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Skull Morphology of *Gregorymys* and Relationships of the Entoptychinae (Rodentia, Geomyidae)

JOHN H. WAHLERT¹ AND RICHARD A. SOUZA²

ABSTRACT

Comparison of skull morphology of type specimens of *Gregorymys formosus* and *G. curtus* with that of other entoptychines and geomyoid rodents supports inclusion of both the Geomyinae and Entoptychinae in the family Geomyidae. The chief shared, derived characters of the two subfamilies are: great dorsal extent of the alisphenoid for origin of a deep anterior division of the temporal muscle; presence of a large squamosal protuberance that redirects the pull of the posterior part of the temporal muscle to a vertical direction; concavity and inclination toward the incisors of the diastemal

palate; narrowed interparietal bone. Anteromedial processes of the auditory bullae that meet in the midline just in front of basioccipital bulges are unique, derived features of the Entoptychinae. The sudden appearance of entoptychines and later of geomyines in the fossil record within the United States and lack of intermediate, more primitive cranial remains are explained by a hypothesized center of geomyid and geomyoid evolution in Mexico and Central America. A revised classification of the Geomyoidea is presented.

INTRODUCTION

Matthew (1907: 212–213) described two new species of *Entoptychus*, *E. formosus* and *E. curtus*, based on skulls from the late Arikareean Rosebud beds of South Dakota. *En-*

toptychus had been known previously from the John Day beds of Oregon. Wood (1936b: 9) erected the genus *Gregorymys*, made Matthew's species *G. formosus* its type, and in-

¹ Research Associate, Department of Vertebrate Paleontology, American Museum of Natural History; Associate Professor of Biology, Department of Natural Sciences, Baruch College of the City University of New York.

² Collection Manager, Division of Earth Sciences, Carnegie Museum of Natural History; Department of Geology and Planetary Science, University of Pittsburgh.

cluded *G. curtus*. The geographic and temporal ranges of *Gregorymys* have been further extended:

- G. riggsi* Wood, 1936b: 11. Late Arikarean, Wyoming
- G. douglassi* Wood, 1936b: 12. Late Arikarean, Montana
- G. kayi* Wood, 1950: 335. Miocene, Montana
- cf. *Gregorymys* Martin, 1976. Hemingfordian, South Dakota
- G. larsoni* Munthe, 1977: 2. Late Barstovian or early Clarendonian, Colorado
- G. riograndensis* Stevens, 1977: 25. Late Arikarean, Texas

Wilson (1949) suggested that a partial mandible from the Upper Sespe of California might belong to the genus *Gregorymys*. Rensberger (1971) transferred the species *G. montanensis* Hibbard and Keenmon, 1950, to *Entoptychus* and thereby extended the range of this genus to the Hemingfordian of Montana.

Rensberger (1973a, 1973b) examined closely related genera. *Pleurolicus* and *Tenudomys* precede *Entoptychus* and *Gregorymys* in the stratigraphic record; *Schizodontomys* mostly succeeds them. *Pleurolicus* is known from Montana, Oregon, and South Dakota; *Schizodontomys* from Oregon and South Dakota; *Tenudomys* from Montana and South Dakota. We have not had the opportunity to study these other taxa, but include them in the Entoptychinae. Wahlert (1985a: 17–18) suggested, however, that *Schizodontomys* may be a dipodomyine heteromyid.

Despite the importance of Matthew's two species in the concept of the genus *Gregorymys*, the skull has been figured only for *G. formosus*. Matthew's figures (1907: figs. 24–26) are rough diagrams that contain serious errors in depicting form and omissions of important structures. Rensberger (1971: pl. 15, a–c) presented photographs of the skull in dorsal, ventral, and lateral views; although these are of excellent quality, fine structural details are not revealed.

It is the chief purpose of this paper to show the skulls of *Gregorymys formosus* and *G. curtus* clearly. Both are type specimens of their respective species and are the best preserved skulls known for the genus. Information from specimens of other species is included. The

new description is the basis for cranial comparison with *Entoptychus* and *Pleurolicus*, and for reassessment of the relationship of entoptychines to other geomyoid rodents. Data on *Entoptychus* are derived from Rensberger (1971) and Wahlert (1972, 1985a). Locality data for the types and other specimens from southwestern South Dakota follow Macdonald (1963, 1970).

The specimens are considered in the context of Wahlert's previous work. Skulls of North American protrogomorphs (1974, 1985b), especially those of *Paramys* and *Sciuravus*, serve as examples of primitive rodents. The Eomyidae (1978), Florentiamyidae (1983), and Geomyoidea (1985a) provide a spectrum of characters within the infraorder Geomorpha. Wahlert (1985a) divided the superfamily Geomyoidea into four families—Florentiamyidae, Entoptychidae, Heteromyidae (Heteromyinae, Perognathinae, Dipodomyinae), and Geomyidae (Geomyinae only). This classification is adopted here except that the Entoptychidae are considered a subfamily of the Geomyidae.

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ABBREVIATIONS

Institutions

- AMNH American Museum of Natural History
- CM Carnegie Museum of Natural History

F:AM	Frick Collection, American Museum of Natural History
FMNH	Field Museum of Natural History
KU	University of Kansas
SDSM	South Dakota School of Mines and Technology
TMM	Texas Memorial Museum
UCMP	University of California Museum of Paleontology, Berkeley

Specimen completeness

c	cranium
j	mandible
n	rostrum
o	orbit
p	palate
s	whole skull
t	pterygoid region

SPECIMENS EXAMINED

Gregorymys formosus

AMNH 12887 s type; AMNH 12888 s (damaged): Porcupine Creek, 2 mi NW of Porcupine Post Office, Shannon Co., S. Dak.; Harrison Fm., late Arikareean.

