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ABSTRACT

Rodents from the ?latest Arikareean-medial Hemingfordian faunas from the Zia Sand include one mylagaulid and several geomyoids. The Standing Rock local fauna is considered earliest Hemingfordian or latest Arikareean; its three geomyoid rodents, *Proheteromys cejanus*, new species, *P.* aff. *floridanus* (Heteromyinae), and *Ziamys tedfordi*, new genus and species (Geomyinae) are consistent with such an age but have little value in detailed correlation. *Ziamys* combines geomyine palatal and rostral structure with pleurolicine-like cheek teeth, which contrast strongly with those of *Dikkomys*. *Ziamys* indicates that the Geomyinae evolved from among the Pleurolicinae, but also resembles species of *Gregorymys* sufficiently to suggest an origin near the point of division of Pleurolicinae and Entoptychinae.

The Blick local fauna of medial Hemingfordian age includes a pleurolicine most nearly resembling the Arikareean *Pleurolicus sulcifrons*. The specimen includes dP_4^4, not known for *Pleurolicus*; these teeth resemble those of entoptychines. A similar dP^4 has been described from the Hemingfordian Quarry A, Martin Canyon local fauna. A heteromyid species is represented by a specimen resembling *Proheteromys* and another resembling *Mookomys*; it may lie near the point of origin of the Perognathinae.

Mesogalus aff. *vetus*, from Jeep Quarry, is morphologically intermediate between *M. praecursor* from the Marsland Formation and *M. vetus* of the Sheep Creek local fauna, and supports an age estimate of late medial Hemingfordian for the Jeep local fauna.

INTRODUCTION

The Zia Sand was first distinguished as a formation by Galusha (1966). He included a summary of the field work done by Frick Laboratory parties under his direction. They obtained from the formation a sequence of faunas ranging through most of Hemingfordian (medial Miocene) time, possibly beginning in late Arikareean time. Rocks included in the formation were partly but not entirely the same as were included by Bryan and McCann (1937) in the Lower Gray Member of the Santa Fe Formation (now the Santa Fe Group). Previous publications dealing with rocks assigned to the Zia Sand were summarized by Galusha and Blick (1971, pp. 38-40). They excluded from the Zia Sand, on biostratigraphic evidence, several exposures

[1] Baruch College, the City University of New York.

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included in or correlated with the Lower Gray Member by Bryan and McCann and by Spiegel (1961). The fossiliferous exposures of the Zia Sand lie in Sandoval County, New Mexico, on an arc extending from approximately 40 miles due north to 15 miles west-northwest of Albuquerque. Galusha described two areas of exposure, the type area of the formation and of the Piedra Parada Member, and the type area of the Chamisa Mesa Member. Gawne (MS) described a third area, in and near Canyada Pilares, and studied the faunas, sedimentation, and paleoecology of the three fossiliferous areas.

All the rodents described below were found in quarries reported on by Galusha (1966). Standing Rock Quarry is in the type area of the formation and of the lower member, the Piedra Parada Member, 60 to 65 feet above the base of the type section of both. Blick Quarry is 300 feet above the base of the type section of the Chamisa Mesa Member. Jeep Quarry lies 275 to 300 feet stratigraphically above Blick Quarry, and 75 feet below the base of the Nambé Member of the Tesuque Formation, Santa Fe Group. Mesa Prospect, which produced no rodents, lies 15 feet above Jeep Quarry.

The fossil mammals found in the quarries indicate differences in age and constitute distinctive local faunas. The Standing Rock local fauna includes *Nothocyon* aff. *minor*, *Promartes* cf. *lepidus*, *Daphoenodon*, new species (Hunt, MS), *Cephalogale* sp., *Archaeolagus* cf. *macrocephalus*, *Proheteromys cejanus*, new species (present paper), *P.* aff. *floridanus*, *Ziamys tedfordi*, new genus and species (present paper), *Stenomylus* (*Stenomylus*) sp., aff. *Spizaetus* sp., and Strigiformes. This fauna was assigned a late Arikareean age by Galusha (1966). It has several genera in common with the Harrison Formation of Nebraska; however, more detailed study suggests an age intermediate between the Harrison and Marsland formations, and therefore near the boundary between Arikareean and Hemingfordian age (Gawne, MS).

The Blick local fauna, from Blick Quarry and from Cynarctoides Quarry, which lies at or near the same stratigraphic level, includes *Cynarctoides,* new species A (Gawne, MS), *Tomarctus* sp., *Archaeolagus* sp., *Oreolagus* cf. *nebrascensis*, *Proheteromys* or *Mookomys* sp., *Pleurolicus* cf. *sulcifrons*, *Blickomylus galushai*, *Stenomylus* (*Stenomylus*) sp., Hemicyoninae, and Iguanidae. This fauna correlates best with the medial Hemingfordian Runningwater Formation of Nebraska, Thomas Farm local fauna of Florida, and Martin Canyon local fauna of northeastern Colorado (Gawne, MS).

The Jeep local fauna, from Jeep Quarry, other nearby localities at the same level, and approximately 20 feet of rock below this level, includes *Cynarctoides*, new species B (Gawne, MS), *Promartes* cf. *lepidus*, cf. *Amphicyon* and *Ysengrinia*, Archaeolaginae, *Mesogaulus* aff. *vetus*, *Merycodus* cf. *sabulonus*, *Blickomylus galushai*, *Michenia* sp., *Protolabis* sp., and *Homocamelus* sp. This local fauna is intermediate in age between the medial Hemingfordian Runningwater Formation and the late Hemingfordian Sheep Creek local fauna (Gawne, MS).

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ABBREVIATIONS

The following abbreviations are used to designate institutional collections:

AC, Amherst College

AMNH, the American Museum of Natural History, Vertebrate Paleontology
CM, Carnegie Museum
F:AM, Frick American Mammals, the American Museum of Natural History
FSGS, Florida State Geological Survey
MCZ, Museum of Comparative Zoology, Harvard
UO, University of Oregon

ORDER RODENTIA

SUBORDER SCIUROMORPHA

SUPERFAMILY APLODONTOIDEA

FAMILY MYLAGAULIDAE

Mesogaulus aff. *vetus* (Matthew, 1924)
Figures 1, 2

Mylagaulus vetus Matthew, 1924, pp. 82-84, figs. 6-8.
Mesogaulus vetus: Cook and Gregory, 1941, p. 551.

Referred Specimen. F:AM 51263, palate with right P^4, posterior half of left P^4, and right and left M^2, from Jeep Quarry, Chamisa Mesa Member type section, late medial Hemingfordian in age.

Description and Comparisons. Measurements of the teeth are given in table 1; dental terminology is illustrated in figure 2. P^4 is worn sufficiently that all valleys have formed closed fossettes, although the parafossette is still in contact with the marginal enamel anterolabially. Parafossette and anterior segment of the protofossette have joined to form a Y-shaped lake. The metafossette, aligned with the posterior portion of the parafossette, nearly meets it. The small mesofossette and anterior end of the hypofossette approach the crest separating parafossette and metafossette, so that four lakes converge toward a single point. Isolated from the anterior segment, the posterior part of the protofossette is straight and parallel to the posterior segment of the parafossette.

The protocone is posterior to the middle of the tooth. Lingual to the moderate-sized mesostyle, the paracone is separated from it by a deep parastria; the metacone lies posterior to the mesofossette and mesostyle, with no intervening mesostria; the tooth is thus wider posterior to the mesostyle than anterior to it. Metacone and mesostyle are supported by a distinct root, which ends ventral to the posterolingual root and is much smaller. Enamel covers most of the lingual side of the posterolingual root, but ends ventral to the anterior root lingually and about 1.5 mm. ventral to the roots labially. A thin layer of cement is present on the dorsal two-thirds of the labial sides of the crown, thicker in the parastria and overlapping the dorsal margin of the enamel; traces can also be seen on the lingual side.

In most characters this P^4 lies between *Mesogaulus praecursor* (Cook and Gregory, 1941) of the Marsland Formation (= Upper Harrison Formation) and two species of *Mesogaulus* from the

TABLE 1
Dental Measurements (in Millimeters) of *Mesogaulus*

	Mesogaulus aff. *vetus* F:AM 51263	*Mesogaulus vetus* AMNH 20507
P^4		
Length[a]	7.2	8.0
Width[a]	4.8	4.9
Crown height	9.7[b]	12.3
M^2		
Length[c]	2.9	–
Width[c]	3.5	–

[a]Maximum.
[b]Slightly more worn than AMNH 20507; by comparison with unworn teeth, original height is estimated as less than 11 mm.
[c]Occlusal; tooth heavily worn.

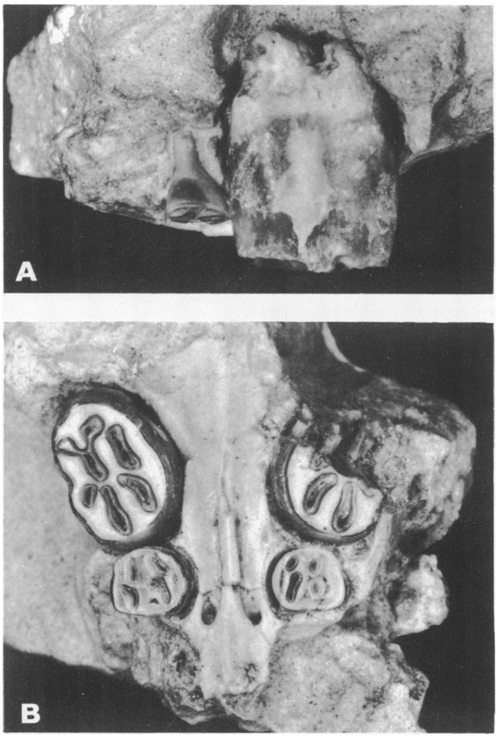

FIG. 1. *Mesogaulus* aff. *vetus*, F:AM 51263. A. Lateral view of RP_4 and M_2. ×3. B. Occlusal view of palate. ×3.

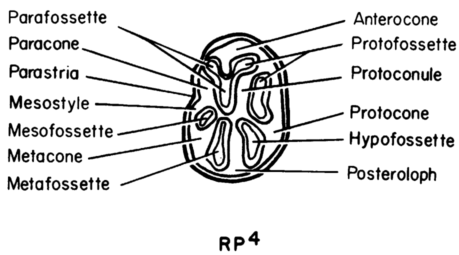

FIG. 2. Diagram showing structures of P_4 described in text. Based on *Mesogaulus* aff. *vetus*, F:AM 51263. ×3.

Sheep Creek local fauna, *M. vetus* and *M. novellus* (Matthew, 1924, pp. 82, 84), the latter also known from Split Rock, Wyoming (Black and Wood, 1956). The fossette pattern is most like that of *M. praecursor*, although lacking a small fossette between hypofossette and metafossette present in *M. praecursor*. Crown height is greater than in *M. praecursor* and less than in *M. vetus* (preserved almost entire in AMNH 20507 from the Sheep Creek local fauna). All three exceed *M. novellus*, which is smaller in all dimensions. P^4 of F:AM 51263 is narrower than in *M. praecursor* and broader than in *M. vetus*. That of *M. novellus* is slightly broader because of its projecting mesostyle; the tooth is as narrow posterior to the mesostyle as anterior to it. *Mesogaulus novellus* and *M. vetus* are similar in most aspects of crown pattern, including the anterior position of the protocone. The Jeep Quarry specimen resembles *M. praecursor* in posterior position of the protocone, and is similar but less extreme in the labial position of metacone and mesostyle and the resulting depth of the parastria. Metacone and mesostyle of *M. praecursor* are supported by a well-separated root subequal in size to the lingual roots, although slightly more ventral on the crown. The root structure of *M. novellus* has not been described; the posterolabial root of *M. vetus* is reduced more than that of F:AM 51263. Enamel covers all the roots of *M. praecursor* and *M. vetus*; the abbreviated enamel development of F:AM 51263 is not seen in other specimens of *Mesogaulus* examined and may be anomalous.

