Relationships of the Florentiamyidae (Rodentia, Geomyoidea) Based on Cranial and Dental Morphology

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ABSTRACT

The family Florentiamyidae is redefined based on derived cranial and dental characteristics that demonstrate monophyly. A unique process from the palatine, together with the alisphenoid, forms the edge of the anterior-alar fissure; the foramen for the descending palatine vein is lateral to the process. The optic foramen is larger than 1.0 mm. Masticatory and buccinator foramina are united with the accessory foramen ovale. The temporal foramen is large. The frontal is wide with roughly parallel, marginal flanges that project over the orbits. An anteriorly concave process on the petrosal descends posterior to the fenestra cochleae. The entostyle in the upper molars is elongated and blocks the lingual end of the transverse valley. The florentiamyids share primitive characters with eomyoids and Sciuravus that are modified in other geomyoids; these indicate that the family is the earliest branch in the phylogeny of geomyoid rodents. Cranial and dental morphology of florentiamyids is described. Variations in tooth crown patterns illustrate possible origin of the typical geomyoid pattern. Evidence of cusp height and wear facets supports the hypothesis that geomyoid teeth are widened by the addition of styles. Completeness of fossil material suggests that florentiamyids were burrowers. The genera Sanctimus and Florentiamys are redefined, and three new species of each genus are named and described. New specimens range in age from late Oligocene to early Miocene. Diagnoses of previously described species are revised. The species S. tiptoni is transferred to the genus Florentiamys; ?S. clasoni and ?F. agnewi are designated as Geomyoidea incertae sedis.

INTRODUCTION

The florentiamyid rodents, heretofore accorded only subfamilial rank, are of especial interest in the study of geomyoid phylogeny. The cheek teeth and skull retain some primitive features that shed light on the development of special characteristics in geomyoids. Known specimens of florentiamyids range in age from late Oligocene into early Miocene time, a span of about eight million years. Their distribution is limited to south-

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western South Dakota, western Nebraska, and southeastern Wyoming, areas that are contiguous.

Two genera of florentiamyid have been named, *Florentiamys* Wood, 1936, and *Sanctimus* Macdonald, J. R., 1970. Although the skulls and jaws of the type species have been described and figured, the three phylogenetic hypotheses proposed for florentiamyids are based on comparison of tooth crown patterns.

Wood (1936, p. 49) said: "The possibility has been suggested on the basis of the genotype that the heteromyids represent a simplification of a *Paramys*-like pattern, with reduction of the anterior and posterior cingula and transformation of the rather crescentic cusps of *Paramys* to conical cusps such as are found in *Heliscomys,* by way of an intermediate stage similar to *Florentiamys.* If this is true, *Heliscomys* is much too specialized to be the ancestor of *Florentiamys,* whether or not it is ancestral to the other heteromyids."

Wilson (1949, p. 116) remarked on the uniqueness of dental structure in *Florentiamys* but said: "In any case, it seems difficult to view *Florentiamys* as anything other than a heteromyid, and it and *Griphomys* together suggest that the ancestors of the Miocene and later geomyoids may have passed through a series of changes somewhat comparable to a *Taxymys* (or *Sciuravus*)–*Griphomys*–*Florentiamys* structural series. The relatively isolated and conical cusps in *Heliscomys* may be in part an end result, not necessarily passed through by all later forms."

Rensberger (1973b, p. 835) derived florentiamyids from *Heliscomys* and said: "Increased molariformity of the premolars represents a reversal of the direction of evolution from the eomyids and ischyromyoids to *Heliscomys,* in which premolars became smaller and simpler."

Heliscomys is an extinct geomyoid that is usually assigned to the Heteromyidae. Specimens are of greater geologic age than the known florentiamyids. Its phylogenetic position and a conception of what characteristics are primitive in geomyoid rodents depend on how one interprets the anatomy of the florentiamyids.

I have made one important revision in cra-

nial terminology. Heretofore, I have followed Hill (1935) in naming the fissure in the posterior part of the orbital depression the sphenoidal fissure. Hill claimed that this opening corresponds to the superior orbital fissure and foramen rotundum in primates, and he did not observe that their homologues are still present in an inner layer of the alisphenoid that invests the brain. The fissure is, in fact, the anterior end of the alisphenoid canal. I have chosen a new name, the anterior-alar fissure, to express its unique position and morphology and its distinctness from the orbital fissure. The abbreviation spn used in my previously published figures is here changed to aaf.

ACKNOWLEDGMENTS

TABLE 1
Cranial Lengths and Widths in Millimeters[a]

	LENGTH					WIDTH		
	Condylo-basilar	Diastemal	Incisive foramen	Palatal	Pterygoid	Palatine	Inter-orbital	Posterior cranial
S. stouti								
F:AM 103385	44.5	16.1	3.8	26.0	7.4	4.9	11.6	—
S. simonisi								
F:AM 103380	49.7	18.7	5.2	30.7	9.2	6.0	14.9	22.0
S. falkenbachi								
F:AM 103383	45.9	15.4	4.2	—	7.1	4.3	—	—
F. loomisi								
ACM 1927-126	46.4	16.0	3.2	27.2	7.0	4.4	—	19.3
F. kingi								
F:AM 103384	46.4	17.2	3.7	27.9	7.5	4.6	13.0	19.4
F:AM 103381	44.2	16.5	3.2	27.0	7.4	5.7	12.5	20.0
F. kennethi								
F:AM 103382	—	15.0	4.1	24.3	—	3.9	—	—
F:AM 103387	—	—	—	—	5.7	5.0	13.5	20.3
YPM 20285	—	15.2	3.6	24.5	6.3	4.8	12.0	—
F. kinseyi								
F:AM 103388	—	14.5	3.5	26.0	—	4.8	—	—
F:AM 103389	—	16.9	3.5	—	—	5.6	12.0	—

[a] See text.

ABBREVIATIONS

The catalogue numbers of specimens contain acronyms of several institutions:

ACM, Amherst College, Pratt Museum
F:AM, Frick Collection, American Museum of Natural History
LACM, Los Angeles County Museum
SDSM, South Dakota School of Mines
YPM, Yale Peabody Museum

Other abbreviations in the Systematics section conform to the notation of specimen completeness used in my previous publications: c, cranium; j, mandible; n, snout; o, orbit; p, palate; s, entire skull; t, pterygoid region.

MEASUREMENTS

For cranial dimensions of florentiamyids see table 1. All measurements were made with a Helios dial caliper with subdivisions of one-twentieth mm marked. Condylobasilar length is measured from the henselion, a line tangent to the backs of the incisor alveoli, to a line that is tangent to the posterior curves of the occipital condyles. Palatal length is from the henselion to the posterior edge of the palate at the midline. Diastemal length is the shortest line between the back of an incisor alveolus and the front of the alveolus of the first cheek tooth on the same side. Pterygoid length is the shortest line from the posterior surface of the third molar to the anterior edge of the foramen ovale. Minimum interorbital breadth is across the frontal bones; cranial width is taken at the most medial parts of the posterior squamosal roots of the zygomatic arches and is across parts of the squamosals, parietals, and interparietal. All skull dimensions have an inherent error brought about by distortion that usually occurs in the course of fossilization. In this particular sample, lateral shortening and dorsoventral expansion predominate.

For the dimensions of cheek teeth and incisors see tables 2 and 3. Maximum dimen-

TABLE 2
Dimensions of Upper Teeth; Width : Length (in Millimeters)

	P^4–M^3	I	P^4	M^1	M^2	M^3
S. stuartae[a]						
LACM 15292	7.0	—	1.5 : 1.8	1.8 : 1.9	2.1 : 1.8	1.8 : 1.6
S. stouti						
F:AM 103385	8.5	1.5 : 3.3	2.6 : 2.4	2.4 : 2.0	2.4 : 2.0	2.1 : 1.9
S. simonisi						
F:AM 103380	9.0	1.5 : 3.3	2.8 : 2.5	2.9 : 2.2	2.8 : 2.1	2.4 : 1.9
S. falkenbachi						
F:AM 103383	9.4	1.7 : 3.1	3.1 : 3.1	2.8 : 2.1	2.7 : 1.7	— : 1.8
F. loomisi						
ACM 1927-126	8.4	1.6 : 3.2	2.5 : 2.4	2.6 : 1.9	2.5 : 1.8	2.1 : 1.7
F. tiptoni[a]						
SDSM 632	7.8	—	2.5 : 2.3	2.5 : 2.1	2.3 : 1.8	1.9 : 1.6
F. kingi						
F:AM 103384	8.6	1.4 : 3.0	2.5 : 2.4	2.5 : 2.0	2.5 : 1.9	2.2 : 1.7
F:AM 103381	—	1.3 : 3.1	2.6 : 2.4	2.5 : 1.9	2.4 : 2.0	—
F. kennethi						
F:AM 103382	7.8	1.3 : 2.7	2.3 : 2.1	2.6 : 2.0	2.4 : 1.9	2.1 : 1.7
F:AM 103387	7.9	—	2.4 : 2.1	2.7 : 1.9	2.6 : 2.0	2.3 : 1.8
YPM 20285	7.9	1.4 : 3.1	2.4 : 2.1	2.5 : 1.9	2.3 : 1.8	2.0 : 1.7
F. kinseyi						
F:AM 103388	9.3	1.2 : 2.7	2.6 : 2.4	2.8 : 2.2	2.7 : 2.2	2.3 : 2.0
F:AM 103389	—	1.3 : 3.0	2.9 : 2.7	3.1 : 2.2	—	—
F: AM 103389a	—	1.5 : 3.0	2.9 : 2.7	— : 2.2	2.7 : 2.2	—

[a] Measurements derived from Macdonald, 1970.

sions of individual cheek teeth were taken parallel and perpendicular to the longest loph of each tooth. In the molars this is the anterior loph or lophid; in the premolars, the posterior one. Crown length of the cheek teeth is measured parallel to the axis of the tooth row. Since this line is not coincident with the segments taken to be the length of each tooth, the sum of individual tooth lengths is not equal to the overall crown length. Interdental wear contributes to error in measurement of true length; it is probably less important in the first and last cheek teeth, which are worn only at one end.