AMNH 12889 np: Porcupine Butte, Shannon Co., S. Dak.; Rosebud Fm., late Arikareean.

F:AM 116846 s: north of Keeline, Niobrara Co., Wyo.; Harrison Fm., early late Arikareean.

SDSM 6279 s: loc. V621, Window Butte. SDSM 6297 np: loc. V6215, Ironcloud Ranch. Wounded Knee area, Shannon Co., S. Dak.; Monroe Creek Fm., late early Arikareean (seen in casts).

Gregorymys curtus

AMNH 12890 s type: about 6 mi E of Porcupine Post Office, Porcupine Creek, Shannon Co., S. Dak.; Harrison or Rosebud Fm., late Arikareean.

AMNH 12891 npo: 4 mi below Porcupine Post Office, Porcupine Creek, Shannon Co., S. Dak.; Harrison Fm., late late Arikareean.

Gregorymys douglassi

CM 1187 np type: Woodin, Silver Bow Co., Mont.; late Arikareean.

Gregorymys riggsi

FMNH P12221 npj type: Raw Hide Creek, Goshen Co., Wyo.; Upper Harrison Fm., late Arikareean.

FMNH P26247 npot; FMNH P26251 npo; FMNH P26254 npot (described by Galbreath, 1967, as *G. curtus*): Tylee Canyon, Wounded Knee area, Shannon Co., S. Dak.; Rosebud Fm., late Arikareean.

TABLE 1
Cranial Dimensions^a of *Gregorymys* (type specimens) in Millimeters

	<i>G. formosus</i> AMNH 12887	<i>G. curtus</i> AMNH 12890
Length:		
Condylbasilar	37.8	37.0 (est) ^b
Diastemal	12.8	13.4 (est)
Incisive foramen	3.1	2.4
Palatal	21.6	22.5 (est)
Pterygoid	4.4 (est)	4.5
Width:		
Palatal	2.4	2.2
Interorbital	5.3	6.4
Posterior cranial	17.0 (est)	—

^a See text.

^b Measurement estimated.

F:AM 116848 sj; F:AM 116849 np: 6 mi southwest of Guernsey, Platte Co., Wyo.; Upper Harrison Fm., late late Arikareean.

F:AM 116850 sj: Royal Valley, Niobrara Co., Wyo.; Upper Harrison Fm., late late Arikareean.

F:AM 116851 s: 2 mi west of Jay Em, Goshen Co., Wyo.; Upper Harrison Fm., late late Arikareean.

F:AM 116852 npj: Sand Gulch, Goshen Co., Wyo.; Upper Harrison Fm., late late Arikareean.

Gregorymys riograndensis

TMM 40635-89 npj type; TMM 40635-107 npc; TMM 40635-116 n; TMM 40635-118 p; TMM 40635-150 n: 2 mi southeast of Castolon, Brewster Co., Tex.; Delaho Fm., late Arikareean.

Pleurolicus sulcifrons

AMNH 7044 npoj (type of *Grangerimus oregonensis* Wood, 1936b: 13); AMNH 7177 c (type of *Pleurolicus diplophysus* Cope, 1881: 381); UCMP 86191 npj; UCMP 86196 npot; UCMP 86198 sj: region of John Day River, Wheeler and Grant Co.'s, Oregon; John Day Fm., late early Arikareean.

MEASUREMENTS

Cranial dimensions of type specimens of *Gregorymys formosus* and *G. curtus* are presented in table 1. "Condylbasilar length is measured from the henselion, a line tangent to the backs of the incisor alveoli, to a line that is tangent to the posterior curves of the

TABLE 2
Dental Dimensions^a of *Gregorymys* (type specimens) in Millimeters

	<i>G.</i> <i>formosus</i> AMNH 12887	<i>G.</i> <i>curtus</i> AMNH 12890
Length:		
P4-M3 (alveolar)	8.4	8.4
P4	2.1	—
M1	1.5	1.5
M2	1.4	1.4
M3	1.4	1.3
I (depth)	2.4	2.2
Width:		
P4	2.4	—
M1	2.4	2.6
M2	2.4	2.4
M3	1.6	1.8
I	2.0	2.1

^a See text.

occipital condyles. Palatal length is from the henselion to the posterior edge of the palate at the midline. Diastemal length is the shortest line between the back of an incisor alveolus and the front of the alveolus of the first cheek tooth on the same side. Pterygoid length is the shortest line from the posterior surface of the third molar to the anterior edge of the foramen ovale" (Wahlert, 1983: 3). Palatal width is the minimum distance between the alveoli of the first molars. Interorbital width is the minimum breadth taken with caliper jaws in the orbits. Posterior cranial width is taken at the most medial parts of the posterior squamosal roots of the zygomatic arches and is across parts of the squamosals, and parietals.

Dental measurements are given in table 2. Alveolar length of the cheek teeth is taken from the edge of the maxilla at the front of the fourth premolar to the edge at the back of the third molar. Length of individual teeth is a measurement only of the wear surface. Greatest width is the maximum dimension, not necessarily at the wear surface.

COMPARATIVE CRANIAL MORPHOLOGY

New illustrations are given of the type specimens of *Gregorymys formosus* (figs. 1

and 3) and *G. curtus* (fig. 2). Symmetrical features were reflected where bone is damaged; other specimens were examined to restore missing details. Morphology that is uncertain is indicated by dashed lines. The figures are thus idealized diagrams of the two skulls and not direct representations of specimens. The arching of the skull roof is different in lateral views; deformation of the skulls, especially of *G. curtus*, makes the degree of difference uncertain. Illustrations of the dentitions (fig. 4) are presented merely to fill a surprising omission from the literature.

