including, 1973 are in the collection of the Peabody Museum of Natural History at Yale University. In 1974, a joint Yale University-University of Michigan team under the direction of the authors continued this work in the central Big Horn Basin. All mammal fossils collected in 1974 (except the primates, which are at Yale) are in the collection of the Museum of Paleontology at the University of Michigan. Collections made by Yale

University parties subsequent to 1974 have not been included in this report. A small collection of Lysite mammals was made by a University of Michigan field party in 1976 in the vicinity of Red Butte in the central basin, part of which has been included in this study. To date, a total of over 400 fossil localities (numbered from 1-434) have been discovered in the central Big Horn Basin.

In 1965, Grant E. Meyer and Leonard Radinsky measured a stratigraphic section approximately 1800 ft. (550 m) thick across the entire study area. This section forms the basis for most of the analysis of *Pelycodus* presented here. Some 84 localities were tied directly into the original section by Meyer and Radinsky. Another section measured subsequently by Neasham and Vondra added 19 more localities to the basic section. The remainder of the localities yielding *Pelycodus* that are included in this analysis were interpolated into the basic section using *both* geographic proximity to localities already in the basic section and comparison of the average size of the given *Hyopsodus* sample to that from nearby localities. The final complete stratigraphic sequence of localities is given in Gingerich (1976a, fig. 2). In 1976, David Shankler and Scott Wing of Yale University began measuring new stratigraphic sections in the central Big Horn Basin to correlate all of the fossil localities on the basis of stratigraphy alone. Thus, hopefully, there will be no need in the future to interpolate localities based on the morphology of *Hyopsodus*. The new stratigraphic study is unlikely to change our understanding of the relative position of localities very significantly, and we have thus continued to use the basic sections measured earlier by Meyer and Radinsky.

Some results are included here based on recent work by 1975 and 1976 University of Michigan field parties working in the Sand Coulee area of the Clark's Fork River drainage in the northern Big Horn Basin. All of the described specimens of Sand Coulee *Pelycodus* came from localities actually in measured stratigraphic sections.

The geographic distribution of North American localities yielding *Pelycodus* is shown in text-fig. 1. The areas yielding the biggest collections are the San Juan Basin of New Mexico; the Four Mile area in northern Colorado (McKenna, 1960); the Washakie Basin (Gazin, 1962; Savage *et al.*, 1972); the Wind River Basin (Guthrie, 1967, 1971); the Big Horn Basin and the Powder River Basin (Delson, 1971) of Wyoming. A small collection of *Pelycodus trigonodus* from the Golden Valley Formation in southwestern North Dakota (Jepsen, 1963) is the only North American sample from outside of the map area shown in text-fig. 1.

During the Paleocene and Eocene, erosion of the mountains and aggradation of the basins in western North America kept pace and maintained a fairly mature topography (Van Houten, 1944). Thus, there was relatively little faunal endemism within sedimentary basins. The species of *Pelycodus* from New Mexico appear to have been virtually identical to their correlative counterparts in Wyoming, and there is no evidence that any part of the known geographic range of North American *Pelycodus* was isolated for a significant time from any other part (although some disruption of large populations by rivers and other natural barriers was probable; also, as mentioned above, European species of *Pelycodus* were early isolated from the North American species). Wherever they have been studied to date, North American species of *Pelycodus* appear to fit into the patterns presented here based on Big Horn Basin collections. *Copelemur* appears also to have had a broad geographic distribution in North America (it is not known from Europe), but *Copelemur* is most common in southern faunas. It became established in the Big Horn Basin only during the latter part of the Lysite and early Lost Cabinian. Climate and ecology were undoubtedly responsible for the more limited distribution of *Copelemur*.

DENTAL VARIATION IN *PELYCODUS*

The dentition is probably the most important single anatomical system in living mammals for systematic and evolutionary study. Most living mammals can be identified to genus or species from
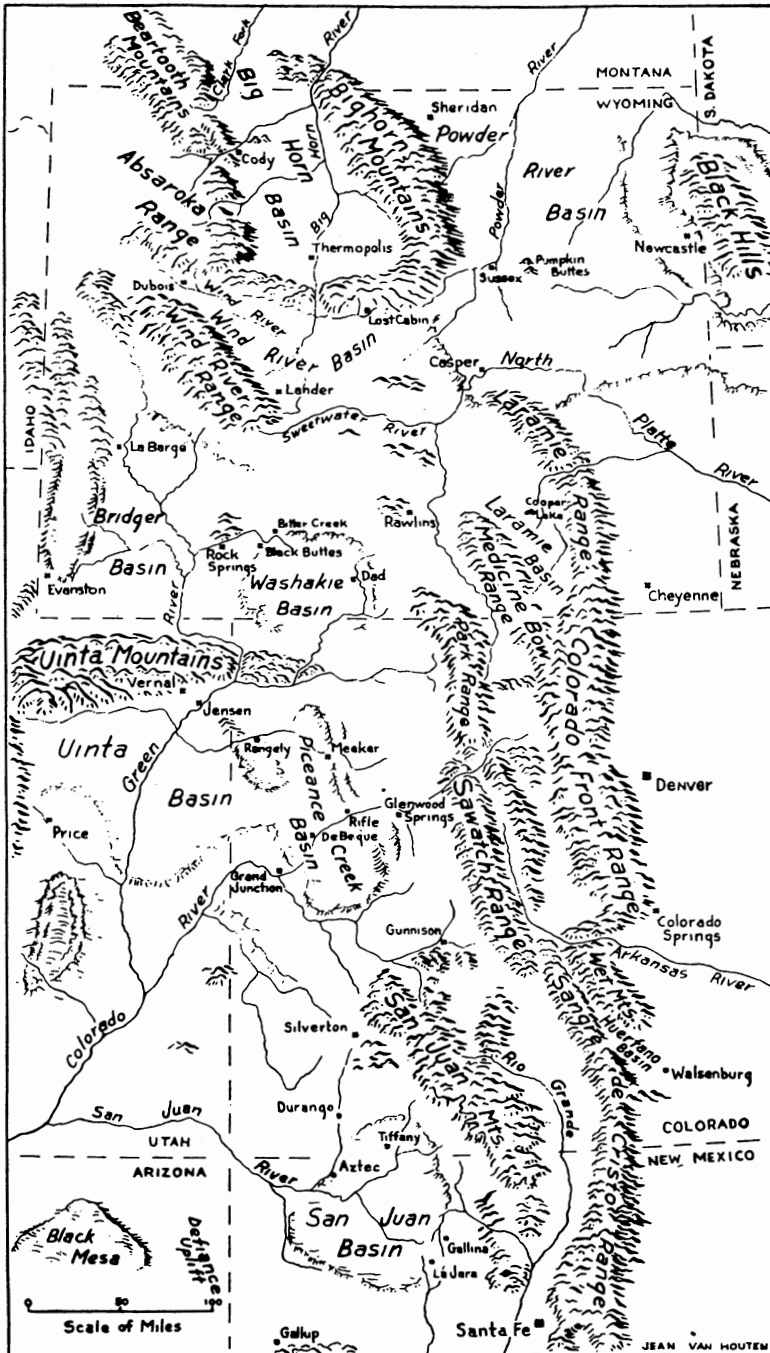
TEXT-FIG. 1 – Sketch map of Rocky Mountain intermontane basins in the western United States, showing the geographic position of localities mentioned in the text. *Pelycodus* is also known from North Dakota, and it gave rise to a major radiation of Adapidae in Europe. The occurrence of some of the same species in localities ranging from the Big Horn Basin to the San Juan Basin suggests that early Eocene populations of *Pelycodus* enjoyed a broad pangeographic distribution possibly covering most of the western United States. Figure from Van Houten (1945).

TABLE 1 — Summary of measurements of the lower and upper cheek teeth of *Pelycodus ralstoni* from University of Michigan Locality SC-4 in the Sand Coulee area, northern Big Horn Basin, Wyoming. M. Depth is depth of mandibular ramus measured below M_1; L, length; W, width; n, sample size; OR, observed range; x, sample mean; s, standard deviation; V, coefficient of variation; V*, coefficient of variation of log (L x W) at each tooth position. Measurements in mm.

		n	OR	$\overline{x}$	s	V	V*
P_3	L	2	2.7–2.9	2.80	.14	5.1	12.1
	W	2	1.9–2.4	2.15	.35	16.4	
P_4	L	10	2.9–3.5	3.14	.21	6.7	5.8
	W	10	2.3–2.9	2.46	.18	7.2	
M_1	L	16	3.4–4.0	3.67	.14	3.8	3.3
	W	16	2.9–3.6	3.14	.19	5.9	
M_2	L	20	3.5–4.0	3.71	.16	4.3	3.3
	W	20	3.2–3.8	3.44	.16	4.7	
M_3	L	5	4.7–5.2	4.90	.24	4.8	3.0
	W	8	3.0–3.4	3.11	.15	4.7	
M. Depth		14	7.0–8.5	7.69	.46	6.0	--
P^3	L	4	3.0–3.2	3.08	.10	3.1	—
	W	4	3.3–3.6	3.45	.13	3.7	
P^4	L	4	3.0–3.6	3.38	.26	7.8	—
	W	4	4.1–4.8	4.45	.31	7.0	
M^1	L	4	3.5–3.7	3.60	.08	2.3	—
	W	4	5.0–5.4	5.23	.21	3.9	
M^2	L	8	3.6–3.8	3.64	.07	2.0	—
	W	8	5.5–6.2	5.93	.26	4.3	
M^3	L	3	2.8–3.2	3.00	.20	6.7	—
	W	3	4.3–4.9	4.67	.32	6.9	

their teeth alone. Thus the fact that many fossil mammals, including *Pelycodus* and *Copelemur*, are known primarily from their teeth and jaws is not the handicap for systematic and evolutionary studies that it might at first appear to be. Other anatomical systems in these extinct genera, for which we have little or no knowledge, were undoubtedly evolving along with the dentition. However, if only one anatomical system could be chosen for evolutionary study, the dentition would probably be the first choice, and it is indeed fortunate that this is the system preserved in the fossil record. Teeth are involved in the mastication of food, and the complicated pattern of cusps and crests characteristic of the teeth of different mammalian groups reflects the dietary preference of the group as

TABLE 2 — Summary of measurements of the lower cheek teeth of *Pelycodus mckennai* sp. nov. from Yale Locality 363 in the central Big Horn Basin, Wyoming. Abbreviations as in Table 1. Measurements in mm.

|		n	OR	$\bar{x}$	s	V	V*
P_3	L	6	2.8–3.1	2.93	.12	4.1	
	W	6	2.0–2.3	2.17	.10	4.8	4.5
P_4	L	11	3.1–3.6	3.36	.17	5.2	
	W	10	2.3–2.8	2.56	.16	6.4	5.4
M_1	L	16	3.7–4.3	3.98	.16	4.0	
	W	15	2.9–3.7	3.34	.23	6.8	3.9
M_2	L	19	3.8–4.5	4.03	.18	4.5	
	W	20	3.4–4.1	3.76	.18	4.7	3.1
M_3	L	14	4.8–5.7	5.31	.28	5.3	
	W	15	3.0–3.7	3.36	.18	5.3	3.1

well as its heritage. The fact that there is a single definitive set of permanent teeth that form within the jaw before they erupt is of great importance because it removes the necessity to correct tooth measurements for ontogenetic change in size. Within groups of related mammal species, body size is highly correlated with tooth size. In primates, for example, the correlation of tooth length with body weight has been estimated at .956 by Kay (1975), and similar values obtained for other tooth size/body size correlations in mammals (Gould, 1975; Gingerich, 1976b). Tooth size, like body size, varies within recognized limits within a living species, and this variance has a high additive genetic component (i.e., high heritability, Bader, 1965). In sum, the insight that teeth offer for comparisons of changes in body size, and for study of dietary adaptations make them ideal for detailed evolutionary studies.

We have measured all of the teeth from two of the largest samples of *Pelycodus* from single localities, and these measurements are summarized in Tables 1 and 2. The coefficient of variation of tooth size in these single locality samples is well within the range of variability of living primates (Gingerich, 1974).

The distribution of variation in size of the first lower molar in three fossil samples is compared to the distribution in two living species in text-fig. 2. The major difference between the two living Madagascar indriids *Avahi laniger* and *Propithecus diadema* is a difference in body size, *Propithecus* weighing about four times as much as *Avahi*. This body size difference is accurately reflected in the difference in tooth size seen in text-fig. 2. Similarly, the major difference between the extinct species *Pelycodus ralstoni* and *Pelycodus abditus* was probably one of overall body size also. Judging from the difference between the sizes of teeth characterizing the two, *P. abditus* probably averaged about twice the body weight of *P. ralstoni*. *Adapis magnus* is a European adapid species that is included in text-fig. 2 for comparison, but will not be further discussed here (see Gingerich, 1977a,b).

