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Kirkomys, a New Florentiamyid (Rodentia, Geomyoidea) from the Whitneyan of Sioux County, Nebraska

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ABSTRACT

Kirkomys milleri, a new genus and species of florentiamyid, is described from a partial skull. Participation of the palatine in the lateral wall of the anterior-alar fissure and long entostyle in the upper molars are derived characters shared with other florentiamyids. However, frontal flanges over the orbits are lacking; the position and size of certain foramina and the morphology of the premolar parallel conditions in living geomyoids and are derived relative to those in *Florentiamys* and *Sanctimus*. *Kirkomys* probably represents a florentiamyid lineage that is separate from these two

genera. *Heliscomys schlaikjeri* is transferred to *Kirkomys* on evidence of dental morphology.

Wear on the upper teeth indicates propalinal chewing. Certain facets show that lower teeth were widened by buccal styles. The crown pattern of the upper cheek teeth is similar to that of *Perognathus*. However, the teeth of *Kirkomys*, like those of other florentiamyids, are bunodont and broadened by an anteroposteriorly elongated entostyle. The diet was probably less abrasive than that of *Perognathus*.

INTRODUCTION

Wahlert (1983) described skulls and dentitions of several new florentiamyid species and concluded that the family Florentiamyidae is the earliest defined branch of the Geomyoidea. He argued against Rensberger's (1973c) hypothesis that proposed a reversal in the direction of premolar evolution and

thus later origin for the family. A new florentiamyid, *Kirkomys milleri*, new genus and species, which reopens the case, has come to light; it is geologically older and has more derived premolar morphology than specimens known heretofore.

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ABBREVIATIONS

Catalogue numbers of specimens contain the following acronyms:

AMNH, American Museum of Natural History
F:AM, Frick Collection, American Museum of Natural History

MCZ, Museum of Comparative Zoology, Harvard University

SYSTEMATICS

SUBORDER MYOMORPHA

INFRAORDER GEOMORPHA THALER, 1966

SUPERFAMILY GEOMYOIDEA WEBER, 1904

FAMILY FLORENTIAMYIDAE WOOD, 1936

KIRKOMYS, NEW GENUS

TYPE SPECIES: *Kirkomys milleri*, new species.

ETYMOLOGY: Named for Dr. Kirk Miller, vertebrate physiologist at Franklin and Marshall College.

DIAGNOSIS: Smaller than *Florentiamys* and *Sanctimus*; P⁴ with protocone and supporting root anterior, and paracone and protostyle absent; incursive foramina very short, about 12 percent of disaternal length; posterior pal-