Upper premolars from Quarry A, Martin Canyon local fauna, assigned to *Mesogaulus paniensis* by Wilson (1960, p. 50) and Galbreath (1953, p. 95) are, as both authors observed, close to *M. praecursor* in morphology. However, on the basis of Wilson's figures 47-49, the metacone is as far lingual in these specimens as in *M. vetus* and *M. novellus*, situated directly behind the paracone rather than labial to it as in *M. praecursor* and F:AM 51263; the mesostyle projects labial to both. As in *M. praecursor*, the premolars are larger in occlusal area and lower than those of F:AM 51263.

The second molars of F:AM 51263, deeply worn, resemble those of *M. novellus*, AC 10315 (Black and Wood, 1956, fig. 4a); they are nearly square, convex lingually, with four remaining fossettes. The enamel is thickest lingually, thin posteriorly, and missing anterolabially because of wear against the premolar. Part of the alveolus of M^3 is preserved.

Discussion. This mylagaulid is a structural intermediate, if not a phylogenetic link, between *Mesogaulus praecursor* of the Marsland Formation and *M. vetus* of the Sheep Creek local fauna. Relative to *M. praecursor*, the Jeep Quarry form has reduced the width of P^4, and in particular the metacone and mesostyle and their supporting root. It has increased the crown height, but retained the posterior position of the protocone. As Cook and Gregory pointed out (1941, pp. 551-552), *M. praecursor* provides an intermediate between *Mylagaulodon angulatus* and later mylagaulids; in four of the five characters of *M. praecursor* given by these authors as primitive, the Jeep Quarry specimen is intermediate between *M. praecursor* and *M. vetus*. (The fifth, the relative development of the anterocone, cannot be determined in F:AM 51263 because of wear.) Despite its small size, low crown height, and projecting mesostyle, *M. novellus* is as advanced in protocone and metacone position as *M. vetus*; it may represent an early offshoot evolving parallel with *M. vetus*, but cannot be considered the most primitive species of *Mesogaulus* as suggested by Black and Wood (1956, p. 684). *Mesogaulus paniensis* appears to be more closely related to *M. novellus* than to *M. vetus*.

SUBORDER MYOMORPHA

SUPERFAMILY GEOMYOIDEA

FAMILY HETEROMYIDAE

Discussion. The division of the Geomyoidea into Heteromyidae and Geomyidae is retained here, but is open to question. Rensberger (1973b) believed the Entoptychinae and Pleurolicinae were derived from a common stem descended from *Heliscomys*. Evidence given below suggests that the Geomyinae were derived from the Pleurolicinae. The Geomyidae would thus be a monophyletic group. However, it remains possible that the Pleurolicinae were descended from *Heliscomys*; that the Florentiamyinae and Entoptychinae, with their more complex premolars, were descended from *Proheteromys*, already in existence in the Orellan; and that the Geomyinae were derived separately from among the Heteromyinae. Aside from this question of monophyly, the differences between the Heteromyidae and Geomyidae are of smaller magnitude than those separating other rodent families.

The cusp terminology employed here for the geomyoid rodents is that of Rensberger (1971, 1973a). It is illustrated in figure 3 in the present paper. It differs from that of Wood (1935a, fig. 1a) only in the identification of cusps of P_4. A number of versions of Wood's terminology, meant to express various authors' theories of cusp homologies, have appeared since 1935, making it necessary to specify the terminology employed. Rensberger's terminology is used here in a topographic sense, and does not necessarily imply homology with similarly named cusps in nongeomyoid rodents.

Measurements in table 2 were made with a mechanical-stage measuring microscope. In cases where caliper measurements were also made, the microscope measurements tended to exceed those made with calipers.

SUBFAMILY HETEROMYINAE

PROHETEROMYS WOOD, 1932

Standing Rock Quarry has produced parts of at least five individuals of *Proheteromys.* These form parts of two coprolite-like specimens interpreted as owl pellets. F:AM 25365 was contained in a pellet with a geomyine, F:AM 25364, referred to a new genus described below. F:AM 25366, a second pellet, includes parts of four individuals, 25366 *a*, *b*, *c*, and *d.* F:AM 25366 *b* and *d* present morphologic and size differences from *a* and *c*, and will be discussed separately.

Proheteromys cejanus, new species
Figures 4, 5

Holotype. F:AM 25365, partial maxilla with P^4-M^2, partial right and left rami with complete dentitions, and phalanges.

Type Locality. Standing Rock Quarry, Piedra Parada Member type section.

Referred Specimens. F:AM 25366 *a*, partial skull with I^1 and articulated right ramus with I_1 and M_{1-3}; and 25366 *c*, partial skull with I^1, left jaw with I_1-M_3, partial right jaw with I_1, and associated M^{1-2} and M_{2-3}.

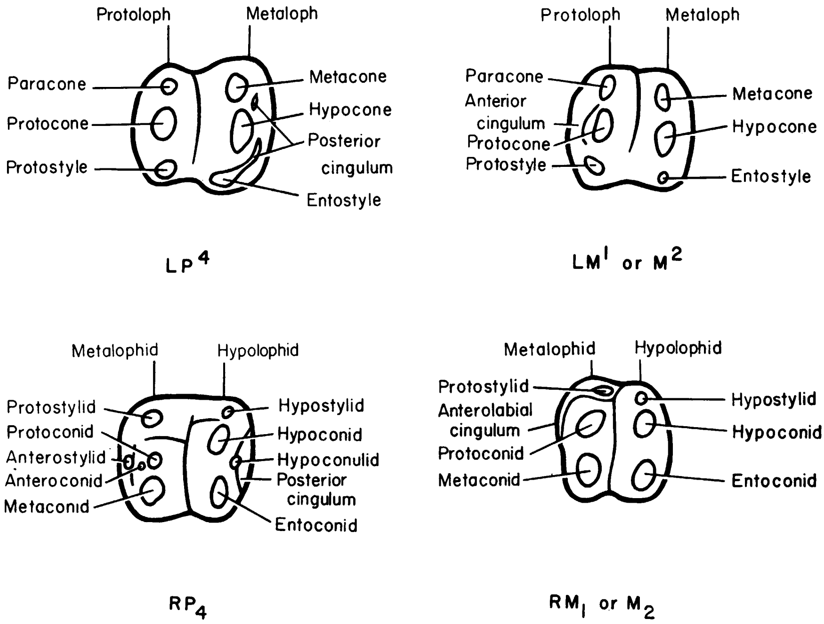

FIG. 3. Diagram of cheek teeth of a hypothetical geomyoid rodent showing cusp terminology used in text.

Etymology. Named for the Ceja del Rio Puerco, the escarpment at the north end of which is Standing Rock Quarry.

Diagnosis. Distinguished from *Proheteromys sulculus* by asulcate upper incisors, stronger anterior cingulum on M^1 and M^2, and higher central connection between lophs of M_2 than M_1. Distinguished from *P. ironcloudi* by larger size, absence of anterior cingulum lingual to protoconid of M_1 and M_2, and absence of labial connection between lophs of M_3.

Description. The skull of F:AM 25366 *a* lacks the cranium posterior to the frontals. Its length from front of incisors to front of orbit (measured at the most anterior point of the posterodorsal margin of the zygomatic arch) is 10 mm., and from front of incisors to back of frontals is about 18 mm. Fused without visible suture, the frontals are unusually narrow for a heteromyine. The minimum interorbital width, 3.9 mm., is 39 percent of the orbit-incisor length, compared with 71 percent for a specimen of *Heteromys* measured and 72 percent for a specimen of *Perognathus*; it resembles modern geomyines more closely. The side of the rostrum is perforated by a large vacuity into which the infraorbital canal opens, a character of all modern heteromyids (Miller and Gidley, 1918, p. 434; Wilson, 1936, p. 21). The skull of F:AM 25366 *c* is slightly smaller (incisor-orbital length 9.3 mm., incisor-posterior frontal length 16.9 mm.). In heteromyid fashion, the rostrum projects anterior to the incisors as a tube. The light zygomatic arch is oriented like those of *Heteromys* and *Perognathus*.

The incisor-condyle length of the right jaw of F:AM 25366 *a* is 15 mm. The coronoid process is subequal in elevation to the condyle. In lateral view the jaws show a strong masseteric ridge running anterodorsally to end abruptly just behind the mental foramen and at the same level, about two-thirds of the height of the jaw; jaw depth below P_4 is 3.2 mm.

The incisors are narrow and elongate in cross section. The lower incisors are slightly concave medially and nearly as wide posteriorly as anteriorly. The asulcate upper incisors are about three-fourths as wide posteriorly as anteriorly.