Body size is probably the most important single dimension in determining an animal's adaptation. Given the ecological and physiological importance of body size (see Hutchinson and McArthur, 1959; McNab, 1971; etc.), we have concentrated on body size in the following analysis of evolutionary
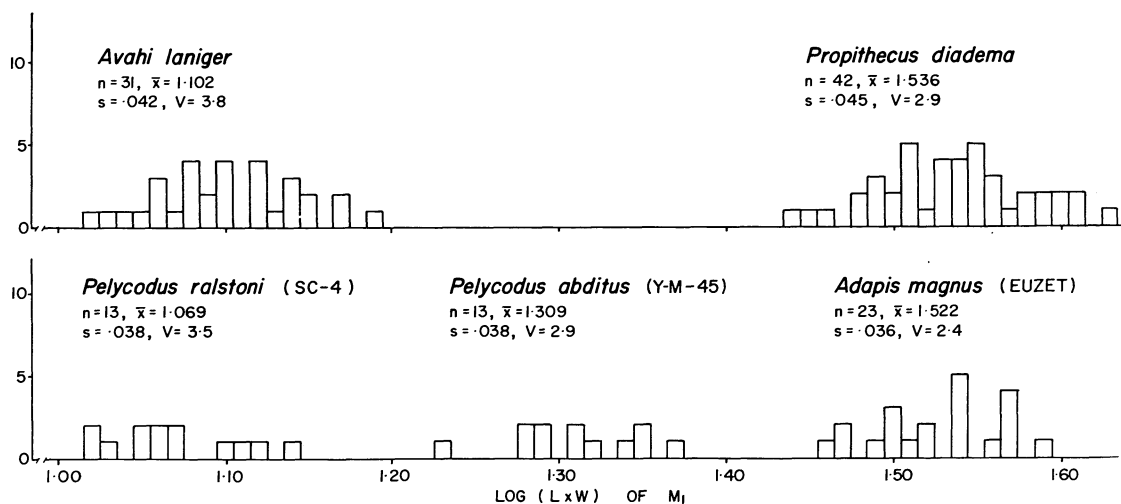
TEXT-FIG. 2 – Dental variation in two living species of lemuriform Indriidae (*Avahi* and *Propithecus*) compared with dental variation in three species of Eocene lemuriform Adapidae (*Pelycodus* and *Adapis*, each fossil sample from a single locality). Note similar coefficients of variation in living and fossil samples. Use of log M_1 size is justified in Gingerich (1974). Locality SC-4 is at level 210 m in text-fig. 11. Locality Y-M-45 is the type locality of *Pelycodus abditus*, at level 1140 ft in text-fig. 10.

change in *Pelycodus*. Other characters, such as mesostyle and hypocone development, have been studied whenever possible, but the fact remains that the most significant way that successive species of *Pelycodus* differ is in tooth size and, by inference, body size.

SYSTEMATIC REVISION

The evolutionary patterns outlined in the following section of this paper were originally determined from a study of the fossils and stratigraphic framework before any species names were (or could be) applied to the patterns. Once the patterns were known, it was possible to search the literature, compare the various available species types, and apply names to successive segments of the evolutionary lineages. Since use of the valid names will facilitate subsequent discussion, we present the systematic revision before the evolutionary patterns, although the latter formed the basis of the systematic revision.

All of the available species names for North American *Pelycodus* and the new genus *Copelemur* are listed in Table 3. It should be noted that we studied the entire typodigm (the entire sample of a species from its type locality) whenever possible, and this population sample was used for comparison when identifying our collections to species. The type locality and minimum sample size studied for each typodigm are listed in Table 3 (note that the given n includes only the specimens that preserved M_1). Eight early Eocene species of North American Adapidae were generally recognized as valid before this study, and we now recognize ten species as valid. While we have described several new species, we have not in any way changed the basic concept of what constitutes a species in these early primates – the average duration of a species remains essentially unchanged since Matthew's (1915) revision. In recognizing that Gray Bull beds make up almost half of the Wasatchian, during which *Pelycodus* changed very significantly, we feel justified in describing one new species intermediate between two of the previously recognized species.

TABLE 3 – Species of *Pelycodus* and *Copelemur* described from western North America. Species recognized as valid in this revision are numbered in the order in which they were described. Locality and size of M_1 are given for each typodigm. Abbreviations as in Table 1. Measurements in mm.

	Species	Type Locality	n	OR	$\bar{x}$	s	V
(1)	*Prototomus jarrovii* Cope, 1874 [Type species of *Pelycodus*]	Arroyo Blanco, San Juan Basin, New Mexico	2	1.37–1.41	1.390	.028	2.0
(2)	*Pelycodus frugivorus* Cope, 1875	Arroyo Almagre, San Juan Basin, New Mexico	4	1.17–1.22	1.195	.021	1.7
	Pelycodus angulatus Cope, 1875 [Indeterminate]	Arroyo Almagre, San Juan Basin, New Mexico	—	—	—	—	—
(3)	*Tomitherium tutus* Cope, 1877 [Type species of *Copelemur*]	?Arroyo Almagre, San Juan Basin, New Mexico	3	1.31–1.36	1.343	.020	1.5
	Pelycodus nunienus Cope, 1881 [Synonym of *P. frugivorous*]	Lost Cabin beds, Wind River Basin, Wyoming	14	1.17–1.31	1.252	.041	3.3
	Notharctus venticolis Osborn, 1902 [Synonym of *P. jarrovii*]	Lost Cabin beds, Wind River Basin, Wyoming	20	1.33–1.46	1.379	.039	2.8
(4)	*Pelycodus ralstoni* Matthew, 1915	3 mi. SE mo. Pat O'Hara Creek, Sand Coulee area, northern Big Horn Basin, Wyoming	12	.98–1.09	1.048	.033	3.1
(5)	*Pelycodus trigonodus* Matthew, 1915	Dry Camp 1, 1910, 5 mi. S of Otto, central Big Horn Basin, Wyoming	7	1.15–1.32	1.202	.059	4.9
	Notharctus limosus Gazin, 1952 [Synonym of *P. frugivorous*]	La Barge fauna, SW¼ Sec. 33, T32N, R111W, Sublette Co., Wyoming	1	1.17	—	—	—
(6)	*Pelycodus? praetutus* Gazin, 1962 [now placed in *Copelemur*]	1¼ mi. S Bitter Creek Station, Sweetwater Co., Wyoming	1	1.06	—	—	—
(7)	*Pelycodus mckennai*, new species	SC-133, NE¼, S1, T55N, R102W, northern Big Horn Basin, Wyoming	4	1.10–1.19	1.147	.046	4.0
(8)	*Pelycodus abditus*, new species	Y-M-45, NW¼, Sec. 33, T49N, R95W, Big Horn Co., Wyo., central Big Horn Basin, Wyoming	13	1.23–1.37	1.309	.038	2.9
(9)	*Copelemur feretutus*, new species	Lysite member, central T39N, R90W, Fremont Co., Wind River Basin, Wyoming	2	1.16–1.18	1.170	.014	1.2
(10)	*Copelemur consortutus*, new species	Lost Cabin beds on Alkali Ck., 5 mi. NW of Arminto, Wind River Basin, Wyoming	5	1.10–1.13	1.116	.016	1.4

Pelycodus Cope, 1875

Prototomus (in part), Cope, 1874, p. 14.
Pelycodus Cope, 1875, p. 13. Type: *Prototomus jarrovii* Cope.
Tomitherium (in part), Cope, 1877, p. 137.
Notharctus (in part), Osborn, 1902, p. 195.
Cantius Simons, 1962, p. 5. Type: *Protoadapis eppsi* Cooper.

North American species.– *Pelycodus ralstoni* Matthew, *P. mckennai*, nov., *P. trigonodus* Matthew, *P. abditus*, nov., *P. frugivorus* Cope, *P. jarrovii* (Cope).

European species.– *Pelycodus eppsi* (Cooper), *Pelycodus savagei* Gingerich.

Known distribution.– Early Eocene (Wasatchian) of North America, and early Eocene (Ypresian) of Europe.

Diagnosis.– Species of *Pelycodus* differ from contemporaneous species of *Copelemur* in having a more closed talonid basin on the lower molars, usually lacking a notch or valley between the ento-conid and hypoconulid, and differ from all contemporaneous species of *Copelemur*, except *C. tutus*, in being significantly larger. Differ from species of later *Notharctus* in lacking symphyseal fusion. Differ from species of *Smilodectes* in having less compressed lower premolars and more distinct paraconids on the lower molars.

Discussion.– In the past, *Pelycodus* and *Notharctus* have usually been distinguished by the degree of development of the hypocone and mesostyle on the upper molars (see Osborn, 1902; Matthew, 1915). The development of both hypocones and mesostyles in the evolution of *Pelycodus* was very gradual, and placing the species *frugivorus* (= *nunienus*) and *jarrovii* (= *venticolis*) in *Notharctus* on this characteristic is unnatural in that it implies a diphyletic origin of *Notharctus* (see text-figs. 10, 13). It also has the effect, given our present understanding of the synonomy involved, of placing the type species of *Pelycodus* in the genus *Notharctus*. An equally arbitrary, but more natural and stable diagnosis of *Pelycodus* and *Notharctus* involves placing the early Eocene species in *Pelycodus*, and the middle Eocene species in *Notharctus*. Symphyseal fusion of the mandibular rami provides a useful morphological character for separating the two and this is the basis of the diagnosis proposed here: *Pelycodus* lacks symphyseal fusion, whereas the left and right mandibular rami are coossified in *Notharctus*. Undoubtedly, samples intermediate between *Pelycodus jarrovii* and *Notharctus tene-brosus* or *Notharctus pugnax* will be found in which some specimens within a single species have fusion while others do not. This illustrates the arbitrary nature of separation of the most advanced species of *Pelycodus* from the most primitive species of *Notharctus*. At the present time, lack of symphyseal fusion is the most useful characteristic diagnosing *Pelycodus* from *Notharctus*.

In an earlier paper, Gingerich (1976a) extended the stratigraphic range of North American *Pely-codus* back into the Clarkforkian. That extension of range was based on an uncatalogued Princeton University tooth of *Pelycodus* labeled in pencil as coming from the "Paint Creek locality" (Univ. Michigan Loc. SC-143). The tooth in question is too large to belong to *Pelycodus ralstoni* (see Gingerich, 1976a, fig. 7), the earliest species from North America, and we suspect that the specimen in question is mislabeled. Higher stratigraphic levels are exposed in the vicinity of Paint Creek that do yield *Pelycodus*. Recent intensive collecting at locality SC-143 has resulted in a good Clarkforkian fauna with no trace of *Pelycodus*. Two seasons of collecting in the Sand Coulee area by University of Michigan parties has established clearly that the Sand Coulee fauna with *Pelycodus ralstoni* overlies beds yielding a Clarkforkian fauna. The two faunas are distinctive, and *Pelycodus* has never been found in the lower one.

Pelycodus ralstoni Matthew, 1915

Text-fig. 13

Pelycodus ralstoni Matthew, 1915, p. 436, fig. 4-6.
Pelycodus ralstoni (in part), Dorr, 1952, p. 90.

Type.— AM 16089, a right maxilla with P^4-M^3 from "3 miles southeast of the mouth of Pat O'Hara Creek" in the Clark Fork or "Sand Coulee" drainage basin, northwestern Wyoming. The exact locality of origin of this sample has not yet been relocated, but study of archives at the American Museum of Natural History suggests that this is in the vicinity of University of Michigan localities SC-89 and SC-139.

Diagnosis.— Smallest North American species of *Pelycodus*, differs from *P. mckennai* and later species in being significantly smaller, almost always lacking any hypocone development or mesostyle crest, and in having a narrower, more rounded heel on M_3. North American *Pelycodus ralstoni* closest to *P. eppsi* in Europe, appears to differ from it in lacking incipient hypocone on basal cingulum of latter. Also, type sample of *Pelycodus eppsi* falls at the very lower end of the size range in the typodigm of *P. ralstoni*.

Age and Distribution.— Lowest Wasatchian faunal interval, "Sand Coulee" beds and equivalent, known from northwestern Wyoming.

Description.— New collections made by University of Michigan field parties in the past two years have greatly increased the number of specimens and knowledge of the dental morphology of *Pelycodus ralstoni*. The lower dental formula of *Pelycodus ralstoni* is 2.1.4.3, and the upper formula is presumably the same. UM 66365 preserves partial alveoli for a small I_1 and a larger I_2, the root of the lower canine, and roots or crowns of all four premolars. The mandibular symphysis in this specimen, as in all later *Pelycodus* as well, was unfused.

One mandible, UM 64828, preserves the lower canine intact. The lower canine in this specimen of *Pelycodus* resembles the lower canine of a male squirrel monkey (*Saimiri*) in size and morphology, having a pointed tip projecting vertically about 5.5 mm above the base of the enameled crown. The root of the canine was much larger than the crown, being larger in both maximum diameter and root length (about 7 mm long). Thus the crown and crown/root relationships in the earliest adapid *Pelycodus* are very different from those in the earliest North American omomyid *Teilhardina americana*, which has a more premolariform crown set on a relatively much smaller root (Bown, 1976). Both could plausibly be derived from an ancestor like early Paleocene *Purgatorius* (Clemens, 1974), but Adapidae and Omomyidae show considerable subsequent divergence in anterior dental morphology. A long wear facet down the back of the crown indicates that the lower canine of *Pelycodus ralstoni* occluded in front of a similarly projecting, interlocking upper canine. Specimen UM 66365 has a significantly smaller canine root than UM 64828, suggesting that some sexual dimorphism was present even in the earliest Adapidae. The canine morphology and occlusion characteristic of Adapidae and most anthropoid primates were present in the earliest adapid for which canines are known.

