Skull Morphology and Relationships of Geomyoid Rodents

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ABSTRACT

Analysis of cranial and mandibular morphology, especially the foramina and structures relating to the masticatory musculature, supports monophyly of the living Heteromyidae. The family includes two major divisions, the Heteromyinae on the one hand, and the Perognathinae and Dipodomyinae on the other. Derived features of *Schizodontomys* suggest that the genus may be an early member of the Dipodomyinae. The Heteromyidae and Geomyidae, containing only the Geomyinae, share common ancestry. The Entoptychidae are tentatively placed as the sister group of these two families; the Florentiamyidae appear to be the earliest known branch of the geomyoid clade. The Geomyoidea, which includes these families, and the extinct Eomyoidea comprise the infraorder Geomorpha. A classification of the Geomorpha that reflects these phylogenetic hypotheses is presented.

INTRODUCTION

Two basic theories on the interrelationships of geomyoid rodents have been proposed. In the traditional view the geomyids (pocket gophers), and the heteromyids (kangaroo rats and pocket mice) are two monophyletic groups that are descended from a common ancestor. In the alternative view recent geomyids and their supposed relatives, which are extinct, are derived independently from heteromyids. Published studies have stressed morphology of the teeth and of cranial structures associated with the muscles of mastication; they have not resolved this controversy.

I have attempted to find cranial characters that can be added to the diagnoses of groups of living geomyoids. The new evidence agrees with common, current subdivisions. The family Geomyidae, subfamily Geomyinae, contains four genera—*Geomys, Orthogeomys, Pappogeomys,* and *Thomomys.* The family Heteromyidae contains three subfam-

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ilies that each include two genera: Heteromyinae—*Heteromys* and *Liomys*; Perognathinae—*Chaetodipus* and *Perognathus*; Dipodomyinae—*Dipodomys* and *Microdipodops*. I examined the published descriptions of skulls of extinct taxa to find characters that indicated relationships to these groups. *Entoptychus, Pleurolicus,* and *Schizodontomys* have heretofore been regarded as constituting one or more subfamilies within the Geomyidae. Cranial evidence of the Florentiamyidae (Wahlert, 1983) and the Eomyoidea (Wahlert, 1978) is included in the discussion of phylogenetic relationships; complete data are available in the previous publications. Supposed cranial remains of *Heliscomys* have been described; since their generic assignments are uncertain (Wahlert, 1983, 1984) I have omitted them.

Rodents of the superfamily Geomyoidea and its sister taxon, the extinct Eomyoidea, have a sciuromorphous lateral masseter. The geomyoids are distinguished by bilophodont cheek teeth and the presence of fur-lined cheek pouches that open lateral to the mouth in living forms. The concept of the Geomyoidea, its subdivisions and their contents developed gradually. Important early contributions were summarized by Coues (1877), Wood (1935), and Russell (1968).

The Geomyinae are burrowers that range from western Canada to Panama. Their fossil record extends back to the early Miocene and is restricted to North America with the possible exception of a Miocene fossil from Shantung, China (Li, 1974). The Heteromyidae are small, scampering and jumping rodents that range from southwestern Canada to northern South America. Their fossil record goes back farther in time, to the early Oligocene, and is entirely North American.

The living heteromyids have certain cranial and dental characters that are regarded as primitive among geomyoid rodents. The oldest supposed heteromyid, *Heliscomys*, is more ancient than other undisputed geomyoid fossils. For these reasons systematists expect that the ancestors of all geomyoids were heteromyid-like rodents. The traditional phylogenetic hypothesis, that geomyids and heteromyids are two monophyletic groups descended from a common, heteromyid-like ancestor, developed in the initial decades of the twentieth century. Wood (1935) presented a detailed phylogeny of heteromyids that included the known extinct and living taxa, and he discussed their relationship to geomyids. The first challenge to the traditional view was made by Wilson (1936); he suggested that the extinct and living geomyid subfamilies had separate ancestry in the Heteromyidae. Both hypotheses have been further elaborated by later authors.

Wood (1935) proposed that the Dipodomyinae and Perognathinae are each other's closest relatives and that together they share with the Heteromyinae a common ancestry in the Oligocene genus *Heliscomys*. The crown morphology of geomyid cheek teeth could also be derived from that of *Heliscomys,* but Wood believed the morphologic gap between this genus and the John Day geomyids to be so great and the time interval so short as to preclude the possibility of ancestor-descendant relationship. Recent studies of the Heteromyidae by M. S. Hafner (1982) and Hafner and Hafner (1983) support Wood's hypothesis of relationship among the subfamilies.

A new subfamily of heteromyids, the Florentiamyinae, was described by Wood (1936a). The skull of *Florentiamys loomisi,* on which the subfamily is based, is heteromyid-like but has many primitive features. The tooth crown pattern appears more primitive than that of *Heliscomys.* Wood concluded (*ibid.,* p. 47) that this florentiamyine species could not be "a direct ancestor of the heteromyids, though it might be a structural ancestor." Wahlert (1983) described new specimens of florentiamyids and found a combination of cranial characters indicating that the group is neither ancestral to nor derived from heteromyids.

Wood (1936b) discussed the relationships of the Entoptychinae, an extinct geomyid subfamily of mid-Tertiary age, and remarked that "the evidence of the skulls is at least as strong for geomyine affinities as the evidence of the teeth is for heteromyid ones" (*ibid.,* p. 4). He described a new genus, *Dikkomys,* as representative of an early stage in differentiation of the Geomyinae. This new material did not serve to link the Geomyinae unequivocally to a particular branch of the Entoptychinae, but Wood found some points of similarity to the genus *Pleurolicus.*

Russell (1968) revised the systematics of the Geomyinae. He agreed with Wood on the ancestral position of *Dikkomys*. He derived the geomyines and entoptychines from a hypothetical ancestor. Rensberger (1971, 1973a) divided the early geomyids into two subfamilies, the Entoptychinae and Pleurolicinae, and he added (1973b) the Florentiamyinae to this lineage. In his phylogeny (*ibid.*) *Heliscomys* is shown as the common ancestor of geomyids and heteromyids.

In the alternative phylogenetic hypothesis, the Geomyinae are considered to be derived from the Heteromyidae at a time later than the origin of the Entoptychinae; the heteromyids, which include *Heliscomys*, are a paraphyletic stem group. Wilson (1936) described a late Miocene geomyine, *Pliosaccomys*; he pointed out many heteromyid-like features of the dentition and suggested that the genus may illustrate a morphological stage passed through by the modern Geomyinae. Since the earlier entoptychines are more specialized than this genus in certain respects, Wilson proposed that they might represent an earlier branch from the central stock.

A second challenge to monophyly of the Heteromyidae was posed by Shotwell (1967). On the basis of new specimens, he described the tooth crown patterns in *Pliosaccomys* as a developmental step from that in *Dikkomys*. Morphological similarities led him to conclude that the Geomyinae are closely related to the dipodomyine heteromyids; that *Pleurolicus*, too, resembles the dipodomyines and may be a part of this lineage; and that *Entoptychus* appears to parallel the Geomyinae in structure but is not a close relative.

Lindsay (1972) presented a phylogenetic tree of heteromyids that incorporated many of these ideas. *Heliscomys*, the common ancestor, was placed in the Perognathinae. The Geomyinae and Dipodomyinae were two branches of a distinct lineage. The Heteromyinae comprised a fourth division; inclusion of *Pleurolicus* as the earliest representative of this subfamily appears to have been based on the work of Reeder (1956). The Entoptychinae were shown as a fifth derivative from *Heliscomys*. The Florentiamyinae were omitted.

Rensberger posed a similar challenge to monophyly of the Heteromyidae. He (1971,

p. 66, fn.) stated that assignment of the Entoptychinae to the Geomyidae may be artificial and that the family is then only a grade. He pointed out (*ibid.*, p. 156) that dental similarities suggest independent origin of the modern Geomyinae from the subfamily Heteromyinae.

In this paper I use aspects of cranial morphology to investigate the interrelationships of heteromyid and geomyid subfamilies. I have grounded the study in recent taxa, because skulls are abundant, and the contents of any foramen can be checked by dissection. This information is sufficient to test the monophyly of the living heteromyids. The extinct taxa are examined in the context of the cranial evidence that defines living taxa and the concepts of character polarity in the Geomorpha that were developed in previous publications (Wahlert, 1978, 1983).

ACKNOWLEDGMENTS

and described the anatomy of *Geomys* and *Dipodomys*. He carried out this independent study project under my direction, when he was a biology major at Franklin and Marshall College.

