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Two New Rodent Genera from the Oligocene White River Formation

(FAMILY HETEROMYIDAE)

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The Oligocene White River formation of the Great Plains has yielded an assemblage of terrestrial vertebrates remarkable for its diversity as well as for the size of the available collections. Examination of the monograph of Scott and Jepsen (1937–41), as well as numerous subsequent contributions, for example, those of Wilson (1949) and Galbreath (1953), suggests that the known species represent rather closely the mammalian community as it existed at the time of deposition. Perhaps least fully known, despite the summary of Wood (1937), is the microfauna of the deposits. The present contribution describes two new heteromyid rodents from the Oligocene of the Great Plains; one of these forms has been discussed previously by Galbreath (op. cit.). The terminology used in describing dental cusps is diagrammed in figure 205.

For the loan of the specimens discussed herein, I am indebted to Dr. C. W. Hibbard, University of Michigan Museum of Paleontology (UMMP), Dr. J. L. Kay, Carnegie Museum of Pittsburgh (CMP), and W. D. Turnbull, Chicago Natural History Museum (CNHM). For the preparation of the illustrations I am grateful to R. A. Norris, Department of Zoology, University of Wisconsin. Financial assistance was received from the Research Committee, University of Wisconsin Graduate School, during the preparation of this report.

Class **MAMMALIA**

Infraclass **Eutheria**

Order **Rodentia**

Family **Heteromyidae**

Library of Congress Catalog Card Number: 60–14725

No. 890

Apletotomeus,[1] new genus

Type species.—Apletotomeus crassus, new species.

Distribution.—Middle Oligocene Brule formation of Nebraska, South Dakota, and eastern Colorado.

Diagnosis.—Molariform teeth brachydont, strongly rooted, with cusps rising but weakly above crown; true molars strongly sexcuspi-

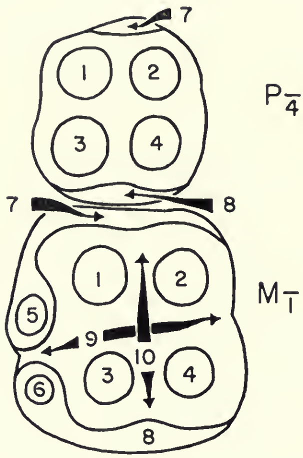

FIG. 205. Diagrammatic representation of the occlusal surface of the left $P_{\overline{4}}$–$M_{\overline{1}}$ in a generalized heteromyid. 1, protoconid; 2, metaconid; 3, hypoconid; 4, entoconid; 5, protostylid; 6, hypostylid; 7, anterior cingulum; 8, posterior cingulum; 9, transverse valley; 10, antero-posterior valley. Application of uniform terminology to $P_{\overline{4}}$ and $M_{\overline{1}}$ varies from the nomenclature suggested by Wood and Wilson (1936).

date, but with slight basal conjunction of laterally adjacent cusps evidencing slight bilophodonty; anterior and posterior cingula present and prominent. Above characteristics much as in the genus *Heliscomys* Cope or *Akmaiomys* (new genus, hereinafter described). $P_{\overline{4}}$ nearly quadrate, quadricuspidate, relatively large, not reduced as in *Heliscomys;* lacks central accessory cusp present on anterior lophid of *Akmaiomys.* Lower incisor sharply recurvate, relatively much broader in cross section than that of *Heliscomys, Akmaiomys,* or *Proheteromys* Wood, being in width equal to or greater than $M_{\overline{1}}$; broad anterior enamel face of incisor nearly flat. Ramus basally much broader and more massive than in *Proheteromys* (of Wood, 1935), *Akmaiomys,* or *Heliscomys;* masseteric crest prominent and shelf-like,

[1] From απλετος, immense, boundless, and τομευς, incisor or cutting tooth.

running anteriad to terminate abruptly below mental foramen; length of jaw greater than in *Heliscomys* but less than in *Proheteromys parvus* Troxell; length of diastema shorter than length of molariform tooth row, whereas in *Proheteromys parvus* the reverse applies; depth of ramus at $M_{\overline{1}}$ greater than alveolar length.