Several specimens (e.g., UM 64828, 66365) preserve the root of P_1, and it is consistently single-rooted, but no specimens have yet been found preserving the crown. The remainder of the dentition has been adequately described by Matthew (1915).

Measurements of the first lower molar of the type sample of *Pelycodus ralstoni* are summarized in Table 3 (see also text-figs. 2, 10-13). Measurements of a somewhat larger sample from Sand Coulee locality SC-4 are summarized in Table 1.

Discussion.— In addition to the sample from the Big Horn Basin described by Matthew (1915), the species *Pelycodus ralstoni* has been recognized in the Hoback Basin of western Wyoming. Specimen UM 27243 figured and described by Dorr (1952) is M_3 of the artiodactyl *Diacodexis*, but
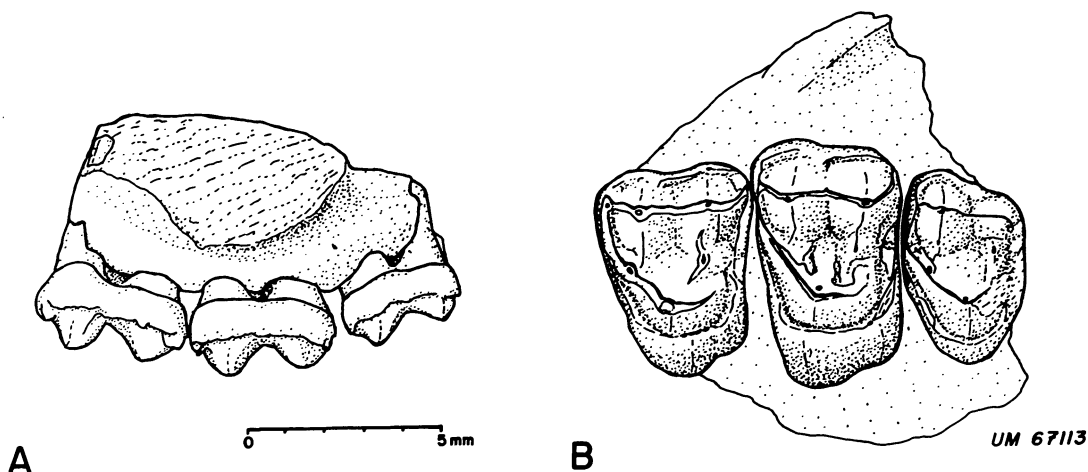
TEXT-FIG. 3 — Type specimen of *Pelycodus mckennai*, UM 67113 from Locality SC-133, a left maxilla in (A) lateral and (B) occlusal views.

another mandible fragment found among the unidentified teeth from Dorr's Hoback Formation Locality 2 does appear to belong to *Pelycodus ralstoni*. The new specimen, a left mandible fragment with P_4-M_1 is now catalogued as UM 67569.

Typodigm.— The following specimens of *Pelycodus ralstoni* are known from the type locality: AMNH 16088, 16089 (type), 16090, 16091, 16093, 16095-16097, 94313, 94316, 94405, 94408, 94421, 94434.

Numerous additional specimens of this species are present in the AMNH, UM and PU collections.

Pelycodus mckennai, new species

Text-figs. 3, 13

Pelycodus ralstoni, McKenna, 1960, p. 76. Dorr and Steidtmann, 1971, p. 26. Delson, 1971, p. 339.
Pelycodus cf. *ralstoni*, Wilson, 1955, p. 514, fig. 1-2.

Type.— UM 67113, a left maxilla with M^{1-3}, collected in 1976 by K. D. Rose from UM locality SC-133 in the Sand Coulee area (NE¼, S1, T55N, R102W, Park Co., Wyoming).

Diagnosis.— Differs from *Pelycodus ralstoni* in being significantly larger and in having a relatively broader heel on M_3. Differs from other species of *Pelycodus* in being smaller and in having no mesostyle crest, or a small mesostyle crest present at low frequencies in samples from individual localities.

Etymology.— Named for Dr. M. C. McKenna, American Museum of Natural History, in recognition of his many contributions to the study of Eocene primates and other mammals.

Age and Distribution.— Lower Wasatchian faunal interval, "lower Gray Bull" beds and equivalent, known from northern Wyoming (Powder River Basin, Big Horn Basin, Hoback Basin) and northern Colorado (Four Mile fauna).

Description.— The dental morphology of this species is very similar to that described above for *Pelycodus ralstoni*, the two differing only as noted in the diagnosis. Nevertheless, *Pelycodus mckennai* is distinctive and can be relatively easily distinguished from *P. ralstoni* and *P. trigonodus* when a representative sample is available. Tooth measurements for the typodigm are given in Table 4.

TABLE 4 — Summary of measurements of the lower and upper cheek teeth of *Pelycodus mckennai* from the type locality, University of Michigan locality SC-133, in the Sand Coulee area, northern Big Horn Basin, Wyoming. Abbreviations as in Table 1. Measurements in mm.

		$\underline{n}$	$\underline{OR}$	$\underline{\bar{x}}$	$\underline{s}$	$\underline{V}$	$\underline{V^*}$
P_2	L	1	2.6	—	—	—	—
	W	1	1.5	—	—	—	—
P_3	L	0	—	—	—	—	—
	W	0	—	—	—	—	—
P_4	L	1	3.2	—	—	—	—
	W	1	2.6	—	—	—	—
M_1	L	4	3.9–4.2	4.05	.17	4.3	4.0
	W	4	3.2–3.7	3.48	.22	6.4	
M_2	L	3	3.8–4.4	4.10	.30	7.3	4.5
	W	3	3.7–4.1	3.90	.20	5.1	
M_3	L	1	5.6	—	—	—	—
	W	1	3.7	—	—	—	—
M. Depth		4	7.5–8.9	7.90	.67	8.5	—
P^3	L	1	3.4	—	—	—	—
	W	1	3.6	—	—	—	—
P^4	L	1	3.5	—	—	—	—
	W	1	4.7	—	—	—	—
M^1	L	2	4.0	—	—	—	—
	W	2	5.2–5.6	—	—	—	—
M^2	L	1	3.8	—	—	—	—
	W	1	6.8	—	—	—	—
M^3	L	1	3.2	—	—	—	—
	W	1	5.1	—	—	—	—

One exceptionally complete mandible, PU 17417 from the Hackberry Hollow locality, is worthy of note. It preserves alveoli for a small central incisor, a slightly larger lateral incisor, a canine measuring 2.3 by 1.7 mm at the base of the crown (most of the crown itself is missing), the intact crown of P_1, roots for P_2, and the remainder of the teeth intact (M_1 broken). By comparison with UM 65304, a presumed male of *P. mckennai* with a canine crown measuring 2.8 by 2.3 mm at the base, the Princeton specimen would appear to be a female.

A maxilla of *P. mckennai* (UM 63266) collected by W. Jungers retains alveoli for the upper canine and P^{1-2}, and the cheek teeth P^{3-4}, M^{1-3}. Five mandibles (UM 65686, 66249, 67089, 67513,

PU 17417) show that a total of four premolars were present in each lower jaw. UM 66940 is a crushed partial skull of this species including the left occiput and mastoid region, and a portion of the left auditory region, but it has not yet been cleaned sufficiently to describe here.

Discussion.— McKenna (1960, p. 76) tentatively synonymized *Pelycodus ralstoni* and *P. trigonodus* because a sample he studied from the Four Mile area of northwestern Colorado was intermediate between the two. McKenna recognized that only a detailed biostratigraphic study of *Pelycodus* specimens from Willwood Formation of the Big Horn Basin would determine the validity of *P. trigonodus*. Now that such a study has been completed, it is clear that both *Pelycodus ralstoni* and *Pelycodus trigonodus* are valid and that an intermediate species *P. mckennai* is sufficiently distinctive to warrant recognition. A sample of specimens (numbered AMNH 93656, 93657, 93661) from the East Alheit locality (Four Mile fauna) was studied in detail, and it matches the type sample of *P. mckennai* from the Big Horn Basin almost exactly. Twenty-one first lower molars have a mean value for the log (L x W) of M_1 of 1.147 (OR = 1.08-1.20, s = .031). Of the ten upper molars studied from East Alheit, eight had no trace of a mesostyle, two had a very weak mesostyle crest, and none had a distinct mesostyle.

Two upper molars, UM 59895, 59899, described by Dorr and Steidtmann (1971) from Locality 29, Sublette County, Wyoming, appear to belong to *Pelycodus mckennai* rather than *P. ralstoni*, but the specimens by themselves are inadequate for certain identification. They both measure 4.0 mm in length, which accords better with *P. mckennai* than *P. ralstoni*, and both lack any trace of a mesostyle. Similarly, the size measurements given by Delson (1971) for *Pelycodus* from the Powder River Basin, if all are from the same restricted stratigraphic interval, indicates that they represent *P. mckennai* rather than *P. ralstoni*.

Wilson (1955) described an interesting anomaly in a specimen of *P. mckennai* (KU 8508) from the Big Horn Basin — the specimen apparently has a smaller supernumerary M_3 following the normal M_3. A similar anomaly has recently been noted by one of us [P. D. G.] in a specimen of European *Adapis*.

Typodigm.-- The sample from the type locality consists of the following specimens: UM 67087, 67089, 67102, 67107, 67113 (type), and 67123.

In addition, large collections of this species from lower Gray Bull localities are in the AMNH, PU, UM, YPM, and other museums.

Pelycodus trigonodus Matthew, 1915

Text-figs. 4, 13

Pelycodus frugivorus, Osborn, 1902, p. 193, fig. 21. Loomis, 1906, p. 281, fig. 3.
Pelycodus trigonodus Matthew, 1915, p. 436, fig. 7-8.
*Pelycodus frugivorus* (in part), Matthew, 1915, p. 439, fig. 12-14.
Pelycodus cf. *trigonodus*, Gazin, 1962, p. 27.
Pelycodus cf. *ralstoni*, Jepsen, 1963, p. 679. West, 1973, p. 750.

Type.— AMNH 15017, associated upper and lower jaws, from American Museum Dry Camp 1, Big Horn Basin, 1910 expedition, a locality approximately 5 miles south of Otto, Wyoming.

Diagnosis.— Differs from *Pelycodus ralstoni* and *P. mckennai* in being larger, and having a small to medium mesostyle crest. Differs from *P. abditus* and *P. jarrovii* in being smaller, differs from *P. abditus*, *P. jarrovii*, and *P. frugivorus* in having less well developed mesostyles and generally lacking hypocones.

Age and Distribution.— Middle Wasatchian faunal interval, "upper Gray Bull" beds and equivalent, known from western North Dakota (Golden Valley Fm.), northwestern Wyoming (Big Horn Basin), and southwestern Wyoming (Washakie Basin).
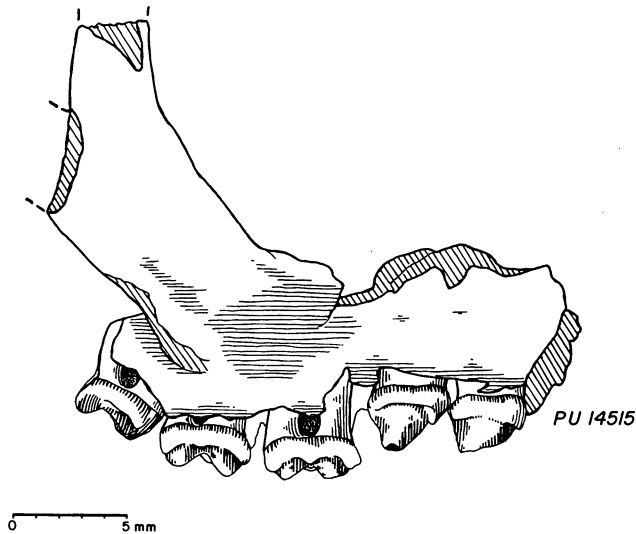
TEXT-FIG.: 4 — Right maxilla of *Pelycodus trigonodus*, PU 14515, in lateral view showing first evidence that a postorbital bar was present in this species.

Description.— As is the case in the transition from *Pelycodus ralstoni* to *P. mckennai*, the transitions from *P. mckennai* to *P. trigonodus*, and from *P. trigonodus* to *P. abditus* appear to have been continuous and gradual. Thus the boundary between each successive species is necessarily arbitrary. Nevertheless, *P. trigonodus* represents a distinctive stage of evolution in *Pelycodus* that can be recognized, given adequate samples, by its characteristic size range and molar construction. The upper molars generally have a mesostyle crest but lack hypocones, retaining instead the broad postprotocingulum that characterizes early species of *Pelycodus*.

PU 14515 is a badly broken partial skull of *Pelycodus trigonodus* collected from the McCullough Peaks by F. B. Van Houten in 1937. This specimen preserves much of the upper molar series, but it is most important in showing that *Pelycodus* had a fully developed postorbital bar (text-fig. 4), as in later *Notharctus* and other Adapidae.

Discussion.— Loomis (1906) described and figured the first specimens of this species from the Big Horn Basin. His figure 3 is an illustration of ACM 3414.

Gazin (1962) referred specimens of *Pelycodus* from Bitter Creek in southern Wyoming to this species. We have studied two of these, mandibles YPM 14068 and 15285, which were both collected by Smith and Heisey for O. C. Marsh in 1882 from the "light colored beds." Both appear to be almost identical with the type specimen of *P. trigonodus*, and the one preserved M_1 has a log (L x W) = 1.20, matching that for the type sample of *P. trigonodus*.

