

PHYLOGENY AND BIOGEOGRAPHY OF THE GENUS *ANSOMYS* QIU, 1987 (MAMMALIA: RODENTIA: APLODONTIDAE) AND DESCRIPTION OF A NEW SPECIES FROM THE BARSTOVIAN (MID-MIOCENE) OF MONTANA

SAMANTHA S. B. HOPKINS

Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley 94720, <shopkins@socrates.berkeley.edu>

ABSTRACT—New aplodontid material recovered from Hepburn's Mesa, Montana, stimulated reexamination of *Ansomys*, a genus of aplodontid previously known only from Asia. A cladistic analysis of the known species of *Ansomys*, as well as new material from Hepburn's Mesa and a few other morphologically similar species, prompted reconstruction of the biogeographic history of the genus. One new species, *A. hepburnensis*, from the Barstovian of Montana, is described, and two other species, *A. nexodens* and *A. descendens*, are placed in *Ansomys* rather than in *Pseudallomys* and *Plesispermophilus*, respectively. Addition of these three species to *Ansomys* extends its distribution throughout the Holarctic in the mid-Miocene. Stratigraphic ranges combined with phylogenetic relationships between species suggest this wide distribution as early as the late Oligocene, which is unique among aplodontid genera. The distribution, the rarity, the unusually small size, and the complex cusp morphology of *Ansomys* suggest a very specialized ecology for members of this clade.

INTRODUCTION

A PLODONTOID RODENTS are abundant and diverse in Oligocene and Miocene faunas of North America, although they are represented today by a single living species, *Aplodontia rufa* Rafinesque, 1817, the mountain beaver or sewellel. Fossil discoveries in the past two decades have made it clear that aplodontoids were quite diverse outside North America as well. Aplodontoids from all the major morphological groups, including prosciurines (Schmidt-Kittler and Vianey-Liaud, 1979), aplodontines (Schlosser, 1924), mylagaulids (Shevyreva, 1971; Wu, 1988), allomyines (Rensberger, 1983), and meniscoomyines (Wang, 1987), have been found in Eurasia. Some evidence even suggests that allomyines, one of the most speciose aplodontoid groups in the early Miocene, may have originated in Europe (Rensberger, 1983). Therefore, determining the relationships among the taxa found in Europe, Asia, and North America is essential to understanding the evolutionary history of the group.

The fauna of Hepburn's Mesa, Montana, is mid-Miocene (Barstovian North American Land Mammal Age) and includes abundant small mammal remains (Burbank and Barnosky, 1990). It has been interpreted to represent an arid or semiarid environment (Barnosky and Labar, 1989) due to the great diversity of geomorphs in the fauna and the presence of interbedded saline lake deposits. Also occurring in the Hepburn's Mesa fauna are jaws and teeth of a new form of aplodontid, which is morphologically quite different from any other known from the Miocene of North America. Comparisons with published accounts of described aplodontid genera showed this species to be most similar to species in the genus *Ansomys* Qiu, 1987 known from the late Oligocene and middle Miocene of Europe and Asia (Qiu, 1987), and to *Pseudallomys* Korth, 1992 known from the late Oligocene of Montana (Korth, 1992). This study focuses on determining relationships between the species previously attributed to the Ansomomyinae (Qiu, 1987), *Pseudallomys*, and the new species from Hepburn's Mesa.

MATERIALS AND METHODS

In order to understand evolutionary relationships, a phylogenetic analysis of the known ansomyine species, the Hepburn's Mesa species, and *Pseudallomys nexodens* Korth, 1992 was performed. Characters were coded from all known published images and descriptions, as well as from the hypodigm of the Hepburn's Mesa species and the holotype of *Pseudallomys nexodens*. Publications from which images and measurements were derived include Dehm (1950), Korth (1992), Lopatin (1997), Qiu (1987),

Qiu and Sun (1988), Rensberger and Li (1986), and Schmidt-Kittler and Vianey-Liaud (1979). All of the known species of *Ansomys* are included, as well as *Plesispermophilus descendens* (Dehm, 1950), which was placed in the subfamily Ansomomyinae by Qiu (1987) and Qiu and Sun (1988). According to the diagnosis for the group, the Hepburn's Mesa material has all of the characters of an ansomyine, so all members of this group were considered important for determining evolutionary relationships. *Plesispermophilus atavus* Schmidt-Kittler and Vianey-Liaud, 1979 and *P. angustidens* Filhol, 1883 were cited as possible members of the subfamily (Qiu, 1987), so they were included in order to determine whether they were closely related to the other ansomyine taxa. *Pseudallomys nexodens*, the only known species of *Pseudallomys*, was included due to its morphological similarity and geographical proximity to the Hepburn's Mesa material. The genus *Prosciurus* Matthew, 1903, coded from images in Korth (1989), was used as an outgroup to root the cladogram.

The data matrix includes 31 characters, all from the cheek tooth morphology. These characters are listed in Appendix 1 and the dental terminology used is illustrated in Figure 1. Characters were chosen so as to be variable within the ingroup and yet not to be highly variable among the representatives of an individual species. One of the greatest difficulties in this analysis was the relatively small sample sizes and fragmentary representation of some taxa. Three of the included species, *Pseudallomys nexodens*, *Ansomys shanwangensis* Qiu and Sun, 1988, and *Ansomys shantungensis* (Rensberger and Li, 1986), are each known only from a single type specimen, and only two of the ingroup taxa could be coded for the entire set of characters. The data matrix was analyzed using maximum parsimony in PAUP 4.0b5 (Swofford, 2001). I estimated branch support using Bremer indices (Bremer, 1994), which determine how many steps must be added to the length of the tree in order to collapse a particular branch.

PHYLOGENETIC RELATIONSHIPS

The consensus phylogeny generated by the first run of the analysis (Fig. 2) supported monophyly of the group including previously cited ansomyines, *Pseudallomys*, and the new aplodontid from Hepburn's Mesa. There was, however, relatively little resolution within the ansomyine clade and branch support was relatively poor. An examination of the three trees with the shortest tree lengths (Fig. 3) showed that the most likely reason for the lack of resolution in the higher branches of the clade is the uncertainty in the placement of *Ansomys crucifer* Lopatin, 1997. This is not surprising, because only 10 of the 31 characters are

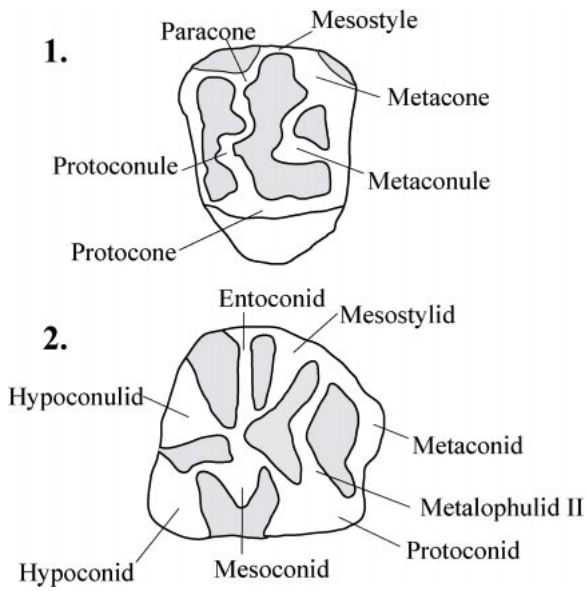


FIGURE 1—Dental terminology. 1, Left upper M1 or M2, anterior to left. 2, Right lower M1, anterior to right.