Apletotomeus crassus, new species

Holotype.—UMMP 25893 (figs. 206, 207, 210), left partial ramus with $I_{\overline{1}}$, $P_{\overline{4}}$–$M_{\overline{3}}$; collected in 1948 by C. W. Hibbard and party.

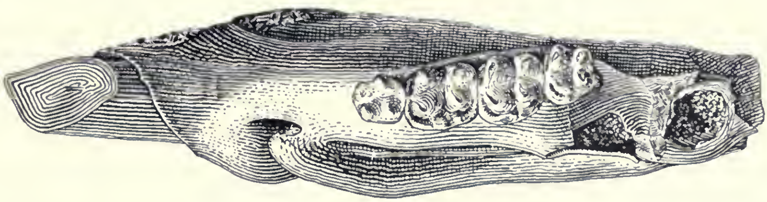

FIG. 206. *Apletotomeus crassus*, new genus and species. Holotype, UMMP 25893. Occlusal view of left lower jaw; approximately × 9½.

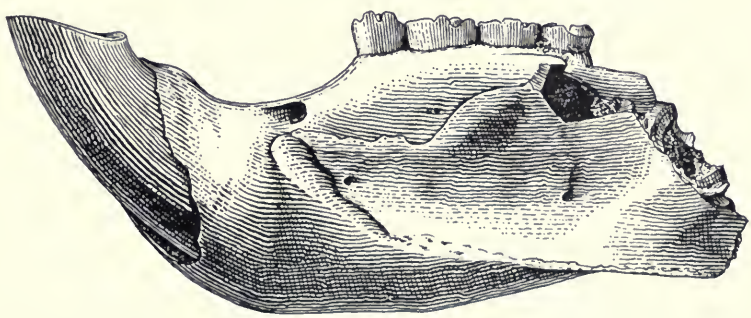

FIG. 207. *Apletotomeus crassus*, new genus and species. Holotype, UMMP 25893. Lateral view of left lower jaw; approximately × 9½.

Hypodigm.—The holotype, from the "Oligocene–Orellan" (from label), Bill Grimm Ranch, NW. ¼, sec. 35, T. 33 N., R. 56 W., Sioux County, Nebraska. Tentatively referred, CMP 8664, partial left ramus with $I_{\overline{1}}$, $M_{\overline{1}}$–$M_{\overline{3}}$, Middle Oligocene Lower Brule, 3½ miles south of Scenic, Pennington County, South Dakota.

Diagnosis.—As for genus.

Description.—This species represents the largest mammal yet described, the dentition of which resembles that of *Heliscomys*. The ramus of the holotype is half again as long as that of *Heliscomys* and is several times the mass. The jaw is very deep; at the level of $M_{\overline{1}}$ the distance from the alveolar border to the base is slightly greater than the length of the molariform tooth row. Basally, the ramus is broad, the ventral border curving gently from the ventro-medial margin to the lateral border of the shelf formed by the ventral masseteric ridge. The latter structure is very prominent and is broadly expanded over its entire length; it passes anteriad nearly parallel with the occlusal plane until, at the level of the anterior border of $M_{\overline{1}}$, it turns abruptly dorsad (fig. 207). The crest terminates anteriorly at a tuberosity just beneath and slightly anterior to the mental foramen. The dorsal masseteric ridge is also prominently evident as it passes posteriad parallel with the occlusal plane from the dorsal extension of the tuberosity to a point opposite the center of $M_{\overline{1}}$, whence it passes postero-dorsad to the anterior base of the ascending process of the ramus. Near the dorsum of the ramus, the planes of the medial and lateral surfaces of the jaw are nearly parallel; dorsally the jaw is narrow, being but slightly wider than the tooth row (fig. 206). The ramus flares ventro-laterad to the prominent masseteric crest and expands to the basal breadth described above. The area between the two masseteric ridges is rugose and very irregular. The presence of small foramina also characterizes this rough area, which is bordered posteriorly by smooth bone, beginning at about the level of $M_{\overline{3}}$.