SPECIMENS EXAMINED

All recent specimens are from the collection of the Department of Mammology, American Museum of Natural History, and bear the acronym AMNH. The generic and specific names are in accord with Hall (1981) as it has been updated by Dr. Karl Koopman from the papers of Anderson (1966), Best (1978), Hafner and Hafner (1983), Nader (1978), and Williams and Genoways (1978, 1980, 1981).

Geomys arenareus. 132080, Otero Co., N. Mex. *Geomys bursarius.* 3467, Hennepin Co., Minn.; 6399, Aransas Co., Tex.; 121661, Adams Co., Nebr.; 130275, Brazos Co., Tex. *Geomys personatus.* 2727, 2977, Nueces Co., Tex. *Geomys pinetis.* 23023–23024, Camden Co., Ga.; 23036, Glynn Co., Ga.; 166457, Clarke Co., Ala.; 166538, Pinellas Co., Fla.

Orthogeomys cavator. 18846, Panama. *Orthogeomys cherriei.* 140385, Costa Rica. *Orthogeomys cuniculus.* 206830, Oaxaca, Mexico. *Orthogeomys dariensis.* 37982, Panama. *Orthogeomys grandis.* 123388, Honduras; 167393, 171622, 185055, Oaxaca, Mexico. *Orthogeomys heterodus.* 139272, 139762, Costa Rica. *Orthogeomys hispidus.* 79104, Guatemala; 148005, Tamaulipas, Mexico; 165989, 178729, Oaxaca, Mexico; 177335, Veracruz, Mexico. *Orthogeomys underwoodi.* 123389, Costa Rica.

Pappogeomys bulleri. 4303, Jalisco, Mexico. *Pappogeomys castanops.* 63812, San Luis Potosí, Mexico; 136722, Brewster Co., Tex.; 188613, 188617, Chihuahua, Mexico. *Pappogeomys gymnurus.* 26168, 26184, 26220, Jalisco, Mexico. *Pappogeomys merriami.* 10881, Veracruz, Mexico; 143208, Distrito Federál, Mexico. *Pappogeomys tylorhinus.* 143555, Distrito Federál, Mexico.

Thomomys bottae. 13837, 124268, Merced Co., Calif.; 124230, San Bernardino Co., Calif.; 132034, Otero Co., N. Mex.; 132077, Bernalillo Co., N. Mex. *Thomomys bulbivorous.* 40581, Multonomah Co., Oreg. *Thomomys monticola.* 121122, Tuolumne Co., Calif.

Thomomys talpoides. 123145, Rio Blanco Co., Colo. *Thomomys umbrinus.* 15784, 17513, Chihuahua, Mexico.

Heteromys anomalus. 14755, Venezuela; 34593, Tolima, Colombia; 186715, Trinidad. *Heteromys australis.* 32959, Cauca, Colombia. *Heteromys desmarestianus.* 79248, Guatemala. *Heteromys gaumeri.* 91197, Yucatán, Mexico. *Heteromys lepturus.* 172467, 172482, Veracruz, Mexico.

Liomys adspersus. 147781, Panama. *Liomys irroratus.* 189221, 189223, Oaxaca, Mexico. *Liomys pictus.* 143452, 190271, Oaxaca, Mexico; 24258, Sinaloa, Mexico. *Liomys salvini.* 79271, Guatemala; 126291, 128159, Honduras; 177012, Chiapas, Mexico.

Chaetodipus baileyi. 136973, 136975, Pima Co., Ariz. *Chaetodipus californicus.* 4559, Orange Co., Calif. *Chaetodipus fallax.* 3250, Orange Co., Calif. *Chaetodipus formosus.* 122256, Washoe Co., Nev. *Chaetodipus hispidus.* 3192, Cameron Co., Tex. *Chaetodipus intermedius.* 132458, Lincoln Co., N. Mex. *Chaetodipus nelsoni.* 21009, Durango, Mexico. *Chaetodipus penicillatus.* 139586, San Diego Co., Calif.; 171029, Sonora, Mexico. *Chaetodipus pernix.* 25902, Sinaloa, Mexico. *Chaetodipus spinatus.* 31838, Baja Calif., Mexico.

Perognathus amplus. 136987, Pima Co., Ariz. *Perognathus fasciatus.* 6708, Shannon Co., S. Dak. *Perognathus flavescens.* 6692, Navajo Co., Ariz. *Perognathus flavus.* 8755, Bexar Co., Tex.; 132441, Colfax Co., N. Mex. *Perognathus longimembris.* 138595, Kern Co., Calif. *Perognathus parvus.* 33505, Malheur Co., Oreg.

Dipodomys agilis. 94303, San Diego Co., Calif. *Dipodomys deserti.* 139605, Yuma Co., Ariz.; 145389, Pinal Co., Ariz. *Dipodomys heermanni.* 124158, San Luis Obispo Co., Calif. *Dipodomys merriami.* 184199, Pima Co., Ariz.; 188637, Chihuahua, Mexico. *Dipodomys ordii.* 39815, Malheur Co., Oreg.; 124717, Beaver Co., Utah. *Dipodomys panamintinus.* 138663, Tulare Co., Calif. *Dipodomys spectabilis.* 145390, Pinal Co., Ariz. *Dipodomys venustus.* 145108, Monterey Co., Calif.

Microdipodops megacephalus. 135602, 135610, 135612, Washoe Co., Nev.; 140689, Elko Co., Nev.

Mr. Timothy Hall dissected a specimen of *Geomys bursarius* from Douglas Co., Kansas, and of *Dipodomys ordii* from Thomas Co., Nebraska. I dissected a specimen of *Thomomys bottae.*

LIVING GEOMYOIDS

CRANIAL FORAMINA

A guide to the foramina in each of the four living subfamilies is presented in figures 1 through 4. A small, median interpremaxillary foramen is present immediately behind the incisors in geomyines; the structure is lacking in heteromyids. The incisive foramina of geomyines, heteromyines, and perognathines are situated in the anterodorsal part of a pair of depressions in the diastema; the length of these deep openings is 15 percent or less of the diastemal length. A spur of the maxilla reaches the back of each foramen in most specimens; in others the median and lateral parts of the premaxilla meet behind the foramina, and the maxilla is excluded from their margins. The posterolateral extensions of the premaxillaries are usually longer than the median spine of that bone between the two foramina. In dipodomyines the incisive foramina are at the surface in the diastema and occupy from 22 to 38 percent of its length; the premaxillary-maxillary suture intersects the lateral margins of the incisive foramina near the middle.

The posterior palatine foramina are in the maxillary-palatine suture in all taxa except *Microdipodops,* where they are within the palatine bones. The maxillary-palatine suture is fused in many of the geomyine specimens. The major pair of these foramina ranges in position through a zone that extends from the middle of the first molar to the junction of the second and third molars. In geomyines a deeply incised furrow runs forward from each foramen; in some specimens excavation of the palatine also extends posteriorly from each foramen. The palate in heteromyids is flat or has shallow furrows. A variable number of small foramina commonly occur in the palate of geomyoids.

The back of the palate is peculiar. The palatine bones extend posteriorly and form a pair of depressions, the parapterygoid fossae, which are separated by a median ridge. The fossae are dorsal to the level of the anterior part of the palate. They are shallow in *Microdipodops* and shallow and anteroposteriorly short in *Perognathus.* Merriam (1895) described these structures in the Geomyinae but did not mention their function. Our dissections of *Geomys* and *Thomomys* revealed that the fossae house salivary glands. In *Dipodomys* an anterior part of the internal pterygoid muscle originates here (Howell, 1932, p. 412). Foramina occur in the region. In most geomyoid specimens the posterior maxillary foramen is present laterally in the maxillary-palatine suture just posterior or medial to the third molar. The foramen is usually small and is underthrust by a flange of the maxilla; the foramen is absent in some specimens. A foramen is always present in the anterior end of each fossa. In geomyines it plunges dorsally or anterodorsally and appears to join the canal of the descending palatine artery. Hill (1935, p. 124) stated that in geomyines it transmits the palatine vein. In heteromyids the foramen opens dorsally into the anterior part of the sphenopterygoid canal. Hartman (1980) stated that this parapterygoid foramen transmits a vein in *Dipodomys.* A medial foramen in the wall separating the fossa and nasal passage is common in *Liomys* and *Heteromys* and occurs in some geomyine specimens. It appears to have been covered by membrane; in a few specimens it is present on only one side. In geomyines the roof of the fossa ranges from solid to lacy. In most geomyine specimens, but not in heteromyids, a furrow passes from the fossa onto the palate; in some specimens it is covered by bone and forms a short canal through the back of the palate. Dissection of *Geomys* and *Thomomys* revealed that the palatine vein runs posteriorly through the furrow to join the internal maxillary vein. This route is an alternative to the primitive, dorsal course in which the vein ascends through the posterior maxillary foramen, and it may account for the small size and variability of the aperture.

