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GEOMYID RODENTS FROM THE MIDDLE TERTIARY

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The Geomyidae, or pocket gophers, are an exclusively North American family of burrowing rodents. Their present range covers western United States, Mexico, and much of Central America, with extensions into Canada and southeastern United States. Fossil members of the family are known from many horizons in the middle and later Tertiary of the United States, but the descriptions are scattered through a considerable literature, and are rather unsatisfactory for the purposes of the evolutionary paleontologist, so that very little is known of the evolutionary trends within the family. The only detailed study, that of Cope, 1884, pp. 855–870, deals only with the John Day forms, and is very inadequately illustrated. In order to lay the foundations for such a knowledge, a detailed study, particularly of the teeth, is needed. The present preliminary study is restricted to the earlier members of the family, as they are represented by larger collections than are the later members, and are a rather homogeneous unit. Furthermore, without a detailed study of all the recent forms, which is at present impracticable, few results of importance could be derived from such late Tertiary geomyids as have been described up to now.

The author is indebted to the authorities of the American Museum, and particularly to Dr. Walter Granger, for permission to study their material and for the facilities for doing so. Figures 1, 3 to 13, 19, 21 to 24, and 32 have been made by Mildred Clemens of the Museum staff, the others being by the author. Thanks are also due to Mr. H. J. Cook of Agate, Nebraska, for the loan of specimens of geomyids from the Harrison, and for pointing out localities where profitable search could be made for other geomyid material. Mr. E. S. Riggs of the Field Museum, Dr. C. L. Gazin of the National Museum, and Mr. J. J. Burke of the Carnegie Museum have very kindly loaned specimens whose descriptions are included in this paper. Dr. C. L. Camp of the University of California permitted me to study the material in the collections there. The execution of this study was assisted by a grant from the Marsh Fund of the National Academy of Sciences. The study was made while the author was Cutting Traveling Fellow in Columbia University.

The Geomyidae may be described as "Sciuromorph" rodents with "skull fossorial; zygoma robust; infraorbital foramen always at end of a long canal, its orifice protected from muscle pressure by counter sinking in an oblique sulcus; frontal without postorbital process" (Miller and Gidley, 1918 pp. 433–434); molars based on a two-lophed, six-cusped pattern, fundamentally identical with that in the Heteromyidae; premolars similar to those in the more advanced forms of heteromyids; cheek teeth progressively hypsodont, usually evergrowing, ultimately with enamel reduced to anterior, posterior, and median plates, or eventually to but a single plate; incisors primitively smooth, progressively develop one or more sulci. Range: Middle Oligocene to Recent, of North and Central America.

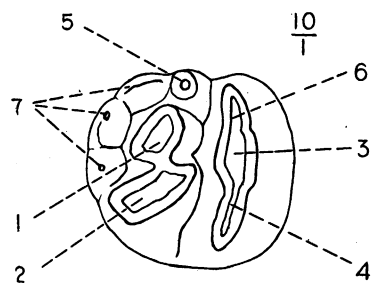

Fig. 1. Diagram of cusps of right lower premolar of an entoptychine.

1 = protoconid; 2 = cusp of uncertain homologies; 3 = hypoconid; 4 = metaconid; 5 = protostylid; 6 = hypostylid; 7 = cusps of the anterior cingulum, the lingual one probably being the anteroconid.

The geomyids fall very distinctly into two groups, named by Miller and Gidley the Entoptychinae and the Geomyinae. These seem entirely worthy of subfamily distinction, and at present no intermediate stages are known, although *Gidleumys*, from the White River, presents many features common to both groups, occupying a position rather similar to that of *Heliscomys* among the heteromyids. Both this form, however, and all the known members of the Entoptychinae, are already too specialized in other directions to be ancestral to the Geomyines, a position occupied by the new form, *Dikkomys*, described below.

The terminology of the cusps (Fig. 1) is the same as that adopted for the Heteromyidae in a revision of the fossil members of that group (Wood, 1935). The cusps in the upper teeth appear to be the normal mammalian cusps, with the addition of two cingulum cusps on the lingual side, as in the heteromyids.

Gidleumys adspectans, new genus, new species[1]

Figure 2

HOLOTYPE.—U. S. N. M. No. 13748, fragment of the left maxilla with P^4–M^1 left.

HORIZON AND LOCALITY.—Middle Oligocene White River (Brule) of South Dakota.

DIAGNOSIS.—Teeth brachydont; cusps still clearly differentiated; cingulum cusps definitely smaller than primary cusps; P^4 with a strong anterior cingulum cusp and a two-cusped protoloph.

The premolar of this animal is quite distinctive, in the large basal cusp developed from the anterior cingulum (Fig. 2), which might be called an anterocone, to correspond with the terminology used in the lower teeth (Fig. 1). While this cusp is high and well developed, it is only about half as high as the rest of the crown. The protoloph is formed of two cusps, which seem without question to be the paracone and

Fig. 2. *Gidleumys adspectans*, holotype. U.S.N.M. No. 13748, P^4–M^1 left. × 5.

protocone. This apparently represents an early divergence from some, at least, of the heteromyids, in which the protoloph is reduced to a single cusp. There is no trace of an internal cingulum cusp on the protoloph, which apparently separates it from some at least of the Entoptychines (especially the genus *Entoptychus*), which have three-cusped protolophs. The metaloph is formed of the usual three cusps (metacone, hypocone, and entostyle), with a minute accessory cuspule behind the hypocone. M^1 is six-cusped, with the crests well developed, but not to the point of obliteration of the individual cusps. The internal cingulum is weak. The teeth of this animal are massive and plump, resembling some of the Miocene heteromyids in general appearance, but differing in the details of the pattern, as well as being an earlier development of the same type of tooth. The latter item seems to have been a universal differentiation between the heteromyids and the geomyids.

This form unquestionably represents an Oligocene geomyioid. Its large size and progressive character show that it represents a different line from that of its contemporary, the heteromyid *Heliscomys*, though

[1] This genus is named in honor of Dr. J. W. Gidley, one of the leading American workers on fossil rodents. The species is named for Dr. C. L. Gazin, who very kindly allowed me to study and describe this important specimen.

the two are reasonably closely related. As the tooth pattern of *Gidleumys* is what would be expected in a geomyid of this age, it seems reasonable to include it in that family. Due to the apparently excessive development of the anterocone, however, this form does not seem to represent an ancestor of the later members of the family, but rather an aberrant side line, which can not with safety be referred to either of the subfamilies. Some species of entoptychines possess an anterior cingulum, but none show any trace of an anterocone except in the milk premolar. Three lophs are also present on the milk teeth of recent geomyids (see Merriam, 1895, Pl. XVI, figs. 1 and 3). There is, however, too little difference in wear between the premolar and the molar to permit the tooth in *Gidleumys* to be a milk tooth. Although the anterocone might have been secondarily reduced in later forms, it seems more probable that this animal represents an aberrant and otherwise unknown line.

Entoptychinae, Miller and Gidley 1918

Angular portion of mandible mostly below alveolar level; cheek teeth rooted, progressively ever-growing; upper incisors primitively smooth, sometimes develop a groove at the median margin; lophs of cheek teeth unite first at edge of protomere; upper and lower premolars resemble molars in pattern, forming, upon wear, two crests, uniting at one or both ends, but not divided into two lobes; protostylid of lower molars sends cingulum onto anterior face of teeth, reaching as far as protoconid, from which an additional stylid may develop.

GENERA.—*Pleurolicus*, *Gregorymys*, *Grangerimus*, and *Entoptychus*. Lower Miocene of western United States.

This subfamily is rather distinct from the Geomyinae. There are many features, however, particularly in the skull, which are close to the latter group. But in the dentition, many of the included forms are closer to the heteromyids than to the Geomyinae. This is particularly true in the manner of development of P_4 of *Gregorymys* (see below, pages 9–12, Figs. 12 and 15). As, however, the evidence of the skulls is at least as strong for geomyine affinities as the evidence of the teeth is for heteromyid ones, and as the lower premolar of *Grangerimus* and *Entoptychus* approaches more nearly to what we find in the Geomyinae, it is best to leave this group near the geomyines for the present, at any rate.

It is unfortunate that, with so much excellently preserved skull material, the limbs should be almost entirely unknown. What few fragments have been found, however, would indicate that these animals had

not developed the specialized burrowing habits of the modern geomyids, and were probably not much more adapted for burrowing than is the modern prairie-dog. This is in accord with the early horizon at which they are found. Perhaps they became extinct because they were unable to compete with the more highly specialized Geomyinae, which were in part, at least, contemporaneous with them, lived in the same areas, and presumably in the same ecologic niches.

PLEUROLICUS COPE, 1870

GENOTYPE.—*P. sulcifrons* Cope.

DIAGNOSIS.—Cheek teeth medium crowned, with strong roots; enamel not prolonged onto roots, but ends as a nearly even line at the base of the crown; lophs of upper teeth unite progressively from lingual to buccal side; never an anterior cingulum on P^4; anterior end of masseteric crest is low and ends below anterior root of P_4; large interparietal and shallow pit between M_3 and base of coronoid, as in *Thomomys*.

Pleurolicus sulcifrons Cope 1878

Figures 3 and 4

COPE, 1884, Pl. LXIV, figs. 6, 9.

SYNONYM.—*Pleurolicus diplophysus* Cope, 1881*a*.

