Chapter 4

The Antiquity of *Rhizomys* and Independent Acquisition of Fossorial Traits in Subterranean Muroids

LAWRENCE J. FLYNN[1]

ABSTRACT

In parallel with the growing body of molecular data bearing on the relationships of muroids, particularly subterranean lineages, the relevant fossil record has improved to the point that its data constrain scenarios of evolution about both the timing and mode of evolution of burrowing muroids, especially bamboo rats, blind mole rats, and zokors. Morphologists have considered these groups phylogenetically distinct from each other, but the three lineages appear to be related as a monophyletic Family Spalacidae, sister taxon to all other living muroids, based on both nuclear and mitochondrial genes. Although living genera are fully subterranean, the fossil record shows that the three groups evolved burrowing characteristics independently. Bamboo rats (Rhizomyinae) have the longest fossil record, extending into the Late Oligocene, but do not show fossorial traits until the Late Miocene. Blind mole rats (Spalacinae) have a fossil record nearly that long, and its early members also lack burrowing traits. Zokors (Myospalacinae) show characteristics considered derived relative to other groups, and have a shorter fossil record. The fossil record of the Tribe Rhizomyini, living Asian bamboo rats, extends to about 10 million years ago, with early species distinct at the generic level from living *Rhizomys.* The oldest well-known species assignable to an extant genus is *Rhizomys (Brachyrhizomys) shansius* from the early Pliocene of Yushe Basin, China, north of the geographic range of modern *Rhizomys.* A hypothesis of close relationship of bamboo rats, blind mole rats, and zokors leads to a reevaluation of affinities of certain Asian fossil taxa and reevaluation of polarity of some features, but molecular data are not yet robust enough to clarify interrelationships of the groups. Morphological and fossil data suggest that myospalacines are more closely related to rhizomyines than to spalacines, and that known Early Miocene rhizomyines are close to the stem zokor morphotype.

INTRODUCTION

"The panoply of adaptations necessary for living underground in tubular burrows has dramatically defined the blind mole rat phenotype, which facilitates their diagnosis but obscures phylogenetic connections to other muroid rodents." This wonderful statement from Musser and Carleton (2005) could be applied as readily to bamboo rats as to *Spalax*, the blind mole rat. Truly subterranean small mammals are obliged to spend at least 95% of the time underground. Given this condition, adaptive constraints are focused such that phylogenetically remote taxa converge in body form, limb proportions, and skull structure. Old World burrowers like bamboo rats and blind mole rats look like North American gophers and even superficially like lipotyphlan moles. Nevo (1999) explored this very subject in his book on subterranean mammals. Since phenotypic resemblance of rodent burrowers is not an especially strong argument for close relationship, fossorial lineages have been classified separately, often at the family level. Ironically, recent molecular work suggests that several different burrowers constitute, in fact, a monophyletic group.

My personal fascination with bamboo rats and relatives began with research on the Siwalik fossil record of the Indian subcontinent, which contains the lion's share of what is known of the history of the group. The Late Tertiary basins of China, in which I

---

[1] Peabody Museum of Archaeology and Ethnology, Harvard University, Cambridge, MA 02138 (ljflynn@fas.harvard.edu).

have had the pleasure to work with colleagues in the field, also produce bamboo rats, as well as the endemic fossorial muroids known as zokors. It is the fossil record of China that provides knowledge delimiting the origin of the bamboo rat *Rhizomys,* and includes remains of other enigmatic muroid precursors.

This study begins with description of the oldest fossil skull and postcrania of the genus *Rhizomys*, which derives from Pliocene Epoch rocks of Yushe Basin, Shanxi Province, People's Republic of China, and is housed in the American Museum of Natural History, New York. It demonstrates the generic identity of other less complete remains of bamboo rats from the fossil record of China, and sheds light on the systematics of older bamboo rats. This analysis leads to a discussion of the phylogenetic relationships of bamboo rats and the relevant fossil record, given that recent molecular work argues for strong affiliation with *Spalax* and with the diverse but local zokors of eastern Asia. Previously, most systematists had considered the common origin of bamboo rats, *Spalax*, and zokors to be remote in time and likely not monophyletic. Finally, enigmatic elements in the fossil record of China are placed in the context of the evolutionary history of higher muroids, given a hypothesis of close relationship of these burrowing groups.

MUROID SYSTEMATICS

Musser and Carleton (2005) give a thorough accounting of the history of muroid classification. For the purposes of this paper, it is sufficient to note that the monophyly of Muroidea is not a question, nor is (for the moment) the close relationship of South Asian bamboo rats (*Rhizomys* and *Cannomys*) and African mole rats (*Tachyoryctes*). Relevant to the issues explored herein, however, is the family-level division of Muroidea and implied close relationships within those families.

