The Harrymyinae, a New Heteromyid Subfamily (Rodentia, Geomorpha), Based on Cranial and Dental Morphology of *Harrymys* Munthe, 1988

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ABSTRACT

Harrymys irvini Munthe, 1988, and *H. woodi* (Black, 1961) are transferred from the Florentiamyidae to the Heteromyidae and given subfamilial status as the Harrymyinae. The skull and dentition of *Harrymys irvini* are redescribed and reillustrated. The genus shares with heteromyids a rostral perforation medial to the infraorbital foramen, stapedial canal enclosed by bone, parietal somewhat retreated from occiput, and origin of temporal muscle restricted to lateral portion of cranium. The bulla shows unique ventral enlargement. Other distinguishing derived characters are shared with various other geomyoid taxa. Primitiveness of *Harrymys* is indicated by posterior position of the ethmoid foramen and unflared superior angular process of the mandible. The lower dentition is unusual; its retained ectolophid together with proximity of protostylid and hypostylid produces an R pattern with wear; transverse lophids are embayed posteriorly. Traditional comparative and PAUP analyses together suggest placement of the Harrymyinae as the earliest branch of the Heteromyidae. The contemporary fossil heteromyids are surveyed for similar, derived cranial and dental characters. No other genus can, at this time, be placed with certainty in the new subfamily.

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INTRODUCTION

Munthe (1988) named and described *Harrymys,* a new rodent from the Split Rock local fauna of Miocene, late Hemingfordian age, and he assigned the genus to the geomyid subfamily Florentiamyinae. The type specimen consists of a nearly complete skull and mandibles. Dr. William Korth, on looking at the published figures, exclaimed to me that the teeth are not florentiamyid-like. The Museum of Paleontology, University of California at Berkeley, kindly lent me the specimen for restudy.

The skull, like the dentition, is not that of a florentiamyid. It is a geomyoid not easily assignable to any family or subfamily. A new, comparative description of the specimen was undertaken in order to place *Harrymys* in the phylogeny of geomyoids. Since my approach to the description of crania is somewhat untraditional, with its emphasis on cranial foramina, I have extended Munthe's account considerably; further preparation has also revealed new data. I comment on his text only when we disagree about the morphology. Munthe described the dentition from the type and many partial specimens that I have not seen. I have incorporated his description of the teeth of *H. woodi.*

New illustrations are given of the type of *Harrymys irvini* (figs. 1 and 2). Symmetrical features of the skull were reflected to fill in areas damaged on one side. Morphology that is missing and thus uncertain was reconstructed with dashed lines. The position of hamular processes of the pterygoid region and styloid processes of the bullae that might have met them posteriorly were indicated only with a question mark; restoration in a particular way could bias assessment of relationship. Lateral compression of the actual specimen has been removed in the drawing by appropriate widening of the skull and rotation of the anterior ends of the bullae medially. The figures are thus idealized diagrams of the specimen and not direct representations of it. Many bone fragments fitted onto the mandibles and provided a complete picture of its shape except for the coronoid process.

This investigation allowed me to recast for computer analysis the comparative data of

my previous studies of the Geomorpha (Wahlert, 1978, 1983, 1984, 1985a; Wahlert and Souza, 1988), and of a manuscript (in press) about the fossil history of heteromyids. Publications of other paleontologists are cited in the text. Many comparative points were also checked against a sample of fossil geomyids and recent geomyines and heteromyids at the American Museum of Natural History. The complete list of character states and the comparison of taxa are presented in Appendices A and B.

Taxonomic usage throughout the text is consistent with the following classification of the Geomorpha (Wahlert, 1985a, as modified by Wahlert and Souza, 1988), a monophyletic taxon within the rodent Suborder Myomorpha:

Infraorder Geomorpha
Superfamily Eomyoidea
  Family Eomyidae
Superfamily Geomyoidea
  Family Florentiamyidae
  Family Geomyidae
    Subfamily Entoptychinae
    Subfamily Geomyinae
  Family Heteromyidae
    Subfamily Heteromyinae
    Subfamily Perognathinae
    Subfamily Dipodomyinae

mens to conduct this research. I appreciate the continuing guidance of Mr. Chester Tarka and Ms. Lorraine Meeker, who prod me to improve the quality of my illustrations.

SYSTEMATICS

SUBFAMILY GEOMYOIDEA BONAPARTE, 1845

FAMILY HETEROMYIDAE GRAY, 1868

SUBFAMILY HARRYMYINAE, NEW SUBFAMILY

DEFINITION: See generic diagnosis.

HARRYMYS MUNTHE 1988

GENOTYPIC SPECIES: *Harrymys irvini* Munthe, 1988.

REVISED DIAGNOSIS (based primarily on *H. irvini*): Large heteromyid rodent with rostral perforation, stapedial canal enclosed by bone, parietal somewhat retreated from occiput, and origin of temporal muscle restricted to lateral portion of cranium; unique ventral expansion of auditory bulla. Retaining the following primitive features that are altered in living heteromyids: complete accessory foramen ovale; temporal foramen present; no flange on frontal projecting over orbits; unflared superior angular process of mandible; incisors without ornament. Other apomorphic characters shared with various geomyoid taxa: incisive foramina about 45 percent of diastemal length; auditory bullae of thin bone, large ventrally with anteromedial processes that meet in midline; mastoid chambers enlarged posteriorly and dorsally; squamosal emarginate posteriorly. Cheek teeth moderately protohypsodont and rooted, bilophate, each transverse loph, except perhaps hypolophid of m3, widened by stylar cusp. Upper cheek teeth wearing to U pattern open buccally; M3 early enclosing central valley as basin. Retention of ectolophid in lower cheek teeth producing H pattern with wear; proximity of protostylid and hypostylid ultimately forming connection and isolating buccal flexid as lake and changing crown to R pattern. Metalophid embayed posteriorly between protoconid and metaconid by tip of lingual flexid. Hypolophid embayed posteriorly between hypoconid and entoconid; V shaped with an-

terior point connected to protoconid by ectolophid; small cusp, which may be a hypoconulid, variably present at posterior end of embayment.

Harrymys irvini Munthe, 1988

TYPE SPECIMEN: UCMP (University of California Museum of Paleontology) 122004; nearly complete skull and mandibles.

REFERRED SPECIMENS: See Munthe (1988: 68).

TYPE LOCALITY AND AGE: Split Rock local fauna (UCMP locality V69190), Fremont Co., Wyoming; Arikaree Formation, late Hemingfordian age.

DIAGNOSIS: Larger than *H. woodi,* see tables 2 and 3; anterior cingulid in lower molars bent posteriorly toward protostylid and forming prominent anterobuccal corner in crown.

Harrymys woodi (Black, 1961)

TYPE SPECIMEN: YPM (Yale University Peabody Museum) 14038; left ramus with I-m1.

REFERRED SPECIMENS: None.

TYPE LOCALITY AND AGE: Section 23, T10N, R5E, Meagher Co., Montana. Deep River fauna, ?late Hemingfordian. Black (1961) stated "Deep River Formation," but this is of Arikareean age and distinct from the Deep River fauna of Hemingfordian and Barstovian age (Savage and Russell, 1983, place *D. woodi* in the Barstovian).

DIAGNOSIS: Smaller than *H. irvini*; see tables 2 and 3; anterior cingulid in m1 extending posterolaterally toward protostylid in long curve that is oblique to axis of tooth.

CRANIAL DIMENSIONS

The condylobasilar length of the skull of *Harrymys irvini,* measured between the posteriormost parts of the incisor alveoli and the occipital condyle is 41.4 mm on the left side, which appears relatively undistorted. The diastemal length, the shortest distance between the alveolus of the incisor and fourth premolar on one side is 12.0 mm. The incisive foramina are 5.4 and 5.5 mm long and begin about 3.8 mm posterior to the incisor

alveoli. The minimum interorbital width across the frontals is 6.9 mm and appears to be undistorted despite lateral compression of the specimen; this width is almost at the dorsalmost extent of the orbits and is approximately equal to the greatest width of the rostrum. Minimum palatal width between fourth premolars is 3.1 mm; it may have been slightly reduced by compression.

COMPARATIVE CRANIAL MORPHOLOGY

Four views of the skull of *Harrymys irvini* are given in figure 1. The diastemal palate of *Harrymys* is broadly concave in lateral view. The concavity is deepest just anterior to the middle of the diastema, and the rostrum everywhere appears tall. In geomyids—geomyines and extinct entoptychines—the deepest point is near the incisors, and in lateral view the rostrum tapers anteriorly. In heteromyids and extinct florentiamyids the diastema is relatively flat. The rostrum is tall and untapered in florentiamyids, which have primitive skull morphology; it is tapered in heteromyids. The tips of the nasal bones in *Harrymys* are broken, and their anterior extent cannot be determined. Munthe (1988: 72) stated that the nearly complete right premaxilla indicates that this bone extended forward and supported prominently projecting nasals. The premaxilla is no longer so complete; Munthe did not figure the right side of the specimen.