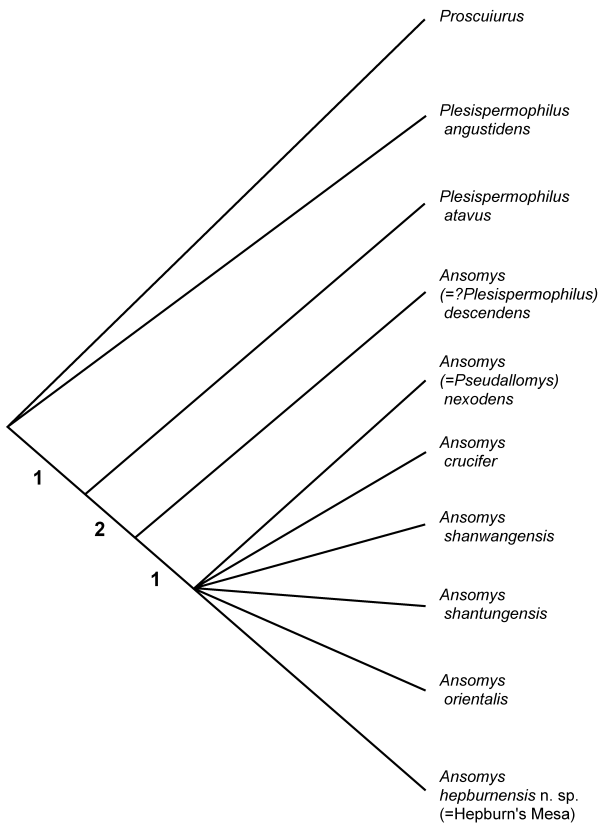
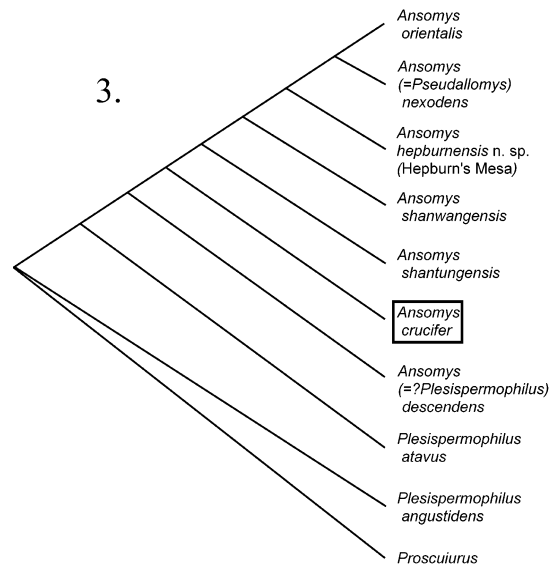
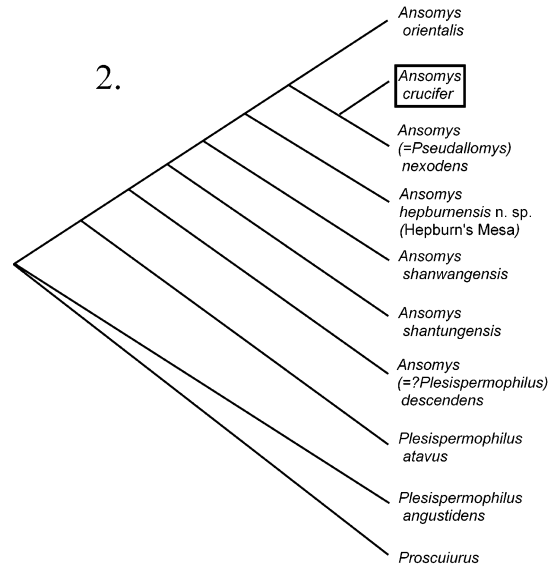
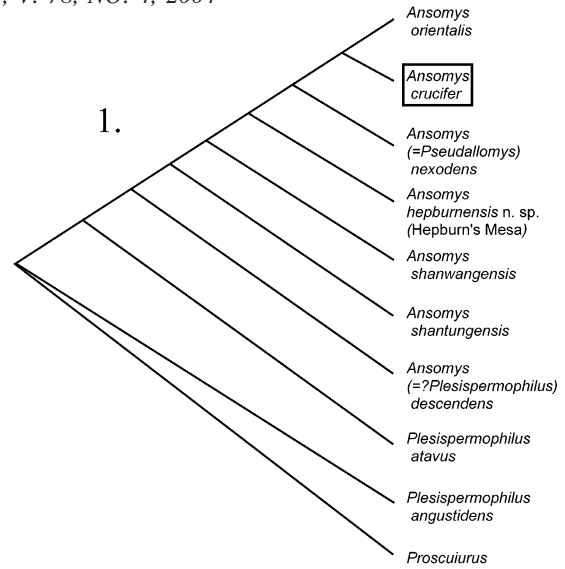


FIGURE 2—Strict consensus of three most parsimonious trees for analysis including *Ansomys crucifer* Lopatin, 1997. Numbers below branches indicate Bremer indices. Total tree length = 44 steps. CI = 0.705. RI = 0.690. RC = 0.486.

coded for *A. crucifer*, which is represented by only a single lower P4. Because this poorly known taxon obscured what signal might be present in the other ansomyine taxa, it was removed from the analysis. Another taxon, *A. shantungensis*, is represented by a single lower M1–2, but it was stable in all the cladistic analyses in a basal position relative to the other species, so the poor representation does not appear to affect resolution of the phylogeny. The second iteration of the analysis (in the absence of *A. crucifer*) recovered a single most parsimonious tree (Fig. 4). Whereas support for many branches still was not very strong, the greater resolution provided a starting point for understanding relationships among species of *Ansomys*.

The results of this phylogenetic analysis of the ansomyine clade (Fig. 4) clarify several questions about relationships of the attributed species. First, *Plesispermophilus angustidens* does not appear to fall within the ansomyine clade. This species consistently falls out basal to the ansomyine clade, unresolved with the outgroup. Thus, this analysis finds no support for the possibility of *P. angustidens* as the ancestor to ansomyines. *Plesispermophilus atavus*, however, appears to be basal to the ansomyines and may represent the ancestral morphology, although the branch support for this node is relatively poor, and hence the relationship is somewhat uncertain.

Also important is the nesting of *Pseudallomys* within the genus *Ansomys*. The only way to designate *Ansomys* as a monophyletic group is to include *Pseudallomys nexodens*, which requires that the monotypic genus *Pseudallomys* be subsumed within *Ansomys*. More difficult is the question of whether to include *Plesispermophilus? descendens* in *Ansomys*. The nodes above and below *P?. descendens* are both fairly well supported, and the original definition of *Ansomys* specifically excluded *P?. descendens*, but the support is stronger for the group that unites all other *Ansomys* and *P?. descendens*. This well-supported node provides an obvious morphological break with which to diagnose the genus.

While the intrageneric relationships are not very strongly supported, it is clear that the most basal species is *Plesispermophilus? descendens*. *Ansomys shanwangensis* and *A. shantungensis* also appear to be fairly basal, and *A. orientalis* Qiu, 1987, *P. nexodens*, and the Hepburn's Mesa apodontid all appear to be more derived members of the clade. The position of *A. crucifer* is unclear due to the lack of adequate material for character coding. These intrageneric relationships are subject to some uncertainty, however, as the branch support within the ingroup is not very strong.

Stratigraphic data for the species of *Ansomys* suggest a substantial gap in preservation of *Ansomys* over a period of more than 10 million years through the late Oligocene and early Miocene; however, this divergence in the Oligocene is constrained by two of the species, *A. shantungensis* and *A. nexodens*. The single known specimen of *A. shantungensis* was drawn from a well core, and was placed in the late Oligocene on the basis of the "stage of evolution" (Rensberger and Li, 1986). This analysis, however, suggests that the stage of evolution would more likely place this species in the middle Miocene. However, a recent revision of the faunas from the Junggar Basin (Ye et al., 2003) indicates a more positive stratigraphic placement for the type of *A. shantungensis* in the late Oligocene, and refers to material of a similar, undescribed apodontid that occurs in the late Oligocene-early Miocene Tiersihabahe fauna of the Junggar Basin. The other putative Oligocene species, *A. nexodens*, comes from a known locality in the early Oligocene (Orellan NALMA) of Montana (Korth, 1992),

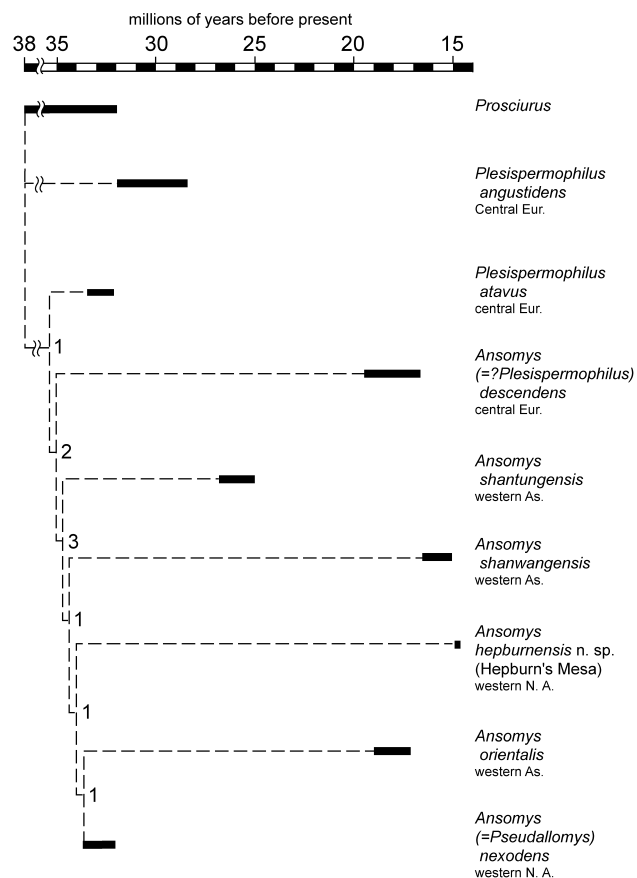


FIGURE 4—Single most parsimonious tree for analysis without *Ansomys crucifer* showing geographic and stratigraphic distributions. Solid bars represent approximate stratigraphic ranges and dashed lines indicate extended ranges inferred from phylogenetic relationships. Numbers to the right of branches indicate Bremer indices. Total tree length = 43 steps. CI = 0.721. RI = 0.700. RC = 0.505.