Subdivisions of Muroidea have been evident for many years, and these are treated extensively by Musser and Carleton (2005). While many authors have preferred to utilize the family-level category to recognize these subdivisions, others, including Carleton and Musser (1984) and McKenna and Bell (1997), have elected to give them lower rank (subfamily), pending more data to clarify interrelationships. Such data are emerging from molecular as well as anatomical studies. These tend to endorse the higher categories that are evidenced by morphology (15 subfamilies according to Carleton and Musser, 1984), and to define clusters of them, which correspond to family-level taxa, fewer in number. Current molecular studies (Steppan et al., 2004; Jansa and Weksler, 2004) are beginning to survey Muroidea broadly, but individual efforts still sometimes miss key taxa. The integrative analysis of Musser and Carleton (2005) draws on molecular and morphological data and recognizes six families within Muroidea: Platacanthomyidae (usually not treated in molecular work), Calomyscidae, Nesomyidae, Cricetidae, Muridae, and Spalacidae. Steppan et al. (2004) and Jansa and Weksler (2004) show Spalacidae to be the sister taxon to all other extant Muroidea.

The family-level taxon Spalacidae has come to be seen as a basal survivor of the fabulous radiation leading to crown-group muroids. Spalacidae would be an ancient branch of living Muroidea. Other more primitive muroids, logically treated as independent families, are all extinct. Hence the Eocene and early Oligocene radiations of muroids should be recognized at the family rank (e.g., Eumyidae, Pseudocricetodontidae, Paracricetodontidae, Eucricetodontidae, Tachyoryctoididae; see Ünay-Bayraktar, 1989), and not lumped in Cricetidae. Coming from the molecular work, however, is the somewhat surprising linkage of *Spalax* and *Rhizomys* + *Cannomys* + *Tachyoryctes* with the fossorial zokor *Myospalax*. Musser and Carleton (2005) illustrate the colorful history of classification of these genera and show that they have been associated in the past, but not usually together to the exclusion of all other muroids. Şen (1977) did suspect that these genera belonged together in Family Spalacidae. This is an exciting and testable hypothesis of relationship that makes review of the fossil record of these groups relevant. I begin with the bamboo rats.

ABBREVIATIONS

AMNH   American Museum of Natural History, New York
F:AM   Frick mammal fossil collection of the American Museum of Natural History
Fm.   formation
GSP   Geological Survey of Pakistan
MCZ   Museum of Comparative Zoology, Harvard University, Cambridge, MA
THP   Tianjin Huang Pei, fossil collections of the Tianjin Museum of Natural History, P.R.C.

COMPARISONS: Among a large suite of specimens in the collections of the Vertebrate Zoology Division of the AMNH and in the Mammal Department of MCZ, useful comparisons were made among *Rhizomys pruinosus pruinosus* (AMNH 113477), *Rhizomys pruinosus senex* (MCZ 35935, 35936), *Rhizomys sinensis vestitutus* (MCZ 7559, 7560), *Rhizomys sinensis wardi* (AMNH 115527, 115528), *Rhizomys sumatrensis* (MCZ 61049), and *Cannomys badius* (AMNH 163644, 163645). The AMNH Division of Paleontology also houses several series of elements attributed to fossil *Rhizomys troglodytes*, for example, AMNH 18407 and 18409. Also examined were *Eospalax fontanierii* (MCZ 19896), ''*Myospalax* cf. *cansus*'' (AMNH 135358, probably *Eospalax fontanierii*), *Spalax microphthalmus* (AMNH 228), *Spalax ehrenbergi* (MCZ 61376) and *Tachyoryctes* sp. (AMNH 54305, 187461).

SYSTEMATICS

Tribe Rhizomyini Winge, 1887
Genus *Rhizomys* Gray, 1831
Subgenus *Brachyrhizomys* Teilhard de Chardin, 1942

DIAGNOSTIC FEATURES: The Tribe Rhizomyini is equivalent to Flynn's (1982, 1990) subfamily Rhizomyinae, diagnosed by derived characters including reduction of the ventral slit of the infraorbital foramen, ridge absent on lower incisor enamel, small posterolingual reentrant on m3, reduced incisive foramina, and a host of fossorial features (chisel incisor, strong coronoid process on deepened mandible, modified humerus with broad epicondyles and strong deltoid crest, broad skull with flaring zygoma and lambdoid crest). The genera *Rhizomys* and *Cannomys* are distinguished from earlier taxa by the apomorphic high, round infraorbital foramen lacking a ventral slit, and the latter is derived in its short M3 and m2, reduced posterolophid on m2, and three crests on M2 and m2. *Rhizomys* has a deep dentary and its masseteric crest terminates below the front of m1 or beyond, without an anterior extension, four-crested M1–2 (strong mesoloph), mesolophid indistinct on m3. The subgenus *Brachyrhizomys* is characterized by features that are likely primitive: lower crowned than living *Rhizomys*, m2 longer than wide until late wear, posterolophid on m3 incompletely isolated, masseteric crest not extending past anterior root of m1, lower diastema not shortened. *Brachyrhizomys* appears to be derived in proodonty, but shares this trait with *Cannomys*.

Rhizomys (Brachyrhizomys) shansius
Teilhard de Chardin, 1942

HOLOTYPE: IVPP 31.096, right dentary with incisor, m1–3; coronoid process, condyle and angle of the mandible missing.