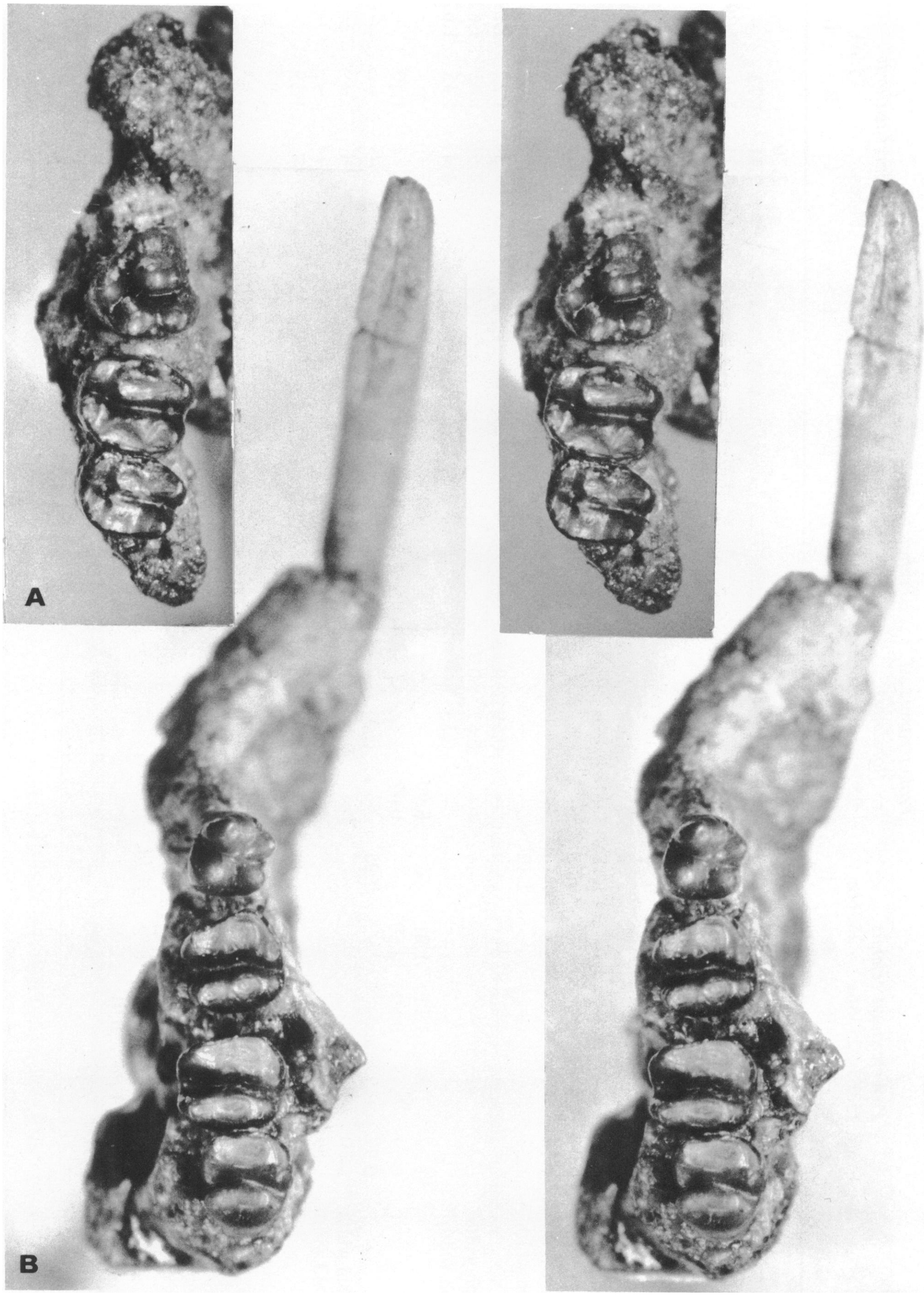

FIG. 4. Holotype of *Proheteromys cejanus*, new species, F:AM 25365. Occlusal, stereo views. A. Partial maxilla with P^4-M^2. ×12. B. Distorted ramus with I_1-M_3. ×12.

TABLE 2
Dental Measurements (in Millimeters) of Geomyoid Rodents

	Proheteromys cejanus F:AM 25365		*P. cejanus* 25366*a*	*P. cejanus* 25366*c*		*Proheteromys* aff. *floridanus* 25366*b*		*P.* aff. *floridanus* 25366*d*	*Proheteromys* or *Mookomys* sp. 51301	25369	25368	*Pleurolicus* cf. *sulcifrons* 51309		*Ziamys tedfordi* 51264		*Z. tedfordi* 25364	
	R	L	R	R	L	R	L	L	L	L	L	R	L	R	L	R	L
I^1 length[1]	–	–	1.30	–	1.32	0.95	–	–	–	–	–	2.20	–	–	2.30	–	–
I^1 width	–	–	0.74	–	0.59	0.52	–	–	–	–	–	1.31	–	–	2.41	1.73	–
P^4 length	1.26	–	–	–	–	–	–	–	–	–	–	–	–	–	2.21	2.56	2.39
P^4 protoloph width	0.77	–	–	–	–	–	–	–	–	–	–	–	–	–	1.76	–	–
P^4 metaloph width	1.30	–	–	–	–	–	–	–	–	–	–	–	–	–	2.19	–	–
M^1 length	1.08	–	–	–	0.94	–	0.71[2]	–	–	–	–	1.74[2]	–	1.40	1.31	1.24	1.33
M^1 protoloph width	1.30	–	–	–	1.32	–	1.00	–	–	–	–	2.55	–	2.20	2.11	2.14	2.15
M^1 metaloph width	1.30	–	–	–	1.28	–	0.96	–	–	–	–	2.51	–	2.12	2.06	1.96	2.05
M^2 length	0.94	–	–	–	0.88	–	–	–	–	–	–	–	–	1.32	1.31	1.17	1.33
M^2 protoloph width	1.26	–	–	–	1.16	–	–	–	–	–	–	–	–	2.09	1.97	2.24	2.02
M^2 metaloph width	1.24	–	–	–	1.12	–	–	–	–	–	–	–	–	2.00	2.01	–	1.81
M^3 length	–	–	–	–	–	–	0.59	0.58	–	–	–	–	–	–	1.34	1.22	1.29
M^3 protoloph width	–	–	–	–	–	–	0.67	0.71	–	–	–	–	–	–	1.56	1.45	1.62
M^3 metaloph width	–	–	–	–	–	–	0.55	–	–	–	–	–	–	–	1.47	1.45	1.62
I_1 length[1]	1.22	1.24	1.11	1.21	–	0.90	–	–	–	1.00	–	–	–	–	–	–	–
I_1 width	0.59	0.65	0.60	0.60	–	0.47	–	–	–	0.50	–	–	–	–	–	1.70	–
P_4 length	0.97	0.99	–	–	0.95	–	0.76	–	1.36	1.18	–	–	–	–	–	–	–
P_4 metalophid width	0.80	0.84	–	–	–	–	–	–	1.07	0.94	–	–	–	–	–	–	–
P_4 hypolophid width	0.89	0.90	–	–	–	–	0.74	–	1.29	1.20	–	–	–	–	–	–	–
M_1 length	1.09	1.11	–	–	1.14	–	1.05[3]	–	–	–	1.27	–	2.22	–	–	1.39	–
M_1 metalophid width	1.12	–	–	–	–	–	1.08	–	–	–	–	–	2.42	–	–	1.93	–
M_1 hypolophid width	1.13	1.17	–	–	1.05+	–	1.04	–	–	–	1.40	–	2.40	–	–	2.03	–
M_2 length	1.09	1.05	1.18	1.05	1.04	–	–	–	–	–	–	–	2.30	–	–	1.32	–
M_2 metalophid width	1.24	1.25	–	1.30	1.12+	–	–	–	–	–	–	–	2.38	–	–	–	–
M_2 hypolophid width	1.18	1.20	–	1.30	–	–	–	–	–	–	–	–	2.38	–	–	–	–
M_3 length	0.99	0.96	0.97	0.96	0.98	–	–	–	–	–	–	–	–	–	–	1.39	1.40
M_3 metalophid width	1.06	1.06	0.91	1.04	–	–	–	–	–	–	–	–	–	–	–	1.78	1.84
M_3 hypolophid width	0.91	0.97	–	0.95	–	–	–	–	–	–	–	–	–	–	–	1.52	1.44

[1] Anteroposterior, measured in plane perpendicular to shaft.
[2] $M^{1 \text{ or } 2}$.
[3] $M_{1 \text{ or } 2}$.

The protocone of P^4 of F:AM 25365 is central and about one and one-half times as wide as long; it bears a paracone, a swelling on the labial side of the protocone just below its apex. The transverse valley is a narrow cleft slightly more shallow centrally than labially or lingually; the lophs would join centrally very late in wear. The three-cusped metaloph is curved in occlusal view, concave anteriorly. The central hypocone is largest; the lower metacone, occupying nearly as much area, would merge indistinguishably with the hypocone early in wear. The entostyle is as high as the hypocone but narrower-based and anteroposteriorly elongate, separated from the hypocone by a valley little deeper than that between hypocone and metacone, and also by a persistent vertical groove on the anterior face of the loph. A low cingulum crest joins the posterolabial side of the entostyle to the hypocone apex; another tiny cuspule or short cingulum lies behind and between hypocone and metacone, closer to the hypocone.

Of the protoloph cusps of M^1, the protocone is largest; the paracone, probably subequal in height, is closely joined to it; and the oval protostyle, lower and smaller in basal area than either, lies partly anterolingual to the protocone. The latter projects posterior to the protostyle and paracone, which are joined anterior to it by a continuous cingulum. Hypocone and metacone unite at an early stage of wear; the anteroposteriorly elongate entostyle is lower, separated from the hypocone by a valley about as deep as that between protocone and protostyle. All anteroposterior valleys are shallower than any part of the transverse valley. Entostyle and protostyle form a notch constricting the lingual end of the transverse valley; with wear, the lophs would first join lingually, then between protocone and hypocone to form a small, ephemeral lake. M^1 of F:AM 25366 *c* is similar, but the lingual connection between lophs is stronger and the central weaker.

M^2 of F:AM 25365 is similar to M^1 but smaller, with a stronger lingual connection between lophs. M^3 is not preserved.

The metalophid of P_4 of F:AM 25365 is tricuspid, with subequal metaconid and protostylid flanking a smaller protoconid (or anteroconid) joined at its base to the metaconid. The valley between protoconid and protostylid is blocked anteriorly by a short, anteromedially directed anterior cingulum nearly as high as the protoconid. The large entoconid and smaller hypoconid are not joined into a loph. On the right P_4, hypoconid and protostylid, and metaconid and entoconid, are weakly joined. The two posterior cusps would thus remain separate with wear, forming separate connections with the metalophid. The labial cusps are closer together than the lingual. The labial valley of the left P_4 is shallowest of the three, the posterior intermediate, and the lingual deepest; with wear, the hypoconid would join first the metalophid, then the entoconid. P_4 of F:AM 25366 *c* lacks the protoconid, but is similar in lacking any connection of the posterior cusps. Labial, posterior and lingual valleys are subequal in depth; the anterior is about half as deep. A short, low cingulum joins metaconid and protostylid at the anterior margin of the tooth.

The hypolophid of M_1 of F:AM 25365 is lower than the metalophid. The conical protoconid is the largest cusp of the metalophid; the transversely oval metaconid is closely joined to the protoconid and nearly as large. The low protostylid is transversely narrow and anteroposteriorly elongate, with half of its length projecting posterior to the protoconid. It is only poorly differentiated from the cingulum which joins it to the posterolingual corner of the protoconid. The hypoconid is slightly larger than the entoconid; the circular hypostylid is smaller and lower, separated from the hypoconid by a valley deeper than that between hypoconid and entoconid. The transverse valley is deflected posterolabially between stylids; it is shallowest there, deepening gradually between protoconid and hypoconid, and more steeply between metaconid and entoconid. M_1 of F:AM 25366 *c* is similar, but with a central connection equaling the low labial connection in height.

Compared with that in M_1, the transverse valley of the right M_2 of F:AM 25365 is less strongly deflected. The transverse valley is shallowest between stylids; the valley also shallows between protoconid and hypoconid, forming a central connection late in wear. The central connection of the left M_2 is nearly as high as that between stylids. M_2 of F:AM 25366 *c* has a well-developed H-pattern, with a stronger central connection and weak labial connection. F:AM 25366 *a* has a weaker central connection, which is still stronger than that between stylids. In each specimen, the central connection is stronger on M_2 than on M_1.

The protostylid of M_3 of F:AM 25365 projects only slightly posterior to the protoconid; otherwise the metalophid is like those of the anterior molars. The hypostylid forms a weak shoulder on the hypoconid. The transverse valley is shallowest centrally and deepens symmetrically both labially and lingually, with no connection between stylids. The hypolophid is lower and transversely narrower than the metalophid. The right M_3 of F:AM 25366 *c* is similar; the left, and the right of F:AM 25366 *a*, lack the hypostylid.

Comparisons. Proheteromys cejanus differs from *P. sulculus* (Wilson, 1960, pp. 75-78) in its asulcate upper incisors; P^4 with a paracone and without an entostyle-protocone connection; M^{1-2} with better developed anterior cingula; more posterior mental foramen; P_4 lacking a hypostylid; and H-pattern better developed in M_2 than in M_1, and even stronger in M_3. The two species are similar in size and in the nature and extent of variation in P_4. An H-pattern is variably present in M_{1-2} of both, and may isolate a small labial lake; M_3 bears a central connection in both. Jaw morphology is generally similar. If the teeth from the same sample described as *Mookomys* cf. *formicorum* (Wilson, 1960, pp. 78-79) are included in *P. sulculus*, a possibility recognized by Wilson and supported by Black (1963, pp. 496-497), the range of variation of the premolars of *P. sulculus* is increased and includes forms similar to those of *P. cejanus*.