Compression has exaggerated the narrowness of the diastema in ventral view. Interpremaxillary foramina are lacking as in eomyids, heteromyids, florentiamyids, and most entoptychines. The incisive foramina are narrow and broaden posteriorly. The premaxillary-maxillary suture runs anteriorly to meet the lateral edges about one-third of the length from the posterior ends. The intersection is farther anterior in dipodomyines and at the posterior end of the foramina in the rest of the Geomorpha. The foramina in *Harrymys* occupy 45 to 46 percent of the diastemal length, a proportion similar to that in *Paramys, Sciuravus,* and *Prosciurus,* 39 to 48 percent. The foramina are relatively shorter in all other members of the Geomorpha:

Eomyidae, 24–40 percent; Florentiamyidae, 12–28; Entoptychinae, 16–32; Geomyinae, Heteromyinae, and Perognathinae, 15 or less; and Dipodomyinae, 22–41.

The cheek tooth rows are nearly parallel with only slight anterior convergence. Interdigitations at the posteromedial edge of the maxilla show that the maxillary-palatine suture crossed the palate medial to the anterior part of the first molar. Posterodorsal curvature of the shallow arterial groove on the left suggests that the palatine foramina may have been in the suture medial to the junction between the first and second molars. A moderately large and round posterior maxillary foramen is posterior to the third molar; the maxilla bounds it anteriorly and laterally and the palatine posteriorly and medially. The foramen is smaller and has a lenticular shape in other geomyoids; it is incompletely enclosed in some eomyids.

The back of the palate on either side of the choanal region slopes dorsally toward the pterygoid fossae and forms a pair of very shallow parapterygoid depressions; breakage precludes complete description of their morphology. Parapterygoid depressions characterize the Geomyoidea and are lacking in the Eomyoidea. In florentiamyids they form broad shelves between the levels of the palate and of the roofs of the pterygoid fossae; the relief is slight, perhaps because the pterygoid fossae in this family are shallow and not perforated by a sphenopterygoid canal. *Harrymys* has the canal, but the depressions are not as pronounced as those in geomyids and heteromyids.

Harrymys was fully sciuromorphous like all of the Geomorpha. The origin of the rostral part of the lateral masseter is clearly marked by a dorsal ridge that runs far onto the premaxilla from the anterodorsal edge of the maxillary root of the zygoma. Its anterior end turns ventrally and disappears. *Harrymys* shows the geomorph character of a long infraorbital canal that is low on the rostrum and depressed into the rostral wall at its anterior end, the infraorbital foramen. The presence of a rostral perforation medial to the foramen is attested by a hole through the bone that has a smoothly curved edge; I believe this aperture is not an artifact of com-
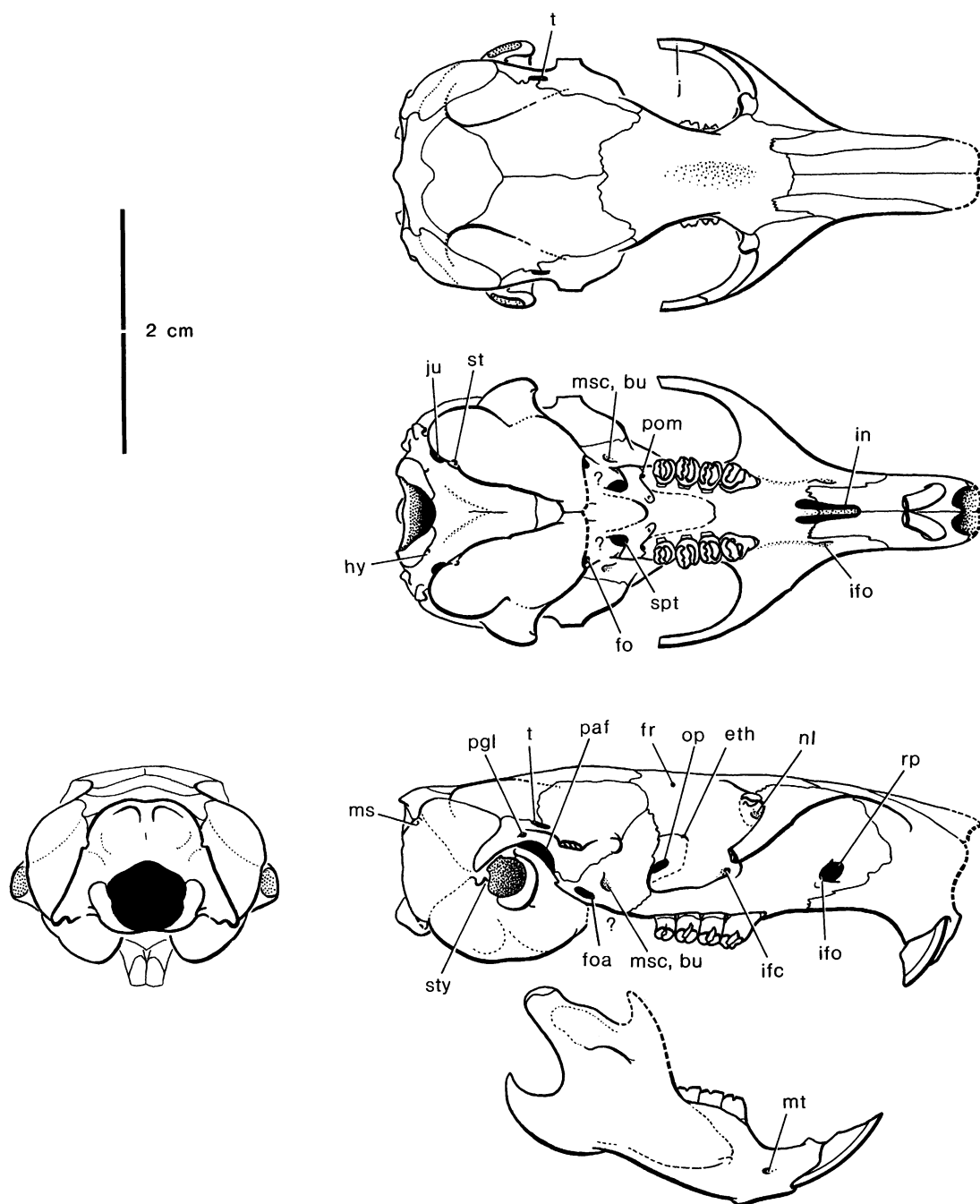
Fig. 1. *Harrymys irvini,* UCMP 122004 type, four views of the skull. Abbreviations for foramina and other features: **bu**, buccinator; **eth**, ethmoid; **fr**, frontal; **fo**, foramen ovale; **foa**, accessory foramen ovale; **hy**, hypoglossal; **ifc**, infraorbital canal; **ifo**, infraorbital foramen; **in**, incisive; **ju**, jugular; **ms**, mastoid; **msc**, masticatory; **mt**, mental; **nl**, nasolacrimal; **op**, optic; **paf**, posterior alar fissure; **pgl**, postglenoid; **pom**, posterior maxillary; **rp**, rostral perforation; **spt**, sphenopterygoid canal; **st**, stapedial; **sty**, stylomastoid; **t**, temporal; **j**, jugal bone. Anterior alar fissure (aaf), not labeled, marked by curved edge at back of orbit.

pression. All heteromyids possess a large ros-
tral perforation, a feature that is lacking in
all other members of the Geomorpha. Ar-
cuate compression fractures set apart the
strong maxillary brace of the zygoma from
the lamina that grades into the rostral wall.
These accidental features are prominent in
Munthe's illustrations (1988: figs. 15, 16); I
have omitted them.

The nasolacrimal foramen is partially pre-
served on the right side of the specimen. It
is in the primitive position in the lacrimal
bone anterodorsal to the orbital aperture of
the infraorbital canal as in other geomorph
rodents; the lacrimal process overhangs it.
The course of the lacrimal canal is indicated
on the left side by white coloration of the
bone. The initial part of the canal is vertical;
it then runs horizontally in the rostrum and
turns medially just above the rostral perfo-
ration. The anterior tip of the jugal bone is
preserved on the right side; the bone is very
short and slender and does not approach the
lacrimal. Restriction of the anterior extent of
the jugal is characteristic of geomyoids. The
jugal extends to the lacrimal in some eomyids
(Wilson, 1949: 35, and fig. 1; Wood, 1974:
fig. 27).

The orbital wall is severely fractured. The
presence or absence of ossification at the
junction of frontal, maxillary, and lacrimal
bones and the nature and position of the
sphenopalatine foramen cannot be deter-
mined. The ethmoid foramen is dorsal to the
posterior part of the second molar and is ei-
ther in the orbitosphenoid-frontal suture or
in the frontal close to the suture. The foramen
is situated as far posteriorly in florentiamyids
and some eomyids. It is somewhat farther
anterior in geomyids and heteromyids. The
optic foramen is dorsal to the third molar
and was probably larger than 1.0 mm. Its
position, like that in entoptychines, hetero-
myids, and some eomyids, is intermediate
between the primitive site, posterior to M3
as in most florentiamyids, and the derived
site, above the anterior half of M2 as in geo-
myines. The apparent large size matches only
that of florentiamyids, perognathines, and di-
podomyines. The presence and position of
an interorbital and a dorsal palatine foramen
cannot be determined. The absence of arterial

channels on the bone suggests that the sphe-
nofrontal foramen may have been lacking. A
small frontal foramen is present near the dor-
salmost edge of the orbit, dorsal to the an-
terior part of the optic foramen; the aperture
is common in rodents and transmits the fron-
tal diploic vein.

