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Cranial Foramina and Relationships of the Eomyoidea (Rodentia, Geomorpha). Skull and Upper Teeth of *Kansasimys*

JOHN H. WAHLERT[1]

ABSTRACT

Derived characters of the incisive foramen, infraorbital canal, sphenopalatine foramen, transverse canal, sphenopterygoid foramen, carotid canal, and temporal foramina are shared by eomyids and geomyoids (Geomyidae and Heteromyidae). Three of these characters are shared with myoxoids, dipodoids, and muroids. These facts support the hypothesis that eomyids and geomyoids had common ancestry in a stem species from which no other rodent groups are descended. The family Eomyidae is raised to equal rank, Eomyoidea. Likewise, the inclusive infraorder Geomorpha and rodents traditionally considered myomorphs shared unique common ancestry and are placed together in the suborder Myomorpha. *Yoderimys* and *Kansasimys* are primitive in the infraorbital canal and lack of interorbital foramen, but *Kansasimys* shares derived tooth crown morphology with other eomyoids. The skull of *Kansasimys* is distinguished by large size and by peculiarities of the premaxillary-maxillary suture, temporal-supraorbital crests, and occiput; the teeth resemble those of *Adjidaumo*.

INTRODUCTION

Extinct eomyid rodents are known from both North America and Europe. The present paper deals only with North American forms, and among these only with the forms for which some skull material is known. Despite these restrictions it is possible to propose a phylogenetic hypothesis and to consider the problem of relationships of the family. The hypothesis is intended as a partial framework for students of the group to supplement or falsify with other morphologic evidence. The only link with Old World forms is provided by *Adjidaumo* which is probably congeneric with *Omegodus* (=*Eomys*) (Fahlbusch, 1973, p. 169; Wood, 1974, p. 62).

The history of eomyid taxonomy has been presented amply by Wood in 1937 and in 1974. Hypotheses as to the relationships among North American members of the group and of the family to other rodents are as follows. The genus *Yoderimys* is set apart in a subfamily, Yoderimyinae, because of its distinctive cheek tooth crown pattern, which is similar to that of the Cricetidae (Wood, 1955). The remaining forms discussed exhibit typical eomyid crown patterns which when worn suggest the Greek

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letter omega. They can be divided, following Burke (1934), into two groups: in *Adjidaumo, Viejadjidaumo, Aulolithomys,* and *Kansasimys* the cheek teeth are bunodont, whereas in *Paradjidaumo* the teeth are higher crowned and more markedly lophate. Black (1965) presented a fuller discussion of possible relationships of North American genera.

Wilson (1949a, p. 48), on the basis of detailed comparison of dental and cranial characters, stated, "The writer feels that the Eomyidae should perhaps be viewed as a relatively primitive group of rodents which departed from the same branch of the Aplodontoidea that gave rise to the heteromyids and muroids—all those being about equally remote from one another, but the heteromyids and eomyids less so; all of closer affinity to one another than to the sciurids and castorids." The Eomyidae would then be a family in the Myomorpha.

A second hypothesis is that eomyids are members of the suborder Sciuromorpha because of their sciuromorphous jaw musculature. Cope (1874) placed the North American eomyids in the Sciuridae. Miller and Gidley (1918) made them a family of sciuroids. Wood (1937) included European genera in the group and placed it as a family in the Sciuromorpha.

Allen (1877, p. 945) doubted Cope's assignment of eomyid genera to the Sciuridae and, instead, referred them, *incertae sedis*, to the Ischyromyidae. Simpson (1945), likewise, did not associate eomyids with geomyoids and assigned them to the Aplodontoidea, which have protrogomorphous jaw musculature.

There are several plausible hypotheses relating the Eomyidae to another family of rodents. Scott (1895, p. 286) appears to have been the first to suggest that eomyids are related to heteromyids and geomyids. Harris and Wood (1969) proposed that eomyids may have given rise to heteromyids and that *Meliakrouniomys* could be a transitional genus. However, the lower incisors I have examined of *Omegodus, Adjidaumo, Paradjidaumo,* and *Yoderimys* have a unique derived arrangement of uniserial enamel lamellae; the lamellae are longitudinal rather than being transverse as in the other geomyoid families examined. Upper incisors of eomyids have the usual type of uniserial enamel. The Eomyidae are monophyletic on the basis of this derived character and cannot have given rise to the Heteromyidae. Both families may share common ancestry in a form with the more common enamel type. I prefer to follow Emry (1972) in removing *Meliakrouniomys* from the Eomyidae; the enamel structure of this genus is, as yet, unknown.

Although the eomyids have been assigned by some authors to the Sciuromorpha, the only candidate for possible close relationship is the castoroid *Eutypomys* (Miller and Gidley, 1918, p. 435; Wood, 1937, p. 234; Schaub, 1958, p. 785; Wahlert, 1977). Within the Myomorpha there are three possibilities of relationship, to the Muroidea, the Dipodoidea, or the Myoxoidea. The derived condition of longitudinal enamel lamellae was found by Korvenkontio (1934) in the lower incisors of dipodoids and some myoxoids. Whether this is in detail like the enamel in eomyids awaits investigation with the scanning electron microscope. Among protrogomorphous rodents, dental resemblance of eomyids to *Sciuravus* has been noted (Wood, 1937, p. 239; Wilson, 1949b, p. 112; Black, 1965, p. 42).

I have not heretofore studied the myomorph rodents. For the purpose of comparison I examined one specimen of each of the following genera in the hope of discerning which character states of the cranial foramina are primitive to the suborder and which are derived: *Glis, Graphiurus, Allactaga, Zapus, Sicista, Peromyscus, Neotoma, Sigmodon, Oryzomys, Calomys, Mystromys, Cricetus, Myospalax, Typhohlomys, Nesomys, Lophiomys, Ondatra, Clethrionomys, Lagurus, Microtus, Tatera, Cricetomys, Dendromus, Deomys, Steatomys, Rattus, Otomys, Spalax,* and *Rhizomys.* Fossil skulls of *Eumys elegans* and *Cricetops dormitor* in the American Museum of Natural History were included also.

With regard to the cranial foramina of eomyids, I point out the places where my observations on the same specimens differ from those of Wilson (1949a) and Wood (1974). There are many points of skull morphology on which I do not agree with these authors. Since this is not the subject of the paper, I do not spell them out, but instead present new illustrations of *Paradjidaumo*, *Viejadjidaumo*, and *Aulolithomys*. My own conception of how these are to be restored is the source for my differences of opinion.

I am grateful to the curators of vertebrate paleontology at the Field Museum of Natural History, Chicago, the Natural History Museum of Los Angeles County, the Texas Memorial Museum, and the University of Nebraska State Museum for the loan of eomyid specimens. Dr. Larry Martin supplied a cast of the type of *Kansasimys*. At the American Museum of Natural History, Drs. Karl Koopman and Guy Musser aided me in selection of myomorph specimens; they and Drs. Richard Tedford, Malcolm McKenna, and Eugene Gaffney suggested improvements in the manuscript. Mrs. Jacqueline Tung aided me in curatorial details of the study, and Mr. Otto Simonis with specimen preparation. Preparation was funded by National Science Foundation Grant number DEB76-82644. Mrs. Katherine Wahlert typed the manuscript.