Proheteromys ironcloudi (Macdonald, 1970, p. 42) is smaller than *P. cejanus*. P_4, which lacks a protoconid, is very like that of F:AM 25366 *c*, although the labial cusps are more strongly joined than the anterior and the anterior cingulum is more obliquely oriented. M_1 may have been more elongate; it has been shortened by interdental wear. Protostylids of M_{1-2} project farther back, but are no more distinct from the cingula, and a short anterior cingulum is present lingual to the protoconid of each. *Contra* Macdonald, a central connection is absent from M_1, although present on M_2. M_3 has both central and labial connections, enclosing a labial lake. Molars of the two species are similar in the lack of posterior cingula or hypoconulids and in the posterior increase in height of the central connection between lophs.

Macdonald (1963, pp. 183-186) has described three species of *Proheteromys*, *P. bumpi*, *P. gremmelsi*, and *P. fedti*, from the early Arikareean Sharps Formation of South Dakota. The number of species represented is questionable; the range of morphological variation is similar in magnitude to that seen in the sample of *P. sulculus* from Quarry A in the Martin Canyon local fauna (Wilson, 1960, pp. 75-79), but size variation may be greater. Macdonald (1963, p. 183) considered *Proheteromys bumpi* the most advanced of these species; it is, however, difficult to distinguish, except by larger size, from *Proheteromys incohatus* from the Orellan of Weld County, Colorado (originally described as *Akmaiomys incohatus* by Reeder, 1960, pp. 518-521; referred to *Proheteromys* by Black, 1965, p. 46). As Reeder noted, the latter species bears two anteromedial cusps on P_4: an elongate cusp between metaconid and protostylid, and a cingular cusp anterior and connected to the first. A similar condition is seen in F:AM 25365, where a cingulum lies anterolabial to the large medial cusp. The central cusp of the protolophid appears to be the anteroconid of Wood (cf. Wood, 1935a, p. 173, description of *Peridiomys rusticus*) and the protoconid or protoconid-anteroconid of Rensberger (1971, pp. 123-124). The cingulum cusp of *P. incohatus* is either absent or merged with the protoconid in *P. bumpi*; in the holotype a short anterior cingulum joins the fronts of protostylid and protoconid. The protoconid of *P. bumpi* is, in any case, more elongate than that of F:AM 25365. On P_4 hypostylid and hypoconulid are variably present, and the entoconid tends to be transversely elongate, constricting the posterior valley. As in *P. cejanus*, the posterior cusps are not joined into a loph. As in most species of *Proheteromys*, the labial cusps are closer together than the lingual.

The protostylids of M_{1-3} are larger, more conical, better separated from the cingulum, and project farther posteriad than those of *P. cejanus*. M_{1-2} have posterior cingula, bearing hypoconulids in one specimen, and short anterior cingula lingual to the protoconids. The central connection on M_2 is no stronger, possibly weaker, than that of M_1 and is always weaker than the labial connection. M_1 appears relatively more elongate than in *P. cejanus*. M_3 has no labial connection, although the hypostylid is larger than in *P. cejanus*.

The molars of *P. gremmelsi* are like those of *P. bumpi*. The conical anterior cuspule of P_4 is probably a cingulum cusp (anterostylid) rather than an anteroconid or protoconid. The two anterior cusps are placed unusually close together, as in *P. parvus*. The posterior cusps are separate; a low hypoconulid or short posterior cingulum blocks the posterior valley. The central connection between molar lophs decreases in height posteriorly through the molar series.

Proheteromys fedti, smallest of the Sharps Formation species, is near the size of *P. cejanus*. As in *P. gremmelsi*, the anteromedial cusp of P_4 corresponds to the cingular cusp of other geomyoids rather than the protoconid or anteroconid. The labial valley is blocked by a conical stylar cusp, and the posterior by a hypoconulid, both lacking in *P. cejanus*; otherwise the tooth is much like that of F:AM 25366 *c*. M_{1-2} have anterior cingula lingual to the protoconids, short posterior cingula, larger and more posterior protostylids, and higher labial connections between lophs. The central connection is stronger on M_2 than on M_1, but still weaker than the labial.

Proheteromys floridanus (Wood, 1932, pp. 45-46; Black, 1963, pp. 492-497) differs more strongly from *P. cejanus*. It is smaller and lacks a paracone on P^4. The posterior cusps of P_4 form a loph, which is usually joined centrally to the metalophid. There is no anterior central cusp. Two hypoconulids are sometimes present. Lower molars lack both labial and central connections between lophs. M_3 has no hypostylid.

Proheteromys parvus, of uncertain age (Wood, 1935a, pp. 170-172; fig. 5), differs from *P. cejanus* in having strong posterior cingula on P_4-M_2 and more anterior protostylids on M_{1-2}; it resembles *P. cejanus* and the species from the Sharps Formation in the separation of P_4 hypoconid and entoconid.

Proheteromys matthewi (Wood, 1935a, p. 170, fig. 96a; Macdonald, 1963, p. 186) from Marsland-equivalent rocks of South Dakota, is higher crowned. P_4 lacks any anterior central cusp, and its posterior cusps form a strong loph. Both labial and central connections of the lophs of M_1 are higher, isolating a relatively persistent lake.

?*Mookomys bodei* (Wilson, 1949, pp. 58-60, pl. 1, figs. 5, 6) from the ?Arikareean upper part of the Sespe Formation of California is very like *Proheteromys cejanus* in P^4 and M_1 morphology, and in lack of loph development on P_4; it differs in larger size, central connection of P_4 cusps, and higher union of the styles of M^{1-2}.

Discussion. The presence or absence of anterior central cusps on P_4 has borne considerable weight in distinguishing species and genera of geomyoid rodents. It appears, however, that the number and identity of such cusps has been a source of confusion. Rensberger (1971, fig. 67) identified the central cusp of the anterior loph of P_4 of entoptychines as the protoconid, and likewise the central cusp variably present in *Pleurolicus* as the protoconid (1973a, fig. 6). The latter is similar in morphology and position to the more posterior of the central metalophid cusps of some specimens of *Proheteromys*. The central cusp of *P. incohatus*, for example, appears homologous, as it is similarly joined at its base to the metaconid (Reeder, 1960, p. 519). The "anteroconid" of *Peridiomys* (Wood, 1935a, figs. 97, 100) also appears homologous to the protoconid (*sensu* Rensberger, 1971, 1973a). Rensberger applied the term "anteroconid" to an accessory cusp of the P_4 metalophid, illustrated in entoptychines, *Heteromys* and *Heterogeomys*. No separate anteroconid (*sensu* Rensberger) has been identified in *Proheteromys*. Rensberger introduced the term "anterostylid" for an anterior cingulum cusp. Such a cusp is variably present in *Proheteromys*; in some specimens lacking it, an anterior cingulum is present. The names applied by Rensberger to the cusps of P_4, employed here, may not correctly express homologies to cusps in other groups of mammals; such homologies are not well understood and may not exist. However, by recognizing that any of three anterocentral cusps may be present in some geomyoids, he has made possible a reinterpretation of the significance of the occurrence of such cusps in early heteromyids.

It is becoming clear that where adequate samples of early and medial Miocene species of *Proheteromys* are available they are characterized by high variability, particularly in the occurrence of accessory cusps on P_4. For example, within the samples from Thomas Farm (Black, 1963, pp. 492-497) and Martin Canyon Quarry A (Wilson, 1960, pp. 75-79) cited above, the protoconid, anterostylid, both, or neither may be present. The presence or absence of these accessory cusps is not a reliable taxonomic character, particularly when used in identifying single specimens or small samples.

Rensberger (1973b, p. 847, fig. 5) considered *Heliscomys* ancestral to *Proheteromys* and *Mookomys* as well as to the later geomyids, in part because it has been reported from Chadronian deposits and *Proheteromys* has not. Our knowledge of Chadronian microfaunas is still limited, however. The presence of both protoconid and anterostylid and of strong posterior and anterior lingual cingula on P_4 of *Proheteromys incohatus* from the Orellan suggests the possibility that such complexity, rather than the smaller size and simplicity of P_4 of *Heliscomys*, is primitive for heteromyines. *Proheteromys cejanus* might be derived from the species or group of species from the Sharps Formation, some of which approach *P. incohatus* in morphology, by simplification through loss of cingula and accessory cusps. *Proheteromys ironcloudi* of the Monroe Creek Formation of South Dakota, smaller in size, appears intermediate in morphology; its range of variation is unknown. *Proheteromys sulculus* from Quarry A, Martin Canyon local fauna, is also close to *P. cejanus*; it is best distinguished by its sulcate upper incisors. *Proheteromys sulculus* could be derived from *P. ironcloudi*, the upper incisors of which are not known, or from *P. cejanus*. *Proheteromys matthewi* represents a distinct advance over the other species discussed in its greater crown height and in the strong posterior loph and lack of cingula and accessory cusps of P_4. ?*Mookomys bodei*, of uncertain age, is similar in most features to *P. cejanus*, although its P_4 is of perognathine aspect.

Proheteromys aff. *floridanus* Wood, 1932
Figures 5, 7

Referred Specimens. F:AM 25366 *b*, partial skull with I^1, right and left jaws with I_1-P_4, and left $M^{1 \text{ or } 2}$, $M_{1 \text{ or } 2}$, and M_3, and F:AM 25366 *d*, left M^3, both part of the owl pellet also containing F:AM 25366 *a* and *c*, from Standing Rock Quarry (E. Extension), Piedra Parada Member type section.

Description and Comparisons. Preserved parts of the skull of F:AM 25366 *b* include the anterior skull roof and rostrum. The premaxillae are convex and unfused ventrally. The incisor-orbital length appears less than in *P. cejanus*, but cannot be measured. The fused frontals, although narrowed by crushing, are broader than those of *P. cejanus* (interorbital width 6.3 mm., as preserved); skull proportions appear closer to those of *Heteromys* or *Perognathus*.

The jaws have an incisor-condyle length of 12.5 mm. The coronoid process rises well above the condyle; the latter is not so far above the occlusal plane as in *P. cejanus* or modern *Heteromys*. The mental foramen lies at half the height of the jaw; the masseteric ridge ends just behind it. The jaw is deepest, 2.4 mm., below P_4, relatively shallower than in *P. cejanus*.

I_1 is narrow in cross section (table 2), straight medially, and relatively shorter and broader than that of *P. cejanus*. I^1 is asulcate, no wider labially than lingually in cross section, and likewise shorter and broader than that of *P. cejanus*.

P^4 is not preserved. $M^{1 \text{ or } 2}$ bears an anterior cingulum only between protocone and metacone, not continuing across the protocone to the protostyle. The styles are higher than in *P. cejanus*, meeting to form a high lingual connection; there is no central connection. Cusps are poorly differentiated on the small M^3. The low, transversely narrow metaloph is joined lingually to the protoloph; the shallow transverse valley deepens labially. F:AM 25366 *d*, a more heavily worn M^3, shows a narrow labial connection as well; wear has isolated a small labial lake.

