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William W. Korth

*Rochester Institute of Vertebrate Paleontology*

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**RODENTS FROM THE LATE HEMPHILLIAN (LATEST MIOCENE),  
SIOUX COUNTY, NEBRASKA**

William W. Korth

Rochester Institute of Vertebrate Paleontology  
928 Whalen Road  
Penfield, New York 14526

*ABSTRACT*

Only one rodent specimen has been previously described from the late Hemphillian ZX Bar local fauna from Sioux County, Nebraska—the holotype of the heteromyid *Perognathus coquorum* Wood. A re-examination of this specimen has led to its allocation to the dipodomyine heteromyid genus *Prodipodomys* Hibbard. An additional specimen of a fossil rodent has been recognized from the ZX Bar fauna that is referable to a new species of the primitive geomyid *Pliogeomys*, *P. russelli*.

† † †

Skinner et al. (1977) listed the late Hemphillian mammalian fauna from ZX Bar local fauna and in-

Table 1. Measurements of the dentition of the holotypes of *Pliogeomys russelli* and *Prodipodomys coquorum*. Abbreviations: a-p, anteroposterior length; tr, maximum transverse width; tra, anterior transverse width (metalophid); trp, posterior transverse width (hypolophid); ht, height of crown. All measurements in mm.

	<i>P. russelli</i> FAM 81069		<i>P. coquorum</i> AMNH 97845	
p4	a-p	1.77	a-p	1.23*
	tra	1.14	tra	1.04*
	trp	1.60	trp	1.32*
			ht	1.50
m1	a-p	0.85	a-p	1.38*
	tr	1.60	tra	1.63*
			trp	1.56*
			ht	0.93
m2	a-p	0.98		
	tr	1.69		
Length of diastema		3.40		5.03
Depth of mandible		5.15		4.41

\* measurements taken from Wood (1935: table II).

cluded only a single rodent specimen, the holotype of the heteromyid *Perognathus coquorum*. This species was described by Wood (1935) from the East *Pliohippus* Draw quarry in Sioux County, Nebraska. This specimen had been misplaced in the collections of the American Museum of Natural History (AMNH) for several years. In search of the collections of uncataloged rodent specimens, this specimen was found along with an additional mandible belonging to a primitive geomyid from the same locality. A re-examination of the type of *P. coquorum* and the geomyid mandible has led to the recognition of two typically late Hemphillian genera of rodents.

Dental nomenclature used below follows that of Rensberger (1973). Upper cheek teeth are indicated by capital letters, and mandibular teeth are denoted by lower case letters.

**SYSTEMATICS**

Order RODENTIA Bowdich, 1821  
Family Heteromyidae Gray, 1868  
Subfamily Dipodomyinae Gervais, 1853  
Genus *Prodipodomys* Hibbard 1939  
*Prodipodomys coquorum* (Wood, 1935)  
(Fig. 1A and B, Table 1)

*Perognathus coquorum* Wood, 1935

**Type and only specimen:** AMNH (American Museum of Natural History specimen) 97845, partial right mandible with incisor and p4-m2 (listed as HJC 702 by Wood, 1935: 105). **Horizon and locality:** NW ¼, sec. 32 or SW ¼ sec. 29, T26N, R55W, Upper Johnson Member, Snake Creek Formation, Sioux County, Nebraska. **Age:** Late Hemphillian (latest Miocene). **Emended diagnosis:** Large species; cheek teeth lower crowned than other species; transverse lophs of lower molars not convergent buccally; cheek teeth more

strongly rooted.

**Discussion.** Wood (1935: 105-07) fully described the type and only specimen of *Perognathus coquorum*. The only aspect of the mandible not described or figured by Wood (1935: figs. 28 and 29) was the masseteric scar on the lateral side of the mandible. The masseteric scar is typical for heteromyids, a small shelf that extends anterior to p4. The bony ridge is dorsally placed and its anterior end extends into the diastema, similar to that in species of *Dipodomys* and *Prodipodomys*.

Although Wood (1935) referred this species to *Perognathus*, stating that it was distinguished from other species by lower crown height of the cheek teeth, the crown height is much higher than any species of that genus. Martin (1984) calculated a crown height index for p4 and m1 in Recent *P. parvus* and several Tertiary species of *Perognathus*. He (Martin, 1984:

figs. 2 and 3) divided the height of the hypolophid of p4 and the metalophid of m1 by their respective anteroposterior lengths. The highest index for p4 was 0.8 and for m1 was 0.7. These indices for the holotype of *P. coquorum* are 1.22 for p4 and 0.84 for m1, markedly higher than any species of *Perognathus*.

