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PLEISTOCENE *PHENACOMYS* FROM KANSAS WITH REMARKS ON OTHER FOSSIL RECORDS

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Phenacomys occurs in the Middle and Late Pleistocene of Kansas. It cannot be derived from any known *Pliophenacomys* and is now thought by us to be an Early Irvingtonian immigrant to North America. *"Pliomys" deeringensis* is a *Phenacomys*, and there is no record of *Pliomys* ever having occurred in North America.

Die Fossiliengeschichte von *Phenacomys* wird diskutiert und neues Material aus dem Mittelpleistozän von Kansas beschrieben. *Phenacomys* kann nicht von *Pliophenacomys* hergeleitet werden und wird statt dessen als Einwanderer nach Nordamerika im frühen Irvingtonian angesehen. Da *"Pliomys" deeringensis* ebenfalls zu *Phenacomys* gehört, gibt es keinerlei Beleg dafür, dass *Pliomys* Nordamerika erreicht hat.

† † †

INTRODUCTION

The spruce, heather, and tree voles of the genus *Phenacomys* (including *Arborimus*) are notable both for their present boreal distribution and for their primitive rooted molars which lack crown cementum. These are features that do not separate *Phenacomys* from many fossil arvicolids, but do separate it from any other living North American genus (Guilday and Parmalee, 1972). Fortunately other characters may be applied to the fossils. Two of these are the reduction of the thickness of the enamel on the edges that occlude last on each dental triangle (the trailing edges, *see* Greaves, 1973), and the shifting of the tooth axis so that the labial triangles are smaller than the lingual triangles in the lower molars, and the labial triangles are larger than the lingual triangles in the upper molars. This shifting of the tooth axis also occurs in bog lemmings (Lemminae) and is discussed by Koenigswald and Martin (1984). Both of these features are more strongly expressed in the modern species than in the earlier forms found in North American Arvicolid Zone (NAAZ) V (*see* Martin, 1979 for a discussion of the North American Arvicolid Zones).

Another suite of characters which may be applied to the recognition of arvicolid taxa was recently described by Koenigswald (1980). This is the arrangement of the apatite prisms and interprismatic substance which make up the enamel of the molars. Koenigswald recognized three major arrangements of apatite prisms which he decribed as radial, lamellar, and tangential enamel (Fig. 1).

All known arvicolids have radial enamel in the molars which is strengthened in advanced forms by the progressive addition of one or more of the other enamel types (Koenigswald, 1980). The local arrangement of the different enamel types within the enamel band of a dentine triangle is called *Schmelzmuster* (Koenigswald, 1980). It is genetically controlled and continuous throughout the height of the molar. Because of the propalinal jaw movement in arvicolids, every alternating triangle possesses a leading edge as well as a trailing edge. The two basic possibilities for enamel configuration are whether or not the *Schmelzmuster* is identical in both the leading and the trailing edge. If they are identical the *Schmelzmuster* is classified as symmetrical, whereas in an asymmetrical *Schmelzmuster* leading and trailing edges are basically differ-

