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Late Eocene Rodents (Mammalia) from Inner Mongolia[1]

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INTRODUCTION

Until recently one of the great gaps in the earlier Tertiary record of rodents was the absence of Eocene rodents from Central Asia. Now, however, reports of upper Eocene rodents from the areas of Irdin Manha and Ula Usu, Inner Mongolia, have come as a result of the work of the Sino-Soviet Paleontological Expedition in 1959 (Chow and Rozhdestvensky, 1960), and a systematic study by Li (1963) documented the first Asian occurrence of a paramyid and sciuravids from the upper Eocene of Inner Mongolia and Honan, North China, respectively. In addition to these records, a re-examination of the collections of the Central Asiatic Expeditions of the American Museum of Natural History, made in the 1920's and in 1930, has revealed the lower jaws and teeth of the upper Eocene rodents that are reported in the present paper. Paramyids and a new genus, possibly having affinities with sciuravids, are represented.

The Inner Mongolian localities of the Central Asiatic Expeditions where these rodents were found are: Irdin Manha; Chimney Butte, North Mesa; Camp Margetts; near Camp Margetts; 7 miles west of Camp Margetts; and 25 miles east of Iren Dabasu. According to Radinsky (1964), the first two of these, Irdin Manha and the Ulan Shireh formation at Chimney Butte, North Mesa, produce faunas that are

[1] Publications of the Asiatic Expeditions of the American Museum of Natural History, Contribution No. 156.

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similar in age, older than the Shara Murun fauna, and thus approximately early late Eocene in age. Faunas from localities in "Irdin Manha" beds at and in the vicinity of Camp Margetts may not be homogeneous; though late Eocene in age, their precise age and ecologic relationships to Irdin Manha faunas are uncertain. Position within the upper Eocene of ?Irdin Manha beds 25 miles east of Iren Dabasu is likewise uncertain.

Thanks are extended to Mr. John J. Burke for suggesting a study of the collections of fossil rodents of the Central Asiatic Expeditions; to Drs. Leonard B. Radinsky and Malcolm C. McKenna for finding the specimens in the collections and for discussions of Mongolian stratigraphy and faunas; and to Dr. McKenna for the loan of specimens. I appreciated also discussion of these rodents with Drs. Craig C. Black, Abbé René Lavocat, Robert W. Wilson, and Albert E. Wood. The photographic illustrations were prepared by Mr. Chester Tarka. This study was facilitated by a grant from the Gulf Oil Corporation.

SYSTEMATIC DESCRIPTIONS

ORDER RODENTIA

FAMILY PARAMYIDAE

Paramyid spp.

Three localities yielded paramyids of a rather generalized nature that seem to fit within the paramyine-reithroparamyine groups of Wood (1962). The known specimens form an inadequate basis for detailed systematic determinations but show that at least two and possibly three species are represented.

Five isolated teeth, A.M.N.H. No. 20176, including three incisors, left P_4, and right M_1 or M_2, are from the Irdin Manha beds (Central Asiatic Expedition, 1923). Although the association of these specimens may be questioned, reference of the premolar and molar to one species is suggested by similarities in size and general morphology. The well-worn premolar has a marginal, non-crested entoconid separated by a groove from the short posterolophid. The molar, less worn, has a small trigonid basin, marginal entoconid, curved posterolophid, and strong ectolophid. The entoconid is not crested, but a cuspule occurs lateral to it.