Both P_4s of F:AM 25366 *b* are preserved. The left consists of a circle of cusps around a central pit, the center of which lies between hypoconid and entoconid. The metaconid is larger than the protostylid and separated from it by an anterolabially-directed valley shallower than the central pit. At the anterior end of this valley is a small anterostylid. The posterior valley is deeper, although still shallower than the central pit. Between this valley and the hypoconid is a small hypoconulid poorly separated from the hypoconid. In contrast to most species, the lingual cusps are closer together than the labial; in fact, the metaconid and entoconid are poorly separated even at the apex. A shallow valley separates protostylid and hypoconid. With wear, the cusps would form two anteroposteriorly oriented lophs concave toward the center of the tooth; they would merge anteriorly, then posteriorly to form a circle. The right P_4 is like the left except that the hypoconulid is less distinct, and the lingual cusps are as well separated as the labial.

$M_{1 \text{ or } 2}$ of F:AM 25366 *b* lacks both central and labial connections; the transverse valley is of uniform depth. The conical protostylid lies almost entirely posterior to the protoconid and is well separated from the cingulum, which is represented by a second stylar cusp anterolabial to the protoconid and joined more strongly to it than to the protostylid. The large conical protoconid is placed slightly farther anteriorly than the metaconid. The circular hypoconid is likewise larger than the entoconid and projects anterior to it; the hypostylid is small and conical, lying on a transverse line with the entoconid. Transverse valley and metalophid are thus convex anteriorly in occlusal view. No anterior lingual cingulum, posterior cingulum, or hypoconulid is present.

These specimens are most similar in size and morphology to *Proheteromys floridanus* (Wood, 1932, pp. 45-46; Black, 1963, pp. 492-497). Wood described the upper incisors of the latter species as asulcate. $M^{1 \text{ or } 2}$ of F:AM 25366 *b* is like MCZ 8470 (Black, 1963, fig. 4e) in position and size of cingula; the styles, which fuse to close the transverse valley lingually in both are broader, as in FSGS V-6016 (Black, 1963, fig. 4d). M^3 has a narrower metaloph than FSGS V-6028 (Black, 1963, fig. 4f), more nearly resembling that of *Heteromys*, and the protostyle stands high above the entostyle rather than joining it in a smooth shelf.

The normal P_4 of *P. floridanus* (Black, 1963, pp. 494-495, fig. 4i-k) is very unlike that of F:AM 25366 *b*, with transverse lophs joined by a central crest and without an anterostylid. However, two small hypoconulids may be present (e.g., FSGS V-6014, Black, 1963, fig. 4i). MCZ 8485 (Black, 1963, fig. 4 l) approaches F:AM 25366 *b* in having the labial cusps joined more closely than the anterior and a deep central pit; it lacks accessory cuspules.

The hypolophid of $M_{1 \text{ or } 2}$ appears little lower than and as cuspidate as the metalophid, thereby contrasting with *P. floridanus*. The anterior cingulum of *P. floridanus* fails to show the division into two well-separated cusps seen in F:AM 25366 *b*. The transverse valley is of uniform depth in both.[1] Black's figures 4m and 4n (1963) show a short cingulum between hypoconid and entoconid; no such structure is present in F:AM 25366 *b*.

Discussion. Although distinguished from *Proheteromys floridanus* by the structure of P_4 and M^3, the Standing Rock Quarry form resembles the Thomas Farm species in most characters of the molars, in the small size of M^3 (described by Black, 1963, as reduced), and the asulcate incisors. In view of the poor preservation of the specimen, as well as of the wide ranges of variation of species of *Proheteromys* demonstrated by Black (1963) and Wilson (1960), the lack of osteological material of *P. floridanus*, and the occurrence of most of the features of the P_4 of F:AM 25366 *b* as variants in *P. floridanus*, the erection of a new species for this specimen would not be justified.

SUBFAMILY HETEROMYINAE OR PEROGNATHINAE

Proheteromys or *Mookomys* sp.
Figure 8

Referred Specimens. F:AM 25369, left ramus with I_1 and P_4; F:AM 51310, left ramus with P_4; and F:AM 25368, $LM_{1 \text{ or } 2}$, all from Blick Quarry, Chamisa Mesa Member type section.

[1]On the basis of a sample of 23 specimens, Black stated that the lophs are not connected; Wood (1947, p. 484) described two specimens as having an anterior spur from the hypoconid which he considered to be the beginning of the H-pattern.

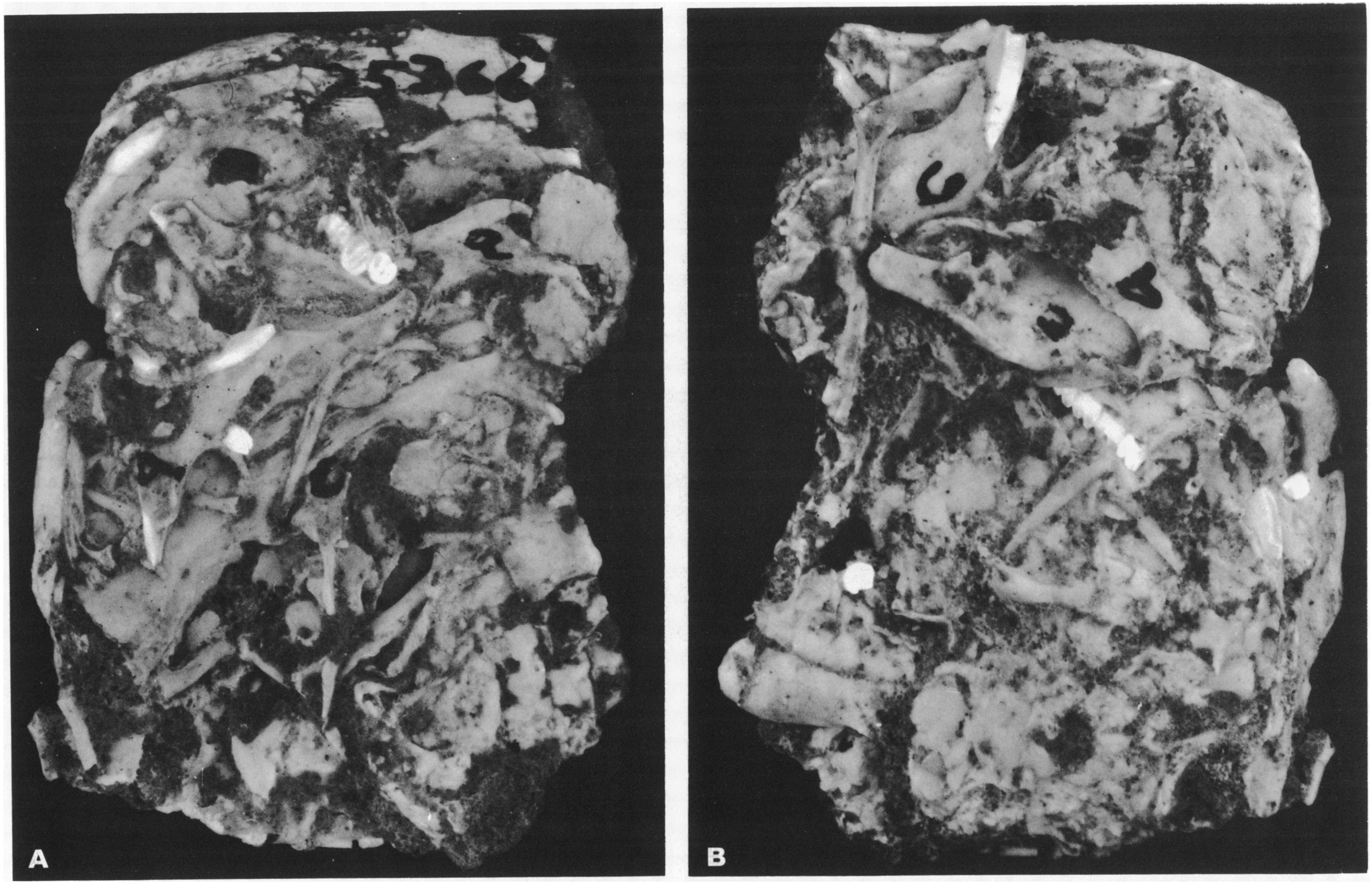

FIG. 5. Owl pellet, F:AM 25366. ×4. A. *Proheteromys cejanus*, new species, 25366 *a*, skull and right jaw, and 25366 *c*, skull; *Proheteromys* aff. *floridanus*, 25366 *b*, ventral view of right jaw, left jaw with P_4, and distorted rostrum lying under incisors of 25366 *a*. B. Reverse side. *P. cejanus*, 25366 *a*, skull; 25366 *c*, partial right jaw and complete left jaw with complete dentition. *P.* aff. *floridanus*, 25366 *b*, crushed skull; right jaw with P_4; and $M_{1 \text{ or } 2}$. See figure 6 for diagram showing positions of specimens.

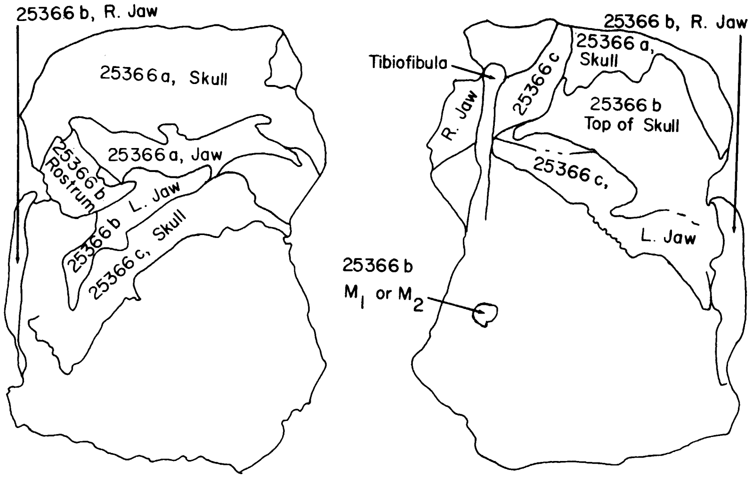

FIG. 6. Diagram showing positions of specimens of *Proheteromys* in owl pellet, F:AM 25366. ×2. Compare with figure 5.

Description. The jaw of F:AM 25369 is shallow, deepest (2.7 mm.) below P_4, its length including the incisor slightly exceeding 16 mm. The mental foramen is at three-fourths the height of the jaw, midway between P_4 and I_1. The masseteric ridge is strong anteriorly, ending abruptly behind and above the mental foramen, and remains distinct posteriorly to the limit of preservation below the coronoid process. The latter is small and lower than the condyle.

The incisor is long and narrow in cross section, little wider labially than lingually, and with a shallow medial concavity. In lateral view the incisor is unusually straight, and ends in a low swelling below the coronoid process approximately at the occlusal plane.

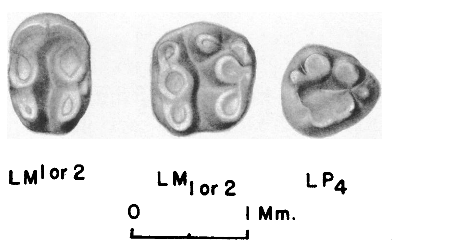

FIG. 7. *Proheteromys* aff. *floridanus*, F:AM 25366 *b*. Cheek teeth, anterior toward right of figure. ×15.