REFERRED MATERIAL: THP 14.183, right dentary fragment with incisor, m2–3; F:AM 117337, cranium and mandible with complete dentition, atlas + axis, partial rib cage and clavicle fragment, right scapula, left and right humerus and ulna, right distal femur fragment, and tibia diaphysis.

LOCALITIES AND AGE: All specimens from Pliocene deposits of Yushe Basin, Shanxi Province, China. North of the Yellow River, in central Shanxi, this basin is north of the range of *Rhizomys* at present. The holotype is of imprecise provenance; THP 14.183 is from Baihaicun, upper Gaozhuang Fm. or lower Mazegou Fm.; F:AM 117337 is from Zhaozhuang, Mazegou Fm., age about 3.5 million years ago (megaannum, Ma). The age range for known fossils, at most 4.5 – 3 Ma, is quite possibly shorter, ~4–3.3 Ma (time scale of Cande and Kent, 1995).
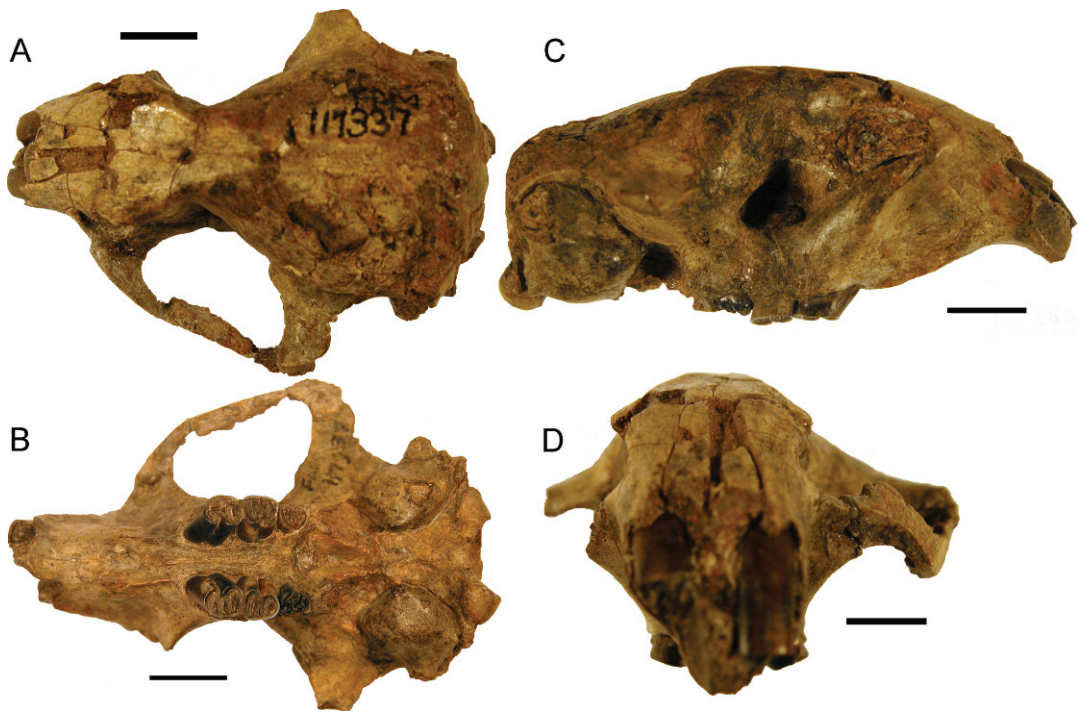
Fig. 1.   Cranium of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337), in dorsal (A), ventral (B), right lateral (C), and anterior (D) views. Scale bars equal 1 cm.

SUPPLEMENTED DIAGNOSIS: *Brachyrhizomys* about the size of smaller individuals of *Rhizomys sinensis* or *R. pruinosus* but with lower crowned molars; skull with proodont incisors, weak lambdoid crest, gently convex occiput nearly vertical and not expanded dorsoventrally; lingual reentrant on M1 short and not convergent with middle buccal reentrant, m2 not wider than long and with persistent anterolingual enamel lake, mandible with diastema not shortened.

DESCRIPTION OF CRANIUM: The skull of *R. shansius* is very much like that of living *Rhizomys*, showing the overprint of adaptations for a fossorial lifestyle. It is compact, stoutly built, with heavy rostrum and broad braincase. There is a narrow interorbital constriction and the occiput supports heavy musculature. The upper diastema rises anteriorly toward the heavy incisors. Tooth rows are set close, with small incisive foramina several mm anterior to them. Significantly different, however, is that the skull, especially the occiput, is lower than that of the high

skull of living species; the occiput is clearly wider than high, and less sloping. F:AM 117337 represents a young individual, with last molar still erupting and not yet showing attrition (fig. 1).