and hence is more difficult to understand. This occurrence implies, because of its early occurrence, that all other lineages of *Ansomys* are present, but not preserved from the early Oligocene through the early Miocene. While this is possible, given the relative rarity of *Ansomys* in the faunas in which it occurs, the magnitude of the range extensions implied indicate a need for a more careful examination of the collection history of this specimen.

SYSTEMATIC PALEONTOLOGY

Abbreviations.—CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; UWBM, Burke Museum, University of Washington, Seattle.

Order RODENTIA Bowdich, 1821
Superfamily APLODONTOIDEA Matthew, 1910
Family APLODONTIDAE Trouessart, 1897
Genus ANSOMYS Qiu, 1987

Sciurodon? DEHM, 1950, p. 334–336, figs. 5–8.
Plesispermophilus? SCHMIDT-KITTLER AND VIANEY-LIAUD, 1979, p. 54–55, fig. 11; QIU, 1987, p. 284, 287–290; QIU AND SUN, 1988, p. 54.
Prosciurus? RENSBERGER AND LI, 1986, p. 764, figs. 1–1, 1–3, 2.
Pseudallomys KORTH, 1992, p. 171, fig. 1.

Type species.—*Ansomys orientalis* Qiu, 1987.

Referred species.—*A. (=Sciurodon?) descendens* (Dehm, 1950). *A. (=Pseudallomys) nexodens* (Korth, 1992). *A. crucifer*

FIGURE 3—Three most parsimonious trees yielded by parsimony analysis of matrix, including *Ansomys crucifer*.

Lopatin, 1997. *A. shantungensis* (Rensberger and Li, 1986). *A. shanwangensis* Qiu and Sun, 1988. *Ansomyx hepburnensis* n. sp.

Revised diagnosis.—Cheek teeth brachydont, unlike menisco-myines and aplodontines, but with high cusps and crests, accounting for roughly a third of the total tooth height, unlike prosciurines; mesostyle large and bifid; labial surfaces of metacone and paracone flat; ectoloph with a unique shape, unlike that of any other aplodontid genus, having a broad, squared labial flexure and shaped overall like the cross section of a flat-brimmed hat; lingual surface of protocone curved dorsoventrally, unlike menisco-myines and aplodontines; upper molars with single metaconule, unlike allomyines; main cusps of lower teeth anteroposteriorly compressed and transversely elongated, yielding thin crests, which are more sloping and lower between cusps than in allomyines; accessory crests very small (less than 0.2 mm in length); M_{2-3} have low, crestlike metaconid, without distinct cusp, unlike all other aplodontids.

Description.—Small, lower molars less than 2 mm in length (except the M_3 of *A. nexodens*, which is 2.6 mm long) and 2.2 mm in width and upper molars less than 2 mm in length and 3 mm in width; P^4 anterostyle large, dividing into a pair of cusps; lingual crest of metaconule joining protoconule, not protocone; protoconule on M^3 large; entoconid large, with long crest extending labially; anterior crest of protoconid of P_4 large, curved lingually; metaconid on M_1 shifted labially, anteroposteriorly compressed; mesostylid of M_{2-3} generally large, similar in size to entoconid.

Discussion.—All the species attributed herein to *Ansomyx* except *A. nexodens* and the new species from Hepburn's Mesa were previously attributed to the subfamily Ansomyinae by Qiu (1987). The morphological similarity and close phylogenetic affinity among the referred species indicate that assignment to a single genus is the best taxonomic representation of their evolutionary relationships. This is the most strongly supported clade in the analysis, and would likely have had even stronger support were it not for the inclusion of the poorly preserved taxon *Ansomyx shantungensis*. *Ansomyx shantungensis* has a stable position in the analysis, but its many uncoded characters reduces the number of steps necessary to destroy resolution of the *Ansomyx* clade. Whereas more material from *A. descendens* or *A. nexodens* could possibly lead to their removal from the genus, there is at this time inadequate evidence to declare them significantly different from the other, previously described *Ansomyx* material. The material available for both *A. descendens* and *A. nexodens* shows all the diagnostic characters for *Ansomyx* as described by Qiu (1987) except that in *A. descendens* the anterior cingulum is not connected to the protocone and the anterior crest of the hypoconid is connected to the mesoconid. The latter character is present to a lesser degree in other species definitely attributed to *Ansomyx*, as well as in *Plesispermophilus atavus*. Although there is a strongly supported clade including all the previously described *Ansomyx*, *A. nexodens*, and the Hepburn's Mesa aplodontid without *A. descendens*, drawing the base of the genus at this point would simply force the erection of a new, monotypic genus for *A. descendens*. Because this would unnecessarily proliferate taxonomic terminology, and is not clearly morphologically justified, *Ansomyx* is here emended to include *A. descendens*.

One factor that complicates the problem of phylogenetic analysis of *Ansomyx* is the extremely small sample size for most of the species of the genus. The only taxa represented by a large sample are *A. orientalis* and *A. hepburnensis* n. sp., both of which are described from numerous isolated teeth. *Ansomyx nexodens* is described from a single jaw fragment, *A. shanwangensis* from a single skeleton, and *A. crucifer* and *A. shantungensis* each from an individual tooth. *Ansomyx descendens* is described from less than a half dozen specimens. Such poor representation precludes

coding of some characters and complicates the process of understanding phylogeny, but these species clearly form a monophyletic group. Additional specimens that preserve hitherto unknown elements could alter the interpretation of the relationships among species of *Ansomyx*.

ANSOMYS DESCENDENS (Dehm, 1950) new combination

Sciurodon? descendens DEHM, 1950, p. 334–336, figs. 5–8.

Plesispermophilus? descendens [sic] (Dehm, 1950) SCHMIDT-KITTLER AND VIANEY-LIAUD, 1979, p. 54–55, fig. 11; QIU, 1987, p. 284, 287–290; QIU AND SUN, 1988, p. 54.

Revised diagnosis.—Smaller than all other species of *Ansomyx* except *A. hepburnensis* n. sp., which is similar in size; lower molars less than 1.5 mm in transverse (TR) width and 1.7 mm in anteroposterior (AP) length, upper molars less than 1.5 mm long and 2.0 mm wide; only species in which mesoconid is connected to the hypoconid in lower cheek teeth by a crest on the labial margin of the tooth; entoconid of M_{1-2} narrow, curved, with anterior face of cusp concave; entoconid crest strongly connected to posteriad-trending mesostylid; anterior crest of protocone in M^{1-2} not connected to anterior cingulum; protoconule with only one anteriorly directed crest connecting to anterior cingulum, on lingual side of cusp.

Material examined.—Figures of types from Institut für Paläontologie und historische Geologie der Universität, München, specimens 1937-II-10294 (type) LP₄, 1937-II-10296 RM₁₋₂, 1937-II-10295 RM₁, 1937-II-10297 LM¹. Figures examined in Dehm, 1950 and Schmidt-Kittler and Vianey-Liaud, 1979.

Discussion.—A new species of aplodontid was originally described by Dehm (1950) and tentatively assigned to *Sciurodon* Schlosser, 1884. Schmidt-Kittler and Vianey-Liaud (1979) reasigned it tentatively to *Plesispermophilus?* but misspelled the specific epithet. This species was referred by Qiu (1987) to a new subfamily, the Ansomyinae, with the misspelling perpetuated, and the error was repeated in Qiu and Sun (1988). The specimens referred to the species are the same in all of the above publications.

ANSOMYS NEXODENS (Korth, 1992) new combination

Pseudallomys nexodens KORTH, 1992, p. 173, fig. 1.