The ventral root of the anterior alar fissure
rises just posterior to the third molar as in
perognathines and *Microdipodops*; it is far-
ther anterior in other heteromyids and geo-
myids, and more posterior in florentiamyids.
The maxilla and alisphenoid interdigitate over
a broad area as in all geomyoids except flo-
rentiamyids. The palatine does not partici-
pate in the root of the fissure as it does
uniquely in florentiamyids. The alisphenoid
bone extends dorsally to about three-quarters
of the orbital height in the posteromedial part
of the orbit. The dorsal extent is similar to
that in entoptychines, less than in geomyines
and florentiamyids, and greater than in het-
eromyids. Its surface appears to be marked
by a slight dorsal ridge that may delimit the
dorsal extent of a deep, anterior division of
the temporalis muscle, a condition that typ-
ifies the geomyids. The squamosal bone also
extends far dorsally, just to the skull roof; it
separates the alisphenoid and parietal in all
of the Geomorpha. The squamosal is high in
all but the eomyids.

Masticatory and buccinator foramina are
probably joined in the single aperture that is
strongly concave anteriorly in the alisphe-
noid wall. Masticatory and buccinator fo-
ramina are joined as a single aperture in het-
eromyines and *Dipodomys*; they are usually
separated in other heteromyids and geo-
myids. In both eomyids and florentiamyids
they are combined with the accessory fora-
men ovale as a single aperture in the pos-
teroventral part of the alisphenoid. Breakage
on the right side of the specimen reveals that
the masticatory and buccinator nerves and
the internal maxillary artery entered the skull
together via the alisphenoid canal. The en-
trance is within the anterior end of the fo-
ramen ovale. The masticatory and buccina-
tor nerve canal diverges dorsally in the
alisphenoid bone. A short distance anterior
to this point, the alisphenoid canal is open
medially into the cranium. It continues into

the orbit as part of the anterior alar fissure. No foramen for the internal maxillary artery is present medial to the masticatory foramen; such an opening is seen in geomyines and heteromyines.

The lateral pterygoid flange, though broken, reaches the auditory bulla and encloses the accessory foramen ovale as in entoptychines. The flange rarely reaches the bulla in living heteromyids and geomyines, and the accessory foramen ovale is seldom enclosed. The foramen ovale itself is bounded posteriorly by the bulla, a geomyoid condition, and it is separated from the posterior alar fissure by the alisphenoid bone. Such a separation is unusual; it occurs in *Gregorymys* and *Entoptychus* but not in other geomyids and heteromyids. Florentiamyids lack a posterior alar fissure. In eomyids the foramen ovale is completely surrounded by bone of the pterygoid fossa, and a posterior alar fissure is absent except in *Kansasimys*. The posterior alar fissure in *Harrymys* extends from the alisphenoid-squamosal suture posterodorsally to the level of the glenoid fossa. The broad dorsal part of the aperture suggests that functionally it incorporates the postglenoid foramen. However, a tiny postglenoid foramen is present in the squamosal immediately posterodorsal to the fossa. In eomyids and florentiamyids the postglenoid foramen is moderately large and surrounded by the squamosal bone. In living geomyids and heteromyids the postglenoid foramen is continuous with the posterior alar fissure or is divided from it by only a prong of the squamosal. The seemingly superfluous postglenoid foramen in *Harrymys* is seen also in *Entoptychus* and *Gregorymys curtus*. Munthe showed (1988: fig. 15) holes in the anteroventral surface of the posterior zygomatic root; these are an artifact of preparation and are not true foramina.

The lateral edge of the entrance into the sphenopterygoid canal is preserved on the left side. The entrance is large and situated in the anteromedial part of the pterygoid fossa. The internal pterygoid muscle extended anterodorsally into the canal and would have filled the space between the back of the parapterygoid depression and the roof of the pterygoid fossa. This condition is seen in all geomyids and heteromyids. The roof of the pterygoid

fossa is entire in florentiamyids. Some eomyids may have a failure of ossification in the fossa, but there is no evidence that the aperture transmitted the internal pterygoid muscle. Traces of the sphenopalatine vacuities and transverse canal are obliterated by damage to the specimen of *Harrymys*. The lateral walls of the choana and the hamular processes are also missing.

Munthe (1988: 73) stated: "The posterior part of the basisphenoid is preserved between the converging margins of the bullae. It is significantly more ventral than the surface of the basioccipital, so the anterior part of the basioccipital appears to be deeply depressed between the bullae in ventral view. The basioccipital is overlapped by the basisphenoid, rather than meeting it in a simple contact." Further cleaning of the specimen revealed that this description is incorrect. The basioccipital and basisphenoid bones form a continuous surface that narrows anteriorly and has a sight anterodorsal inclination. The two bones meet, as usual, in a butt joint. The region of apparent overlap is merely irregular corrosion of the anterior end of the basioccipital. A prominent keel extends anteriorly from the condyles; it narrows to a point that merges into the plane of the basioccipital shortly posterior to the suture with the basisphenoid.

The auditory bullae and mastoid chambers are large. In lateral view the bullae project ventrally in a long anteroposterior curve, and they appear proportionally larger dorsoventrally than in any other geomyoid rodent. In ventral view, broad anteromedial extensions of the bullae meet in the midline. These are damaged, and the presence or absence of styloid processes projecting from them toward the hamular processes, like those in entoptychines, cannot be determined; such processes are present, but small, in dipodomyines. Damage to the left bulla shows that the bone is a thin lamina. The bulla consists of a plain lamina of bone in eomyids and florentiamyids, and the lamina is extremely thin in dipodomyines. Other living geomyoids have a bulla with vesicular internal structure. Lateral compression may have narrowed the bullae in *Harrymys*, but the one on the right looks relatively uncrushed. In the drawing I

have rotated the bullae outward at the posterior ends in order to align the anteromedial processes.

There is no evidence for anterior passage of the internal carotid artery on the medial side of the bulla or of a gap between the wall of the bulla and the basioccipital. These features could have been obliterated by the evident compression of the specimen. The stapedial foramen is large and enters the medial wall of the bulla anteroventral to the jugular foramen. Exposure of the middle ear on the left shows that the stapedial artery crossed the promontorium laterally within a bony tube. The stapedial foramen is present in eomyids, florentiamyids, entoptychines, perognathines, and dipodomyines. It is a tiny perforation in geomyines and is entirely lacking in heteromyines. In eomyids and florentiamyids a groove on the promontorium marks the lateral course of the stapedial artery. The artery is enclosed in a bony tube in perognathines and dipodomyines; in some specimens there is a ventral opening in the tube at mid-course. Munthe (1988: 73) noted "a small foramen low on the dorsomedial wall of the bulla, which may be the jugular foramen." I cannot find this aperture; the jugular foramen is not in this position. He remarked (1988, pp. 73–74) that "the carotid canal is a large vertical foramen at the base of the dorsomedial bulla wall." This opening is, in fact, the stapedial foramen.

The jugular foramen is a lenticular slot between the basioccipital and the posteromedial part of the auditory region. The hypoglossal foramen is a single opening medial to the jugular foramen and mostly hidden by an anterior lip from the articular surface of the condyle.

A small fragment of the stylohyoid is preserved on the posteroventral surface of the left bulla. Only the anteroventral part of the bony meatus of the ear protrudes from the bulla. The stylomastoid foramen is immediately posterior to the meatus.

The mastoid region is enlarged posteriorly and dorsally and constricts the occiput slightly. The squamosal bone is excavated posteriorly and the dorsal part of the mastoid is broadly exposed. Munthe (1988: 73) apparently called this part of the mastoid the "squamosal bulge." The degree of mastoid

enlargement is greater than that in entoptychines and almost as much as in *Perognathus*. Geomyines and heteromyines show no distinct enlargement, whereas the amount in dipodomyines is huge. *Perognathus* differs from *Harrymys* in that dorsal expansion extends anteriorly above the meatus; the wall of the entire auditory chamber has a frothy texture; and the occiput is somewhat constricted. In dipodomyines expansion continues in front of the meatus itself; the mastoid is also expanded medially and greatly constricts the occiput and interparietal. The size and position of the mastoid foramen of *Harrymys* cannot be established with certainty.

A temporal foramen of moderate size is present posterodorsal to the posterior root of the zygoma and dorsal to the posterior alar fissure. It is surrounded chiefly by the squamosal, but the parietal reaches it posterodorsally. The temporal foramen is present in florentiamyids and entoptychines. It is absent in eomyids and living geomyoids.

The dorsal view reveals other important morphological features of the skull. The nasal bones do not project as far posteriorly as the premaxillae, a condition that is common in geomyoids. The frontal has no trace of a median suture. Obliteration of the suture is usual in dipodomyines and perognathines; the character is variable in geomyids; the suture or parts of it remain visible in heteromyines. The narrowest interorbital width across the frontals is where the orbital wall rounds into the skull roof as in geomyines. In heteromyids and florentiamyids a ridge marks the junction of the wall and roof; it is least well developed in *Microdipodops*. In entoptychines the greatest interorbital width is high but within the orbits. The temporal crests of *Harrymys* are lyrate as is common in heteromyids and florentiamyids; the strong channels for muscle origin are separated by a large, wide interparietal bone. The muscle scars extend, albeit faintly, onto the exposed mastoid bone. The posteriormost part of the skull roof is occupied by a bow-shaped extension of the occipital bone. It extends anterolaterally on each side to reach the posteriormost part of each parietal. The parietals thus end at about the midpoint of the interparietal. Such short parietals occur in perognathines and to a much greater extreme in dipodomyines (see figures

in Hall, 1981). The convex occiput of heteromyines contains the rudiment of the condition, with the interparietal projecting farther posteriorly than the parietals. In geomyids and florentiamyids the parietals extend to the occipital plane.