SPECIMENS EXAMINED

Abbreviations: Specimen completeness: c, cranium; n, snout; o, orbit; p, palate; s, entire skull; t, pterygoid region. Institutions: AMNH, the American Museum of Natural History; F:AM, Frick: American Museum Collection; FMNH, Field Museum of Natural History; LACM, Natural History Museum of Los Angeles County; TMM, Texas Memorial Museum; UNSM, University of Nebraska State Museum.

Yoderimys lustrorum: FMNH, PM 431 npo, ½ mi. NNE of Big Cliff, Presidio Co., Texas, early Chadronian.

Aulolithomys bounites: TMM 40492-2A npo, red mound N of Big Cliff, Presidio Co., Texas, early Chadronian.

Viejadjidaumo magniscopuli: TMM 40492-2B s, red mound N of Big Cliff, Presidio Co., Texas, early Chadronian.

Adjidaumo minutus: UNSM 04952 npo, near Trigonias Quarry, Weld Co., Colorado, ?Chadronian.

Paradjidaumo trilophus and P. sp., cf. *trilophus*: AMNH 8751 npo, Castle Rock, Cedar Creek, Logan Co., Colorado, probably Orellan; AMNH 96855 npo, AMNH 96967 npo, AMNH 96997 npo, AMNH 97000 npo, Chalky Buttes, Slope Co., North Dakota, probably Orellan; F:AM 102150 npot, Orin Junction, Converse Co., Wyoming, Orellan; F:AM 102151 npo, F:AM 102152 npo. Plunkett locality, Parsons Ranch, Sioux Co., Nebraska, Orellan; F:AM 102153 s, 1 mi. SW of Kraft Ranch house, F:AM 102154 po, 1½ mi. S. of Kraft Ranch buildings, Niobrara Co., Wyoming, Chadronian; LACM (CIT) 618 s, LACM (CIT) 891 npo, SE of Douglas, Converse Co., Wyoming, probably Orellan.

Kansasimys duibius: F:AM 97824 s, Edson Quarry, Marshall Ranch, Sherman Co., Kansas, late Hemphillian.

CRANIAL FORAMINA

Specimens of the genera described are illustrated in a series of figures: *Paradjidaumo* (fig. 1), *Adjidaumo* (fig. 2), *Viejadjidaumo* (fig. 3), *Aulolithomys* (fig. 4), and *Kansasimys* (fig. 6). Wood (1974, figs, 27, 28, 31, 34, and 35) presented additional views of the Vieja specimens, including *Yoderimys*.

The ratio of length of the incisive foramina to diastemal length, measured in a direct line from the back of the incisor alveolus to the front of the alveolus of the first cheek tooth, is .40 in *Yoderimys*, .34 in *Adjidaumo*, .31 in *Viejadjidaumo*, .25 in *Aulolithomys*, .25 in *Kansasimys*, and ranges from .24 to .31 in nine specimens of *Paradjidaumo*. The lateral margins of the foramina are intersected near the back by the premaxillary-maxillary suture, which runs posteriorly away from them at the beginning of its course; in *Kansasimys* the suture crosses the diastemal palate behind the foramina and flanks an anterior prong of the maxilla that reaches the medial margins of the foramina.

The posterior palatine foramina face anteroventrally and are within the palatine bones medial to the anterior half or middle of the second molar in *Paradjidaumo*, and to the back of the first molar in *Aulolithomys*, a point on which I disagree with Wood (1974, p. 74). The foramina are not symmetrical in the specimen of *Viejadjidaumo*; that on the right is medial to the back half of the first molar and that on the left to the junction of the first and second molars. Likewise in *Kansasimys*, the foramen on