The diastemal palate is broadly concave and inclined upward toward the incisors as it is in other entoptychines but less so than in geomyines. Interpremaxillary foramina are usually lacking; a pair of tiny foramina flank the median premaxillary suture in two specimens of *Pleurolicus*. The incisive foramina are short and narrow with the posterior ends depressed into the palate. The premaxillary-maxillary suture runs anteriorly to meet the foramina at their posterolateral edges. The incisive foramina occupy 16 to 26 percent of the diastemal length, a high figure compared with living geomyines, heteromyines, and perognathines, but in accord with other entoptychines and florentiamyids.

The posterior palatine foramina are in the maxillary-palatine suture; they are medial to some part of the zone from the middle of the first to the middle of the second molar, a common position in rodents. One or two additional paired or unpaired foramina occur posterior to these in some specimens of *Pleurolicus*. Tooth rows converge and the palate narrows anteriorly as in other entoptychines and geomyines. The degree of convergence is much greater than in *Pleurolicus*.

The back of the palate is peculiar as in all geomyoid rodents. The palate slopes dorsally on either side of the choanal region toward the pterygoid fossae and forms a pair of parapterygoid fossae; these depressions are shallow in *G. curtus*, considerably deeper in *G. riggsi*, and even more pronounced in *G. formosus*. In geomyines and heteromyids the posterior edges of the depressions have a ventral inclination that is lacking here. The posterior maxillary foramen is posterior to the third molar; the maxilla bounds it laterally and the palatine medially.

Gregorymys was fully sciuromorphic and shows the geomorph character of a long infraorbital canal that is low on the rostrum and is depressed into the rostral wall at its anterior end, the infraorbital foramen. A small hole is present in the wall of this depression only in the type specimen of *G. formosus*; the region is more commonly imperforate.

The nasolacrimal foramen, which is the entrance to the lacrimal canal, is in the primitive position in the lacrimal bone anterodorsal to the orbital aperture of the infraorbital canal. The initial part of the canal is nearly vertical. The process of the lacrimal bone that overhangs it is small. The region where lacrimal, frontal, and maxillary bones meet is imperfectly preserved, but there appears to be little room for a gap or nonossification as is common in geomyoids.

The sphenopalatine foramen is dorsal to the anterior part of the first molar in *G. formosus* and *G. curtus*, and to the junction of the fourth premolar and first molar in *G. riggsi*. This range is the same as in other geomyoids. The orbital lamina of the palatine appears to reach the sphenopalatine foramen and to exclude the orbitosphenoid from its margin in *G. formosus* (AMNH 12887), whereas both bones appear to reach the foramen in *G. curtus*. The former condition is recorded in *Entoptychus* (Wahlert, 1985a: fig. 5). The character may well vary. Palatine participation in the margin is primitive in rodents (Wahlert, 1974). The frontal bone appears to be barely excluded from the margin of the foramen; exclusion of the frontal is a common, but not universal, character in geomyoids.

The ethmoid foramen is in the orbitosphenoid-frontal suture dorsal to the posterior part of the first molar in *G. formosus* and *G. curtus*. It is farther anterior in *G. riggsi* and is dorsal to some part of the sphenopalatine foramen. Its position is within the range seen in heteromyids and geomyines.

The optic foramen is about 1.0 mm in diameter, a size that is common in rodents but bigger than in geomyines. The foramen appears to have been dorsal to the third molar in damaged remains of *G. formosus*; this position is seen in heteromyids. It is farther anterior in *G. curtus*, dorsal to the second molar, and in *G. riggsi* dorsal to the junction

of the first and second molars. In *Pleurolicus* (UCMP 86196) the anterior part of the foramen is dorsal to the second molar. These positions are seen in geomyines. The orbital wall is complete as in *Heteromys* and *Liomys*, and there is no unossified area between the orbitosphenoid and frontal bones as often occurs in geomyines. The border of a sphenofrontal foramen is preserved on the right side of the type specimen of *G. formosus*; it is dorsal to the anterior-alar fissure in the alisphenoid-frontal suture. This foramen is rarely seen in fossil skulls of the Geomorpha. It has been noted in an eomyid (Wahlert, 1978: fig. 3) and in a florentiamyid (Wahlert, 1983: 12). Among living geomyoids the foramen is present only in *Dipodomys* and possibly in *Perognathus* (Wahlert, 1985a: 8).

The dorsal palatine foramen is in the maxillary-palatine suture dorsal to the junction of the second and third molars in *G. formosus* and dorsal to the second molar in *Pleurolicus* (UCMP 86196), common positions in rodents. It is probably hidden within the anterior-alar fissure of other species. The ventral root of the anterior-alar fissure rises from above the posterior part of the third molar in *G. formosus*, from above the posterior part of the second molar in *G. curtus*, and from above the anterior part of the second molar in *G. riggsi*. This range is comparable to that in heteromyids and geomyines, but it is far anterior to the position in florentiamyids and eomyids. No interorbital foramen was found. A gap between the orbitosphenoid and palatine in *G. formosus* and *Pleurolicus* (UCMP 86196) may indicate the presence of a sphenopalatine vacuity.