MORPHOLOGY OF THE MANDIBLE

The left and right mandibles together give a nearly complete morphological picture except for the coronoid process (fig. 1). The mental foramen is approximately ventral to the midpoint of the diastema; it is somewhat more than halfway above the ventral edge of the jaw. I do not agree with Munthe's statement (1988: 74) that it is positioned high on the lateral surface of the mandible. The lower masseteric crest has very low relief posteriorly at the root of the angular process. Relief increases anteriorly and an inclined shelf is formed ventral to the fourth premolar. The upper masseteric crest has no relief and is defined only by a slight change in orientation of the surface. The upper crest descends from the anterior edge of the coronoid process; it curves ventrally to meet the anterior end of the lower crest below the front of the alveolus of p4, as in geomyids. The end of the fossa is farther anterior in florentiamyids. In heteromyids the prominent lower crest extends farther anterodorsally.

In ventral view the large but slender angle is disposed in a straight line with the medial edge of the mandible; the tip of the superior angular process projects laterally to a small degree. This is similar to the eomyid and florentiamyid conditions. I find no evidence that the angle might have been flattened when the skull was compressed. In heteromyids the angle is large, and the tip is flared laterally. The angle of the mandible in *Entoptychus* resembles that of heteromyines, but the pronounced lower masseteric crest and accompanying breadth of the jaw in ventral view are similar to the derived geomyine condition. In geomyines the body of the angle is merely a ridge, and the process forms a strong lateral projection. In heteromyids the angle is large and the tip is flared laterally. If the occlusal surface of the cheek teeth is taken as

horizontal in lateral view, the condyloid process of *Harrymys* extends very slightly beyond the tip of the angular process. In dorsal view the spindle-shaped condyle is oriented anteroposteriorly, and its width is slightly more than one-half its length. The right mandible preserves the positional relationship of the condyloid process to the body of the mandible more accurately than the left; only the right mandible can be articulated with the skull for both chewing and gnawing occlusion. The semilunar notch between the angular and condyloid processes is deep.

Although the coronoid process is missing, curvature of edges leading into it, both anteriorly and posteriorly, indicates that it was quite large. It is similar in relative size to the process in eomyids (Wood, 1974) and entoptychines (Rensberger, 1971), larger than that in florentiamyids and heteromyids, and smaller than that in geomyids. The mandibular notch between coronoid and condyloid processes does not extend deeply into the lamina of the mandible; in geomyids the long coronoid process makes the notch deep.

The lower incisor is long, and the posterior end of the alveolus bulges laterally from the mandible below the mandibular notch. A distinct fossa dorsomedial to it marks the insertion of the posterior part of the medial masseter. The bulge of the incisor alveolus is present in all members of the Geomorpha (for eomyids see figures in Black, 1965; Wood, 1974; Comte and Vianey-Liaud, 1989). The great length of the alveolus appears to be the chief cause of the bulge in florentiamyids. A second factor, the presence of a concavity for insertion of the posterior part of the medial masseter, is observed as primary in *Microdipodops*. The position of the bulge in *Harrymys* is posterior to that in eomyids and florentiamyids and similar to the position in perognathines, heteromyines, and *Microdipodops*. The bulge is between the superior angular and condyloid processes in geomyines and *Dipodomys*; Wahlert (1985a) failed to note the posterior position in the latter taxon.

In medial view the large mandibular foramen is at the base of the condyloid process close to its posterior edge. The ascending lamina of the jaw arises lateral to m2. There is no depression between it and m3 for in-
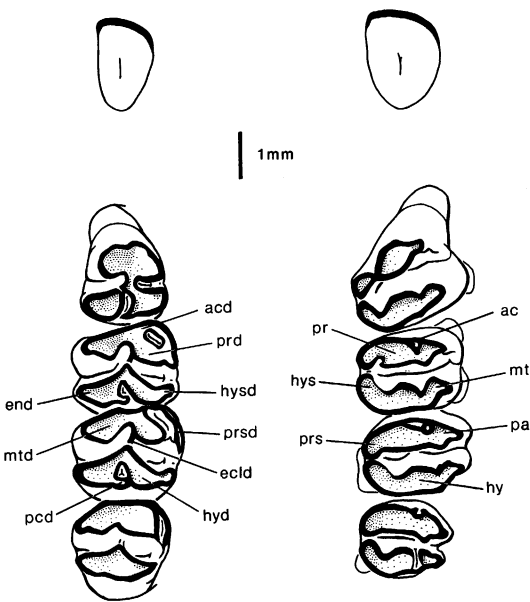
Fig. 2. *Harrymys irvini*, UCMP 122004 type, lower right and upper left dentitions in crown view and incisor cross sections (approximate). Abbreviations: **ac**, anterior cingulum; **acd**, anterior cingulid; **ecld**, ectolophid; **end**, entoconid; **hy**, hypocone; **hyd**, hypoconid; **hys**, hypostyle; **hysd**, hypostylid; **mt**, metacone; **mtd**, metaconid; **pa**, paracone; **pcd**, posteroconid or cingulid; **pr**, protocone; **prd**, protoconid; **prs**, protostyle; **prsd**, protostylid.

sertion of the posterior part of the medial masseter; in this *Harrymys* is like heteromyids. The surface of the angle forms a shallow concavity. The insertion of the digastric muscle is marked by a ventral projection or chin beneath the diastema. The symphysis is not fused.

DENTITION

Dimensions of the teeth of *H. irvini* are presented in tables 1 and 2; crown views are

TABLE 1
Tooth Row Lengths (mm)
Harrymys irvini

	L P4-M3	R p4-m3	L p4-m3
Alveolar	8.4	8.4	8.4
Enamel crown	8.2	8.0	7.9
Occlusal	7.3	7.3	7.2

TABLE 2
Tooth Dimensions (mm)
Harrymys irvini

	R and L	I	i	
Depth		2.15	2.0	
Maximum width		1.6	1.25	

	L	P4	M1	M2	M3
Occlusal length		1.9	1.7	1.7	1.6
Maximum crown width		2.5	2.4	2.4	2.0

	R and L	p4	m1	m2	m3
Occlusal length		1.7	1.8	1.8	1.7
Maximum crown width		1.9	2.2	2.4	2.1

illustrated in figure 2. Measurements were taken with a Helios dial caliper accurate to 0.05 mm. Three different measurements of tooth row length are given, since not all may be available in a particular fossil specimen. Dimensions of the cheek teeth were measured in two different ways. Occlusal length, the only consistent dimension that can be taken for all cheek teeth, is not constant and changes over time with shortening of teeth due to interdental wear and with lengthening due to crown wear in P4 and p4, since these teeth broaden anteriorly toward the base. Maximum width of each tooth is constant until late in wear. The greatest width in premolars is across the posterior loph/id; in molars it is across the anterior loph/id. In M2 the two lophs are almost equal in length. Black (1961: 16) gave dimensions of the two lower teeth p4 and m1, known in *H. woodi*; I have checked them against the figure and find them to be occlusal crown measurements (table 3). The teeth are smaller than those of *H. irvini*; the sum of their occlusal lengths is 84 percent of that in *H. irvini*, but they are proportionally longer.

TABLE 3
Tooth Dimensions (mm)
Harrymys woodi[*]

	L	p4	m1
Occlusal length		1.45	1.50
Maximum crown width		1.30	1.65

[*]from Black, 1961, p. 16.

The cheek teeth of *H. irvini* (fig. 2) have been described in detail by Munthe (1988). I restate only morphology that appears to be of taxonomic significance. The teeth are protohypsodont (sensu Mones, 1982: 110) in moderate degree. The cusps of the upper teeth are joined by wear into lophs. The transverse lophs are extended lingually by the presence of styles as in all other geomyoids. In this specimen the lophs are about to join lingually into a continuous U pattern that is common in geomyoids. The buccal flexus on each tooth is open and will remain so until the tooth is nearly worn out; its floor is about 0.5 mm from the base of the enamel crown in the molars. The base of the buccal flexus is slightly higher and this distance greater in P4. In M3 apposition of the paracone and metacone will close the buccal end of the flexus and form a central lake. Paracone and protocone are united as a large, anterior cusp in P4; a narrow wear facet descends into a ridge on the lateral side of this cusp. The protostyle is also large, and the tooth retains a molarlike appearance rather than the triangular one common in geomyoids. There is no evidence of an entostyle; florentiamyids have both an entostyle and a hypostyle. A trace of a very low anterior cingulum remains on M1 and M2. Long anterior cingula are present in florentiamyids and in eomyids, which also have posterior cingula. The protostyle is partly separated from the protocone in M1 by a shallow valley that sits much farther apically than the central valley of the buccal flexus. The metacone is mostly separated from the hypocone in M3. These features presumably were present in each tooth early in the wear sequence. Upper teeth of *H. woodi* are not known.

The cusps of the lower teeth are also joined by wear into lophs that are widened buccally by styles. The protostylid is a ridge that connects directly with the anterior cingulid. It is separated from the protoconid by a shallow valley that joins the buccal flexid far above its base. The left dentition, which is slightly less worn than the right, shows that this feature is present in all of the cheek teeth including p4. The Y pattern of valleys in lower molars occurs in florentiamyids, many extinct heteromyids (Wood, 1935), and in *Pleurolicus* (Wood, 1936: fig. 8; Gawne, 1975: fig.