HOLOTYPE.—Amer. Mus. No. 7165, part of skull.

HORIZON AND LOCALITY.—Middle John Day Beds of Oregon.

DIAGNOSIS.—Deep groove in frontals between orbits, due to elevation of temporal ridges; protoloph of P^4 distinctly shorter than metaloph; anterior loph of P_4 three-cusped with anteroconid extending back to unite with hypolophid.

Previous authors have based the definition of the species of this subfamily almost entirely on the supraorbital ridges. They are quite characteristic, though intergradations sometimes appear to occur. These ridges are extensions of the temporal crests, which may reach as far forward as the anterior end of the orbit. They do not appear to be sexual differences, being associated with corresponding dental variations. This species is separated from all the other members of the genus by the possession of supraorbital crests.

The diagnostic teeth of this species are the premolars. P^4 has an apparently one-cusped protoloph, and a three-cusped metaloph, which unite first at the lingual side (Fig. 3). The crest connecting the two lophs apparently represents (by analogy with the Heteromyidae and by comparison with other geomyids) an internal cingulum, which did not, however, develop a protostyle in this species. An anterior cingulum is present at the base of the crown. In P_4 (Fig. 4), there is a well-developed anteroconid between the two main cusps of the trigonid (see Fig. 1). The anteroconid extends well back between the other two cusps, and makes the first point of union of the lophs lie in the center

of the tooth. There is a clear indication of an H-pattern in the lower molars, not only the two cusps of the external cingulum, but also the protoconid and hypoconid, being approximated to each other.

This species seems to be one of the more specialized members of the genus, in the development of the strong temporal crests and the large size of the anteroconid. The simplicity of the protoloph of P^4 is prob-

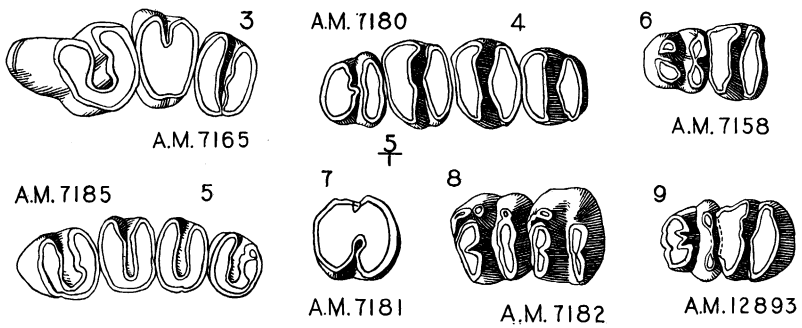

Fig. 3. *Pleurolicus sulcifrons*, holotype, A.M. No. 7165, P^4–M^3 left.
Fig. 4. *Pleurolicus sulcifrons*, referred specimen, A.M. No. 7180, P_4–M_3 right.
Fig. 5. *Pleurolicus leptophrys*, referred specimen, A.M. No. 7185, P^4–M^3 left.
Fig. 6. *Pleurolicus leptophrys*, referred specimen, A.M. No. 7158, P_4–M_3 right.
Fig. 7. *Pleurolicus copei*, paratype, A.M. No. 7181, P_4 right.
Fig. 8. *Pleurolicus copei*, paratype, A.M. No. 7182, M_{1-2} right.
Fig. 9. *Pleurolicus dakotensis*, holotype, A.M. No. 12893, P_4–M_1 left.
All figures five times natural size.

ably secondary. It is not clear whether or not the anterior cingulum of this tooth is primitive. This species seems somewhat separated from the other members of the subfamily, in which the union of the crests through the styles is emphasized, and approaches more closely to the Geomyinae, in which the union of the lophs in the center of the tooth is the characteristic condition. While the premolar is verbally suggestive of the geomyines in that the union of the lophs occurs in the center first, the close approximation of the lophs throughout their entire lengths is a more fundamental resemblance to the other entoptychines, as are also the characters of the upper teeth, and warrant the retention of the species in this subfamily, though with suggested relationships to the geomyines.

The specimen described by Cope (1881*a*) as *P. diplophysus* (Amer. Mus. No. 7177) is the brain case of a young individual which does not appear distinguishable from *P. sulcifrons*. Cope characterized the species

as having separate temporal crests, as in *P. leptophrys*, and distinct otic and mastoid bullae. These characters are all due to the youth of the animal, whose sutures are still wide open, that between the two interparietals being still in existence, as well as that between the tympanic and mastoid bullae. The temporal crests, though separate, approach each other. There is a distinct depression between the temporal crests in the orbital region, which suggests a young *P. sulcifrons* in which the crests had not been fully elevated. This animal may be considered, for the present, merely an immature, though fully grown, *P. sulcifrons*.

Pleurolicus leptophrys Cope 1881*a*

Figures 5 and 6

COPE, 1884, Pl. LXIV, figs. 7–8.

HOLOTYPE.—Amer. Mus. No. 7174, damaged skull with worn teeth.

HORIZON AND LOCALITY.—Holotype from Lower Miocene Middle John Day Beds of Oregon; referred specimens from Upper and Lower Rosebud of South Dakota.

DIAGNOSIS.—No supraorbital ridges, frontal being smooth; protoloph of P^4 almost as long as metaloph; anterior loph of P_4 with but two cusps, uniting with the ends of hypolophid, surrounding a central basin.

In the upper premolar (Fig. 5), the elongated protoloph shows three cusps. Whether or not this is primitive can not yet be demonstrated. The crests of this tooth unite first at the lingual side, and seem next to unite buccally, to surround a basin. The enamel lake of the upper teeth lasts longest in M^3, and next longest in the premolar. The absence of the anteroconid in P_4 (Fig. 6) is very definitely primitive, as is the distinct separation of all the cusps of this tooth. There is a minute hypostylid on the premolar, suggesting the initial stage in the development of the cingulum. There is no suggestion of an H-pattern in the lower molars of this species. In M_1 of the figured specimen, a small enamel fold appears between the protoconid and the protostylid, which seems to be the same fold that appears in that location in *Heteromys* and related genera of heteromyids. The smooth frontal region, with no trance of supraorbital crests, seems probably to represent a primitive condition.

Two lower jaws in the American Museum collections, from the Rosebud (Amer. Mus. No. 13758 from the Lower Rosebud and Amer. Mus. No. 12896 from the Upper Rosebud, both from South Dakota) do not at present appear distinguishable from *P. leptophrys*. The premolar is almost identical, while the chief differences in the molars are the slightly less angular antero-external corner, which may represent solely differ-

ences in the amount of wear. The second of these two specimens, from the Upper Rosebud, is the animal referred to by Matthew (1907, p. 214) as a heteromyid, related to *Heteromys*. The smaller animal which Matthew mentions has been described elsewhere (Wood, 1935, p. 170) as a heteromyid.

P. leptophrys appears to be the most primitive known member of the Entoptychinae, and at the same time, one of the earliest. It is probably not ancestral to any of the others, many of which are its contemporaries, but it seems justifiable to consider it the structural ancestor of the subfamily.

Pleurolicus copei, new species

Figures 7 and 8

HOLOTYPE.—Amer. Mus. No. 7175, front part of a skull.

PARATYPES.—Amer. Mus. No. 7181, lower jaw with P_4–M_2; Amer. Mus. No. 7182, lower jaw with M_{1-2}.

HORIZON AND LOCALITY.—Middle and upper John Day Beds of Oregon.

DIAGNOSIS.—Largest known species of the genus; frontal region slightly concave but nearly flat and very broad; P^4 with a broad anterior basal cingulum.

This species combines characters of both *P. leptophrys* and *P. sulcifrons*, although it is probably not closely related to the latter. M^{1-2} are compressed anteroposteriorly. M^3 is rather large. As indicated, there is a broad basal cingulum at the anterior end of the upper premolar, which does not, however, bear any cusps. The teeth of the holotype are very highly worn, and show almost nothing of the pattern. P^4 is probably a derivative of the type of premolar found in *P. leptophrys*, the union of the two lophs being buccad of the center of the tooth, though not at the buccal margin (Fig. 7). The lower molars are almost square. In unworn teeth (Fig. 8), the anterior part of the external cingulum gives rise to two cusps, the second one appearing antero-external to the protoconid and antero-mesiad to the protostylid.

Pleurolicus dakotensis, new species

Figure 9

HOLOTYPE.—Amer. Mus. No. 12893, lower jaw with P_4–M_1 left.

HORIZON AND LOCALITY.—Lower Rosebud, Porcupine Creek, South Dakota.

DIAGNOSIS.—Anterior loph of P_4 three-cusped, as in *P. sulcifrons;* lophs unite as in *P. leptophrys;* H-pattern in molars very faint; hypolophid of P_4 only two-cusped.

In this species, the pattern as shown in *P. leptophrys* is further developed. The anteroconid is of considerable size (Fig. 9), but does not show any tendency to move posterad, as it seems to have done in

P. sulcifrons. The posterior crest has only two cusps, as in *P. leptophrys*, which seems to be a primitive character. This species is probably a descendant of something fairly close to *P. leptophrys.*

GREGORYMYS, NEW GENUS[1]

GENOTYPE.—*Entoptychus formosus* Matthew, 1907.