The mental foramen opens into a deep depression which is about one-third the length of the diastema anterior to $P_{\overline{4}}$. The diastemal length is somewhat less than the alveolar length; the curvature of the dorsal surface of the diastema is rather abrupt, the middle portion being less concave than are the anterior and posterior elevations to the alveoli. The plane of the symphysis is almost exactly parallel to the inner molariform alveolar border, indicating nearly parallel tooth rows in the lower jaws. The flat alveolar surface is in the form of an acute isosceles triangle with the teeth running along the lingual edge. The lateral border runs posteriad with a slight concavity near the anterior base of the ascending process. In addition, it is evident that a deep pit is present between $M_{\overline{3}}$ and the ascending process, the dorsal surface dropping abruptly postero-laterad from the alveolus of $M_{\overline{3}}$ to a level just superior to the incisor. Although the area immediately anterior to the mandibular pit is broken out along with the base of the ascending ramus, the smoothness and regularity of a portion of the break in the pit at the level of the posterior border of $M_{\overline{3}}$ indicate the probable position of a mandibular foramen.

The incisor is very large in cross section, relative to the width of the molariform teeth (cf. figs. 207 and 209). The radius of curvature of the incisor is short, conforming to the relative shortness of the ramus. Since the known specimens of rami are broken posteriorly, the configuration of the capsule of the incisor and the processes cannot be determined.

As in *Heliscomys*, the molariform teeth are brachydont (figs. 207, 210). $P_{\overline{4}}$ is quadrituberculate, with the anterior two cusps slightly closer together than are the posterior. Unfortunately, the antero-internal border of this tooth has been broken in the holotype so that the size of the metaconid cannot be determined with accuracy. It appears to have been equal in size to the hypoconid and entoconid, the protoconid being somewhat smaller than the other three. A small conulid arises from the anterior cingulum in connection with the antero-lateral border of the metaconid. A prominent cingulum is present, connecting the hypoconid and entoconid posteriorly.

$M_{\overline{1}}$ and $M_{\overline{2}}$ are nearly equal in size (Table 1), both taking a form that is nearly rectangular (figs. 206, 210). The four primary cusps are appreciably more prominent than the two lateral stylids which, however, are distinct and form with the other cusps a sextuberculate occlusal surface. The protostylid extends posteriorly into the transverse valley, causing this depression to run postero-buccad from the protoconid-hypoconid line to the tooth border. The hypostylid rises just posterior to the hypoconid-entoconid axis, thus causing the hypolophid which forms with wear to curve postero-laterad. A very broad anterior cingulum is present the entire width of both teeth and curves posteriad laterally to connect with the protostylid. The latter structure rises above the level of the cingulum and is present at this stage of wear as a separate cusp with a distinct separation from the arcuate crest of the cingulum.

The protoconid and metaconid are conjoined as a metalophid by short ridges which join somewhat nearer the former cusp and thence run anteriad to the cingulum. A distinct depression is present between the metaconid and the anterior cingulum. The curving valley separating the protostylid and the external cingulum from the protoconid is deep and, with wear, would persist nearly as long as the transverse valley. The latter is deepest at its confluence with the lateral valley which runs in an antero-posterior direction separating the principal cusps from the stylids. From this point the floor of the transverse valley rises slightly to the lateral tooth border and more appreciably to the basal level of the four primary cusps, at which point it is still slightly deeper than the antero-posterior valley separating the four primary cusps.

The hypoconid and entoconid are broadly connected by basal extensions which adjoin near the anterior border of the cusps. The antero-posterior valley between them thus is interrupted in a manner similar to that of the metalophid. The hypoconid is connected basally to the hypostylid, but the latter rises as an apically independent structure. A posterior cingulum extends nearly the width of the tooth in $M_{\overline{1}}$, but is prominent only between the hypoconid and entoconid in $M_{\overline{2}}$. A tiny but distinct cusplet arises from this posterior cingulum in connection with the entoconid in $M_{\overline{1}}$.