Jepsen (1963, see also West, 1973) listed the species *Pelycodus* cf. *ralstoni* in his faunal list from the Golden Valley Formation in North Dakota. This record is based on three isolated teeth: an upper M^2 (PU 17234) measuring 4.3 mm in length, 6.8 mm in width; an uncatalogued M^1 measuring 4.1 mm in length and 5.7 mm in width; and an M_2 (PU 17269) measuring 4.7 mm in length and 4.3 mm in width. These teeth resemble *P. trigonodus* most closely in size and in having a small to medium-sized mesostyle crest on the upper molars, and they are here referred to *P. trigonodus* rather than *P. ralstoni*.

TABLE 5 – Measurements of the type and a referred specimen of *Pelycodus abditus*. Measurements in mm.

UM 66000 (type) Mandibular dentition			AMNH 15018 Maxillary dentition		
Tooth	Length	Width	Tooth	Length	Width
P_3	3.5	2.4	P^3	4.1	4.4*
P_4	4.0	3.0	P^4	4.0	5.7
M_1	4.8	4.4	M^1	4.7	6.7
M_2	4.9	4.7	M^2	4.9	7.9
M_3	6.1	4.2	M^3	4.3	6.0

* estimated

Typodigm.– The type sample consists of some seven mandibles, a maxilla, and a crushed palate: AMNH 15017 (type), 15029, 15050, 15054, 15057, and 16152.

In addition, there are numerous referred specimens of this species in the AMNH, PU, UM, YPM, and other museum collections.

Pelycodus abditus, new species

Pl. 1, fig. 1; text-fig. 13

Pelycodus nuniensis, Loomis, 1906, p. 282, fig. 5.
Pelycodus jarrovii (in part), Matthew, 1915, p. 438, fig. 9, 10.
Pelycodus cf. *jarrovii*, Kelley and Wood, 1954, p. 344, fig. 4d.
Pelycodus near *jarrovii*, Gazin, 1962, p. 28.

Type.– UM 66000, right and left mandibles collected by G. Gunnell and B. H. Smith from Yale-Michigan Locality 45, southwest of Red Butte in Section 33, T49N, R95W, Big Horn County, Wyoming.

Diagnosis.– Differs from *Pelycodus ralstoni, P. mckennai*, and *P. trigonodus* in being larger, having a stronger mesostyle, and usually a distinct but small hypocone. Differs from *P. frugivorus* in being larger but having a less well developed mesostyle and hypocone. Differs from *P. jarrovii* in being smaller and having a less well developed mesostyle and hypocone.

Etymology.– *abditus*, L., hidden or concealed, in reference to the long period during which this species was incorrectly hidden under the name *P. jarrovii*.

Age and Distribution.– Upper Wasatchian faunal interval, "Lysite" beds and equivalent, known chiefly from northwestern Wyoming (Big Horn and Wind River Basins), but also from southwestern Wyoming (Fossil Basin).

Description.– The type specimen of *Pelycodus abditus*, a mandible, is illustrated in Plate 1, fig. 1, and one of the best upper dentitions is the maxilla AMNH 15018 illustrated by Matthew (1915, fig. 9). Measurements of these specimens are given in Table 5. Measurements of M_1 in the typodigm are summarized in Table 3.

EXPLANATION OF PLATE 1

(All figures twice natural size)

Figure 1 – Type specimen of *Pelycodus abditus*, UM 66000, left and right mandibles in occlusal view, stereophotograph.

Figure 2 – Topotype of *Pelycodus jarrovii*, AMNH 16298, left mandible with M_{1-2} in occlusal view, stereophotograph.

Figure 3 – Topotype of *Copelemur tutus*, AMNH 16206, left mandible with M_{1-2} in occlusal view, stereophotograph.
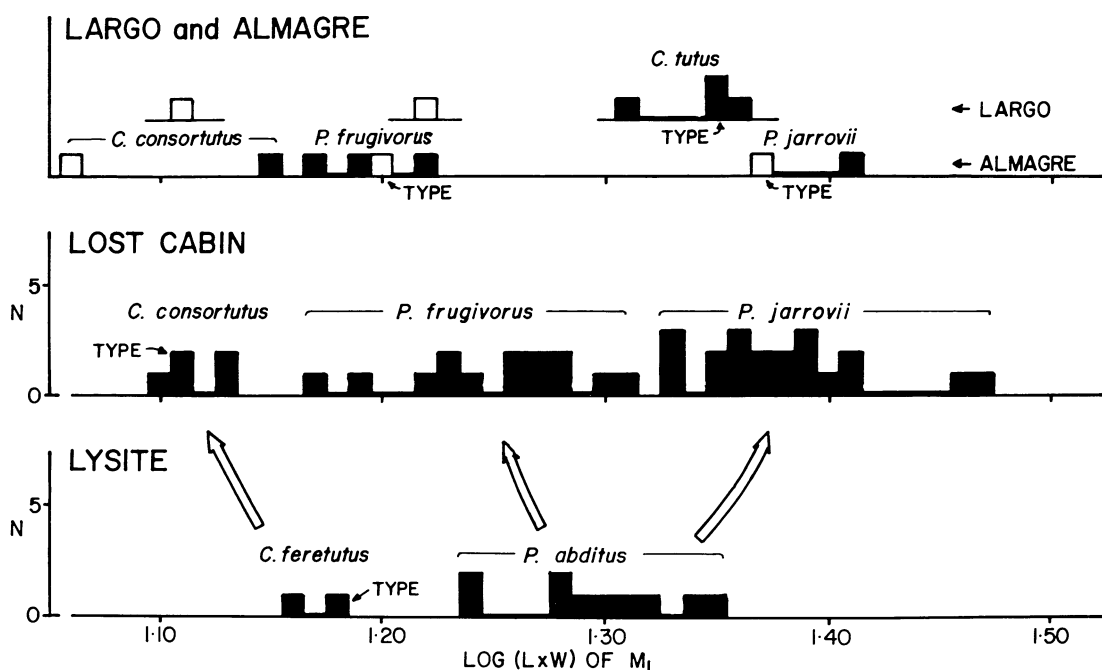
TEXT-FIG. 5 – Comparison of the pattern of variation in tooth size in early Eocene Adapidae from the San Juan Basin (Largo and Almagre beds) with that in the Wind River Basin (Lost Cabin and Lysite beds). Two species are present in the Lysite beds, and three are present in the Lost Cabin beds in the Wind River Basin. Samples from both the Largo and Almagre facies match Lost Cabin adapids most closely in size (shown here) and other morphological characteristics. Type specimens are indicated whenever possible. Open squares are estimates based on M_2 where M_1 is not preserved. Evidence for phylogenetic relationships shown by arrows is shown in text-fig. 10.

The type specimen (Pl. 1, fig. 1) consists of left and right mandibular rami, narrowing at the front to form a V-shaped mandible with an unfused symphysis. Roots and/or tooth crown are preserved for the canine, four permolars, and three molars in the type. YPM 26524, an early representative of *P. abditus* from Yale Locality 268, preserves alveoli showing that there were clearly two small incisors in the mandible of this species, the central one being slightly smaller than the lateral one.

The upper dentition of *Pelycodus abditus* (text-fig. 13) is distinctive chiefly because it has a distinct mesostyle crest and a small but distinct hypocone on the upper molars.

Discussion.– The first description and illustration of specimens of *Pelycodus abditus* was early in this century by Loomis, who published a figure of ACM 3542 (Loomis, 1906, fig. 5). Loomis described these under the name *Pelycodus nuniensis* Cope, an obvious *lapsus calami* for Cope's *Pelycodus nunienus* (see below).

An additional confusion regarding this species was created inadvertently by Matthew (1915), who designated a specimen (AMNH 15018) of this species as a neotype of *Pelycodus jarrovii*. Cope (1874) originally described *P. jarrovii* from New Mexico, but the type specimen was lost sometime before Matthew's revision. No collections from the Almagre and Largo beds of New Mexico include the species represented by AMNH 15018, although "Lost Cabin" age specimens of *Pelycodus* are clearly represented (text-fig. 5). As discussed below, *P. jarrovii* is a senior synonym of the species usually referred to under the name *P. venticolis*. Hence it is necessary to redescribe the collections

identified by Matthew (1915) and subsequent authors under *P. jarrovii* as a new species, for which the name *Pelycodus abditus* is proposed.

Typodigm.— The type sample of *P. abditus* includes the following: UM 65956, 65960, 65984, 65997, 66000 (type), YPM 18639, 18641-18644, 18649, 18679, 23218, 23284, 23285, 23323, 24391, 27148, 30425, 31000, 31010, 31052, and 33293.

Numerous additional specimens of this species are in the collections of ACM, AMNH, PU, UM, USNM, and other museums, the collections from "Lysite" beds of the Big Horn Basin and Wind River Basin (Guthrie, 1967) being the most important.

<p align="center">*Pelycodus frugivorus* Cope, 1875</p>

<p align="center">Text-fig. 6c</p>

Pelycodus frugivorus Cope, 1875, p. 14.
Tomitherium frugivorum, Cope, 1877, p. 144, Pl. 39, fig. 16.
Pelycodus nunienum Cope, 1881, p. 187.
Pelycodus frugivorus, Cope, 1885, p. 230, Pl. 15a, fig. 4-5.
Notharctus nunienus, Osborn, 1902, p. 195, fig. 20b, 22. Matthew, 1915, p. 444, fig. 19. Granger and Gregory,
    1917, p. 845.
Notharctus limosus Gazin, 1952, p. 22, Pl. 1, fig. 6-8. Gazin, 1962, p. 29, Pl. 4, fig. 5.
Notharctus cf. *nunienus*, Gazin, 1962, p. 30.
Notharctus nunienus (in part), Robinson, 1966, p. 31, Pl. 8, fig. 3. Guthrie, 1971, p. 63.

Type.— Unnumbered mandible with M_{2-3} in Cope collection from lower Eocene of New Mexico (Almagre beds), specimen now lost. Cope (1875) gives measurements of the type as follows: M_2 length and width, 4.5 and 4.0 mm; M_3 length and width, 6.0 and 3.5 mm. AMNH 16209 from New Mexico agrees very closely with these measurements. AMNH 16212 appears to be the best topotype of *P. frugivorus* collected to date.

Diagnosis.— Differs from *P. ralstoni* and *P. mckennai* in being larger, from *P. abditus* and *P. jarrovii* in being smaller (see Table 3). Differs from *P. ralstoni, P. mckennai, P. trigonodus,* and *P. abditus* in having stronger mesostyles (usually distinct cusps) and stronger hypocones.

Age and Distribution.— Upper Wasatchian faunal interval, "Lost Cabin" beds and equivalent, known from northwestern Wyoming (Big Horn and Wind River Basins), southwestern Wyoming (Green River Basin), southern Colorado (Huerfano Basin), and northern New Mexico (San Juan Basin).

Description.— The most complete lower jaw of *Pelycodus frugivorus*, AMNH 12736 from the Wind River Basin, was figured by Matthew (1915, fig. 19). It originally had a complete canine, and the crowns of P_2-M_3 intact (text-fig. 6c). At some time subsequently, before it was refigured by Gregory (1920, Pl. 36), the crown of the canine and part of P_3 were broken and lost. Nevertheless, the specimen shows the unfused symphysis, projecting canine, normally proportioned P_4 with distinct paraconid and metaconid, molars with distinct paraconids, and closed talonid basins characteristic of *P. frugivorus*. The two topotypes mentioned above, AMNH 16209 and 16212 from the San Juan Basin, agree in most details, but have a slightly better developed entoconid notch on M_2 and a narrower rounded heel on M_3. Comparison with other specimens from Lost Cabin beds of the Wind River Basin (e.g., PU 20590) and USNM 19294 (holotype of "*N. limosus*") from the Green River Basin, indicates that an entoconid notch and rounded M_3 heel also occur in some specimens from Wyoming.