9) at early stages of wear. The hypostylid is a single cusp; it may be lacking in m3. A central ridge extends posterolingually from the medial side of the protoconid. An arm from the hypoconid and another from the metaconid converge anteriorly and unite just before meeting this ridge. The hypolophid thus appears as a wide V with the apex anterior and a shallow valley or embayment posterior. A cusp that is associated with the entoconid sits posterior to the valley. With wear the cusp joins the entoconid and is like a posterior cingulid; the subsequent union of the cusp with the hypoconid isolates the posterior valley as a lake.

The central ridge separates the basins of the lingual and buccal flexids. If one follows Butler (1985: 393), "... crests that separate homologous basins are themselves homologous," the ridge may be called the ectolophid, a retained primitive feature. The floor of the lingual flexid is somewhat less than 0.5 mm from the base of the enamel crown in molars; the floor is higher and the distance is greater in p4. Munthe (1988: 82) pointed out that "the lingual flexid curves sharply anteriorly at the center of the tooth." Thus the metalophid, like the hypolophid, has a posterior embayment. The base of the protostylid and that of the hypostylid are conjoined, and the buccal flexid is deepest within the tooth; it makes a pit between this low, stylar union and the ectolophid. The ectolophid is higher than the stylar union in p4 but decreases in relief progressively in the molars. The teeth wear first to an H pattern with the flexid open externally; then the buccal flexid closes to produce an R-shaped wear pattern. It appears that, once formed, the H pattern would persist longer in the anterior teeth. The H pattern occurs variously in extinct heteromyids. Eomyids possess a complete ectolophid of high relief near the center of each tooth. Merriam (1895: 16, fig. 2) illustrated such connections in all of the lightly worn molars of a living geomyine, *Heterogeomys*.

Munthe (1988: 82) described the lower molars of *H. woodi* as follows: "[They] show the *Harrymys* generic characters of distinctly separated cusps, deep and anteriorly projected lingual flexid, and early central lophid connection between the hypoconid/entoconid and protoconid." They are much smaller than

the molars in *H. irvini*; the central ridge (ectolophid) is variably developed and not as prominent as in *H. irvini*.

All four incisors are complete, and there are no fortuitous breaks that expose the cross sections. The incisor cross sections in figure 2 are composites derived from superposition of the oblique wear surface onto the actual cross-sectional dimensions of the tooth. The upper and lower incisors are nearly equal in depth, but the uppers are considerably wider than the lowers. The greatest width in both is near the front. The anterior enamel faces of upper and lower incisors are smooth and rounded. The upper incisors bear no trace of the strong longitudinal groove or grooves that are present in living perognathines, dipodomyines, and in many geomyines; there is no hint in *H. irvini* of a flattened anterior face as in heteromyines. In geomyids, lower incisors with broad, flat anterior faces are very common but not universal. Munthe (1988: 82) stated: "The incisor of the *H. woodi* type mandible is similar to that of the *H. irvini* type except that it has a sharp anterobuccal corner, which produces a flat anterior face." Dr. Karl Koopman (personal commun.) pointed out to me that this is within the limit of variation in living *Dipodomys*; *D. microps* has flat-faced lower incisors, whereas the surface is rounded in other species.

DISCUSSION AND CONCLUSION

Munthe (1988) placed *Harrymys* in the geomyid subfamily Florentiamyinae on the basis of resemblances between the skulls: morphology of external nares; depth, width, and morphology of the rostrum; degree of opisthodonty in upper incisors; narrowness of palate; development of bullae; narrowness of posterior part of skull; fragile zygomatic arches; and general skull proportions. He noted two differences: shorter incisive formaina and square outline of zygomatic arches in *Florentiamys*.

I have set the skull of *Harrymys irvini* next to the type skull of *Florentiamys loomisi*. The resemblances are superficial. Incompleteness of the nares in both specimens precludes meaningful comparison. Similar rostral profile and degree of opisthodonty can be found among paramyids (see figures in Wood, 1962)

and similar opisthodonty among the geomorph rodents. Relative narrowness of the posterior part of the skull is due in part to lateral compression; certainly in burrowing rodents the cranium is wider, but this degree of narrowness does not appear unusual for a rodent. Thin zygomatic arches are common throughout the Rodentia, and among the Geomorpha they are notable in eomyids and especially in heteromyids. I do not understand Munthe's description of the "square zygomatic arches" in *Florentiamys*. There is more than one shape to the arches in florentiamyids (Wahlert, 1983: figs. 4, 6; 1984: fig. 1).

General skull proportions also differ between *Harrymys* and *Florentiamys*. The rostrum is shorter in *Harrymys*; the diastema is 29 percent of condylobasilar length, whereas in *Florentiamys* it is 34 percent. Similarly, the distance from the back of M3 to the condyle is 50 and 46 percent of the condylobasilar length. The ratios of alveolar length of the cheek tooth row to condylobasilar length are nearly alike, 20.5 and 19.5 percent. Palatal width compared with condylobasilar length is as close to that in some heteromyine specimens as to that in *Florentiamys*. The incisive foramina of *Harrymys* are proportionally long for a geomorph rodent. There are many other points of morphological difference between *Harrymys* and florentiamyids. *Harrymys* lacks two important derived characters of florentiamyids: participation of the palatine in the lateral wall of the anterior alar fissure and union of masticatory and buccinator foramina with the accessory foramen ovale. *Harrymys* has many other features that are more derived than the corresponding characteristics in florentiamyids: rostral perforation present (but see Wahlert, 1983 and 1984, for expression of uncertainty about the condition in florentiamyids); broad suture between alisphenoid and maxilla; sphenopterygoid canal opening within pterygoid fossa; bullae large ventrally with anteromedial processes meeting in midline; mastoid chambers expanded posteriorly and dorsally, and squamosal posteriorly recessed; parietal not extending to occiput. *Harrymys* is not a florentiamyid, nor can it stand in ancestral or descendant relationship to any member of that family.

In order to place *Harrymys* in the geomyoid phylogeny, I have compared the cranial features with those of other taxa in light of previous hypotheses of relationships within the Geomorpha (Wahlert, 1985a, as modified by Wahlert and Souza, 1988). I also assigned numerical values to discrete cranial and dental character states (appendix 1), transcribed the data as a matrix (appendix 2), and used Swofford's (1989) PAUP program (Phylogenetic Analysis Using Parsimony), Macintosh version 3, to generate the most parsimonious phylogenetic trees. Both methods produced similar results and raised similar questions; I discuss them together.

Outgroups used in determining character polarity are the extinct genera *Paramys* and *Sciuravus* of North America (Dawson, 1961; Wood, 1962; Wahlert, 1974, 1985b) and the Eomyoidea (Wilson, 1949; Wood, 1974; Wahlert, 1978; Comte and Vianey-Liaud, 1989). Sciurids (data from Wahlert, 1972) were included in the PAUP analysis as a rough measure of its reliability. Information on incisor enamel structure was taken from Wahlert (1968, 1983, 1989) and Wahlert and Koenigswald (1985). Parameters of the PAUP analysis were as follows: characters unordered; "branch-and-bound" method used to identify all optimal trees; unrooted trees rooted using outgroup method; character-state optimization by delayed transformation (DELTRAN).

Analysis of the data matrix, omitting *Harrymys,* yielded a tree in accord with previously published work. The length of this tree was 119 steps, and the consistency index (CI) 0.561. Such a high degree of homoplasy is consistent with published phylogenetic analyses of the geomyoid rodents. There were eight instances of evolutionary reversal at various nodes. As expected, the sciurid branch is between the primitive ischyromyoids, *Paramys* and *Sciuravus,* and the Geomorpha; no special relationship of sciurids to either group is implied here. The shortest tree that included *Harrymys* placed the taxon as sister group to the clade Geomyidae + Heteromyidae. Its length was 132 steps and CI 0.520.

Prior cogitative analysis of the data yielded several possible relationships for *Harrymys*; the strongest were placement as sister taxon to the entire Heteromyidae or to the Dipo-

domyinae. Since none of these hypotheses was more than seven steps longer than the shortest tree, the "exhaustive search" algorithm of PAUP was used to identify all trees equal to or less than seven steps longer than the shortest tree. The 50 trees generated were manually checked to identify equivocal transformations. There were three reasonable possibilities: *Harrymys* could be a sister group to the heteromyid subfamilies, tree length 133, CI 0.516; to the dipodomyine genera, length 138, CI 0.496; and to *Entoptychus* and *Gregorymys,* length 136, CI 0.504. The remaining possible position, as sister to the Perognathinae + Dipodomyinae, evidently has a tree length greater than any in this set.

The particular tree that I believe to be most likely places *Harrymys* within Heteromyidae as the sister group to the heteromyid subfamilies (fig. 3); this tree is only one step longer than the shortest. *Harrymys* and heteromyids share the prominent rostral perforation, anteromedial to the infraorbital foramen (character 10[state 1], see appendix A), a derived feature that is a unique character among rodents. In this scheme, each lineage examined is set apart by its own combination of derived characters. Changes in character states progress toward greater derivation along the main axis, and the seven reversals that occur are primarily in the branches leading to the various terminal taxa.

Harrymys possesses several additional heteromyid characters: stapedial canal enclosed by bone (34[1]), parietal somewhat retreated from occiput (37[1]), and origin of temporal muscle rstricted to lateral portion of cranium (39[1]). Other characters—position of anterior alar fissure relative to cheek teeth (14), width of maxillary-alisphenoid suture (16), and presence of boss anterior to glenoid fossa (19)—which are noted as changing from states 0 to 1 at the heteromyid limb, have advanced from 1 to 2 in its geomyid sister taxon; stage 1 may be the prior condition for both geomyids and heteromyids.