SYSTEMATICS

SUBORDER MYOMORPHA

INFRAORDER GEOMORPHA THALER, 1966

SUPERFAMILY GEOMYOIDEA WEBER, 1904

FAMILY FLORENTIAMYIDAE WOOD, 1936

REVISED DIAGNOSIS: Special process from palatine, together with alisphenoid, forming edge of anterior alar fissure; dorsal aperture of 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. Temporal foramen large, dorsal to postglenoid foramen. Frontal transversely wide with roughly parallel, marginal flanges over orbits. Descending process, concave anteriorly, on petrosal posterior to fenestra cochleae. Entostyle of upper molars elongated and blocking lingual end of transverse valley.

SANCTIMUS MACDONALD, J. R., 1970

TYPE SPECIES: *Sanctimus stuartae* Macdonald, J. R., 1970.

REVISED DIAGNOSIS: Protostyle of P^4 large, closely connected to anterolingual side of protocone, divided from entostyle by shallow valley. Protostylid single in P_4.

TABLE 3
Dimensions of Lower Teeth; Width : Length (in Millimeters)

	P_4-M_3	I	P_4	M_1	M_2	M_3
S. stuartae[a]						
LACM 15292	7.0	—	2.1 : 1.8	2.2 : 1.8	2.2 : 2.0	1.9 : 1.5
S. stouti						
F:AM 103385	8.5	1.3 : 2.7	1.9 : 2.0	2.2 : 2.0	2.3 : 2.0	2.2 : 2.0
S. falkenbachi						
F:AM 103383	9.5	1.5 : 2.9	2.5 : 2.8	2.5 : 2.0	2.7 : 2.0	2.4 : 2.0
F. loomisi						
ACM 1927-126	8.5	1.4 : 2.6	1.9 : 2.1	2.3 : 2.2	2.4 : 2.2	2.1 : 1.8
F. kingi						
F:AM 103384	8.6	1.4 : 2.7	2.0 : 2.4	2.2 : 2.2	2.4 : 2.1	2.2 : 2.0
F. kennethi						
F:AM 103382	7.9	1.2 : 2.2	1.8 : 1.9	2.2 : 2.0	2.4 : 2.0	2.0 : 1.9
F:AM 103386	8.7	1.2 : 2.9	2.0 : 2.5	—	—	2.2 : 2.0
F:AM 103387	8.1	1.3 : 2.6	1.8 : 2.0	2.3 : 2.0	2.4 : 2.0	2.1 : 1.9
YPM 20285	—	1.2 : 2.6	—	—	2.3 : 1.8	2.0 : 1.5
F. kinseyi						
F:AM 103388	9.3	1.1 : 2.2	2.0 : 2.3	2.3 : 2.3	2.6 : 2.3	2.3 : 2.2
F:AM 103389	9.1	1.3 : 2.9	2.1 : 2.3	2.4 : 2.2	2.6 : 2.2	2.2 : 2.0
?F:AM 103379	9.0	1.4 : 2.6	2.2 : 2.4	2.3 : 2.1	2.5 : 2.1	2.2 : 2.0
?*F. agnewi*[b]						
SDSM 55120	—	—	1.7 : 1.8	2.0 : 1.8	—	—
?*S. clasoni*						
SDSM 54388	—	—	1.7 : 2.0	2.0 : 1.9	—	—

[a] Measurements derived from Macdonald, 1970.
[b] *Ibid.,* 1963.

Sanctimus stuartae Macdonald, J. R., 1970

TYPE SPECIMEN: LACM 15292 (sj). J. R. Macdonald, 1970, figure 23; Rensberger, 1973, figures 2, 3.

TYPE LOCALITY AND AGE: LACM 1819, Wounded Knee area, Shannon Co., S.D.; near top of Sharps Formation, early Arikareean (late Oligocene).

REVISED DIAGNOSIS: Small skull. Crown lengths of upper and lower cheek teeth low (tables 2 and 3). P_4 unusually short and rounded, lacking hypostylid, both exceptions for the genus.

Sanctimus stouti, new species

TYPE SPECIMEN: F:AM 103385 (sj); figures 2A and 6.

TYPE LOCALITY AND AGE: Muddy Creek, Niobrara-Platte Co. boundary, Wyo.; Monroe Creek Formation, early Arikareean (late Oligocene).

ETYMOLOGY: Named for Prof. T. Mylan Stout, vertebrate paleontologist at the University of Nebraska, Lincoln, who guided me in the initial stages of this study.

DIAGNOSIS: Dimensions of skull and dentition larger than *S. stuartae* (tables 1–3). P_4 longer, possessing hypostylid as do other species of the genus.

Sanctimus simonisi, new species

TYPE SPECIMEN: F:AM 103380 (s); figures 2B, 4, and 7.

TYPE LOCALITY AND AGE: Muddy Creek, Niobrara-Platte Co. boundary, Wyo.; Monroe Creek Formation, early Arikareean (late Oligocene).

ETYMOLOGY: Named for Mr. Otto Simonis, preparator of fossil mammals at the American Museum of Natural History.
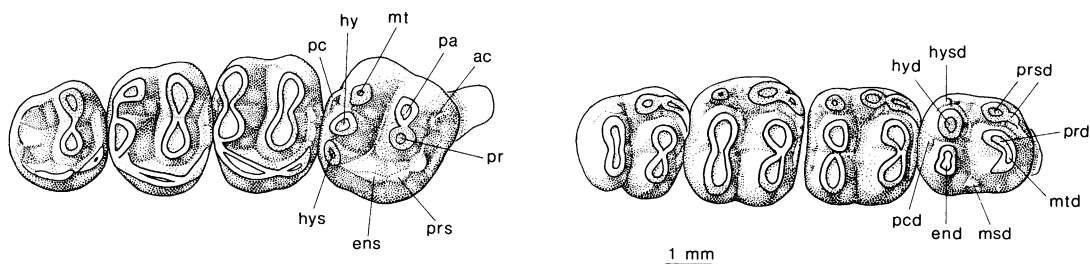
FIG. 1. *Florentiamys loomisi,* ACM 1927-126. Upper right and lower left cheek teeth. *Abbreviations:* ac, anteroconid; end, entostylid; ens, entostyle; hy, hypocone; hyd, hypoconid; hys, hypostyle; hysd, hypostylid; msd, mesostylid; mt, metacone; mtd, metaconid; pa, paracone; pc, posterocone or cingulum; pcd, posteroconid or cingulum; pr, protocone; prd, protoconid; prs, protostyle; prsd, protostylid.

DIAGNOSIS: Zygomatic arch heavier and skull longer and broader than other species (table 1); maxillary part of arch strongly bowed; posterior opening of alisphenoid canal visible just anterior to combined accessory foramen ovale, masticatory and buccinator foramina.

Sanctimus falkenbachi, new species

TYPE SPECIMEN: F:AM 103383 (npcj); figures 2C and 8C.

TYPE LOCALITY AND AGE: First breaks, 6 or 7 miles S of Harrison, Sioux Co., Nebr.; Harrison Formation, late Arikareean (early Miocene).

ETYMOLOGY: named for Mr. Charles Falkenbach, collector of this and several other florentiamyid specimens in the Frick Collection.

DIAGNOSIS: Hypertrophy of protostyle giving P^4 unique anterolingual bulge; premolars unusually large relative to other cheek teeth (tables 2 and 3). Protoconid anteroposteriorly
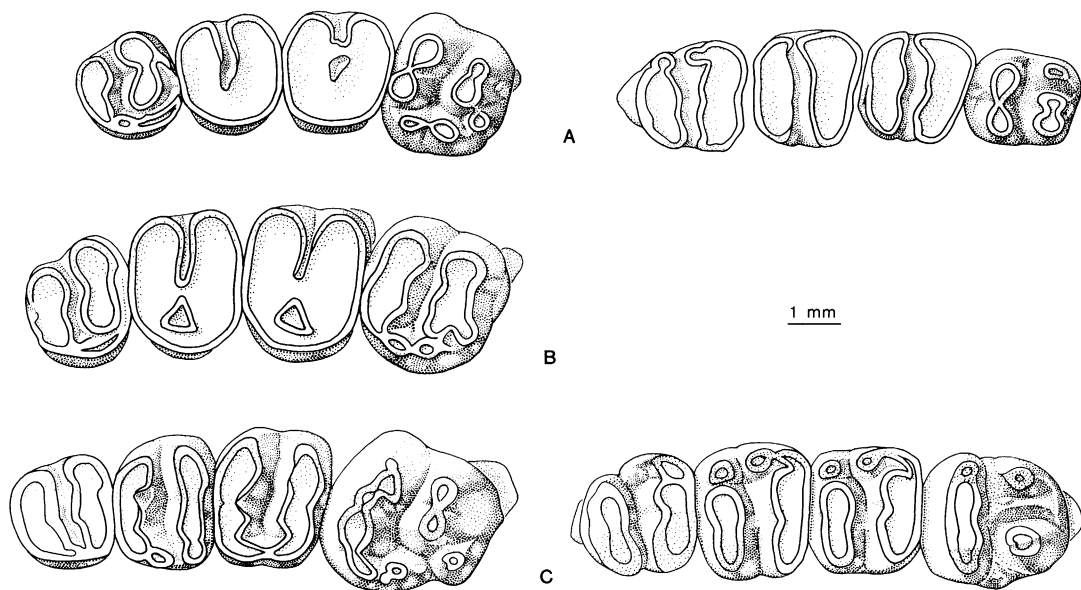