The infraorbital foramen is not visible in front view, because its lateral margin is flush with the wall of the snout. The infraorbital canal in geomyines is ventral or medial to the long incisor alveolus, whereas in heteromyids, which have a shorter incisor, it is ventral to the alveolus. The infraorbital canal emerges
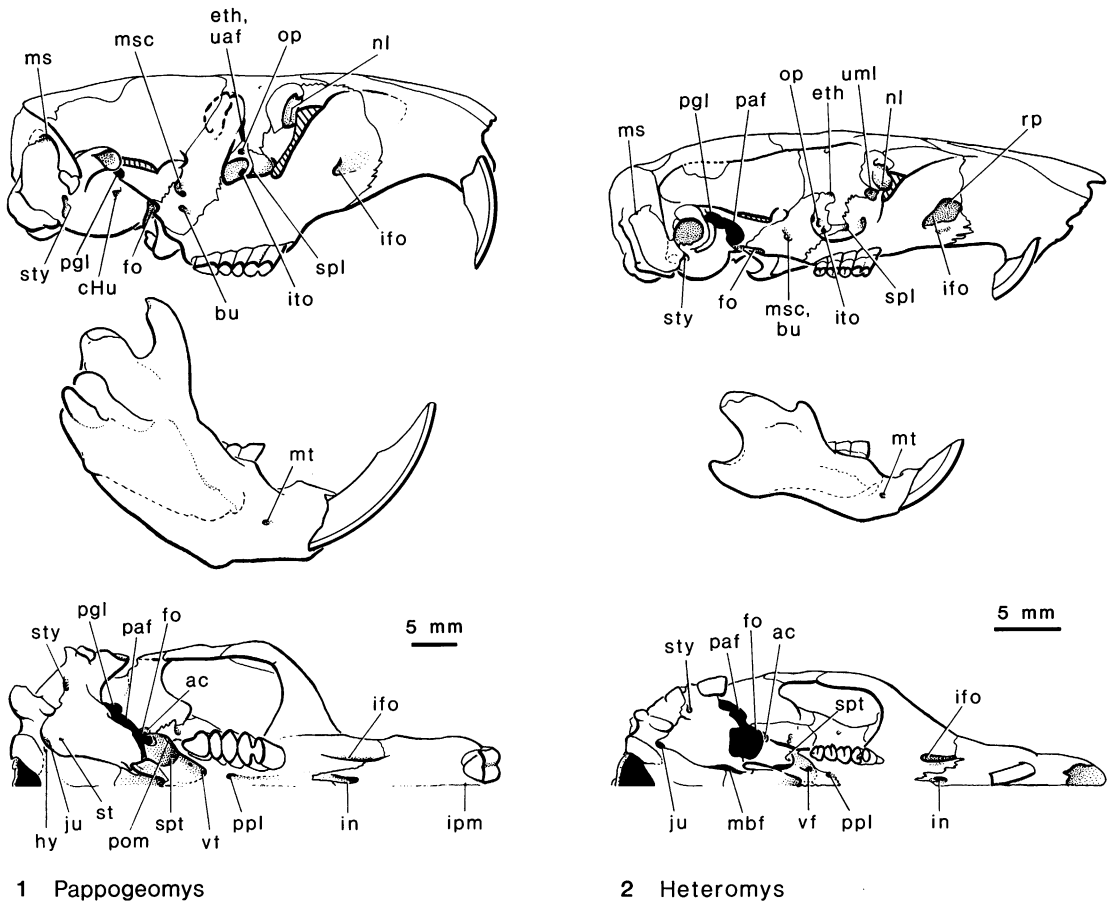
1 Pappogeomys

2 Heteromys

FIG. 1. *Pappogeomys merriami*, AMNH 143208.
FIG. 2. *Heteromys lepturus*, AMNH 172467. Skulls. Cross hatching indicates imagined cut through bone.

Abbreviations: For foramina and other structures (as named): ac, posterior aperture of alisphenoid canal; asq, anterior squamosal; bu, buccinator; cHu, canal of Huguier; eth, ethmoid; fo, foramen ovale; foa, accessory foramen ovale; hy, hypoglossal; ifo, infraorbital; in, incisive; ipm, interpremaxillary; ito, interorbital; ju, jugular; mbf, fissure medial to bulla; ms, mastoid; msc, masticatory; mt, mental; nl, nasolacrimal; op, optic; paf, post-alar fissure; pgl, post glenoid; pom, posterior maxillary; ppl, posterior palatine; rp, rostral perforation; spl, sphenopalatine; spt, sphenopterygoid canal; spv, sphenopalatine vacuity; st, stapedial; sty, stylomastoid; t, temporal; uaf, unossified area between alisphenoid and frontal bones; uml, unossified area between maxillary and lacrimal bones; vf, venous foramen in parapterygoid fossa.

at a depression in the side of the snout. In geomyines the depression has a medial wall, but in heteromyids the bone always is perforated; the prominent hole in the maxilla was covered by membrane in life. The premaxillary-maxillary suture is anterior to the depression in most geomyine specimens. In heteromyines, *Microdipodops,* and some specimens of perognathines the suture runs into the perforation, whereas in *Dipodomys*

and other perognathines a thin lamina of the maxilla surrounds the anterior end of the perforation. The scar of the superficial masseter is spread ventral and posteroventral to the foramen in geomyines. It is more restricted in most heteromyid specimens, and the scar is confined ventral to the foramen. The length of the infraorbital canal in most geomyines is between 15 and 20 percent of the condylobasilar length; in *Thomomys* the range is
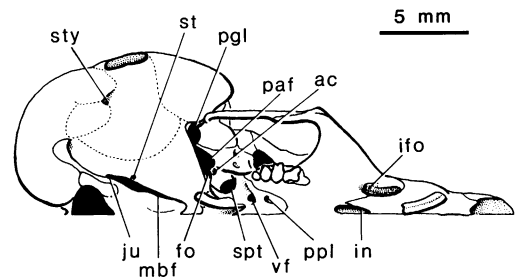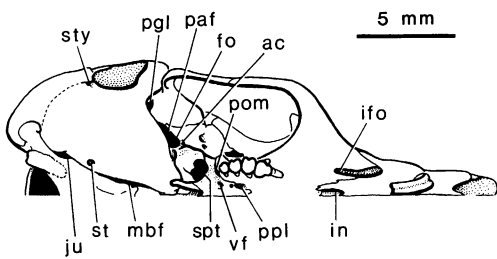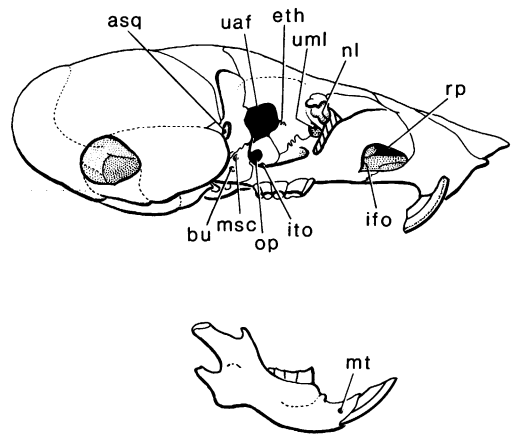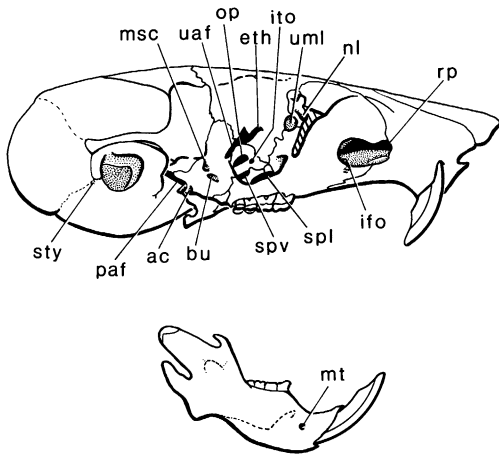
3 Perognathus   4 Microdipodops

FIG. 3. *Perognathus amplus,* AMNH 136987.
FIG. 4. *Microdipodops megacephalus,* AMNH 135612. Skulls. Abbreviations as in figure 2.

from 11 to 15 percent, and in *Liomys* from 19 to 24 percent. The anterior alveolar foramen is hidden deep within the canal.