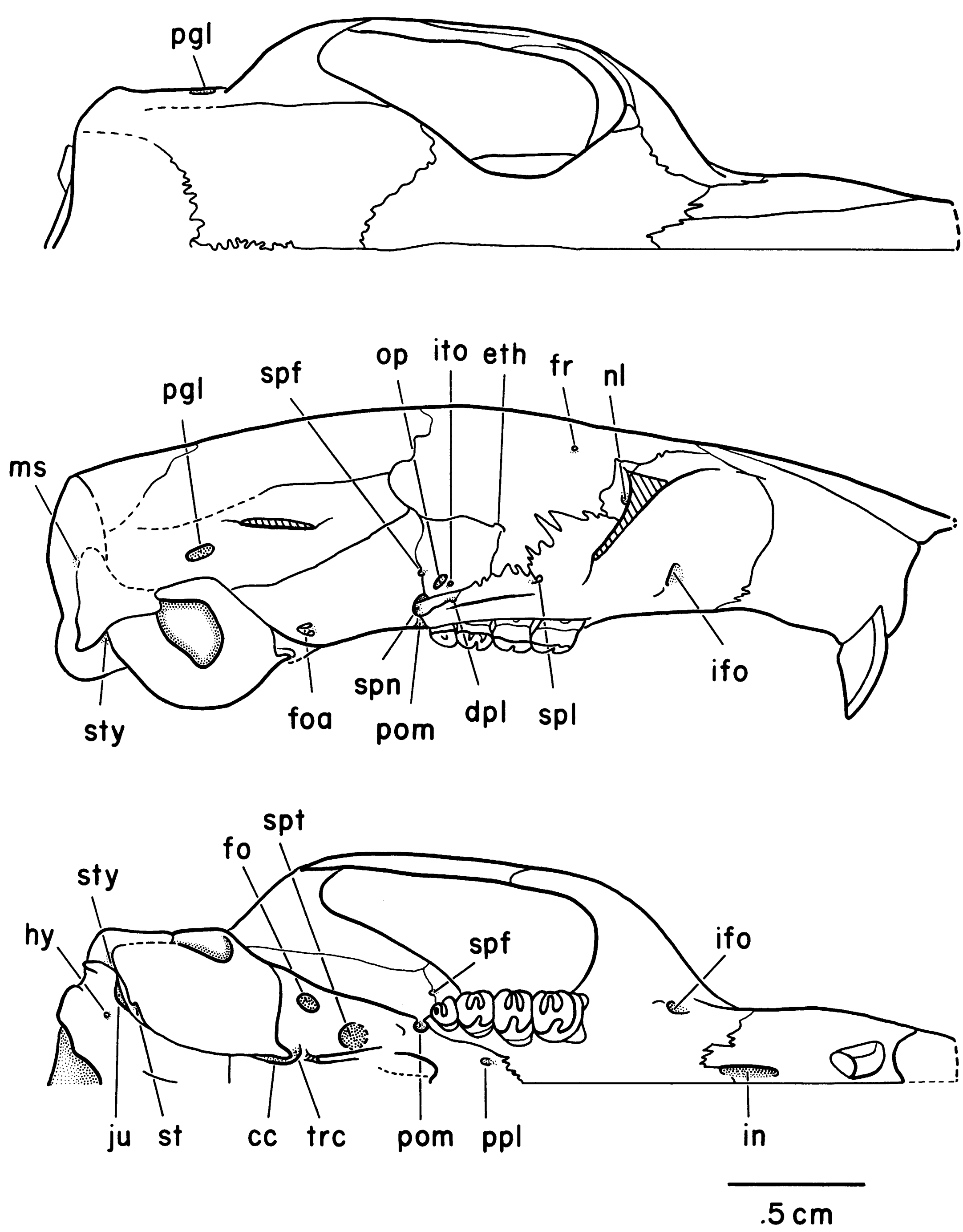

FIG. 1. Skull of *Paradjidaumo trilophus* based on LACM (CIT) 618, dorsal, lateral, and ventral views. Abbreviations: asc, alisphenoid canal; cc, carotid canal; dpl, dorsal palatine; eth, ethmoid; fo, foramen ovale; foa, foramen ovale accessorius; fr, frontal; hy, hypoglossal; ifo, infraorbital; in, incisive; ito, interorbital; ju, jugular; mlf, middle lacerate; ms, mastoid; nl, nasolacrimal; op, optic; paf, post-alar fissure; pgl, postglenoid; pom, posterior maxillary notch; ppl, posterior palatine; spf, sphenofrontal; spl, sphenopalatine; spn, sphenoidal fissure; spt, sphenopterygoid; st, stapedial; sty, stylomastoid; trc, transverse canal. Dashed line, probable position; hatched areas, cut through bone; dashed and dotted line, broken edge; stippling indicates positions of foramina.

the right is medial to the middle of the second molar and that on the left to the back half of that tooth. Smaller foramina are present in the palatine behind the first pair in *Viejadjidaumo* and some specimens of *Paradjidaumo*. The palate of *Yoderimys* is damaged, and details cannot be determined. The maxilla ends behind the cheek teeth in a point. Between the point and the pterygoid region a slight notch is formed in *Viejadjidaumo*; in *Paradjidaumo* a foramen that opens dorsally in the floor of the sphenoidal fissure is enclosed. In *Kansasimys* the foramen is deep in the anterior portion of the pterygoid fossa.

Jaw musculature was sciuromorphous, and the infraorbital canal is well developed, horizontal, and low on the side of the snout in all genera. In front view it is nearly vertical, but the top is a little farther lateral than the bottom. The canal averages 3.0 mm. in length. *Kansasimys*, which is quite large and was not included in the average, has a canal 5.1 mm. long. The lateral margin of the anterior aperture, the infraorbital foramen, is just anterior to the roughened area, the equivalent of a masseteric tubercle, that was the site of origin of the anterior superficial division of the lateral masseter. There is no trace of this roughening in *Kansasimys*. The canal itself is somewhat depressed into the side of the snout in *Paradjidaumo* and also, to a lesser degree, in *Adjidaumo*, *Viejadjidaumo*, and *Aulolithomys*. The condition is absent in *Yoderimys* and *Kansasimys*. Wilson (1949a, p. 37) remarked that "immediately inside the entrance, the internal wall of the canal may be perforate as in the Heteromyidae, but to a less degree." One specimen examined by Wilson, LACM (CIT) 618, was subjected to dorsoventral pressure which flattened and slightly rotated it during fossilization; the other, LACM (CIT) 891, was laterally compressed. This motion compressed the snouts and produced the apparent perforations; undistorted specimens show no trace of them. None of the specimens were broken so as to show the anterior alveolar foramen. In *Kansasimys* a foramen is present in the premaxilla anterior to the infraorbital.

The lacrimal region is damaged in all specimens. Enough of the lacrimal bone remains in *Adjidaumo*, *Paradjidaumo* (AMNH 96855), *Viejadjidaumo*, and *Aulolithomys* to show that it surrounds the opening to the nasolacrimal canal. The opening is dorsal to the posterior aperture of the infraorbital canal. The course of the nasolacrimal canal is visible through the bone on the left side of LACM (CIT) 618. It swings anteriorly, runs dorsal to the infraorbital canal, and passes medially under the incisor just anterodorsal to the infraorbital foramen.

The sphenopalatine foramen is dorsal to some portion of the area extending from the back part of the fourth premolar to the middle of the first molar. It is within the maxilla, the malar and palatal parts of which meet in a nearly vertical suture above it. The orbitosphenoid and the orbital process of the palatine are substantially posterior to it. In *Aulolithomys* a slip of the frontal dips close to the foramen which is divided into anterior and posterior apertures. Nutritive foramina are present in the orbital floor of all genera.

The ethmoid foramen is dorsal to the junction of the first and second molars in *Paradjidaumo*, *Adjidaumo*, and probably in

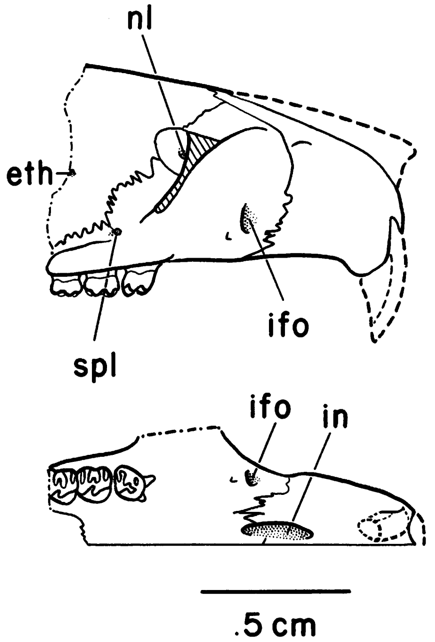

FIG. 2. Skull of *Adjidaumo minutus*, UNSM 04952, lateral and ventral views (composites of right and left sides). See figure 1 for abbreviations.