When *Harrymys* stands as a first branch of the Heteromyidae, all but one of its distinctive characteristics represent evolutionary reversals or instances of homoplasy. *Harrymys* is unique in the great ventral inflation of its auditory bullae (27[2]). The rostrum lacks the derived anterior taper (3[0]), and the incisive
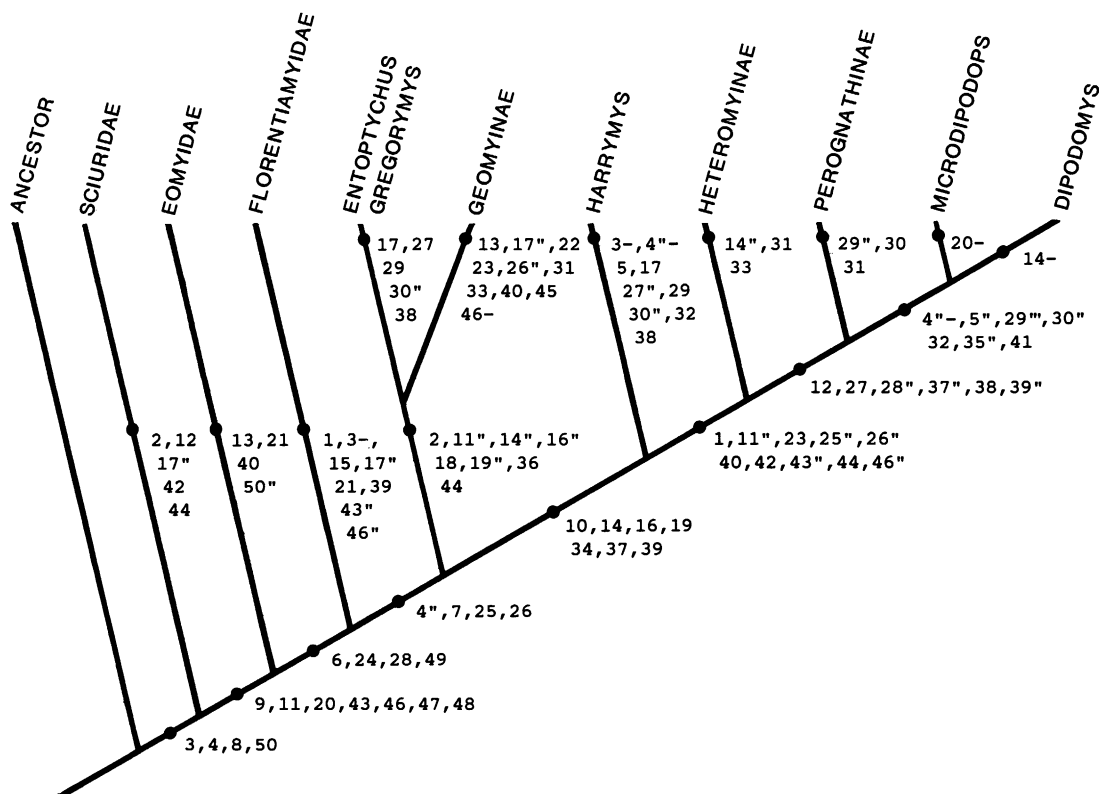
Fig. 3.   Cladogram showing *Harrymys* as the first branch of the Heteromyidae. Numbers refer to characters in appendix A. All characters are at state 0 in the ancestral taxon (based on *Paramys* and *Sciuravus*). Listing of a number by itself indicates change to state 1; a number followed by double or triple prime ["] indicates change to second or third states; a number followed by minus [−] indicates reversal from that state to a lower one. No special relationship of the Geomorpha to the Sciuridae is proposed.

foramina, as in dipodomyines, have reverted to a proportionally longer size (4⁰). The intersection of premaxillary-maxillary suture with the incisive foramen is not at the back but farther forward (5¹), a position intermediate between the primitive (5⁰) and dipodomyine conditions (5²). The dorsal extent of the alisphenoid is moderate (17¹), greater than in other heteromyids and eomyids (17⁰), but less than or equal to the extent in florentiamyids and geomyids (17²). Dorsal inflation of the mastoid (29¹) is similar in degree to that in *Entoptychus* and *Gregorymys* but less than that in perognathines (29²) and dipodomyines (29³). Anteromedial bullar processes that meet at the midline (30²) are similar to those in *Entoptychus* and *Gregorymys* and dipodomyines; the condition is approached in perognathines (30¹). That the bullar wall

is a thin lamina of bone (31⁰, 32¹) as in dipodomyines is perhaps a consequence of its great inflation. Posterior emargination of the squamosal and exposure of the underlying mastoid roof (38¹) occur also in *Entoptychus* and *Gregorymys,* perognathines, and dipodomyines. If *Harrymys* is a heteromyid, then two important derived characters that it lacks must have arisen in parallel between geomyids and all other heteromyids: the ethmoid and other orbital foramina are far anterior (11²), and the superior angular process of the mandible is flared laterally (44¹).

Placement of *Harrymys* in the Dipodomyinae, as the sister taxon to *Microdipodops* and *Dipodomys,* would require 14 evolutionary reversals in the extinct genus. This group of characters is not associated with any one cranial function, and does not appear to sup-

port the possibility of paedomorphosis. It is unlikely that *Harrymys* is a dipodomyine. I have also rejected the association of *Harrymys* with entoptychids, because the latter possess derived features in common with geomyids.

Since Munthe described *Harrymys* as a florentiamyid, he did not explore possible relationships to extinct heteromyids. Heteromyids contemporary with and older than *Harrymys* have been described. Hemingfordian contemporaries include: *Proheteromys* (Heteromyidae, incertae sedis—Wahlert, in press); perognathines—*Mookomys, Trogomys, Stratimus,* and *Perognathus*; dipodomyines—*Cupidinimus* and *Peridiomys*; and *Schizodontomys* of controversial phylogenetic position. Except for *Schizodontomys*, the cranial remains are inadequate for detailed comparison with *Harrymys*. The partial incisive foramina illustrated for *Trogomys* (Reeder, 1960) might have been long. The premaxillary-maxillary suture appears to meet the lateral margin quite far anterior to the back; Reeder's text, however, contradicts this picture and states that the suture crosses the foramina "at or near their posterior borders" (Reeder, p. 126). Useful cranial material of *Mookomys* and *Perognathus* of Hemingfordian age has not been described. *Cupidinimus* evidently had an enlarged dorsal mastoid chamber, and the parietals did not reach the occiput (Wood, 1935: 127). Descriptions of cranial material of *Peridiomys* are unhelpful.

Three specimens of *Schizodontomys harkseni* have been described and the cranial remains figured (Macdonald, 1970, as *Grangerimus harkseni*; Rensberger, 1973; K. Munthe, 1981). Korth et al. (1990) named a new species *S. amnicolus* and figured the skull. It is possible to make a composite of cranial features from these data. Uncertainty about the validity of a composite exists for two reasons. Authors do not describe or illustrate all of the same features. The dentition of *S. amnicolus* does not match Rensberger's (1973) generic definition. The genotypic species, *S. greeni* Rensberger, 1973, consists of a partial left mandible with p4 and m1. Rensberger included *S. harkseni* and *S. sulcidens* in the genus. Characters of the anterior part of p4, given in the generic definition, occur in all

three species: "Metalophid of P_4 with two cusps; lingual cusp larger, oval or D-shaped; accessory cusps other than small anteroconid absent" (Rensberger, p. 60). The diagnosis of *S. amnicolus,* given by Korth et al. (1990: 33), includes the statement: "P_4 with anteroconid and variable other cuspules." Of the three lower premolars figured (fig. 3B, C, D), only one has a D-shaped lingual cusp; the type (incorrectly noted as USNM 26681 in the figure) does not.

The skulls attributed to *Schizodontomys* have the heteromyid character of a large rostral perforation and sharp frontal crests that slightly overhang the orbits. The sphenopalatine foramen is dorsal to M1. The incisive foramina are rather short. The junction of the premaxillary-maxillary suture with the foramen is different in illustrations of Rensberger and of Korth et al. In Rensberger's photograph (1973: pl. 5b), the suture appears to intersect the foramina near their posterior ends; Korth et al. (1990: fig. 2) showed the suture intersecting the foramina near the middle. The palatine foramina are far anterior, medial to M1, and there is usually a smaller posterior pair. The palatine bone extends anteriorly as far as the posterior border of P4. At least one large foramen occurs at the anterior end of each parapterygoid fossa. The pterygoid fossa opens anterodorsally into a sphenopterygoid canal. The auditory bulla forms the posterior border of the foramen ovale. The stapedial artery was present and enclosed, at least partially, by a bony tube on the promontorium. The auditory bullae are inflated ventrally to such a degree that the anterior ends meet in the midline. The mastoid is somewhat inflated both posteriorly and dorsally, and the squamosal bone is posteriorly emarginated. The walls of the bulla and mastoid chambers are thin, noncancellous bone. The frontoparietal suture is posteriorly convex. The origin of the temporal muscle is restricted to the lateral parts of the cranial vault. In the mandible the lower masseteric crest extends as far as or farther than the anterior margin of p4. The coronoid process obscures m3 in lateral view. According to K. Munthe (1981: 9) "the angular process, also similar to that in *Heteromys,* exhibits a gentle lateral bending and has no distinct lateral process."