DIAGNOSIS.—Teeth high crowned but rooted, forming central lakes in both upper and lower molars upon wear; highly worn teeth never develop the interrupted enamel characteristic of *Entoptychus;* P^4 bearing accessory cusps; P_4 with multicuspidate anterior cingulum.

RANGE.—Rosebud and Lower Harrison of South Dakota and Nebraska and beds of similar age in Wyoming and Montana.

Gregorymys formosus (Matthew)

Figure 10

SYNONYM.—*Entoptychus formosus* Matthew, 1907, Figs. 24–26.

HOLOTYPE.—Amer. Mus. No. 12887, a skull with teeth.

HORIZON AND LOCALITY.—Upper Rosebud of South Dakota.

DIAGNOSIS.—Frontal region with supraorbital ridges; slight groove at median margin of upper incisors; P_4 large with a complete anterior cingulum; upper premolar very large, with single-cusped protoloph.

RANGE.—Rosebud and Lower Harrison of South Dakota and Nebraska and beds of similar age in Wyoming and Montana.

The skull is long, with the nasals and premaxillary extending the same distance caudad. The temporal crests are high, and unite posterior to the orbits. The nasals are flat in cross section. There is no lacrymal process. The lophs of the cheek teeth unite progressively from protomere to paramere, leaving but a small and short-lived lake in the center of the crown. P^4 has a protoloph apparently formed of but a single cusp, whereas there are four cusps in the metaloph, an accessory cuspule appearing between the hypocone and the entostyle, as in *Gidleumys.* In the lower premolar, there is a strong, continuous anterior cingulum (Fig. 10). In this species, as in the genus as a whole, P^4 is by far the largest tooth in either series. It is, however, proportionately larger in this species than in any other.

Gregorymys curtus (Matthew)

Figures 11 to 13

SYNONYM.—*Entoptychus curtus* Matthew, 1907.

HOLOTYPE.—Amer. Mus. No. 12890, a damaged skull with teeth.

HORIZON AND LOCALITY.—Upper and Lower Rosebud and Lower Harrison of South Dakota and Nebraska.

[1] I take great pleasure in naming this genus for Professor W. K. Gregory, in appreciation of his ever-ready assistance and encouragement to my studies on fossil rodents.

DIAGNOSIS.—Frontal region smooth; upper incisor asulcate; protoloph of P_4 with two cusps; lower premolar with four-cusped anterior cingulum; accessory cuspule at antero-external margin of cingulum of lower molars.

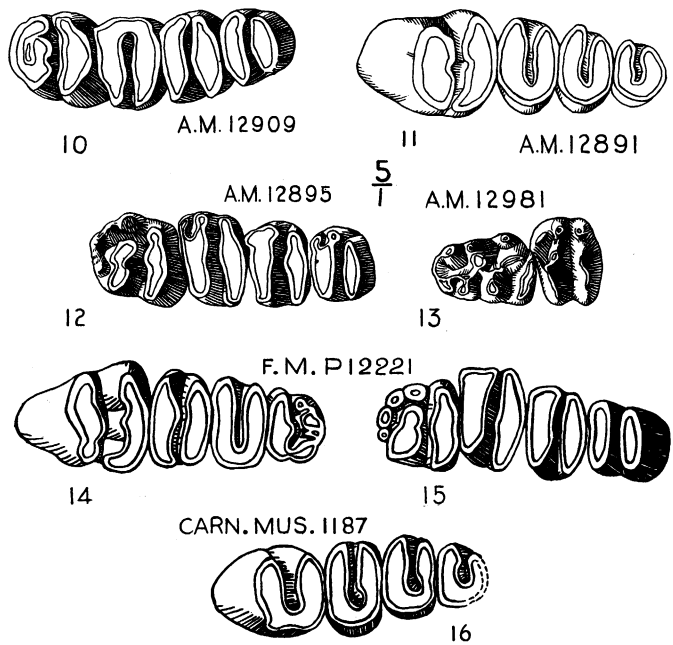

Fig. 10. *Gregorymys formosus*, referred specimen, A.M. No. 12909, P_4–M_3 right.

Fig. 11. *Gregorymys curtus*, referred specimen, A.M. No. 12891, P^4–M^3 left.

Fig. 12. *Gregorymys curtus*, referred specimen, A.M. No. 12895, P_4–M_3 right.

Fig. 13. *Gregorymys curtus*, referred specimen, A.M. No. 12981, DP_4–M_1 left, reversed.

Fig. 14. *Gregorymys riggsi*, holotype, Field Museum No. P12221, P^4–M^3 left.

Fig. 15. *Gregorymys riggsi*, holotype, Field Museum No. P12221, P_4–M_3 left.

Fig. 16. *Gregorymys douglassi*, holotype, Carnegie Museum No. 1187, P^4–M^3 left.

All figures five times natural size.

The skull in this species is short, with very low, rounded supraorbital ridges uniting at the level of the middle of the orbit. The nasals do not reach as far caudad as do the premaxillaries, and are rounded in cross section. There is a lacrymal process extending into the orbit. The upper-premolar is extremely large, and the molars taper rapidly to the end of the series (Fig. 11). On wear, a central lake is formed in P^4, and there

is a trace of one of the molars, although none of the lakes are large. In the lower teeth (Fig. 12), the cusps are clearly determinable. The molars show the accessory cingulum cuspule very distinctly. The anterior crest of the premolar is formed of the cingulum which has given rise to the protostylid and three anterior cusps, of which the lingual one is perhaps the anteroconid.

The most interesting specimen referable to this species is a lower jaw with the milk premolar (fig. 13). This tooth is surprisingly complicated for such an early stage. Moreover, it shows no apparent similarity to the milk teeth of the living gophers, which may be due to the lack of comparable material in the same stage of wear. Merriam's figure (Merriam, 1895, Pl. XVI, fig. 2) shows the earliest stage in wear of a milk tooth of a Geomyine that I know of. The milk tooth in *G. curtus* is much longer and distinctly narrower than is P_4. The postero-internal portion of the tooth consists of four cusps surrounding a central basin, which seem to be homologous to the four primary cusps of the permanent premolar. Buccad of the protoconid is a large protostylid. The posterior migration of this cusp and of the protoconid has impinged upon the hypostylid until it is reduced to a very faint basal cingulum. A cusp which seems to be the anteroconid is connected by a crest to the space between the two principal anterior cusps. The anterior part of the tooth is formed by a semicircle of cingulum cusps, connecting at both ends with the anteroconid. There are five clearly distinguished cusps in this semicircle, and the cingulum crest at the anterior end of the tooth is swollen, foreshadowing a sixth cusp. The pattern is thus fundamentally the same as that of DP_4 of *Heteromys* or *Dipodomys*, and shows some resemblances to the permanent tooth which replaces it. Whether or not this tooth would support placing this subfamily among the Heteromyidae rather than among the Geomyidae would depend entirely upon the pattern of the unworn milk teeth in the modern members of the latter group. Such teeth have yet to be described.

The original specimens of this species were from the Rosebud of South Dakota. A number of isolated teeth in the author's private collection, from ant hills in the Lower Harrison, a mile north and east of Agate, Nebraska, seem indistinguishable from this species.

Gregorymys riggsi, new species

Figures 14 and 15

HOLOTYPE.—Field Mus. No. P12221, anterior part of skull with associated lower jaws.

HORIZON AND LOCALITY.—"Arikaree Beds, Miocene, Raw Hide Creek below OLO Ranch, Wyoming." Lower Miocene.

DIAGNOSIS.—Distinct though shallow groove in center of upper incisor; gentle supraorbital ridges, not uniting until behind the orbits, if then; protoloph of P^4 three-cusped, the central cusps of the two lophs almost uniting; metaloph of M^3 four-cusped; deep masseteric fossa in mandible.

This species appears to be quite close to *Gregorymys formosus* in the development of the central sulcus of the upper incisors and in the pattern of P_4. The faint groove in the upper incisor suggests that these grooves are not sudden acquisitions, but are acquired gradually, and that this is an initial step. The nasals are slightly arched in cross section, and, as mentioned in the diagnosis, the supraorbital ridges are low and unite far back.

P^4 has become entirely molariform with a three-cusped protoloph. This is an approach toward *G. curtus*. The accessory cusp of the metaloph of M^3 is probably of little significance. The upper teeth decrease progressively in size from P^4 to M^3 (Fig. 14).

In P_4, there is clearly shown an anterior cingulum (Fig. 15), continuous with the external cingulum. Three cusps are developed from the former, not counting the protostylid. M_1 shows marked thinning of the enamel on its anterior face. No trace of such thinning appears on any of the other teeth, either in the upper or the lower jaw.

A second specimen (F. M. No. 12220) is referred to this species. It is definitely smaller in all its dimensions by five to ten percent. The crowns seem to be lower, and the groove in the incisor shallower in this specimen. The differences do not seem, however, to be of more than individual significance.

These two specimens were the lowest that Mr. Riggs found in this particular area, occurring about one or two hundred feet below the *Diceratherium* Zone.

Gregorymys douglassi, new species

Figure 16

HOLOTYPE.—Carnegie Mus. No. 1187, anterior part of skull.

HORIZON AND LOCALITY.—Lower Miocene, Goodin, about three or four miles north of Divide, Montana. Collected by Earl Douglass, Aug. 27, 1903.