A slightly smaller paramyid is represented by A.M.N.H. No. 80800 (fig. 1), a left jaw fragment with M_{2-3} from the "Irdin Manha" beds, 7 miles west of Camp Margetts (labeled also "probably below Houldjin gravels"). The teeth are simple. M_2 has a small, non-crested entoconid and a short posterolophid that is separated from the entoconid by a

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF PARAMYID TEETH

	A.M.N.H. No. 20176	A.M.N.H. No. 20235	A.M.N.H. No. 80800	A.M.N.H. No. 80801
P_4				
Anteroposterior	3.9	—	—	—
Width of trigonid	3.0	—	—	—
Width of talonid	3.6	—	—	—
M_1				
Anteroposterior	—	—	—	2.2
Width of trigonid	—	—	—	2.1
Width of talonid	—	—	—	2.2
M_2				
Anteroposterior	—	—	3.4	2.3
Width of trigonid	—	—	3.4	2.4
Width of talonid	—	—	3.7	2.4
M_3				
Anteroposterior	—	—	4.1	—
Width of trigonid	—	—	3.5	—
Width of talonid	—	—	—	—
Molar				
Anterposterior	3.9	4.7	—	—
Width of trigonid	3.6	4.9	—	—
Width of talonid	3.8	4.4	—	—

shallow groove. The lower incisor is narrower anteriorly than the incisors included in A.M.N.H. No. 20176. The masseteric fossa reaches forward to a line below the middle of M_2. Slightly smaller teeth, a weaker ectolophid, and the absence of a cuspule lateral to the entoconid differentiate the molars of this paramyid from the molar in A.M.N.H. No. 20176, but whether specific or individual differences are involved remains a question.

A larger paramyid, A.M.N.H. No. 20235, left M_1 or M_2, comes from the ?Irdin Manha beds, 25 miles east of Iren Dabasu. Metalophulid II is longer than that in A.M.N.H. Nos. 20176 and 80800, and the entoconid is crested and separated by a deeper groove from the posterolophid, which has a slightly raised hypoconulid. The tooth resembles the paramyine tooth from near Irdin Manha described by Li (1963, p. 160, pl. 1, fig. 3) in having a crested entoconid, complete ectolophid, and in the general shape of the posterolophid, but it has a longer metalophulid II and is slightly larger. The similarities suggest relationship, but whether the two teeth represent the same paramyid species cannot be determined from available specimens.

?PARAMYID SP.

A rodent smaller than the above paramyids, A.M.N.H. No. 80801, left jaw with M_{1-2} from "Irdin Manha" beds at Camp Margetts, has teeth so worn and eroded as to make identification difficult. However, paramyid affinities are suggested by the marginal entoconid, short, anteroposteriorly narrow posterolophid, and the general proportions of the molars. On the jaw a large mental foramen is in line with the anterior wall of P_4, and a small pit below the talonid of P_4 may be a second mental foramen. The species represented is different from the paramyids discussed above.

FAMILY ?SCIURAVIDAE

ADVENIMUS,[1] NEW GENUS

TYPE SPECIES: *Advenimus burkei*, new species.

REFERRED SPECIES: *Advenimus bohlini*, new species.

DISTRIBUTION: Late Eocene, Inner Mongolia.

GENERIC CHARACTERS: Dental formula, $_{1\ 0\ 1\ 3}$. Cheek teeth brachydont; increase in size from P_4 to M_3; having four cuspate conids, of which lingual conids of molars are crested and forming transverse lophs following wear. On molars trigonid basin oriented anteroexternally to posterointernally, open posteriorly; metalophulid II short; posterior wall of metaconid descending steeply into central basin; ectolophid weak, well set in from buccal wall. Hypoconulid very prominent, essentially independent cusp on little-worn M_{1-2}, large but less distinctly cuspate on M_3. P_4 having anterior cingulum, hypoconulid relatively smaller than on molars.

Advenimus burkei,[2] new species

Figures 2–4

TYPE SPECIMEN: A.M.N.H. No. 26664, partial left jaw with M_{1-3}, broken incisor.

HYPODIGM: Type, and A.M.N.H. No. 26665, partial right jaw with P_4–M_2.