Revised diagnosis.—Larger than *A. descendens*, *A. hepburnensis* n. sp., and *A. orientalis*; lower molars greater than 1.9 mm in length and width and M_3 longer than in any other species of *Ansomyx*; mesoconid separate from hypoconid, not connected labially; entoconid crest broad, straight except in M_2 , in which the entoconid is curved slightly anteriorly; entoconid crest crossed by small accessory crest, an incipient connection between entoconid and mesostylid crests; mesostylid curving posteriad; talonid basin of M_3 wider relative to trigonid than in other species for which M_3 is known, except *A. hepburnensis*, which has a similarly wide talonid basin; molars longer relative to width than in all other species, except *A. descendens* and *A. shanwangensis*; M_3 with small labial cingulum on anterior face of protoconid, unlike all other *Ansomyx*.

Material examined.—Holotype, CM 11898, partial right dentary with M/1-M/3.

Occurrence.—South side of Dry Hollow, sec. 5 or 6, T5N, R3E, Dunbar Creek Formation, Toston area, Broadwater County, Montana.

Discussion.—Phylogenetic analysis nests this species deeply within the clade of species previously attributed to Ansomyinae. The genus is a well-supported clade and represents a unique morphology, as discussed previously. Even if this species were basal to the rest of the *Ansomyx* clade (excluding *A. descendens*), designating *Pseudallomys* as a separate genus requires a separate

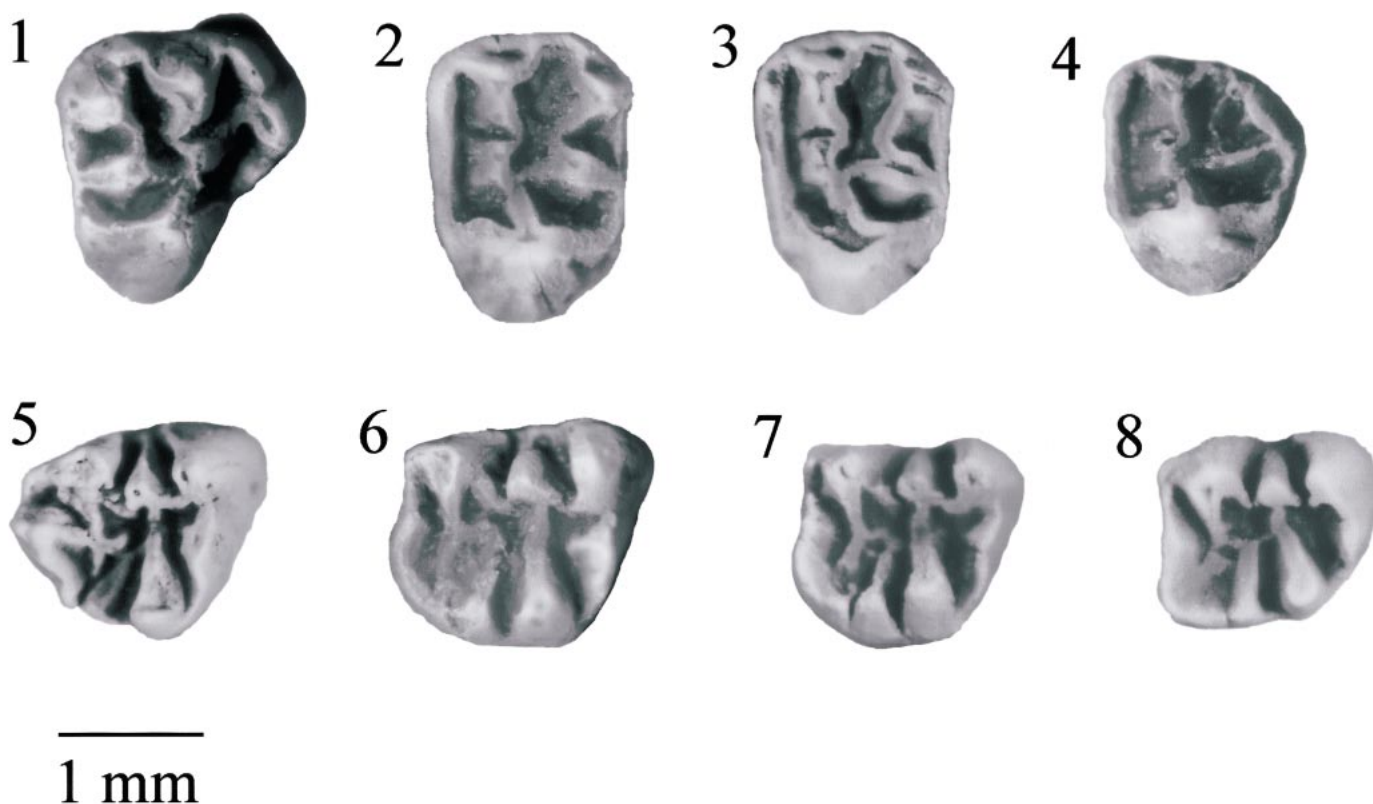


FIGURE 5—Isolated molar teeth of *Ansomys hepburnensis* n. sp. 1, CM 61220, RP₄, 2, CM 75611 LM¹ or ², 3, CM 75605 LM¹ or ², 4, CM 75618 LM³, 5, CM 75637 RP₄, 6, CM 63300 RM₁, 7, CM 75625 RM₂, 8, CM 63306 RM₃. Labial at top.

genus for each species. Thus, *P. nexodens* is placed within the genus *Ansomys*.

ANSOMYS HEPBURNENSIS new species

Figures 5, 6, Table 1

Diagnosis.—Smaller than all other *Ansomys* except *A. descendens*, lower molars less than 1.9 mm in length and 1.7 mm in width, averaging roughly 1.6×1.5 mm, upper molars less than 1.6 mm long and 2.0 mm wide and averaging approximately 1.3×1.7 mm; mesoconid separate from hypoconid, not connected labially; entoconid crest on all lower cheek teeth broad and straight, with no accessory crests or connections to mesostylid, unlike all other species of *Ansomys*; mesostylid straight; talonid of M₃ broad, similar in width to trigonid basin; lower molars not much longer than wide, unlike *A. nexodens*, *A. shanwangensis*, and *A. descendens*; M₃ protocone without labial cingulum; anterior crest of protocone well connected to anterior cingulum; protoconule on upper molars lack prominent crest or crests connecting to anterior cingulum, unlike all other *Ansomys*.

Description.—**Lower jaw:** There are two partial dentaries known for *A. hepburnensis*, CM 64461 and 63300, both of which are missing the incisor and portion of the jaw anterior to the alveolus for P₄ and the posterior region of the jaw. CM 64461 preserves the entire tooththrow, although it is quite worn, and most of the masseteric fossa. The description of jaw morphology is derived entirely from these two specimens. The tooththrow is short, with anteroposteriorly shortened lower molars which overlap laterally, placing the metaconid of one tooth immediately lingual to the hypoconulid of the tooth anterior to it. This shortening of the tooththrow is also apparent in all of the other species of *Ansomys* for which associated dentitions are known. The major cusps of the lower teeth are generally anteroposteriorly compressed and

the entoconid, mesostylid, and metaconid have large, prominent labiolingual crests. The masseteric fossa is deep relative to other derived prosciurines, with a groove along the dorsal edge which hooks slightly dorsally at its anterior edge, as in all but the most basal aplodontids. The ventral edge is straight, reaching the ventral edge of the jaw immediately below the hypoconid of M₂. From what little of the posterior portion of the jaw that is preserved, it appears that the angular process of the jaw is expanded as in allomyines, meniscomyines, and aplodontines, with two parts to the angular process, one of which is located medial to the plane of the jaw at its most ventral point and the other of which is slightly dorsal to this process and lateral to the plane of the jaw. This state is not developed in other prosciurines, and is very strongly developed in the modern *Aplodontia* Richardson, 1829. The type of *A. hepburnensis* preserves the posterior portion of the masseteric fossa, and the divergence of the two parts of the angular process is apparent from this area of the jaw.