The lacrimal foramen is anterodorsal to the orbital aperture of the infraorbital canal. The lacrimal spine overhangs it to a varying degree. The descending channel and lateral margin of the foramen are formed by the lacrimal bone posteriorly and by the maxilla anteriorly. In geomyines the initial course of the lacrimal canal is ventral or posteroventral. The canal passes ventrolateral to the end of the incisor alveolus, which extends low and terminates at or in the root of the zygoma; at this point the lacrimal canal is lateral to the infraorbital canal. The lacrimal canal then ascends anteriorly until it is dorsal to the infraorbital foramen, where it may form a bulge

in the rostral depression. In heteromyids the incisor alveolus ends high on the snout and does not obstruct passage of the lacrimal canal. The canal has an anterior orientation; it begins dorsolateral to the posterior entrance to the infraorbital canal. The infraorbital canal is visible through the thin wall of the rostrum and can be seen to pass dorsomedial to the perforation. A nonossification is common in geomyines and heteromyids at or near the intersection of the frontal-maxillary suture and the edge of the lacrimal bone. It is usually absent in *Dipodomys.*

The sphenopalatine foramen is medial to the alveolar capsules that protrude into the orbit in geomyines. Its position in living forms ranges from just anterior to the capsule of the first molar to the space between the capsules

of the first and second molars. In heteromyids the sphenopalatine is dorsal to a portion of the range from the junction of the fourth premolar and first molar to the posterior part of the first molar. The maxilla always forms the anterior and ventrolateral boundaries of the aperture and never surrounds the entire opening. The orbital lamina of the palatine reaches the back of the foramen in most specimens; the frontal and orbitosphenoid bones participate in the margin of the foramen in some specimens. Variation in the number of bones bounding the sphenopalatine foramen is great, and no taxonomic significance can be assigned to any particular combination of them.

Ossification of the dorsal part of the orbitosphenoid and posteroventral part of the orbital lamina of the frontal is commonly incomplete in geomyines. This aperture is confluent ventrally with the optic foramen and dorsally with the ethmoid foramen in many specimens. Commonly, it extends ventrally between the orbitosphenoid and alisphenoid bones and is continuous with the anteriorly enlarged orbital fissure. Among heteromyids complete orbital walls are found in *Heteromys* and *Liomys.* The nonossified area is present in *Microdipodops* and some specimens of *Dipodomys,* and it is large in all perognathines. The orbital fissure is large in all heteromyids, and a thin bar of bone separates it from the posterior part of the optic foramen.

The ethmoid foramen is dorsal to a zone that extends from the middle of the first molar to the middle of the second. It is united with the nonossified area in many geomyine specimens, in perognathines, *Microdipodops,* and many *Dipodomys.* In other geomyine and *Dipodomys* specimens it is within the frontal bone. In heteromyines it is in or near the frontal-orbitosphenoid suture.

The optic foramen in *Heteromys* and most geomyine specimens is less than 1 mm in diameter, about 1 mm in *Liomys,* and larger than 1 mm in perognathines and dipodomyines. It is completely surrounded by the orbitosphenoid in heteromyids except some perognathine specimens; the degree to which it is enclosed varies in geomyines. The position of the optic foramen ranges from above the junction of the first and second molars to

the middle of the second molar in geomyines. It is farther posterior in most heteromyids and ranges from the junction of the second and third molars to a position posterior to the third. An interorbital foramen is present in the orbitosphenoid bone anteroventral or ventral to the optic foramen in geomyines and heteromyines. The interorbital foramen is present in a few specimens of perognathines; this suggests that it may be united with the large optic foramen in the rest of the perognathine specimens and in the dipodomyines. Hartman (1980) called this aperture the presphenoid foramen; he observed it and recorded its variability in *Dipodomys.* The lateral sides of the orbitosphenoid are flattened where the internal pterygoid muscle originates. In heteromyines the area is posteroventral to the optic foramen; in some dipodomyines it extends farther anteriorly. In geomyines, too, it extends anteriorly and is ventral to the optic foramen. The region is not sculpted in this fashion in perognathines.

The dorsal palatine foramen is hidden within the anterior-alar fissure (formerly termed sphenoidal fissure) in geomyines and is medial or anteromedial to the anterior edge of the fissure in heteromyids. In most specimens the foramen is between the alveoli of the second and third molars.

The sphenofrontal foramen is lacking in all but *Dipodomys* where it may be the large opening in the dorsal curve of the anterior-alar fissure. The content of the opening has not been verified by dissection. The foramen is not seen, but may be included in the large orbital nonossification in *Perognathus.* Both of these heteromyid genera have a stapedial artery that retains all three branches (Bugge, 1971, p. 347), and the foramen is to be expected. Nutritive foramina are present in the maxillary floor of the orbit.

The ventral root of the anterior-alar fissure, which is formed by the maxilla and alisphenoid bones, arises above a zone that ranges from the second molar alveolus to the junction of the second and third molar alveoli in geomyines. It arises dorsal or slightly anterior to the third molar in heteromyines, usually just posterior to the third molar in perognathines and *Microdipodops,* and posterior to that tooth in *Dipodomys.*

The internal maxillary artery runs within

the alisphenoid canal up to the level of the masticatory foramen where its medial wall ends, and the passage joins the sphenopterygoid canal. This anterior opening can be seen within the masticatory foramen in geomyines, *Heteromys,* and some *Liomys.* In dipodomyines and perognathines the enclosed part of the alisphenoid canal is extremely short. Masticatory and buccinator foramina are separated in *Microdipodops,* most specimens of geomyines and many perognathine specimens. The foramina are joined as a single aperture in heteromyines and *Dipodomys.* Hartman (1980) incorrectly called this the foramen ovale; he noted that it is occasionally divided in *Dipodomys.* The canals to these foramina open laterally from the enclosed part of the alisphenoid canal.

The lateral pterygoid flange forms the lateral wall of the sphenopterygoid canal. In living geomyoids it usually fails to reach the auditory bulla, and the accessory foramen ovale is rarely enclosed posteriorly by bone. The alisphenoid canal enters the bone anterior to the foramen ovale and just medial to the anterior margin of the accessory foramen ovale. In all specimens the foramen ovale is open posteriorly, and thus is bounded by the auditory bulla. Usually the foramen ovale is continuous laterally with an opening that includes the post-alar fissure and postglenoid foramen. In dissected specimens and in some of the skulls examined, a membrane covers the fissure. In some specimens of *Geomys* and in one of *Liomys* a spur of the alisphenoid dorsolateral to the foramen ovale reaches the bulla and separates the foramen ovale from the post-alar fissure. In most geomyine specimens this spur is present in varying degree but does not reach the bulla. Occasionally the postglenoid foramen is separate and surrounded by the squamosal and the bulla; it is not entirely enclosed by the squamosal.

The sphenopterygoid canal is a prominent feature of the pterygoid region. The internal pterygoid muscle arises from its walls and from a flattened area on the medial wall of the orbit posteroventral to the optic foramen. In *Dipodomys* a large vein emerges from the canal (Howell, 1932, p. 480). The position of the entrance to the transverse canal is variable. In some geomyines it is at the base of the hamular process in the posteromedial wall

of the sphenopterygoid canal; in others it begins laterally, in the medial wall of the alisphenoid canal. It is lacking in some geomyine and most heteromyid specimens.

The carotid foramen is situated medial to the auditory bulla near the junction of the basioccipital and basisphenoid bones. In perognathines it is usually behind the suture. A slight gap between the anterior part of the bulla and the medial basicranial elements enlarges the foramen in heteromyids. The gap is very long in dipodomyines and includes the jugular foramen.

The internal structure of the bulla is vesicular in all geomyoids except dipodomyines. The vesicles are open into the middle ear cavity. The vesicular texture is most extensive in perognathines. The bulla in dipodomyines is made of a thin lamella of bone, but this is achieved through remodeling of a trabecular precursor (Webster, 1975), which is probably the beginning of vesicular texture in other taxa. The auditory bullae are strikingly enlarged in perognathines and are enormous in dipodomyines. In perognathines the anteromedial parts of the bullae, which house the eustachian tubes, approach one another and are appressed to the ventral side of the basisphenoid; in a few specimens these extensions meet in the midline. In dipodomyines the extensions meet in a broad junction and are similarly applied to the surface of the basisphenoid; in these rodents this is the only contact of the anterior and medial sides of the bulla with the rest of the skull.