Harrymys shares many cranial characters with *Schizodontomys,* but there are significant differences. *Harrymys* lacks sharp frontal crests overhanging the orbits. Its incisive foramina are quite long. Bullar processes, and not the chamber walls themselves, meet in the midline. The frontoparietal suture is nearly straight. The m3 is only partially obscured by the coronoid process. The angle is not bent laterally. Thus the skulls of *Harrymys* and *Schizodontomys* are superficially similar, but quite different in detail.

The crown pattern of the lower teeth is the most distinctive feature of the dentition for comparison of *Harrymys* with other geomyoids. The teeth retain primitive geomorph characters: ectolophid which connects metalophid and hypolophid producing H pattern with wear; Y-shaped transverse valley present. Combined with these primitive features, one notes the proximity of protostylid and hypostylid that with wear causes closure of the buccal flexid, and the presence of both a deep posterior embayment of the metalophid between the protoconid and metaconid, and of a posterior valley and cusp that intervene between the hypoconid and entoconid. The separation of cusps in the lophids may be an exaggeration of the primitive condition that can be seen in florentiamyids. With the possible exception of *Stratimus,* the lower teeth of Hemingfordian heteromyids, described above, lack these distinguishing, derived features.

The X or H patterns of worn crowns, in which the transverse lophs are joined at the middle of the tooth, have received frequent comment in descriptions of extinct heteromyid taxa. The two patterns have not been carefully distinguished, however. Presence of an ectolophid, a primitive feature, should produce an H pattern as in *Harrymys.* Transverse crests that simply broaden toward each other near the base would join late in wear and produce an X pattern. The ectolophid is a prominent feature of many eomyid dentitions, though it is placed more lingually. The H or X pattern may also be an early, transitory condition in geomyid molars. The Y form of the transverse valley occurs in florentiamyids, most heteromyids, and in pleurolicines.

The proximity of protostylid and hyposty-

lid, that produces closure of the buccal flexid, and converts the H to an R pattern, occurs in a few other extinct heteromyids, in some *Pleurolicus* specimens, and in two supposed geomyids. *Prodipodomys*? *mascallensis* Downs, 1956 (fig. 7), has a very worn dentition with an X or H pattern in p4 and tiny lakes, which are the remains of buccal flexids in m1 and m2. Downs stated (p. 224): "It is probable that *P.*? *mascallensis* is nearer Dipodomyinae than Perognathinae in the relative depth of mandible, and the slight tendency to high crown, size, and incipient H-pattern in molars." The type specimen is from the Mascall fauna of Grant Co., Oregon, and is of early Barstovian age. The length of the tooth row is about 60 percent of that in *Harrymys irvini.* The teeth are much too worn for traces of a posterior embayment of the lophids to remain. Upper teeth were not found. Shotwell (1967: 24) described the morphology of less worn teeth in *P.*? *mascallensis*; it confirms the potential for formation of an R pattern in lower teeth. He stated that the first contact between lophids is at the styles in m1, and it is central in m2 and m3. Cusps of the hypolophid are separated initially by a groove, but there is no posterior embayment of the crest. Shotwell did not find any known genus that was an entirely satisfactory place for this species; he said (p. 26) that its phylogenetic position "... is one in a group of rodents which has relationships with apparently both heteromyids and geomyids." Lindsay (1972: 59) transferred the species to a new genus *Mojavemys*; he proposed its derivation from *Dikkomys* or *Trogomys.*

An R pattern of wear has been illustrated in *Oregonomys sargenti* (Shotwell, 1956: fig. 6A; 1967: fig. 8 as *Perognathus sargenti*; Martin, 1984: fig. 15), a heteromyid of late Hemphillian Age from the McKay Reservoir local fauna, Umatilla Co., Oregon. Shotwell (1956) named the species as a member of the genus *Perognathus,* but he pointed out (p. 731) that "unlike other forms of *Perognathus* the two lophs of the molars are connected by a small ridge twinned on the p4." *Harrymys* and the other species of *Oregonomys* have but a single connecting ridge on p4. Lower molars of all species of *Oregonomys* (Martin, 1984: fig. 14) show a slight posterior embayment in the

metalophid between the protoconid and metaconid, but there is no deep embayment of the hypolophid as in *Harrymys*. Comparison of published measurements shows that the tooth row is about 70 to 75 percent as long as that of *H. irvini*. Martin (1984) described upper teeth from the type locality. The chief difference from *Harrymys* is that the protoloph of the premolar is short and is dominated by a large, anterior cusp; the protostyle appears to be absent. A cranial fragment of *Oregonomys pebblespringsensis* was figured by Martin (1984: fig. 12a, b); the few details known are similar to *Harrymys*. In dorsal view it appears that the parietals do not reach the occiput, and the interparietal is almost square. The bullae are missing, but symmetrical curves lateral to the parietal bones indicate that they were large with a substantial dorsal chamber in the mastoid. The bullar walls are not trabecular, but numerous supporting struts are present. The stapedial canal is partially ossified.

Korth et al. (1990) described *Stratimus* as a perognathine from the early Hemingfordian Runningwater Formation of Dawes County, Nebraska. In the mandibular dentition (Korth et al., fig. 1) p4 possesses a strong anteroposterior ectolophid. Molars form an X pattern with wear; the transverse lophids of the molars appear to unite at the middle of each tooth because of their shape and not via an ectolophid.

Rensberger (1973: fig. 26) illustrated an R pattern in m1 and m2 of *Pleurolicus dakotensis*. The premolar, however, lacks an ectolophid, and the pleurolicine skulls illustrated are similar to those of entoptychines and not to *Harrymys*. The specimen is of late, early Arikareean age.

Skwara (1988) described and figured individual teeth identified as "*Proheteromys* sp. intermediate species" from the Topham local fauna of Saskatchewan. Korth et al. (1990: 30) pointed out that many of the lower teeth have the characteristic hypolophid of *Stratimus strobeli* and resemble it in size. Skwara stated that the fauna is most like that of Split Rock, Wyoming. The isolated right m1 or m2 (pl. 25, fig. 5 of Skwara) is very similar in crown pattern to that of *Harrymys* but smaller in dimensions.

The lower dentitions of two supposed geomyids, *Dikkomys* and *Lignimus*, resemble those of *Harrymys*. Crown heights are greater than in *Harrymys*, but roots are present on the cheek teeth. Wood (1936) described *Dikkomys matthewi* from isolated teeth recovered from the late Arikareean Harrison Formation near Agate, Sioux Co., Nebraska. He placed it in the Geomyinae. Cheek teeth are hypsodont and rooted. Lower p4, m1, and m2 show an H pattern; the M1 is worn to a reversed N pattern, which is wholly unlike the crown pattern in *Harrymys*. Galbreath (1948) described and figured an entire lower dentition from the so-called Upper Rosebud near Wounded Knee, Shannon Co., SD, that is of late Arikareean age. The m1 and m2 of this specimen are worn to an R pattern. The stated occlusal length of the lower dentition is 90 percent of that of *H. irvini*. Green and Bjork (1980: figs. 2, 3, 4) illustrated wear stages in individual teeth collected at the Hemingfordian Black Bear Quarry II, Bennet Co., South Dakota. They (p. 348) stated: "The cristid mesiobliqua begins at the center of the protoconid and is posterolingually directed to the entoconid." However, the figure shows that, unlike the teeth in *Harrymys*, the cristid (the ectolophid) extends from the metaconid to the hypolophid. This difference shifts the posterior embayment of the metalophid to continuity with the buccal flexid, a character which might be variable and thus trivial. Initially the hypolophid is indented posteriorly in p4 and m1 (the authors stated that m2 and m3 are similar); a cusp is present in this valley in some specimens of p4. The metalophid is also indented posteriorly. The upper teeth are unlike those of *Harrymys*, and confirm Wood's illustrations. Green and Bjork made no mention or show of stylids on lightly worn p4 and m1. Kron (1988: 80) stated: "Lower molars do have a hypostylid. The protostylid is normally reduced."

Black (1961: fig. 5b) illustrated p4 and m1 in a fragmentary left ramus of a new species, *Dikkomys woodi*, from the ?Hemingfordian Deep River Formation, Meagher Co., Montana. The teeth are slightly smaller than those of *D. matthewi*. The R pattern is present in both teeth; the metalophids of p4 and m1 are posteriorly embayed, and the hypolophid of p4 and possibly of m1 is indented posteriorly by a shallow valley. Munthe (1988: 82) reas-

signed the species as *Harrymys woodi*. Russell (1968) transferred Galbreath's specimen of *D. matthewi* to *D. woodi*; I agree with Munthe (1988: 83) (for the reasons he gave) that Russell was in error, and the original attribution stands.