P₄.—The metalophulid II is complete and proceeds posteriorly from the metaconid, then turns at a 90-degree angle and meets the protoconid as a labiolingual crest. At the bend in the metalophulid II, a pair of accessory crests proceeds lingually and posteriorly, forming a cross-shaped intersection. The metaconid is transversely compressed and possesses two posterior crests, one along the lingual edge of the tooth and one which forms the metalophulid II. The mesostylid is small, perhaps half the size of the large, prominent entoconid. The labial crest of the entoconid is straight, connecting directly with the posterior edge of the mesoconid. There is no connection between the mesostylid and entoconid, as is present in most species of *Ansomys*. The hypoconulid is large and somewhat triangular in shape. The hypoconid is slightly smaller than the hypoconulid and positioned immediately labial to it. The hypoconid is connected on its lingual side to the

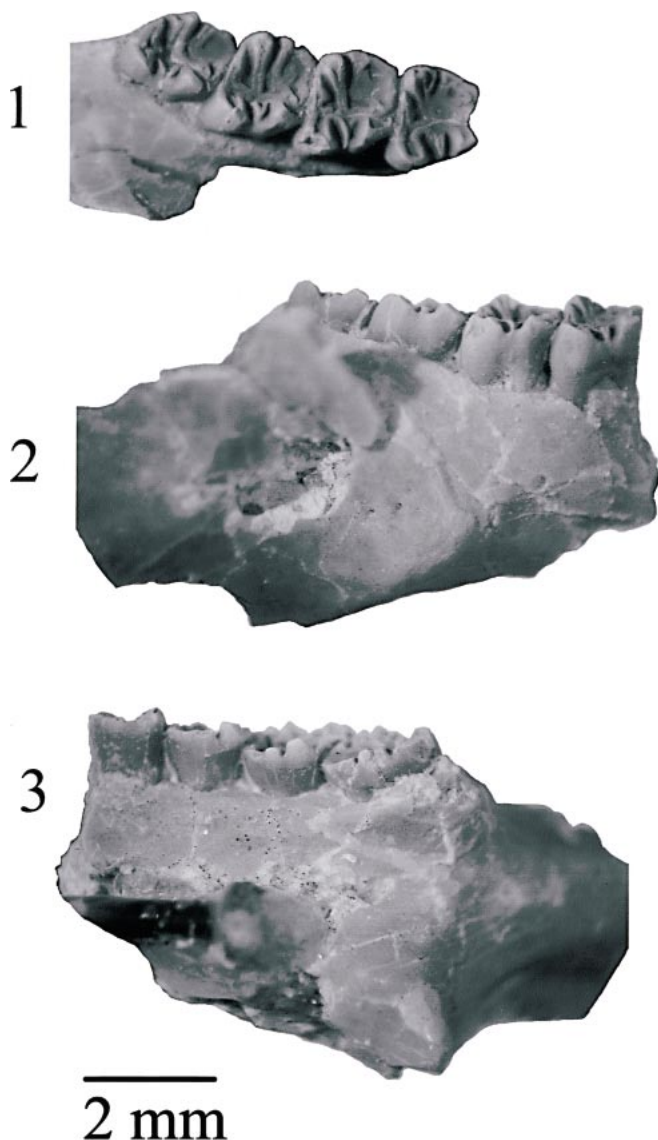


FIGURE 6—Type specimen of *Ansomys hepburnensis* n. sp., CM 64461, right dentary with P_4 through M_3 . 1, Occlusal view; 2, labial view; 3, lingual view.

mesoconid, but the anterolabial crest of the hypoconid ends on the tooth's labial margin, unconnected to the mesoconid. The mesoconid is relatively labial in position, and its labial surface is close to vertical, not low-angled and sloping, as in some other species of *Ansomys*. The protoconid is also transversely compressed, and has a small, anteriorly directed crest which hooks only very slightly lingually.

M_{1-2} .—The talonid basin and posterior cusps of M_{1-2} are similar to P_4 ; the main differences between these teeth are in the anterior cusps and the shape of the trigonid. The metaconid is a low, crestlike cusp, lower than in P_4 and higher in M_1 than in M_2 . The metaconid of M_1 is shifted labially and located near the middle of the anterior cingulum; in M_2 it is located just labial to the anterolingual corner of the tooth. The metaconid crest proceeds along the lingual edge of the tooth, ending in a small, secondary mesostylid. There is a small gap in the lingual cingulum between this small mesostylid and the primary mesostylid. The mesostylid is slightly larger than in P_4 , with a crest oriented labiolingually, parallel to the entoconid crest. The labial crest of the mesostylid

ends in the center of the tooth, where it joins a small, anteroposteriorly oriented accessory crest connecting to the metalophulid II. The metalophulid II is present on the protoconid, but mostly absent on the metaconid, with only a short extension of the interior crest of the protoconid toward the metaconid. In the space surrounding this crest there are two or three tiny incipient cusps, the exact positions of which vary from one specimen to another. The anterior crest of the protoconid joins with the labial crest of the metaconid, forming the anterior cingulum; in M_2 , unlike M_1 , the anterior crest of the protoconid hooks slightly labially before turning lingually to join the metaconid.

M_3 .—The cusp morphology of M_3 is very similar to that of M_{1-2} , with a few minor differences. The metalophulid II is completely absent on the metaconid, lacking even the small crest present in the other molars, and the metaconid is placed right at the anterolingual corner of the tooth. The anterior cingulum forms a 90-degree bend at the metaconid and proceeds posteriorly, ending just anterior to the mesostylid. There is no secondary mesostylid on M_3 . The entoconid slants slightly anteriorly, joining the center of the mesoconid, rather than its posterior edge, as in the other lower cheek teeth. The hypoconulid is greatly reduced and more closely joined with the hypoconid. Finally, the relative dimensions of M_3 differ from M_{1-2} , in that M_3 is transversely narrower relative to its length than M_{1-2} , and the talonid narrows posteriorly.

P^4 .—The fourth premolar of *A. hepburnensis* is similar in size to M_{1-2} , although it is longer anteroposteriorly due to the presence of the anterocone. The protocone is large and prominent, with a rounded lingual surface and strong crests extending anterolabially toward the anterocone and posterolabially toward the posterior crest of the metaconule. The metaconule is long and transversely compressed, roughly three times as long as it is wide. The anterior crest of the metaconule meets the protoloph at the lingual edge of the protoconule, and the posterior crest of the metaconule meets the posterior edge of the tooth. The metaloph is formed by the labially directed crest from the metaconule to the anterior edge of the metacone. The posterior cingulum is poorly developed, not strongly enclosing the posterior fossettes. The metacone is somewhat transversely compressed and rectangular, roughly twice as long as wide, and has a flat or very slightly convex labial face. The mesostyle is low, barely enclosing the central transverse valley, and bifid, forming a hat-shaped ectoloph. The anteroposterior length of the mesostyle is roughly half that of the metacone. The paracone is larger than the metacone and roughly triangular, with crests connecting to the mesostyle, anterocone, and protoconule. The labial face of the paracone is slightly convex. The crest connecting the paracone and anterocone bends labially, forming a small anterostyle that slopes posterolabially down the face of the tooth. The anterocone is doubled, with two distinct cusps, both of which are ovate, with long axes directed anterolingually. A low cingulum is developed between the lingual anterocone and the protocone, and the shape of this anterior face of the premolar indicates the presence of a third premolar similar in size to those present in other prosciurines, though no third premolars of *Ansomys* have been identified from Hepburn's Mesa. The protoconule is small and roughly square, with a pair of poorly defined crests extending anterolabially to the labial edge of the lingual anterocone.

M^{1-2} .—The first and second molars, as in many rodents, are indistinguishable as isolated teeth in *Ansomys*. The protocone is similar in morphology to that of P^4 , being large and located directly lingual to the central transverse valley. The anterior and posterior crests are both thick and prominent and make near 90-degree turns at the anterior and posterior tooth margins. The lingual surface of the protocone is curved and there are dorsoventral grooves anterior and posterior to the cusp. The posterior cingulum is weak, as in P^4 . The metaconule is transversely compressed and

acutely triangular, widest anteriorly and tapering posteriorly into a crest that reaches the posterior margin of the tooth. The anterolingual crest joins the proto-loph at the lingual edge of the protocone, closing the lingual end of the central transverse valley, and the anterolabial crest bends labially to join the metacone. The metacone is rectangular, about 1.5 times as long anteroposteriorly as it is wide. The labial face of the metacone is flat. The mesostyle is similar to that of the P⁴, except that it is longer, roughly equal in length to the metacone. The paracone is triangular, as in P⁴, and has a flat labial face. Crests extend from the paracone posterolabially to the mesostylid, lingually to the protoconule, and anterolabially to the anterior cingulum. The anterior cingulum is well developed and straight, connecting the paracone and protocone. The protoconule is square, with a pair of poorly defined crests extending down the anterior surface of the cusp, but not reaching the anterior cingulum. There is a low, poorly defined labiolingually oriented crest traveling the length of the central transverse valley, highest near the labial end of the valley.