The tips of the incisors, nasals, and bits of the premaxillas are missing due to breakage. The incisors were proodont unlike living *Rhizomys*, in which they recurve and are directed ventrally. The incisors appear to be rooted above M1. The snout (fig. 2) is broad posteriorly, and narrows steadily anteriorly; conversely the nasals broaden anteriorly. The narrow posterior limits of the nasals are adjacent to the posterior borders of the premaxillae. Together, these make a jagged intersection with the frontals opposite the posterior rim of the high infraorbital foramen. The dorsal aspect of the infraorbital foramen is ringed by the maxilla. The foramen transmits the deep portion of the masseter, whose scar extends slightly beyond the foramen onto the premaxilla. Anterior to the infraorbital foramen, the premaxilla-
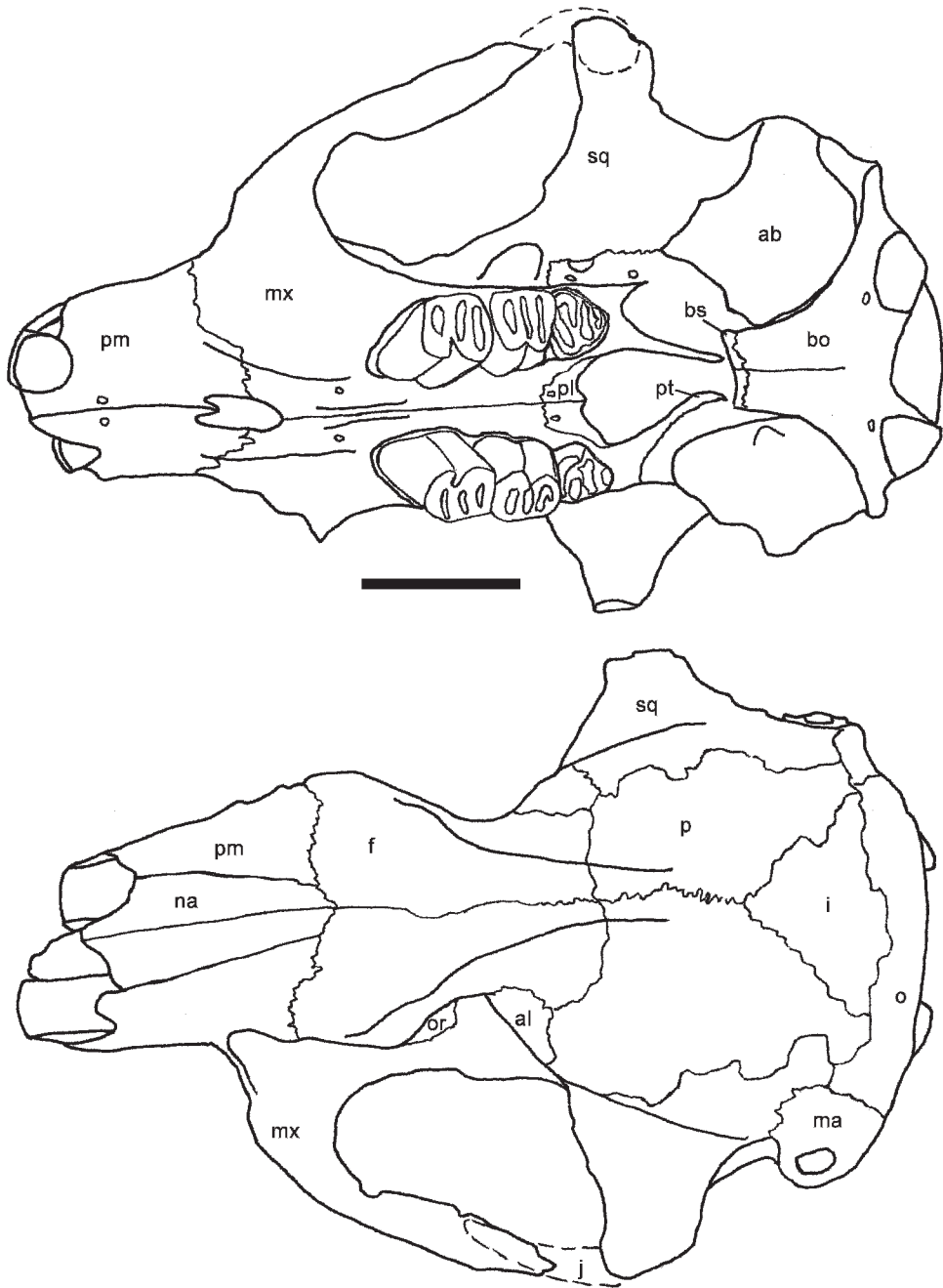
Fig. 2.   Line drawing of the skull of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337), in ventral (above) and dorsal (below) views; 1 cm scale. View is slightly angled to show features of the orbit (deep fissure from ventral view; some of the orbitosphenoid from dorsal view, on the side of the orbit, above the maxilla floor). Abbreviations: **al** (alisphenoid), **ab** (auditory bulla), **bo** (basioccipital), **bs** (basisphenoid), **f** (frontal), **i** (interparietal), **j** (jugal), **ma** (mastoid), **mx** (maxilla), **n** (nasal), **or** (orbitosphenoid), **p** (parietal), **pl** (palatine), **pm** (premaxilla), **pt** (pterygoid), **sq** (squamosal).