The alisphenoid bone extends dorsally to about three-quarters of the orbital height in the posteromedial part of the orbit. A deep division of the temporal muscle arose on its channeled surface, as in living geomyines. In *G. formosus* (AMNH 12887) a low, median crest is roughly parallel to the anterior and posterior edges of this extension. Among the geomyines only *Thomomys* lacks the low median crest in the area of muscle origin. This orbital portion of the muscle must have run almost vertically to its insertion on the mandible. The alisphenoid has a similar dorsal extent in *Entoptychus*, florentiamyids, and living geomyines; its condition is not record-

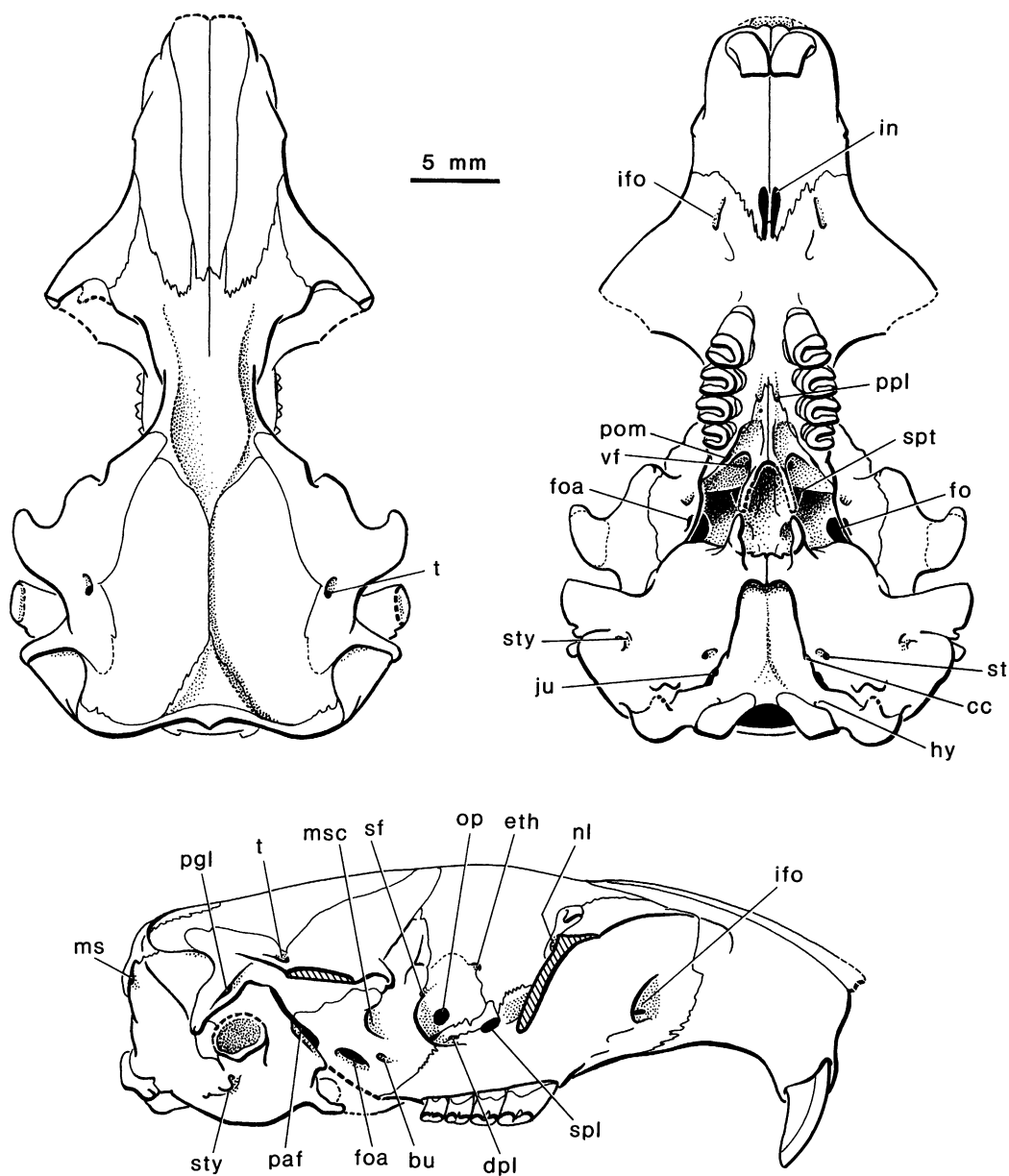


Fig. 1. *Gregorymys formosus*, AMNH 12887. Restoration of skull. Cross hatching indicates imagined cut through bone; dashed lines, uncertain morphology. Anterior alar fissure forms large C-shaped edge in posterior part of orbit.

Abbreviations: For foramina and other structures (as named): **bu**, buccinator; **cc**, carotid canal; **dpl**, dorsal palatine; **eth**, ethmoid; **fo**, foramen ovale; **foa**, accessory foramen ovale; **hy**, hypoglossal; **ifo**, infraorbital; **in**, incisive; **ju**, jugular; **ms**, mastoid; **msc**, masticatory; **nl**, nasolacrimal; **op**, optic; **paf**, postalar fissure; **pgl**, post glenoid; **pom**, posterior maxillary; **ppl**, posterior palatine; **sf**, sphenofrontal; **spl**, sphenopalatine; **spt**, sphenopterygoid canal; **st**, stapedial; **sty**, stylomastoid; **t**, temporal; **vf**, venous foramen in parapterygoid fossa.