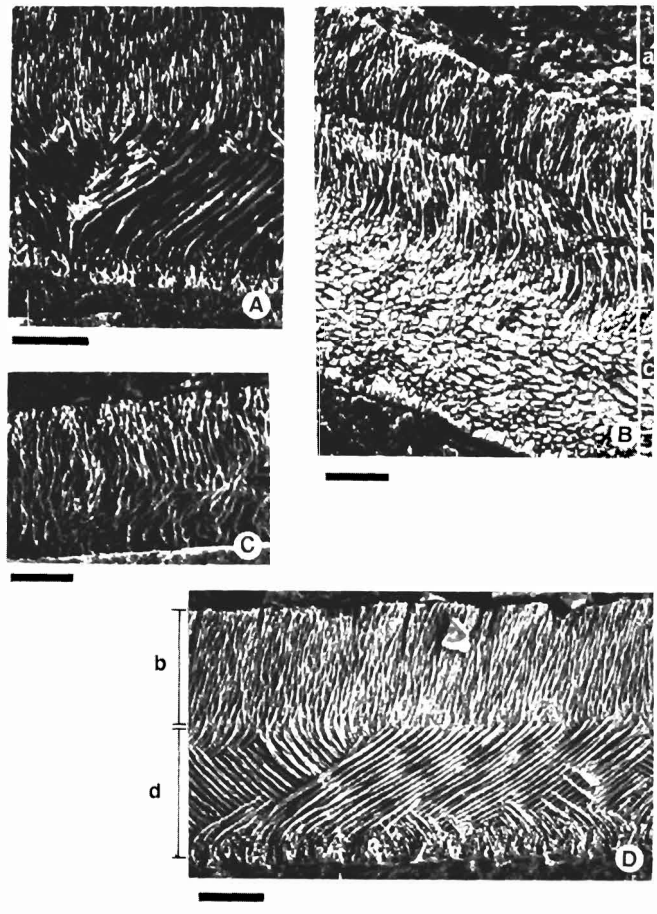

FIGURE 1. SEM photographs of cross-sections from *Phenacomys* molars. Scale = 20 u. A-B. *Phenacomys* sp., from the Wilson Valley Local Fauna, left M_3, KUVP 49,438. A. Leading edge with radial enamel at the top and lamellar enamel at the bottom. B. Trailing edge. a = dentine; b = radial enamel, c = tangential enamel. C-D. *Phenacomys intermedius,* from the Recent of Alaska. C. Trailing edge, top radial enamel, bottom tangential enamel. D. Leading edge b = radial enamel; d = lamellar enamel.

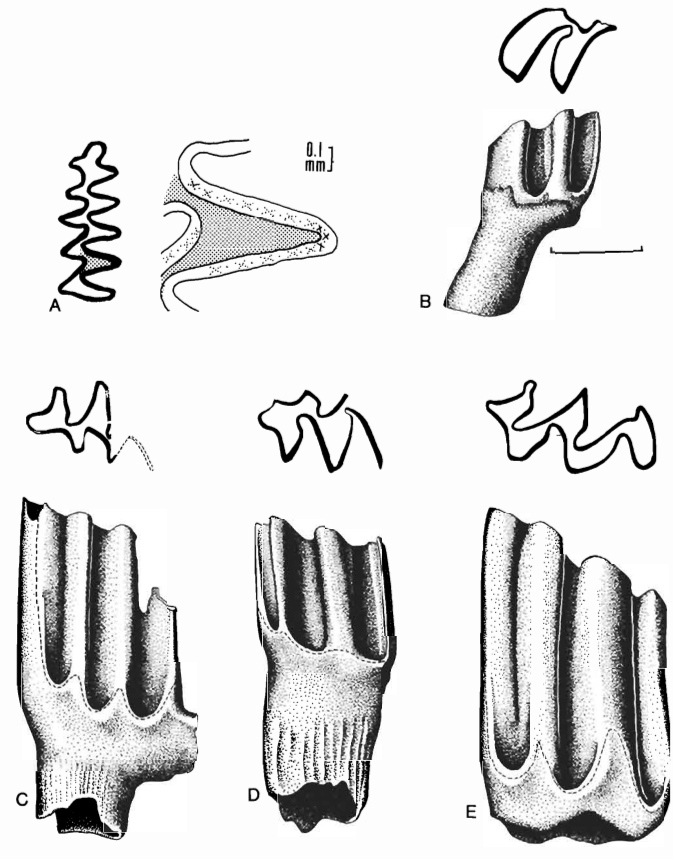

FIGURE 2. A. *Schmelzmuster* of *Pliophenacomys* (from Koenigswald, 1980, code for structures in Fig. 3, E). B-E. *Phenacomys* sp., from the Wilson Valley Local Fauna. B. Partial left M_3, KUVP 49,438. C. Partial left M_1, KUVP 49,434. D. Partial right M_1, KUVP 49,437. E. Partial right M^1, KUVP 49,435.

ent. *Pliophenacomys* (Fig. 2, A) exhibits symmetrical *Schmelzmuster* and *Phenacomys* (Fig. 3, A-C) asymmetrical *Schmelzmuster.* It does not seem possible to develop a symmetrical *Schmelzmuster* out of an asymmetrical one, but a symmetrical *Schmelzmuster* can become secondarily assymmetrical, when the thickness of the trailing edges are reduced without reduction of the leading edges. In an asymmetrical *Schmelzmuster,* as in *Phenacomys,* the leading edges tend to all be of one type and all trailing edges are of another. The enamel of the trailing edge of the posterior loops on the lower molars and the anterior loops of the upper molars is called closing enamel (Koenigswald, 1980); it may differ somewhat from the other trailing edges in being more conservative when the others are reduced in thickness.