One of the best upper dentitions is a specimen, AMNH 4735 from the Wind River Basin, figured by Cope in 1885 (Pl. 15a, fig. 4; see also Osborn, 1902, fig. 20b; and Gregory, 1920, Pl. 35, rev.). It shows very distinct mesostyle cusps, especially on M_2, and worn but distinct hypocones.
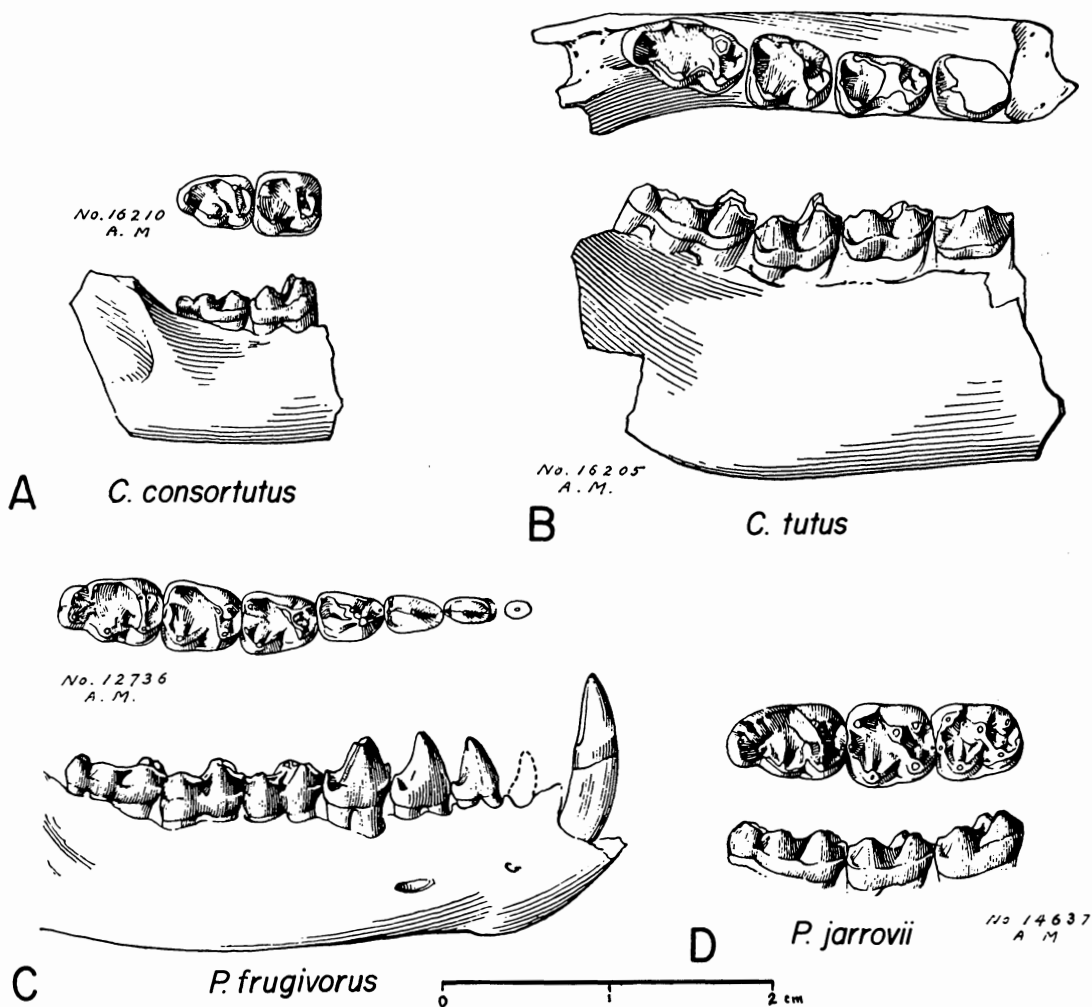
TEXT-FIG. 6 – Comparison of the right mandibular dentition of four species of Adapidae from the Almagre and
              Largo beds of the San Juan Basin, New Mexico, all drawn at the same scale. A and B are *Cope-
              lemur*, C and D are *Pelycodus*. All specimens in AMNH. Drawings from Matthew (1915), slightly
              more than twice natural size.

Discussion.– Cope described *Pelycodus frugivorus* in 1875, based on a specimen from New Mexi-
co. Five years later Wortman collected similar specimens in the Wind River Basin of Wyoming, and
Cope (1881) named these *P. nunienus*, a name he subsequently synonymized with *P. frugivorus*
(Cope, 1885). The chief character that distinguished them was the twinned hypoconulid on M_3
in *P. nunienus* and its absence in *P. frugivorus*. Cope (1885) concluded that this was probably just
individual variation, a conclusion further substantiated by the variation described above in Wind
River specimens.

Subsequently, Osborn (1902) and Loomis (1906) incorrectly identified specimens of *P. trigonodus*
as Cope's *P. frugivorus*, and resurrected the name *P. nunienus* for the more advanced Wind River
forms with quadrate molars, shifting the species to *Notharctus* on this account. This confusion of

P. frugivorus with *P. trigonodus*, and subsequently with *Copelemur feretutus* (see below), obscured both the true relationships of the species and the correlation of New Mexico Eocene strata with those of Wyoming. After restudying all of the collections available from New Mexico, including those made by Simpson in the late 1940's and early 1950's (Simpson, 1948, 1951), it is possible to arrive at a clearer understanding of the New Mexico Adapidae.

Two species of *Pelycodus* and two species of the new genus *Copelemur* are represented (text-figs. 5, 6). *P. frugivorus* occurs in both the lower (Almagre) and upper (Largo) beds of the San José Formation in New Mexico. It is most common in the lower beds, and Almagre Arroyo would appear to be the type locality of *P. frugivorus* (Simpson, 1951, p. 16-17). Species of *Pelycodus* as advanced as those from the Almagre and Largo beds do not appear elsewhere until the equivalent of the Lost Cabin beds in Wyoming. For these and other faunal reasons, it appears likely that the Almagre and Largo faunas are very close to each other in age, and correlative with the Lost Cabin beds in northern Wyoming.

The species *"Notharctus limosus"* occurs together with *P. jarrovii* in the Green River Basin (Gazin, 1952) and it is morphologically indistinguishable from *P. frugivorus*, hence the two are almost certainly synonymous.

Some specimens from the Huerfano lower faunal zone labeled *Notharctus nunienus* by Robinson (1966) belong to *Pelycodus frugivorus*, but *Pelycodus jarrovii* is also represented. Specimens from the upper faunal zone are not included, and will be discussed elsewhere in connection with a revision of *Notharctus* and *Smilodectes*.

Typodigm.— The exact locality where the type specimen of *P. frugivorus* was found cannot be determined, and the type itself is lost, but the following specimens representing this species were found in the lower or Almagre beds in New Mexico: AMNH 16212, 48956, 48959, 55506, 55512, 55513. The following specimens of *P. frugivorus* come from the upper or Largo beds: AMNH 16208, 16209, 55502, 55503.

In addition, a large number of specimens of *P. frugivorus* are known from the Wind River Basin, including AMNH 4734 (type of *P. nunienus*), 4735, 12736, PU 18366, and 20590. Other specimens of *P. frugivorus* include USNM 19294 (type of *P. limosus*, from Green River Basin), YPM 27294 (Big Horn Basin), and AMNH 55224 and UCM 32157 (Huerfano Basin). Additional specimens are housed in all of the above museums.

Pelycodus jarrovii (Cope, 1874)

Pl. 1, fig. 2; text-figs. 6d, 7

Prototomus jarrovii Cope, 1874, p. 14.
Pelycodus jarrovii, Cope, 1875, p. 14. Cope, 1881, p. 187. Cope, 1885, p. 228.
Tomitherium jarrovii, Cope, 1877, p. 137, Pl. 39, fig. 17-18.
Pelycodus tutus (in part), Cope, 1881, p. 187. Cope, 1885, p. 228, Pl. 25a, fig. 103. Osborn, 1902, p. 194.
Notharctus venticolis Osborn, 1902, p. 195. Matthew, 1915, p. 443, fig. 16-18. Granger and Gregory, 1917, p. 846. White, 1952, p. 192. Gazin, 1952, p. 24.
*Pelycodus jarrovii* (in part), Matthew, 1915, p. 438.
Notharctus cf. *venticolis*, Gazin, 1962, p. 30.
Notharctus nunienus (in part), Robinson, 1966, p. 31.
Notharctus venticolis (in part), Guthrie, 1971, p. 63.

Type.— Unnumbered mandible with broken M_2 and intact M_3 in Cope collection from lower Eocene of New Mexico (Arroyo Blanco), specimen now lost. Cope (1874) gives measurements of the type as follows: M_2 width, 5.0 mm; M_3 length and width, 7.0 and 4.5 mm. This is the specimen figured by Cope (1877) in his Plate 39, figure 17. AMNH 16298, a mandible with M_{1-2} appears to
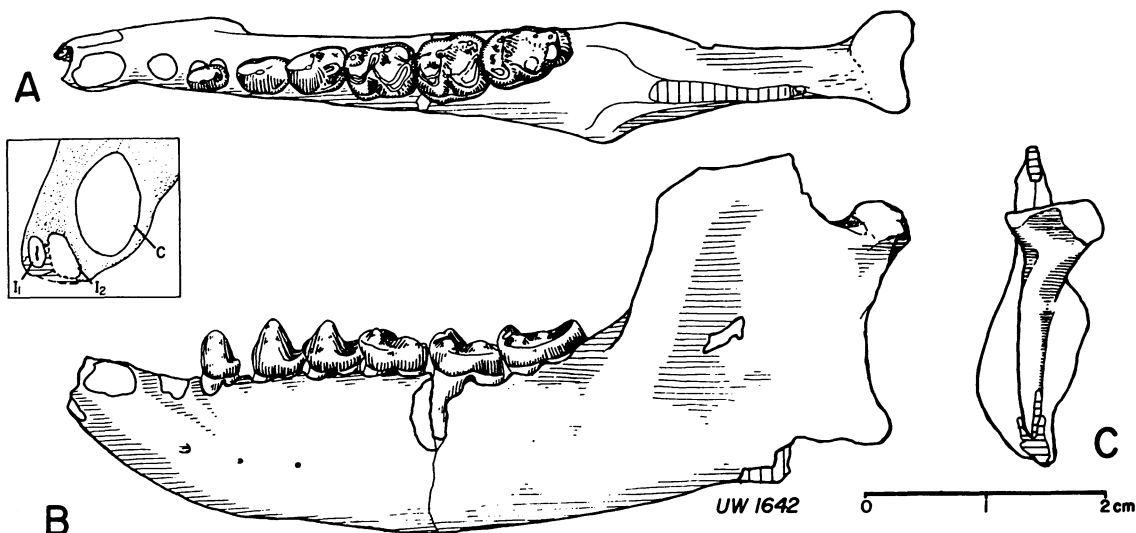
TEXT-FIG. 7 – Right mandible of *Pelycodus jarrovii*, UW 1642, from the Red Desert area, Sweetwater County, Wyoming. Specimen in (A) occlusal, (B) lateral, and (C) posterior view. Inset shows the relative size of the root of I_1 and the alveoli for I_2 and the canine, in an enlarged, oblique, anterior view looking down the alveoli.

be the best topotype of *P. jarrovii* collected to date. Note that the specimen designated a neotype of *P. jarrovii* by Matthew, 1915, belongs in fact to *P. abditus*.

Diagnosis.– Differs from all other species of *Pelycodus* in having a well developed mesostyle and hypocone on the upper molars.

Age and Distribution.– Upper Wasatchian faunal interval, "Lost Cabin" beds and equivalent, known from northwestern Wyoming (Big Horn and Wind River Basins), southwestern Wyoming (Green River Basin), southern Colorado (Huerfano Basin), and northern New Mexico (San Juan Basin).

Description.– One of the most complete mandibles of *Pelycodus jarrovii* is UW 1642 (text-fig. 7), which preserves the root of a very small central incisor, the alveoli for a larger I_2, a still larger canine, and a small P_1, as well as the intact crowns of P_2-M_3. The lower molars of *P. jarrovii* are broad and flat, resembling other species of *Pelycodus*. The symphyseal area in UW 1642 is well preserved and the rami clearly were not coossified. The articular condyle is also well preserved in this specimen, and it has the "bean-shaped" appearance Gregory (1920, p. 145) described in middle Eocene *Notharctus*. The canine alveolus in UW 1642 measures about 4.2 mm by 2.5 mm. By comparison AMNH 14655, another mandible of *P. jarrovii* described by Gregory (1920, fig. 44-45), has a stout projecting lower canine of much greater diameter, suggesting that the former is a female and the latter is a male.

A crushed partial skull of *P. jarrovii* (AMNH 14656) is known from the Wind River Basin that preserves the upper incisors and upper canine (Gregory, 1920, fig. 31, 52). The central incisor has a broad spatulate crown, while the lateral one has a much smaller and almost pointed crown. The upper canine in this specimen of *P. jarrovii* is a very large, narrow, dagger-like tooth resembling that in males of highly dimorphic species of monkeys. The upper premolars and molars are typical of

those of most *Pelycodus*, except that the molars have prominent mesostyles and hypocones (text-fig. 13).

Discussion.— Cope's original type specimen of *Pelycodus jarrovii* consisted of a mandible fragment with the talonid of M_2 and a complete M_3 from the San Juan Basin of New Mexico. According to Simpson (1951, p. 14-15) it came from Arroyo Blanco. The type was illustrated by Cope (1877, fig. 17), but unfortunately was lost before any subsequent scholar was able to study it. Osborn (1902) hardly mentioned *P. jarrovii* in his paper describing "*Notharctus venticolis*" from the Wind River Basin. Matthew (1915) might perhaps have recognized the synonymy of *P. jarrovii* and "*N. venticolis*," but he misinterpreted the teeth preserved in a topotype of *P. jarrovii* (AMNH 16298), thinking that the preserved teeth were M_2 and a broken M_3. They are in fact M_1 and M_2, indicating a larger species than Matthew judged *P. jarrovii* to be. Restudying all of the San Juan Basin *Pelycodus* and *Copelemur*, and plotting them on a size axis (text-fig. 5), it is clear that AMNH 16298 (solid square at right) represents the same species as the type specimen of *P. jarrovii* (open square). The only possible confusion would be with *Copelemur tutus*, a species with very different molar morphology. Comparing the specimens of *P. jarrovii* from the Almagre beds of New Mexico with those from the Wind River Lysite and Lost Cabin beds of Wyoming (text-fig. 5), it is clear that *P. jarrovii* is conspecific with "*Notharctus venticolis*," from the Lost Cabin beds.