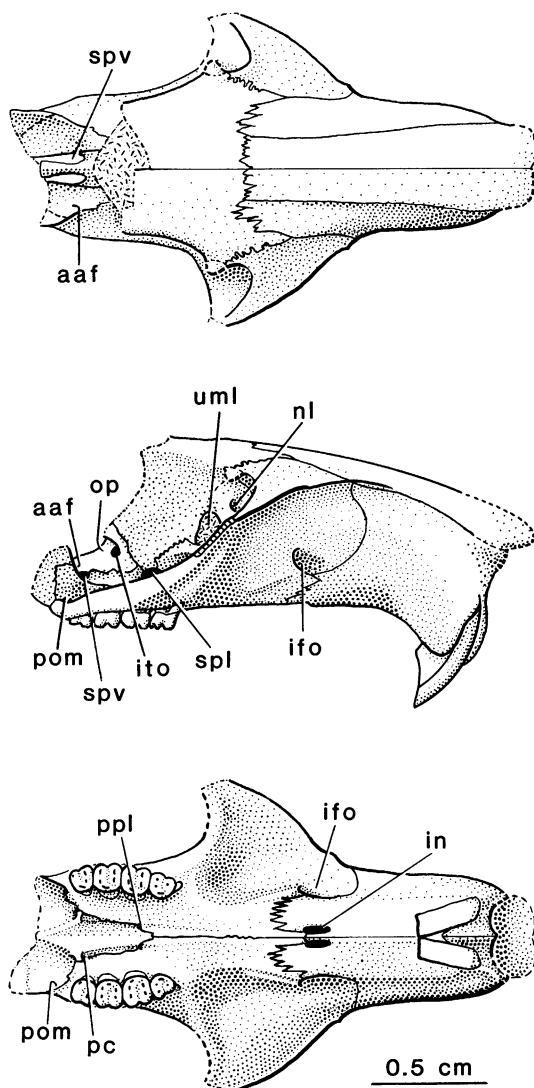


FIG. 1. Skull fragment of *Kirkomys milleri*, F:AM 105337, in dorsal, lateral, and ventral view. Dashed lines indicate broken edges; cross hatching, imagined cut through bone. Abbreviations for foramina and other apertures (as specified): aaf, anterior-alar fissure; ifo, infraorbital; in, incisive; ito, interorbital; nl, nasolacrimal; op, optic; pc, palatine canal; pom, posterior maxillary; ppl, posterior palatine; spl, sphenopalatine; spv, sphenopalatine vacuity; uml, unossified area in maxillary-lacrimal suture.

atine, dorsal palatine, sphenopalatine, and optic foramina and anterior-alar fissure farther anterior than in *Florentiamys* and *Sanc-*

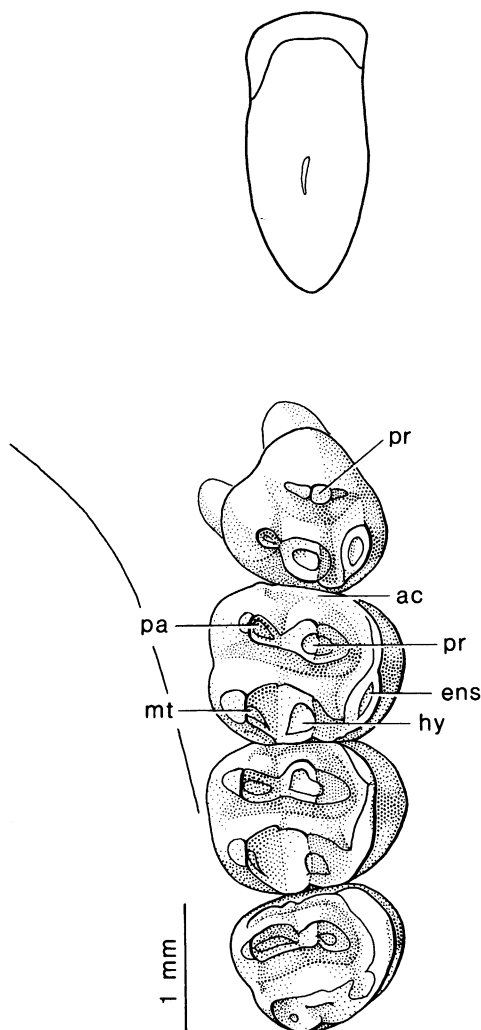


FIG. 2. Upper right dentition of *Kirkomys milleri*, F:AM 105337, including I (left side, reversed), P⁴-M³, and curve of maxillary root of zygoma. Abbreviations: ac, anterior cingulum; ens, entostyle; hy, hypocone; mt, metacone; pa, paracone; pr, protocone.

timus; no marginal flanges on frontal bones over orbits.

Kirkomys milleri, new species

TYPE SPECIMEN: F:AM 105337, snout, palate, orbit; figures 1, 2, and 4A.

TYPE LOCALITY, AGE AND STRATIGRAPHY: West end of Court House Rock, Sioux Co., Nebr.; Brule Formation, Whitneyan (early late

Oligocene). 54 feet below unconformity between Gering Formation and underlying Brule. Specimen is noted on section of area by Morris F. Skinner as about 30 feet below upper ash and about 15 feet below specimen he identified as *Hyracodon*.

ETYMOLOGY: Same as for genus.

DIAGNOSIS: Cheek teeth proportionally larger than in *K. schlaikjeri*, having deep separation between protocone and entostyle; posterior cingulum absent on P⁴; anterior cin-

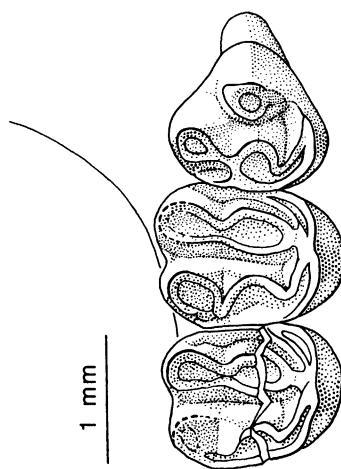


FIG. 3. Upper right dentition of *Kirkomys schlaikjeri*, MCZ 7335, including P⁴-M² and curve of maxillary root of zygoma.

gula on molars narrow; maximum curvature of edge of maxilla into zygoma anterior to P⁴.