*M*³.—The third molar is transversely narrower than the first and second molars. The protocone is large and T-shaped, with anterior, posterior, and labial crests radiating at right angles. The posterior cingulum is rounded, connecting the posterior crest of the protocone to the metacone. The metaconule is modified into a thin crest that proceeds anteriorly from the posterior cingulum just lingual to the metacone, turning sharply labially at the center of the tooth and extending to the labial edge of the metacone. There is a small crest extending from the bend in the metaconule anteriorly to the center of the posterior side of the protoconule, closing the central transverse valley. The metacone is elongated along the posterolabial corner of the tooth, forming the labial half of the posterior cingulum. The mesostyle is essentially absent on *M*³. The paracone is similar in morphology to that of *M*¹⁻², triangular with a flat labial face. The protoconule is small and rectangular, slightly wider transversely than it is long. The anterior crests present on the protoconule of *M*¹⁻² are absent in *M*³.

Etymology.—For the type locality, Hepburn's Mesa.

Types.—Holotype, CM 64461, partial right dentary with P4-M3, Hepburn's Mesa, Montana, CM Locality #1935, Chalk Cliffs South, Unit 16 microfossil quarry, Figure 6.

Paratype series: CM 63300, partial R dentary with M1; CM 63308, 75629, RM₁; CM 75626, LM₂; CM 75625, RM₂; CM 63306, 64150, RM₃; CM 75604, 75605, 75611, 75646, LM¹⁻²; CM 75606, RM¹⁻²; CM 75617, 75618, LM³; CM 75634, LP₄; CM 75637, RP₄; CM 75616, LP₄; CM 61220, RP₄, Hepburn's Mesa, Montana, CM Locality #1935, Chalk Cliffs South, Unit 16 microfossil quarry.

Other material examined.—CM 64104, 75635, LM₁; CM 63299, 64200, 64231, 75628, 75630, 75631, UWBM 76668 RM₁; CM 75623, UWBM 76667, 76670, LM₂; CM 63479, 75627, RM₂; CM 64202, UWBM 76671, LM₃; CM 75638, 75645, UWBM 76669, 76673, RM₃; CM 63498, 63575, 63987, 64032, 64133, 64203, 64439, 75603, 75607, 75612, 75641, 75642, LM¹⁻²; CM 63568, 63745, 64126, 64127, 64160, 64279, 64280, 64405, 64406, 64462, 75601, 75602, 75608, 75613, 75614, UWBM 76666 RM¹⁻²; CM 63752, 64159, 75600, 75621, LM³; CM 63900, 63903, 75620, 75643, UWBM 76664, 76665, 76672, RM³; CM 63814, 75636, LP₄; CM 63751, 64162, 64285, 75610, 75644, RP₄; CM 63772, 75615, 75639, 75640, UWBM 76674, 76675, 76690, LP₄; CM 63826, 64407, RP₄; 13 additional lower molars, CM 63470, 63776, 63973, 64080, 64311, 75619, 75622, 75624, 75632, 75648, UWBM 76680, Hepburn's Mesa, Montana, CM Locality #1935, Chalk Cliffs South, Unit 16 microfossil quarry.

Occurrence.—Early Late Barstovian NALMA, locality dated to between 14.9 and 14.7 Ma (Barnosky and Labar, 1989; Barnosky and Barnosky, 1990).

Discussion.—*Ansomys hepburnensis* is an important addition

to the fossil record of this genus. Besides *A. orientalis*, this is the only species of *Ansomys* for which a sample of more than a half dozen specimens is known, and it is one of only three species (with *A. orientalis* and *A. shanwangensis*) for which the complete cheek tooth dentition is known. The spatial and temporal position of *A. hepburnensis* is also important; its occurrence in the mid-Miocene of North America provides a link between the late Oligocene North American species *A. nexodens* with the mid-Miocene occurrences in China, Kazakhstan, and Europe. This gives some suggestion of the biogeographic complexity within *Ansomys*. Finally, *A. hepburnensis* adds to the known diversity of Miocene aplodontids in the Rocky Mountains, known to be represented by three other aplodontid lineages, aplodontines, allomyines, and meniscomyines, as well as mylagaulids. Aplodontids are now extinct east of the Sierras, but the occurrence of *A. hepburnensis* in the Barstovian of Montana indicates that they maintained significant diversity in that region as recently as 15 million years ago.

DISCUSSION AND CONCLUSIONS

The morphology of *Ansomys* is unique among mid-Miocene aplodontoids and is unusual among those found in the late Oligocene. First, few aplodontoids are so brachydont, and only *Ansomys* remains so in the mid-Miocene. Allomyines are the only other aplodontoid group in the mid-Miocene in which cusps are recognized in the teeth of adults, yet they are much higher-crowned than *Ansomys*, as well as generally larger in body size. Also, the development of internal crests within the tooth basin, particularly in the lower teeth, is unusual in *Ansomys*. Again, allomyines are the only other late Oligocene aplodontids that have this complex cusp morphology. *Ansomys* is distinct from allomyines in lacking a strongly developed ectoloph, and in the absence of evidence for increasing hypsodonty or robustness of the dentition through time, whereas allomyines possess these features (Rensberger, 1983). Clearly, *Ansomys* represents a unique ecomorph within the Aplodontoidea and may shed some light on questions of the evolution of hypsodonty in the aplodontoid lineage. By the mid-Miocene, two other aplodontoid lineages, the Aplodontinae and the Mylagaulidae, had developed hypsodont teeth. *Ansomys* and the Allomyiinae remained brachydont in the mid-Miocene, though they were higher cusped than most Oligocene aplodontoids. An understanding of the ecological differences between hypsodont and brachydont lineages of aplodontoid rodents could help to elucidate the causes of the evolution of hypsodonty in Miocene rodents.

The geographic distribution of known species of *Ansomys* (Fig. 7) suggests that it possessed a strong capacity for dispersal. Species are known from Montana and China in the late Oligocene, and the mid-Miocene distribution extends from Germany through Kazakhstan and eastern China to Montana. Hypotheses about the biogeographic history of the group are suggested by the cladogram, though the accuracy of those interpretations is, of course, limited by the assumption that the cladogram represents the actual phylogeny of the taxon. Interestingly, the most parsimonious cladogram suggests the possibility of two separate immigrations between Asia and North America. Based on the hypothesized relationships expressed in Figure 4, the genus appears to have originated in Europe (1, Fig. 7), as suggested by the presence of both the putative sister taxon, *Plesispermophilus atavus*, and the most basal species, *Ansomys descendens*, in Europe. Then, *Ansomys* seems to have invaded Asia, as indicated by the presence of *Ansomys shanwangensis* (2, Fig. 7) and *Ansomys shantungensis* (3, Fig. 7) in eastern China. If *A. crucifer* (7, Fig. 7) is placed at this point in the cladogram, as suggested in Figure 3.3, it may represent part of the path of this immigration event, as it is found in Kazakhstan (path a, Fig. 7). If, alternately, it nests higher in the