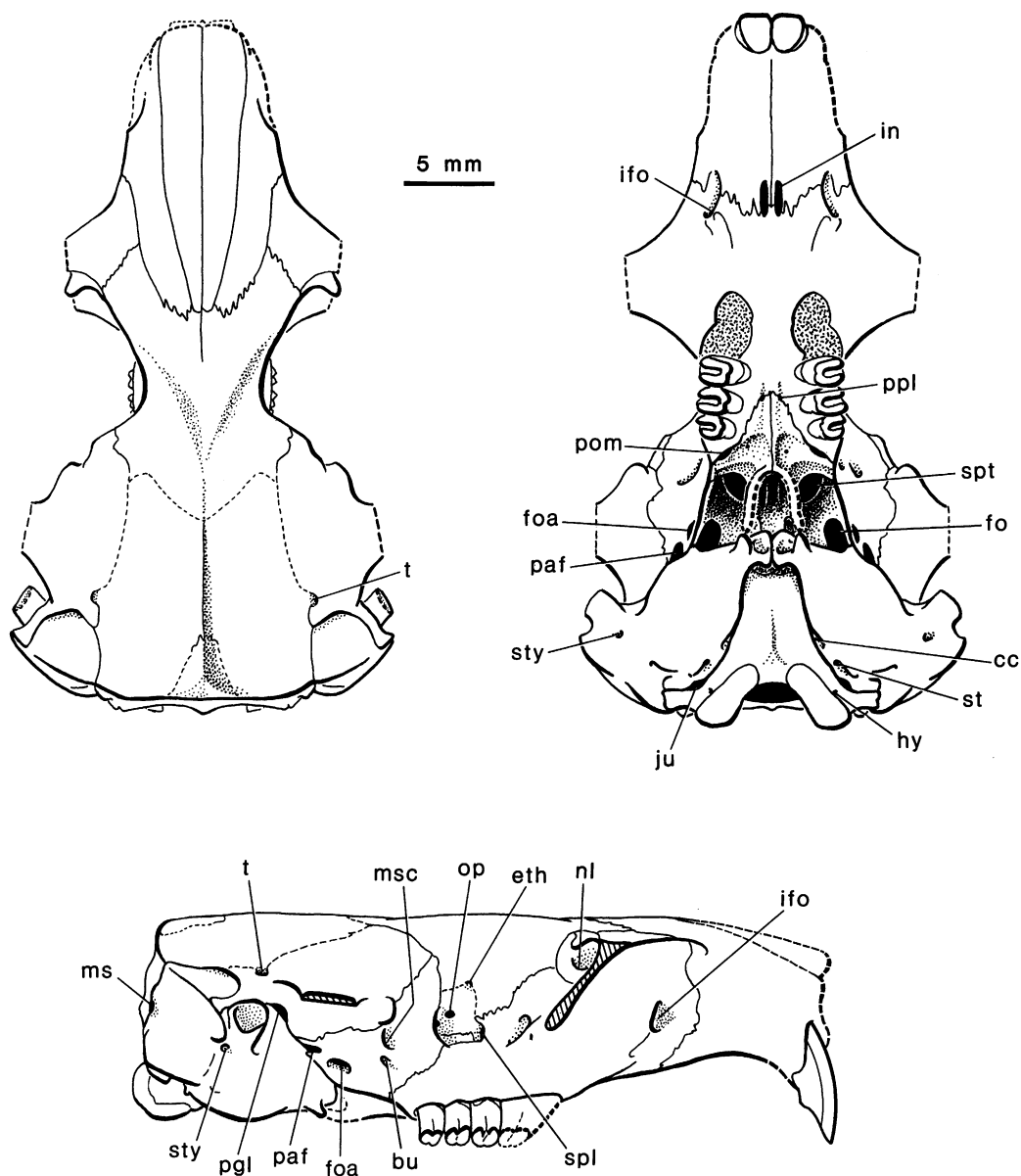


Fig. 2. *Gregorymys curtus*, AMNH 12890. Restoration of skull. Notation and abbreviations as in figure 1.

ed in *Pleurolicus*. The alisphenoid is low in heteromyids. The squamosal is also extended dorsally, especially in *G. formosus*, *Entoptychus*, *Pleurolicus*, and geomyoids. The anteroventral margin of the alisphenoid makes a broad suture with the posterior end of the maxilla, a characteristic of other entopty-

chines, heteromyids, and geomyines. The union of these elements is narrower in *Pleurolicus*, but not so narrow as in *florentiomyids*.

Masticatory and buccinator foramina are usually separated. In one specimen of *G. curtus* (AMNH 12890) they are separated on the

left side but are joined as a single aperture on the right. No foramen is seen in the medial wall of the masticatory foramen for passage of the internal maxillary artery; such a hole has been reported in geomyines, *Heteromys*, and *Liomys* (Wahlert, 1985a: 9).

The lateral pterygoid flange is prominent and reaches the auditory bulla. The accessory foramen ovale is fully surrounded by bone in *Gregorymys* and *Entoptychus*. In living heteromyids and geomyines the flange rarely reaches the bulla, and the accessory foramen ovale is seldom enclosed. Rensberger (1973a: 40) stated that *Pleurolicus* shows the geomyine condition in which the "foramen ovale" (= accessory foramen ovale) is not enclosed ventrally. The region may be damaged, and this description is open to question.

The alisphenoid canal enters the alisphenoid bone at the anterior end of the foramen ovale. The foramen ovale is bounded posteriorly by the auditory bulla, a geomyoid condition, but in *Gregorymys* and *Entoptychus* the alisphenoid separates it laterally from the postalar fissure, a rare feature in geomyoids. The two apertures are continuous in *Pleurolicus* (UCMP 86198). In *G. formosus* the postalar fissure is continuous dorsally into the postglenoid foramen, which is between the squamosal and the bulla. A posterior flange of the squamosal separates these two apertures in *G. curtus* and *Pleurolicus*; this variation also occurs in living geomyoids. *G. formosus*, *Entoptychus*, and *Pleurolicus* have a slitlike foramen in the prong of the squamosal that extends posterolaterally to the mastoid. Wahlert (1985a: 11, fig. 5) has called this the postglenoid foramen. The problem of naming these openings is postponed to the discussion.