FIG. 2. *Sanctimus.* Cheek teeth. A. *S. stouti,* F:AM 103385, composite of upper left and right, lower left. B. *S. simonisi,* F:AM 103380, upper right. C. *S. falkenbachi,* F:AM 103383, upper right, lower right reversed.
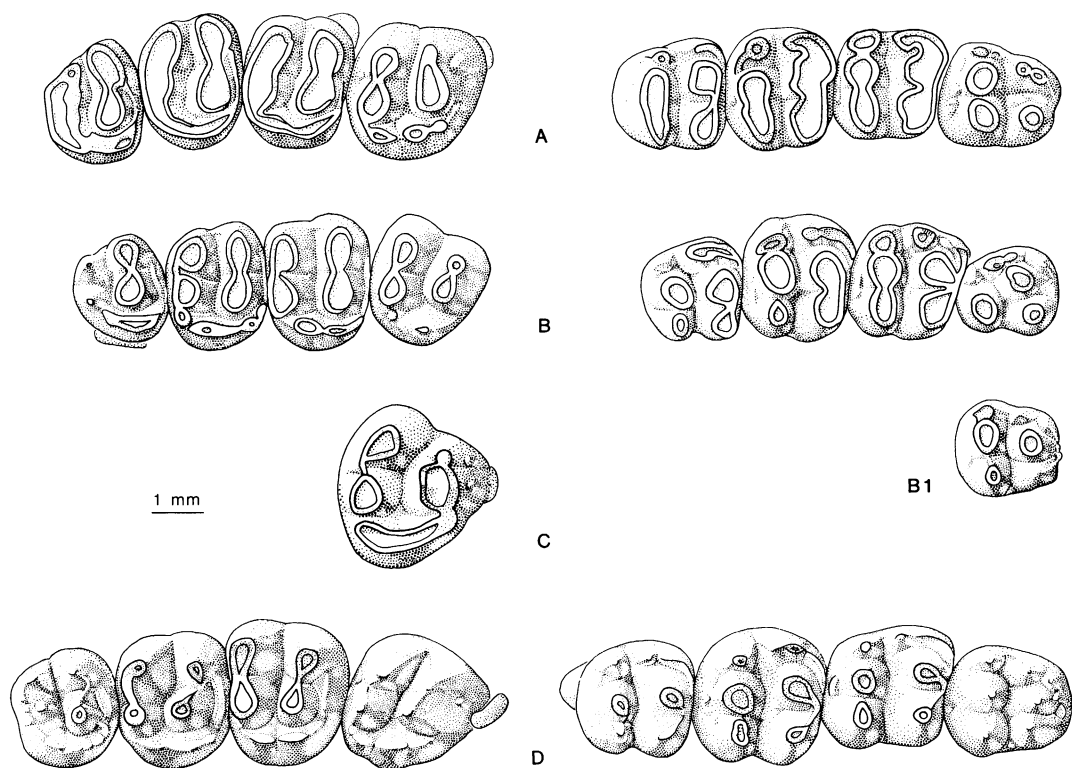
FIG. 3. *Florentiamys*. Cheek teeth. A. *F. kingi*, F:AM 103384 upper right, lower left. B. *F. kennethi*, F:AM 103382, upper left reversed, lower left with malformed P_4. B1. F:AM 103382, right P_4 reversed. C. *F. kinseyi*, F:AM 103389, right P^4. D. *F. kinseyi*, F:AM 103388, upper right, lower left.

elongated and low mesostylid blocking lingual end of transverse valley in P_4; posterior cingulum lacking on lower cheek teeth. Front of lower incisors rounded, not slightly flattened as in other florentiamyid species.

FLORENTIAMYS WOOD, 1936

TYPE SPECIES: *Florentiamys loomisi* Wood, 1936.

REVISED DIAGNOSIS: Protostyle small, continuous with entostyle in P^4; protostylid double in P_4.

Florentiamys loomisi Wood, 1936

TYPE SPECIMEN: ACM 1927-126 (sj and postcranial elements); figure 1. Wood, 1936, figures 1–7.

TYPE LOCALITY AND AGE: Five miles SE of Hagie, along north face of 66 Mountain, Goshen Co., Wyo.; Gering or Monroe Creek Formation, early Arikareean (late Oligocene).

REVISED DIAGNOSIS: Anterior cingulum forming broad shelf in upper molars and giving M^3 a rounded appearance; cingulum present anterior to protocone in P^4. Low mesostylid blocking lingual end of transverse valley in P_4; anterior cingulum present on lower molars, developed most clearly on M_1.

Florentiamys tiptoni
(Macdonald, J. R.), 1970

TYPE SPECIMEN: SDSM 632 (p fragment). J. R. Macdonald, 1970, figure 24; Rensberger, 1973b, figure 4.

TYPE LOCALITY AND AGE: SDSM V6215, Ironcloud Ranch, Shannon Co., S.D.; Monroe Creek Formation, early Arikareean (late Oligocene).
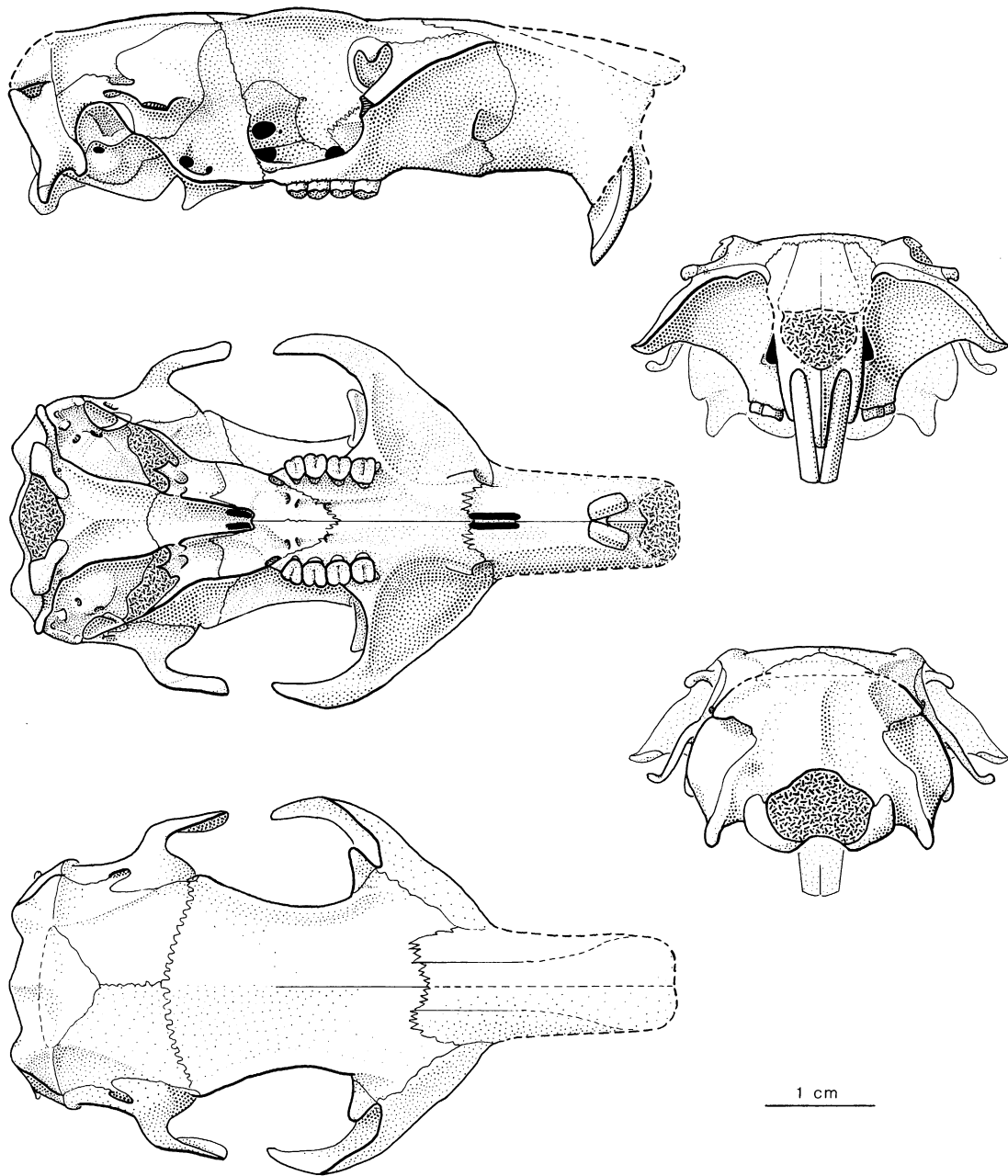
FIG. 4. *Sanctimus simonisi*, F:AM 103380. Skull. Dashed lines indicate restoration; cross hatching, imagined cut through bone.

REVISED DIAGNOSIS: Small *Florentiamys* (table 2). Molars forming series of distinctly graded sizes with M^1 largest; anterior cingulum forming narrow shelf in upper molars.

Florentiamys kingi, new species

TYPE SPECIMEN: F:AM 103384 (sj); figures 3A, 5, 8A, 8B, and 9.