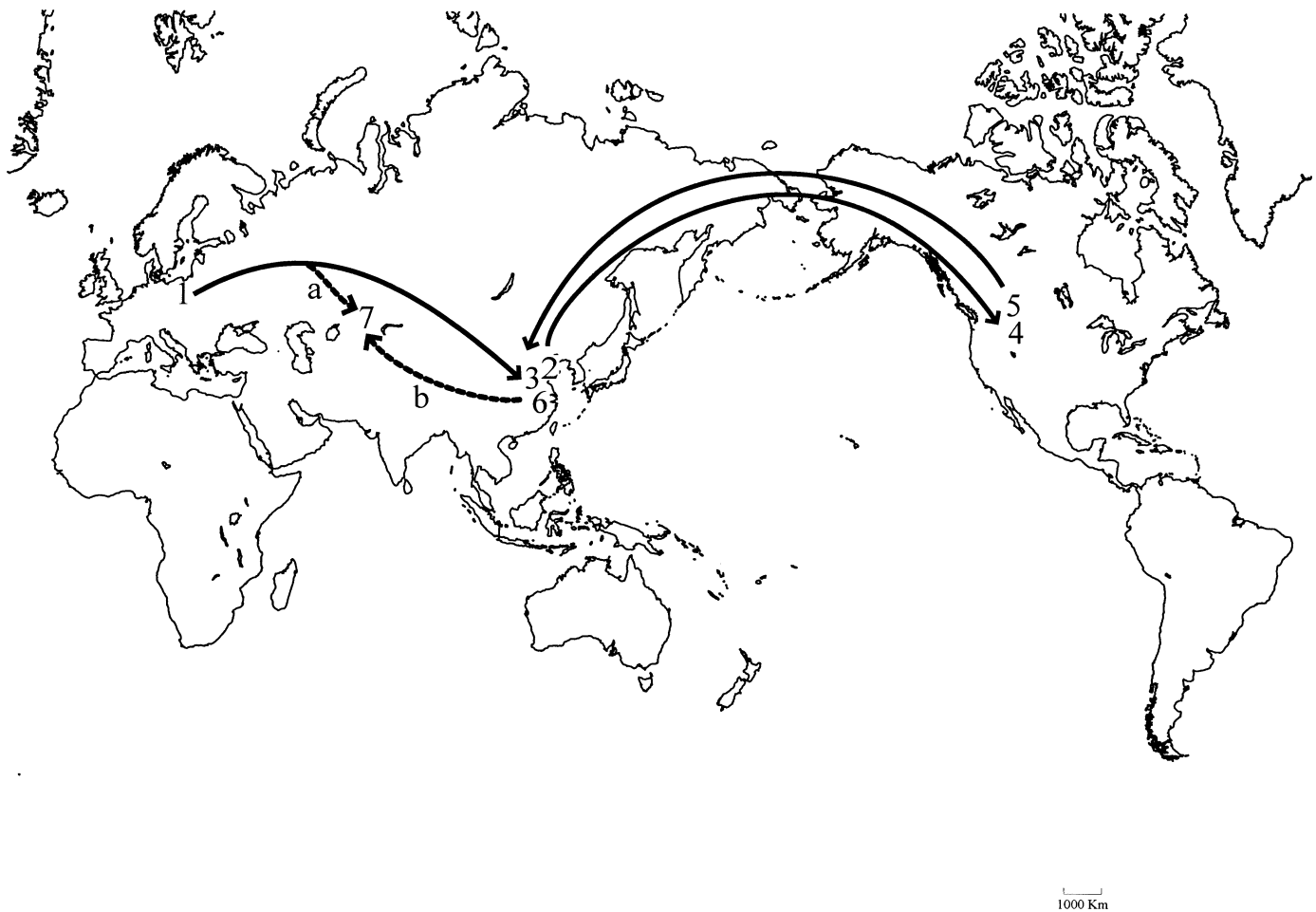


FIGURE 7—Geographic distribution and possible migration history of *Ansomys* species. Arrows indicate hypothesized dispersal paths, and numbers correspond to the locations where each of the taxa are found. Dashed lines indicate the different possible paths for the ancestor of *Ansomys crucifer*, which differ depending on which of the three cladograms in Figure 3 is used. 1, *A. descendens*; 2, *A. shantungensis*; 3, *A. shanwangensis*; 4, *A. hepburnensis* n. sp.; 5, *A. nexodens*; 6, *A. orientalis*; 7, *A. crucifer*.

tree, as suggested in Figure 3.1 or 3.2, it is likely to represent a subsequent western immigration from eastern China (path b, Fig. 7). From China, the most parsimonious resolution suggests two scenarios. One possibility is the invasion of North America by the lineage that led to *A. hepburnensis* n. sp. (4, Fig. 7) and *A. nexodens* (5, Fig. 7), followed by a subsequent return to Asia by the lineage that contains *A. orientalis* (6, Fig. 7). The other possibility is that the two North American species represent separate immigrations from Asia. Both scenarios are equally parsimonious. Although the biogeographic scenarios presented above are subject

to some doubt, due to the lack of strong support for precise intrageneric relationships and the poor fossil record, it is clear that the widespread distribution of the species within *Ansomys* indicates a history of large-scale migration. This point alone is interesting, given that the species are all small in body size (Table 2), and that the one surviving species of aplodontid (*Aplodontia rufa*) shows both a small home range size and a poor capacity for long-distance dispersal (Carraway and Verts, 1993).

One interesting characteristic of *Ansomys* is the infrequent occurrence and fragmentary preservation generally characteristic of

TABLE 1—Tooth measurements for specimens of *Ansomys hepburnensis* n. sp. SD = standard deviation, OR = observed range. All measurements in mm.

Element	Length				Width			
	<i>n</i>	Mean	SD	OR	<i>n</i>	Mean	SD	OR
P ⁴	11	1.78	0.104	1.63–1.96	11	1.90	0.151	1.67–2.15
M ¹⁻²	25	1.33	0.084	1.15–1.56	21	1.82	0.154	1.52–2.05
M ³	8	1.34	0.085	1.22–1.48	7	1.59	0.144	1.30–1.74
P ₃	8	1.58	0.144	1.30–1.74	11	1.45	0.185	1.26–1.81
M ₁	9	1.62	0.186	1.37–1.85	8	1.55	0.118	1.30–1.67
M ₂	7	1.52	0.096	1.41–1.67	6	1.51	0.123	1.30–1.67
M ₃	8	1.47	0.112	1.26–1.63	7	1.32	0.100	1.15–1.44

TABLE 2—Body mass reconstructions for known species of *Ansomys* (except *A. crucifer*, for which there is no data about the length and width of the lower first molar). Body masses are computed using the equation developed by Legendre (1986) for the correlation between lower first molar area and body mass in rodents.

	Average ml length	Average ml width	Average ml area	Estimated body mass (g)
<i>Ansomys hepburnensis</i> n. sp.	1.64	1.56	2.57	46.4
<i>Ansomys nexodens</i>	1.93	1.97	3.80	92.9
<i>Ansomys orientalis</i>	1.75	1.71	2.99	60.9
<i>Ansomys shantungensis</i>	1.86	1.77	3.29	72.1
<i>Ansomys shanwangensis</i>	2.05	2.05	4.20	110.9
<i>Ansomys descendens</i>	1.7	1.4	2.38	40.6

the species in the genus. This rarity may simply be a function of the taphonomy and collection history of the localities where *Ansomys* has been found, it may also be that it indicates low abundance in the communities from which the fossil assemblages were derived. If species of *Ansomys* were rare in ancient communities, that would provide a possible explanation for why there are so few known species and specimens, despite its wide geographic distribution and the abundance of faunas of the appropriate age. Another possible explanation for this spotty distribution is that *Ansomys* was an ecological specialist, and thus occurred very intermittently over the landscape, associated with the distribution of a particular habitat type. Finally, it is possible that collection bias toward larger specimens has limited the discovery of further remains of *Ansomys*, which is characterized by small body size. The first and third arguments are supported somewhat by the stratigraphic fit of the phylogenetic hypothesis. Both of these arguments suggest that the known occurrences do not faithfully record all the places and times where *Ansomys* existed. All of the species of *Ansomys* except *A. nexodens* and *A. shantungensis* are middle Miocene. *Ansomys nexodens*, the most derived species in the genus, is late Oligocene (Orellan NALMA) in age (Korth, 1992), and *A. shantungensis* was suggested from its stage of evolution to be mid- to late Oligocene in age (Rensberger and Li, 1986). This pattern may indicate an inaccurate phylogeny; but more likely, given the paucity of known specimens, the fossil record of *Ansomys* simply does not record much of its evolutionary history. Even in the absence of more complete material, this group of aplodontids illustrates an interesting Miocene biogeographic history and adds to the known morphological and lineage diversity of Oligo-Miocene aplodontid rodents.

ACKNOWLEDGMENTS

I thank A. Barnosky for providing mentorship and guidance throughout the project. P. Holroyd also provided copious advice, particularly with respect to applied phylogenetics. C. Beard and A. Tabrum, CM, provided access to specimens and casts used in this study. R. Emry, J. Martin, and an anonymous reviewer provided helpful reviews of the manuscript. I would also like to express my appreciation to E. Davis for informative discussions about methodology, as well as for moral support. Collection of Hepburn's Mesa fossils was made possible by funds from National Science Foundation grants BSR-8612959 and BSR-8746769 to A. Barnosky. Research was also supported by a National Science Foundation Graduate Research Fellowship. This is UCMP publication # 1828.

REFERENCES

BARNOSKY, A. D., AND W. J. LABAR. 1989. Mid-Miocene (Barstovian) environmental and tectonic setting near Yellowstone Park, Wyoming and Montana. *Geological Society of America Bulletin*, 101:1448–1456.