The masseteric scar in species of *Perognathus* is ventral to the diastema and descends posteroventrally, whereas in *Prodipodomys* and *Dipodomys* the scar is more dorsal, extends into the diastema, and is nearly horizontal. The masseteric scar on the holotype of *P. coquorum* is identical to that of *Prodipodomys* rather than that of *Perognathus*.

The greater crown height of the cheek teeth and morphology of the masseteric scar of "*Perognathus*" *coquorum* more closely approaches that of *Prodipodomys* than it does *Perognathus* and should be referred to the former.

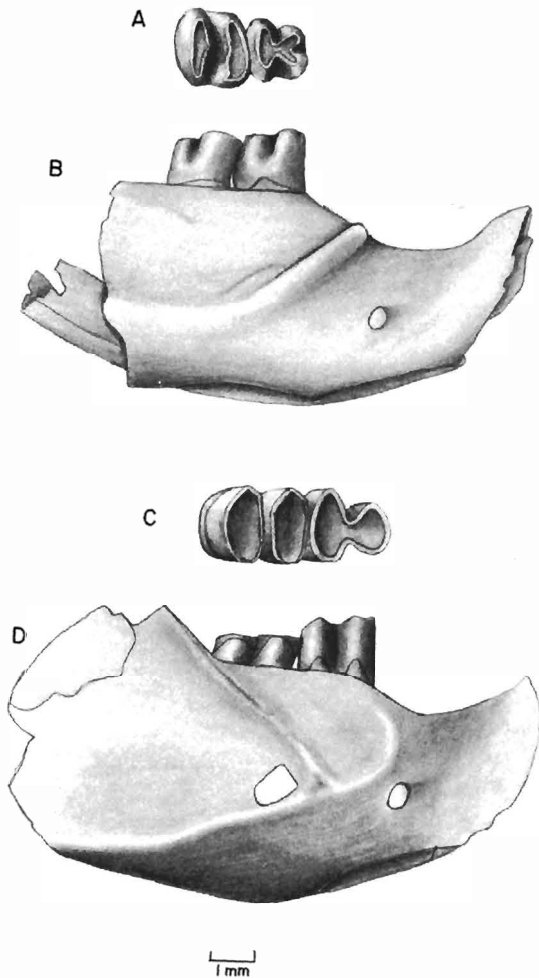


Figure 1. Holotypes of *Prodipodomys coquorum*, AMNH 97845 and *Pliogeomys russelli*, AMNH 80169. A-B, *P. coquorum*. A, occlusal view p4-m1. B, lateral view of mandible. C-D, *P. russelli*. C, occlusal view of p4-m2. D, lateral view of mandible.

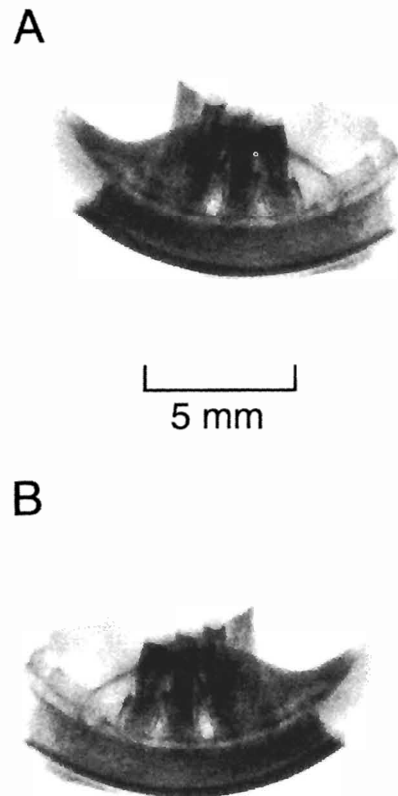


Figure 2. X-ray positives of *Pliogeomys russelli*, AMNH 80169. A, medial view. B, lateral view.

Among species of *Prodipodomys*, *P. coquorum* is distinguished by its larger size, lower crown height of the cheek teeth (there is only a slight indication of enamel an chevron p4) with well defined roots, and the lophs on the lower molars parallel and not convergent lingually. These lophs converge toward the center of the tooth on molars of *Prodipodomys* and unworn molars of *Dipodomys* (for examples see Wood, 1935: figs. 28–29, 73–90; Tomida, 1987: fig. 15 for *Dipodomys*; and Zakrzewski, 1969: fig. 5, 1970: fig. 1 for *Prodipodomys*).