The sphenopterygoid canal is a prominent feature of the pterygoid region as it is in living geomyoids. It is immediately posterior to the parapterygoid depression. Rensberger (1971: 96) said that in *Entoptychus* "the anterior ends of the pterygoid fossae are closed, not open as in the geomyines." However, *G. formosus*, *G. curtus*, and *Pleurolicus* (UCMP 86198) retain clear evidence for a large opening in the dorsal roof of the pterygoid fossa. The posterolateral edge of this opening is marked by a smooth, curved edge of bone, and, medial to the opening, the presphenoid/orbitosphenoid element is laterally com-

pressed; these features approximate the heteromyine condition. The morphology of the region suggests the presence of a large, vertical internal pterygoid muscle whose origin on the walls of the fossa was extended dorsally in conjunction with opening of the roof of the fossa. This is a geomyoid condition. No trace of a transverse canal was found; it is lacking in some geomyines and most heteromyids.

The auditory bullae are enlarged and unusual. They are somewhat inflated ventrally. Broad anteromedial processes meet in the ventral midline of the skull, and the anterior end of the basisphenoid protrudes ventrally as a pair of bulges immediately posterior to them. The processes are not so broad in *Pleurolicus*. Similar processes and basioccipital bulges are known only in dipodomysines. The processes conceal the carotid foramina. In *Gregorymys* a groove in the medial edge of each bulla, alongside the basioccipital, marks the course of the internal carotid artery. There may have been a slight gap or fissure between the basioccipital and adjacent bulla/petrosal in *Gregorymys*, as occurs in *Pleurolicus*, *Entoptychus*, and also in dipodomysines.

The bullae are preserved unbroken, or they are missing, and internal texture of the bone may only be guessed. The mastoid region of one specimen, *G. riggsi* (AMNH 116851), is damaged, and the bone is clearly trabecular. This is the typical bullar structure of geomyoids. The bullae of *Entoptychus* are not apparently trabecular (Wahlert, 1985a: 12). In dipodomysines the bone of the bulla and mastoid regions is a single, thin layer.

The stapedial foramen is large and enters the medial wall of the bulla anteroventral to the jugular foramen as in perognathines and dipodomysines. The foramen is lacking in heteromyines and is marked only by a pit in geomyines. The stylomastoid foramen is posteromedial to the long bony meatus, as it is in geomyines.

The mastoid region is enlarged and broadly exposed on the occiput, which is narrow, and on the skull roof, where the squamosal is posteriorly excavated. A similar condition occurs in perognathines and dipodomysines. The small mastoid foramen is situated dorso-medially in the mastoid-occipital suture.

The jugular foramen is a lenticular slot between the basioccipital and the postero-

medial part of the petrosal. In *Pleurolicus* and *Entoptychus* it is continuous with the fissure medial to the bulla. The hypoglossal foramen, which may consist of two small openings, is medial to the jugular foramen and is underthrust by the anterior edge of the occipital condyle; it faces anterolaterally.

A small temporal foramen is present posterodorsal to the squamosal root of the zygoma. The squamosal-parietal suture dips down to it. Similar temporal foramina occur in other entoptychines and florentiamyids but not in living heteromyids and geomyines.

Dorsal views of *Gregorymys* skulls show other important cranial features. The nasal bones do not extend as far posteriorly as the premaxillae, a common but not universal characteristic of geomyoids. The narrowest dimension of the interorbital width is within the orbits and not at the edge of the skull roof as in heteromyids. *G. formosus* has strong supraorbital crests that are lacking in other species; these unite dorsal to the squamosal root of the zygoma to form the medial sagittal crest. This condition occurs also in mature *Entoptychus* specimens. Lyrate temporal crests in *Pleurolicus* may be close together but do not join to form a single, medial crest (Rensberger, 1973a: 38). Only a slender lateral prong of the emarginate squamosal extends posteriorly, a condition like that in perognathines. The interparietal bone is a narrow wedge between the parietals (it is bell-shaped in *Pleurolicus*) and has very slight lateral extent in the three genera of entoptychines. The condition is geomyine-like. The bone is wide in heteromyines and perognathines; its width is clearly limited by dorsal exposure of the inflated bullae in dipodomysines.

The presence of a median sagittal crest is evidence that the origin of the temporal muscle extended to the midline of the skull in these specimens. It is least prominent in *G. riggsi*. There is a large squamosal protuberance anteromedial to the glenoid fossa. In living geomyines this acts as a pulley that makes the contractile force of the posterior part of the temporal muscle operate vertically (Wahlert, 1985a: 10). Rensberger (1971: 104) recorded a similar process in *Entoptychus*; he illustrated the structure in *Pleurolicus* (1973a: pl. 2, a, b). The process is present but weak in perognathines and heteromyines.

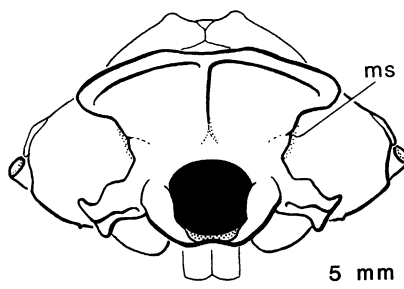


Fig. 3. *Gregorymys formosus*, AMNH 12887. Restoration of skull, posterior view. ms, mastoid foramen.