DIAGNOSIS.—No supraorbital crest; faint groove at median margin of upper incisor; cheek teeth as in *G. curtus*, but P^4 smaller and M^{1-2} compressed anteroposteriorly; crowns high.

This species appears to be quite close to *Gregorymys curtus*. The lack of supraorbital ridges, the three-cusped protoloph of P^4, and the large size of the upper premolar, tend to associate it with that species. There

are, however, several features separating the two. These are the faint groove in the incisor, the proportionately smaller size of P^4, the antero-posterior compression of M^{1-2} and the definitely smaller dimensions in every respect (see Table I).

A specimen in the collections of the American Museum (Amer. Mus. No. 21342), consisting of P^4–M^2 right, collected by Dr. C. C. Mook in 1925, near Silverbow, Montana, is very close to, if not identical with, this species. It differs in being about ten percent larger in all measurements. The differences in proportions (see Table I) seem to be differences in stage of wear, the American Museum specimen being less worn. In the latter specimen, the enamel is greatly thinned on the posterior side of the molars, and there is a suggestion of cement at the base of the crowns. There is, however, the same antero-posterior compression of the molars that was indicated as characteristic of *G. douglassi*. The American Museum specimen is from beds of uncertain age. Dr. Mook's field identification was Oligocene, but he informs me that there are numerous isolated patches of Tertiary beds near Silverbow, some of which are certainly Oligocene. Others may be Miocene as far as he knows, but all were grouped as Oligocene in the field in the absence of evidence to the contrary. The similarity of this specimen to the type of *G. douglassi* warrants the tentative conclusion that the beds in which it was found are also of Lower Miocene age.

This genus forms a closely united group, set apart from the other members of the subfamily by the large size of the premolars, the well-developed anterior cingulum of P_4 which has developed a series of accessory cuspules, and in the tendency for a formation of a three-cusped protoloph on P^4. These species are a progressive group, paralleling *Entoptychus* in many respects, but clearly represent a rather distinct side line (see Fig. 33). In particular, they differ from all forms of *Entoptychus* in the heteromyid-like specialization of the lower premolar, which has developed an anterior cingulum with several small accessory cuspules. *Entoptychus*, on the other hand, has a reduced anteroconid, and little or no trace of an anterior cingulum.

Grangerimus oregonensis, new genus, new species[1]

Figures 17 and 18

HOLOTYPE.—Amer. Mus. No. 7044, damaged skull with lower jaws.

HORIZON AND LOCALITY.—Lower Miocene Upper John Day Beds, John Day River, Oregon.

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[1] I take great pleasure in naming this genus for Dr. Walter Granger, in appreciation of his kindness in allowing me free access to the fossil rodents of the American Museum.

DIAGNOSIS.—Molars high crowned but rooted; P^4 with single cusped protoloph; slight tendency for development of lakes in upper molars; H-pattern in lower molars; P_4 with anteroconid but only a trace of anterior cingulum; base of lower incisor forms knob on ascending ramus; anterior face of upper incisors slightly rounded; slight supraorbital ridges, with no trace of their uniting to form a sagittal crest.

While this form approaches *Gregorymys* in a number of particulars, having attained nearly the same stage in the development of hypsodonty, nevertheless it is clearly on an entirely distinct line, as exemplified by the fact that the lower premolar shows only a very slight trace of an anterior cingulum, connected to the anteroconid. This cingulum may be the initial stage in the development of the type found in *Gregorymys*. The pattern of the tooth (Fig. 18), with protoconid, mesoconid, and anteroconid, is quite close to that which occurs in *Pleurolicus*. This last genus is certainly close to *Grangerimus*, and is probably ancestral, though it is probable that all the known species are evolving in other directions. There are, however, sufficient points in which *Grangerimus* has advanced over *Pleurolicus* to necessitate its being considered a distinct genus. The crowns of all the cheek teeth are much higher than in *Pleurolicus*. The forward position of the anteroconid of the premolar is quite distinct from anything seen in *Pleurolicus*, as is also the presence of a short anterior cingulum. The anteroconid unites with the antero-lingual cusp as in *Entoptychus*, instead of being free or equally close to both the latter and protoconid, as in *Pleurolicus* and *Gregorymys*. Moreover, the upper incisors are more nearly flat than in *Pleurolicus*, and the lower incisor is longer and more powerful, as is indicated by the knob for its base on the ascending ramus. The relationships of *Grangerimus* are almost equally close with *Entoptychus*, to which this form seems structurally ancestral (Fig. 33). The anteroconid, however, is much smaller than in *Entoptychus*. The less accentuated hypsodonty and the presence of roots tend further to separate this form from *Entoptychus*. The H-pattern of the lower molars is further developed than in *Gregorymys* (see Figs. 10, 12, and 15). In the upper teeth, the most distinguishing feature is the apparent presence of but one cusp in the protoloph of P^4, which distinguishes this species from all other known members of the subfamily except *Pleurolicus sulcifrons*.

This form shares with *Gregorymys* and *Pleurolicus* the possession of a short, broad skull, as contrasted with the highly compressed and elongate skull of *Entoptychus*. Although this last type of skull must have been derived at some time from a shorter and relatively broader skull, there was probably a considerable time between the Lower Miocene

and the period in which the common ancestor of the two genera lived. One of the most unusual features about this entire subfamily is the presence of all stages, primitive to specialized, in beds of essentially the same age, and their almost complete absence in beds of any other age.

ENTOPTYCHUS COPE, 1878

GENOTYPE.—*E. cavifrons* Cope.

RANGE.—Middle and Upper John Day Beds of Oregon.

DIAGNOSIS.—Cheek teeth rootless with greatly elongated crowns; enamel extends farther down the posterior side of the lower and anterior side of the upper teeth than it does elsewhere, being particularly limited on the buccal and lingual sides of the crown; interruptions develop in the enamel after wear; protoloph of P_4 almost as long as metaloph, being formed of three cusps; incisors smooth and flat; infraorbital foramen separated from the masseter by a crest; skull much more elongate and fossorial in habitus than in any other member of the subfamily.

This genus represents the end stage of an early side line of geomyioids, which have so many similarities to the recent geomyids that they must be included in the same family. The masseter muscle was as advanced as in the modern gophers, extending above and anterior to the infraorbital foramen. In the lower jaw, the masseteric crest ends below the premolar. There are numerous striking similarities to heteromyids in the teeth, most expecially recalling the Heteromyinae. The great complexity of the anterior part of P_4 is very like the conditions developed in *Heteromys*. The premolars become elongate upon wear, as in *Liomys*.

In the reduction of the enamel to anterior and posterior plates, this genus closely simulates the geomyines. This reduction occurs in all species of the genus, and serves as a distinction from *Gregorymys* and *Grangerimus*. Some of the figures of *Entoptychus* shown below do not indicate the presence of interruptions, since they represent young individuals, so as to show as much of the pattern as is possible. The breaks appear early in life, though not as early as in the Geomyinae. P^4_4 possess anterior and posterior enamel plates and central lakes. In the lower molars, the enamel is preserved only as a lake and a posterior blade. In the upper molars, it remains on the anterior face instead of the posterior. There is frequently a basal posterior cingulum on M_{2-3}. The depression between M_3 and the base of the coronoid process is of considerable, and sometimes of great, depth, though never with a foramen in the depression as is so often the case among heteromyids.

The habitus of the skull in this genus is that of a highly adapted burrowing form. The elongate nasal region, in contrast to the shortened cranial portion, is similar to what is found among the Geomyinae. The wide diastema, with protruding incisors, which meet at an acute angle,

suggests the use of the incisors for burrowing rather than for gnawing, and is similar to occurrences among the Bathyergidae, Spalacidae, and other digging rodents. (For a fuller discussion of the anatomy of the skull, see Cope 1884, pp. 855–858.) The skeleton, according to Cope (*op cit.*, p. 857) most nearly resembles that of *Thomomys*.

Entoptychus cavifrons Cope, 1878

Figures 19 and 20

COPE, 1884, Pl. LXIV, fig. 4.

HOLOTYPE.—Amer. Mus. No. 7052, a skull with worn teeth.

HORIZON AND LOCALITY.—Middle and Upper John Day Beds of the John Day River, Oregon. Holotype from Upper John Day.

DIAGNOSIS.—Elevated frontal ridges as in *Pleurolicus sulcifrons;* P^4 large, increasing markedly in area of grinding surface upon wear; anteroconid and lingual cusp of P_4 connected by crest; protoconid enlarged with incipient protostylid; trace of cingulum from protoconid toward anterior end of tooth; M^3 reduced.

The holotype of this species is the skull of a mature individual, with fully worn teeth, which show nothing except the enamel lakes and plates. For this reason the tooth illustrations are based on other individuals, which seem, on the basis of skull characters and length of the tooth row, to belong to this species. The nasals taper to the posterior end, and do not reach as far back as do the premaxillaries. The supraorbital ridges are clearly shown, and bound a lower central region, which gave the name to the species. The teeth, while hypsodont, are not as elongate as in *E. planifrons*. The nasal region is not as much arched as in this last form, the top of the skull being much more nearly a level plane. The lower premolar of this species, as of the other members of the genus, differs from that of *Gregorymys* in developing an antero-posterior subdivision of the anterior loph, between the anteroconid and the protoconid, and in the reduction (if it were ever present) of the anterior cingulum.