The *Schmelzmuster* of *Phenacomys* (Fig. 1; Fig. 3, A) consists of two-layered enamel on both the leading and trailing edges. On the leading edges the outer layer is radial enamel and the inner layer is lamellar enamel (Fig. 1, A and D). The lamellar enamel extends around the apex of each triangle where it ends in a single layer of radial enamel. The trailing edges have an outer layer of tangential enamel along most of their length (Fig. 1, B and C). This is a relatively derived *Schmelzmuster,* and is comparable to that found in advanced species of *Mimomys* like *M. polonicus.*

Clethrionomys and *Mimomys* have independently developed a *Schmelzmuster* similar to that of *Phenacomys,* but the *Phenacomys* lineage can be differentiated from them by other morphological features. The shift of the tooth axis as well as

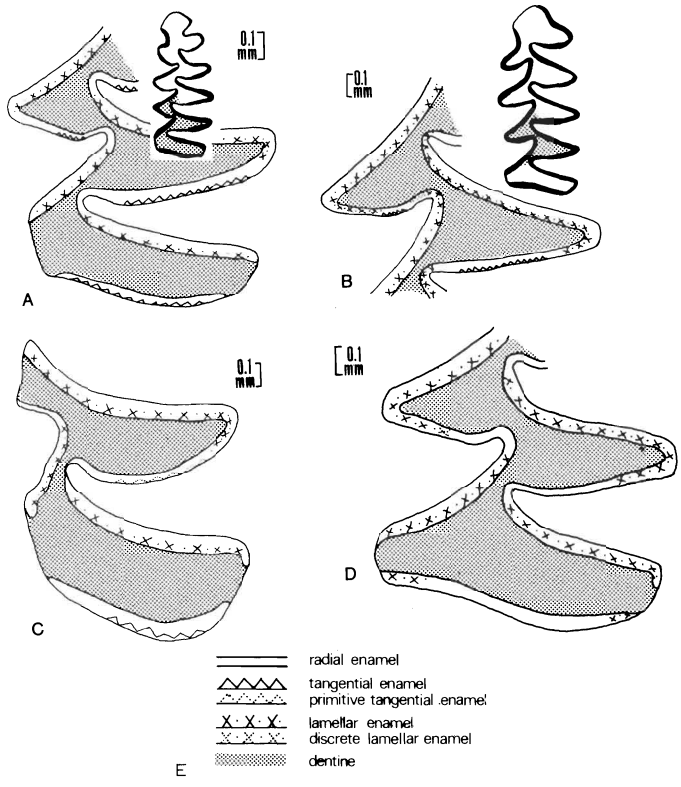

FIGURE 3. Graphic representations of the *Schmelzmuster* of selected arvicolids (A, B, and D from Koenigswald, 1980). A. *Phenacomys intermedius*, B. *Phenacomys deeringensis*. C. *Phenacomys* sp., KUVP 49,438. D. *Pliomys lenki*. E. Code for enamel structures (note that radial enamel within the enamel band is left white).

the lack of cement are the most obvious of these features. The existence of parallel evolution in the *Schmelzmusters* of arvicolids has to be taken into account when close relationships seem to be indicated for taxa with similar *Schmelzmusters*. When two taxa are separated by different *Schmelzmusters* that cannot be arranged within one evolutionary line, then their common ancester would have lacked one or both *Schmelzmusters* and would likely date back to a very early stage in the arvicolid radiation.

Phenacomys is presently restricted to North America and has not been found in the fossil deposits of Eurasia. Because of this distribution, it has generally been supposed that *Phenacomys* originated in North America, although it is rare as a fossil prior to the Wisconsinan. The Late Pleistocene distribution of *Phenacomys* has been well summarized by Guilday and Parmalee (1972).