Zakrzewski (1970) referred a jaw from the Hemphillian Saw Rock Canyon fauna of Kansas to *Prodipodomys* sp. It was distinguished from the contemporaneous *P. griggsorum* by its larger size, deeper jaw, lower-crowned cheek teeth with better-developed roots, lower placement of the mental foramen on the mandible, and relatively shorter diastema. *Prodipodomys coquorum* shares all of these features with the Saw Rock Canyon specimen. It is quite likely that the specimen described by Zakrzewski (1970) is referable to *P. coquorum*.

*Prodipodomys coquorum* is morphologically transitional between a perognathine and a dipodomyine. The change in the masseteric scar and increased crown height of the cheek teeth of *P. coquorum* separates it from other perognathines. However, the occlusal pattern does not differ significantly from later Clarendonian or Hemphillian species of the perognathine *Cupidinimus* (Barnosky, 1986; Baskin, 1979). This combination of a more primitive dentition and derived mandible in *P. coquorum* supports the hypothesis that the origin of the dipodomyines is likely from a *Cupidinimus*-like perognathine sometime in the late Clarendonian or earliest Hemphillian.

Voorhies (1975) described a Clarendonian dipodomyine *Eodipodomys* from Nebraska and suggested that it was ancestral to later dipodomyines, already having attained greater hypsodonty of the cheek teeth and modifications of the limb bones and skull. Zakrzewski (1981) argued that *Eodipodomys* was an early sidebranch of the dipodomyines and that *Prodipodomys* was a much more likely ancestor to *Dipodomys* even though the earliest species of *Prodipodomys* had lower crowned cheek teeth than *Eodipodomys*. In fact, *Eodipodomys* has a perognathine masseteric scar on the mandible unlike that of *Prodipodomys* and *Dipodomys*, and the upper incisor of *Prodipodomys* is grooved (as in *Dipodomys*) whereas that of *Eodipodomys* is asulcate. There are also species of *Prodipodomys* that have the rudiments of enamel failure and greater crown height of the cheek teeth typical of *Dipodomys*. As suggested by Zakrzewski (1981), it appears that *Eodipodomys* was an early dipodomyine, but not directly ancestral to Recent *Dipodomys*.

*Prodipodomys coquorum* represents a primitive species of the genus that may have been ancestral to later, more advanced species of *Prodipodomys* (greater crown height, enamel failure, and weaker root development of cheek teeth). The stratigraphic position of *P. coquorum* (late Hemphillian) is also consistent with this interpretation.

Family Geomyidae Bonaparte, 1845  
Subfamily Geomyinae Bonaparte, 1845  
Genus *Pliogeomys* Hibbard, 1954  
*Pliogeomys russelli* n. sp.  
(Figs. 1C and D; Table 1)

**Type specimen and only specimen:** AMNH 81069, partial right mandible with i1 and p4-m2. **Horizon and locality:** *Pliohippus* Draw, NW ¼, sec. 32 or SW ¼ sec. 29, T26N, R55W, Upper Johnson Member, Snake Creek Formation, Sioux County, Nebraska. **Age:** Late Hemphillian (latest Miocene). **Diagnosis:** Slightly larger than *P. parvus*, smaller than all other species of the genus; cheek teeth lower crowned and more strongly rooted than in other species except *P. parvus*; heteromyid projection of masseteric scar on mandible reduced, dorsal ridge of masseteric scar weakly developed, and medial ridge weak, becoming a shallow groove posteriorly; mental foramen anterior to masseteric scar. **Etymology:** Patronym for R. J. Russell for his work on pocket gophers. **Description:** The mandible of AMNH 81969 is dorsoventrally deep (5.15 mm depth below m1). The diastema and short and shallow with no indication of a diastemal notch. The ventral ridge of the masseteric scar is well developed, originating from the area of the angle and running anterodorsally, ending anteriorly just anterior to the tooth row. The anterior end of the ventral ridge curves posteriorly, connecting to a faint dorsal ridge. The medial ridge fuses with the ventral ridge about 1.4 mm posterior to the anterior extent of the ventral ridge and runs posterodorsally toward the anterior edge of the ascending ramus. After about 1.5 mm from the junction with the ventral ridge, the medial ridge becomes a narrow, shallow groove. The mental foramen is anterior to the masseteric scar, just below mid-depth of the mandible. The posterior portion of the mandible is lacking and the coronoid process, condyle, and angle are missing. Just posterior to the junction of the medial and ventral ridges of the masseteric fossa there is a small circular hole where the bone has been broken away. This marks the presence of a bony capsule for the base of the premolar. Medially, on the ascending ramus a basitemporal fossa is present but shallow.