maxilla suture drops vertically to intersect the middle of the incisive foramen. The muscle scar of the lateral masseter clearly extends anteriorly on the side of the rostrum beyond this suture. Anterior to the scar is a shallow depression in the premaxillary bone, posterior to the incisors. Because the origin of the lateral masseter is highly developed, it suppresses completely the zygomatic plate, fusing it onto the side of the snout. The infraorbital foramen is high and rounded, fully modern, except that it is proportionately larger than in living species. The anterior root of the zygoma of F:AM 117337 is broken on both sides and the lacrimal bone is not preserved. The lacrimal may contribute to the dorsal aspect of the anterior root of the zygoma in living species but, in any case, does not touch the premaxilla. The heavy left zygomatic arch flares broadly laterally. It was broken during preparation, but the small jugal (fig. 2) was located and replaced. The arch is not as deep dorsoventrally as in living species, and the contribution to it by the jugal bone is smaller.

In dorsal aspect, the interorbital region of the skull is constricted, narrower than the rostrum, rounded around the braincase. Scars for the temporalis muscle begin at the anterior margin of each orbit and converge posteriorly but do not meet. Temporal ridges can be traced caudally to the interparietal and nearly to the occiput before they turn laterally. Both the degree of interorbital constriction and convergence of scars as parasagittal crests are a function of size and individual age. The frontal bones contribute to the anterior portion of the braincase and terminate somewhat posterior to the interorbital constriction. Bones of the cranial vault are thick with sutures reinforced by overlapping laminae of bone, particularly between parietal, interparietal, supraoccipital, and squamosal. Hence, tracing sutures is complicated by minor spalling of laminar bone from the fossil. The parietals roof most of the braincase; the occipital plate does not encroach upon them from behind. The large interparietal is roughly triangular, not subrectangular as in many muroids, and it is large for *Rhizomys*, not overlain posteriorly by the supraoccipital as it is nearly completely so in living species. The occipital is gently convex, not flattened or surmounted by a distinct flange of bone. From the occipital condyles, barely visible in dorsal view, the occiput rises vertically and curves gently rostrally. The dorsal view of the strongly inclined occiput of living *Rhizomys* reveals the condyles prominently.

In posterior view the braincase is much wider than high. Mastoids are prominent. Dorsolateral to them, a wing of the squamosal extends above and medial to the bony auditory tube (broken on the left side). The foramen magnum is large relative to modern *Rhizomys*. Bullae are large and heavy, with a short bony auditory tube present. The bony auditory tube terminates at the level of the posterior root of the zygoma, and does not extend dorsolaterally above the zygoma as in living *Rhizomys*. Paroccipital processes, although broken, probably were not as big as in living species. In ventral view, the basioccipital extends to the mouth of the eustachian canal of the bulla. Wings of the pterygoids are broken, and most of the basisphenoid is missing (fig. 2). The basicranium is telescoped, shortened as in living *Rhizomys*. The telescoping places the bullae adjacent to the pterygoid vacuities. The deep pterygoid vacuities and mesopterygoid fossa accommodate the pterygoid musculature that counters the strong temporalis. The vacuities retain some matrix, obscuring details of the foramen ovale, the middle lacerate foramen, and the alisphenoid canal.

The rostrum and palate are strongly built. Penetrating the bone near the midline and posterior to each incisor are small premaxillary foramina. The rostrum is constricted on each side by the heavy masseteric musculature, which builds a flange of bone along the posterior half of the diastema. These ridges flank short, closely paired incisive foramina, whose posterior ends are 4.4 mm anterior to the alveolus rim for M1. Molar rows are set close and diverge somewhat posteriorly. A ridge down the center of the palate is bounded on each side by a narrow trough. The palatine bone tightly rounds the maxillary alveolus for M3 and contributes to the posterior margin of the hard palate. It terminates with a V-shape at the maxilla, with rostral apex and opposite the boundary between M2 and M3. Posterior palatine

foramina are weakly defined, apparently located at the border with the maxilla. Because the hard palate extends caudally only to the middle of M3 in this young individual, the palatine contribution to the hard palate is minor. The palate ends about 1.7 mm anterior to the posterior rim of the alveolus for M3. The otherwise concave posterior margin of the palate has a midline knob. Laterally, the maxilla extends as a process behind each M3 and is continuous with the pterygoid plate.