Robinson (1966) described all the specimens of Adapidae from the Huerfano Basin as "*Notharctus nunienus*," but it appears that this is a mixed grouping. The smaller specimens from the lower beds are *Pelycodus frugivorus*, whereas one larger specimen (AMNH 56546) from the lower beds is *P. jarrovii*. Specimens from the upper beds in the Huerfano Basin will be considered in a later study of *Notharctus* and *Smilodectes*.

A part of what Guthrie (1971) called *Notharctus venticolis* actually belongs to *P. frugivorus*, while the larger specimens represent *P. jarrovii*.

Typodigm.— *Pelycodus jarrovii* is a rare species in New Mexico, and only two specimens from the type area are known in existing collections: AMNH 16298 and AMNH 55514.

In addition, we have studied many specimens of *P. jarrovii* in the ACM, AMNH, PU, UCM, UW, and YPM collections. Others are preserved in the USNM. Some of the best specimens, in addition to the large American Museum collection and those described above, are ACM 10092, 10280; PU 13424, 13445, 18367, 20592; and YPM 27788.

                                    Copelemur, new genus

Tomitherium (in part), Cope, 1877, p. 141.
Pelycodus (in part), Cope, 1881, p. 187.
Pelycodus?, Gazin, 1962, p. 28.
Notharctus (in part), Guthrie, 1971, p. 63.

Type species.— *Tomitherium tutum* Cope.

Included species.— *Copelemur praetutus*, (Gazin), *C. feretutus*, nov., *C. consortutus*, nov., and *C. tutus* (Cope, type species).

Known distribution.— Early Eocene (Wasatchian) of North America. *Copelemur* appears to be characteristic of more southern faunas within North America.

Diagnosis.— Species of *Copelemur* differ from *Pelycodus, Smilodectes,* and *Notharctus*, in generally having an open talonid on the lower molars, with a more distinct entoconid notch. All except *C. tutus* differ from contemporary species of *Pelycodus* in being smaller and generally having less well developed hypocones and mesostyles. Differ from species of *Notharctus* in lacking symphyseal fusion. Differ from species of *Smilodectes* in having less compressed lower premolars and more distinct paraconids on the lower molars.

Etymology.– Named for Edward Drinker Cope, who originally described the type species exactly a century ago. Suffix *lemur* refers to the lemuriform affinities of this genus among archaic primates.

Discussion.– The species of *Copelemur* have long been confused with species of *Pelycodus* and *Notharctus*, to which they are closely related. Matthew (1915, p. 441) recognized that the species "*Pelycodus*" *tutus*, here placed in *Copelemur*, differed markedly from other species of *Pelycodus* in the placement of the entoconid on the lower molars and its connection to the metaconid via a prominent crest. In his original description of *praetutus*, Gazin (1962, p. 28) referred it and *C. tutus* questionably to the genus *Pelycodus*, and suggested that they might represent a distinct genus. He refrained from placing *C. praetutus* and *C. tutus* in a new genus because species of *Pelycodus* and *Notharctus* sometimes approach them in the distinctive construction of the entoconid corner of the tooth. *Pelycodus* and *Notharctus* do not show the entoconid notch and metaconid-entoconid crest developed to the degree seen in the species here placed in *Copelemur*. The best evidence that a distinct clade is represented by the species here placed in *Copelemur* is their separation as a distinctive smaller lineage evolving in parallel with *Pelycodus abditus* and *P. frugivorus* in the late Wasatchian of the Big Horn and Wind River Basins (text-fig. 10).

As indicated by text-fig. 10 also, *Copelemur* is abundant in the Big Horn Basin for only a short time, represented by a relatively small interval of the Lost Cabin beds. It is rare both before and after this interval in the Big Horn Basin, although it apparently lived for a somewhat longer period in the Wind River Basin. Two lineages of *Copelemur*, one of *Pelycodus jarrovii*-sized animals and the other smaller, are present in the San Juan Basin in strata equivalent to the Lost Cabin beds (text-fig. 5), suggesting that possibly *Copelemur* was a more tropical form than *Pelycodus*. The available evidence indicates that *Copelemur* was relatively more common and more diversified in southern faunas within North America.

Copelemur praetutus (Gazin, 1962)

Pelycodus? *praetutus* Gazin, 1962, p. 28, Pl. 4, fig. 2-4.

Type.– USNM 22262, a right mandibular ramus with broken P_3, broken P_4, and M_{1-2} from 1¼ miles south of Bitter Creek Station, Sweetwater County, Wyoming.

Diagnosis.– Smallest species of *Copelemur*. Differs from *C. feretutus*, *C. consortutus*, and *C. tutus* also in having relatively narrower molars.

Age and Distribution.– Gazin (1962) states that the type specimen comes from strata correlative with the lowest Wasatchian "Sand Coulee" beds, however the presence of *Pelycodus trigonodus* from the same locality indicates that the age is probably mid-Wasatchian and equivalent to the "upper Gray Bull." *Copelemur praetutus* is known with certainty only from the type locality. Two specimens from Yale Locality 365 (U. Gray Bull beds) in the Big Horn Basin are very close to *C. praetutus* in size (text-fig. 10), but they do not have the very deep entoconid notch seen in the type. These two specimens possibly indicate an extension of the range of *C. praetutus* to the Big Horn Basin but more complete specimens will be required to confirm this.

Description.– The type specimen of *Copelemur praetutus* shows an unfused mandibular symphysis, alveoli for a lower canine, a single-rooted P_1, and double-rooted P_2 and P_3, with broken P_{3-4} and intact M_{1-2}. P_4 measures 3.4 mm in length and 2.4 mm in width. M_1 measures 3.8 by 3.0 mm, and M_2 measures 4.0 by 3.3. The morphology of these teeth is very similar to that seen in small *Pelycodus* except that a deep notch separates the entoconid from the hypoconulid crest on M_1 and M_2. This entoconid notch opens the talonid medially. The entoconid itself is connected to the back of the metaconid by a strong crest. The paraconids on M_1 and M_2 are rather anteriorly placed, giving these two teeth relatively open trigonids as well. One specimen, YPM 14698, is a left M_3 from
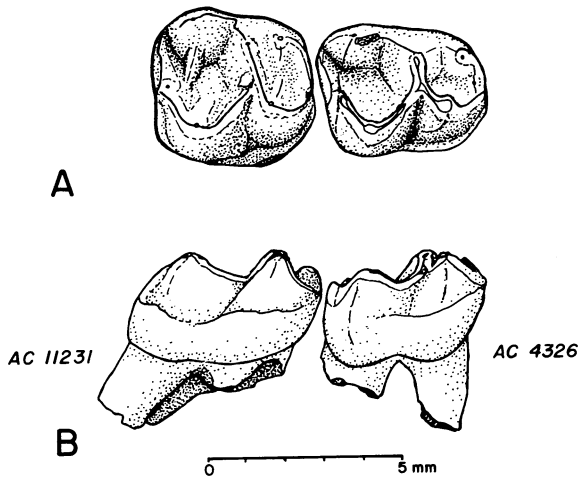
TEXT-FIG. 8 – Type and referred specimen of *Copelemur feretutus* in (A) occlusal and (B) lateral view. ACM 4326 (type) is a right M_1, ACM 11231 is a right M_2, both from Lysite beds in the Wind River Basin.

Bitter Creek Station allocated to this species by Gazin (1962). It measures 5.4 mm in length, 3.4 mm in width, and has a relatively closed trigonid with the reduced paraconid apparently joined to the front of the metaconid. The heel of M_3 is narrow and curved.

Discussion.– The upper dentition of this species is unknown, and the variation in morphology of the lower cheek teeth is inadequately known. A thorough new study of the Bitter Creek Station district is in progress by Savage, Waters, and Hutchison (1972) that should greatly increase our understanding of the morphology and stratigraphic distribution of *Copelemur praetutus*.

Typodigm.– USNM 22262 (type), YPM 14697, and YPM 14698.

Copelemur feretutus, new species

Text-fig. 8

Pelycodus cf. *frugivorus*, Kelley and Wood, 1954, p. 344, fig. 4e.
Pelycodus frugivorus (in part), Guthrie, 1967, p. 21.

Type.– ACM 4326, an isolated right M_1 from the Lysite member, Wind River Formation, Wind River Basin, Wyoming.

Diagnosis.– Differs from *C. praetutus* and *C. consortutus* in being significantly larger, and from *C. tutus* in being significantly smaller. Differs from *C. praetutus* in having relatively broader molars, with the paraconid more closely approximated to the metaconid on M_1 and M_2. Differs from *C. consortutus* and *C. tutus* in having less well developed hypocones and mesostyles on the upper molars.

Etymology.– *fero*, L., to carry or bear, in reference to the probable role of this species in the line leading to *C. tutus*.

Age and Distribution.– upper Wasatchian faunal interval, "Lysite" beds and equivalent, Wind River and Big Horn Basins, northwestern Wyoming.

Description.– There are no mandibles of this species preserving the anterior dentition. M_1 is preserved in two specimens, ACM 4326 (type) and PU 18166. In the type, M_1 measures 4.2 mm in

TABLE 6 — Summary of measurements of the lower and upper cheek teeth of *Copelemur feretutus* from the type locality, Lysite member, Wind River Basin, Wyoming. Measurements in mm. Abbreviations as in Table 1.

		$\underline{n}$	$\underline{OR}$	$\overline{x}$	$\underline{s}$	$\underline{V}$
M_1	L	2	4.1–4.2	4.15	—	---
	W	2	3.5–3.6	3.55	—	---
M_2	L	6	4.0–4.5	4.25	.19	4.4
	W	6	3.6–4.2	3.95	.24	6.1
M_3	L	4	5.3–5.8	5.55	.24	4.3
	W	4	3.3–3.6	3.45	.13	3.7
M^1	L	4	3.8–4.0	3.93	.10	2.4
	W	4	5.3–6.2	5.75	.42	7.3
M^2	L	2	4.2–4.3	4.25	—	---
	W	2	6.3	—	—	—
M^3	L	2	3.4–3.5	3.45	—	---
	W	2	5.2	—	—	---

length and 3.6 mm in width. M_1 has an open trigonid, but in M_2 and M_3, the paraconid is closely approximated to the metaconid to form a closed trigonid. In M_1 and M_2 (text-fig. 8) there is usually a distinct entoconid notch separating the entoconid from the hypoconulid. M_3 has a small rounded heel on the talonid like that in *C. praetutus*.

Two maxillae, ACM 4325 and PU 18365, preserve upper M^{1-3}. The former has a moderate mesostyle crest on the upper molars but it is much weaker on molars of the latter. The hypocone appears to have been weakly developed in both. The upper molars do not differ greatly from those of early *Pelycodus*.

Measurements of the upper and lower dentition of *Copelemur feretutus* are given in Table 6.

Discussion.– The specimens from Lysite beds referred to *Pelycodus frugivorus* by Kelley and Wood (1954) and by Guthrie (1967) all appear to belong to *Copelemur feretutus*. A histogram showing the relationship of these specimens to the contemporary *Pelycodus abditus* from the Lysite is shown in text-fig. 5.

Typodigm.– The following specimens come from the Lysite member of the Wind River Formation, Wind River Basin, Wyoming: ACM 2416, 2509, 2510, 2511, 2821, 2925, 4322, 4325, 4326 (type), 11173, 11231; PU 17691, 18166, 18365.
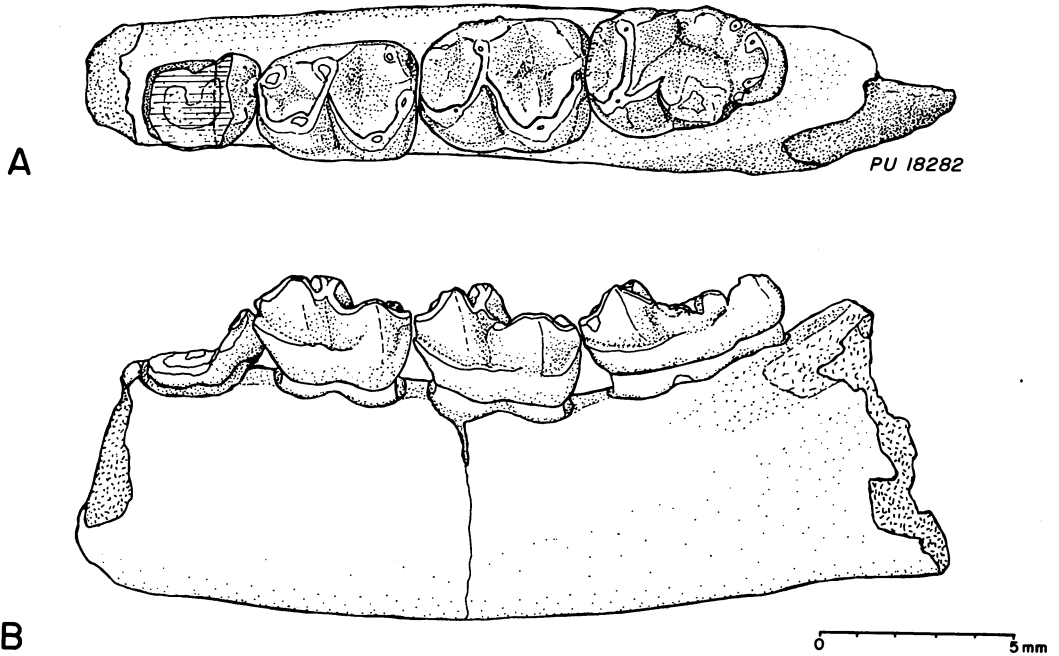
In addition, there are a small number of specimens from upper Lysite equivalent beds in the Big Horn Basin that belong to this species. These include YPM 18669, 23258, and 30393.