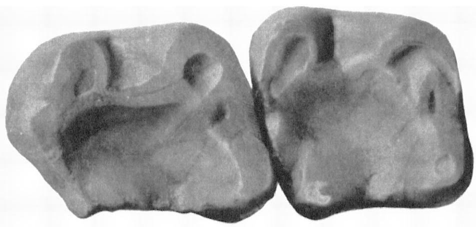
[1] From Latin *advena* (stranger) and *mus* (mouse).

[2] For John J. Burke, in appreciation of his work on earlier Tertiary rodents.

Horizon and Locality: Upper Eocene, "Irdin Manha" formation; near Camp Margetts, Mongolia (Central Asiatic Expedition, 1930).

Specific Characters: On P_4 well-developed cingular shelf on anterior wall, talonid slightly narrower than trigonid, hypoconid low. Entoconid crest on M_1 directed posterior to hypoconid, on M_2 toward or anterior to hypoconid. Masseteric fossa extending forward to line below middle of M_2.

1



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Figs. 1, 2. Occlusal views of rodent teeth. 1. Paramyid sp., A.M.N.H. No. 80800, left jaw with M_{2-3}. ×8. 2. *Advenimus burkei*, A.M.N.H. No. 26665, right jaw with P_4–M_2. ×12.

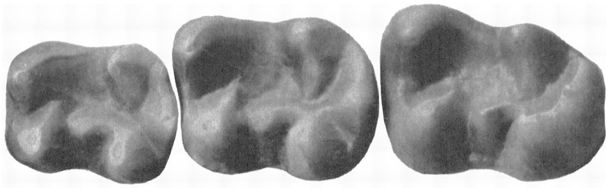
Description: (Additions to generic and specific characters). Both specimens represent relatively young individuals, having little wear on the cheek teeth, more in A.M.N.H. No. 26665 (fig. 2) than in A.M.N.H. No. 26664 (fig. 3). The teeth increase in both transverse and anteroposterior dimensions from P_4 to M_3. The premolar differs from the molars in having a shelf-like cingulum low on its anterior face and a relatively smaller, anteroposteriorly compressed hypoconulid. The hypoconid is lower than the hypoconulid and the other conids and has the appearance of a rounded anteroexternal swelling on the flank of the compressed hypoconulid. The ectolophid is rudimentary, the metaconid is not

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF *Advenimus* AND CF. *Advenimus* SP.

	A. burkei		*A. bohlini*	Cf. *Advenimus* sp.		
	A.M.N.H. No. 26664	A.M.N.H. No. 26665	A.M.N.H. No. 26294	A.M.N.H. No. 26291	A.M.N.H. No. 26292	A.M.N.H. No. 26293
P_4						
Anteroposterior	—	2.0	1.4	2.0+	—	*ca.* 2.2
Width of trigonid	—	1.4	0.9	1.7+	—	—
Width of talonid	—	1.3+	1.0	1.8	—	—
M_1						
Anteroposterior	2.3+	2.1	1.5	2.2	2.3	2.3
Width of trigonid	1.7	1.6	1.1	2.0	2.0	2.0
Width of talonid	1.8+	1.8+	1.3	2.0+	2.1	2.2
M_2						
Anteroposterior	2.7	2.2+	1.6	2.5	2.8	2.6
Width of trigonid	2.0+	1.9	1.3+	2.5	2.4	2.6
Width of talonid	2.1+	2.1+	1.4	2.5	2.6	2.7+
M_3						
Anteroposterior	2.9	—	—	2.9+	3.2	—
Width of trigonid	2.2	—	—	2.5	2.5	—
Width of talonid	2.0	—	—	2.3	2.6	—
P_4–M_3, length	—	—	—	9.6	—	—
M_1–M_3, length	7.6	—	—	7.6	8.0	—
Width of lower incisor	*ca.* 1.2+	—	—	1.4	1.5	—
Inside depth of jaw at M_1	*ca.* 5.7	—	3.4	7.4+	7.5	—