P_4 of F:AM 51310 is larger and relatively higher crowned than that of *Proheteromys cejanus*. The metaconid and smaller protostylid are circular conical. Between them and set off from them by faint grooves is a protoconid which reaches a height above the transverse valley approximately half that of the metaconid apex, and joins with the protostylid and metaconid to form a metalophid. Weak ridges running anterocentrally from the metaconid and protostylid meet in a short anterior cingulum below the level of the protoconid. Entoconid and hypoconid are transversely elongate, but separated by a posterior valley nearly as deep as the transverse valley; the "hypolophid" would form only shortly before joining the metalophid. The transverse valley is shallowest centrally and just labial of center, deepening labially and lingually.

P_4 of F:AM 25369 is similar but simpler; its metalophid is narrower and lacks the protoconid, its metaconid and protostylid joining posterocentrally at about one-third the height of the metaconid apex above the transverse valley. The anterior cingulum is weaker, a swelling forming a convexity on the anterior margin of the tooth. The transverse valley is shallowest between proto-

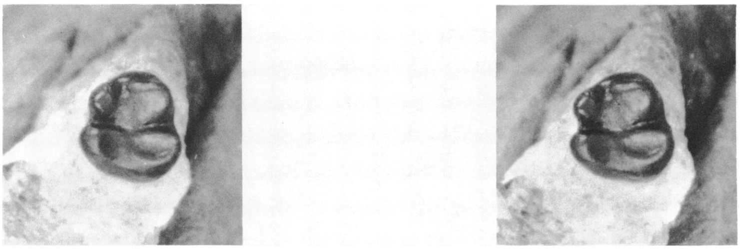

FIG. 8. *Proheteromys* or *Mookomys* sp., F:AM 51310. LP_4, occlusal, stereo view. ×10.

stylid and hypoconid; the posterior valley is little higher.

$M_{1\ or\ 2}$, F:AM 25368, is higher crowned than those of *P. cejanus* and more advanced in loph development; all traces of separate cusps disappear within one-fourth of the height of the loph above the transverse valley. The styles are nearly as high as the major cusps, but smaller based. The protostylid, the labial half of which is missing, lies almost entirely posterior to the protoconid; it is joined to the anterolabial corner of the protoconid by the cingulum which is thus oriented anteroposteriorly, not forming a Y-pattern. No other cingulum is present. The transverse valley is shallowest between the styles and deepens lingually, with no central connection.

Comparisons and Discussion. F:AM 51310 is heteromyine in the presence of a protoconid on P_4, and resembles *Proheteromys cejanus* in bearing an anterior cingulum as well and in the weak connection of the posterior cusps. There are also, however, strong similarities to *Mookomys altifluminus*, described as a perognathine, in the greater crown height, broad medial connection of P_4 lophs tending to be highest just labial of center, and transversely elongate posterior cusps of P_4. The resemblance of F:AM 25369 to *Mookomys* is even greater, differing only in larger size. The lophodonty of the molar is a further resemblance. Differences between F:AM 51310 and F:AM 25369 are of the same kind and degree as seen within the samples of *Proheteromys cejanus* and *P. sulculus* and do not justify placing the specimens in different subfamilies. The Blick Quarry form, although larger, may be an intermediate between *Proheteromys* and *Mookomys.*

Peridiomys rusticus (Matthew, 1924, p. 85; Wood, 1935a, pp. 172-174) of the Barstovian Lower Snake Creek local fauna is another possible descendant of the Blick Quarry form. It differs in larger size; greater crown height, with the additional length of enamel largely below the transverse valley; hypostylid present on P_4; connection of the anterior cingulum of the lower molars to the protoconid farther lingual, forming a Y-pattern; and central connection between lophs of the lower molars. The lack of the latter character in the single molar from Blick Quarry is inconclusive, as the central connection varies from absent to higher than that of *P. rusticus* in both *Proheteromys cejanus* and *P. sulculus*. The protoconid, the connection of lophs just labial of center, and the transversely elongate posterior cusps of P_4 of *Peridiomys rusticus* are similarities to the Blick Quarry form.

FAMILY GEOMYIDAE

SUBFAMILY PLEUROLICINAE

Pleurolicus sp.

Figure 9

Referred Specimen. F:AM 51309, partial dentition including both upper incisors, RdP^4, $LM^{1\ or\ 2}$, and LdP_4-M_2, from Blick Quarry, Chamisa Mesa Member type section.

Description and Comparisons. This specimen most nearly resembles *Pleurolicus sulcifrons* from the John Day Formation, Oregon. The upper incisors are relatively narrower than those of *P. sulcifrons* cited by Rensberger (1973a, p. 44); the ratio of width to depth, measured in cross section, is 0.59, compared with 0.64 and 0.66 for specimens of *P. sulcifrons*. However, the immaturity of F:AM 51309 may be responsible for the narrowness of the incisors. The anterior enamel band is more rounded than those of specimens of *P. sulcifrons* observed; its convexity increases from the medial to the lateral margin, without forming a lateral angle.

The protoloph of $M^{1 \text{ or } 2}$ is straight; its three cusps are separate for about one-fifth of the crown height of the tooth. The protostyle is slightly narrower than the paracone and protocone. The protocone apex lies posterior to those of the paracone and protostyle, which are joined by an anterior cingulum slightly higher than the valleys separating the cusps. The metaloph of F:AM 51309 is convex posteriorly, the metacone and entostyle being anterior to the hypocone and separated from it by valleys shallower than those of the protoloph. The entostyle is elongate anteroposteriorly, little better separated from the protostyle than from the hypocone; the lingual connection would form early in wear. The entostyle projects farther anterior than in other specimens of *Pleurolicus*, deflecting the transverse valley anteriorly; in this it resembles *Entoptychus* rather than *Pleurolicus* (Rensberger, 1973a, p. 47).

M_1 and M_2 of F:AM 51309 resemble specimens of *P. sulcifrons*, in particular AMNH 7182 [paratype of *P. copei* (Wood, 1936, p. 8, fig. 8); *P. copei* has been referred to *P. sulcifrons* by Rensberger (1973a, p. 17)], in size; crown height; depths of transverse and longitudinal valleys; and development of a small cusp on the cingulum "antero-external to the protoconid and antero-mesial to the protostylid" (Wood, 1936, p. 8). This small cusp is more strongly joined to the protostylid than to the protoconid. The longitudinal valleys are less than one-fourth as deep as the transverse valleys. The transverse valley separating the anterior cingulum from the protoconid is little deeper than that between protoconid and protostylid. The anterior cingulum is stronger in F:AM 51309 than in *P. sulcifrons*. M_2 has a central connection much lower than the labial connection, seen also in AMNH 7182. M_{1-2} differs from most specimens of *P. sulcifrons*, but resembles AMNH 7182 and a few other specimens (Rensberger, personal commun.), in the lack of an anterior projection of the center of the hypolophid.

Pleurolicus sp. from Blick Quarry is larger than the species of *Schizodontomys* and *Tenudomys* described by Rensberger (1973a). It resembles *P. sulcifrons* and differs from *Schizodontomys* in the posterior position of the protostylid of M_1 and M_2, shallowness of the lake enclosed by the anterior cingulum of M_1, and rounded anterolingual corner of $M^{1 \text{ or } 2}$. Crown height of F:AM 51309 is similar to that of *P. sulcifrons*, exceeding that of *Tenudomys*.

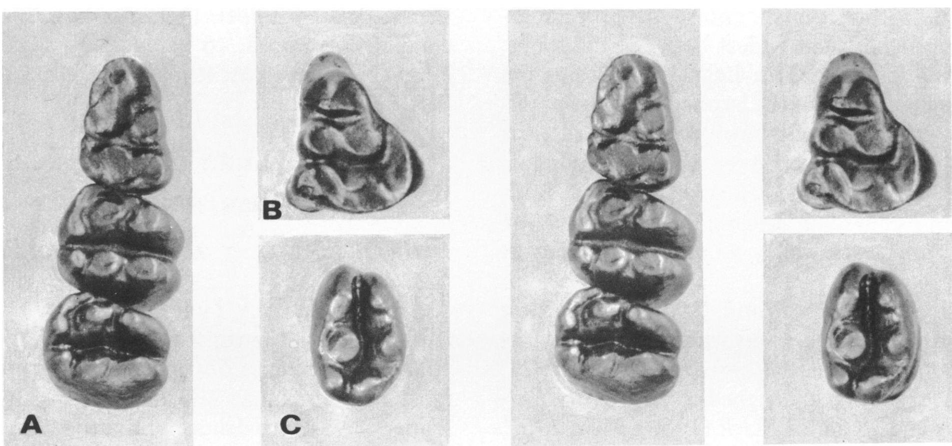

FIG. 9. *Pleurolicus* cf. *sulcifrons*, F:AM 51309. Occlusal, stereo views. A. LdP_4-M_2. ×7. B. RdP^4. ×7. C. $LM^{1 \text{ or } 2}$. ×7.

DP_4 is heavily worn, but in those points that can be compared is like that of *Entoptychus* (Rensberger, 1971, pp. 121-123, figs. 67, 68 h, pl. 6 i).[1] The single wear facet anterior to the transverse valley is interrupted only by a lingual notch and a small anterolabial enamel patch now isolated from the tooth margin, but near the position of the notch between anterior and labial cingulum cusps in *Entoptychus*. The hypolophid is not joined to the metalophid by a crest as it is in *Thomomys* and *Gregorymys* (Rensberger, 1971, fig. 67). The most posterolingual of the anterior semicircle of cingulum cusps is separated from the metalophid by an anteroposteriorly short, transversely elongate notch as in *Entoptychus*; the corresponding "notch" of *Liomys* is widely open because of the absence of the lingual cingulum cusps. A short posterior cingulum or hypoconulid was present. A narrow process of the hypostylid projects anteriorly at the tooth margin, nearly closing the transverse valley.

The triangular, three-lophed dP^4 is less deeply worn than dP_4. The anteroloph consists of one large triangular cusp; it is widest posteriorly, about half as wide as the metaloph. The straight protoloph includes subequal, conical protocone and paracone. Hypocone and metacone are wider than long, the metacone directed anterolabially so that its base meets that of the paracone; the metaloph is thus concave anteriorly. The strong transverse crests described by Rensberger in *Entoptychus* are absent. Protostyle and entostyle are fused to form a high, anteroposterior, ridgelike cusp, highest and widest between the lophs; it is nearly unworn. This lingual ridge joins the anterolingual corner of the hypocone to the anterolingual corner of the protocone and extends anteriorly as a low crest to the posterolingual angle of the anterocone. Cingula are absent. Both transverse valleys are thus closed lingually; the posterior transverse valley would close labially at a late stage of wear.

Teeth assigned by Wood (1935b) and Black (1960) to *Palustrimus* have been recognized as dP^4s of entoptychines (Rensberger, 1968, 1971; Black, 1969). Black assigned *P. lewisi* to *Entoptychus* and *P.* sp. of Black (1960), MCZ 7353, to *Gregorymys*. The latter identification is confirmed by Macdonald's figure (1970, fig. 17b) of dP^4 of *Gregorymys formosus*, SDSM 6297, which differs from MCZ 7353 in the lack of the small accessory cusp in the floor of the second transverse valley and in the apparently unicuspid anteroloph. The specimens are similar in the width of the anterior crest and in the presence on protoloph and metaloph of small styles separate from the narrow lingual crest. *Entoptychus*, including "*P. lewisi*," lacks the lingual crest.