One's first impression of the lateral view of F:AM 117337 is that the skull is deep dorsoventrally, a characteristic of *Rhizomys*. The skull roof is arched, highest above the back of the orbit. Deepening is accomplished mainly by dorsoventral expansion of the maxilla, which accommodates the high-crowned molars. The orbit and its structures are extended dorsoventrally, with simultaneously increased basicranial flexion. The expanded maxilla is consistent with the deep rostrum, which rises steeply toward the incisors. The anterior root of the zygoma is anterior to M1. The posterior root begins above the back of M3, is expansive antero-posteriorly, and rises gently rearward. It ends at the posterolateral extent of the temporal ridge, which passes above the auditory tube of the bulla. This tube is more elongate and extends dorsally above the level of the zygoma in living *Rhizomys*. The glenoid fossa is wide and elongate. The heavy posterior root of the zygoma is supported by a large squamosal bone. Relative to the squamosal, the small alisphenoid is squeezed with the maxilla and contributes to the back of the orbit. Posteriorly, the alisphenoid shows a notch, which may represent the anterior opening of the alisphenoid canal. Anterior to this are two foramina, apparently equivalent to the buccinator and masticatory foramina of geomyids (Wahlert, 1985), which also have a deep skull. The floor of the orbit, maxillary bone, is excavated deeply into the skull and includes pits for the sphenoidal (anterior alar) fissure and optic foramen. A small foramen above M1 in the maxilla may be the sphenopalatine. The small orbitosphenoid is located anteriorly at the midlevel of the orbit, and deep within it. The orbitosphenoid and alisphenoid are barely in view from

the dorsal aspect (fig. 2). These bones are relatively larger than in living *Rhizomys*, which has a relatively more vertically expanded maxilla. Correlated to the more vertically expanded maxilla, the orbit is less deeply excavated above the molar roots in living species.

MANDIBLE: The unfused mandible has a large, rugose contact surface between dentaries that brings the chisel-shaped incisors close together. Molar occlusal surfaces are tilted inward. The diastema (10.3 mm for the left dentary) is neither as shortened nor as concave dorsally as in living species. Jaw depth is considerable: measured externally, 14 mm below m1, and 13.5 mm below m2. In the young individual represented by F:AM 117337 (fig. 3), m3 is erupting, which makes the measurement of 14.2 mm an underestimate for the length of the tooth row. (The distal wall of m3 slopes ventrally and posteriorly, which makes measurements of the occlusal surface dependent on wear stage). The ventral border of the mature, and larger, THP 14.183 is damaged so that the depth of 15.3 mm below the back of m1 in this specimen is an underestimate for the original; its tooth row length at the alveoli is 14.75 mm. The dentary has a high condyle (10.5 mm above the m2 alveolus in F:AM 117337) and strong coronoid process, perhaps stronger and more vertical than in living species. A prominent coronoid correlates with strong temporalis muscles which stabilize the jaw as the head is lifted during chisel-tooth burrow excavation. The incisor is rooted in a capsule lateral to the condyle. The capsule of this young bamboo rat is smaller and does not extend as far posteriorly as in observed living *Rhizomys*. (*Cannomys* exhibits a condition in which the extended capsule rises above and dominates the adjacent condyle.) The strong upper and lower masseteric crests meet below the front of m1 as a rounded scar without anterior extension. Anterior to it is the mental foramen, above the midline of the dentary, at the back of the diastema. The ascending ramus is broad anteroposteriorly, and rises opposite m2, close to the tooth row and without a defined pocket next to the teeth. The mandibular foramen is above the distal part of m3, not well posterior to it as in living

Fig. 3. Internal (above) and external views of the left dentary, and dorsal view of the right dentary (below) of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337); scale bars equal 1 cm.

species. The angular process is more caudally extended than in living *Rhizomys*, beyond the limit of the condyle and incisor capsule.

DENTITION: The stout upper incisor is broad mediolaterally (3.45 mm) in relation to its parasagittal length (4.25 mm). Its enamel cap is gently rounded and wraps about three-tenths of the way onto the lateral side of the incisor. There is no major ornamentation—only gentle rugosities on the enamel. The lower incisor (3.91 × 4.35 mm) is heavier, with the enamel cap somewhat less rounded than that of the upper incisor. Enamel wraps just over a quarter of the way onto the lateral side of the incisor. Only minor rugosities ornament the enamel. Although the enamel is considerably darkened, there are mottled traces of original orange pigmentation. The more mature individual THP 14.183 has a larger lower incisor, 4.55 mm wide.

Molar dimensions (length × width) are cited here as maxima, including expanded bases of crowns (not occlusal wear surface; hence, measurements are greater than in table 1). Measurements draw on information from the left and right sides of the skull (differentially preserved and exposed). M1 (6.0 × 4.4 mm) is noticeably longer than wide and moderately high crowned (4 mm crown height visible lingually, less than its length or width). The tooth is higher crowned lingually than buccally and appears to have four roots, one anterolingual root well developed and directed anteriorly for support. The rounded occlusal outline has one lingual reentrant, which extends nearly to the base of the crown. In occlusal view, the reentrant is short and directed anteriorly toward the first of three buccal transverse enamel lakes. Consequently, the tooth exhibits four lophs: anteroloph, protoloph, mesoloph, and combined metaloph-posteroloph. M2 is more squared in its major dimensions (4.3 × 4.25 mm), although it is narrower posteriorly than anteriorly. It has the same four transverse lophs, but the lingual reentrant is directed toward the middle enamel lake, and possibly joined it in early wear. M3 is just erupting, making its measurement (3.8 × 3.6 mm) difficult. It has the same four lophs, although the posteroloph is short due to the rounded nature of the back of the tooth. The lingual