The stapedial foramen is absent in heteromyines and absent or marked only by a pit or tiny perforation in geomyines. The foramen is of moderate size in perognathines and dipodomyines and enters the medial wall of the bulla anteroventral to the jugular foramen. In dipodomyines it is quite far anterior, and the course of the stapedial canal is posterolateral. Bugge (1971) observed that in *Perognathus* and *Dipodomys* the stapedial artery supplies blood to the dura mater, orbit, and upper and lower jaws; this is the primitive pattern in rodents. In *Geomys* the external carotid has, via anastomosis, taken over the entire area of stapedial supply. Bugge did not examine the carotid circulation in heteromyines.

The jugular foramen is a lenticular slot be-

tween the basioccipital and the postero-medial part of the auditory bulla and periotic. It is open anteriorly into a gap between the anterior parts of these elements in dipodomyines. The hypoglossal foramen is single or multiple and faces anterolaterally toward the jugular foramen; in some specimens it is hidden by an anterolaterally projecting flange from the ventral surface of the basioccipital. Temporal foramina are absent in most specimens. Dipodomyines have one or two foramina in the squamosal bone dorsal to the zygomatic root; they are just in front of the anterior bulge of the inflated auditory bulla. I have named the aperture the anterior squamosal foramen; Hartman (1980) called it the squamosal foramen.

The stylomastoid foramen is between the bony auditory tube and the mastoid. These two elements are often fused. In many specimens a furrow leads ventromedially from the foramen; it runs along the anterior edge of the paroccipital process and approaches the jugular foramen. The feature is not seen in dipodomyines. The mastoid foramen in geomyines is a thin slit dorsal to the medial part of the mastoid on the face of the occiput, and it is overhung by the edge of the occipital bone in many specimens. The foramen is minute or absent in heteromyids. Tiny condyloid foramina are variable in their presence or absence.

OTHER CRANIAL FEATURES

The adductor musculature of the jaw has shifted anteriorly in geomyoids relative to that in primitive rodents. The sciuromorphous condition in which the origin of the lateral masseter extends anteriorly onto the rostrum illustrates this point. The shift is apparent also in the temporal and internal pterygoid muscles and in the insertion of the lateral masseter on the mandible. The origin of the internal pterygoid muscle is described above in conjunction with the orbit and the sphenopterygoid canal.

The origin of the temporal muscle differs among geomyoids. The muscle is extensive in geomyines; a median sagittal crest is common but not universal in the family. A pair of temporal crests occurs in some specimens of each genus and is most common and far-

thest lateral in *Thomomys*. The temporal muscle is smaller in heteromyids. Temporal crests are far lateral in heteromyines, and the narrow origin of the muscle reaches the back of the squamosal. The inflated bulla in perognathines and dipodomyines restricts the muscle origin still more, and it does not extend posteriorly beyond the zygomatic root.

The temporal muscle is modified uniquely in geomyines. Dissection of *Geomys* and *Thomomys* revealed that a tough, smooth capsule of connective tissue covers the protuberance of the squamosal anterior to the glenoid fossa. A part of the posterior division of the temporal muscle rides over this pulley-like structure, and the direction of its force is made vertical to the skull axis. The deep anterior part of the temporal muscle arises in a unique fossa on the posterior wall of the orbit. The alisphenoid bone forms most of the fossa and ascends almost to the skull table; it is separated from the parietal by the long anterodorsal extension of the squamosal. The fossa is a single channel in *Thomomys*. In the other living geomyines a vertical ridge divides the dorsal part of the fossa in two.

In heteromyines and perognathines the protuberance on the squamosal is present but weaker than in most geomyids; its function has not been verified by dissection. The structure is not present in dipodomyines. In heteromyids there is no furrow in the orbit that would indicate the presence of a special anterior part of the temporal muscle; the alisphenoid bone does not ascend to the skull table, and it usually meets the squamosal near the middle of the vertical dimension of the orbit.

The mandibles of heteromyids and geomyines are markedly different. In heteromyids the angle of the jaw is a distinct flange that curves ventrolaterally from the body of the ramus. It terminates posterodorsally in a flaring superior angular process. Howell (1932, p. 411) observed that in *Dipodomys* the posterior part of the deep lateral masseter, which he termed masseter posterior, inserts on the lateral and medial surfaces of this process, which he distinguished from the angle. The region is similar in other heteromyids. Nikolai and Bramble (1983) proposed that the eversion of the angular process reduces

crowding of the mandible by the enlarged bullae in perognathines and dipodomyines. Since a somewhat everted angle occurs in heteromyines, which lack great bullar inflation, the design may be associated primarily with a certain mode of chewing and gnawing. In geomyines the angle is reduced and does not form anything more than a ridge on the body of the ramus; the superficial masseter and internal pterygoid insert here on the lateral and medial sides of the jaw, respectively. The superior angular process is robust and projects laterally from the back of the ramus; the insertion of the posterior part of the deep lateral masseter surrounds it. Hill (1937, p. 104) called the structure the angular process, and Merriam (1895) labeled it the angle in his figures. Such usage is incorrect, since the true angle is associated with insertion of the superficial masseter and internal pterygoid muscles.

The coronoid process, on which the temporal muscle inserts, is strong in geomyines and extends farther dorsally than the condyloid process. It is much weaker and less extensive in heteromyids. In geomyines the insertion of the temporal muscle is primarily on the medial side of the process and in a prominent depression (the basitemporal fossa of Russell, 1968) that extends anteriorly between the process and the last two molars. The depression is shallowest in *Thomomys,* and it is lacking in heteromyids. In some specimens of *Dipodomys* a depression is present, but it is associated with the mandibular foramen. In geomyines this foramen is posterior to the depression.

The alveolus of the lower incisor is long and produces a lateral bulge on the mandible. In geomyines the bulge is between the superior angular process and the condyloid process; in heteromyids it is farther anterior. The posterior part of the medial masseter inserts between the alveolar bulge and the condyloid and coronoid processes in geomyines; the insertion is usually marked by a pit in geomyines, but it is not a distinct structure in heteromyids.

The insertions of the lateral and medial divisions of the masseter create a shallow masseteric fossa on the lateral side of the mandible. The fossa is roughly triangular, and an apex marks the anteriormost extent of the insertion. The single mental foramen is anterior to this point. In all geomyoids the apex is farther forward than in primitive rodents. In geomyines it is ventral to the anterior part of the fourth premolar. In heteromyids the apex is usually extended by a ridge or is itself anteroventral to that tooth.

EXTINCT TAXA

In addition to the florentiamyids, described elsewhere (Wahlert, 1983, 1984), cranial remains of three other extinct geomyoid taxa are known in detail sufficient for inclusion in this study. *Entoptychus* occurs in the early Miocene John Day Formation of Oregon, and *Pleurolicus* in slightly older levels of the same formation. Rensberger (1971, 1973a) and Wahlert (1972) described these skulls. *Schizodontomys* of early middle Miocene age occurs in both the upper part of the John Day Formation and strata of similar age in South Dakota; Rensberger (1973a) described a partial skull, and Munthe (1981) expanded this description with a more complete cranium and partial skeleton. All of these taxa bear the hallmarks of the Geomyoidea, but they have a variety of specializations.

Entoptychus (fig. 5) retains certain primitive characters that do not occur in the living geomyines and heteromyids. The accessory foramen ovale (identified by Rensberger as the foramen ovale) is enclosed within the alisphenoid; the foramen ovale appears to be between the pterygoid region and the bulla. The alisphenoid reaches the bulla and separates the foramen ovale from the post-alar fissure. Rensberger (1971) said that the sphenopterygoid canal is lacking. I have disagreed (1972), but the region is damaged in all specimens that I have seen. This detail is an important point in placement of the group and should be reexamined. The postglenoid foramen is within the squamosal bone, and a temporal foramen is present above the posterior part of the zygomatic root.

Entoptychus shares certain derived features with the heteromyids and geomyines. A temporal tuberosity is present on the squamosal bone anterior to the glenoid fossa. The superior angular process projects laterally from the mandible.