Entoptychus planifrons Cope, 1878

Figures 21 and 22

COPE, 1884, Pl. LXIV, figs. 1, 1*a*, 1*b*, 1*c*, and 1*d*.

LECTOHOLOTYPE.—Amer. Mus. No. 7029, a skull with lower jaws. Cope designated no type either in 1878 or in 1885, and hence I designate this specimen the lectoholotype, since it is the first specimen he discusses (1884, pp. 858–860) and much the best preserved.

DIAGNOSIS.—Frontal region flat, with no trace of temporal crests; P^4 smaller than in *E. cavifrons* and M^3 larger; cheek teeth about twenty-five per cent longer (antero-posterior measurement) than in *E. cavifrons*.

This species, in spite of its similarity in size and general appearance, is not sufficiently close to *E. cavifrons* to warrant uniting them in the

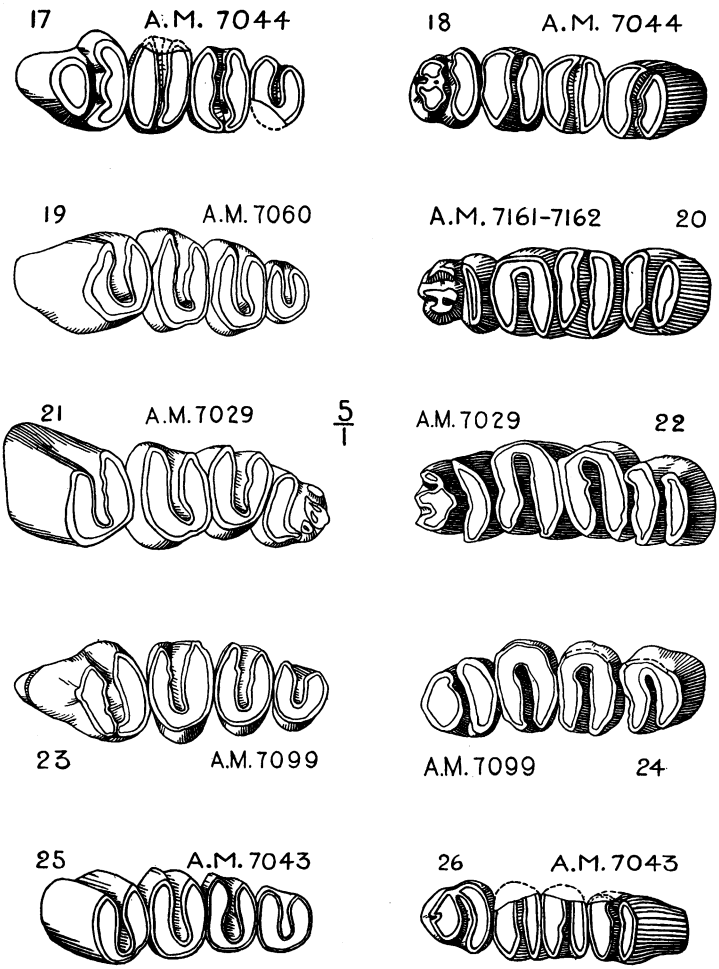

Fig. 17. *Grangerimus oregonensis*, holotype, A.M. No. 7044, P^4–M^3 left.
Fig. 18. *Grangerimus oregonensis*, holotype, A.M. No. 7044, P_4–M_3 right.
Fig. 19. *Entoptychus cavifrons*, referred specimen, A.M. No. 7060, P^4–M^3 left.
Fig. 20. *Entoptychus cavifrons*, referred specimens, A.M. Nos. 7161–7162, P_4–M_3 right.
Fig. 21. *Entoptychus planifrons*, holotype, A.M. No. 7029, P^{4-3} left.
Fig. 22. *Entoptychus planifrons*, holotype, A.M. No. 7029, P_4–M_3 right.
Fig. 23. *Entoptychus germannorum*, holotype, A.M. No. 7099, P^4–M^3 left.
Fig. 24. *Entoptychus germannorum*, holotype, A.M. No. 7099, P_4–M_3 right.
Fig. 25. *Entoptychus minor*, holotype, A.M. No. 7043, P^4–M^3 left.
Fig. 26. *Entoptychus minor*, holotype, A.M. No. 7043, P_4–M_3 right.

All figures five times natural size.

same species. It is entirely possible that the difference in the crests is one of sex. However, until that shall have been established or at least rendered probable by future work, it is best to continue to regard these crests as specific characters. Furthermore, the tooth rows of *E. planifrons* are almost twenty five per cent longer than in *E. cavifrons*, which, aside from any differences in the rest of the animal, is sufficient to warrant their separation. I identified a number of specimens in the collections of the University of California as being either *E. cavifrons* or *E. planifrons* on the basis of length of tooth rows, and found that in every instance the frontal region was in accord with the conclusions based on the teeth. This strongly suggests that the frontal crests may be valid specific distinctions.

In the upper teeth, the enamel breaks (not shown in the figures, which are of a young specimen) appear first on the buccal side. The teeth are very high crowned, much higher than in *E. cavifrons*, being as long as in recent geomyids, although the two lophs are preserved as discrete units for a longer time in the fossil. In the upper teeth, the enamel breaks appear last in the premolar, whereas in the lowers, they occur in the premolar before they do in M_3. In the molar series, the breaks appear first in the first molar and last in the third. The anterior loph of P_4 is three-cusped, as in *E. cavifrons*, and unites with the center of the posterior loph, suggesting relationships with *Pleurolicus sulcifrons* or *P. copei*, and with the Geomyinae. The distinct H-pattern of M_3 is suggestive of the same ancestry. The flat frontal region also resembles that of *P. copei*. The grinding surface of the cheek teeth slopes sharply downward from front to rear.

The pit between M_3 and the coronoid process is shallow, as in *Pleurolicus* The skull is strongly arched. The auditory region is quite progressive, and resembles that of the modern geomyines. There is no appreciable sagittal crest, and the temporal crests are very faint. The snout is long, being half the length of the skull, and the post-palatal region is only a quarter of the total length. The skull is like that of *E. minor*, but is more advanced, in this resembling *E. cavifrons*.

Entoptychus germannorum, new species[1]

Figures 23 and 24

COPE, 1884. Pl. LXIV, figs. 5, 5*a*, and 5*d* (figured as *E. crassiramis*).

HOLOTYPE.—Amer. Mus. No. 7099, damaged skull with jaw.

[1] It gives me great pleasure to name this species for John and Louise Germann, staff artists of the American Museum, in appreciation of their continued assistance to me in all the phases of illustration of scientific publications.

HORIZON AND LOCALITY.—Middle John Day Beds of Butte Creek, Wasco County, Oregon.

DIAGNOSIS.—Frontal ridges extremely strong and high; teeth relatively low-crowned for *Entoptychus;* basal anterior cingulum on P^4; M^3 reduced, M_3 not; suggestion of cement at the base of the teeth; size about equal to *E. planifrons.*

In most respects, this is one of the most primitive species of the genus, though in some items, such as the presence of the cement, it is highly specialized. The crowns are definitely shorter than in any other species, as is indicated by the cingulum at the anterior end of P^4. There is, however, no trace of roots in the type and only known specimen. M^3 is reduced as in *E. cavifrons.* There is no indication of an H-pattern in the lower molars. The cement seems to be forming as a growth around the base of the crowns, but has not begun to grow up the sides to any extent. In this character, this species resembles the specimen of *Gregorymys* from Silverbow, Montana, referred to *G. douglassi* (see above, p. 13).

In the skull, the cranium represents about a third of the total length, which is a primitive condition for this genus. The temporal and frontal ridges are unusually strong and regular. They begin to converge from the anterior end of the orbits, and unite to form a strong sagittal crest. If these crests are valid criteria for distinguishing species in this subfamily, there can be no doubt of the distinctness of this form. In addition, however, this species is separable on the basis of the dental characteristics pointed out above. It seems to represent a somewhat modified (particularly in the development of the cement) descendant of the common ancestor of the genus, and is, all in all, the most primitive known species of the genus. In spite of this, it is distinctly separated from the other known forms, being the only one in which cement has been developed. The characters of the skull mentioned in Cope's discussion of *E. crassiramis* (Cope, 1884, pp. 864–865) are based on the holotype of this species. The skull of *E. crassiramis* is still essentially unknown (see below, p. 24).

Entoptychus minor Cope, 1881*a*

Figures 25 and 26

COPE, 1884, Pl. LXIV, figs 3, 3*a*, and 3*b*.

HOLOTYPE.—Amer. Mus. No. 7043, a skull with left ramus of lower jaw.

HORIZON AND LOCALITY.—Middle John Day Beds of Oregon.

DIAGNOSIS.—Smallest member of the genus; teeth high crowned; enamel breaks develop late in life; P_4 of the simple type with two main subdivisions of the anterior loph; slight depression in the frontal region due to faint supraorbital crests.

This is one of the more primitive species of the genus. The skull proportions are more like those of *Gregorymys* or *Grangerimus* than is the case with most of the species referred to *Entoptychus*. The rostrum is rather short. The dorsal surface of the skull is essentially smooth, though there are slight traces of frontal ridges, most clearly indicated by the presence of a slight median depression in the frontal region.