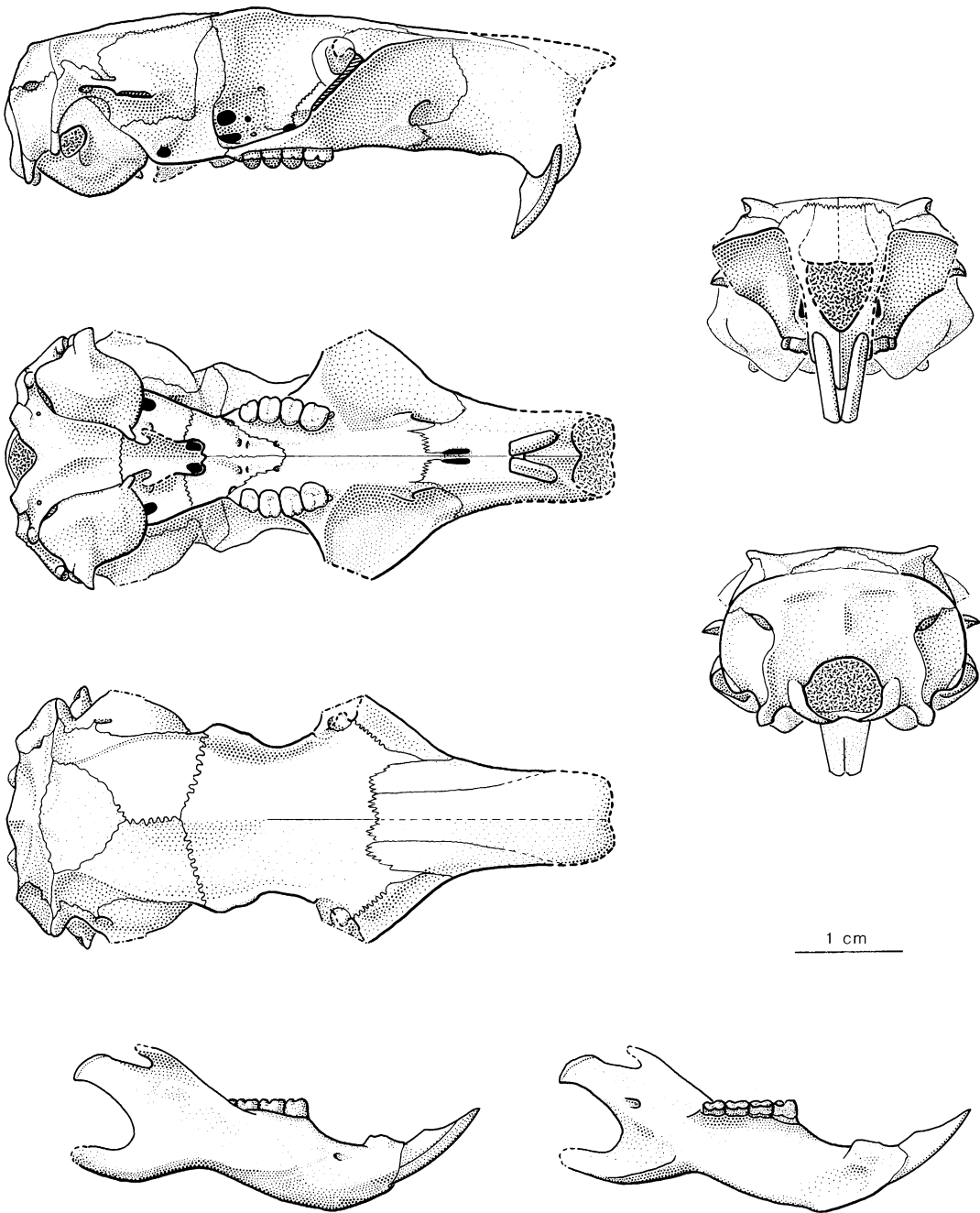TYPE LOCALITY AND AGE: Willow Creek,

FIG. 5. *Florentiamys kingi,* F:AM 103384. Skull. Dashed lines indicate restoration; cross hatching, imagined cut through bone.

Niobrara Co., Wyo.; Gering Formation, early Arikareean (late Oligocene).

REFERRED SPECIMENS: F:AM 103381 (s),

Little Muddy Creek, Niobrara Co., Wyo.; Gering Formation, early Arikareean (late Oligocene).

ETYMOLOGY: Named for Dr. David B. King, developmental biologist at Franklin and Marshall College.

DIAGNOSIS: Same size as *F. loomisi* (tables 1–3). Anterior cingulum forming narrow shelf in upper molars, present anterior to protocone in P^4. Protoconid forming low, anteroposteriorly elongated ridge on buccal side of metaconid, and mesostylid absent in P_4; anterior cingulum lacking in lower molars.

Florentiamys kennethi, new species

TYPE SPECIMEN: F:AM 103382 (npj and postcranial elements); figure 3B and 3B1.

TYPE LOCALITY AND AGE: Horse Creek, Goshen Co., Wyo.; Gering Formation, early Arikareean (late Oligocene).

REFERRED SPECIMENS: F:AM 103386 (j), Little Muddy Creek, Niobrara Co., Wyo.; F:AM 103387 (potcj and postcranial elements). Three miles ENE of Tremain Station, Goshen Co., Wyo.; both Gering Formation. YPM 20285 (npotj), Muddy Creek, Niobrara-Platte Co. boundary, Wyo.; Monroe Creek Formation. All sites early Arikareean (late Oligocene).

ETYMOLOGY: Named in memory of Dr. Kenneth R. John, formerly vertebrate biologist at Franklin and Marshall College.

DIAGNOSIS: Skull and dentition smaller than in *F. loomisi* (tables 1–3); optic foramen dorsal and posterior to M^3. P^4 somewhat triangular with anterior end rotated lingually so that root of paracone is more nearly anterior, and protostyle and entostyle probably united in single, large, lingual cusp; anterior cingulum absent in P^4, forming narrow shelf in upper molars. Mesostylid absent in P_4 and anterior cingulum lacking in lower molars.

COMMENT: Left P_4 in type specimen is malformed; the protoconid is exceptionally large, and other cusps are displaced (fig. 3B and 3B1).

Florentiamys kinseyi, new species

TYPE SPECIMEN: F:AM 103388 (npj immature); figure 3D.

TYPE LOCALITY AND AGE: Three miles ENE of Tremain Station, Goshen Co., Wyo.; Gering Formation, early Arikareean (late Oligocene).

REFERRED SPECIMENS: F:AM 103389 (n), figure 3C; F:AM 103389a (P^4–M^2); ?F:AM 103379 (j); Little Muddy Creek, Niobrara Co., Wyo.; Gering Formation, early Arikareean (late Oligocene).

ETYMOLOGY: Named for Dr. W. Fred Kinsey, anthropologist and Director of the North Museum, Franklin and Marshall College.

DIAGNOSIS: Skull and dentition larger than in *F. loomisi* (tables 1–3). P^4 quite triangular and rotated so that root of paracone is anterior; anterior cingulum forming narrow shelf in upper molars. Lacking mesostylid in P_4 and anterior cingulum in lower molars.

COMMENT: The cranial dimensions of the type specimen are low, because the individual is immature (table 1); the cheek teeth are little worn. The incisor enamel of F:AM 103379 is not pigmented, and the shape of the tooth, broadest posterior to the middle, differs from that of the type. A lower jaw, included in the field package with referred specimens, F:AM 103389 and F:AM 103389a, is not definitely associated with either; the P_4 has a single protostylid as in *Sanctimus*, but the dental dimensions best match this species of *Florentiamys*.

GEOMYOIDEA *INCERTAE SEDIS*

?*Florentiamys agnewi*
Macdonald, J. R., 1963

TYPE SPECIMEN: SDSM 55120 (j). J. R. Macdonald, 1963, figure 18.

TYPE LOCALITY AND AGE: SDSM V5360, Shannon Co., S.D.; Sharps Formation, early Arikareean (late Oligocene).

COMMENT: A small, peculiar geomyoid (table 3). Protostylid displaced posteriorly in P_4 and M_1; protostylid and hypostylid joined and blocking buccal end of transverse valley in M_1.

?*Sanctimus clasoni*
(Macdonald, J. R.), 1963

TYPE SPECIMEN: SDSM 54388 (j). J. R. Macdonald, 1963, figure 12.

TYPE LOCALITY AND AGE: SDSM V5350, Shannon Co., S.D.; Sharps Formation, early Arikareean (late Oligocene).

REFERRED SPECIMENS: Six partial mandibles (J. R. Macdonald, 1970).
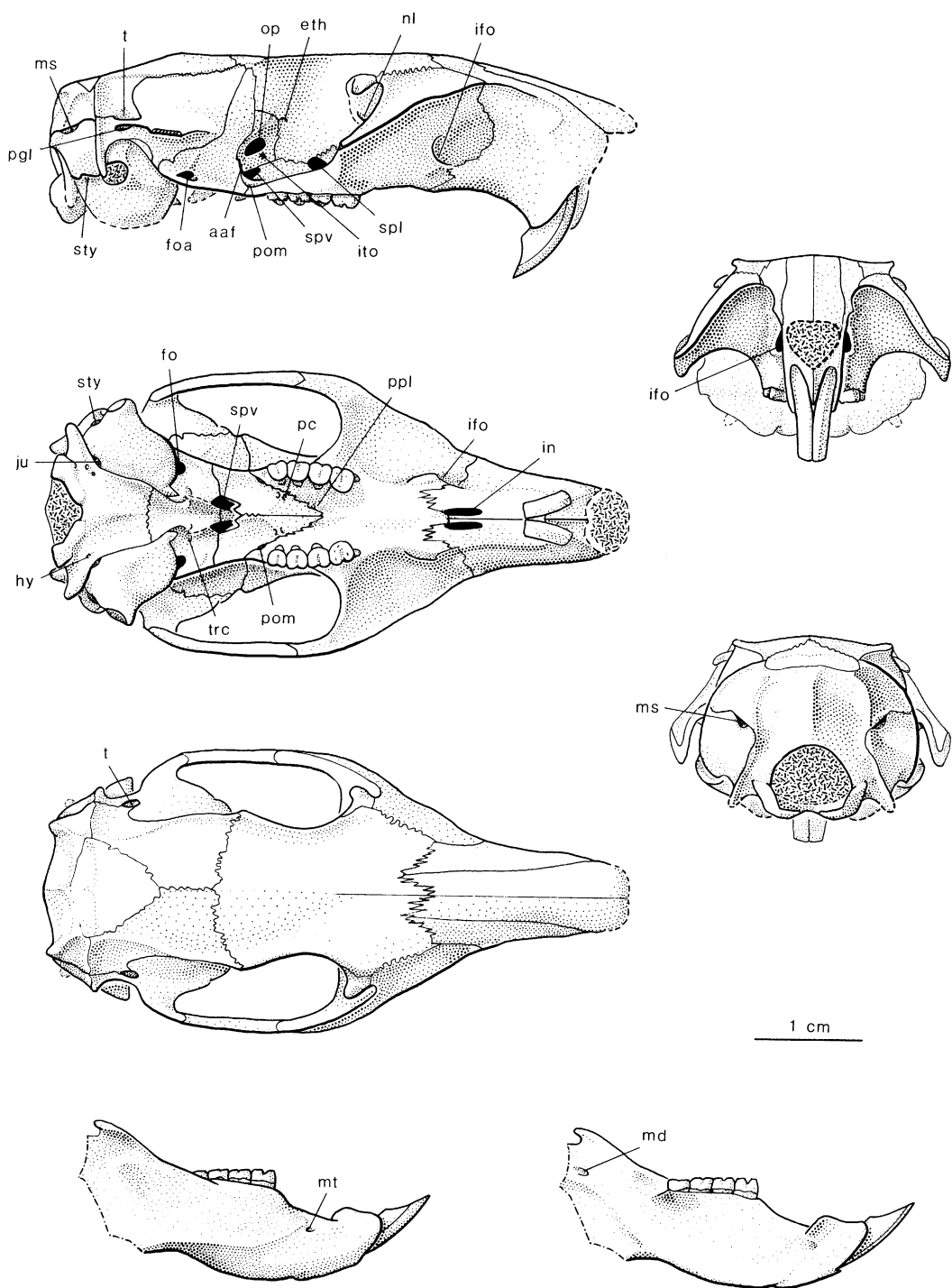
FIG. 6. *Sanctimus stouti,* F:AM 103385. Skull. Dashed lines indicate restoration; cross hatching, imagined cut through bone. *Abbreviations:* aaf, anterior-alar fissure (=spn, sphenoidal fissure, of previous publications); eth, ethmoid; fo, foramen ovale; foa, accessory foramen ovale; hy, hypoglossal; ifo, infraorbital; in, incisive; ito, interorbital; ju, jugular; md, mandibular; ms, mastoid; mt, mental; nl, nasolacrimal; op, optic; pc, palatine canal; pgl, postglenoid; pom, posterior maxillary; ppl, posterior palatine; spl, sphenopalatine; spv, sphenopalatine vacuity; sty, stylomastoid; t, temporal; trc, transverse canal.