crested, and the entoconid, though basically cuspate, displays a trace of a crest directed toward the hypoconulid. On the anterior surface of P_4 a flattened wear facet occurs on the protoconid; a smaller facet, on the metaconid. Anterior wear on P_4 in rodents is normally produced through occlusion with P^3, and these facets suggest that P^3 was present in *Advenimus*. On each molar the metaconid crest forms the anterolingual wall, the ectolophid is better developed than on P_4, and a mesoconid occurs on the ectolophid. The pattern of M_1 resembles that of M_2 in most features, but these teeth differ in the orientation of the entoconid crest. On M_1 the relatively straight crest is directed obliquely backward toward the groove between the hypoconid and hypoconulid. On M_2 the crest is variable but forms a more complete hypolophid; in A.M.N.H. No. 26665



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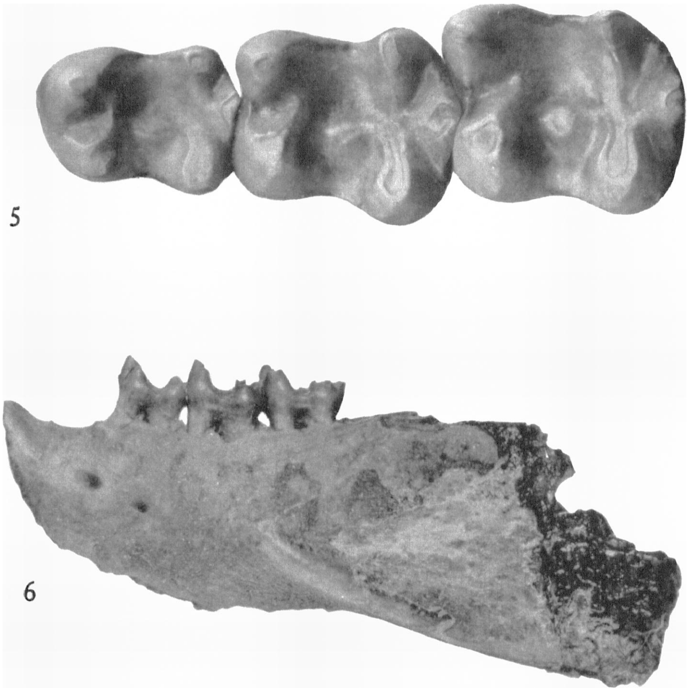
FIGS. 3, 4. *Advenimus burkei*, type specimen, A.M.N.H. No. 26664, left jaw with M_{1-3}. 3. Occlusal view of teeth. × 10. 4. Lateral view of jaw. × 5.

it is directed toward the hypoconid; and in A.M.N.H. No. 26664 it is slightly concave anteriorly and directed toward the ectolophid just anterior to the hypoconid. The large hypoconulid on M_{1-2} is crested buccally and lingually. The hypolophid on M_3 is concave anteriorly and is in contact with the ectolophid in front of the hypoconid. On this tooth the hypoconulid is not a distinct cusp, as on the more anterior teeth, but rather seems to be incorporated into a posterolophid that is in contact with the posterior side of the hypoconid.

The lower incisor, as shown by a broken cross section in A.M.N.H. No. 26664, is transversely narrow and has very slightly convex anterior, medial, and lateral walls. The jaw (fig. 4), incompletely known, has a shallow masseteric fossa that is bordered by a distinct ventral ridge and a less well-marked dorsal rim. Two mental foramina are shown by A.M.N.H. No. 26665, a larger one in line with the anterior wall of P_4, and a smaller, with the talonid of that tooth.



FIGS. 5, 6. *Advenimus bohlini*, type specimen, A.M.N.H. No. 26294, left jaw with P_4–M_2. 5. Occlusal view of teeth. ×20. 6. Lateral view of jaw. ×7.

Advenimus bohlini,[1] new species

Figures 5, 6

TYPE SPECIMEN: A.M.N.H. No. 26294, partial left jaw with P_4–M_2.

HYPODIGM: Type only.