M^1 is proportionately unusually large in this species, a distinction from the other members of the genus. The teeth are fairly high crowned, but the enamel breaks develop late in life. In the lower premolar, there is evidence for only two cusps in the anterior loph, and it seems reasonably certain that the unworn pattern was probably something like that of *Grangerimus* (Fig. 18). The third molars are essentially unreduced.

Entoptychus sperryi Sinclair, 1905

Figures 27 and 28

SINCLAIR, 1905, Pl. XIV, figs. 6–9.

SYNONYM.—*E. rostratus* Sinclair, 1905.

HOLOTYPE.—Univ. California, Vert. Pal. No. 649, skull with badly worn teeth.

HORIZON AND LOCALITY.—Upper John Day, University of California Locality No. 849, Haystack Valley, Oregon.

DIAGNOSIS.—One of the largest and most specialized species of the genus; teeth extremely large in proportion to skull length; supraorbital crests arise near anterior end of orbit and meet near level of glenoid, uniting at posterior end of frontals; anterior loph of P_4 formed of at least three distinct cusps; anterior edge of metaloph of P^4 essentially straight.

This species is larger than any other except *E. crassiramis*. It is probably not related to the latter, but forms the end stage of a line arising in *E. cavifrons*.

The cheek teeth are very high crowned. In the holotype, the buccal and lingual interruptions have been completely developed, and the enamel has also been worn away from the anterior face of the lower molars. The anterior loph of P_4 shows unmistakable traces of three independent cusps, which would group this species with *E. cavifrons* and *E. planifrons*. The third molars are somewhat reduced. There is no trace of cement on the cheek teeth.

The frontals extend forward between the nasals for a distance of about 3.0 mm. The supraorbital crests begin near the anterior end of the orbit, a short distance mediad of the actual edge of the orbit. They meet at the posterior end of the frontals, at about the level of the center of the glenoid. The meatus is unusually long and tubular. There is an infinitesimal groove at the median margin of the upper incisor, although, for all intents and purposes, these teeth are entirely smooth.

The mandible is as specialized as that of any member of the subfamily. There is a pit several millimeters deep between the third molar and the coronoid process. The germ of the incisor forms a large knob on the ascending ramus, postero-latero-dorsad of M_3. The upper end of the angle, instead of being more or less in the plane of the jaw, is directed outward, at right angles to the rest of the mandible, for a distance of about 9 mm. I have seen no other entoptychine with this character. The masseteric fossa ends below the premolar.

Presumably associated with this specimen are a few portions of the skeleton. There are several phalanges, but little can be told of them in the absence of comparable material. The first four cervicals are also preserved. These have not been fully prepared, but they seem rather large. There does not appear to be any evidence of antero-posterior compression, much less fusion of the separate bones as in certain heteromyids.

The type of *E. rostratus* Sinclair (U. Cal. No. 1651) is from the same level and same general region of the John Day Beds (U. Cal. Locality 855). There are slight differences in size and proportions between it and *E. sperryi*, but they do not seem to me to be of sufficient importance to warrant the retention of this as a distinct species, in the absence of the frontal region and of the teeth in *E. rostratus*. The skull is slightly longer than that of *E. sperryi* (55.5 mm. instead of 50), while the post-dental region is distinctly longer (20.5 mm. instead of 16). The width across the zygomata is 35 mm. in both, and that across the bullae essentially the same (approximately 28 mm.). A process of the frontal extends forward 5.0 mm. between the nasal and the premaxillary, whereas in *E. sperryi* it is essentially absent. The process of the frontals between the nasals is 2.5 mm. long instead of 3.0 as in *E. sperryi*. At the anterior end of the orbit, there are slight rugosities which suggest the similarly placed ones in *E. sperryi*, which mark the anterior end of the supraorbital crests in that form. These differences seem to fall within the limits of individual variation.

The upper incisors seem to be more curved than those of *E. sperryi*, though this may be due to the breaking of the anterior end of the skull in *E. rostratus*. There is a very faint groove at the median margin of the upper incisor. The cheek teeth are extremely worn and broken. The first two molars (M^3 is missing on both sides) have been worn until the central lake has been entirely destroyed. No enamel is present at all on M^2, and it is restricted to the anterior faces of P^4–M^1. There is a minute central lake in P^4. This tooth has not increased at all in antero-

posterior diameter in spite of the great amount of wear it has undergone. The differences in the measurements of the cheek teeth, as listed in Table I, do not seem to be of any significance, in view of the highly worn and broken nature of the teeth of *E. rostratus*.

Since this species is from the same area and horizon as the type of *E. sperryi*, is of approximately the same size in all significant measurements that could be taken, shows considerable agreement in such details of the teeth as could be determined, and has had many of the diagnostic parts broken or lost, it seems entirely justifiable to consider it a synonym of *E. sperryi*.

Entoptychus lambdoideus Cope, 1881*a*

Figure 29

COPE, 1884, Pl. LXIV, figs. 2, 2*a*, and 2*b*.

HOLOTYPE.—Amer. Mus. No. 7041, damaged skull.

HORIZON AND LOCALITY.—Middle John Day Beds of Oregon.

DIAGNOSIS.—Clearly marked temporal crests uniting just behind the eyes, at posterior end of frontals; temporal crests leave the rim of orbit with a definite angle instead of a curve; P^4–M^2 of uniform size.

The crowns of the teeth in the type and only known specimen show but little trace of the pattern (Fig. 29). The median valleys, however, are quite shallow, indicating that the crowns were not as high in this as in some of the other species. The teeth are unusually long antero-posteriorly in proportion to their transverse diameter, being distinctly more circular than in any other species of the genus. The skull as a whole is more nearly like that of *E. planifrons* than it is like any other member of the genus, though the shape of the temporal crests is quite distinct from anything that I have observed elsewhere within the subfamily. The crests meet at the posterior end of the frontals, as in *E. sperryi*, to which this species may be related. There is a shallow pit on the side of the maxillary in front of and slightly laterad of the premolar.

Entopytychus crassiramis Cope, 1878

Figures 30 and 31

The specimen figured in COPE, 1884, Pl. LXIV, and referred to this species has been described above as the type of *E. germannorum*.

LECTOHOLOTYPE.—Amer. Mus. No. 7094,[1] a plate. Referred specimens: Amer. Mus. Nos. 7095–7098, lower jaws.

HORIZON AND LOCALITY —Middle John Day beds, John Day River, Oregon.

[1] Cope originally did not select a type. In 1884, he said the species was established on mandibular rami, even though both uppers and lowers were included in the description. Matthew (in the catalog of the American Museum) selected the partial skull, No. 7094, as the type. Since it is impossible to determine which jaws were the ones referred to by Cope, none of them having been figured or described, I have followed Matthew, and hereby designate Amer. Mus. No. 7094 the lectoholotype.

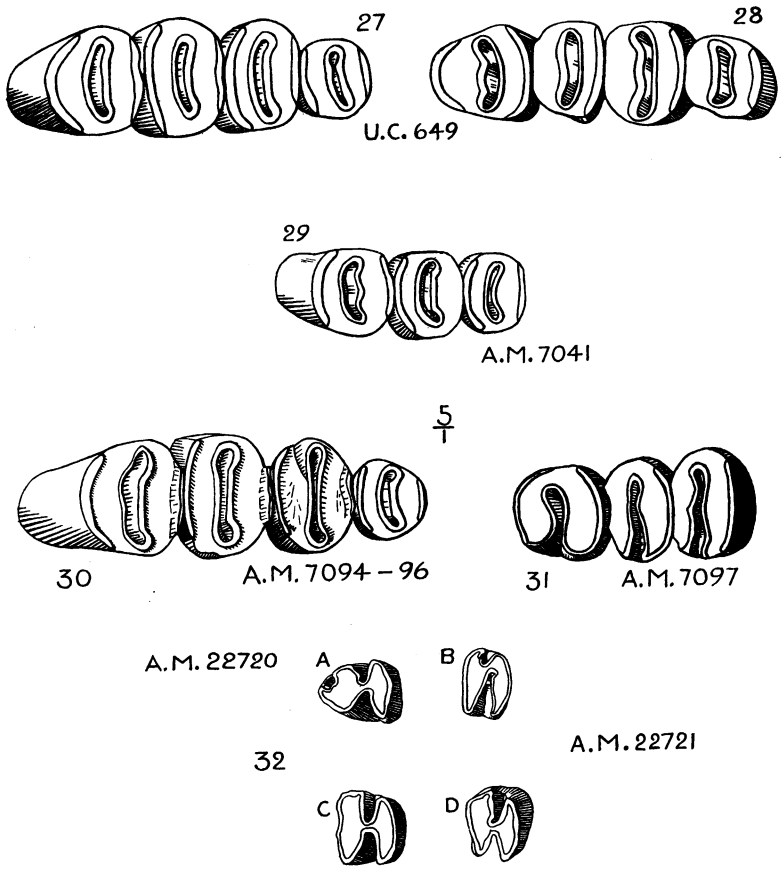

Fig. 27. *Entoptychus sperryi*, holotype, Univ. Cal. Vert. Pal. No. 649, P^4–M^3 left.

Fig. 28. *Entoptychus sperryi*, holotype, Univ. Cal. Vert. Pal. No. 649, P_4–M_3 right.

Fig. 29. *Entoptychus lambdoideus*, holotype, A. M. No. 7041, P^4–M^3 left.

Fig. 30. *Entoptychus crassiramis*, composite of holotype, A. M. No. 7094 and referred specimen, A. M. No. 7096, P^4–M^3 left.