Copelemur consortutus, new species

Text-fig. 6a, 9

Pelycodus frugivorus (in part), Matthew, 1915, p. 439, fig. 11.
Notharctus nunienus (in part), Guthrie, 1971, p. 63.

TEXT-FIG. 9 – Type specimen of *Copelemur consortutus*, PU 18282, a left mandible with M_{1-3} in (A) occlusal and (B) lateral view.

Type.– PU 18282, a left mandible collected in 1931 from Alkali Creek, 5 miles northwest of Arminto, Wyoming.

Diagnosis.– Differs from *Copelemur feretutus* and *C. tutus* in being smaller. Differs from *C. feretutus* in tending to have larger mesostyles on the upper molars. Differs from *C. tutus* in retaining more distinct paraconids on M_1 and M_2. Differs from *C. praetutus* in having relatively broader lower molars, with the paraconids on M_1 and M_2 more closely approximated to the metaconids.

Etymology.– *consors*, L., brother, sister, or partner, in reference to the close relationship of this species to its sister species *Copelemur tutus*.

Age and Distribution.– Upper Wasatchian faunal interval, "Lost Cabin" beds and equivalent, known from New Mexico (San Juan Basin), and northwestern Wyoming (Wind River and Big Horn Basins).

Description.– The sample of *Copelemur consortutus* from the type locality is small, consisting of only five mandibles and an isolated upper tooth (see Table 7). For this reason much of the following description will be of a slightly earlier and larger sample of Big Horn Basin specimens from Yale Localities 174, 192, and 193.

One specimen, YPM 28178, preserves the front of the mandible, with an unfused symphysis, alveoli for the canine, a single-rooted P_1, and double-rooted P_2, and the crowns of P_{3-4} and M_1. YPM 28196 and 28258 preserve the crowns of P_{3-4} and M_{1-3}. P_3 has a simple, sharply pointed crown without accessory cusps. P_4 has a similarly sharp protoconid with a small paraconid and a distinct metaconid. The heel of P_4 has a distinct hypoconid and it is extended posteromedially somewhat as in *C. tutus* (AMNH 16205). M_1 and M_2 in most specimens have a deep entoconid notch,

TABLE 7 — Measurements of the lower dentition of *Copelemur consortutus* from the type locality in the Wind River Basin. Measurements in mm. Abbreviations as in Table 1.

	P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W
PU 18282 (type)	—	—	4.0	3.2	4.1	3.5	5.2	3.2
PU 20591	3.6	2.6	3.8	3.4	3.9	3.6	5.1	—
PU 20593	3.6	2.6	4.0	3.4	—	—	—	—
PU 20593	—	—	3.9	3.2	4.2	3.7	—	—
PU 20595	—	—	4.1	3.3	4.2	3.6	5.2	3.1

but the type specimen and several others (e.g., YPM 28239) have this feature less well developed than most. The heel of the talonid on M_3 has the narrow rounded shape typical of *Copelemur*, but a few specimens show a tendency toward developing a median fissure and twinned hypoconulids.

The maxillary dentition is best represented by YPM 27292, having P^4 and M^{1-3} in almost perfect condition. This specimen (from Yale Locality 192) has a small mesostyle crest and no trace of a hypocone on the postprotocingulum of M^1 and M^2. Another specimen from the same locality, YPM 29703, has small hypocones on M^1 and M^2. In most features the upper cheek teeth of *Copelemur consortutus* resemble closely those of early *Pelycodus trigonodus*.

Discussion.— The size of first lower molars in *Copelemur consortutus* from Lost Cabin beds in the Wind River Basin is plotted in text-fig. 5. Comparing this distribution with specimens from Lost Cabin equivalent strata in the San Juan Basin, and comparing the specimens from both areas, it appears that the same species is represented. AMNH 16210 (figured by Matthew, 1915) and AMNH 55504 appear especially close to the type of *C. consortutus*, although there are some minor differences in cusp pattern, especially on the trigonid of M_3.

In measuring specimens from the Lost Cabin beds, Guthrie (1967) confused three species as two, and his measurements were thus incorrect as a result. The distribution of M_1 size from that interval is given in text-fig. 5, which clearly shows that there is more variation than can be accommodated in two species. This difference is important, as it helps to clarify the relationship of Wind River Lost Cabin deposits to those in the Big Horn Basin (compare text-fig. 10 here with fig. 7 in Gingerich, 1976a). Strata equivalent to typical Lost Cabin beds are clearly represented in the Big Horn Basin.

Typodigm.— Five specimens are known from the type locality in the Wind River Basin: PU 18282 (type), 20591, 20593, and 21759.

In addition, the following specimens are known from the San Juan Basin: AMNH 16210, 55501, 55504, 55515, 55518, and 55530. Numerous specimens from the Big Horn Basin are preserved in the Yale collection, among them YPM 27292, 28178, 28196, 28225, 28235, 28239, 28258, 28274, 28287, 29703.

<div align="center">

Copelemur tutus (Cope, 1877)

Pl. 1, fig. 3; text-fig. 6b

</div>

Tomitherium tutus Cope, 1877, p. 141, Pl. 39, fig. 19.
Pelycodus tutus (in part), Cope, 1881, p. 187. Cope, 1885, p. 228.

Pelycodus tutus, Matthew, 1915, p. 441, fig. 15.
Pelycodus? *tutus*, Gazin, 1962, p. 29.

Type.— Unnumbered right mandible with P_{3-4} and M_1, now lost, from the Wasatchian of New Mexico. AMNH 16206 (Pl. 1, fig. 3) is a good topotype preserving M_1 and M_2.

Diagnosis.— Differs from other species of *Copelemur* in being significantly larger (see Table 3).

Age and Distribution.— The type comes from Almagre or Largo strata, late Wasatchian age, "Lost Cabin" beds equivalent, known only from the San Juan Basin of New Mexico.

Description.— The type specimen of *Copelemur tutus* was well figured by Cope (1877, Pl. 39, fig. 19); it shows clearly the very deep entoconid notch on M_1 characteristic of this species and of the genus. Cope (1877, p. 142) published the length and width of M_1 as well, so the species is well established even though the type specimen is lost. M_1 in the type measured 5.0 mm in length and 4.5 mm in width.

Cope's type specimen preserved alveoli for the lower canine, a single-rooted P_1, double-rooted P_2, and the crowns of P_{3-4} and M_1. Three additional mandibles are known, which show that open trigonids characterize all the lower molars, the paraconids being small and rather anteriorly placed. M_1 and M_2 have the very deep entoconid notch characteristic of the genus (text-fig. 12). M_3 has a simple, narrow, rounded heel on the talonid. Otherwise the lower dentition most closely resembles that of *Pelycodus*.

A single upper molar, M^1 or M^2 (AMNH 55462) is known that has a relatively small hypocone, and a small but distinct mesostyle cusp connected to the ectoloph by a fine crest. A paraconule is present, but there is no metaconule, and there is no lingual cingulum on this particular tooth.

Discussion.— *Copelemur tutus*, the type species of the genus, is a rare but distinctive element in the Wasatchian fauna of the San Juan Basin. Judging from the distribution shown in text-fig. 5, it is possible that *C. tutus* in the Largo replaced *Pelycodus jarrovii* ecologically, the latter apparently being confined to the Almagre facies.

Gazin (1962, p. 29) questioned whether this species really belongs in the genus *Pelycodus*. It is clearly distinctive and we have placed it in the new genus *Copelemur*, but it is nevertheless most closely related to *Pelycodus*.

Typodigm.— AMNH 16205-16207, 55462. No other specimens of this species are known.

PHYLOGENY AND EVOLUTION

At the beginning of this paper we outlined our approach to phylogeny reconstruction for groups of animals that have a reasonably dense and continuous fossil record. The first requirement is a sound stratigraphic framework, and it has been provided in the present case by the measured stratigraphic sections of Meyer and Radinsky, and Neasham and Vondra. The second requirement is a detailed study of morphological variation within each locality sample — this too has been done, as was illustrated above in the section of the paper on dental variation in *Pelycodus*. The final step in organizing data for stratophenetic analysis is to integrate the distribution of variation seen in each locality sample or stratigraphic interval into the general stratigraphic framework.

The organization of dental size and variation in early Eocene Adapidae from the central Big Horn Basin in Wyoming is illustrated in the raw data plotted in text-fig. 10. This data has been further interpreted, based on stratophenetic linking of very similar samples in adjacent stratigraphic intervals, and it yields the pattern of lineages shown by dashed lines in text-fig. 10. Studied in stratigraphic context, it is clear that a single lineage of *Pelycodus* was present in the Big Horn Basin through most of the Wasatchian, but two lineages are present in Lost Cabin beds. Furthermore, a distinct lineage of *Copelemur* is present in both Lysite and Lost Cabin beds in the Big Horn Basin (and possibly in upper Gray Bull beds as well).

Given the pattern of phylogeny in text-fig. 10, and the details of morphological change discussed in the section of this paper on systematics, it is possible to subdivide each lineage into a sequence of valid species. *Pelycodus ralstoni* evolved into *P. mckennai*, which evolved into *P. trigonodus*, and so forth. While the distinction between lineages is nonarbitrary, it must be emphasized that the exact boundary between successive species within a lineage is arbitrary (although each species as a whole can be distinguished morphologically). No natural breaks are obvious, and it is necessary for ease of discussion and for use in biostratigraphy to make essentially artificial boundaries between species. It turns out, largely for historical reasons, that these correspond fairly well with established subdivisions of the Wasatchian (Sand Coulee, lower Gray Bull, etc. — which themselves are poorly defined at present). Since the boundaries between time successive species must be time-parallel to make taxonomic diversity reflect biological diversity, the successive species of *Pelycodus* can potentially serve as a useful substitute in zonation of the Wasatchian, pending a full scale faunal study of this interval of evolutionary history. In this connection it is important to emphasize that the distinctions between species are based on comparisons of whole samples from each locality, and the transitions between species appear in every case to be continuous and gradual. Thus any zonation based on *Pelycodus* could be used, at best, to subdivide the Wasatchian into five subunits.

Our primary interest in studying *Pelycodus* and *Copelemur* has not been biostratigraphic zonation of the Wasatchian, but rather the patterns of phylogeny and evolution exhibited by these genera. The genealogical relationships of the species of *Copelemur* are still somewhat obscure, owing to the inadequate stratigraphic record of these species. The only reasonably certain relationship is the ancestor-descendant relationship of *C. feretutus* and *C. consortutus*. Within *Pelycodus*, on the other hand, we can be much more certain about genealogical relationships. The four species from *P. ralstoni* to *P. abditus* appear to be a single ancestor-descendant sequence, with *P. abditus* giving rise to both *P. frugivorus* and *P. jarrovii*.

As we discussed in the introductory sections of this paper, body size is an important component of an animal's adaptation, and tooth size provides an important basis for studying relative body size. The pattern of change seen in tooth size (and, by inference, in body size) is shown in text-figs. 10 and 11. The major lineage of *Pelycodus* became progressively larger through the course of the Wasatchian, except for *P. frugivorus* which became smaller. The one lineage of *Copelemur* documented in text-fig. 10 also became smaller. *Pelycodus frugivorus* and *P. jarrovii* apparently exhibit some kind of character divergence in geological time, although this has not yet been fully studied.

For comparison, one of us (P. D. G.) has initiated a new collecting program in Wasatchian sediments of the northern Big Horn Basin (Sand Coulee area) where fossils are abundantly preserved in a well exposed sequence of sediments spanning the "Sand Coulee" through upper "Gray Bull" faunal subdivisions. In two seasons to date more than 200 mandibles and maxillae of *Pelycodus* have been collected, although section measuring is still in progress and only 35 of these can yet be plotted stratigraphically. These are plotted in text-fig. 11 on a vertical scale adjusted to be comparable to that in text-fig. 10. Even given the small number of samples available to date, it is clear that the same pattern of *Pelycodus ralstoni* evolving into *P. mckennai* which in turn becomes *P. trigonodus* is shown here as was shown in the central Big Horn Basin. Obviously, an important future step will be to study *Pelycodus* in southern Wyoming, Colorado, or New Mexico in a similar way to see if the evolutionary patterns seen there are the same. The fact that several species, such as *P. frugivorus* and *P. jarrovii*, are found in both New Mexico and Wyoming strongly suggests that similar phylogenetic patterns will be found in both areas, but it is nevertheless of great importance to test this.