HORIZON AND LOCALITY: Upper Eocene, Ulan Shireh formation; Chimney Butte, North Mesa, Shara Murun region, Mongolia (Central Asiatic Expedition, 1928).

SPECIFIC CHARACTERS: Smaller than *A. burkei*. On P_4 rudimentary cingulum on anterior wall, talonid slightly wider than trigonid. On M_{1-2} hypoconulid less crested than in *A. burkei*, entoconid crest directed toward hypoconid. Masseteric fossa extending forward to line between M_1 and M_2, V-shaped anteriorly.

DESCRIPTION: (Additions to generic and specific characters). The pre-

[1] For Birger Bohlin, in appreciation of his extensive studies on Asian fossil rodents.

molar in this smaller species of *Advenimus* (fig. 5) differs from that in *A. burkei* in having a less well-developed anterior cingulum, a wider talonid than trigonid, and a better developed hypoconid, which resembles in general that on the molars. The entoconid crest is directed toward the hypoconulid. A wear facet on the anterior face of the protoconid, as in *A. burkei*, suggests that P^3 was present. The hypoconulids of P_4 and M_1 appear to be more rounded and cuspate, with less lateral and medial cresting, than those of *A. burkei*. An anterior ridge connects the hypoconulid of M_2 to the posteromedial side of the hypoconid. The entoconid crests of M_{1-2} are directed toward the hypoconid, forming essentially complete hypolophids.

The masseteric fossa is bounded ventrally by a strong ridge (fig. 6), more prominent than that in *A. burkei*. Although the known jaw is incomplete, the posteriormost part preserved shows that the ventral edge of the jaw is bent inward somewhat. Two mental foramina are present, the larger in line with the anterior wall and the smaller with the middle of P_4.

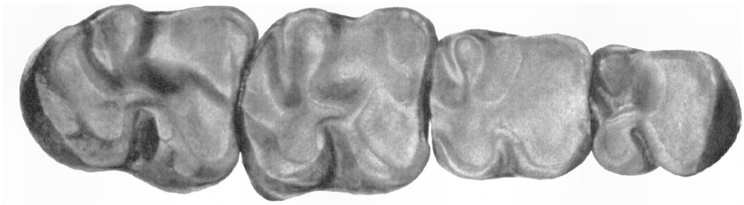
Cf. *Advenimus* sp.

Figures 7, 8

Specimens: A.M.N.H. Nos. 26291, incomplete right jaw with P_4–M_3; 26292, incomplete left jaw with M_{1-3}; 26293, incomplete right jaw with P_4 (broken), M_{1-2}.

Horizon and Locality: Upper Eocene, Ulan Shireh formation; Chimney Butte, North Mesa, Shara Murun region, Mongolia (Central Asiatic Expedition, 1928).

Description and Discussion: The cheek teeth of these three specimens are well worn. The pattern that remains on the molars (fig. 7) shows the following characters: protoconid with short metalophulid II; metaconid as the highest cusp and forming anterointernal wall of tooth; ectolophid well set in and uniting the protoconid and hypoconid; well-developed posterolophid; hypolophid directed toward hypoconid on M_1, anterior to hypoconid on M_{2-3}. On P_4 a flattened wear facet occurs on the anterobuccal side, the crest of the entoconid extends back toward the small, raised hypoconulid, and in A.M.N.H. No. 26293 a trace of an anterior cingulum is present on the anterior wall. The teeth increase in size from P_4 to M_3. The lower incisor in broken section is narrow transversely. The masseteric fossa extends forward to a line below the trigonid of M_2 or between M_1 and M_2 and is bordered ventrally by a strong ridge. The ridge continues for a short distance anterior to the fossa also (fig. 8). Two



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8

FIGS. 7, 8. Cf. *Advenimus* sp. 7. A.M.N.H. No. 26291, right jaw with P_4–M_3. Occlusal view of teeth. ×10. 8. A.M.N.H. No. 26293, right jaw with P_4–M_2. Lateral view of jaw. ×3.