Fig. 31. *Entoptychus crassiramis*, referred specimen, A. M. No. 7097, P_4–M_3 right.

Fig. 32. *Dikkomys matthewi*.

(a) Holotype, A. M. No. 22720, P_4 right.
(b) Referred specimen, A. M. No. 22721, M^1 right.
(c) Referred specimen, A. M. No. 22721, M_1 left.
(d) Referred specimen, A. M. No. 22721, M_2 left.

All figures five times natural size.

DIAGNOSIS —Largest known member of genus; teeth proportionately large; no supraorbital ridges

This species is represented by much more fragmentary material than is the case with the other members of the genus. The holotype is a partial skull with the cheek teeth and the frontal region, but with both ends broken off. It has slightly larger teeth than any of the specimens referred to the same species. It seems probable, however, that all of these largest forms are conspecific. The lower teeth referred to this species are certainly distinct from *E. sperryi*, the only other species of comparable size (see Figs. 28 and 31). There is a fairly deep, round pit by the base of the coronoid process. There appear to have been no supraorbital crests. Other information about the skull and skeleton is lacking.

The first three of the upper cheek teeth are subequal in size. The enamel breaks are very well developed, and the enamel is much reduced on the posterior side of the teeth, although it stands up as a high, narrow blade. M^3 is somewhat smaller than are the other teeth. The enamel has been worn away from the anterior face of the molars in the specimen figured. The lower premolar is much less cut into by wear than are the molars, indicating that the crowns are worn away with considerable rapidity in this species. The individual cusps of the molars seem to have been rather distinct. The premolar seems to have belonged to the group with two main cusps in the anterior loph, rather than to the three-cusped division.

This species is clearly differentiated from all the others except *E. sperryi* on the basis of size. It is separable from the latter by the differences in the supraorbital crests and in the pattern of the teeth. *E. crassiramis* can be considered as the end stage of a series which has retained many primitive characters, but has specialized in the excessive hypsodonty of the cheek teeth. In this character, it is certainly the most specialized member of the subfamily that has as yet been described.

Two specimens from the Pliocene have been referred to this genus. A careful study of both specimens, made at the University of California in May, 1935, has convinced me that neither can be referred to *Entoptychus*, or even to the Geomyidae, for reasons outlined below.

Entoptychus minimus Kellogg, 1910

KELLOGG, 1910, Fig. 15. U. Cal. No. 12569, from the Thousand Creek Beds of Nevada.

This form is clearly not referable to *Entoptychus*. It has rooted cheek

teeth, although they are rather high crowned. The stage of hypsodonty is about that of various contemporary heteromyids. The structure of P_4 is quite distinct from that of any known geomyid, and is that of the Heteromyinae. The pattern of the molars is likewise more heteromyid than geomyid. In particular, the details of the teeth indicate that this form is congeneric with *Diprionomys agrarius* (Wood, 1935, pp. 178–198). This is being treated more fully in another connection.

Entoptychus? sp. Hall, 1930

HALL, 1930, Fig. 1. U. Cal. No. 29633, from the Barstow Beds of California.

Hall very tentatively identified this specimen as a geomyid, and considered that if it belonged to the family, it was probably *Entoptychus*. The lingual margin of the tooth is divided into two columns, but the outer half bears a broad, shallow basin, separating the paracone from the metacone. Viewed from the anterior side, however, it is seen that the lingual half is higher crowned than is the buccal. In view of this and the pattern of the crown, this tooth probably represents an upper deciduous premolar of a rabbit.

Geomyinae Miller and Gidley, 1918

Angular portion of mandible mostly above alveolar level; upper incisors of most forms sulcate, frequently with several grooves; cheek teeth ever-growing in the living forms, progressively extremely hypsodont; lophs of cheek teeth unite first at the center of the tooth; premolars of modern forms bilobed whereas molars have only one column; skull extremely fossorial in pattern; skeleton also highly adapted for digging, all the modern forms being burrowers.

GENERA.—*Dikkomys*, *Thomomys*, *Geomys*, *Pappogeomys*, *Cratogeomys*, *Platgeomys*, *Orthogeomys*, *Heterogeomys*, *Macrogeomys*, *Zygogeomys* and *Plesiothomomys*. Lower Miocene of Nebraska, later Tertiary of Kansas and Nebraska, Pleistocene of Maryland, Pleistocene and Recent of western United States, and Recent of western Canada, southeastern United States, Mexico, and Central America.

This subfamily represents a higher grade of specialization than do the Entoptychinae, which they seem to have replaced almost as soon as the two groups came into competition. At present nothing is known of the origin, and very little of the evolution of the Geomyinae. The later Tertiary forms that have been described are all close to the recent species, and show little or nothing of the origin of the group. The genus *Dikkomys*, described below, is considered to represent an early stage in the differentiation of the subfamily, but is of uncertain relationships.

Dikkomys matthewi, new genus, new species[1]

Figure 32

HOLOTYPE.—Amer. Mus. No. 22720, P_4 right.

PARATYPES.—Amer. Mus. No. 22721, M^1 right, M_1 and M_2 left.

HORIZON AND LOCALITY.—Lower Harrison, one mile north and east of Agate, Nebraska, in ant hills at edge of breaks.

DIAGNOSIS.—Geomyine type of premolar, the crests uniting in the center of the teeth in an H-pattern; teeth rooted, but hypsodont and lophodont; enamel complete throughout life.

The teeth of this species seem to form an ideal starting point for the evolution of the later Geomyinae. The premolar pattern is essentially identical with that which the more primitive of the living forms retain, with its two loops uniting just buccad of the center of the tooth (Fig. 32*a*). These two loops are homologous to the two lophs of the entoptychines. The small anterior cuspule on P_4 of *D. matthewi* is apparently part of an anterior cingulum. The buccal half of the median valley is much shallower than is the lingual half.

The pattern of the lower molars is very similar in its fundamentals to that of P_4, consisting of two lophs uniting slightly buccad of the center of the tooth (Fig. 32*c* and *d*). A trace of the external cingulum may be seen connecting the buccal margins of the two lophs. Here again, the buccal half of the valley is much shallower than the lingual half.

In the upper molar (Fig. 32*b*), the cingulum is reduced and almost lost, though the two cusps formed from it are retained. The union of the two lophs is between protocone and entostyle, the lingual valley being minute.

In all of these teeth, there is little or no trace of individual cusps. The lophs are strong and high, but clearly developed roots are still present on all the teeth, and the enamel is not extended down onto the sides of the roots. The molars are clearly separable from those of the modern Geomyinae in the retention of two distinct columns. This is, however, obviously a primitive character, and is no more than would be expected in an ancestral form.

The origin of this genus, its exact relationships to the entoptychines and to the later geomyines, are still uncertain, but it seems very probable that *Dikkomys* is at least structurally ancestral to the later forms, and hence closest to *Thomomys*. It is quite distinct from *Entoptychus*, but is suggestive of *Pleurolicus sulcifrons*. The specializations needed to derive the later Geomyinae from this form as far as it is known are increased hypsodonty, loss of the roots, reduction of the median valley of

[1] This generic name is intended to suggest relationships with *Thomomys*.

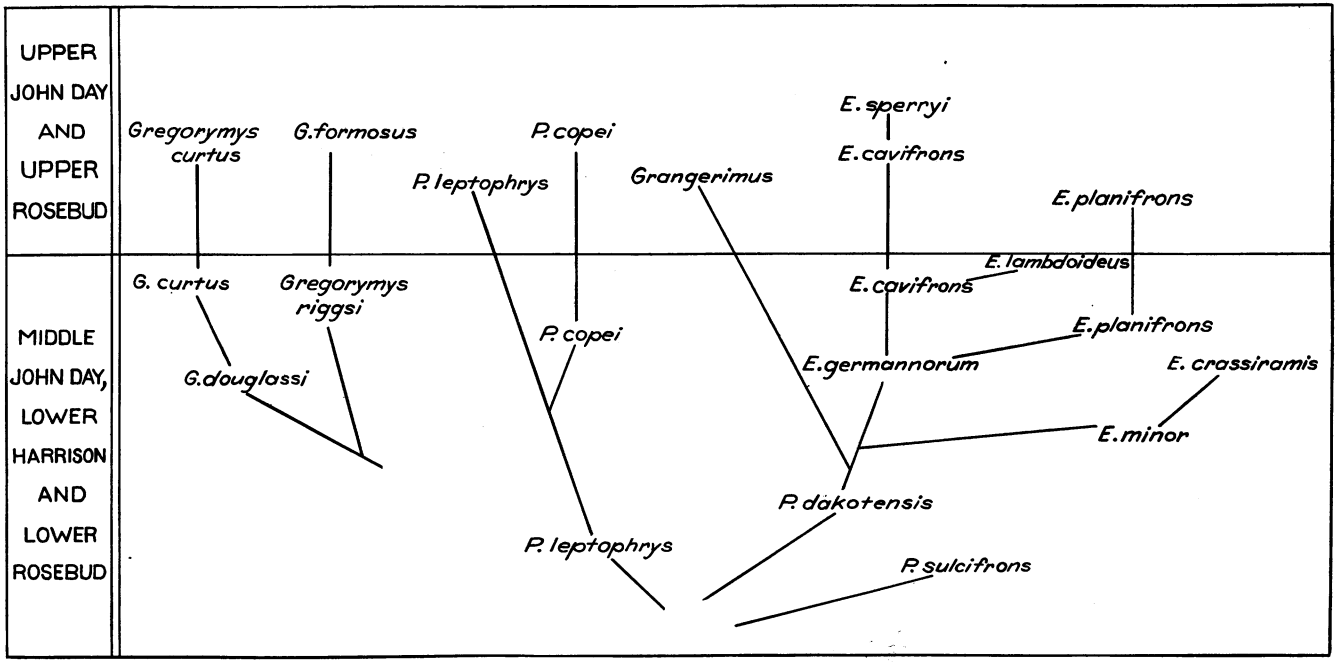

Fig. 33. Tentative chart of structural relationships of the Entoptychinae.