Kirkomys schlaikjeri (Black, C.C.), 1961

TYPE SPECIMEN: MCZ 7335, fragment of right maxilla with P⁴-M²; figure 3 and table 1.

TYPE LOCALITY AND AGE: NW side of Sixty-Six Mountain, Goshen Co., Wyo.: Gering equivalent, early Arikarean (late Oligocene).

DIAGNOSIS: Cheek teeth proportionally smaller than in *K. milleri* and having shallow separation between protocone and entostyle; posterior cingulum present on P⁴; anterior cingula on molars wider than in *K. milleri*; maximum curvature of edge of maxilla into zygoma lateral to P⁴.

SKULL AND DENTITION

Description of the skull is based on the specimen of *Kirkomys milleri* (fig. 1), unless *K. schlaikjeri* is mentioned. Dimensions of the skull are as follows: diastemal length, 10.4 mm, from back of incisor alveolus to root of P⁴ on same side; incisive foramen length, 1.3 mm; palatal length, approximately 16.2 mm, from backs of incisor alveoli to broken end of palate at midline; palatal width, 2.9 mm, minimum distance between alveoli of M¹s.

The diastema is nearly flat, and the small incisive foramina situated near its midpoint occupy only 12 percent of its length. The foramina are intersected at the back by the premaxillary-maxillary suture, which runs posteriorly away from them. The posterior palatine foramina are medial to the middle of M¹ in *K. milleri* and to the junction of M¹ and M² in *K. schlaikjeri*; they face anteroventrally in the maxillary-palatine suture; shallow furrows lead a short distance anteriorly from them. The posterior part of the palate has paired depressions, and a groove leads anteriorly from each toward the posterior palatine foramina. A boss on the palatine, where it changes slope, may be the remains of a bridge across each groove to the maxilla; this bridge encloses the palatine canal. The posterior maxillary foramen is a long, lenticular opening immediately posterior to M³ and dorsomedial to the maxillary spine.

Both specimens are fully sciuromorphic. In ventral view the curve of the edge of the maxilla into the zygoma is farther anterior in *K. milleri* (figs. 2 and 3). The infraorbital canal is long and measures about 3.7 mm. It begins in the orbit anterodorsal to P⁴ and emerges in a depression low on the side of the rostrum. The lateral wall of the infraorbital foramen is flush with the rostrum; the medial wall at the foramen was entire but is now damaged in its deepest recess. The premaxillary-maxillary suture is anterior to the depression but curves posteroventrally along its ventral margin. The origin of the superficial masseter is indicated by a narrow, roughened strip that slants posteroventrally from the lower edge of the infraorbital foramen.

The lacrimal canal is visible through the wall of the rostrum; it runs anteriorly from

the nasolacrimal foramen in the anterodorsal curve of the orbit, descends lateral to the incisor alveolus, and turns medially above the depression for the infraorbital canal. An unossified area forms a gap in the orbital wall at the junction of the lacrimal, frontal, and maxillary bones. The sphenopalatine foramen is dorsal to the posterior part of P⁴ and to most of M¹; it is surrounded by the frontal, maxillary, and palatine bones; the orbitosphenoid is close to the foramen but apparently does not reach it. The ethmoid foramen is not preserved. Most of the margin of the optic foramen is missing, but a saddle on the orbitosphenoid indicates that it was dorsal to M². An interorbital foramen, anteroventral to the optic, perforates the orbitosphenoid bone dorsal to the anterior portion of M². A large sphenopalatine vacuity extends from the middle of M³ posteriorly to be hidden by the wall of the anterior-alar fissure. The dorsal palatine foramen, hidden from view in the illustration, is in the maxillary-palatine suture dorsal to the posterior part of M¹; it is close to the sphenopalatine foramen and to the posterior palatine foramen, which is the opposite end of the canal for the descending palatine artery.