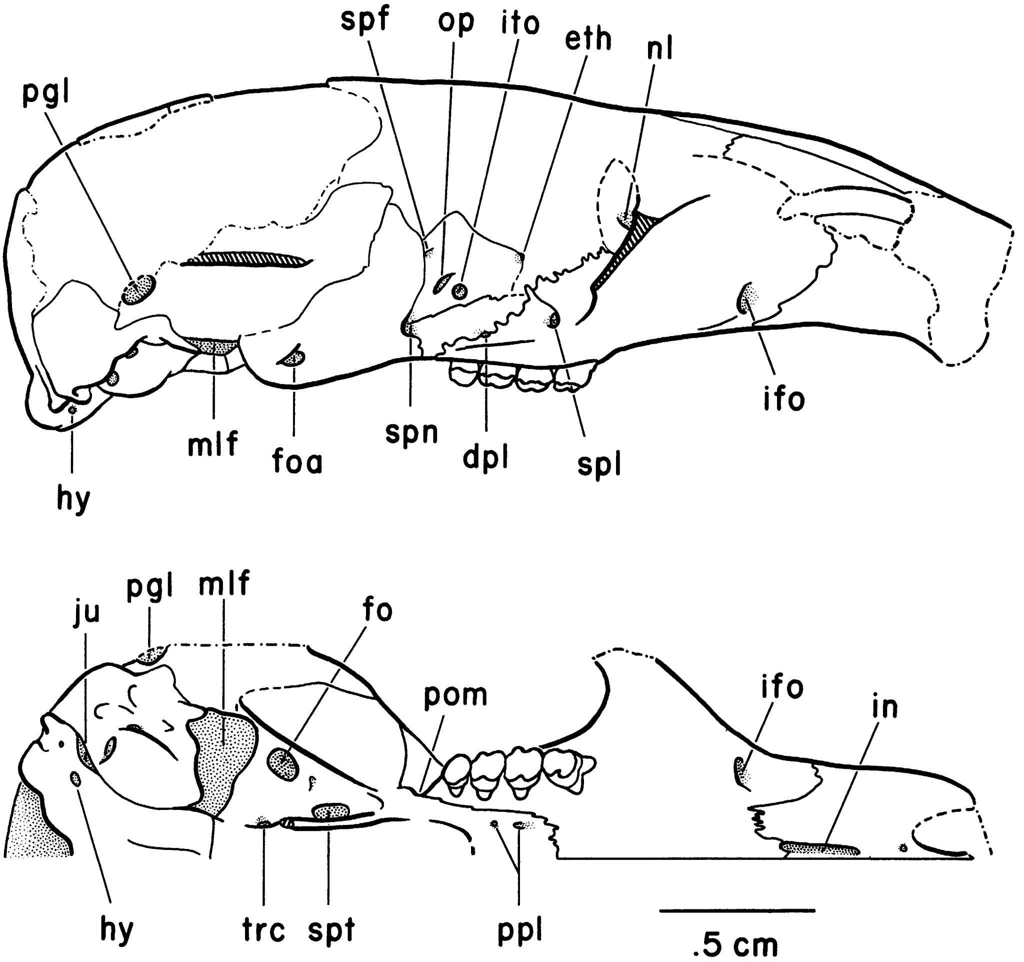

FIG. 3. Skull of *Viejadjidaumo magniscopuli*, TMM 40492-2B, lateral and ventral views. See figure 1 for abbreviations.

Viejadjidaumo and *Aulolithomys*. *Yoderimys* specimens do not preserve this detail; it was probably posterior to the spot labeled as such by Wood (1974, fig. 35). The foramen is large in *Kansasimys* and dorsal to the hindmost part of the second molar. The orbitosphenoid reaches the foramen in every case known. A slight lip of the frontal overhangs the foramen except in *Kansasimys*. A minute vascular foramen in the frontal at the dorsal edge of the orbit may or may not be present.

The diameter of the optic foramen, which is within the orbitosphenoid, is less than a millimeter in all the genera; the foramen is not preserved in *Aulolithomys* or *Adjidaumo*, both of which are broken anterior to it. The optic foramen is dorsal to the last molar or dorsal to and slightly behind that tooth. It is separated from the sphenoidal fissure by a moderately wide lamella of bone in *Yoderimys*, *Kansasimys*, and *Viejadjidaumo*, and by a narrow bar in *Paradjidaumo*. A single, large interorbital foramen is present in *Paradjidaumo*, *Aulolithomys*, and *Viejadjidaumo* just anteroventral to the optic foramen. The aperture is absent in *Yoderimys* and *Kansasimys*; the region is not preserved in the specimen of *Adjidaumo*. Wood (1974, p. 82) described a peculiar foramen in *Yoderimys* in the maxilla and canal in the orbitosphenoid and suggested that these might be a primitive version of what I term the interorbital foramen. These structures appear to be the result of a fracture in the fossil and not part of the skull morphology. I do not agree that a suture divides the orbitosphenoid into two parts but attribute this also to fracturing. Wilson's figure of *Paradjidaumo* (1949a, fig. 2), to which Wood compared *Yoderimys*, shows a similar division of the orbitosphenoid. There is no trace of a division in undistorted specimens, but it is common in crushed ones; the so-called suture is merely a zone of weakness.

The sphenofrontal foramen is absent in *Kansasimys*. It is present in *Viejadjidaumo* in the orbitosphenoid-alisphenoid suture. A small foramen appears to be present in one specimen of *Paradjidaumo*, LACM (CIT) 618, at the junction of the orbitosphenoid, alisphenoid, and frontal bones. There is no channel in the surface of the orbitosphenoid anterior to it. A swell in the alisphenoid that runs posterodorsally from the foramen may represent an internal channel. The sutures in other specimens are disturbed sufficiently to mask the evidence of this foramen. The dorsal palatine foramen is in the maxillary-palatine suture dorsal to a part of the zone between the back of the second molar and the middle of the third. The sphenoidal fissure is posterodorsal to the last molar. In *Kansasimys* it is separated at its opening from the cranial cavity by a wall of bone, whereas in *Paradjidaumo* it is open medially.

In *Kansasimys* the pterygoid fossa is deep and begins medial to the back of the third molar; the lateral pterygoid flange terminates at the anterior end of the foramen ovale. The masticatory and buccinator foramina are united to comprise a single aperture close to the foramen ovale in the lateral wall of the alisphenoid. In *Paradjidaumo* and *Viejadjidaumo* the pterygoid fossa is shallow, and the lateral pterygoid flange which bridges the foramen ovale forms the ventral margin of the combined masticatory and buccinator foramina. If a foramen ovale accessorius is present, it is part of this single aperture. Wood (1974, figs. 27 and 28) labeled this aperture as the foramen ovale. One specimen of *Paradjidaumo*, F:AM 102150, has a separate buccinator foramen on the left side; the right side is damaged. In both *Kansasimys* and *Paradjidaumo* the alisphenoid canal begins anteromedial to the foramen ovale; this is probably the arrangement in *Viejadjidaumo*, also.

In *Paradjidaumo* and *Viejadjidaumo* the

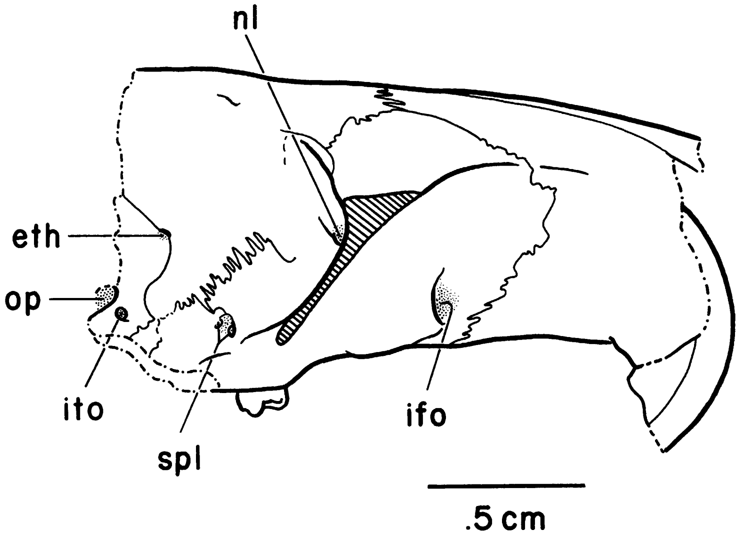

FIG. 4. Skull of *Aulolithomys bounites*, TMM 40492-2A, lateral view. See figure 1 for abbreviations.

pterygoid fossa is a relatively flat triangular surface which dips dorsally at its posterior edge. The palatine thins posteriorly and fails to overlap the curved anterior border of the pterygoid; an aperture is formed in the anterior part of the fossa. Wilson (1949a, p. 39) identified this as a sphenopterygoid foramen, and, I believe, it may be a rudimentary one on the basis of its location. A similar opening is present in *Viejadjidaumo*; it was not figured by Wood (1974). In *Kansasimys* the anterior portion of the pterygoid fossa is set apart from the posterior by a transverse ridge of bone. Within this anterior division there is a small, well-defined foramen.