This is not intended as a Phylogenetic Chart, nor are the relative positions of the species indicative of stratigraphic level, except the division into the upper and lower portions.

the molars so that but a single column remains, and the limitation of the enamel to certain portions of the periphery of the crown.

The picture presented by the mid-Tertiary representatives of the Geomyidae is a most unusual one. They are essentially unknown in the Oligocene. Throughout the later Tertiary, from Middle Miocene on, they are rather rare as fossils. In looking at the Lower Miocene, however, one sees a large number of forms that are referred to this family. With one exception, they belong to an isolated and relatively compact group, which was separated by Miller and Gidley as a distinct subfamily. The origin and evolution of the various lines within this subfamily can not be traced at the present moment, due to the essential contemporaneity of all the forms that have as yet been described. An attempt has been made to work out the structural relations of this group, without any wish to express genetic relationships (Fig. 33).

In many respects the Entoptychinae are a group intermediate between the Geomyinae and the Heteromyidae, but they seem best to be classed with the former on the basis of skull structure, since the pattern of the cheek teeth is indecisive in this case. The habitus of this subfamily, in part at least, seems to have been fossorial, though they were not as far advanced along these lines as are the Geomyinae. The apparent sudden disappearance of the entoptychines after John Day and Rosebud time may be due to competition with the better-fitted Geomyinae, or may merely indicate that we have not as yet found the later Entoptychinae, microfauna being relatively rare in most Miocene deposits. The appearance of the earliest known geomyine in the same beds as the later entoptychines may or may not be of significance in this connection.

One point of considerable importance is the great similarity in cheek-tooth pattern between the geomyids and the heteromyids. This similarity, frequently so great as to amount almost to identity, is a strong indication of close relationship between the two families. It is a matter of importance to the paleontologist, however, that, although the two families may arrive at the same results in essentially the same manner, nevertheless the geomyids do it, usually, one epoch earlier than do the heteromyids.

TABLE I.—COMPARATIVE MEASUREMENTS OF GEOMYID UPPER TEETH

(All Measurements in Millimeters)

	P^4, antero-posterior, crown	P^4, width protoloph	P^4, width metaloph	M^1, antero-posterior	M^1, width protoloph	M^1, width metaloph	M^2, antero-posterior	M^2, width protoloph	M^2, width metaloph	M^3, antero-posterior	M^3, width protoloph	M^3, width metaloph
Gidleumys adspectans (Type: U. S. N. M. No. 13748)	3.05	2.43	2.68	2.22	2.56	2.54	..	..	..	..	..	..
Pleurolicus leptophrys (A. M. No. 7185)	1.85	1.74	2.01	1.47	2.09	1.94	1.35	1.93	1.82	1.28	1.63	1.39
P. sulcifrons (A. M. No. 7165)	2.40	1.20	2.24	1.65	2.21	2.14	1.52	2.12	1.97	..	..	..
P. copei (Type: A. M. No. 7175)	2.63	1.79	2.83	1.66	2.76	2.56	1.63	2.48	2.32	1.79	1.95	1.69
Gregorymys formosus (Type: A. M. No. 12887)	2.50	2.30	2.40	1.82	2.44	2.21	1.48	2.21	1.80	1.59	1.70	1.27
G. curtus (A. M. No. 12891)	2.40	2.30	2.60	1.41	2.35	2.30	1.41	2.10	1.85	1.41	1.62	1.42
G. riggsi (Type: F. M. No. P12221)	2.14	2.40	2.85	1.58	2.40	2.12	1.47	2.37	2.12	1.45	1.82	1.66
G. douglassi (Type: C. M. No. 1187)	1.82	1.92	1.95	1.53	2.20	1.94	1.46	1.96	1.78	1.30	1.67	1.27
G. douglassi, referred specimen (A. M. No. 21342)	2.05	1.92	2.31	1.80	2.55	2.21	1.45	2.36	1.90	..	..	..
Grangerimus matthewi (Type: A. M. No. 7044)	2.08	1.64	2.32	1.63	2.31	..	1.59	2.23	2.18	1.41	..	1.56
Entoptychus cavifrons (A. M. No. 7060)	1.87	1.82	1.96	1.48	2.24	2.14	1.34	2.19	1.94	1.08	1.48	1.43
E. planifrons (Type: A. M. No. 7029)	1.98	1.98	2.08	1.82	2.37	2.20	1.62	2.25	1.87	1.81	1.82	1.38
E. germannorum (Type: A. M. No. 7099)	1.95	1.99	2.36	1.75	2.24	2.07	1.70	2.25	2.15	1.38	1.58	1.44
E. minor (Type: A. M. No. 7043)	1.50	1.80	1.98	1.50	2.08	1.93	1.35	1.93	1.73	1.43	1.58	1.35
E. sperryi (Type: U. Cal. No. 649)	2.57	2.82	2.65	2.07	3.03	2.92	1.95	2.87	2.56	1.83	2.02	1.83
E. rostratus (Type: U. Cal. No. 1651)	2.38	2.19	2.42	1.78	2.33	..	1.63	2.21	..	..	..	..
E. lambdoideus (Type: A. M. No. 7041)	2.18	2.16	2.24	1.83	2.26	2.20	1.63	2.05	1.93	..	..	..
*E. crassiramis** (Type: A. M. No. 7094)	2.80	2.62	3.02	2.34	3.18	2.98	2.16	2.96	2.80	1.86	2.08	1.75
Dikkomys matthewi (A. M. No. 22721)	..	..	..	1.30	1.70	1.62	..	..	..	..	..	..

* First two measurements based on A. M. No. 7096, an animal of approximately the same size as No. 7094.

TABLE II.—COMPARATIVE MEASUREMENTS OF GEOMYID LOWER TEETH

(All Measurements in Millimeters)

	P_4, antero-posterior	P_4, width metalophid	P_4, width hypolophid	M_1, antero-posterior	M_1, width metalophid	M_1, width hypolophid	M_2, antero-posterior	M_2, width metalophid	M_2, width hypolophid	M_3, antero-posterior	M_3, width metalophid	M_3, width hypolophid
Pleurolicus sulcifrons (A. M. No. 7180)	1.76	1.60	1.89	1.80	2.32	2.25	1.75	2.36	2.18	1.53	1.90	1.65
P. leptophrys (A. M. No. 7158)	1.43	1.32	1.67	1.57	1.95	1.92	..	2.10	2.05	..	..	..
P. copei (A. M. Nos. 7181, 7182)	2.20	1.86	2.11	1.79	2.34	2.26	1.75	2.36	2.36	..	..	..
P. dakotensis (Type: A. M. No. 12893)	1.57	1.46	2.13	1.54	2.08	2.13	..	..	..	..	..	..
Gregorymys formosus (A. M. No. 12909)	2.30	2.05	2.25	1.58	2.22	2.37	1.52	2.25	2.07	1.55	2.07	1.55
G. curtus (A. M. No. 12895)	2.19	2.01	2.23	1.78	2.26	2.31	1.57	2.22	2.01	1.52	1.95	1.60
G. riggsi (Type: F. M. No. P12221)	2.18	1.97	2.42	1.56	..	..	1.56	2.15	2.11	1.52	1.75	1.62
Grangerimus matthewi Type: A. M. No. 7044)	1.70	1.53	1.93	1.66	1.98	1.96	1.66	2.07	2.03	1.67	1.98	1.73
Entoptychus cavifrons (A. M. No. 7162. M_1 = A. M. No. 7161)	1.58	1.38	1.77	1.57	1.93	2.07	1.49	2.07	2.07	1.30	1.79	1.76
E. planifrons (Type: A. M. No. 7029)	1.88	1.57	2.10	1.81	2.33	2.43	1.76	2.13	2.23	1.75	2.05	2.03
E. germannorum (Type: A. M. No. 7099)	1.98	1.54	2.02	1.52	2.22	2.15	1.53	2.09	2.07	1.63	1.85	1.85
E. minor (Type: A. M. No. 7043)	1.66	1.38	1.84	1.40	..	..	1.35	..	..	1.36	..	..
E. sperryi (Type: U. Cal. No. 649)	2.64	1.93	2.43	1.88	2.38	2.68	2.08	2.56	2.71	2.00	1.96	2.06
E. crassiramis (A. M. No. 7097)	2.38	2.01	2.38	1.68	2.55	2.71	1.62	2.73	2.91	..	..	..
Dikkomys matthewi (Type: A. M. No. 22720 and A. M. No. 22721)	1.93	1.30	1.43	1.55	1.83	1.74	..	..	..	..	..	..

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