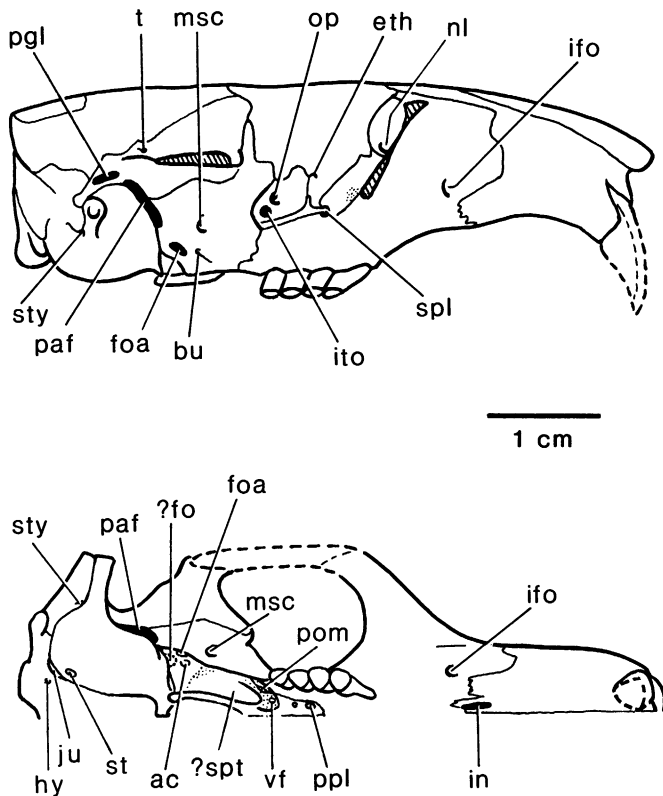*Entoptychus* has derived characters of its

FIG. 5. *Entoptychus* sp., University of California Museum of Paleontology no. 65251. Skull. Abbreviations as in figures 1 and 2. Modified from Wahlert (1972, fig. 19).

own. The posterior part of the squamosal is narrow above the auditory tube. The auditory bullae, which are not trabecular, are swollen ventrally; anteromedial processes from opposite sides touch in the midline just anterior to a peculiarly swollen region of the basioccipital and basisphenoid. Rensberger reported that a narrow slit separates the bulla and basioccipital; it is confluent posteriorly with the jugular foramen. A fossa for insertion of the temporalis muscle occurs on the mandible lateral to M_3; it is not as pronounced as that of geomyines.

The skull of *Pleurolicus* is not as fully known. Rensberger stated that the pterygoid fossa is shallow. The postglenoid foramen is situated between the squamosal and the auditory tube. There is a single temporal foramen. A large temporal tuberosity can be seen on the squamosal anterior to the glenoid fossa in Rensberger's figure and plates of skulls.

The superior angular process projects laterally. Specialization of the auditory and basicranial regions is like that of *Entoptychus*; the bullae are somewhat more inflated. Rensberger also described skeletal remains and found many features indicating fossorial specialization in *Entoptychus* (1971, p. 140) and *Pleurolicus* (1973a, p. 81).

Schizodontomys is superficially similar to these two genera, but Munthe (1981) noted important differences. The infraorbital foramen appears to be enlarged by an unossified area anterior to the canal. The sphenopterygoid canal is present posterior to the shallow parapterygoid fossa. The foramen ovale is enlarged by a gap between the pterygoid region and the bulla. The accessory foramen ovale and temporal foramen are lacking. The postglenoid foramen, between the squamosal bone and the auditory bulla, is confluent with the post-alar fissure; the alisphenoid bone sepa-
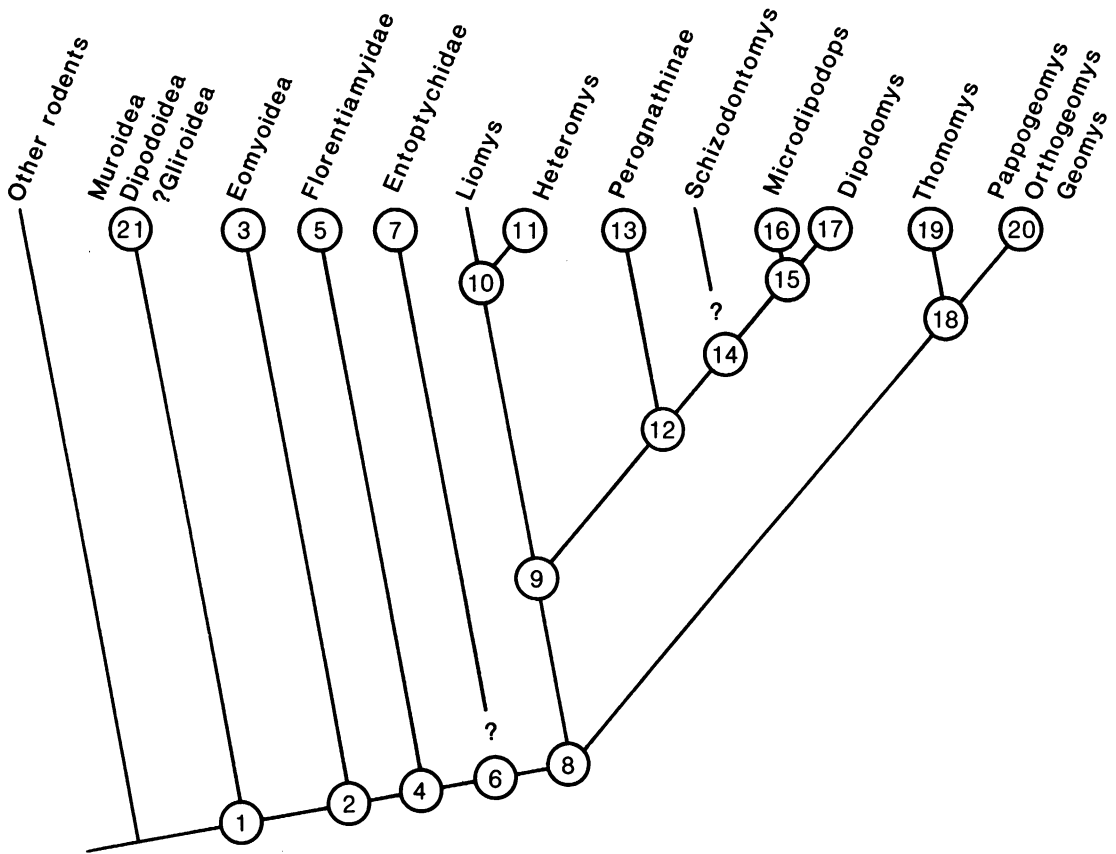
FIG. 6. Proposed relationships of the Geomyoidea. Numbers at nodes correspond to numbers in discussion.

rates this aperture from the foramen ovale. Masticatory and buccinator foramina are confluent. As in *Entoptychus* and *Pleurolicus* there is a stapedial foramen; the bony tube for the artery is preserved crossing the promontorium. The auditory bullae are inflated and meet in a broad junction in the ventral midline, but the basioccipital is not swollen behind the junction. Inflation of the auditory region exceeds that of *Entoptychus* and *Pleurolicus,* since the mastoid is swollen posteriorly and dorsally. The posterior part of the squamosal is very narrow above the auditory tube. There is no area of the orbit specialized for origin of a part of the temporal muscle. The angle of the jaw exhibits gentle lateral bending and the superior angular process is not set apart. The extent of the incisors is as in heteromyids. Munthe described the skeleton of *Schizodontomys* and found many features indicating that it was at least quadrupedally saltatorial; she pointed out that these specializations make it morphologically intermediate between *Heteromys* and *Dipodomys.*

DISCUSSION

The data of cranial foramina and other characters that were observed support the traditional hypothesis of relationships among living geomyids. The cladogram (fig. 6) and following summary of shared, derived characters add to the basis of this phylogeny and include data from extinct taxa. Numbers in the list correspond to numbered nodes in the cladogram. Additional characteristics of the living taxa may be found in the recent analyses by Hall (1981); Rensberger and Wood best summarized other characters of the

extinct taxa in the papers cited. The spectrum of primitive and derived conditions of characters is based on comparison with *Paramys, Sciuravus,* and a sample of muroid rodents (Wahlert, 1974, 1978).