TABLE 1
Cranial and Dental Measurements (mm)[a] of F:AM 117337, *Rhizomys (Brachyrhizomys) shansius*

Occipitonasal length[b]	55
Zygomatic breadth	46
Interorbital breadth	9.7
Length of rostrum[b]	21
Breadth of rostrum	15.6
Breadth of braincase	24.9
Height of braincase	20.0
Length of diastema	17.9
Length of incisive foramina	4.8
Breadth of incisive foramina	2.5
Length of bony palate	17.6
Breadth across bony palate at M1	3.1
Postpalatal length	20.2
Breadth of mesopterygoid fossa	6.5
Length of bulla	10.7
Crown length of M1-M3[c]	12.2
Breadth of M1, M2, M3[c]	3.9, 3.8, 3.2
Crown length of m1-m3[c]	14.2
Breadth of m1, m2, m3[c]	3.5, 4.4, 4.4

[a] After Musser et al. (2005: fig. 3).

[b] Underestimated due to breakage.

[c] Molar dimensions are at the occlusal surface, and are therefore minimum measurements for these little-worn teeth (the occlusal wear surface is larger in later wear stages).

reentrant is confluent in early wear with both the anterior and middle buccal enamel lakes.

Lower molars are lower crowned, with less noticeable unilateral height (higher crowned buccally). The first molar (5.2 × 3.95 mm) is well worn although m3 is not fully erupted, and shows primarily five transverse lophs (anterolophid, metalophid, mesolophid, hypolophid, and posterolophid). The mesolophid is a long lingual continuation of the protoconid. A large enamel lake separates the mesolophid from the metalophid and is just closing off from the buccal wall of the tooth at this stage of wear. This lake parallels the major buccal reentrant between protoconid and hypoconid. The posterior enamel lake is small. The m2 is square (4.9 × 4.95 mm; THP 14.183 is somewhat bigger [Flynn, 1993]) and has four major lophs. The short mesolophid joins the anterior loph through the protoconid. Posterolingual to the mesolophid is the hypolophid, which joins the posterolophid lingually. In early wear a small enamel lake in the anterolingual corner of the tooth demar-

Fig. 4. Forelimb of *Rhizomys (Brachyrhizomys) shansius* (F:AM 117337). A, right humerus in medial view; B, left humerus in posterior view; C, lateral view of proximal right ulna; D, medial view of left proximal ulna. Scale bar equals 1 cm.

cates a remnant of the lingual anterolophid. In later wear the mesolophid joins the hypolophid and all lingual reentrants are closed off. The m3 is much like m2 but is longer, especially due to the posterior wall being expanded backward toward its base (7.2 × 5.3 mm). Its small anterolingual lake is persistent and the mesolophid is less prominent, more rapidly merged by wear with the hypoconid. The posterolophid is a simple, prominent, arcuate structure, completely isolated from the rest of the crown by a long reentrant that closes off lingually during moderate wear. The right m3 of F:AM 117337 is somewhat more erupted than the left, shows a bit of wear on its cusp tips although they are below the level of m2, and is partially prepared out of its crypt (allowing crude measurement; crown height about 5.5 mm). It has two lingual reentrants in early wear.

POSTCRANIA: Portions of the axial skeleton of F:AM 117337 are preserved. The broad atlas-axis complex is stoutly built as in living bamboo rats. The proximal two-thirds of a clavicle, 21 mm long, is nearly straight and missing its curved distal end. It is comparable to the stout clavicle of living *Rhizomys*, rather than the more slender clavicle of *Tachyoryctes* or *Cannomys*. The five ribs preserved in near-anatomical position, plus association with other parts of the skeleton and the nearly complete skull, suggest that the specimen was not transported or torn apart by a predator, but perhaps was preserved in its burrow.

The appendicular skeleton includes several parts of each forelimb. The right scapula, with prominent spine but broken acromion and coracoid process, is elongate (24.4 × 11 mm); the supraspinous fossa is narrow, much less expanded than in living species. The ulna (fig. 4) is heavy and anteroposteriorly deep. Broken distally, it exceeds 31.5 mm in length. The olecranon process is prominent, the length from the proximal surface of the trochlear notch to the tip being 9.3 mm. There is a heavy coronoid process and prominent supinator crest running distally from it.