mental foramina, one below the trigonid of P_4 and a larger one slightly higher and more anterior in position, occur in A.M.N.H. Nos. 26291 and 26293; in A.M.N.H. No. 26292 a single elongate foramen, constricted posteriorly and present below P_4, may represent a fusion of two foramina. The rodent represented by these specimens is considerably larger than *Advenimus bohlini*, which is also from the Ulan Shireh formation at Chimney Butte, North Mesa, but only slightly larger than *A. burkei* from the "Irdin Manha" beds near Camp Margetts.

Although comparisons and a determination of the affinities of this larger Ulan Shireh rodent are difficult on the basis of available specimens, the following similarities suggest relationship to *Advenimus:* increase in size of cheek teeth from P_4 to M_3; general pattern of molars having short metalophulid II and hypolophid, ectolophid well set in; anterior cingulum and reduced hypoconulid on P_4; transversely narrow incisor;

position and development of masseteric fossa; two mental foramina. In the stage of wear shown in A.M.N.H. Nos. 26291, 26292, and 26293, the molars have a simple posterolophid that, although elevated somewhat, does not resemble the cuspate hypoconulid found in this region in *A. burkei* and *A. bohlini.*

Until the rodent represented by these specimens is known from less worn teeth, it seems desirable to leave its taxonomic assignment indefinite. Though similarities in several characters suggest reference to *Advenimus*, known specimens of this rodent show a generalized enough pattern to resemble also the tooth from Honan referred to by Li (1963, p. 157) as *Sciuravus* sp.

DISCUSSION

Relationships of *Advenimus*

A combination of characters, including a reduced P_4, the proportions of the tooth row with increase in size of teeth from P_4 to M_3, and the enlarged, prominent hypoconulid on the molars, sets *Advenimus* apart from other known early rodents. In the basic structure of the cheek teeth, however, *Advenimus* has several characters in common with the Sciuravidae. Among these characters are: brachydonty; entoconid well developed on molars, separated posteriorly from posterolophid, and crested to form more or less complete hypolophid; and metalophulid II short, directed posterointernally. *Advenimus* resembles sciuravids also in the position of the anterior border of the masseteric fossa below M_1 or the region between M_1 and M_2. If occlusal wear on P_4 has been interpreted correctly (see descriptions), P^3 was present in *Advenimus*, and thus its dental formula, $\frac{1}{1}\frac{0}{0}\frac{2}{1}\frac{3}{3}$, would correspond to that in sciuravids. Among sciuravids that are older than or contemporary with *Advenimus* may be found certain features suggestive of the distinctive characteristics of *Advenimus*. For example, P_4 is reduced in *Sciuravus? rarus* of the middle Eocene (Wilson, 1938, pp. 136–137) and *S. powayensis* of the upper Eocene (Wilson, 1940, p. 89). The middle Eocene *S. bridgeri* has a moderately well-developed hypoconulid (Wilson, 1938, p. 134) that, although much less prominent than that of *Advenimus*, might suggest a potential among sciuravids for the development of the emphasized hypoconulid characteristic of *Advenimus*.

Thus, on the basis of known lower jaws and teeth, *Advenimus* seems to be morphologically closest to the sciuravids. How much taxonomic weight should be placed on these similarities is, however, uncertain. As Wilson (1949, p. 96) has pointed out, the pattern of the upper teeth, particularly the structure of the hypocone, may be more significant taxonomically for primitive rodents than that of the lower teeth. Until it is more completely known, in light of its distinctive characters and the very incomplete earlier Tertiary record of rodents in Asia, only a tentative familial reference of *Advenimus* to the ?Sciuravidae is considered here to be the most reasonable expression of its probable relationships.