Phenacomys occurs in the Wisconsinan Trapshoot Local Fauna near Plainville, Rooks County, Kansas. Eighteen other species of mammals (Stewart, 1978) including *Clethrionomys gapperi, Microtus montanus, Thomomys talpoides,* and *Spermophilus kimballensis,* occur with it in this fauna and form a distinctly boreal assemblage. Stewart and Rogers (1984) report a pollen profile indicating a grassland containing scattered pine trees. This is consistent with the montane-conifer parkland which was thought by Martin and Neuner (1978) to be the habitat of the *Camelops-Navahoceros* Faunal Province. The Trapshoot Local Fauna must have been situated close to the ecotone between the *Symbos-Cervalces* and *Camelops-Navahoceros* faunal provinces as typical *Symbos-Cervalces* faunas are known some 200 km east of it. Stewart has recently developed an additional Wisconsinan (16,700 ybp and 17,930 ybp) biota, the Coon Creek Local Biota, in Graham County, Kansas. The biota comprises a boreo-montane assemblage including *Phenacomys*. It has produced macrofossils (needles) of limber pine (Wells, 1983).

Phenacomys also recently has been reported from the Late Pleistocene of south-central Nebraska (Corner, 1982). Michael R. Voorhies (personal communication) has found another Wisconsinan record of *Phenacomys* in the Smith Falls Local Fauna of northern Nebraska. (*see* TER-QUA Symposia Series, vol. 2, *in press*). We would suggest one other possible occurrence in western Nebraska. The Uptegrove Local Fauna of Miocene age included a diverse microfaunal component including an extinct ground squirrel, *Spermophilus kimballensis* (Kent). A *Thomomys* skull from the same fauna was recognized by Kent (1967) to be from a Pleistocene burrow intruded into the Miocene sediments. Martin (1975) described an arvicolid from this fauna as *Propliophenacomys uptegrovensis,* supposedly of Late Miocene age. It now seems likely that most of the microfauna associated with the Uptegrove Local Fauna is the result of Pleistocene intrusion by burrowing. The primitive aspects of *P. uptegrovensis* (lack of cement and rooted teeth) are consistent with *Phenacomys,* and it should be considered a Pleistocene record of that genus (Voorhies, 1984). This interpretation could be confirmed by analysis of the tooth enamel histology of one of its molars.

Hibbard (1944) referred two isolated upper first molars from the Wilson Valley Local Fauna to (?) *Phenacomys*. These upper molars are rooted and lack cement, but they have low dentine tracts when compared to those in the M^1 of modern *Phenacomys*. If correctly assigned to *Phenacomys,* they were at the time of their publication the oldest record for this genus in North America and were the only published record from Kansas (*see* Guilday and Parmalee, 1972). After the discovery of *Phenacomys* in the Trapshoot Local Fauna (Stewart, 1978) we became interested in this other Kansas record and searched the unidentified microtine teeth from the Wilson Valley Local Fauna for additional specimens (Fig. 2, B-E). We found (Fig.

2) the anterior portions of two lower first molars, KUVP 49,434 and KUVP 49,437, the posterior portion of an M_3, KUVP 49,438, and two M^1s, KUVP 49,436 and KUVP 49,435. The lower molars lack cement and have high dentine tracts on the anterior loop. The labial triangles are smaller than the lingual triangles and the anterior enamel of the alternating triangles is thicker than the posterior enamel. At least five alternating triangles posterior to the anterior loop are present on M_1. The M^1 consists of anterior loop followed by three alternating triangles and posterior loop. The dentine tracts on this tooth are lower than in Recent species of *Phenacomys;* this is a primitive feature. There is also less reduction in enamel thickness than in the modern species (Fig. 1).

The M_3, KUVP 49,438, was examined for its *Schmelzmuster* (Fig. 1, A-B; Fig. 3, C). The leading edges are two-layered with an inner layer of lamellar enamel and an outer layer of radial enamel. This arrangement carries around the apex of the anticline, but the trailing edge proper is composed of two layers with an inner radial and an outer tangential layer. This *Schmelzmuster* confirms the assignment of these teeth to *Phenacomys*. The Wilson Valley Local Fauna (KUVP Kansas Coll. Loc. Lincoln County-00) occurs just below a lens of Pearlette-like ash (Zakrzewski, 1976; Zakrzewski and Kolb, 1982); these ashes usually date at about 600,000 ybp. Associated fauna from this locality includes *Sorex cinereus, Spermophilus lorisrusselli, Mictomys meltoni,* and *Microtus paroperarius,* which puts the Wilson Valley Local Fauna quite clearly in NAAZ V. Eshelman and Hager (1984) reported an additional Irvingtonian record of *Phenacomys* from the Cudahy-equivalent Hall Ash Local Fauna in Jewell County, Kansas. A volcanic ash above the fauna produced a date of 700,000 ybp and may represent the same event as for the Little Sioux Local Fauna.