Table 1.—MEASUREMENTS OF SPECIMENS OF *APLETOTOMEUS*
(In millimeters)

		UMMP 25893	CMP 8664	UMMP 32598
$I_{\overline{1}}$	Greatest width (cross section)	1.02	0.93	0.82
	Greatest length (cross section)	1.55	1.53	1.30
$P_{\overline{4}}$	Width of metalophid	0.72	....	....
	Width of hypolophid	....	....	....
	Antero-posterior length	0.77	....	....
$M_{\overline{1}}$	Width of metalophid	0.97	0.97	....
	Width of hypolophid	0.95	1.00	....
	Antero-posterior length	1.01	1.03	....
$M_{\overline{2}}$	Width of metalophid	1.05	1.03	....
	Width of hypolophid	0.95	0.95	....
	Antero-posterior length	0.97	0.97	....
$M_{\overline{3}}$	Width of metalophid	0.88	0.80	....
	Width of hypolophid	0.73	0.63	....
	Antero-posterior length	0.90	0.77	....
Depth of ramus at $M_{\overline{1}}$		3.9	....	....

$M_{\overline{3}}$ is slightly shorter than $M_{\overline{2}}$ and is but three-quarters the breadth (Table 1). The protostylid and the anterior and external crests of the cingulum are somewhat smaller, but otherwise the anterior portion of the tooth is similar in all respects to that of $M_{\overline{1}}$ and $M_{\overline{2}}$. The transverse valley is appreciably deeper than the antero-posterior one; the lophodonty of this tooth thus is fairly well advanced. The highest point of the transverse valley connects the protoconid and hypoconid, where presumably the two lophids would first join with wear. At the state of wear of the holotype, no hypostylid is observed on $M_{\overline{3}}$, but an angular attritive surface has been formed at the point where the structure may briefly have risen at eruption. A weak posterior cingulum connects the borders of the hypoconid and entoconid of $M_{\overline{3}}$.

Specimen CMP 8664 is nearly equivalent to the holotype in overall size. The ventral masseteric ridge rises somewhat higher than in the type specimen, and the dorsal ridge passes in a nearly straight line from the anterior tuberosity to the ascending ramus. The enclosed lateral surface of the jaw is less irregular, with fewer penetrating foramina. The masseteric tuberosity drops directly into the depression of the mental foramen. The incisor is narrower (Table 1) and appears to have a slightly greater radius of curvature than does that of the type specimen.

$P_{\overline{4}}$ is absent in this specimen. Being less worn, the principal cusps of the molars are more prominent than are those of the holotype. However, the stylids of $M_{\overline{1}}$ are less prominent, as is the entire development of the cingulum. No cusplet arises from the posterior cingulum of $M_{\overline{1}}$. On $M_{\overline{2}}$ the stylids are prominent and well divided from the principal cusps. $M_{\overline{3}}$ is markedly smaller than the comparable tooth of the type specimen. This is not due to state of wear. While the external cingulum of this tooth is still broad, the protostylid as a separate structure is not apparent.

Apletotomeus sp.

A partial left ramus with $I_{\overline{1}}$, UMMP 32598, from the Middle Oligocene, Lower Brule, Oscar Orlander Ranch, Weld County, Colorado, either is representative of a heretofore unknown species of *Apletotomeus* or attests to an extreme of variability in *A. crassus*. Appearing somewhat less specialized than in the type species, the incisor is less heavily recurvate, relatively narrower and of lesser cross-sectional area. The diastemal region is broader and less modified at the mental foramen, while the well-developed ventral masseteric crest is somewhat more abruptly curvate anteriorly than in the holotype. It is unfortunate that the molariform teeth are absent in this specimen.

Akmaiomys,[1] new genus

Proheteromys? Galbreath, 1953, Univ. of Kansas Paleo. Contr., Vertebrata, Art. 4, p. 66.

Type species.—*Akmaiomys incohatus*, new species.

Distribution.—Known only from the Middle Oligocene White River formation, Lower Cedar Creek member (Galbreath, 1953, p. 66) of northeastern Colorado.

[1] From ακμαιος, vigorous, prime, and μῦς, mouse.