- BOWDICH, T. E. 1821. An analysis of the natural classifications of Mammalia for the use of students and travelers. J. Smith, Paris, 115 p.
- BREMER, K. 1994. Branch support and tree stability. *Cladistics*, 10:295–304.
- BURBANK, D. W., AND A. D. BARNOSKY. 1990. The magnetostratigraphy of Barstovian mammals in southwestern Montana and implications for the initiation of Neogene crustal extension in the northern Rocky Mountains. *Geological Society of America Bulletin*, 102:1093–1104.
- CARRAWAY, L. N., AND B. J. VERTS. 1993. *Aplodontia rufa*. *Mammalian Species*, 431:1–10.
- DEHM, R. 1950. Die Nagetiere aus dem Mittel-Miocen (Burdigalium) von Wintershof-West bei Eichstaett in Bayern. *Neues Jahrbuch fuer Mineralogie, Geologie und Palaeontologie. Abhandlungen. Abteilung B: Geologie, Palaeontologie*, 91(3):321–428.
- FILHOL, H. 1883. Description d'un nouveau genre de Rongeurs provenant des Phosphorites du Quercy. *Bulletin de la Société philomathique du Paris*, series 7, 7:99–100.
- KORTH, W. W. 1989. Aplodontid rodents (Mammalia) from the Oligocene (Orellan and Whitneyan) Brule Formation, Nebraska. *Journal of Vertebrate Paleontology*, 9(4):400–414.
- KORTH, W. W. 1992. A new genus of prosciurine rodent (Mammalia: Rodentia: Aplodontidae) from the Oligocene (Orellan) of Montana. *Annals of Carnegie Museum*, 61(3):171–175.
- LEGENDTRE, S. 1986. Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeovertebrata*, 16(4): 191–212.
- LOPATIN, A. V. 1997. The first find of *Ansomys* (Aplodontidae, Rodentia, Mammalia) in the Miocene of Kazakhstan. *Palaeontological Journal*, 31(6):667–670.
- MATTHEW, W. D. 1903. The fauna of the Titanotherium beds at Pipestone Springs, Montana. *Bulletin of the American Museum of Natural History*, 19:197–226.
- MATTHEW, W. D. 1910. On the osteology and relationships of *Paramys* and the affinities of the Ischyromyidae. *Bulletin of the American Museum of Natural History*, 28:43–71.
- QIU, Z. 1987. The Aragonian vertebrate fauna of Xiacaowan, Jiangsu; 7, Aplodontidae (Rodentia, Mammalia). *Vertebrata Palasiatica*, 25(4): 283–296.
- QIU, Z., AND B. SUN. 1988. New fossil micromammals from Shanwang, Shandong. *Vertebrata Palasiatica*, 26(1):50–58.
- RENSBERGER, J. M. 1983. Successions of meniscomyine and allomyine rodents (Aplodontidae) in the Oligo-Miocene John Day Formation. *University of California Publications in Geological Sciences*, 124:1–157.
- RENSBERGER, J. M., AND C.-K. LI. 1986. A new prosciurine rodent from Shantung Province, China. *Journal of Paleontology*, 60(3):763–771.
- SCHLOSSER, M. 1884. Die Nager des Europäischen Terriars nebst Betrachtungen über die Organisation und die geschichtliche Entwicklung der Nager überhaupt. *Paleontographica*, 31:323–328.
- SCHLOSSER, M. 1924. Tertiary Vertebrates from Mongolia. *Palaeontologica Sinica*, series C, 1(1):1–119.
- SCHMIDT-KITTLER, N., AND M. VIANEY-LIAUD. 1979. Evolution des Aplodontidae Oligocenes Européens. *Palaeovertebrata*, 9(2):32–82, 34 pls.
- SHEVYREVA, N. S. 1971. The first find of fossorial rodents of the family Mylagaulidae in the Soviet Union. *Bulletin of the Academy of Sciences of the Georgian SSR*, 62(2):481–484. (In Russian)
- SWOFFORD, D. L. 2001. PAUP: 4.0b5: Phylogenetic Analysis Using Parsimony (and Other Methods). Sinauer Associates, Sunderland, Massachusetts.
- TROUSSERT, E. L. 1897. *Catalogus Mammalium tam viventium quam fossilium*. Nova editio, pt. 2. R. Friedländer und Sohn, Berlin, p. 219–452.
- WANG, B. 1987. Discovery of Aplodontidae (Rodentia, Mammalia) from middle Oligocene of Nei Mongol, China. *Vertebrata Palasiatica*, 25(1): 32–45.
- WU, W. 1988. The first discovery of Middle Miocene rodents from the northern Junggar Basin, China. *Vertebrata Palasiatica*, 26(4):250–264.
- YE, J., J. MENG, AND W. WU. 2003. Oligocene/Miocene Beds and Faunas from Tiersihabahe in the Northern Junggar Basin of Xinjiang. *Bulletin of the American Museum of Natural History*, 279:568–585.

ACCEPTED 25 SEPTEMBER 2003

APPENDIX 1—List of characters.

1. Entoconid crest directed straight to mesoconid on P/4 (1) or not oriented toward mesoconid (0)
2. Hypoconulid connected most strongly to hypoconid (1), to entoconid (2), or neither (0) on P/4
3. Entoconid crest elongated labiolingually (1) or not elongated (0)
4. M/2 metaconid low and crestlike (1) or high and cuspsate (0)
5. M/3 metaconid with crest connecting to protoconid, dividing trigonid from talonid (0) or without crest (1)
6. P4/ anterostyle doubled (1) or single (0)
7. M1–2/ paraconule with a pair of crests extending anteriorly (1) or without crests (0)
8. M/2 entoconid with small, anteriorly hooked crest (1) or without crest (0)
9. Protocone of P/4 with crest extending anterolingually (1) or without (0)
10. M1–2 with small second mesostylid (1) or without (0)
11. Mesostylid on M2–3 large, similar in size to entoconid (1) or small (0)
12. M/1 mesoconid with lingual crest connection to mesostylid (1) or without (0)
13. Anterior cingulum not strongly connected to protocone on M1–2/ (1) or connected to protocone (0)
14. Protoconule on M3/ small (0) or large (1)
15. Anterior crest of hypoconid on M1–3 extending anteriorly to connect to mesoconid crest (1) or not connected to mesoconid crest (0)
16. Mesostyle bifid, ectoloph handle-shaped (1) or mesostyle single (0)
17. Labial surface of ectoloph flat (1), concave (2), or convex (0)
18. Metaconid on M/1 shifted somewhat labially (1) or lingually prominent (0)
19. Metaconid on M/1 anteroposteriorly compressed (1) or not compressed (0)
20. Anterior and posterior faces of M/3 roughly parallel (1) or not parallel (0)
21. M1–2 labiolingually expanded (1) or anteroposteriorly longer than wide (0)
22. Entoconid crest straight (1) or curved (0)
23. Mesostylid crest straight (1) or curved (0)
24. Lingual crest of metaconule joining protoconule (1) or protocone (0)
25. Labial end of central transverse valley open (0) or closed (1)
26. Mesostyle (0) or large (1)
27. Hypocone present (1) or absent (0)
28. Main cusps of lower teeth anteroposteriorly compressed (1) or not compressed (0)
29. Metaconule triangular (1) or round (0)
30. Basal part of hypoconid posterolabially expanded (1) or not expanded (0)
31. Accessory crests in trigonid basin present (1) or absent (0) on molars

APPENDIX 2—Character matrix.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
<i>A. hepburnensis</i> n. sp.	1	1	1	1	1	1	0	1	1	1	0	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	1	
<i>A. orientalis</i>	1	0	1	1	1	1	0	1	1	1	0	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	0	1	1	1	1	
<i>A. shantungensis</i>	?	?	1	1	?	?	?	?	0	?	0	1	0	?	?	?	?	?	?	?	0	1	1	?	?	?	?	?	1	?	1	1
<i>A. crucifer</i>	1	0	1	?	?	?	?	?	1	?	?	0	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	1	?	1	?
<i>A. nexodens</i>	1	1	1	1	1	?	?	0	?	1	0	1	?	?	1	?	?	1	1	0	1	1	0	?	?	?	?	1	?	1	1	
<i>A. descendens</i>	0	1	1	1	?	?	0	1	1	0	1	1	?	1	1	1	1	1	1	?	0	0	0	1	0	1	0	1	1	1	1	
<i>A. shanwangensis</i>	1	1	1	0	?	?	1	1	1	1	0	?	?	0	1	1	1	1	1	1	0	1	1	1	0	1	0	1	1	1	1	
<i>P. atavus</i>	0	1	1	0	0	?	?	0	0	0	0	0	0	0	1	?	?	1	0	0/1	1	1	0	?	?	?	?	0	?	1	1	
<i>P. angustidens</i>	0	1	0	0	1	0	?	0	1	0	0	0	1	1	1	0	2	0	0	0	0	?	?	0	0	0	0	0	1	0	1	
<i>Prosciurus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	?	0	0	0	1	0	0	0	0	