In all three genera the opening of the transverse canal faces laterally into the pterygoid fossa at the base of the medial pterygoid flange. The middle lacerate foramen is small and exposed medial to the anterior part of the bulla in both *Paradjidaumo* and *Kansasimys*. *Kansasimys* is the only specimen that shows a trace of the carotid canal. A faint channel begins at about the middle of the length of the bulla on its medial side and slopes anterodorsally to a point where the basioccipital is bowed away from the bulla and periotic. The specimen of *Paradjidaumo* which retains a bulla on one side is enough disturbed to preclude detection of the canal, a point on which I disagree with Wilson (1949a, p. 39). No trace of the canal was found in *Viejadjidaumo* in which the bullae are not preserved. Wood (1974, p. 67) described a pair of fenestrae flanking the presphenoid in ventral view. I find no distinct edges on the bone surrounding these areas and believe that the fenestrae may be an artifact of preservation.

The single hypoglossal foramen is situated between the occipital condyle and jugular foramen in *Kansasimys*, *Paradjidaumo*, and *Viejadjidaumo*. In the last genus the surface of the promontorium is damaged and no trace of the stapedial artery channel remains. In *Paradjidaumo* (fig. 5) the stapedial foramen is situated between the bulla and periotic just anteroventral to the jugular foramen. A channel for the stapedial artery runs across the back part of the promontorium and is most deeply incised ventral to the fenestra vestibuli. The artery probably exited from the middle ear via a canal presumed to be present in a swell of the periotic that runs anterolaterally from the front of the fenestra vestibuli and is part of the medial wall of the epitympanic recess. A foramen in the thin posterior part of this wall opens between the recess and the facial canal. The facial canal appears to be an open channel posteriorly; its covered portion may have begun just anterior to the fenestra vestibuli dorsal to the presumed canal for the stapedial artery. The stylomastoid foramen occupies its usual position between the front of the mastoid process and the bulla. Structures of the auditory region are not well preserved but appear to be similar in *Viejadjidaumo*.

The bulla and periotic are fused in *Kansasimys*, whereas in the other genera they are not. The stapedial foramen is far forward near the middle of the bulla in its medial wall. The channel for the artery is deeply incised in the promontorium and is presumed to have entered a canal after it passed through the stapes. The facial canal appears to be completely enclosed in the swell of periotic medial to the epitympanic recess. The stylomastoid foramen is in its usual position.

Kansasimys has a post alar fissure that is probably associated with the veinous system;

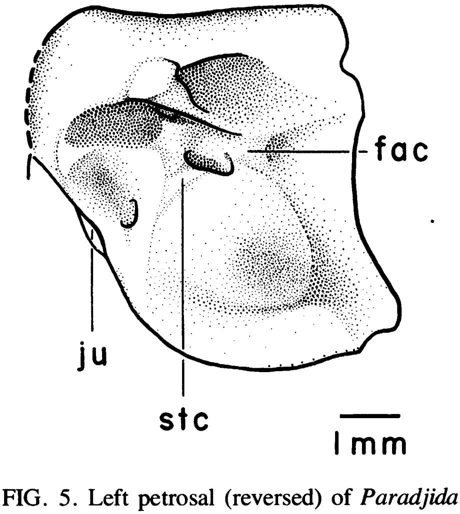

FIG. 5. Left petrosal (reversed) of *Paradjidaumo trilophus*, LACM (CIT) 618. Abbreviations: fac, facial canal; ju, jugular foramen; stc, stapedial artery channel.

Paradjidaumo lacks the structure. The postglenoid foramen appears to be entirely within the squamosal bone in *Paradjidaumo* and *Viejadjidaumo*, but damage has obscured the dorsal and posterior suture of the bone. The foramen is within the squamosal in *Kansasimys*, and its long axis is about 1.9 mm long. The mastoid foramen is at the top of the mastoid in its suture with the occipital; it is double on the right side and single on the left in the specimen of *Kansasimys*. I could not find it in the other specimens. Temporal foramina are absent. Wood (1974, p. 68) described a suprasquamosal foramen in the parietal-squamosal suture in *Viejadjidaumo*; I do not find evidence for such a foramen.

SKULL AND UPPER TEETH OF *KANSASIMYS*

The skull of *Kansasimys* (fig. 6) F:AM 97824 does not have an associated lower dentition. My certainty that it is *Kansasimys dubius* is based on three facts: the skull is that of a large eomyid; a cast of the type mandible and dentition, KU 3582 (University of Kansas, Museum of Natural History), occludes neatly with it; both the type and the new skull are from the same locality, Edson Quarry.

The condylo-basilar length of the skull, measured from the back of the occipital condyle to the back of the incisor alveolus is 40.9 mm; the minimum interorbital width, 9.7 mm; and the distance between the tips of the squamosal prongs of the zygoma, 28.5 mm. The skull has certain characters that are different from those of other eomyids and other rodents. Most striking are the temporal crests which begin laterally at the low lambdoidal crest, define the dorsal margins of the orbits sharply as supraorbital crests, and curve ventrally to terminate each in a boss just posterodorsal to the top of the anterior root of the zygoma. Just anterior to the boss, there is a slight concavity atop the zygomatic root. A lesser but sharp crest on the maxilla and premaxilla marks the anterodorsal limit of the deep lateral masseter more clearly than in other eomyids. The skull table is broad and narrows gradually from the lambdoidal crest to the front of the oribits; it is slightly convex in the parietal region and slightly concave in the frontal.

The morphology of the occiput is striking. In posterior view a strong medial crest extends dorsally from the foramen magnum to the middle of the lamboidal crest. Lateral nuchal crests begin at the lambdoidal crest about two-thirds of the distance from the medial crest to the intersection of the temporal crests. They descend ventrolaterally in two stages, convex laterally to a level at about the top of the foramen magnum, and then concave laterally into the paroccipital processes. A channel that broadens ventrally is formed on the occipital and mastoid between the nuchal crest and the squamosal portion of the lambdoidal crest. Other peculiarities of the skull are noted in the description of cranial foramina.

The cheek teeth (fig. 7A), which include the fourth premolar and three molars, are similar to those of *Adjidaumo* (fig. 7C). They are low crowned, and cusps are distinct parts of the transverse lophs. The mesostyle is lacking. The mesoloph is small and, though worn, appears to be shorter than in *Adjidaumo*. There are several other differences from this genus. In the fourth premolar the protoloph is complete; a bulge in the middle of the protoloph and a low crest running dorsomedially on the anterior side of the protocone, structures lacking in *Adjidaumo*, may be homologous with the medial arm of the anteroloph in *Yoderimys* (fig. 7B). A trace of this arm is present on the first molar, another resemblance to *Yoderimys*. The

TABLE 1
Measurements (in Millimeters) of *Kansasimys dubius*

Incisor width 2.0 depth 2.8
Length of cheek tooth row 8.0
Alveolar length of cheek teeth 8.6

	ap	wa	wp
P^4	2.0	2.1	2.2
M^1	2.1	2.4	2.3
M^2	1.9	2.3	2.1
M^3	1.7	1.9	—

Abbreviations: ap, anteroposterior length; wa, wp, width of anterior and posterior portions along line through transverse loph.