MORPHOLOGY OF THE MANDIBLE

The type specimens of *Gregorymys* lack mandibles; most mandibles referred to the various species are damaged, and processes are broken off. In *G. riggsi* (F:AM 116848 and F:AM 116850) the coronoid process appears to have been large, as would be expected in a rodent with a substantial temporal muscle; there is no depression for muscle insertion between the process and the cheek teeth as in geomyines. The coronoid process is large in *Pleurolicus*, and there is a slight depression for muscle insertion. The masseteric crest is very prominent in *Gregorymys* and *Pleurolicus*, like that described by Rensberger (1971) in *Entoptychus*. His comparative description indicates that the morphology of the mandible is more primitive than that seen in geomyines. The angle in *Entoptychus* terminates in a superior angular process that forms a prominent shelf in advanced forms of the genus; this is a heteromyid-like condition. In geomyines the angle is reduced, but the process remains large and is more dorsally situated.

DENTITION

The upper cheek teeth of *Gregorymys* (fig. 4) conform to the entoptychine crown pattern as described by Rensberger (1971: 70). The teeth wear to a U-shape that is concave outward (buccally). The width of transverse lophs is great and presumably includes the lingual styles that are characteristic of geomyoids. The teeth of the type specimen of *G. formosus* are deeply worn. Further wear would cause

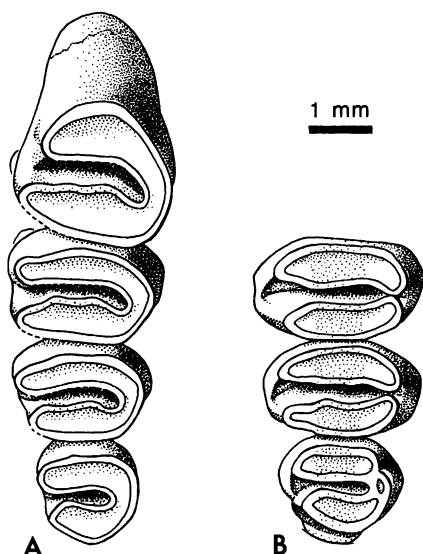


Fig. 4. Upper right cheek teeth of *Gregorymys*—type specimens: (A) *G. formosus*; (B) *G. curtus*. Anterior is at top of page, lingual is to the right.

connection of paracone and metacone, and the central valley would be transformed into a lake in each tooth, as in *Entoptychus*. The enamel extends deeper toward the alveolus on the anterior and posterior ends of the teeth than on lingual and labial sides. The anterior part of P4 is covered by a substance that may be cement. The teeth of the type specimen of *G. curtus* are less worn, and the transverse lophs of M1 and M2 are not quite joined lingually. The median valleys appear to be deepest buccally, and their transformation into lakes by wear is unlikely. The enamel is not extended toward the alveolus on the anterior and posterior parts of the teeth. The teeth of these two species of *Gregorymys* are very similar in size (table 2). Differences may only reflect different stages in wear. Wood (1936b: table 1) also gave dental measurements of the type specimens. These differ slightly from our own; his length of the entire tooth is greater than our wear surface dimension. The incisors have a slight ridge along the anteromedial edge of the enamel face.

DISCUSSION

The skulls of *Gregorymys* and other entoptychines exhibit a combination of primitive

and derived features that place them in the Geomyoidea. Close scrutiny of the crania permits a new assessment of their relationships within the superfamily.

Gregorymys and other entoptychines exhibit typical characteristics of the Geomorpha, which also includes the extinct Eomyoidea: lateral masseter arising on rostrum (sciuromorphy); infraorbital canal long, low on rostrum, and depressed into rostral wall at anterior end; sphenopalatine foramen far anterior, dorsal to M1; wear on cheek teeth forming transverse lophs.

The entoptychines retain primitive features of rodents and other mammals that have a varied record of retention within the Geomorpha: (1) optic foramen about 1.0 mm in diameter, whereas the size is smaller or larger in other geomyoids; (2) stapedial foramen present as in eomyids, florentiamyids, perognathines, and dipodomysines; (3) masticatory and buccinator foramina usually separate and distinct from accessory foramen ovale as in geomyines, perognathines, and *Microdipodops* (a dipodomysine); (4) accessory foramen ovale bounded ventrally by bone, temporal foramen present in or near squamosal-parietal suture, postglenoid foramen within squamosal bone (exception—some *Gregorymys*) as in eomyids and florentiamyids. The entoptychines share no unique derived characters with eomyids. In *G. formosus*, *Entoptychus*, and *Pleurolicus* there appear to be two postglenoid foramina; one is in the primitive position within the squamosal, and the other is confluent with the postalar fissure, the derived position. This shift in venous circulation is apparently completed in *G. curtus* and in living geomyoids.

Several shared derived features unite entoptychines and geomyoids: incisive foramina short, 30 percent or less of diastemal length; parapterygoid fossae present (very shallow in florentiamyids); foramen ovale bounded posteriorly by auditory bulla; anterior part of squamosal extending dorsally as far as or near to skull table; cheek teeth bilophodont. Entoptychines share no unique derived characters with florentiamyids other than dorsal extension of the alisphenoid.

Rensberger (1971) described resemblances and differences between *Entoptychus* and geomyines and heteromyids (Heteromyinae

in his usage). He proposed three alternative phylogenetic hypotheses: (1) entoptychines and geomyines arose independently from a nonfossorial geomyoid; (2) entoptychines and geomyines arose from a semifossorial geomyoid group; (3) entoptychines and geomyines are independent offshoots of the Heteromyidae.