DP^4 of F:AM 51309 differs from the two species of *Gregorymys* and from *Entoptychus* (Rensberger, 1971, pp. 110-113, fig. 68a-c, pl. 6a-e) in the narrowness and unicuspid construction of its anteroloph and also in the fusion of the styles into a broad ridgelike cusp as high as the major cusps of the lophs.

Wilson (1960, p. 79-80) has assigned a similar tooth, KU 10237, from Quarry A, Martin Canyon local fauna, to *Proheteromys* sp. cf. *P. magnus*, but also stated, "If KU 10237 does not pertain to *P.* sp. cf. *magnus*, it probably is the DP^4 of an entoptychine." This tooth differs from F:AM 51309 in the larger size of the central cusps of the protoloph and metaloph, lack of connection of the lingual crest with the anterocone, and relatively greater wear on the lingual crest. KU 10237 is nearly as large as dP^4 of F:AM 51309 and much wider than KU 10238, the upper molariform tooth assigned to *P.* sp. cf. *P. magnus*. DP^4 of F:AM 51309 is narrower than the associated upper molariform tooth. These comparisons appear to exclude KU 10237 from *P.* sp. cf. *P. magnus*; it may be conspecific with F:AM 51309.

SUBFAMILY GEOMYINAE

ZIAMYS, NEW GENUS

Genotypic Species. Ziamys tedfordi, new species.

Included Species. Type species only.

Etymology. Named for the Zia Sand.

Diagnosis. Genus of Geomyinae differing from most Entoptychinae and modern Geomyinae in shape of rostrum (short and broad, deepening gradually posteriorly, lacking both the arch of modern geomyines and the break in slope anterior to P^4 of *Entoptychus*), in which it resembles

[1]Cusp terminology of deciduous teeth follows Rensberger (1971, pp. 110-112, fig. 67).

Gregorymys riggsi; morphology of P^4 (protoloph apparently unicuspid, transversely broad and anteroposteriorly short, joining entostyle and hypocone with wear to form a moderately persistent lingual lake); and relatively brachydont dentition with late-forming connections between lophs (P^4-M^2 lophs join nearly simultaneously at lingual margin and center; M^3 exceptional, with persistent central lake; M_{1-3} with central connection only). In these dental characters *Ziamys* resembles some specimens of *Pleurolicus sulcifrons*. *Ziamys* differs from modern geomyines, and resembles entoptychines and pleurolicines, in its rounded zygomatic arches, simple maxillojugal suture, and lack of an anterior palatine foramen. *Ziamys* differs from entoptychines and pleurolicines, and resembles modern geomyines, in its strongly fused, ventrally convex premaxillae, ventrally depressed palate deeply incised by grooves in some enclosed to form canals, prominent lateral angular process of lower jaw, upper incisors with weak medial groove and deep lateral sulcus, and anteroposteriorly short molars.

Ziamys tedfordi, new species
Figure 10

Holotype. F:AM 51264, a partial skull with nearly complete upper dentition.

Type Locality. Standing Rock Quarry, Piedra Parada Member type section.

Referred Specimen. F:AM 25364, a palate and partial mandible, also from Standing Rock Quarry; found in same owl pellet as F:AM 25365, holotype of *Proheteromys cejanus*.

Etymology. Named in honor of Dr. Richard H. Tedford, Curator of Vertebrate Paleontology, the American Museum of Natural History.

Diagnosis. Same as for the genus.

Description. The holotype, F:AM 51264, is a partial skull lacking most of the cranium and dorsoventrally crushed (fig. 10A, B). The left P^4-M^3, right M^{1-3}, and incisors are preserved. The rostrum is distorted; the premaxillae have been rotated posteroventrally and forced beneath the maxillae at their ventral suture. Thus shortened, the diastema is approximately equal in length to the alveoli of the cheek teeth, 6.7 mm. By the most generous estimate its original length was less than one and one-half times the cheek tooth length. In profile the rostrum appears to deepen gradually posteriorly from the incisors. In dorsal view it is wider than the interorbital area and retains or increases its breadth anteriorly. The nasals are missing. A small foramen perforates each dorsal process medial to the anterior root of the zygomatic arch. Ventrally the rostrum is narrow and transversely convex as in modern geomyines; the premaxillae are completely fused with only a faint ridge marking the midline. The incisive foramina are obscured; the anterior palatine foramen is absent; and the infraorbital canal opens into a short groove just posterior to the maxillopremaxillary suture. The maxillary surface ventral to the groove is smooth, bearing neither a ridge running anteriorly from the P^4 alveolus nor a scar for the M. masseter superficialis tendon. The extreme shortening of the rostrum may have resulted in a more anterior origin for the tendon, in the area obscured by crushing.

The palate between P^4s is equal in width to P^4, and widens only slightly posteriorly. Anteriorly the palate is moderately grooved for the palatal arteries; opposite P^4 the grooves deepen and become enclosed in canals, the right opening opposite the middle of P^4 and the left just posterior to P^4. The palatine, largely missing, extends anteriorly to the front of M^1 at the midline. Along the shallow groove marking its suture with the maxilla are two or more tiny foramina which probably open into the canal. An opening on each maxillopalatine suture dorsal to the back of M^2, exposed by loss of the palatine, may enter the canal for the palatine artery. The surface of the palate lies ventral to the level of the external edges of the cheek tooth alveoli. A slitlike opening posterior to each M^3 may be the foramen identified by Rensberger (1971, p. 96) as that carrying the palatine vein.

The zygomatic process of the maxilla, in dorsal view, meets the rostrum at right angles, but is evenly curved, with no anterolateral angle, and long. Its dorsal surface is broad. The maxillojugal suture is flat, the jugal lying entirely dorsomedial to the maxilla.

F:AM 25364 consists of a palate with all cheek teeth preserved, part of the zygomatic process of the maxilla, most of the right jaw bearing M_{1-3}, and parts of the left jaw crushed against

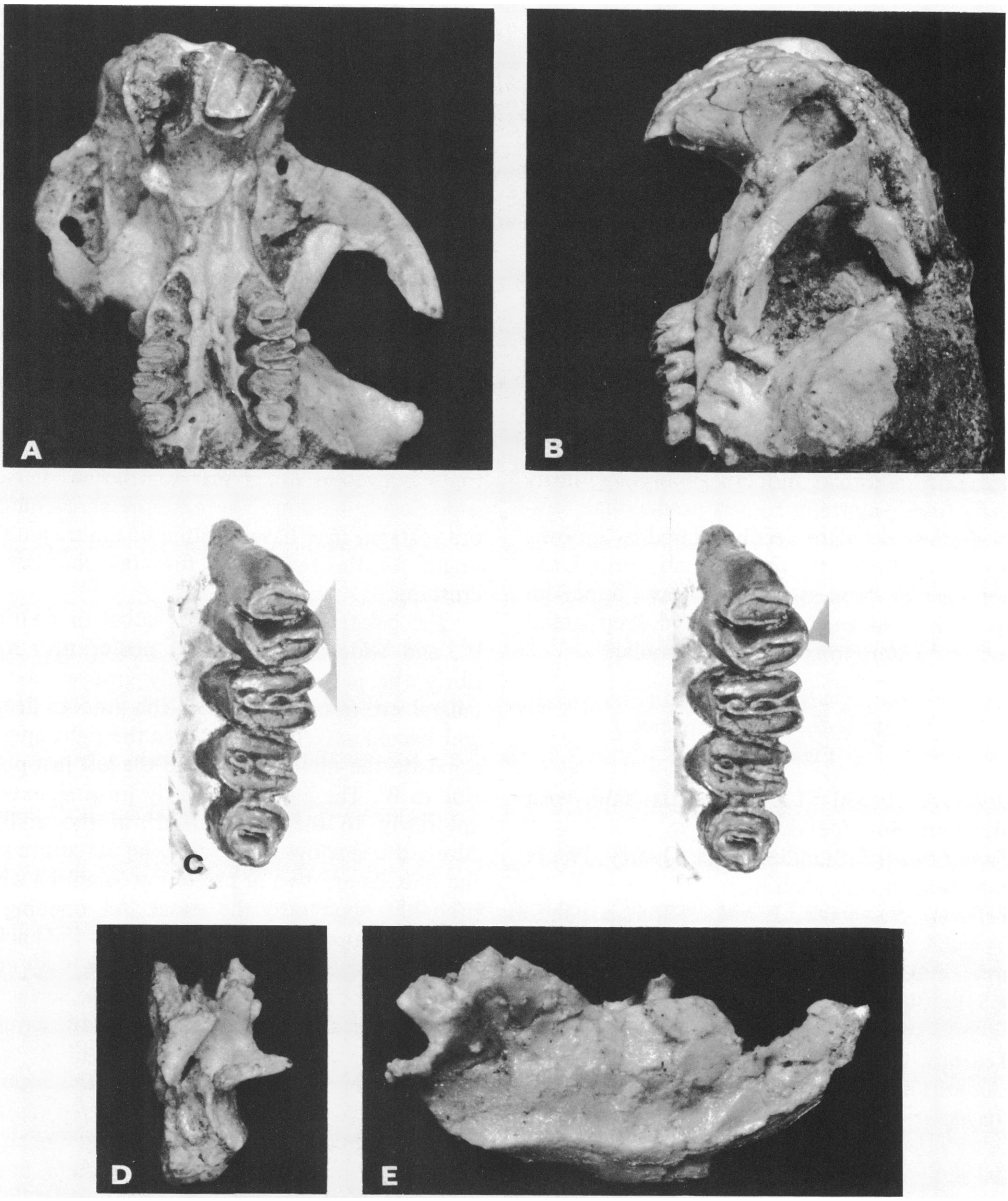

FIG. 10. *Ziamys tedfordi*, new species. A, B, and C, holotype, F:AM 51264. A. Ventral view of skull. ×3. B. Lateral view of skull. ×3. C. Occlusal, stereo view of left cheek teeth. ×7. D and E, referred specimen, F:AM 25364. D. Posterior view of jaw. ×3. E. Lateral view of jaw. ×3.

the right. The bone of the palate is poorly preserved, so that the sutures cannot be located with certainty. The median carina is stronger anteriorly than that of the type; between the cheek teeth the grooves for the palatal arteries are deeply incised but not enclosed. The medial carina and palate lateral to the grooves lie in the same plane, which is ventral to the labial edges of the alveoli. The number and exact position of the posterior palatine foramina cannot be ascertained.

The diastema of the right jaw (fig. 10E) is approximately 5 mm. long. Depth of the horizontal ramus below M_1 is 7 mm. The masseteric crest is strong posteriorly but weakens rapidly after turning dorsad; it is vertical where it lies just posterior to the mental foramen, which is 1.5 mm. anterior to the alveolus of P_4. The masseteric crest is horizontal below the molars, but curves ventrally below the base of the coronoid process. The posteroventral extent of the angular process is unknown. A strong lateral angular process was present (fig. 10D); its base is 3.5 mm. wide, and lies approximately in the occlusal plane. The anterior edge of the coronoid process arises beside M_2, concealing M_3 from lateral view. The ascending ramus is broken away below the points of separation of the coronoid process, condylar process, and incisor root; the bases of these structures have been crushed together.

The upper incisor of the holotype bears a deep groove the deepest point of which lies just lateral of center, and a shallow groove near the medial margin. The central sulcus is broad with gently sloping sides which turn abruptly downward to form an inner, sharply V-shaped valley. The medial groove has a rounded floor. The medial ridge is much lower than the central and labial ridges; all three have rounded crests. The tooth is triangular in cross section, slightly wider than long.