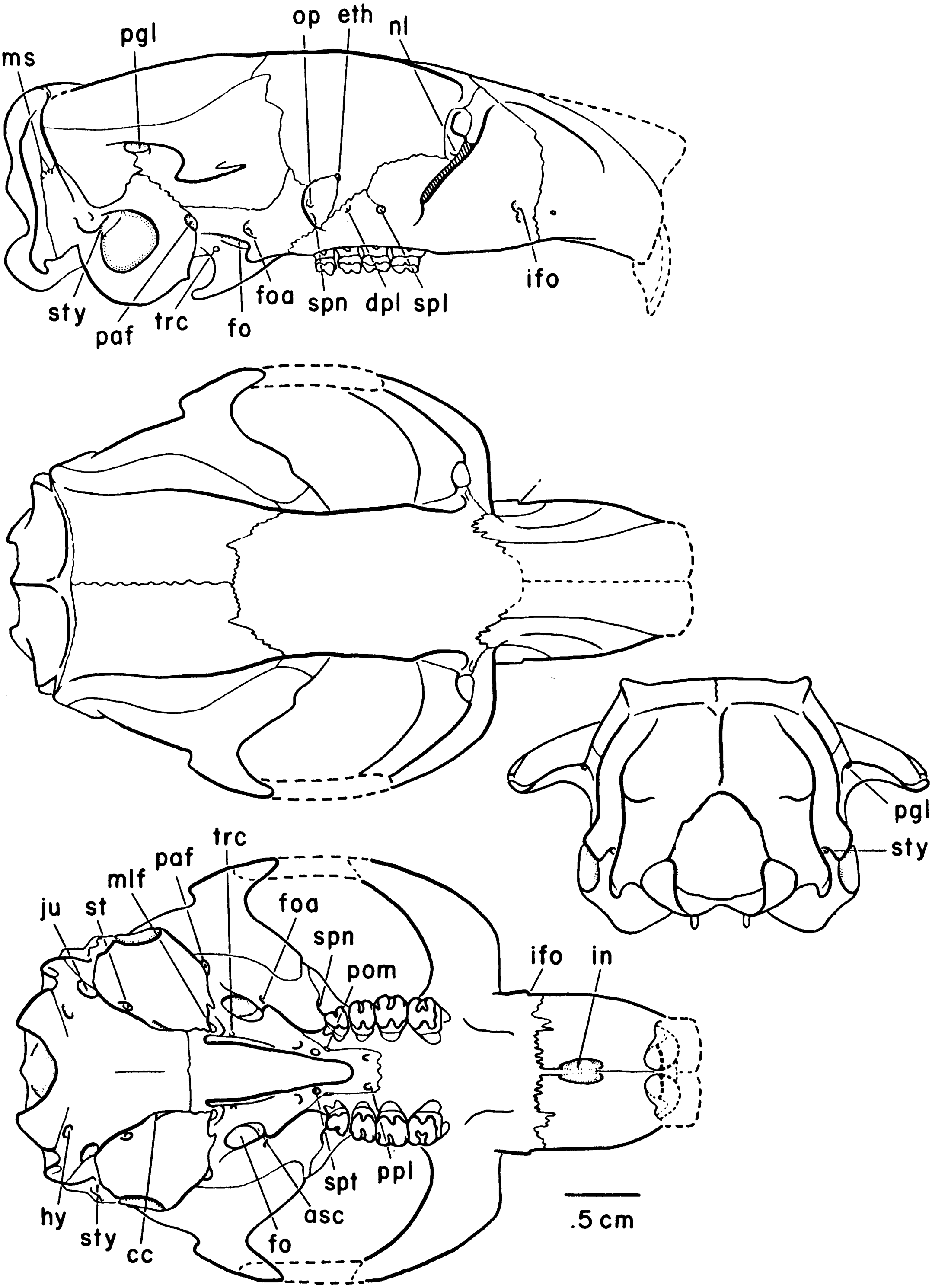

FIG. 6. Skull of *Kansasimys dubius*, F:AM 97824, lateral, dorsal, posterior and ventral views. See figure 1 for abbreviations.

anteroloph of the third molar is shorter labially than in *Viejadjidaumo*. The metacone and hypocone of that tooth are distinct cusps, and the posteroloph is short.

The face of the incisor (fig. 7A) is flatter than that of *Yoderimys* (fig. 7B), *Adjidaumo* (fig. 7C), or *Aulolithomys* and is similar to that of *Viejadjidaumo*. Incisors of the Vieja eomyids have been figured by Wood (1974, figs, 29D, 32C, 35C). The shape in cross section is similar to that of *Viejadjidaumo* but broader in the middle. Dimensions of the teeth are given in table 1.

DISCUSSION

The cranial foramina of eomyids are compared with those of other rodents except hystricomorphs. Comparative data are taken primarily from the thesis and publications of Wahlert (1972, 1974, 1977) and from an unpublished study of the Myomorpha. Additional information is available in Hill (1935), Guthrie (1963, 1969), and Bugge (1970, 1971a, 1971b, 1974). Terminology is taken from Hill with modifications. My observations on muroid rodents do not coincide in all cases with those of

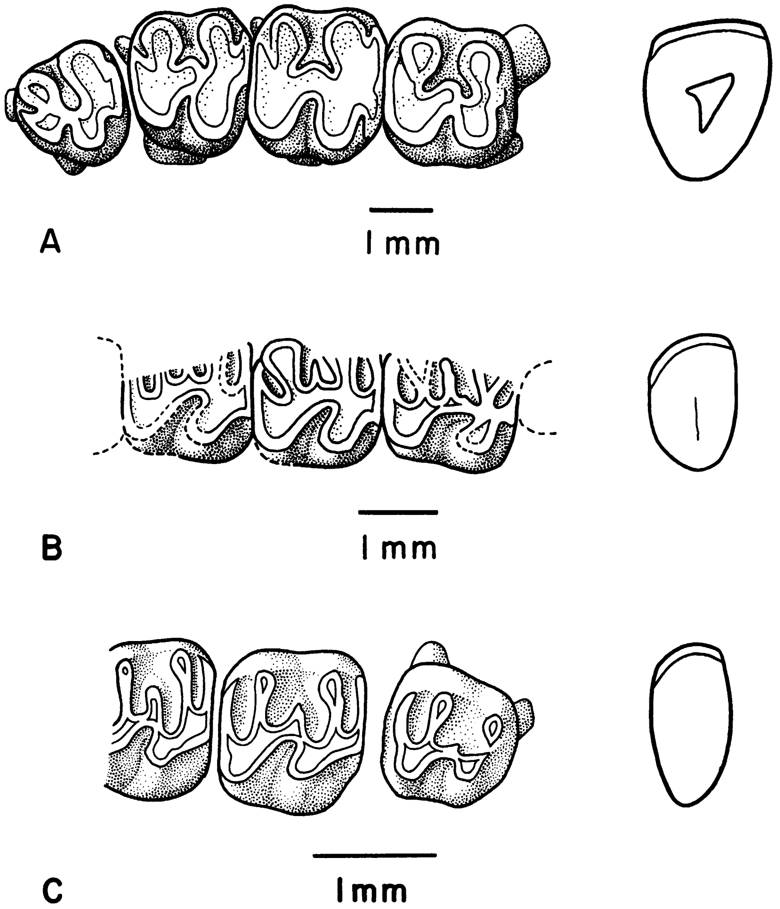

FIG. 7. A. Upper left incisor (reversed) and right cheek teeth of *Kansasimys dubius*, F:AM 97824. B. Upper left incisor and cheek teeth (reversed) of *Yoderimys lustrorum*, FMNH, PM 431. C. Upper right incisor and left cheek teeth (reversed) of *Adjidaumo minutus*, UNSM 04952.