Diagnosis.—True molar teeth as in *Heliscomys* and *Apletotomeus*. $P_{\overline{4}}$ relatively large, unreduced, quadrate, with four principal cusps at the corners of the quadrangle; a fifth, prominent, antero-posteriorly elongate cusp rises between protoconid and metaconid and runs anteriad to an anterior cingulum. Lower incisor relatively procumbent, narrow in cross section, but with anterior enamel surface nearly flat. Ramus broader, relative to width of molars, than in *Heliscomys*, but not as robust as in *Apletotomeus;* masseteric crest very prominent and shelf-like, terminating anteriorly immediately below mental foramen; size slightly larger than that of *Heliscomys vetus* Cope.

Akmaiomys incohatus, new species

Proheteromys? sp. Galbreath, 1953, Univ. of Kansas Paleo. Contr., Vertebrata, Art. 4, p. 66.

Holotype.—CNHM-PM 381 (figs. 208, 209, 211), anterior portion of right ramus with $I_{\overline{1}}$, $P_{\overline{4}}$–$M_{\overline{1}}$.

Hypodigm.—The holotype, from "Mid Oligocene, Lower Brule formation, 6 miles N.E. Gault, Weld County, Colorado" (from label); White River formation, lower Cedar Creek member, Mellinger locality, SE. ¼, sec. 17, T. 11 N., R. 65 W. (Galbreath, 1953, p. 66).

Diagnosis.—As for genus.

Description.—The jaw appears to be slightly longer than that of *Heliscomys vetus* Cope. In depth, however, the ramus is highly expanded, as in *Apletotomeus*, and to a relatively similar extent, to judge from the remaining unbroken anterior basal section. Dorsal to the masseteric ridge the ramus is of a width similar to that of *Heliscomys*. The crest, as in *Apletotomeus*, proceeds anteriad, then dorsad, as a heavily developed shelf (figs. 208, 209) which thus expands broadly the ventral margin of the jaw. Anteriorly the masseteric crest terminates just below the mental foramen, which opens into a slight depression about one-quarter the length of the diastema anterior to $P_{\overline{4}}$ and slightly ventral to the dorsal surface of the diastema. The texture of the lateral surface of the ramus is difficult to determine because of the repeated fracture of the jaw in this region, but the surface appears to have been at least somewhat irregular. The medial surface of the jaw is nearly plane, not strongly concave as in *Apletotomeus*.

The incisor, being nearly equal to $P_{\overline{4}}$ in width (Table 2), is relatively broader in cross section than is that of *Heliscomys*, but the expansion is not comparable to that in *Apletotomeus*, in which the incisor reaches the width of $M_{\overline{1}}$ and is not antero-posteriorly elongate.

This tooth exserts in a flatter arc than the incisor of either *Heliscomys* or *Apletotomeus;* its radius of curvature is greater than that of either genus and is more nearly similar to that of *Proheteromys parvus* Troxell.

The molariform teeth (figs. 209, 211) are brachydont. The unique feature of this specimen is the occlusal pattern of $P_{\overline{4}}$, which is sub-

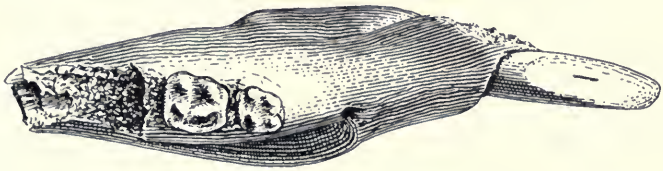

FIG. 208. *Akmaiomys incohatus*, new genus and species. Holotype, CNHM-PM 381. Occlusal view of right lower jaw; approximately × 10.