In addition to evolutionary change in tooth size and body size, one can study the patterns of change in other characters of *Pelycodus* and *Copelemur* as well. An attempt has been made in text-fig. 12 to quantify the acquisition of a mesostyle and hypocone in *Pelycodus*. This clearly happened gradually, the earliest samples of *P. ralstoni* from Sand Coulee beds having neither cusp. Mesostyle crests appear in various stages of development in *Pelycodus* with larger specimens (both within

population samples and comparing successive populations) having stronger mesostyle crests. Finally, both the large and small Lost Cabin species of *Pelycodus* have large *Notharctus*-like mesostyle cusps. The development of the hypocone shows the same pattern, but its development is retarded with respect to the evolution of the mesostyle. Hence the upper Gray Bull species *P. trigonodus* tends to have a distinct mesostyle crest but no hypocone, an interesting example of the mosaic pattern of evolution of morphological characteristics. Schoeninger (1976) studied the functional significance of the evolution of a mesostyle in *Pelycodus* and in the living *Alouatta* and concluded that the mesostyle
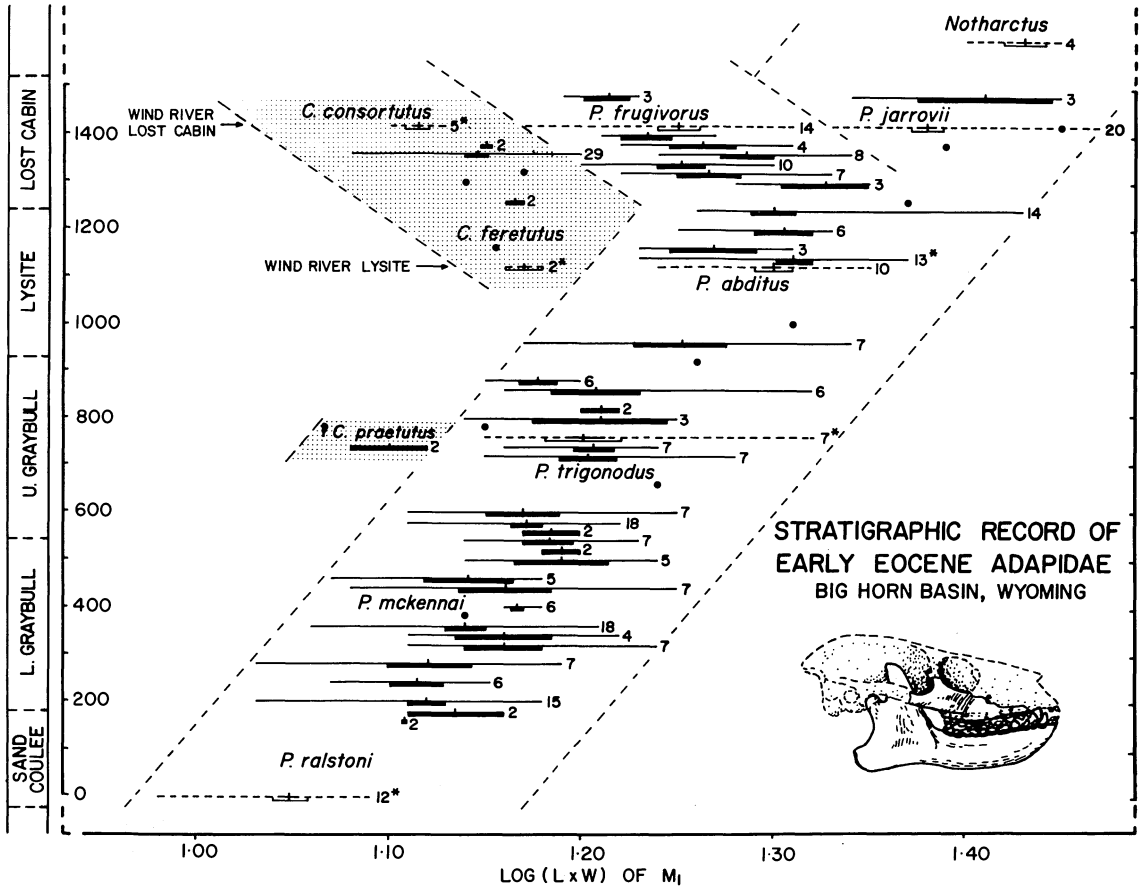
TEXT-FIG. 10 — Stratigraphic distribution of *Pelycodus* and *Copelemur* in the Big Horn Basin, Wyoming, based on collections in the Yale Peabody Museum and the Museum of Paleontology, University of Michigan. Solid lines show sample range, vertical slash is mean, bar is standard error of mean, and small numerals are sample size. Vertical axis is measured stratigraphic section (in feet) spanning most of Wasatchian, dated at approximately 53 my to 49 my before present, based on Gingerich (1976a, fig. 2). Oblique dashed lines show pattern of phylogenetic relationships inferred from data. Horizontal dashed lines with open bars show important samples of *Pelycodus* and *Copelemur* not in measured sections, from: Sand Coulee area (*P. ralstoni*), central Big Horn Basin (*P. trigonodus*), Wind River Lysite beds (*C. feretutus* and *P. abditus*), and Wind River Lost Cabin beds (*C. consortutus, P. frugivorus,* and *P. jarrovii*). Asterisks mark typodigm of valid named species. Pattern for *Pelycodus* modified slightly from Gingerich (1976a, fig. 7) by addition of new samples and reanalysis of Lost Cabin samples. Note close relationship of *P. jarrovii* to sample of *Notharctus* from Carter Mountain in the Big Horn Basin. Note also the separate evolutionary identity of *Copelemur* in the Big Horn Basin.

functions to puncture leaves during the initial stage of their mastication, but no comparable study has been made of the functional significance of the hypocone in *Pelycodus* (or in *Alouatta*). The evolution of the upper molar dentition in the sequence from *Pelycodus ralstoni* to *P. jarrovii* is illustrated in text-fig. 13. Only five stages of evolution are represented, but they illustrate the general trend toward increased size, larger mesostyles, and larger hypocones in this lineage of *Pelycodus*.

As a final point we should consider the relationship of early Eocene Adapidae to their middle Eocene descendants. As text-fig. 10 and all other evidence suggests, *Notharctus* is a direct descendant of *Pelycodus jarrovii*. The species of *Notharctus* present in the Bridger A or "Gardnerbuttean" interval of the middle Eocene (McGrew and Sullivan, 1970; Robinson, 1966) is significantly larger than *P. jarrovii* but otherwise practically indistinguishable. The origin of *Smilodectes*, however, is a more difficult and still unsolved problem. *Smilodectes* could be derived from either *Pelycodus frugivorus*, or from *P. jarrovii*. The latter possibility seems more likely, but further detailed stratigraphic and morphological study will be required to confirm this.

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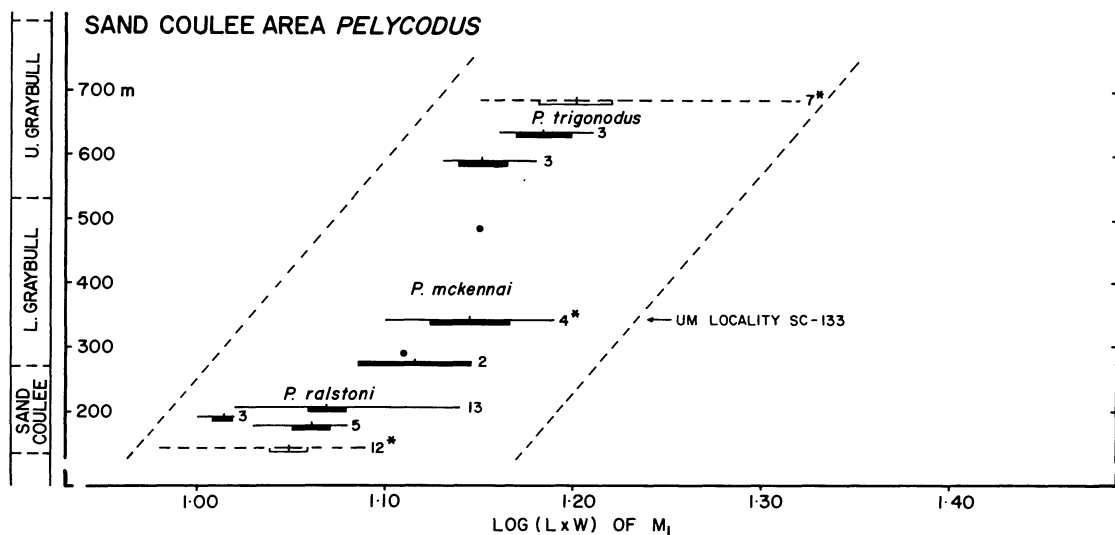
TEXT-FIG. 11 — Stratigraphic distribution of *Pelycodus* in the Sand Coulee area of the northern Big Horn Basin, Wyoming. Vertical scale (in meters) adjusted to match rate of evolutionary change in text-fig. 10. Symbols and type samples of *P. ralstoni* and *P. trigonodus* same as text-fig. 10. All specimens in the Museum of Paleontology, University of Michigan.

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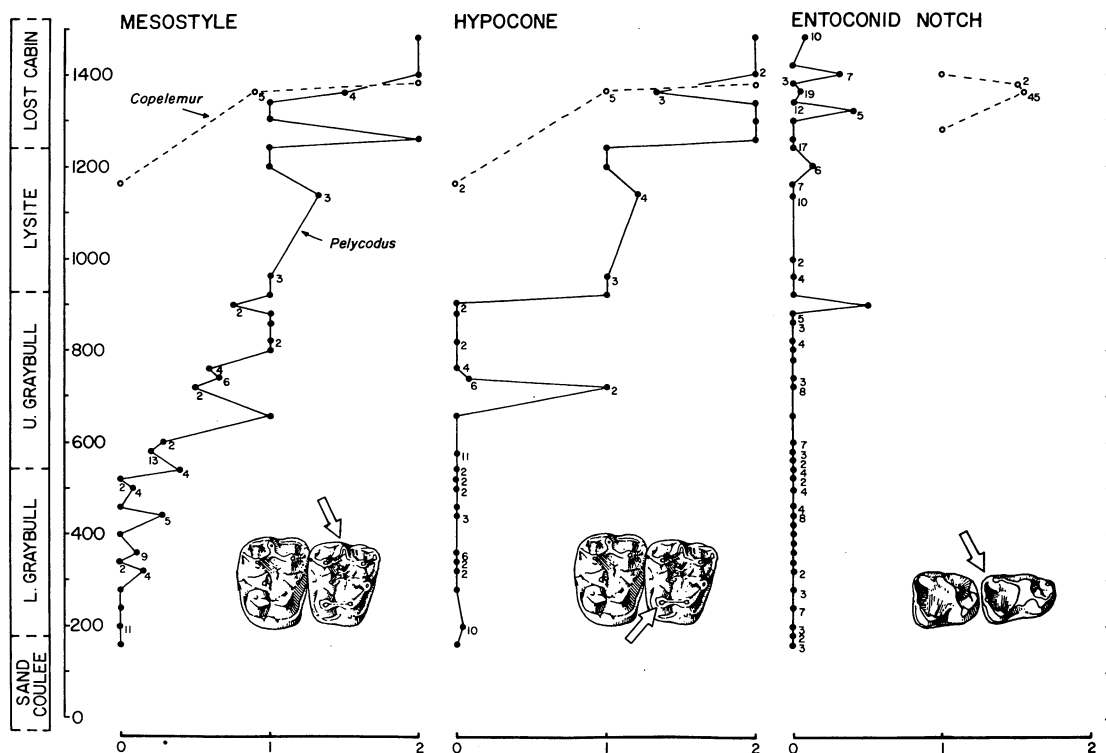
TEXT-FIG. 12 — Pattern of evolutionary change in the mesostyle, hypocone, and entoconid notch in *Pelycodus* and *Copelemur* from the Big Horn Basin, based on collections in the Yale Peabody Museum. Fully developed features are shown by arrows in inset figures. Each character was scored on a scale from 0 to 2 depending on whether it was absent, present, or strongly developed. Vertical axis same as in text-fig. 10. Solid circles and lines show pattern of change in mean values for *Pelycodus*. Open circles and dashed lines show pattern of change in mean values for *Copelemur*. Note that evolution of a mesostyle preceded evolution of a hypocone in *Pelycodus*. Note also failure to establish an entoconid notch in *Pelycodus*, while it characterizes specimens of *Copelemur*.
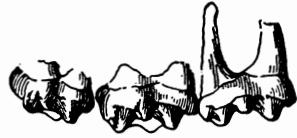
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TEXT-FIG. 13 — Evolution of upper molars in the lineage from *Pelycodus ralstoni* to *Pelycodus jarrovii*, all drawn to same scale. Note increasing size, enlarging mesostyle, and enlarging hypocone as documented in text-figs. 10 and 12. All figures (except B) from Matthew (1915), slightly more than twice natural size.
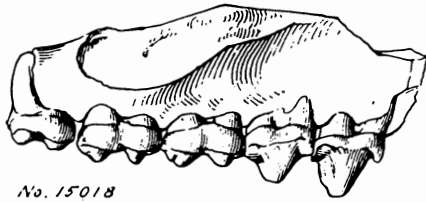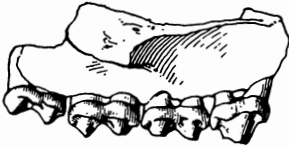
No. 15018
A. M.

No. 14637
A. M.

E

P. jarrovii

D

P. abditus

No. 15017
A. M.

P. trigonodus

C

No. 67113
U. M.
(rev.)

P. mckennai

B

Evolution of Upper Molars
in Early Eocene *Pelycodus*

No. 16089
A. M

P. ralstoni

A

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