Storer (1970) created the genus *Lignimus* and placed it in the Entoptychinae. Specimens are from the upper Barstovian Wood Mountain Formation of Southern Saskatchewan (Storer, 1970: figs. 6–12; 1975: figs. 74–76) and the early, late Barstovian Norden Bridge local fauna of Brown County, Nebraska (Storer, 1973: figs. 12–14). The crown patterns of lower cheek teeth in *Lignimus montis* resemble those of *Dikkomys matthewi*. The ectolophid connects hypolophid and metaconid (Storer, 1975: 102, fig. 75E); both transverse lophids are embayed posteriorly. The teeth are high-crowned and rooted. P4 has a large anterior cusp, in some with a subsidiary cusp at the front, whereas P4 in *D. matthewi* retains paracone and protocone as a distinct protoloph. The sum of average lengths of individual lower teeth amounts to about 70 percent of the occlusal length of the dentition in *Harrymys irvini*; the largest tooth appears to be p4. Korth (1979) suggested that *Lignimus hibbardi* Storer, 1973, may be generically different from *L. montis*; subsequently he (1987) transferred the species to the geomyine genus *Parapliosaccomys*. *Lignimus transversus* Barnosky, 1986, from the Late Barstovian part of the Colter Formation, Teton County, Wyoming, has morphology similar to that of *Harrymys* in the lower molars. Cheek teeth are brachydont and rooted. The ectolophid in m1 (Barnosky, 1986: pl. vC) may unite the hypolophid and protoconid as in *Harrymys,* but the photograph is unclear on this point.

Akersten (1973: 142) considered *Dikkomys* to be a member of the *Lignimus* group of geomyines. He opined that the "strong medial lophid connections and weak or absent labial lophid connections in the lower molars" preclude inclusion of *Dikkomys* within the Geomyinae. Kron in his Ph.D. dissertation (1988: 63) created a new subfamily of florentiamyid which unites *Dikkomys, Lignimus, Harrymys* (noted as "*Dikkomys*"), and a new genus. Further preparation of specimens at the base of the anterior alar fissure has led him to conclude that these taxa belong

to a heteromyid subfamily (Kron, personal commun.).

I consider *Harrymys* to represent a new subfamily, the Harrymyinae, that is an early branch of the Heteromyidae; it shares with them the large rostral perforation that I have seen nowhere else in the Rodentia. As a consequence of this placement, the lateral projection of the superior angular process of the mandible must have arisen independently in heteromyids and geomyids. Such a projection is common among rodents and can be seen in *Aplodontia, Marmota,* and in the myoxids. Retention of an enclosed accessory foramen ovale and of temporal foramina is also seen in the geomyid entoptychines. The presence of anteromedial processes of the bullae that meet in the midline is an instance of convergence with entoptychines and dipodomyines. Enlargement of mastoid chambers and reduction of the bullar wall to a simple lamina occur only in dipodomyines and possibly *Schizodontomys* among geomyoids.

Some of the genera with similar dental characteristics may also belong in the Harrymyinae. Candidates for inclusion are probable heteromyids with an R pattern in the lower molars: *Prodipodomys*? *mascallensis, Oregonomys, Dikkomys, Lignimus montis,* and *Lignimus transversus*. I hesitate to place *Dikkomys matthewi* in this assemblage because the upper molars differ so much from those of *Harrymys*. The barrier to inclusion of any of these taxa in the subfamily is the nearly complete lack of comparative cranial material.

As more material is discovered and described in detail, the complexity of geomyoid phylogeny becomes ever more daunting. It is appropriate to quote the now famous pronouncement of Wood (1935: 250): "The most important point to be emphasized is that 'Parallelism, parallelism, more parallelism and still more parallelism' is the evolutionary motto of the rodents in general and of the heteromyids in particular. This extends to all parts of the body."

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APPENDIX A

Cranial and Dental Character States

1. Shape of diastema in lateral view
    0 flat
    1 curved

2. Slope of diastema in lateral view
    0 not inclined anteriorly
    1 inclined strongly anteriorly

3. Rostrum
    0 not tapered
    1 tapered by descending nasals

4. Incisive foramen length/diastemal
       length
    0 >.40
    1 .20 to .40
    2 .10 to .19

5. Maxillary-premaxillary suture
       intersects incisive foramina
    0 at back
    1 1/3 from back
    2 near middle

6. Parapterygoid fossae
    0 absent
    1 present

7. Sphenopterygoid canal
    0 absent
    1 present

8. Masseter
    0 protrogomorphous
    1 sciuromorphous

9. Infraorbital canal low
    0 lateral to rostrum
    1 depressed into rostrum

10. Lateral wall of rostrum
    0 solid
    1 perforated at infraorbital
       foramen

11. Ethmoid foramen dorsal to
    0 M3
    1 M2, M3 junction
    2 mid M2 to mid M1

12. Optic foramen
    0 1.0 mm
    1 >1.0 mm

13. Optic foramen
    0 1.0 mm
    1 <1.0 mm

14. Anterior alar fissure rises
    0 far posterior to M3
    1 just posterior to M3
    2 above or anterior to M3

15. Anterior edge of anterior alar
       fissure
    0 alisphenoid only
    1 palatine and alisphenoid

16. Suture of maxilla and alisphenoid
       (lateral view)
    0 none
    1 narrow
    2 broad

17. Dorsal extent of alisphenoid
    0 low
    1 moderate
    2 high

18. Anterior division of temporal
       muscle arises on alisphenoid
    0 none
    1 present

19. Boss anterior to glenoid fossa
       redirects temporal muscle
    0 not present
    1 present
    2 very prominent

20. Masticatory and buccinator
       foramina
    0 separate
    1 united in one opening

21. Masticatory and buccinator
       foramina
    0 separated from accessory
       foramen ovale
    1 united with accessory foramen
       ovale

22. Masticatory foramen
    0 lacking medial opening
    1 with medial opening

23. Posterior margin of accessory
       foramen ovale
    0 ossified
    1 not ossified

24. Foramen ovale
    0 surrounded by alisphenoid bone
    1 bounded posteriorly by auditory
       bulla

25. Posterior alar fissure
   0 absent
   1 present but separated from
     foramen ovale
   2 present and joined with foramen
     ovale

26. Postglenoid foramen
   0 in squamosal bone
   1 in squamosal bone; another
     between squamosal and periotic
   2 between bones and continuous
     with posterior alar fissure

27. Auditory bulla with
   0 no ventral inflation
   1 some ventral inflation
   2 great ventral inflation

28. Mastoid, posterior inflation
   0 none
   1 some
   2 great

29. Mastoid, dorsal inflation
   0 none
   1 slight with window in squamosal
   2 great
   3 very great, joins bulla
     anterior to meatus

30. Anteromedial bullar processes
   0 not present
   1 present
   2 present and meeting in midline

31. Bullar texture
   0 not frothy
   1 frothy

32. Thickness of bulla
   0 thick
   1 thin

33. Stapedial artery
   0 present
   1 absent

34. Stapedial canal
   0 open
   1 enclosed by bone

35. Bullar constriction of
     interparietal
   0 none
   1 some
   2 great

36. Interparietal
   0 wide or constricted by bullar
     inflation
   1 narrow but not constricted by
     bullar inflation

37. Parietal
   0 reaches occiput
   1 somewhat retreated from occiput
   2 does not come near occiput

38. Squamosal
   0 entire posteriorly
   1 emarginate posteriorly

39. Origins of temporal muscles
   0 reach or come close to midline
   1 restricted laterally
   2 restricted very far laterally

40. Temporal foramen
   0 present
   1 absent

41. Anterior squamosal foramen
   0 lacking
   1 present

42. Frontal flange over orbit
   0 lacking
   1 present

43. Anterior end of masseteric fossa
   0 posterior to p4
   1 under p4
   2 anterior to p4

44. Superior angular process
   0 in plane of mandible
   1 flared laterally

45. Angle of mandible
   0 large
   1 reduced

46. Relative size of coronoid process
   0 large
   1 small
   2 very small

47. Posterior end of incisor alveolus
   0 in plane of mandible
   1 projects laterally from
     mandible

48. Cheek teeth
   0 cuspidate
   1 lophate

49. Cheek teeth having styles
   0 but not bilophodont
   1 and bilophodont

50. Incisor enamel
   0 pauciserial
   1 uniserial
   2 special uniserial

APPENDIX B
Data Matrix of Cranial and Dental Character States

Taxon	Character states				
Ancestor[a]	00000	00000	00000	00000	00000
Sciuridae	01110	00100	?1000	0200(01)	00(01)0(01)
Eomyidae	0(01)110	00110	(12)01(01)0	00001	1000(01)
Florentiamyidae	100(12)0	1011?	10001	02001	10010
Heteromyinae	10120	11111	20(01)20	10011	0(01)112
Perognathinae	10120	11111	21010	1001(01)	00112
Microdipodops	101(01)2	11111	21010	100?0	00112
Dipodomys	10112	11111	21000	100?1	00112
Entoptychinae[b]	011(12)0	11110	200(23)0	2112(01)	00011
Geomyinae	01120	11110	201(23)0	2212(01)	0111(12)
Harrymys	00001	11111	1?010	11011	00011

Taxon	Character states (continued)				
Ancestor[a]	00000	00000	00000	00000	00000
Sciuridae	(02)0000	0(01)0?0	?000(01)	01(01)10	(012)0001
Eomyidae	00000	?0000	000?1	00100	11102
Florentiamyidae	00100	00000	00010	0(01)200	21111
Heteromyinae	20100	101?0	01011	01210	21111
Perognathinae	21221	1001(01)	02121	01210	21111
Microdipodops	21232	01012	02121	11210	21111
Dipodomys	21232	01012	02121	11210	21111
Entoptychinae[b]	11112	?00?0	10100	00110	11111
Geomyinae	20(01)00	101?0	10001	00111	01111
Harrymys	12112	01010	01110	00100	11111

[a]Ancestor: Based on *Paramys* and *Sciuravus*.
[b]Entoptychinae: Based on *Entoptychus* and *Gregorymys*.