COMMENT: A small geomyoid (table 3) with single protostylid and prominent anterostylid on P_4.

FLORENTIAMYID SKULL AND DENTITION

The features of the skull and jaws are illustrated and labeled in figure 6; for the dimensions of specimens see table 1. The skull is of moderate size. The palate is nearly parallel to the gently arched dorsal surface of the skull. The temporal crests are closest posteriorly where they meet the edges of a large interparietal; they flare anterolaterally to maximum separation at the parietal-frontal junction. The zygomatic arch is slender. The posterior half of the median suture between the frontal bones is fused. The frontal is transversely wide with roughly parallel marginal flanges that extend over the orbits. The palate is wide and flat between the cheek teeth. The paired depressions at the back of the palate that slope posterodorsally into the pterygoid fossae are presumed to have held salivary glands, as they do in living geomyids. The basioccipital is keeled. The auditory bullae are not inflated. The average ratio of certain cranial dimensions compared with condylobasilar length is: diastema, 0.35; entire palate, 0.58; pterygoid region, 0.15.

The incisive foramina are short, 30 percent or less of the diastemal length; their lateral margins are intersected at the back by the premaxillary-maxillary suture. The posterior palatine foramina are medial to the junction of M^1 and M^2 or to the anterior part of M^2, and they are in the maxillary-palatine suture. A canal passes horizontally through the palatine from the anterior end of each depression at the back of the palate to the palate proper; in living geomyids a branch of the descending palatine vein passes through this region.

The florentiamyids were fully sciuromorphous. The infraorbital canal is long and situated low in the rostrum; at its anterior end the canal is sunk into the snout, and the lateral wall of the infraorbital foramen is nearly flush with the rostrum. A hole occurs in the rostrum anteromedial to the infraorbital foramen, however, I do not believe that a true perforation was present; the ragged edges of the aperture and the presence of bone fragments in the region suggest that the wall of the rostrum had been entire but thin. The origin of the superficial masseter is restricted to a low rise ventral and posterior to the infraorbital foramen.

The lacrimal canal runs anteroventrally from the nasolacrimal foramen in the orbit; it is horizontal immediately dorsal to the infraorbital canal, and then it turns medially to pass under the arch of the incisor. A nonossification is sometimes present at the junction of the lacrimal, frontal, and maxillary bones in the wall of the orbit. The sphenopalatine foramen is far anterior, dorsal to M^1; it is bounded by the frontal, maxillary, and palatine bones; the orbitosphenoid does not reach it. The ethmoid foramen is in the orbitosphenoid-frontal suture dorsal to the junction of M^2 and M^3. The optic foramen is larger than 1.0 mm; it is posterodorsal to M^3 except in F:AM 103382, *F. kennethi*, in which the anterior part is dorsal to that tooth. The interorbital foramen passes through the orbitosphenoid ventral or anteroventral to the anterior end of the optic foramen. Traces of the sphenofrontal foramen at the dorsal end of the anterior alar fissure and of a bifurcating furrow that leads from it for the anterior ethmoid and superior ophthalmic arteries are preserved in F:AM 103385, *S. stouti*. The dorsal palatine foramen is in the maxillary-palatine suture dorsal to the junction of M^2 and M^3; it is hidden from view in the illustrations by the orbital bulge of the maxilla over the cheek tooth alveoli.

The anterior-alar fissure (sphenoidal fissure of previous publications; see Introduction) is

$\rightarrow$

FIG. 7. *Sanctimus simonisi,* F:AM 103380. Middle ear, right side. Magnification approximately ×7. Patterned areas are matrix. *Abbreviations:* as, alisphenoid bone; bo, basioccipital bone; etr, epitympanic recess; fco, fenestra cochleae; ff, foramen of Fallopian aqueduct; fv, fenestra vestibuli; ju, jugular foramen; mst, mastoid bone; pop, paroccipital process; prp, petrosal process; stc, stapedial artery canal; sty, position of stylomastoid foramen.
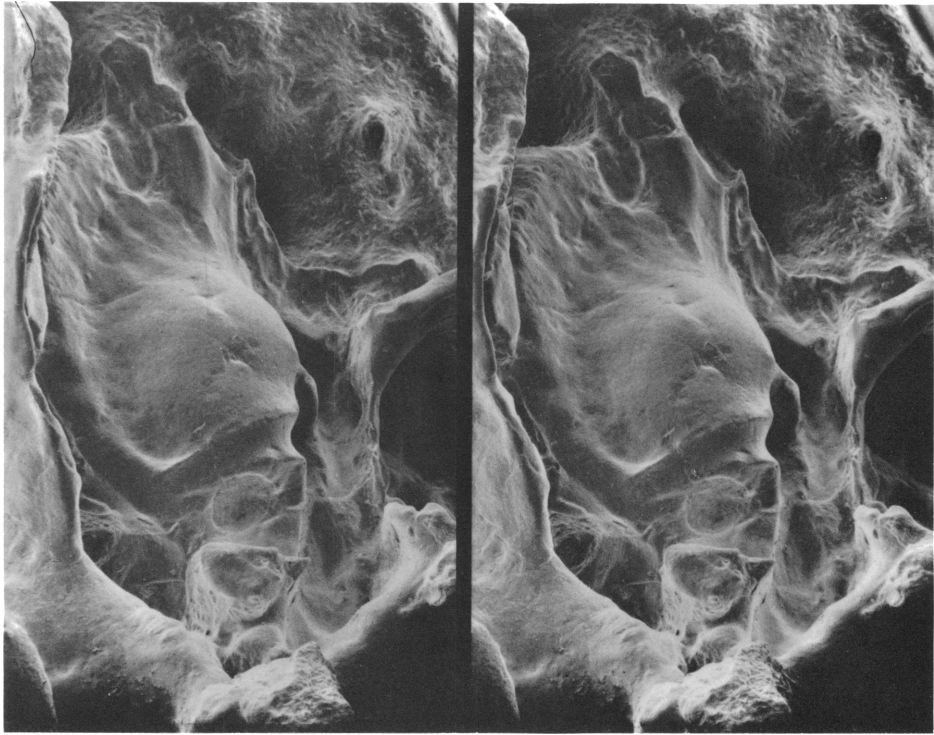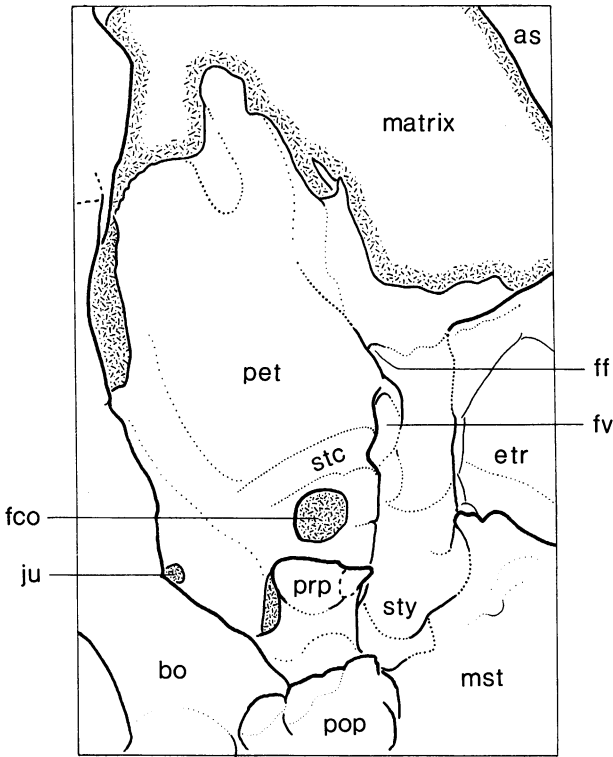
posterior to M^3. The lateral edge of the fissure is formed by the alisphenoid and a unique process of the palatine that rises from the floor of the orbit. The dorsal aperture of the canal for the descending palatine vein is in the maxillary-palatine suture as usual, but it is lateral to the fissure wall rather than anteromedial or medial to it as in heteromyids and geomyids.

The masticatory and buccinator foramina are combined with the accessory foramen ovale. The pterygoid fossa is completely roofed, and there is no trace of a sphenopterygoid foramen. The foramen ovale is bounded posteriorly by the auditory bulla. The entrance to the alisphenoid canal is at the anterior end of the foramen ovale. The posterior part of the alisphenoid canal is combined with the canal of the masseteric and buccinator nerves. The large entrance to the transverse canal is widely separated from the alisphenoid canal; it is located in the roof of the pterygoid fossa between the foramen ovale and the base of the hamular process. The sphenopalatine vacuities are extensive and visible in both ventral view of the nasal passage and lateral view of the orbit. There is no special indication of the internal carotid canal; the artery appears to have turned dorsally between the bony Eustachian tube of the bulla and the junction of the basioccipital and basisphenoid bones.

The stapedial foramen is presumed hidden deep within the aperture of the jugular foramen. A broad furrow for the stapedial artery is marked by crests on the promontorium, which is illustrated in figure 7. The furrow notches the ventral and dorsal margins of the fenestra vestibuli; it is continued anterolaterally by a groove in the wall bounding the epitympanic recess, but this detail is not visible in the view presented. A foramen anterodorsal to the fenestra vestibuli is interpreted as the opening of the Fallopian aqueduct; the facial nerve was exposed within the middle ear as it is in certain insectivores (McDowell, 1958). A process, which is concave anteriorly, descends from the petrosal posterior to the fenestra cochleae. A post-alar fissure between the squamosal bone and the bulla is lacking; a crescent of the petrosal is exposed here.