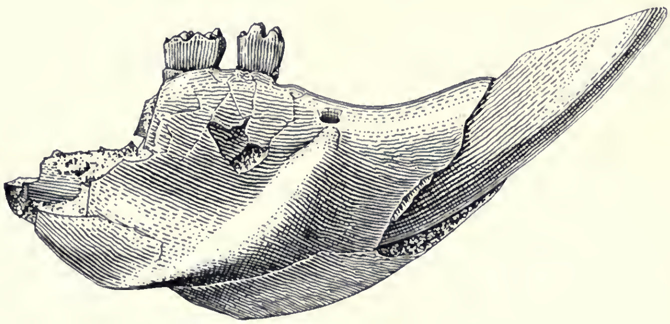

FIG. 209. *Akmaiomys incohatus*, new genus and species. Holotype, CNHM-PM 381. Lateral view of right lower jaw; approximately × 10.

quadrate, quinquecuspidate, and prominent in size. The protoconid is markedly smaller than are the other three primary cuspids, which are nearly equal in size and distinctness. Situated between the metaconid and protoconid, a prominent and distinct cuspid rises from the basin of the crown nearly to the height of the protoconid. This accessory structure seems to be most closely connected basally to the metaconid. From the anterior border of the prominent anterior cingulum a small cusplet rises centrally and connects broadly posteriorly with the accessory cuspid. The origin of the fifth cusp is in doubt; it does not represent a cingular neomorph but rather appears to be derivative from the tooth basin just buccal to the metaconid. At any rate, the pattern is a radical departure from the other known Oligocene heteromyids and cannot be compared with any in this respect. While the small cusplet from the anterior cingulum is present in $P_{\overline{4}}$ of *Apleto-*

tomeus, there is no trace of the prominent accessory cuspid in that genus. In *Akmaiomys* the posterior cingulum is present and prominent, a small cusplet arising centrally therefrom. The valleys of the tooth are nearly identical in depth, except between the metaconid and accessory cuspid, between which the depth is reduced. It is therefore difficult to determine the eventual pattern of $P_{\overline{4}}$ with wear.

TABLE 2.—MEASUREMENTS OF HOLOTYPE OF *AKMAIOMYS INCOHATUS*
(In millimeters)

		CNHM-PM 381
$I_{\overline{1}}$	Greatest width	0.60
	Greatest length (cross section)	1.10
$P_{\overline{4}}$	Width of metalophid	0.63
	Width of hypolophid	0.68
	Antero-posterior length	0.70
$M_{\overline{1}}$	Width of metalophid	0.90
	Width of hypolophid	0.88
	Antero-posterior length	0.95
Depth of ramus at $P_{\overline{4}}$ (approximate)		3.3

$M_{\overline{1}}$ (fig. 211) is quite similar to this tooth of *Apletotomeus,* though the cusps are somewhat more discrete than in the latter genus. The crown is quadrate, with broadly rounded corners. The pattern is sextuberculate, with the four primary cusps nearly equal in height and distinctness and the lateral stylids about two-thirds the height of the principal cusps. The primary cusps are oriented squarely on the crown; the protostylid and hypostylid lie somewhat behind the protoconid-metaconid and hypoconid-entoconid axes, respectively. Thus, the transverse valley runs nearly straight across the tooth but passes slightly posteriad as the protostylid protrudes into the depression at the lateral tooth margin.

The cingulum is very prominent anteriorly, running postero-laterad to connect basally with the otherwise distinct protostylid. Despite their depth, none of the antero-posterior depressions is as deep as the transverse valley; the latter is deepest between the stylids and the lateral cuspids and is shallowest between the metaconid and entoconid.

The hypoconid and entoconid are broadly joined anteriorly and probably would form a lophid sooner than the anterior cusps. A very prominent posterior cingulum, circumventing the hypoconid, connects the hypostylid with the entoconid. A prominent cusplet rises from the cingulum between the posterior borders of the hypoconid and the entoconid.

FIG. 210. *Apletotomeus crassus*, new genus and species. Holotype, UMMP 25893. Occlusal view of left lower tooth row; × 50.