The anterior-alar fissure (sphenoidal fissure of earlier publications) is dorsal to the posterior part of M³. A lamina of the palatine arises above M² from the floor of the orbit and forms the anteroventral edge of the anterior-alar fissure; the alisphenoid continues the wall dorsally. 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 as in *Florentiamys* and *Sanctimus* rather than anteromedial or medial to it as in heteromyids and geomyids.

In dorsal view the rostrum is quite broad and roughly parallel-sided. The intersection of the wall of the orbit and skull roof is rounded; the anterior portion that is preserved shows no trace of the marginal flanges that overhang the orbits in other florentiamyids.

In cross section the incisor (fig. 2) is widest at the middle; the enamel surface is nearly as wide. The enamel is thickest where it curves from the anterior to the lateral side. The lingual wear facet is nearly vertical relative to the plane of the cheek teeth. In front view the

TABLE 1
Dimensions of Upper Teeth (in Millimeters)

<i>Kirkomys milleri</i> , F:AM 105337					
Incisor width	1.0	depth	2.1	enamel thickness	0.2
Alveolar length of cheek teeth	4.9				
Crown length of cheek teeth	4.6				
Crown length : width		P ⁴	M ¹	M ²	M ³
		1.3 : 1.2	1.1 : 1.5	1.1 : 1.5	1.1 : 1.3
<i>Kirkomys schlaikjeri</i> , MCZ 7335		1.1 : 1.2	1.1 : 1.4	1.1 : 1.4	—

incisor tip is worn straight across, and the edge is nearly horizontal. The enamel surface is almost smooth; it grades from cinnamon color at the tip to tawny (Smithe, 1975). The center of curvature of the incisor in lateral view (fig. 1) lies on the surface of the diastema ventral and a very slight distance posterior to the anteriormost point of the maxilla.

The upper cheek teeth are low crowned and display a typical florentiamyid crown pattern that is illustrated in figures 2, 3, and 4A. For dimensions of the teeth see table 1. Lengths of individual cheek teeth were measured along an anteroposterior line that bisects the tooth row; widths are the maximum dimension perpendicular to this line. The greatest width of the dentition is across the anterior part of M². M¹ and M² each have the four primary cusps, and a lingual entostyle that blocks the median transverse valley. The third molar is similar but lacks strong development of a hypocone. All three molars have a low anterior cingulum; only M¹ has a trace of a posterior cingulum. The shallow depression between protocone and entostyle in molars of *K. schlaikjeri* has permitted union of these features with moderate wear. Although the teeth of *K. milleri* are not as worn, I believe that union would occur at a later stage.

The premolar, excluding the anterior root, occupies about 28 percent of the crown length of the tooth row. It is more triangular than the molars, because there is a single anterior cusp, labeled protocone in the illustration; this cusp is aligned, as a protocone would be, with the lingual cusps in the molar teeth, but the anterior position of the anterobuccal tooth root suggests that the cusp may be a united protocone and paracone. A posterior cingu-

lum is present in P⁴ of *K. schlaikjeri*. Black (1961) discounted the taxonomic importance of this feature, because its occurrence and position vary in *Heliscomys*, the genus to which he assigned this species. The greater breadth of the cingula in molars of *K. schlaikjeri* suggests to me that the presence of the cingulum in P⁴ is a significant difference from *K. milleri*.

Although the primary cusps of the cheek teeth form transverse lophs, the wear facets create three anteroposterior crests of the cusps and entostyles; these crests and anteroposterior striations on worn surfaces in *K. milleri* indicate propalinal chewing. Facets on the buccal sides of the paracones and metacones in *K. milleri* demonstrate that protostylids and hypostylids widened the buccal sides of the unknown lower cheek teeth. The specimen of *K. schlaikjeri* appears to have been tumbled before deposition, and wear facets are not defined by clear edges.