The postglenoid foramen is within the squamosal bone below the zygomatic root. The temporal foramen, situated in the squamosal above the zygomatic root, is large; the parietal reaches it dorsally. The mastoid foramen forms an elongated gap dorsal to the mastoid bone.

The lower jaw is sciurognathous. The coronoid process is bent laterally; its posterior edge almost parallels the slope of the dorsal edge of the condylar process. The common base of the two processes rises lateral to M_2 and is set apart from M_3 by a shallow depression. The condyle is anteroposteriorly elongated and transversely narrow. The incisor alveolus bulges laterally below the coronoid process. The angle extends as far posteriorly as the condylar process and farther laterally; its ventral edge is inflected medially. The masseteric fossa is bounded by dorsal and ventral lines; the weakly marked dorsal line is nearly coincident with the leading edge of the coronoid process. The ventral line descends posteroventrally near to the bottom of the jaw and extends to the end of the angular process; it is excavated and most prominent anterior to its intersection with the dorsal line. The symphysis is unfused.

Features of the dentition are illustrated and labeled in figure 1; dimensions are recorded in tables 2 and 3. The cheek teeth are low crowned and have variable traces of anterior and posterior cingula. Wear produces a bilophodont pattern. Upper and lower teeth are widened by addition of stylar cusps. The widths of P^4 and M^1 are greater than those of the corresponding lower teeth, except in *S. stuartae*, LACM 15292; widths of M^2 and M^3 are about equal to those of the corresponding lower molars.

The upper tooth rows converge anteriorly at an angle of about 15 degrees. The upper teeth are widened lingually by the addition of protostyle, entostyle, and hypostyle. The entostyle is elongated and blocks the lingual end of the transverse valley. In decreasing order the cusp heights in M^1 and M^2 are paracone, metacone, protocone, hypocone, and entostyle. The protoloph is defined by wear first, the metaloph, second; the metaloph is then joined with the entostyle to produce a J-shaped loph; finally, the entostyle is united to the protoloph, and the entire crown assumes a U-pattern that is concave bucally.

The metacone and hypocone are weakly defined in M^3. The paracones and metacones of the upper teeth are beveled on the buccal side by the stylar ridge of the lower teeth; the entostyle lacks a lingual bevel. The anterior cingulum, present on M^2 and M^3 and variable on other teeth, extends from the anterior end of the entostyle; it is low on the front of the tooth and ascends apically on the anterior side of the paracone. A trace of the posterior cingulum is rarely present, never on M^3; the cingula remain unworn until a late stage of attrition. The greatest width of the molars is through the protoloph; of P^4, through the metaloph. The protocone is larger than the paracone and is variably united with that cusp in P^4. P^4 is lightly worn relative to the molars and is preceded by a dP^4, the remains of which can be seen in F:AM 103388, *F. kinseyi.*

The lower teeth are widened buccally by addition of a protostylid to the metalophid and a hypostylid to the hypolophid. The metaconid is the highest cusp in M_1 and M_2; stylar cusps are relatively high, but are the lowest features. The hypolophid is usually defined by wear first, the metalophid, second. The protostylid is posterolateral to the protoconid and is separated by a shallow valley from the crescentic cingulum that extends to the anterior side of the protoconid. The metalophid and protostylid are usually joined via a crescentic cingulum prior to union of the hypolophid and hypostylid. Extreme attrition produces a U-pattern that is concave lingually; a very low rise connects the protoconid and hypoconid across the transverse valley; occasionally it is high enough to produce an X-pattern with wear as in YPM 20285, *F. kennethi.* A long, low anterior cingulum is present only in the molar teeth of ACM 1927-126, *F. loomisi.* A posterior cingulum is common, but its presence is variable; it is always lacking on M_3. Cingula are unworn until a late stage of attrition. M_2 is always the widest lower cheek tooth. The greatest width is through the metalophid in molars and through the hypolophid in P_4. P_4 is rectangular; the protoconid is small and occasionally is anteroposteriorly elongated; the protostylid is usually in line with the metalophid; a small hypostylid is present in all taxa except *S. stuartae.*

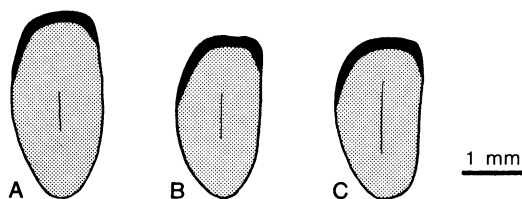The upper incisors are slightly deeper and

FIG. 8. Cross sections of incisors. A and B. *Florentiamys kingi,* F:AM 103384. A. Upper left reversed. B. Lower left. C. *Sanctimus falkenbachi,* F:AM 103383, lower left.

usually a little wider than the lowers; the depth is about twice the width; the greatest transverse width is near the middle. Incisor cross sections are roughly oval (fig. 8). The enamel of upper and lower incisors is pigmented except in F:AM 103379, ?*F. kinseyi,* and the surface is without ornament. The anterior enamel surface of the lower incisors is slightly flattened in all but F:AM 103383, *S. falkenbachi.* The lingual wear facet of the upper incisors is nearly vertical relative to the occlusal plane of the cheek teeth; the center of curvature of the incisor shaft is anterior to the middle of the diastema, just ventral to the anteriormost extension of the maxilla. The center of curvature of the lower incisors is far dorsal to the anteriormost end of P_4.

Enamel microstructure (fig. 9) was examined by scanning electron microscopy; the median sagittal plane of upper and lower incisors was polished, etched with dilute hydrochloric acid, and coated with gold palladium. The enamel is clearly divided into inner and outer parts. The inner part is uniserial; bands extending out from the enamel-dentine junction are one enamel rod thick. Each band is the cut edge of a three dimensional lamella, a sheet of parallel enamel rods. Rods of adjacent lamellae are seen to decussate in transverse section. The total thickness of the enamel in the upper incisor is approximately 145 microns in the plane of section; the uniserial inner part occupies 84 percent of this total. Bands are inclined apically; relative to a perpendicular to the enamel-dentine junction, the inclination is initially steep, about 30 degrees, but it flattens to a lesser inclination of 10 degrees. The section of the upper incisor nearly bisects the angle of decussation, so the rod sections in adjacent bands
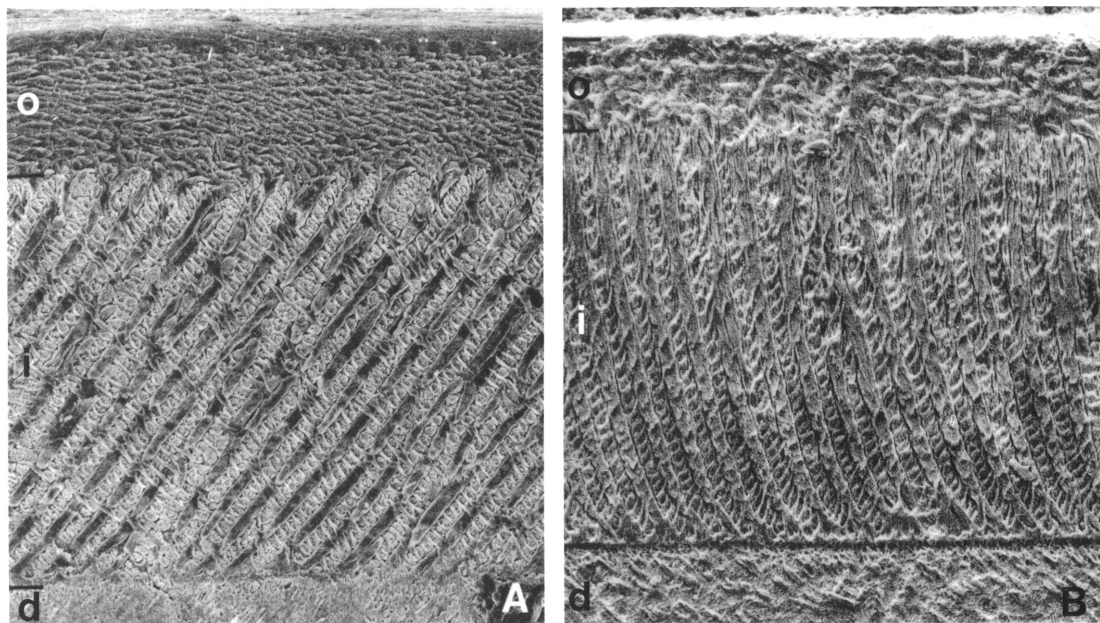
FIG. 9. *Florentiamys kingi*, F:AM 103384. Scanning electron microscope photographs of incisor enamel; median sagittal section. Printed full size. A. Lower left, tip to right; magnification *ca.* ×420. B. Upper left, tip to left; magnification *ca.* ×440. *Abbreviations:* d, dentine; i, inner enamel; o, outer enamel.

appear similar in size. The rods dip from the plane of section at opposite angles in adjacent bands. The total thickness of the enamel in the lower incisors is about 175 microns; the uniserial inner part occupies 75 percent of the thickness. Bands are inclined apically at 40 degrees. The section of the lower incisor is nearly parallel to the rods in one set of lamellae. The cross sections of these rods are extremely elongated. Rods in the other set of

TABLE 4

Primitive Cranial and Dental Characters Shared by Florentiamyids and Other Rodent Groups

	Floren- tiamyidae	*Sciuravus*	Eomy- oidea	*Ento- ptychus*	*Pleu- rolicus*	Hetero- myidae	Geo- myidae
Incisors oval, without ornament	+	+	S	0	0	S	0
Worn cheek teeth with traces of cingula	+	+	S	0	0	S	0
Fourth premolars molariform	+	+	+	+	+	S	+
Palate and diastema gently arched	+	+	+	0	I	+	0
Imperforate rostrum	+	+	+	+	+	0	+
Edge of anterior alar fissure mainly posterior to M³	+	+	+	+	+	S	0
Shallow pterygoid fossa							
Accessory foramen ovale present	+	+	+	0	0	0	0
Stapedial artery present in adult	+	0	+	+	0	0	0
Postglenoid foramen within	+	+	+	+	+	S	0
squamosal bone	+	+	+	S	0	0	0
Temporal foramen present	+	+	?	+	+	0	0