Entoptychines and the living heteromyids and geomyines share a group of derived features: deep pterygoid fossa opening anterodorsally into the sphenopterygoid canal; anteroventral part of alisphenoid having broad suture with posterodorsal end of maxilla; bone of auditory bulla with highly vesicular internal texture (exception *Dipodomys*); superior angular process of mandible flaring laterally. The primitive features of entoptychines that are modified or lost in living geomyoids occur in regions that have undergone continuous modification in the Geomorpha. They do not bar placement of the subfamily within either the Heteromyidae or Geomyidae. The entoptychines, however, like the geomyines, lack the unique defining characteristics of the Heteromyidae: rostral perforation present at and anterior to infraorbital foramen; frontal roof projecting over orbits; origin of temporal muscle restricted to lateral part of skull roof; coronoid process of mandible small and low. The Entoptychinae and Geomyinae do not appear to be offshoots from the Heteromyidae.

The chief question that remains concerns the placement of the Entoptychinae within or outside of the family Geomyidae. The excellent condition of the type specimens of *G. formosus* and *G. curtus* adds important new data.

The greatest similarity of entoptychines and geomyines is the unique design of the temporal muscle and the bones that support it. The alisphenoid bone extends far dorsally and has a clearly marked site for origin of an anterior, deep division of the muscle. The suture between the alisphenoid and posterodorsal part of the maxilla is very broad. A strong boss is present on the squamosal anterior to the glenoid fossa; it redirects the pull of the posterior part of the temporal muscle to a vertical direction. A shallow pit between the third molar and coronoid process in *Entoptychus* and *Pleurolicus* is the site of inser-

tion of part of the temporal muscle on the mandible. The concavity and inclination toward the incisors of the diastemal palate are shared with geomyines but the degree of both is less. The interparietal is narrow.

Geomyines are more distantly derived from a primitive rodent morphology than are entoptychines. The palate in geomyines is narrower and more grooved. The optic foramen is smaller and together with the anterior alar fissure is farther anterior relative to the cheek teeth. The origin of the internal pterygoid muscle extends farther anteriorly through the sphenopterygoid canal into the orbit. Stapedial and sphenofrontal foramina are closed and lost; the external carotid artery has annexed the branches of the stapedial artery by a series of anastomoses (Bugge, 1971). The temporal muscle inserts in part in a prominent pit between the posterior cheek teeth and the coronoid process of the mandible. The angle and superior angular process are greatly modified. The alveoli of upper and lower incisors are considerably lengthened.

The entoptychines are not primitive geomyines but have unique, derived features of their own. Anteromedial bullar processes meet in the midline in a fashion similar to that of dipodomys, presumably an example of convergence. The mastoid region is inflated and exposed on the dorsal skull roof; the squamosal is thereby emarginated posteriorly.

CONCLUSION

The Entoptychinae and Geomyinae appear to have shared common ancestry and to be most closely related to the Heteromyidae among geomyoid rodents. No fossil skulls are known that would link the two subfamilies through intermediate, primitive morphology.

The living geomyines share a host of derived cranial characters that set them apart from all other geomyoid rodents. At the same time, the amount of cranial diversity within the Geomyinae is low. Wahlert (1985a: 17) stated that "such a long list of derived characters that set a group apart from its closest relatives indicates remote common ancestry, or rapid evolution, or a combination of the two hypotheses. . . . The low level of cranial

differentiation among geomyine genera suggests either recent diversification or long conservation of a successful design after a period of rapid evolution." Yet another hypothesis is suggested by this study of *Gregorymys*: that the fossil record samples only outliers from a Mexican and Central American center of geomyid and possibly geomyoid evolution.

Russell (1968: 558) suggested a Central American origin of modern geomyine lineages. His association of extreme fossorial adaptation with pronounced aridity, however, is questionable. Suitability of soil for burrowing appears to be the chief feature limiting the group; environments that the genera inhabit show a considerable range in altitude, temperature, and moisture. Distribution maps (Merriam, 1895; Hall, 1981) of living geomyines show the greatest variety of genera to be in Mexico and Central America. This variety may well reflect both the diversity of local environments and the span of time that geomyines have lived in the region. Wahlert (in press) pointed out that Miocene heteromyids known from the United States and Canada can be associated, on the basis of cranial evidence, with genera that live today in the same areas. Those with more primitive cranial morphology, *Heteromys* and *Liomys*, are chiefly Mexican and Central American, and this, too, may be the center of heteromyid evolution.

If Mexico and Central America are the center of geomyoid evolution, then fossils from the United States represent colonists of favorable northern environments. This would explain the sudden appearance of specialized entoptychines and later of geomyines in the stratigraphic record. The entoptychines share only some derived characters of living geomyines and perhaps show an early stage in specialization of the family. Their own derived features bar them from ancestral status.

Since the Entoptychinae—certainly *Entoptychus*, *Gregorymys*, and *Pleurolicus*—is a clearly defined taxon that shares many unique derived features with the Geomyinae, we place the two subfamilies within the Geomyidae. The following classification revises that of Wahlert (1985a).

Superfamily Geomyoidea Bonaparte, 1845: 5

Family Florentiamyidae Wood, 1936a: 41

Family Heteromyidae Gray, 1868: 201

Subfamily Heteromyinae Gray, 1868: 201

Subfamily Perognathinae Coues, 1875: 277–278

Subfamily Dipodomysinae Gervais, 1853: 245

Family Geomyidae Bonaparte, 1845: 5

Subfamily Entoptychinae Miller and Gidley, 1918: 434

Subfamily Geomyinae Bonaparte, 1845: 5

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