The characteristics that set *Advenimus* most clearly apart from other early rodents seem to associate this rodent with the Ctenodactylidae, rodents that appear first in the upper Oligocene of Mongolia. Comparisons of *Advenimus* with *Karakoromys*, the most primitive upper Oligocene ctenodactylid, show the resemblance most strongly in an increase in the size of the teeth from P_4 to M_3; the reduction of P_4 through diminution of the talonid and especially of the hypoconid, which is a low cusp in *A. burkei* and essentially lacking in *Karakoromys*; and in having an enlarged hypoconulid on the molars and a strong ridge below the masseteric fossa. By the late Oligocene, ctenodactylid cheek teeth are markedly modified from a primitive pattern, with new connections of cusps and lophs that have been related by Bohlin (1946, pp. 82–90) to obliquely forward and inward occlusal movements. One notable difference from the lower molars of *Advenimus* is a shifting forward of the hypolophid, which is in contact with the ectolophid well in advance of the hypoconid in *Karakoromys* and *Tataromys*. Hypolophid-ectolophid contact in *Advenimus* is more like that on dP_4 in *Tataromys* (Bohlin, 1946, fig. 19:27), although some indication of forward migration of the hypolophid contact does occur on M_{2-3} in *A. burkei*. Reduction of P_4 is more advanced in the late Oligocene ctenodactylids than in *Advenimus*, and, in this connection, P^3 is absent. Speculation about relationships among rodents, in which parallelism has been such a common evolutionary feature, is hazardous, especially in a case such as this with no early and middle Oligocene connecting forms known. However, that *Advenimus* may be near a group leading toward ctenodactylids is an interesting possibility based on both morphological and paleogeographic grounds.

Early Tertiary Rodents in Central Asia

Table 3 is essentially a status report on current knowledge of early rodents from Central Asia. The Asian record is still very inadequate. Lower and middle Oligocene records are surely incomplete, and Eocene Central Asian rodents are known from the upper Eocene only. It is hoped that current work will continue to add to the gradually emerging picture of Asian rodent evolution.

A connection between North American and Central Asiatic Eocene and early Oligocene rodents is suggested by the cylindrodontid record and probably also by that of sciuravids, the little-known *Sciuravus* sp. from Honan (Li, 1963, pp. 157–160) seeming to be a generalized sciuravid. *Tsinlingomys*,[1] also from the upper Eocene of Honan, is considered to be a sciuravid by Li (1963, pp. 156–157), but it differs from North American sciuravids in having a complete metalophulid II and masseteric fossa below M_3, which is more posterior than in other sciuravids. Unfortunately, *Tsinlingomys*, like *Advenimus*, is known from lower jaws and teeth only. As in the case of *Advenimus*, *Tsinlingomys* seems closer to sciuravids than to other known rodents, but its distinctive characters and absence of a more complete Asian record seem to favor a more tentative reference to the ?Sciuravidae. The late Eocene was a time when a number of rodent groups experimented with new morphological possibilities, some more successful, in terms of leading toward persistent groups, than others. *Protoptychus*, *Griphomys*, *Protadjidaumo*, *Simimys*, and *Presbymys* in North America and *Gliravus* in Europe are examples of new rodent types

TABLE 3

FIRST APPEARANCE IN ASIA, NORTH AMERICA, AND EUROPE OF RODENT FAMILIES KNOWN FROM THE CENTRAL ASIAN EOCENE AND OLIGOCENE

Family	Asia	North America	Europe
Paramyidae	Upper Eocene	Upper Paleocene[a]	Lower Eocene
Sciuravidae	Upper Eocene[b]	Lower Eocene[a]	—
Cylindrodontidae	Lower Oligocene	Middle Eocene[a]	—
Sciuridae	Upper Oligocene	Middle Oligocene[a]	Upper Oligocene
Ctenodactylidae	Upper Oligocene[a]	—	—
Cricetidae[c]	Lower Oligocene[d]	Lower Oligocene[e]	Lower Oligocene
Zapodidae	Upper Oligocene	Lower Miocene[e]	Upper Oligocene

[a] Earliest record.