The brachydont cheek teeth are worn to within 1 mm. of the base, but the lophs remain distinct. The base of the enamel extends slightly farther dorsad on the anterior than the posterior end of each tooth. The protoloph of P^4, apparently unicuspid, is narrower transversely than the metaloph. Hypocone and metacone are merged with no intervening groove at this wear stage, but are separated from the anteromedially directed entostyle by an anterior, vertical, rounded groove. The entostyle is appressed to the lingual angle of the protoloph, but joins it only 0.5 mm. from the base of the enamel. A central connection between hypocone and protoloph occurs at about the same height; from this point the transverse valley slopes gently labially. A deep pit is enclosed by the protoloph, entostyle, and hypocone; it would persist as a lake after the lophs had otherwise merged. There is no evidence of a posterior cingulum.

The molars are short and broad (table 2). Transverse valleys of M^{1-2} are of nearly uniform depth, although indented by the bases of the anterior cusps. The left M^1 shows a simultaneous formation of lingual and central connections of the lophs, with worn enamel remnants still present between styles and between protocone and hypocone, and a constriction of the valley between paracone and metacone. The original valley floor is limited to a small, shallow, oval, lingual lake and an equally shallow, transversely elongate labial re-entrant. The right M^1, slightly more worn, has dentine exposed in the lingual connection. The lophs of M^2 are joined by enamel and dentine lingually and centrally to completely isolate an ephemeral lingual lake from the shallow labial re-entrant, the latter only faintly indented by the paracone base. The metaloph of M^3 is narrower transversely than the protoloph, joined to it labially and lingually by enamel and exposed dentine to enclose a more persistent central lake, which is indented slightly by the protocone base. The lingual connection is narrower posteriorly, suggesting that the entostyle is more broadly connected to the protoloph than to the hypocone. The metacone is set off by constrictions from both paracone and hypocone. The metaloph is low, its enamel breached only along the posterior margin. If a posterior cingulum was present it was very narrow; the metaloph is not expanded posteriorly.

F:AM 25364 includes a fragment of the enamel band of the upper incisor. The medial groove is more distinct than in 51264, and the central sulcus, although as deep as that of the holotype, is simple with a broad, rounded floor. The cheek teeth are deeply worn. P^4-M^2 retain short labial re-entrants, which would disappear with little more wear. P^4 bears, in addition, a patch of enamel representing the floor of the lingual lake. M^1 and M^2 become even shorter with wear; M^3 is less affected, and the occlusal surface of P^4 is elongated.

The lower incisor has a broad, flat enamel band; the posterior part of the tooth is crushed. P_4 is missing. M_{1-2} are anteroposteriorly short. The metalophid of M_1 is slightly narrower than the hypolophid. At this late stage of wear the lophids are joined broadly centrally and separated by labial and lingual re-entrants. The labial re-entrant consists of a nearly vertical remnant of the anterior wall of the transverse valley, forming a step between the dentine of the lophids. The lingual re-entrant is an infolding of enamel which would disappear with little more wear. M_2 is similar lingually, damaged labially. M_3 also shows lingual and labial re-entrants; the hypolophid thus delimited is shorter and narrower than the metalophid. The lophs of these molars lack marginal connections, and the enamel in the transverse valley rises centrally; however, the wear facets are transversely concave and the central connection may have been little higher than the preserved enamel remnants.

Comparisons. If Rensberger's concept of the Geomyidae (1971, pp. 66-67; 1973a, p. 16) is accepted, *Ziamys tedfordi* may be placed in this group on the basis of its broad rostrum and zygomatic arches; broad, grooved thick-enameled incisors; and narrow palate. Within this family, its short rostrum, fused, ventrally convex premaxillae, deep and sometimes enclosed grooves incised in a ventrally depressed palate, strong lateral angular process of the mandible, doubly grooved incisors, anteroposteriorly compressed molars, apparent union of the entostyle of M^3 with the protoloph, and central union of the lophids of M_{1-3} link *Ziamys* with the modern geomyines. Those characters in which it resembles entoptychines and pleurolicines, e. g., rounded zygomatic arches with simple maxillopalatine sutures, relatively posterior coronoid process, anteromedially-directed entostyle of P^4, and persistent lake of M^3, seem best interpreted as primitive characters shared with some heteromyids. The ventral surface of the rostrum, in profile, shows neither the high arch of the geomyines nor the abrupt rise and break in slope anterior to P^4 of *Entoptychus*; its straight, gently rising line can be matched in some specimens of *Pleurolicus*, and in *Gregorymys riggsi*.

In view of the geomyine characters listed, *Ziamys* shows a surprising lack of dental resemblance to *Dikkomys matthewi*, which by Harrison time had developed some characters typical of advanced geomyines (Wood, 1936, pp. 26-28). The holotype of *D. matthewi*, AMNH 22720, is a P_4, not preserved in *Ziamys*. The paratype, AMNH 22721, includes M^1, M_1, and M_2 of different individuals. All are much higher crowned than in *Ziamys*. M^1 shows an early entostyle-protocone connection which migrates to the lingual margin with wear; a labial connection forms later in wear. This pattern contrasts strongly with the late lingual connection and lack of labial connection of *Ziamys*. M_1, heavily worn, shows a narrow central enamel-dentine crest between lophs, and narrow labial and lingual marginal crests of nearly equal height which would, with additional wear, join the lophs and isolate labial and lingual lakes. M_2 is much less worn, but the central connection is already formed. The labial connection is as high as on M_1, the lingual crest lower. The lower molars therefore also contrast with those of *Ziamys*.

Gregorymys riggsi (Wood, 1936, pp. 9-11) parallels *Ziamys* and *Geomys* in having a weak central groove on its upper incisor, and resembles *Ziamys* in the shortness and ventral profile of its rostrum; its premolar form, however, is entoptychine.

The holotype of *Gregorymys douglassi*,[1] CM 1187 (a cast, AMNH 89745, was used in comparisons), resembles *Ziamys* in the shortness, ventral transverse convexity, and profile of its rostrum. The protoloph of P^4 is narrower than the metaloph, and *contra* Wood (1936, pp. 12-13) shows no evidence of division into cusps. As in *Ziamys*, and unlike *Pleurolicus*, hypocone and metacone merge after moderate wear. The incisor is broad with a faint medial groove. The upper cheek teeth are similar to most pleurolicine and entoptychine specimens in their early lingual connection of the lophs, and are higher crowned than those of *Ziamys* or *Pleurolicus sulcifrons*.

[1]The locality of this specimen is Woodin (misspelled Goodin by Wood, 1936), 3 to 4 miles north of Divide, Silverbow County, Montana.

The palate is moderately sculptured and narrow anteriorly, but widens posteriorly more than does that of *Ziamys*.

The greatest resemblance to the cheek-tooth pattern of *Ziamys* is found in *Pleurolicus sulcifrons*. No specimen shows the combination of characters that distinguish *Ziamys*, but most of them occur in *P. sulcifrons* as variants. Among characters of P^4, the broad but apparently unicuspid protoloph, with the entostyle appressed to it but not joining it until late in wear, is most closely matched in AMNH 7044 (holotype of *Grangerimus oregonensis*; referred to *P. sulcifrons* by Rensberger, 1973a, p. 17; see also Shotwell, 1967, p. 49).[1] The central connection between lophs of P^4, isolating a deep lingual pit, is seen in AMNH 7185. This specimen was referred to *Pleurolicus leptophrys* by Cope (1884, p. 868, pl. LXIV, fig. 8); as noted by McKenna and Love (1972, p. 19), it is not conspecific with the type of that species, which has been referred to *Entoptychus* by Rensberger (1973a, p. 30). AMNH 7185 is here referred to *P. sulcifrons*. More typical specimens of *P. sulcifrons* have a narrower protoloph that joins the metaloph early in wear, and lack a central connection between lophs. In all specimens of *P. sulcifrons* examined, the metacone and hypocone of P^4 remain distinguishable, separated anteriorly by a vertical groove on the anterior face of the metaloph; this groove is absent in *Ziamys*, and the metacone and hypocone merge indistinguishably early in wear.

The lophs of M^{1-2} of *Ziamys* join very late in wear, and lingual and central connections form nearly simultaneously. This condition is approached in AMNH 7044; other specimens, e.g., UO 2810 (Shotwell, 1967, fig. 28), show a central connection well after the styles have joined.

[1]Two pleurolicines described from South Dakota, originally referred to *Grangerimus* [*G. dakotensis* Macdonald, 1963, pp. 182-183, now *Tenudomys*? *dakotensis* (Rensberger, 1973a, p. 80); *G. harkseni* Macdonald, 1970, pp. 39-40, now *Schizodontomys harkseni* (Rensberger, 1973a, p. 69)] differ more strongly from *Ziamys* in their narrow P^4 protolophs and broader palates. AMNH 12982, referred by Macdonald to *G. oregonensis*, is much closer to *Tenudomys*? *dakotensis* in width of palate and P^4 entostyle orientation than to *Pleurolicus*.

The lophs of M_{1-3} of *Ziamys* are joined centrally, but show no labial or lingual connections; all specimens of *Pleurolicus* examined have labial connections, although the height is variable.

Pleurolicus differs from *Ziamys* in its longer molars; narrow, asulcate incisors; longer diastema; wider palate without grooves; unfused premaxillae; and short, deep scar for the M. masseter superficialis tendon, as in entoptychines (Rensberger, 1971, p. 69; 1973a, p. 39).

Discussion. It is clear that *Ziamys* is a geomyine, yet its relation to later members of the subfamily is obscure. *Dikkomys matthewi* is at least contemporary with and probably earlier than *Ziamys tedfordi*. At best, then, *Ziamys* is a late survivor of an ancestral group. The dental differences between the two genera may be byproducts of the hypsodonty of *Dikkomys*; there is no positive evidence, however, that *Ziamys* is a direct ancestor of *Dikkomys*. Among later forms, *Pliosaccomys* (Wilson, 1936, pp. 20-29; Shotwell, 1967, pp. 26-34, 48-50) is a possible descendant. Black (1961, pp. 13-15) argued on the basis of differences in the mode of union of the lophs of the lower molars that *Pliosaccomys* and *Dikkomys* represent different lineages. Shotwell (1967, p. 48) discounted this difference because both labial and central connections occur in both forms, although at different times. Wilson (1936, pp. 20-21) described *P. dubius* as having an unarched rostrum, fused premaxillae, and narrow, heavily sculptured palate. The upper incisors are asulcate. The interrelationships of these Tertiary geomyines cannot be understood until the skull of early Miocene *Dikkomys* is known. In view of Wood's observations (1937, p. 173) of parallel development of grooving in geomyoid incisors, the startling similarity of the upper incisors of *Ziamys* and *Geomys* is unreliable as evidence of a nearer relationship between these genera.

Considered as a representative of an early geomyine radiation, *Ziamys* strongly suggests that the subfamily arose from the Pleurolicinae, with particular affinities with *P. sulcifrons*. A descent from a primitive entoptychine is possible but less likely; *Gregorymys riggsi* and *G. douglassi* resemble *Ziamys* in form of the rostrum, though not of the palate. A third possibility, that the geomyines arose from within the heteromyines independently, cannot be entirely ruled out; as Wood has pointed out, parallelism has been frequent among geomyoids.

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