1. Myomorpha: Carotid canal short, near basisphenoid-basioccipital junction; entrance to transverse canal separated from alisphenoid canal; zygomatic arch slender; incisor enamel with uniserial Hunter-Schreger bands in the *portio interna.*

2. Geomorpha: Fossa on rostrum for anteriorly extended lateral masseter (sciuromorphy); long, low infraorbital canal sunk into side of rostrum at anterior end; sphenopalatine foramen far anterior, dorsal to M^1; interorbital foramen present (apparently united with optic foramen in many perognathine and dipodomyine specimens); wear on cheek teeth forming transverse lophs.

3. Eomyoidea: Complex Schmelzmuster in enamel of lower incisors with uniserial Hunter-Schreger bands longitudinal; sphenopalatine foramen completely surrounded by maxilla; masticatory and buccinator foramina united with accessory foramen ovale; temporal foramen absent.

4. Geomyoidea: Incisive foramina short, 30 percent or less of diastemal length (exception, Dipodomyinae); parapterygoid fossae, usually with foramen, present between palate and pterygoid fossae; auditory bulla forming back of foramen ovale; cheek teeth bilophodont; transverse lophs in upper and lower cheek teeth widened by addition of styles.

5. Florentiamyidae: Special process from palatine, together with alisphenoid, forming edge of anterior-alar fissure; canal for descending palatine vein lateral to anterior-alar fissure; optic foramen larger than 1.0 mm; masticatory and buccinator foramina united with accessory foramen ovale; entostyle of upper molars elongated anteroposteriorly and blocking lingual end of transverse valley.

6. Unnamed node: Pterygoid fossa deep; superior angular process of mandible flared laterally.

7. Entoptychidae: Auditory bullae inflated ventrally with anteromedial processes meeting in midline; gap between bulla and basioccipital; contiguous parts of basioccipital and basisphenoid swollen ventrally.

8. Unnamed node: Fur lined cheek pouch-es present outside the mouth (this character may have arisen at a lower node); incisive foramina 15 percent or less of diastemal length (exception, Dipodomyinae); pterygoid fossa containing entrance to sphenopterygoid canal; origin of internal pterygoid muscle extending through sphenopterygoid canal toward orbit; posterior margin of accessory foramen ovale not ossified, and lateral pterygoid flange often failing to reach auditory bulla; postglenoid foramen between squamosal bone and auditory bulla, often confluent with post-alar fissure; temporal foramen absent; auditory bullae with highly vesicular texture (exception, Dipodomyinae).

9. Heteromyidae: Large perforation of rostrum at and anterior to infraorbital foramen; interpremaxillary foramen absent; posterior end of optic foramen narrowly separated from orbital fissure; mastoid foramen minute or lacking; origin of temporal muscle restricted to lateral part of skull roof; coronoid process on mandible small and low; insertion of masseter on mandible usually marked by ridge extending anteroventral to P_4.

10. Heteromyinae: Ventral root of anterior-alar fissure rising above M^3; masticatory and buccinator foramina united; stapedial and sphenofrontal foramina absent.

11. *Heteromys:* Optic foramen smaller than 1.0 mm.

12. Unnamed node: Optic foramen larger than 1.0 mm; nonossification common dorsal to orbitosphenoid; auditory bullae highly inflated with anteroventral processes approaching each other and touching basisphenoid; squamosal bone extending as thin process posteriorly above bony auditory meatus; origin of temporal muscle restricted chiefly to orbit.

13. Perognathinae: Small skull; large orbital nonossification usually including ethmoid foramen.

14. Dipodomyinae: Auditory bullae further inflated, especially dorsal part; anteroventral processes of bullae meet in broad junction in midline.

15. Unnamed node: Incisive foramina elongated posteriorly with premaxillary-maxillary suture intersecting lateral margins near middle; posterior part of squamosal lacking; postglenoid foramen absent; anterior

squamosal foramen present; further inflation of auditory bullae; gap present between bulla and medial basicranial elements and including carotid foramen at anterior end and jugular foramen at posterior; stapedial canal entering auditory region anterior to its usual position.

16. *Microdipodops*: Posterior palatine foramina in palatine bones (may be primitive condition); bullae slightly more inflated than in *Dipodomys* (Webster and Webster, 1975).

17. *Dipodomys*: Masticatory and buccinator foramina usually united; cheek teeth hypsodont.

18. Geomyidae: Diastema strongly arched; palate deeply furrowed anterior to posterior palatine foramina; furrow or canal connecting parapterygoid fossa and palate; initial course of lacrimal canal ventral; optic foramen smaller than 1.0 mm and far anterior, dorsal to a zone from the junction of M^1M^2 to M^2; nonossification common dorsal to orbitosphenoid; ventral root of anterior-alar fissure above a zone from alveoli of M^2 to M^2M^3 junction; dorsal palatine foramen hidden within anterior-alar fissure; anteromedial opening of alisphenoid canal visible within masticatory foramen; sphenofrontal foramen lacking; stapedial foramen and functional artery lacking; origin of internal pterygoid muscle extending anteriorly through sphenopterygoid canal as far as or beyond optic foramen; posterior part of maxilla meeting anteroventral part of alisphenoid in long suture; boss on squamosal redirecting pull of posterior part of temporal muscle; deep anterior part of temporal muscle arising in broad vertical fossa in orbit; alisphenoid bone extended dorsally almost to skull table and sculpted by fossa for temporal muscle; insertion of temporal muscle in broad pit between coronoid process of mandible and posterior cheek teeth; angle reduced to ridge on mandible; robust superior angular process projecting laterally below condyloid process; alveoli of upper and lower incisors with great posterior extent.

19. *Thomomys*: Infraorbital canal relatively short.

20. *Geomys, Orthogeomys, Pappogeomys*: Fossa on alisphenoid for origin of deep anterior part of temporal muscle divided in two by vertical ridge in dorsal part.

21. Other Myomorpha: Enlarged infraor-bital foramen; lacrimal foramen low in maxilla, medial or anteromedial to infraorbital foramen.

It is tempting to treat sciuromorphy as a primary character and unite the eomyoids, geomyoids, sciuroids, and castoroids in a single taxonomic group as did early mammalogists. However, sciuromorphy, the extension of the origin of the lateral masseter onto the rostrum, has arisen more than once among rodents. The extinct ischyromyoid *Titanotheriomys* is sciuromorphous (Wood, 1976), but it is not related to any of the groups mentioned above. Anterior extension of the origin of the lateral masseter is also a component of the myomorphous condition seen in muroids. The living sciurids exhibit a range in development of the infraorbital canal that makes them more primitive than the known extinct and living Geomorpha. The canal is no more than a hole in the maxillary root of the zygoma in *Protoxerus, Eutamias,* and *Tamias*; it is a long, enclosed passage in most other sciurids (Wahlert, 1972). Emry and Thorington (1982) have described the Oligocene genus *Protosciurus* which has many morphological features that are special to the Sciuridae, but it retains the primitive, protrogomorphous condition in which the origin of the lateral masseter is restricted to the zygomatic arch. Therefore, sciuromorphy does not even apply to all the members of the taxon on which the name is based. In sciurids and castorids the anterior margin of the infraorbital canal projects laterally from the rostrum. The fact that in the Geomorpha the anterior end of the infraorbital canal is depressed into the rostrum and the anterior margin of the canal is flush with the rostral wall may suggest independent origin of sciuromorphy in the group. Anterior extension of the origin of the lateral masseter is a common specialization in rodents. By itself sciuromorphy is not a sufficient criterion on which to base a hypothesis of monophyly. Its indiscriminate use in classification masks the complexity of rodent evolution.

The evidence of cranial foramina that places the Geomorpha in the Myomorpha is slim. This placement is based on the work of Hill (1937) and Wilson (1949). Hill found that many of the characters that geomyoids share with sciurids are interdependent, because they

are related to sciuromorphous origin of the lateral masseter. Some other similarities are retentions of primitive characters. Hill listed many characters of the skull, skeleton, and soft anatomy that are chiefly specializations shared by geomyoids and muroids. He suggested that the Geomyoidea be placed in the Myomorpha. Wilson (1949) compared the skull of *Paradjidaumo,* an Oligocene eomyid, with other sciuromorphous and myomorphous rodents. He, too, distinguished primitive from specialized characters and concluded that "the Eomyidae should perhaps be viewed as a relatively primitive group of rodents which departed from the same branch of the Aplodontoidea that gave rise to the heteromyids and muroids—all three being about equally remote from one another, but the heteromyids and eomyids less so; all of closer affinity to one another than to the sciurids and castorids" (*ibid.,* p. 48). Wilson clearly proposed a monophyletic clade whose branches include the Eomyidae, Heteromyidae, and Muroidea.