[b] See discussion for affinities of Asian "sciuravids."

[c] *Tachyoryctoides*, a cricetid according to Stehlin and Schaub (1951, p. 367), was referred by Bohlin (1946, p. 67) to the Rhizomyidae.

[d] Sannoisian deposits in Shansi (Zdansky, 1930, p. 83).

[e] Upper Eocene if *Simimys* is referable. Wilson (1949, pp. 123–124) favored cricetid reference; Stehlin and Schaub (1951, p. 312) and Wood (1955, p. 179), zapodid.

[1] The spelling *Tsinlingomys* is used in the Chinese text of Li's original description (1963, pp. 151–156), but *Tsinlinomys* appears in his English summary and figure captions. Li has informed me by letter that *Tsinlingomys*, from Tsin-ling Mountain near the fossil-bearing locality, is the correct original spelling.

that appear in the late Eocene; perhaps the Asian *Tsinlingomys* and *Advenimus* represent similarly experimenting lines.

The family that stands out in table 3 as the most isolated is the Ctenodactylidae. As suggested above, *Advenimus* might be near the group that gave rise to these rodents. Whether or not *Advenimus* is involved in the phylogenetic transition, of known rodents sciuravids do seem to be the group in which the ultimate ancestry of ctenodactylids may be found. The basic sciuravid molar plan, with a well-developed hypocone subequal to the protocone in the upper molars and in the lower molars four conids, of which the metaconid and entoconid are lophate, and a well-developed posterolophid, has the potential of developing the ctenodactylid pattern. Further evidence for a sciuravid-ctenodactylid connection is provided by a North American middle Eocene sciuravid, A.M.N.H. No. 12118 (Dawson, 1962), which resembles the ctenodactylids in the reduction of P^4, as well as in having molars with a well-developed hypocone and deep buccal valley, and by other sciuravids that are known to have a reduced P_4.

Probably having an Asiatic origin in the later Eocene or earlier Oligocene, by the time of their late Oligocene appearance ctenodactylids exhibit some diversity, which is illustrated by *Karakoromys*, *Tataromys*, and *Leptotataromys*. The relationship of these Oligocene rodents to later forms was not clear until Bohlin (1946) demonstrated their similarities to the Miocene genus *Sayimys* and, through that genus, to Recent ctenodactylids. The relationship was considered close enough to permit reference of the Oligocene and Miocene forms to the Ctenodactylidae, otherwise known only from Recent representatives. In Bohlin's discussion the designation "Tataromyidae" (quotation marks his) was sometimes employed for the fossils. At the end of the Miocene, ctenodactylids were still present in Central Asia, where *Sayimys* occurs, had spread to southern Asia, where *Sayimys* is known by a jaw from the Nagri Zone of the Siwalik beds (Wood, 1937, pp. 73–76), and had reached into northern Africa, where they are represented by isolated teeth and maxillary fragments in the Moroccan Beni Mellal fauna (Lavocat, 1961, pp. 52–64). The African record extends the geographic range of fossil ctenodactylids to within that of Recent members of the family, Africa north of the equator. Lavocat's separation of ctenodactyloid rodents into the families Tataromyidae, including all fossil forms, and Ctenodactylidae, for Recent representatives, seems to make an unnatural subdivision of these rodents, lacking adequate morphological grounds. *Sayimys*, for example, resembles Recent *Ctenodactylus* more closely in the microscopic structure of the incisor enamel and jaw morphology than it does *Tataromys* (Bohlin, 1946, pp. 112, 131, 143–146), with which it would be united under Lavocat's arrangement. The relationships between these rodents seem to be expressed more clearly, following Bohlin (1946) and Wood (1955), by our utilizing for them one family, the Ctenodactylidae, within which further work may establish adequate morphological grounds for subdivision into well-defined subfamilies.

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