Abbreviations: +, all; I, intermediate; 0, none; S, some. Data from Wahlert (1972, 1974, 1978) and Rensberger (1971, 1973a).
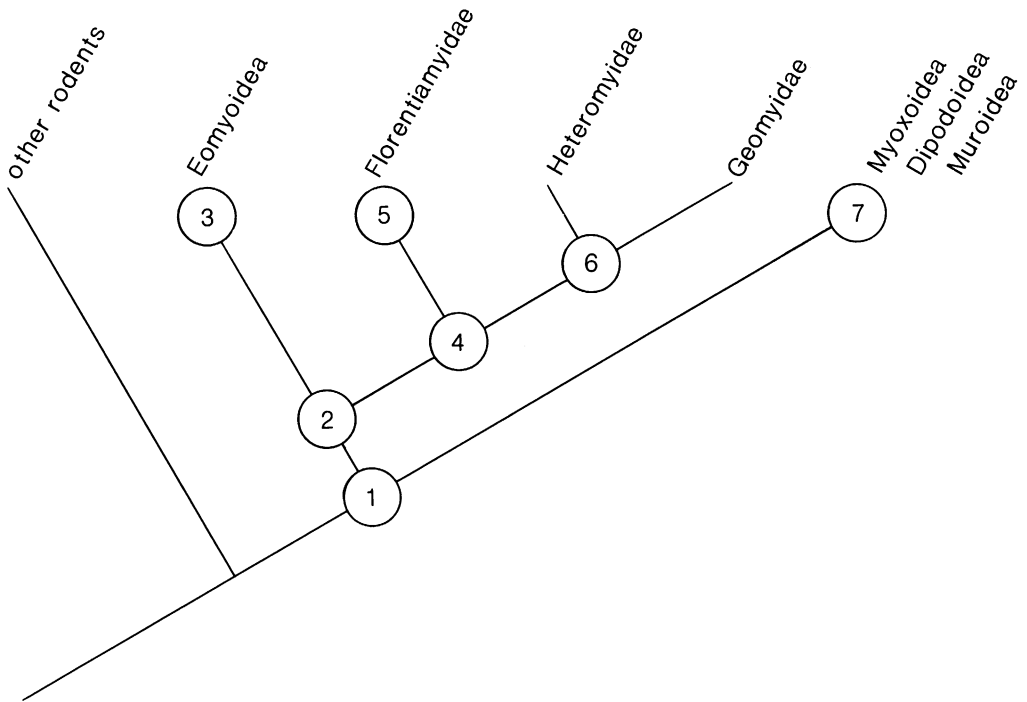
Fig. 10. Proposed relationships of the Florentiamyidae. See discussion below.

lamellae are cut almost transversely; their cross sections are oval, and they dip at a high angle from the plane of section.

DISCUSSION

Florentiamyids, geomyids, and heteromyids share derived cranial and dental characters that indicate unique common ancestry. Different sets of derived characters distinguish the florentiamyids on the one hand and heteromyids and geomyids on the other. Therefore, the florentiamyids constitute a monophyletic group that merits familial rank, because it is not descended from or ancestral to either heteromyids or geomyids. Retained primitive characters (table 4) suggest that the florentiamyids diverged early in geomyoid phylogeny. The full hypothesis of relationship is presented as a cladogram in figure 10. The shared, derived characters that define each node and end point are as follows:

1. Myomorpha: Carotid canal short, lateral to basisphenoid; entrance to transverse canal separated from alisphenoid canal; zygomatic arch slender; incisor enamel uniserial.

2. Geomorpha: Sciuromorphous masseter; long, low infraorbital canal sunk into snout at anterior end; sphenopalatine foramen far anterior, dorsal to M^1; interorbital foramen present; wear on cheek teeth forming transverse lophs.

3. Eomyoidea: Longitudinal enamel lamellae in lower incisors; sphenopalatine foramen surrounded by maxilla.

4. Geomyoidea: Incisive foramina short, 30 percent or less of diastemal length; broad, shallow depression between palate and pterygoid fossa; auditory bulla forming back of foramen ovale; cheek teeth bilophodont; upper teeth widened lingually by addition of protostyle, entostyle, and hypostyle; lower teeth widened buccally by addition of proto-

stylid to metalophid and hypostylid to hypolophid.

5. Florentiamyidae: Revised diagnosis of family.

6. Heteromyidae and Geomyidae: Pterygoid fossa deep, containing entrance to sphenopterygoid canal; posterior margin of accessory foramen ovale not ossified; auditory bulla with vesicular texture at least during development; superior part of angular process of mandible flared laterally.

7. Myoxoidea, Dipodoidea, and Muroidea: Enlarged infraorbital foramen.

Participation of the palatine in the ventral edge of the anterior-alar fissure is a unique character in florentiamyids; it is most simply derived from a rodent more primitive than known heteromyids and geomyids. In primitive rodents, such as *Sciuravus* and *Paramys,* the palatine is exposed between the maxilla and alisphenoid, and the descending palatine vein is not enclosed in bone (Wahlert, 1974). Additional posterior support of the dentition is acquired in geomyoids and many other rodent groups through union of the maxilla and alisphenoid. This bridge encloses the descending palatine vein in a canal; the dorsal opening for the vein is anteromedial to the wall of the anterior-alar fissure, which is formed entirely by the alisphenoid. In florentiamyids the maxilla and alisphenoid meet, but the foramen is lateral to the fissure wall, where it is uniquely formed by a process of the palatine. The florentiamyids must have evolved from a rodent exhibiting the primitive stage with an unenclosed passage. This condition is known in *Viejadjidaumo,* an early Chadronian member of the Eomyoidea, the sister group of the Geomyoidea (Wahlert, 1978).

Other characteristics support the hypothesis that florentiamyids are a primitive branch of geomyoids. In table 4 the florentiamyids are compared with the more primitive *Sciuravus* and eomyoids, to the extinct geomyid genera *Entoptychus* and *Pleurolicus,* and to living geomyids and heteromyids. The florentiamyids share with *Sciuravus* and other early rodents of the family Paramyidae the following primitive characters: moderate size; dorsal surface of skull gently arched with palate and diastema nearly parallel to it; wall of rostrum complete medial to infraorbital fo-

ramen; lateral margins of incisive foramina intersected at back by premaxillary-maxillary suture; sphenopalatine foramen not reached by orbitosphenoid bone; anterior edge of anterior alar fissure posterior to M^3; optic foramen posterior to M^3 (except F:AM 103382, *F. kennethi*); pterygoid fossa with complete roof, lacking sphenopterygoid foramen; accessory foramen ovale present; furrow for stapedial artery present on promontorium; postglenoid foramen surrounded by squamosal bone; angular process of mandible not flared laterally; cheek teeth low crowned, retaining variable traces of anterior and posterior cingula; incisors oval in cross section, depth about twice width with greatest width near middle; incisor surface without ornament.

The palate and diastema of florentiamyids form a gentle arch as in eomyoids and heteromyids. The arch is deeper in *Pleurolicus,* because the diastema is recessed posterior to the incisors and descends posteriorly to accommodate the more protrusive cheek teeth. These trends are exaggerated further in *Entoptychus* and living geomyids. The rostrum in florentiamyids lacks the large perforation so prominent in heteromyids.

Situation of the anterior-alar fissure posterior to M^3 is a primitive character supplanted in living geomyids, many heteromyids, and in other unrelated rodent taxa. In these rodents the fissure is farther anterior, and the alisphenoid and maxilla meet in a suture posterior to the molars; the breadth of the suture corresponds with the anterior position of the alisphenoid margin. The pterygoid fossa is shallow and completely roofed in florentiamyids, whereas in living geomyids and heteromyids it is deep and perforated by the sphenopterygoid canal, which permits anterodorsal extension of the internal pterygoid muscle. An accessory foramen ovale is present in *Paramys* (not reported in Wahlert, 1974) but apparently lacking in *Sciuravus.* The lack of the foramen in living heteromyids and geomyids appears to be a secondary loss associated with remodeling of the alisphenoid; it is not a homologue of the condition in *Sciuravus.* In living geomyoids the position of the postglenoid foramen posterior to the edge of the squamosal may also be a result of this remodeling.

The carotid circulation appears to have been primitive, like that in living perognathine and dipodomyine heteromyids (Bugge, 1971). The furrow that crosses the promontorium is broad and marks the course of a large stapedial artery that probably continued into orbital branches. The sphenofrontal foramen, where the ophthalmic branch emerged from the cranium, is closely associated with the anterior-alar fissure as in the two subfamilies of heteromyids.

The incisors of florentiamyids are primitively oval in cross section. In other geomyoids the incisors are more triangular with the greatest width near the anterior enamel face; the enamel is often flattened anteriorly and grooved. Anterior and posterior cingula are present in florentiamyid cheek teeth, but they are reduced compared to those in eomyoids. Cingula are lacking in other geomyoids except extinct species assigned to *Heliscomys, Proheteromys,* and *Perognathus.* Molariformity in shape and function of the fourth premolars is a characteristic of primitive rodents and geomyoids in general. Although fusion of paracone and protocone and reduction or absence of the protoconid decrease the resemblance of the premolars to the molars in many geomyoids, the tooth remains molar-like in function.

The florentiamyids, geomyids, and heteromyids share some derived characters that do not indicate relationship. Sporadic occurrence of certain characters within geomyoids and differences in basic design indicate parallelism rather than common origin. Coalescence of protocone and paracone and rotation of the anterobuccal root to an anterior position in P^4 are common derived features in geomyoids. A large optic foramen occurs in the dipodomyines. In heteromyids the frontal region is broad and may overhang the orbit slightly, but the edges converge anteriorly rather than being roughly parallel as in florentiamyids.

Comparison of florentiamyids to geomyids, heteromyids, and related, extinct rodents supports Wood's hypothesis that florentiamyids occupy a position morphologically intermediate between primitive rodents and heteromyids, but the florentiamyids gave rise to no other geomyoid taxon. Since the known florentiamyid specimens come from a limited geographic area, and the skulls have unusual derived characteristics, I suspect that the group had a prior history of considerable duration.