DISCUSSION

The two species of *Kirkomys* are very similar. Although the specimen of *K. schlaikjeri* is from a slightly younger horizon, the species appears to be more primitive than *K. milleri*. Anterior cingula of the molars are broad in *K. schlaikjeri*; still greater breadth occurs in eomyids, such as *Yoderimys* and *Adjidaumo*, which are the most primitive branch of the Geomorpha (Wahlert, 1978). The posterior palatine foramina of *K. schlaikjeri* are medial to the junction of M¹ and M² as in *Florentiamys* and *Sanctimus* and similar to the position in eomyids; those of *K. milleri* are farther anterior. The difference in position of

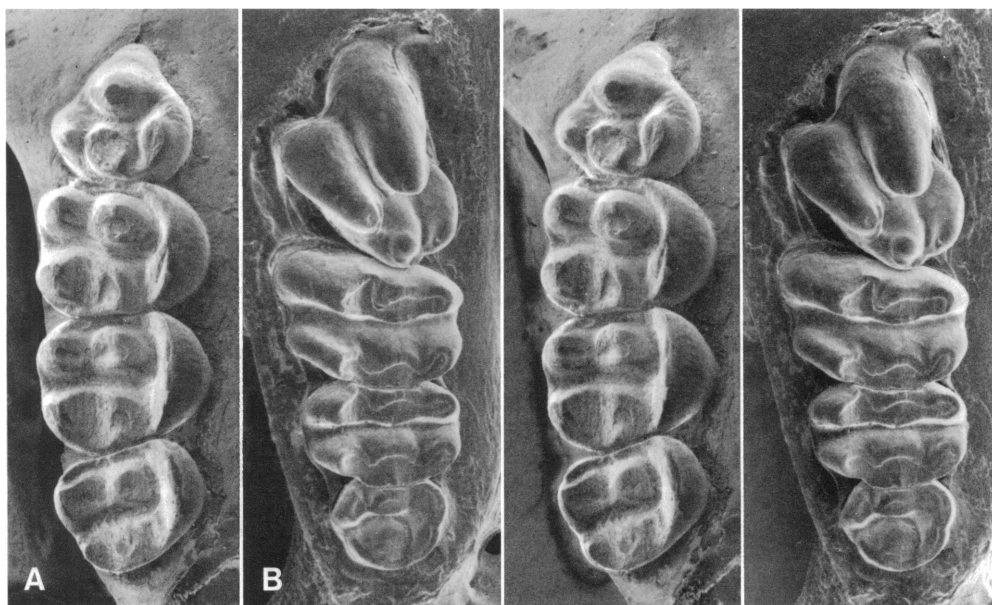


FIG. 4. Stereoscopic scanning electron micrographs of upper right cheek teeth in A. *Kirkomys milleri*, F:AM 105337, magnification approximately $\times 16$; and B. *Perognathus parvus parvus*, AMNH 33505 (Ironsides, Malheur Co., Oregon), magnification approximately $\times 18$.

the zygomatic curve of the maxilla is harder to interpret; *K. milleri* is similar to the eomyids, whereas the more posterior position in *K. schlaikjeri* is like that in *Florentiamys* and *Sanctimus*. Korth (1984) in a study of evolution among early Tertiary rodents proposed that "posterior margin of the anterior root of the zygoma even with the posterior margin of P⁴" is a primitive condition (*ibid.*, p. 64). However, in sciuriform rodents the maxillary root of the zygoma is inclined anteriorly, and the ventral part appears to be shifted posteriorly as a consequence of this tilt; thus the posterior position here may be derived.

Kirkomys possesses some, but not all, of the florentiamyid hallmarks. Chief among them is participation of the palatine bone in the edge of the anterior-alar fissure and consequent position of the dorsal aperture for the descending palatine vein lateral to the fissure wall; the entostyle of the upper cheek teeth is elongated and blocks the lingual end of the transverse valley.

Cranially *Kirkomys* exhibits a mixture of primitive and derived characters that differ

from those of other florentiamyids. The incisive foramina are extremely short, and the posterior palatine, dorsal palatine, and optic foramina and the anterior-alar fissure are more anterior in position than those of *Florentiamys* and *Sanctimus*. These features of *Kirkomys* approach the conditions seen in living geomyoids. The frontal bones, however, lack the marginal flanges that project over the orbits, a derived character in other florentiamyids.