The lower incisor is typically broad with a flattened anterior enamel surface. The cheek teeth have the beginnings of roots at their bases (Fig. 2). The dentine

tracts on the lateral sides of the teeth taper dorsally, ending before reaching the occlusal surface. There is no cement on any of the cheek teeth.

The lower premolar is the largest of the cheek teeth. The anterior column (metalophid) of the lower premolar is convex anteriorly and narrower buccolingually than the posterior column (hypolophid). The buccal re-entrant between the metalophid and hypolophid is not as deep as the lingual. The hypolophid is a wide, straight loph. The enamel that encloses the entire tooth is approximately equal in thickness at all points around the tooth.

The first two molars are nearly identical in size and morphology. Both are anteroposteriorly compressed ovals of enamel surrounding exposed dentine. The third molar is not present in AMNH 80169.

**Discussion.** *Pliogeomys russelli* clearly belongs to *Pliogeomys* rather than any other genus. The cheek teeth are higher crowned than those of *Pliosaccomys* or *Progeomys* with enamel failure not present in the latter two genera. This new species cannot be referred to any of the geomyines that have higher crowned (rootless) cheek teeth such as *Parapliosaccomys*, *Geomys* or *Thomomys*.

*Pliogeomys russelli* is similar in size to the Blancan *P. parvus*, being only slightly larger (Zakrzewski, 1969). It is smaller than any of the other species of the genus. The morphology of the masseter attachment to the mandible and position of the mental foramen in *P. russelli* is intermediate between that of Recent *Geomys* and the primitive condition (Akersten, 1973). This condition is sometimes present in specimens of *P. buisi*. All other species of *Pliogeomys* have the primitive condition.

The crown height of the cheek teeth of *P. russelli* is similar to that of *P. buisi*, higher crowned than *P. parvus* and lower crowned than in *P. carranzai* from the Hemphillian of Mexico (Lindsay and Jacobs, 1985) and a species from the Saw Rock Canyon of Kansas described by Akersten (1973).

When Zakrzewski (1969) described *P. parvus* from the Blancan Hagerman fauna the only other known species of *Pliogeomys* was *P. buisi* from the late Hemphillian of Kansas (Hibbard, 1954). Zakrzewski viewed *P. buisi* as being the ancestor of *Geomys* which first appeared in the Blancan, and *P. parvus* was viewed as the ancestor of the genus (or subgenus of *Geomys*) *Nerterogeomys* which also first appeared in the Blancan.

Akersten (1973), in an unpublished dissertation, noted the combination of primitive and advanced characters of the teeth of *P. parvus* along with the primitive

morphology of the masseteric scar on the mandible, and he suggested that it was distinct from other species of *Pliogeomys* and that it might represent a different genus. Akersten (1973) also recognized an additional species of *Pliogeomys* from the Hemphillian Saw Rock Canyon fauna of Kansas that was more advanced in dental morphology (greater crown height of cheek teeth, etc.) than *P. buisi* from slightly earlier in the Hemphillian. He argued that *P. parvus* represented a separate radiation of *Pliogeomys* that was not related to any later geomyids and that *P. buisi* and the other Kansas species were in the ancestry that led to *Nerterogeomys*.

*Pliogeomys russelli* has cheek teeth that are similar in crown height, enamel failure and root development to those of *P. buisi* and lacks any cement that is present in the higher crowned species. The morphology of the mandible is advanced beyond that of *P. parvus* and the Saw Rock Canyon species of *Pliogeomys*, and therefore is more likely developing in the direction of *Geomys* (Fig. 3).

*Pliogeomys buisi* is not only stratigraphically older than both *P. russelli* and the Saw Rock Canyon species, it appears to be morphologically ancestral to both as well. The Saw Rock Canyon species of *Pliogeomys* has cheek teeth that are advanced over those of *P. buisi* but the masseteric scar on the mandible has the primitive *Nerterogeomys* morphology. Specimens of *P. buisi* vary in the condition of the masseteric scar on the mandible from the primitive condition to an intermediate condition as in the mandible of *P. russelli*. Clearly, both lineages leading to *Geomys* and *Nerterogeomys* can be traced back to *P. buisi* through *P. russelli* and the Saw Rock Canyon *Pliogeomys*, respectively.