The descriptions and figures of cranial remains assigned to *Heliscomys,* which is considered to be a heteromyid (Wood, 1980), do not provide evidence useful in this phylogenetic analysis. The problem is not the incompleteness of the skulls so much as uncertainty about the taxonomic assignment of the specimens. The genus *Heliscomys* is based on the species *H. vetus* Cope, 1873,; the type specimen is a lower dentition which has a small, three-cusped premolar. The crania, except that described by Reeder (1957), lack associated lower dentitions. Galbreath (1961) added further complexity to the problem when he suggested that the species *H. tenuiceps* and possibly *H. vetus* were florentiamyines; the statement implies that *Heliscomys* is not a monophyletic taxon.

Four partial skulls have been attributed to the genus *Heliscomys.* Galbreath (1948, 1961) described and figured specimens of *H. tenuiceps* from the middle Oligocene Cedar Creek beds of Colorado. The skulls resemble those of florentiamyids, but the frontal bone does not form a flangelike projection over the orbit; the critically important edge of the anterior-alar fissure is not preserved. The upper molars have elongated entostyles and transverse lophs that are nearly perpendicular to the axis of the tooth row. Although the premolar has a single, anterior cusp, the tooth shape, as illustrated (*ibid.,* 1948, pl. 3), is florentiamyid-like. Galbreath proposed that the species *H. tenuiceps* linked *Heliscomys* and florentiamyines (*ibid.*), and he concluded that this species and possibly *H. vetus* belonged in the Florentiamyinae (*ibid.,* 1961). Reeder (1957) described another skull from the Cedar Creek beds, and he assigned it to the species *H. vetus.* It, too, lacks the flange over the orbit; Reeder mentioned depressions at the back of the palate that are a characteristic of geomyoids. Setoguchi (1978) figured a damaged rostrum and palate from the late Oligocene strata at Badwater Creek, Wyoming, and referred the specimen to *H. vetus.* The teeth do not resemble those of florentiamyids; the transverse lophs are oblique to the

axis of the tooth row, and the three-cusped premolar is small and sharply triangular.

Rensberger (1973b) placed *Heliscomys* at the base of the geomyoid phylogenetic tree and accepted the small size and simple morphology of the fourth premolars as primitive. The morphology of the upper and lower premolars, however is highly variable in specimens assigned and referred to the species *H. vetus*. Black (1965) described dentitions from the early Oligocene Pipestone Springs local fauna. In all specimens a small cusp is found at the anterobuccal base of the protocone in P^4; four-cusped and three-cusped conditions occur in P_4 of different specimens. Galbreath (1953) observed a similar range of variation in the premolars of the species *H. vetus* from the middle Oligocene Cedar Creek beds of Colorado. Wood (1980) summarized earlier discussions and agreed with the consensus that premolars with four primary cusps are primitive in *Heliscomys*. He suggested that the three-cusped condition is a specialized trend in *Heliscomys* that is apart from the main line of heteromyid evolution.

Wood's conclusion is supported by the evidence of other extinct geomyoid rodents. Wilson (1949) proposed that the ancestors of known geomyoids passed through a series of dental morphologies somewhat comparable to those of *Taxymys* (or *Sciuravus*)–*Griphomys*–*Florentiamys*. Wood (1980) presented a very similar morphologic series that started with the eomyid *Viejadjidaumo* instead of *Taxymys* and suggested *Meliakrouniomys* as an alternative to *Griphomys*. The striking feature of these rodents is that the fourth premolars are four-cusped; *Florentiamys* is similar, but the teeth are widened by the addition of styles. The simplest explanation of the small, three-cusped premolars of *Heliscomys* is that they are a derived morphology.

Wood (1980) suggested that the individual variation of *Heliscomys vetus* in the Oligocene may have been great enough to encompass most of the described species. A second alternative is possible. The florentiamyids, despite their many primitive characters, have not been recognized as older than the late Oligocene; their remains may already be represented in collections as specimens of *Heliscomys*. *Heliscomys tenuiceps* Galbreath, 1948, and *H. schlaikjeri* Black, 1961, are ob-vious candidates for restudy in this light; an elongated entostyle blocks the lingual end of the transverse valley in the upper molars of both species as it does in florentiamyids.

If the presence of four major cusps is primitive in geomyoid premolars, the florentiamyids illustrate origin of the typical geomyoid tooth crown in parallel with heteromyids. The single anterior cusp and root of P^4 is produced through fusion of paracone and protocone and rotation of the tooth; the two anterior cusps in the lower P_4 are the fused protoconid and metaconid and the protostylid. Two lines of evidence, cusp height and wear, demonstrate that widening of geomyoid cheek teeth occurred through the addition of styles, as described by Wood (1935), and not through enlargement of conules. The relative height of cusps is determined by their developmental sequence; higher cusps were initiated earlier (Butler, 1956). In *Paramys* and *Sciuravus* the highest cusps in the upper teeth are the three primary ones followed by the conules. In florentiamyids the lingual styles in the upper molars and the buccal ones in the lowers are not so high as the other cusps; they do not represent part of the original complement of cusps unless a change in time of cusp formation has occurred.

The details of tooth occlusion support the view that styles have been added to the primitive complement of cusps. When the cheek teeth of primitive rodents are occluded, the uppers project farther buccally than the lowers and the lowers farther lingually. The upper teeth bear wear facets on the lingual side but none on the buccal. Lower teeth exhibit the reverse pattern. In the upper teeth of florentiamyids buccal cusps are slightly beveled, whereas the lingual entostyle has a sharp edge. The lowers show a new, slight bevel on the lingual edge. This modification of the primitive pattern of tooth overlap and wear is the strongest evidence of stylar expansion. The condition defines the Geomyoidea. The wear facets are easily observed and can be used to assign isolated teeth to the taxon.

Chewing in all florentiamyids appears to have been propalinal; the lower teeth moved anteriorly across the uppers. The cheek teeth are worn flat. In one specimen of *F. kennethi*, F:AM 103382, the P_4 is malformed (fig. 3B). The enlarged protoconid has worn down the

paracone proportionately. The protoconid has a facet on its posterolateral side that fits against a similar worn surface on the antero-medial side of the metacone. These surfaces mark initial occlusion; the lower jaw then slid forward, and the protoconid abraded the paracone. The distance of anterior jaw movement was about one-half the length of the premolar.

Certain features of crown pattern appear to vary randomly in the florentiamyid specimens, and, although they are distinctive, they do not define groups that could be considered taxa. The presence of cingula is variable among specimens; I have attributed this to loss, which here appears random. The paracone and protocone are united in varying degrees in P^4, and the protoconid is reduced in P_4; surprisingly, skulls with associated jaws show that these features are not correlated with each other.

The completeness of florentiamyid specimens compared with small sample size is remarkable. Collecting preference does not explain this anomaly, because collectors of four different institutions obtained skulls with associated jaws; most of those in the Frick Collection were articulated. Postcranial elements were found with three of the specimens, and at least one partial skeleton was articulated. Many of the florentiamyid specimens experienced little or not transport from the place of death. The bone shows no trace of prolonged subaerial exposure and was presumably unavailable to scavenging animals that might have broken and dispersed the elements. I believe that most of the florentiamyids died and were preserved in burrows. Florentiamyid limbs are not specialized for burrowing, but all of the living geomyoid rodents burrow despite a wide variety of limb morphologies. Reports of fossil heteromyids that were found in burrows suggest similar completeness prior to collection (Voorhies, 1974, 1975). Isolated teeth, described in the literature (L. J. Macdonald, 1972), were collected from anthills; they are not a comparable sample.

Most of the specimens of *Sanctimus* and *Florentiamys* are nearly identical in cranial morphology. The width of the rostrum was cited previously to differentiate the two genera (Rensberger, 1973b); however, the type

specimen of *F. loomisi* is flattened laterally, and the narrow snout is an artifact of preservation. The snouts in other specimens are as broad as in *Sanctimus*. I have used the presence or absence of a valley between the protostyle and entostyle and doubling of the protostylid to define the genera. Subdivision of specimens on the basis of these features is in accord with prior designations of genera. Size differences between some of the species are clear, but in most instances they are not striking.

The anterior alar fissure is not preserved in the skull of *S. stuartae*, the type species of the genus *Sanctimus*. The broad frontal region and the dental morphology support assignment of the genus to the Florentiamyidae. The lower dentition of ?*S. clasoni* (Macdonald, J. R., 1963), does not provide sufficient evidence for assignment to the family.

The species *F. tiptoni* was described originally as *Sanctimus* (J. R. Macdonald, 1970); however, it lacks the defining valley between the protostyle and entostyle, so I have changed its generic assignment. The graded cheek tooth series is unique to *F. tiptoni* among florentiamyids. ?*Florentiamys agnewi* Macdonald, J. R., 1963, is known from a partial lower jaw; the teeth are so peculiar that I am unable to place the taxon. The species *F. lulli* Wood, 1936, was transferred by Wahlert (1976) to the geomyoid genus *Jimomys*.

CONCLUSIONS

The Florentiamyidae is a family of geomyoid rodents that is defined by cranial and dental characters; chief among them is the unique participation of the palatine in the edge of the anterior-alar fissure. Characters shared with the more primitive eomyoids and *Sciuravus* support the hypothesis that the florentiamyid lineage is the earliest defined branch of the Geomyoidea. These characters are supplanted in heteromyids and geomyids through remodeling of the pterygoid region and alisphenoid bone in association with changes in the internal pterygoid and temporal muscles. The hypothesis that florentiamyid dental morphology represents a reversal of crown simplification seen in *Heliscomys* is rejected.

Florentiamyid teeth illustrate the probable mode of development of the typical geomyoid crown pattern. The single, large anterior cusp and root of P^4 arise through reduction of the paracone and its incorporation into the protocone and by lingual rotation of the tooth. Cusp heights and wear patterns support the view that cheek teeth are widened by addition of lingual styles in the upper dentition and buccal styles in the lower.

Completeness of florentiamyid material, and association of skulls, jaws, and postcranial elements in the small sample of known forms suggests preservation in burrows. Isolated fragments of specimens are rare.

The Florentiamyidae include two genera. *Sanctimus* is distinguished by separation of the protostyle from the entostyle in P^4 and the single protostyle in P_4. Three new species are added to the genus; the relationship of ?*S. clasoni* to other geomyoids is deemed uncertain. *Florentiamys* is defined by its small protostyle closely associated with the entostyle in P^4 and by the double protostylid in P_4. Three new species are added to the genus, and *F. tiptoni* is transferred to it; the position of ?*F. agnewi* is uncertain.

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