The dentition resembles that of some extinct *Heliscomys*, a genus of markedly smaller size. The morphology of *Heliscomys* suggests that styler widening of the upper cheek teeth is a shared character among geomyoids, but that the prominence of the entostyle in florentiamyids is a derived condition. Illustrations of upper teeth in *Heliscomys vetus* (Black, 1965, fig. 5f; Setoguchi, 1978, fig. 23c) show variation in development of the entostyle. It is low, but entire, in posterior molars. In the M¹ figured by Setoguchi it is simple and continues into a pronounced anterior cingulum; in that figured by Black the entostyle is in line with the metacone and hy-

pocone and is separated from a posterolingual extension of the anterior cingulum. The division between anterior and posterior parts of the tooth appears to have developed along with the styler shelf in *Heliscomys* and is an independently derived condition.

Dental comparison of *Kirkomys* and *Perognathus* (fig. 4) illustrates the similarities and differences between florentiamyid and heteromyid morphologies. In *Perognathus* the upper cheek teeth are higher crowned, and P^4 - M^2 are clearly divided by the transverse valley. Such a division characterizes unworn teeth of heteromyids (Wood, 1935) and entoptychine and pleurolicine geomyoids (Rensberger, 1971, 1973b). Occlusal wear has shaped the cusps of the teeth into antero-posterior ridges in *Kirkomys* as it does in *Perognathus*. A parallel example of this form of wear and widening of the cheek teeth by addition of styles was diagrammed by Butler (1980) for murid rodents.

The primitiveness of *Kirkomys* relative to *Perognathus* is seen in comparison of enamel thicknesses. There is no marked difference in thickness of enamel on the anterior and posterior sides of the cusps in *Kirkomys*. In *Perognathus* the enamel is thin on the posterior sides and thick on the anterior sides of the lophs. Rensberger (1975) described the increased efficiency of this design when there is high food abrasion. The irregular topography in the tooth crown of *Perognathus* at the stage of wear illustrated is caused by variation in width of the lophs.

The long entostyle is a peculiarity of florentiamyids. Rensberger (1975) pointed out that in young specimens of *Entoptychus* the hypsodont teeth have anteroposterior enamel segments on the lingual side in uppers and on the buccal side in lowers; the extra enamel retards wear and causes these parts of the teeth to stand higher than the rest of the crown; the crown flattens when worn to a depth below this enamel. Florentiamyids have bunodont teeth that become flat when extremely worn. An entostyle is prominent in all, especially in *Kirkomys*; it increases the area of the crown that makes contact with the lower teeth and, thus, decreases occlusal pressure per unit area (Rensberger, 1973a). The large area of contact, especially when combined with propalinal chewing, is an effective

design for exposing new surfaces of food to mechanical breakdown during a single chewing stroke. The food of *Kirkomys* was probably not very abrasive. I have described the entostyle as blocking the transverse valley in the upper molars. During mastication, however, it would have compressed and sheared the food protruding lingually from the transverse valleys that cross and lie between the lower teeth.

It is possible that some fossil specimens described as *Heliscomys* are florentiamyids; *Kirkomys schlaikjeri* is a case in point. The upper dentition of *Heliscomys tenuiceps* (Galbreath, 1948) is similar to that of *Kirkomys*, but the teeth are smaller. Comparison of the skull of *Kirkomys* and the published figure of this species is perplexing, because the premaxillary-maxillary suture and boundary of the orbitosphenoid, as shown by Galbreath (*ibid.*, pls. 2 and 3A) follow unexpected courses. Galbreath (1953) corrected identification of the ethmoid foramen, but he did not recognize that the aperture labeled SF (sphenoidal fissure) is probably the optic foramen. Black (1961) pointed out especial dental resemblance of *K. schlaikjeri* to *H. tenuiceps*.

CONCLUSIONS

Derived cranial morphology, especially anterior position of orbital foramina and anterior-alar fissure relative to the cheek teeth, combined with primitiveness of the frontal roof suggest that *Kirkomys* belongs to a lineage within the Florentiamyidae separate from that of *Florentiamys* and *Sanctimus*. This same combination of characters supports the hypothesis that the single anterior cusp and triangular shape of P^4 are parallel derivations in *Kirkomys* and other geomyoids and not the primitive condition in florentiamyids. The fact that the specimen of *Kirkomys milleri* is geologically older than *Florentiamys* and *Sanctimus* suggests considerable diversity in this little known family.

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