The evidence for relationship of eomyids to heteromyids was set forth by Wilson (1949). Wahlert (1978) included the geomyids in analysis of cranial foramina and reached the same conclusion. Unique, derived characters of the eomyids indicate that they constitute a monophyletic clade that shares its ancestry with the Geomyoidea.

The Geomyoidea share a suite of derived characters that make them distinctly different from the eomyids. Correct identification of the parapterygoid fossae is important. Fossil skulls are often broken immediately behind these fossae, especially if a sphenopterygoid canal is present, and the parapterygoid fossae are easily mistaken for the pterygoid fossae proper.

The skulls of florentiamyids were described by Wood (1936a), Rensberger (1973b), and Wahlert (1983). The group is unusual for its combination of a primitive geomyoid tooth crown pattern with a derived morphology of the anterior-alar fissure and canal for the descending palatine vein that is unique among rodents. Damage anterior to the infraorbital canal makes Wahlert's supposition that the rostrum was imperforate uncertain. On the basis of current knowledge,

placement of the florentiamyids in any other geomyoid group would make the definition of that group unworkable.

The entoptychids share derived characters with geomyids and heteromyids. The superior angular process of the mandible is flared laterally, and the pterygoid fossa is deep if not open dorsally into a sphenopterygoid canal. Retention of primitive characters indicates that the Entoptychidae branched off before the splitting of the Heteromyidae and Geomyidae. These characters are the supposed lack of a sphenopterygoid canal, retention of the temporal foramen, enclosure within a single bone of the accessory foramen ovale and of the postglenoid foramen. *Entoptychus* and *Pleurolicus* lack the rostral perforation seen in heteromyids.

The Heteromyidae and Geomyidae share many derived characters. Chief among them is the presence of a sphenopterygoid canal which permits anterior extension of the internal pterygoid muscle. Hill (1937, p. 159) stated that in heteromyids the internal pterygoid muscle does not invade the sphenopterygoid canal; he said (1935) that the canal is reduced to a foramen for a large vein in *Perognathus, Dipodomys,* and *Microdipodops.* This claim appears to have been based on Howell (1932) whom he cites, and on examination of cleaned skulls of the taxa mentioned. New dissection of *Dipodomys* revealed that a part of the internal pterygoid muscle passes through the sphenopterygoid canal anteriorly to the level of the base of the anterior-alar fissure; passage of a large vein through the canal was verified. Other characters, such as the reduction of the posterior parts of the alisphenoid and squamosal that permits confluence of several foramina may reflect a common, derived arrangement of the masticatory system and supporting bony elements. The fur-lined cheek pouches that are external to the mouth in geomyids and heteromyids may have been present in extinct taxa of the other related groups.

The Heteromyidae are united by the presence of a large perforation in the wall of the rostrum anterior to the infraorbital canal. The importance of this character has been stressed by systematists for more than a century. The reduced temporal muscle origin and small

coronoid process are probably interdependent characters. The Heteromyinae have the most primitive skulls among living geomyoids. It is the shared primitive characters and parallelism in loss of the stapedial artery and forward position of the anterior-alar fissure that make heteromyines and geomyines appear similar.

The perognathine-dipodomyine branch is characterized by enlargement of the auditory bullae and reduction of the squamosal and restriction of the origin of the temporal muscle. The sense of vision appears to be especially important. Anteroventral enlargement of the auditory bullae is accompanied in dipodomyines, as in *Entoptychus,* by separation of the bulla on anterior and medial sides from other bones of the cranium. The separation may reduce transmission through bone of sound that is generated in chewing. The union of bullar processes and contact between this specialized region and the basisphenoid may give the animal a means of distinguishing and ignoring the sound produced in its mouth. The incisive foramina of dipodomyines are very long; their extension far posterior to the premaxillary-maxillary suture indicates that this is a secondarily derived condition. The thin bone of the auditory bulla is remodeled from a trabecular precursor and also appears to be secondarily derived. The remarkable cranial specializations of the Dipodomyinae stand in strong contrast to those of the Geomyinae; close relationship of the two groups is unlikely, and dental similarities are interpreted as parallelism.

The family Geomyidae, which includes only the Geomyinae, is characterized by a complex set of characters that in part reflect extreme specialization. Wilkins and Woods (1983) found that chewing is propalinal in all forms, and they proposed that both masticatory and fossorial adaptations are important determinants of skull form. 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 proposed phylogeny supports remote common ancestry of geomyids and heteromyids. The low level of cranial differentiation among liv-

ing geomyine genera suggests either recent diversification or long conservation of a successful design after a period of rapid evolution.

CONCLUSIONS

The following classification is based on the proposed phylogeny of the infraorder Geomorpha. The genera described in this paper are given in parentheses.

Infraorder Geomorpha Thaler, 1966
    Superfamily Eomyoidea Depéret and Douxami, 1902
        Family Eomyidae Depéret and Douxami, 1902
    Superfamily Geomyoidea Weber, 1904
        Family Florentiamyidae Wood, 1936
        Family Entoptychidae Miller and Gidley, 1918
           (*Pleurolicus* and *Entoptychus*)
        Family Heteromyidae Allen and Chapman, 1893
           Subfamily Heteromyinae Alston, 1876
               (*Liomys* and *Heteromys*)
           Subfamily Perognathinae Coues, 1875
               (*Perognathus* and *Chaetodipus*)
           Subfamily Dipodomyinae Coues, 1875
               (?*Schizodontomys, Microdipodops,* and *Dipodomys*)
        Family Geomyidae Gill, 1872
           Subfamily Geomyinae Baird, 1857
               (*Geomys, Orthogeomys, Pappogeomys,* and *Thomomys*)

This classification is conservative and follows both mammalogists and paleontologists with regard to the taxonomic rank of the living groups. Elevation of the Entoptychidae and Florentiamyidae to families is based on the early branching of these taxa from the geomyoid lineage.

The Geomyidae, which includes only the Geomyinae, has the longest defining list of derived characters among the groups studied; monophyly of this group has not been questioned. I retain the subfamily Geomyinae for two reasons—it is commonly used by mammalogists, and it distinguishes these genera from the entoptychids, which are considered to be a subfamily of the Geomyidae by many paleontologists. Many of the geomyid spe-

cializations are directly associated with changes in the arrangement of the masticatory muscles and in dental morphology. Small size of the optic foramen may be associated with reduction of eyes and life in burrows. The reasons for loss of the stapedial artery and new connections of its branches are obscure.

Monophyly of the Heteromyidae is indicated by reduced temporal musculature and a unique perforation in the rostrum anterior to the infraorbital foramen. Among heteromyids the Heteromyinae are primitive, and they share many primitive cranial features with the Geomyidae. Rensberger (1971) noted this similarity. Enlargement of the bullae and modification of the posterior part of the skull together with large size of the optic foramen characterize the perognathine-dipodomyine branch of the Heteromyidae. The presence of a sphenopterygoid canal and rostral perforation and dipodomyine-like specializations reported by Munthe (1981) permit incorporation of *Schizodontomys* in this lineage. Shotwell (1967) and Lindsay (1972) grouped the living geomyids with the dipodomyines; there is dental similarity, but lack of shared, derived cranial characters belies this proposed relationship.

The Heteromyidae and Geomyidae are each other's closest relatives. The presence of a large sphenopterygoid canal and reduction of the posterior edges of the alisphenoid and squamosal bones characterize these groups.

The data do not support close relationship of living geomyids and extinct entoptychids. The Entoptychidae have a deep pterygoid fossa, but the sphenopterygoid canal is lacking. The alisphenoid bone is extensive posteriorly and encloses the accessory foramen ovale and postglenoid foramen. Despite retention of some primitive characters, there are specializations; the enlarged bullae and anterior separation of bullae from the basioccipital are derived features seen also in dipodomyines. Entoptychids lack the rostral perforation that is a characteristic of the Heteromyidae. Other aspects of skull morphology resemble geomyid specializations; these are interpreted as examples of parallelism that are associated with a burrowing mode of life.

I have described the skulls of the Florentiamyidae (1983) and Eomyoidea (1978) previously. The new data do not contradict the conclusions reached in those studies. The infraorder Geomorpha is used here as a gathering taxon for all of these rodents that share derived features; these include sciuromorphous lateral masseter, long infraorbital canal that is depressed into the rostrum, anterior position of the sphenopalatine foramen, and tooth crown pattern with transverse lophs. Although these rodents are sciuromorphous, other derived characters suggest that they are members of the suborder Myomorpha.

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