Hill. I believe that *Paramys* and *Sciuravus*, based on comparison with other mammals, show conditions of the cranial foramina that are in the main primitive to rodents; in the following remarks on these two genera, this assumption is made.

Shared derived characters indicate relationship, whereas shared primitive characters indicate only that taxa are members of some larger group (e.g., Mammalia, Rodentia, etc.) and are thus shared at a higher level of universality than the subjects at hand. Derived characters of the foramina in eomyids can be distinguished from primitive ones by out-group comparison with those of other rodent groups or with mammals in general. Stratigraphic priority is not necessarily a criterion of primitiveness. Shared derived characters are used to test hypotheses of relationship.

The ratio of incisive foramen to diastemal length is rather low. The highest, in *Yoderimys*, is slightly less than that of *Paramys* and *Sciuravus* and well below that of dipodoids and most muroids; it is similar to that of myoxoids. The total range in other genera includes the range in *Eutypomys*, and overlaps the ranges observed in Oligocene and younger protrogomorphs, sciuromorphs, and some muroids; in geomyids the ratio is much lower. Low magnitude of the ratio is a derived character.

Inclusion of the posterior palatine foramina within the palatine bone is a primitive character retained in some members of diverse rodent groups. Placement relative to the cheek teeth is primitive, also. Presence of a posterior maxillary notch is primitive. Enclosure of a foramen in *Paradjidaumo* is a common derived state in rodents; its dorsomedial location in *Kansasimys* is further derived.

Sciuromorphous jaw musculature is derived. The deep part of the lateral masseter has its origin on both the ventrolateral surface of the zygomatic arch and the side of the snout. It is seen in eomyids, geomyids, heteromyids, castoroids, sciurids, and some ischyromyids. A similar arrangement occurs in the muroid genus *Rhizomys*. However, the rhizomyoid *Tachyoryctes* retains a trace of the muroid zygomatic plate. This suggests that the plate has fused with the side of the snout in *Rhizomys*, and origin of the anterior part of the muscle on the snout has been achieved via a transformation series different from that in sciuromorphous rodents.

In all protrogomorphous rodents the infraorbital canal is short, a mere foramen in the front of the zygomatic arch. A long infraorbital canal is developed in castorids, eomyids, heteromyids, geomyids, and in most sciurids. Slight development of a canal is seen in some specimens of the castoroid genus *Eutypomys*. If sciuromorphy defines a monophyletic assemblage of rodents, then the sciurids and castoroids are its earliest branches, and the geomyids, heteromyids, and eomyids are a monophyletic group. In the last three families, excepting the genera *Yoderimys* and *Kansasimys*, the anterior part of the infraorbital canal is partially sunk into the side of the snout, rather than appearing wholly lateral to it as in other sciuromorphs. The canal can be depressed into the snout because the incisor alveolus does not lie medial to it, except in *Kansasimys*. This is a shared derived character of geomyids and heteromyids; its absence in *Kansasimys* suggests that eomyids have acquired it independently. In muroids the ventral part of the infraorbital foramen, the homologue of the canal, is entirely lateral.

The position of the nasolacrimal foramen within the anterodorsal part of the orbit is primitive. The anterior placement of the sphenopalatine foramen is derived, a character seen only in *Eutypomys* and some castorids. In geomyids and heteromyids it is nearly as far forward. The ethmoid foramen is likewise anterior to its primitive position relative to the cheek teeth, but this is seen commonly among living rodents. Its situation in the frontal-orbitosphenoid suture is probably primitive, also a character of geomyids and heteromyids. The foramen is entirely within the frontal bone in *Sciuravus*, some paramyid specimens, aplodontoids, sciurids, and muroids. In myoxoids and dipodoids failure of ossification in the region makes its position doubtful; in *Zapus*, the foramen is within the frontal. The optic foramen and sphenoidal fissure have no peculiar attributes.

The presence of an interorbital foramen is a derived character seen in three eomyid genera, in ischyromyids, prosciurids, sciurids, castoroids, geomyids, heteromyids, and many myomorphs. The presence of a sphenofrontal foramen is primitive; its absence in *Kansasimys*, derived. Separation of the dorsal palatine from the sphenopalatine foramen is a common derived character in rodents, placement in the maxillary-palatine suture a primitive character shared by all but castoroids.

Union of masticatory and buccinator foramina is a derived character that occurs in members of many rodent groups. The foramen ovale accessorius is probably joined with these foramina, a derived character. The alisphenoid canal and foramen ovale have no unusual features. Separation of the transverse canal posteromedially from the alisphenoid canal is a derived character common to the Myomorpha, rare in sciurids, and seen in *Pleurolicus*. I have not found the canal in other geomyoids. *Eutypomys* is of interest because it has two entrances to the transverse canal, one at the back of the alisphenoid canal, and a second posterior in the pterygoid fossa. The presence of a foramen in the anterior part of the pterygoid fossa is shared with muroids and myoxoids. It may be the precursor of a sphenopterygoid canal like that seen in geomyoids and *Spalax*.

A short carotid canal occurs also in geomyoids and myomorphs, and is probably derived. Presence of a stapedial artery is primitive. Nothing of interest can be said about the jugular, hypoglossal, stylomastoid, mastoid, and postglenoid foramina. Temporal foramina are common in protrogomorphous rodents, castoroids, and sciurids, rare in geomyoids, and usually absent in myomorphs. Their absence in *Paradjidaumo* and *Kansasimys* is a derived character.

CONCLUSIONS

Monophyly of the Eomyidae is based on derived tooth crown morphology and enamel microstructure of lower incisors. All derived characters of the cranial foramina (table 2) are shared with the Geomyidae and Heteromyidae. The three families can be defined as monophyletic most succinctly by a pair of characters: long infraorbital canal and separation of entrance to transverse canal posteromedially from alisphenoid canal. Geomyids and heteromyids are a monophyletic group sharing derived char-

TABLE 2
Derived Characters of Eomyoids Shared With Some Other Rodent Groups

	Eomyoidea	*Paramys* + *Sciuravus*	Ischyromyidea	Castoroidea	Sciuridae	Heteromyidae + Geomyidae	Myoxoidea	Dipodoidea	Muroidea
1. Ratio of incisive foramen length to diastemal length low	+	0	+	+	+	+	+	0	S
2. Infraorbital canal long	+	0	0	S	S	+	0	0	0
3. Sphenopalatine foramen far anterior	+	0	0	S	0	+	0	0	0
4. Entrance to transverse canal separated from alisphenoid canal	+	0	0	0	S	?+	+	+	+
5. Sphenopterygoid foramen present	+	0	0	0	0	+	+	S	S
6. Carotid canal short	+	0	0	0	0	+	+	+	+
7. Temporal foramina rare or absent	+	0	0	0	S	+	+	+	+