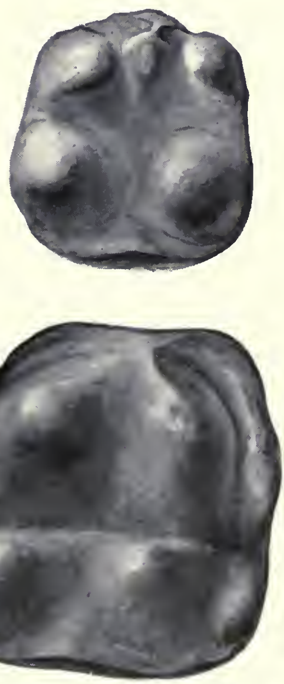

FIG. 211. *Akmaiomys incohatus*, new genus and species. Holotype, CNHM-PM 381. Occlusal view of right $P_{\overline{4}}$–$M_{\overline{1}}$; × 50.

Discussion.—Galbreath (1953, p. 66) made a careful analysis of the specimen of *Akmaiomys* and he was convinced that the animal was not referable to the genus *Heliscomys* but rather fitted into the complex of forms combined as the genus *Proheteromys*. In connection with the present study, the specimen has again been compared in detail with all known relative types. Characteristics of the ramus, as well as of the teeth, show a lack of close relationship to *Proheteromys floridanus* Wood, the type species of the genus. There are, however, a number of features in common with *Proheteromys parvus* Troxell and *P. nebraskensis* Wood. Cuspularity and the conformation of the ramus are similar in general to these characteristics in the latter species. Neither *Akmaiomys* nor *Proheteromys* exhibits the reductive modification of $P_{\overline{4}}$ which characterizes *Heliscomys;* both genera retain well-developed premolars. More specimens are necessary in order to characterize the genus *Akmaiomys* with certainty, but there is little doubt that this specimen represents a generic parameter heretofore undescribed.

The rarity in Oligocene collections of specimens of the rodent genera *Akmaiomys* and *Apletotomeus* relative to those of *Heliscomys, Adjidaumo,* and *Paradjidaumo* may be indicative with respect to the habitats of these forms. In the absence of objective data, it may be postulated that the species represented by larger numbers of specimens in the fossil record lived at or near the site of deposition of sediments. Thus a riparian habitat would be implied for *Heliscomys,* now represented by several scores of specimens in various collections, but *Akmaiomys* and *Apletotomeus,* represented by one and three specimens respectively, might well have occupied a less mesic habitat somewhat distant from the streamside.

The recent revision of the Lower(?) Oligocene Florissant flora by MacGinitie (1953) has provided evidence as to the habitat within which the White River fauna existed. Though deposited at moderate elevation (1000–3000 feet) about 125 miles south-southwest of the principal White River exposures, the remarkable flora enables a reasonable estimate as to the environmental characteristics of the more distant sites of faunal deposition.

A warm-temperate floral facies was inferred for the Florissant on the basis of the environments occupied today by the nearest equivalent species. Average annual temperatures of the western and southern states during the pre-Pliocene Tertiary were higher than today; MacGinitie (op. cit.) stresses that the higher average temperature was due primarily to increase in the thermal minima rather than in the maxima. *Fagopsis*, an ecological equivalent of modern alder or birch, *Zelkova*, an elm-like genus related most closely today to species from southeastern Asia, and *Chamaecyparis*, closely equivalent to the Port Orford cedar, were important plant species of the riparian situation and moist hillsides. Between the mesic fluviatile habitats MacGinitie (op. cit., p. 52) postulates that the vegetation consists of "an open forest of pines and dwarf, mostly evergreen oaks, (encinal), with hardier members of the chaparral forms (*Dodonaea, Mahonia, Schmaltzia,* and *Zyzyphus*) in warm, less favorable niches. The fossil plant association offers nothing to warrant the conclusion that there were widespread grasslands. The evidence favors an open, rather dry forest on the high ground, with grass in the more open areas."

On the basis of the above evidence, the probable environment of the near-by White River may be inferred. There is no evidence for widespread grassland conditions; on the basis of certain of the less common elements of the Florissant, it is suggested that the plains to the east were more xeric in nature than the lacustrine lake and stream borders. MacGinitie (op. cit., p. 59) reaches the conclusion that the "picture indicated is that of a subhumid grassy scrub (probably similar to the thorn-bush and mesquite-grass formations of southwest Texas), with more mesic vegetation in wide flood plains." These, then, are the probable environments within which lived the large Oligocene fauna of the High Plains.

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