## CONCLUSIONS

Both species described here from the late Hemphillian of Sioux County are similar in having relatively advanced morphology of the mandible and primitive dentitions. The occurrence of species of both *Prodipodomys* and *Pliogeomys* in the ZX Bar local fauna also supports the late Hemphillian age of this fauna. These genera are only present in Nebraska in faunas that are either late Hemphillian or "latest" Hemphillian in age (Voorhies, 1990).

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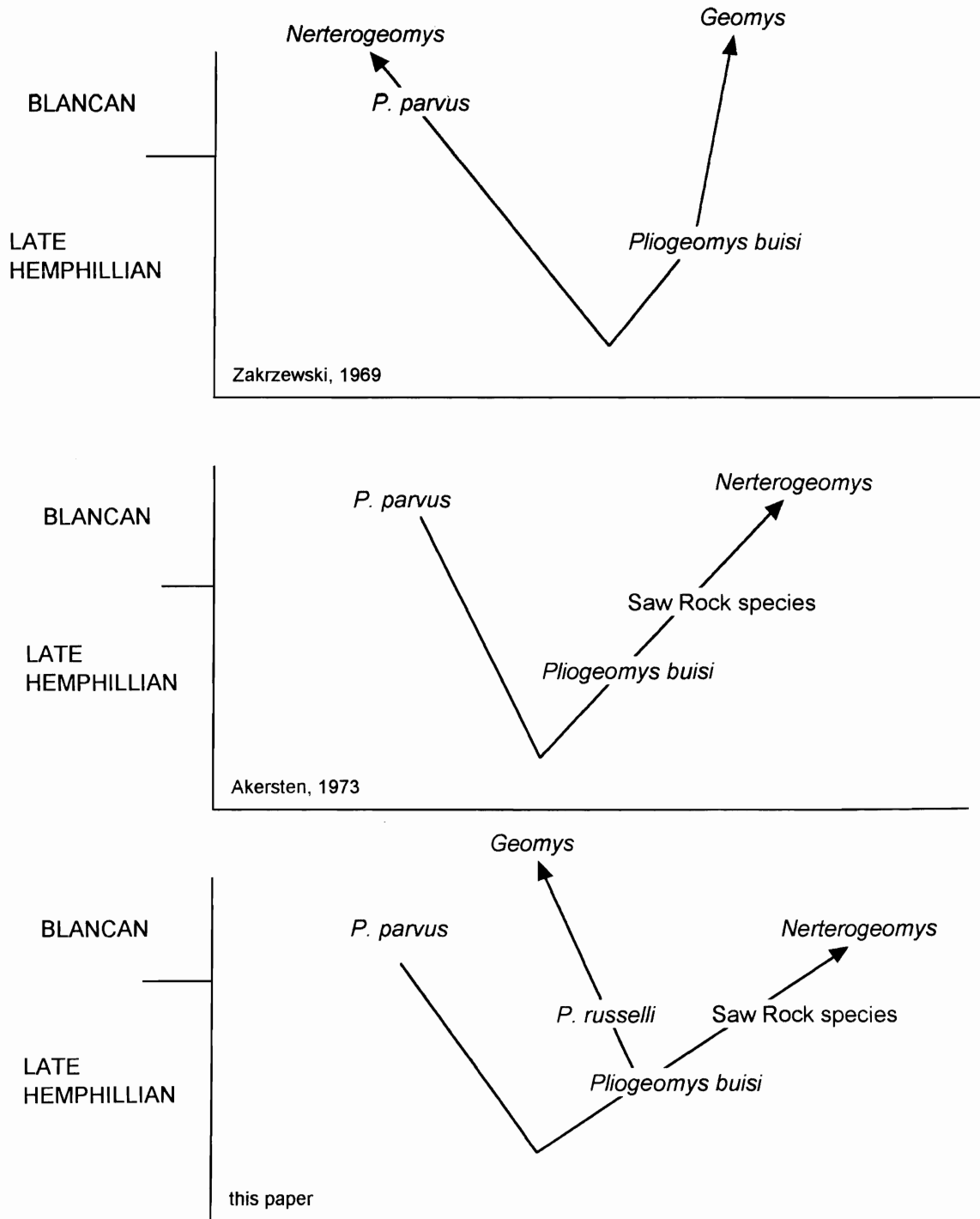


Figure 3. Proposed phylogenies of species of *Pliogeomys*.

visitation grant from the American Museum of Natural History. Dr. W. Akersten provided comparative figures of Tertiary geomyines. Earlier versions of parts of this manuscript were critically reviewed by Drs. R. J. Zakrzewski and A. D. Barnosky.

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