Guilday and Parmalee (1972) also report *Phenacomys* from the Little Sioux Local Fauna in Iowa, beneath a volcanic ash dated at 740,000 ybp (Zakrzewski and Kolb, 1982) and also from Cumberland Cave in Maryland and Trout Cave in West Virginia. The Wilson Valley Local Fauna, Trout Cave, and Cumberland Cave seem to contain faunas of similar age. The only other *Phenacomys* close in age to those from the Wilson Valley, Hall Ash, and Little Sioux local faunas is *Phenacomys deeringensis* (Guthrie and Matthews, 1971) from the Cape Deceit Local Fauna in Alaska. *Phenacomys deeringensis* was originally assigned to *Pliomys* by Guthrie and Matthews (1971) and this assignment has been followed by Repenning (1980), although there is no evidence to support such an assignment and the European students of *Pliomys* have rejected it. Chaline (1977) referred the Cape Deceit taxon to *Phenacomys;* this assignment was supported by Koenigswald (1980) on the basis of the *Schmelzmuster* present (Fig. 3, B). *Pliomys* has a distinct *Schmelzmuster* with the lamellar enamel on the leading edges extending around the apices of the anticlines and into the trailing edges, but not extending far along the trailing edges, which are composed primarily of radial enamel (Fig. 3, D).

Phenacomys deeringensis resembles the Wilson Valley form in height of dentine tracts, crown pattern, distribution of enamel thickness, lack of cement and the presence of roots. *P. deeringensis* is somewhat larger than the Kansas form and additional material is needed from the Wilson Valley Local Fauna in order to work out their exact relationship.

RELATIONSHIPS

The relationships of *Phenacomys* are a matter of speculation. Hibbard (1937) compared *Pliophenacomys* to *Phenacomys* when he created the former genus. Martin (1972) described the most advanced species of *Pliophenacomys (P. osborni)* from deposits belonging to NAAZ III.

Eshelman (1975) discussed the possibility that *P. osborni* was referable to *Pliomys* and possibly to *''Pliomys'' deeringensis*. Examination of *Pliophenacomys primaevus* (Fig. 2, A) and *P. osborni* shows that they share a symmetrical *Schmelzmuster* of three layers with a central layer of discrete lamellar enamel and inner and outer layers of radial enamel. The apex of the angles contains an inner layer of typical lamellar enamel and the apex of the synclines radial enamel. This pattern is unlike the asymmetrical *Schmelzmuster* of *Phenacomys*. Neither *Pliophenacomys primaevus* nor *P. osborni* could have given rise to *Phenacomys*. We have not examined the *Schmelzmuster* of the oldest species of *Pliophenacomys, P. finneyi,* but the chances of *Pliophenacomys* giving rise to *Phenacomys* are considerably reduced. *Pliophenacomys osborni* is correctly assigned to *Pliophenacomys* and should not be confused with *Phenacomys deeringensis*.

The *Schemlzmuster* of *Phenacomys* is unlike that of any known Blancan North American arvicolid, and it now seems likely that *Phenacomys* immigrated to North America from Eurasia as early as NAAZ IV, as R. Martin (1973) has reported it from the Java Local Fauna in South Dakota. In this locality it is associated with *Allophaiomys* sp. and *Mictomys kansasensis*. The Java record is significantly older than the Wilson Valley record and does not fit Repenning's suggestion that *Phenacomys* immigrated into North America in what would correpsond to NAAZ V (Repenning, 1980).

We have not identified any characters that would serve to tie *Phenacomys* to other extant arvicolids. It does not appear to be derived from *Mimomys* and therefore it is probably not closely related to rodents (*Arvicola, Microtus,* etc.) that have such a derivation. We would suggest that the origins of *Phenacomys* probably lie in northern Asia.

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