Symbols: +, all; 0, none; S, some

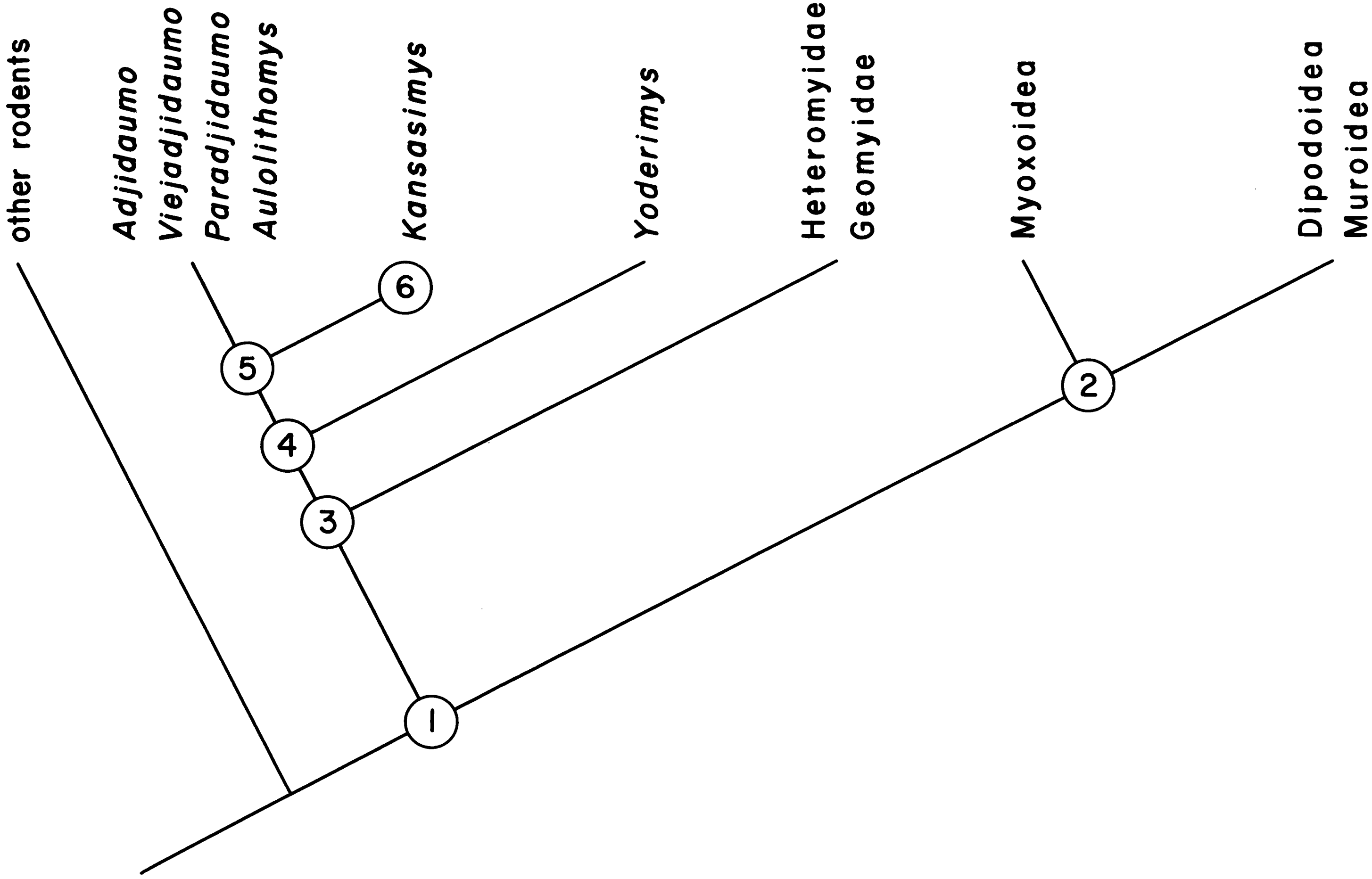

FIG. 8. Proposed relationships among eomyoid rodents and of eomyoids to geomyoids and to myomorphous rodents. Shared derived characters: 1. numbers 4, 6, and 7 of table 2; 2. enlarged infraorbital foramen; 3. sciuromorphy and numbers 1, 2, 3, and 5 of table 2; 4. longitudinal enamel lamellae in lower incisors; 5. eomyid tooth crown pattern; 6. extended temporal crests, premaxillary-maxillary suture behind incisive foramina, loss of sphenofrontal foramen. Multiple taxa at the end of a line represent unresolved polychotomies.

acters: tooth crown morphology basically bilobed, infraorbital canal depressed into snout, pterygoid fossa continued anteriorly as a broad canal into orbit. As remarked above, eomyids cannot be ancestral to heteromyids and geomyids but may share common ancestry with them. Eomyids are proposed as the sister group of geomyids and heteromyids, and the three families united in a monophyletic taxon. This is congruent with other current hypotheses of relationship. The Geomyoidea, Weber, 1904, is taken in its original sense to include only the Geomyidae and Heteromyidae. The Eomyidae are raised to equal taxonomic rank, Eomyoidea. Both superfamilies are united in an infraorder, Geomorpha Thaler, 1966. Study of the Florentiamyinae, a group which may be the most primitive within the Geomyoidea, may serve to test these hypotheses of relationship. I plan to prepare and describe the skulls in the collection of the American Museum of Natural History.

The number of derived characters shared with myoxoids is next largest, followed in turn by those in common with dipodoids and muroids. Separation of the entrance to the transverse from the alisphenoid canal is the most certain derived character shared by them. If these three superfamilies constitute a monophyletic assemblage, then the Geomorpha is its sister group, and the suborder Myomorpha encompasses both groups. A cladogram of proposed relationships is presented in figure 8. Hartenberger (1971) has shown close relationship of myoxoids to certain microparamyines. I believe that the Geomorpha is related to this group as well, and I predict that microparamyine skulls will show the characteristic separation of the entrance to the transverse canal.

If the Castoroidea includes both eutypomyids and castorids (Wahlert, 1977), then the number of derived characters shared with eomyoids is only one, namely the low ratio of incisive foramen length to diastemal length. Likewise, evidence from the sciurids and ischyromyids is not compelling. Derived characters shared with some members of these groups are considered to be examples of parallelism. *Paramys* and *Sciuravus* share no derived characters of the foramina with eomyoids, and separate retention of the eomyoids as a derived group allied to protrogomorphous rodents is not supported.

Skulls of *Adjidaumo*, *Viejadjidaumo*, *Paradjidaumo*, and *Aulolithomys* are similar with regard to cranial foramina. *Kansasimys* is primitive in the position of its infraorbital canal and lack of an interorbital foramen. It shares derived tooth crown morphology with these other genera and has derived characters of its own: temporal crests continuing to anterior end of orbit, premaxillary-maxillary suture crossing diastema posterior to incisive foramina and flanking a maxillary process that runs anterior to the medial margins of the foramina, sphenofrontal foramen absent. I have placed *Kansasimys* as the sister group of the four other genera. *Yoderimys* is likewise primitive with regard to the cranial foramina. It is the only eomyid genus retaining the third upper premolar. The molar crown pattern is the most primitive among eomyoids but has a number of unique derived features. The genus appears to represent a still earlier split in the superfamily. The traditional view of eomyoid relationships is supported. A cladogram of proposed relationships is given in figure 8.

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