The heavy humerus (fig. 4) has fused, or nearly fused epiphyses. With a length of 34.1 mm, its head is large (maximum dimension and its perpendicular are 10.5 × 9.1 mm). The distal end of the humerus is wide, the epicondylar width being 11.6 mm. The

TABLE 2
Comparative Forelimb Measurements[a] (mm) and Ratios of F:AM 117337, *Rhizomys*
(*Brachyrhizomys*) *shansius*, and Other Burrowing Muroids

	HL	HW	HW/L	HD	HD/L	UL	OL	OL/UL
Brachyrhizomys shansius (F:AM 117337)	34.1	11.6	0.34	19.0	0.56	>31.5	9.3	<0.30
Rhizomys pruinosus senex (MCZ 35935)	43.0	14.5	0.34	26.1	0.61	48.4	13.7	0.28
R. pruinosus pruinosus (AMNH 113477)	47.2	14.1	0.30	26.1	0.55	55.5	13.5	0.24
Cannomys badius (MCZ 3617)	25.4	7.1	0.28	15.4	0.61	28.2	7.2	0.25
Tachyoryctes ibeanus (MCZ 8134)	25.6	8.0	0.31	14.1	0.55	30.3	6.5	0.21
Tachyoryctes sp. (AMNH 54305)	24.0	6.9	0.29	13.3	0.55	30.3	6.2	0.20
Tachyoryctes sp. (AMNH 187461)	27.0	7.8	0.29	16.0	0.59	35.0	6.7	0.19
Spalax microphthalmus (AMNH 228)	27.0	9.5	0.35	15.8	0.59	33.0	11.3	0.34
Spalax ehrenbergi (MCZ 61376)	18.0	5.8	0.32	12.2	0.68	24.8	8.8	0.35
Eospalax fontanierii (MCZ 19896)	32.0	14.9	0.47	21.2	0.66	43.2	18.0	0.42
Eospalax fontanierii (AMNH 135358)	31.0	15.1	0.49	19.3	0.62	—	—	—

[a] Measurement abbreviations: HL, humerus length; HW humerus width at the epicondyles; HD, distal extent of the deltoid crest of the humerus (measured from the proximal surface of the head of the humerus); UL, ulna length, OL, olecranon length (measured from the proximal surface of the trochlear notch).

prominent deltoid crest is long, ending about 19 mm from the proximal end of the humerus—over half the length of the bone (56%), similar to other *Rhizomys* (table 2). For example, the larger humerus of AMNH 113477 is 47.2 mm long with deltoid crest length of 26.1 mm, 55% its length; its epicondylar width is 14.1 mm, proportionally somewhat less than F:AM 117337. The humerus of *R. troglodytes* AMNH 18407, nearly twice as long as that of *R. shansius*, has a deltoid crest ratio of 63%.

The hind limb is represented by a right distal femur fragment with total condyle width of 11.1 mm. An associated right tibia is missing its epiphyses. The tibia diaphysis is 34 mm long and relatively slender. The scar for the distal portion of the fibula begins 9 mm from the distal end of the diaphysis. Other elements include a proximal phalanx 8.5 mm long.

The forelimb of F:AM 117337 is clearly modified for burrowing, the ulna having a large olecranon process and strong supinator crest, and the slightly twisted humerus having a heavy deltoid crest and wide epicondyles. Epicondyle width, deltoid crest development, and prominence of the oleceranon process are developed as in the living rhizomyines *Rhizomys, Cannomys,* and *Tachyoryctes* (table 2). *Spalax* is similar, although its olecranon process is relatively longer. All of these observations appear to be independent of

absolute size, as judged from total humerus length, and the features are consistent with burrowing, particularly for rodents that do not rely solely on the forelimbs, but are primarily chisel-tooth diggers. However, the humerus and ulna of zokors, which depend mainly on the forelimb for digging, are strikingly modified. Zokor humeri have prominent deltoid crests that project distinctly from the shaft, and exceedingly broad epicondyles; a tranverse axis through them is angled with respect to the head of the shaft. Humerus width through the epicondyles is nearly half the total length. The olecranon process is long, 42% of ulna length in MCZ 19896, and with a massive proximal tubercle located medially. The forelimbs of zokors show strong adaptations for burrowing, since at least the Late Miocene.

DISCUSSION: Teilhard de Chardin (1942) based his taxon *Brachyrhizomys shansius* on several mandibular fragments from Yushe Basin. Scholars at the Institute of Vertebrate Paleontology and Paleoanthropology determined that the Tianjin collection dentary 31.096 is the type specimen. Its provenance is ''Pre-Villafranchian Pliocene beds of Yushe'' (Teilhard de Chardin, 1942). Of all known specimens, only F:AM 117337 and a few collected in recent years have good stratigraphic provenance. All are mid-Pliocene in age. Teilhard de Chardin (1942) noted the long diastema and corresponding proodonty

of the incisors, although he determined this without the benefit of a skull to observe! He was also impressed by the lower crown height, hence the name *Brachyrhizomys*. In reality, *Brachyrhizomys* specimens including F:AM 117337 are high crowned, although not hypsodont and not as high crowned as living *Rhizomys*. This feature plus those noted above distinguish *Brachyrhizomys* from living species, but they are largely (if not completely) primitive conditions for *Rhizomys*. F:AM 117337 shows, on the other hand, that *Brachyrhizomys shansius* shares many important derived features with living *Rhizomys*. Fundamental is the infraorbital foramen confined to a high position and without ventral slit—it is sealed ventrally by anterior expansion of the deep masseter. *Brachyrhizomys* shares a high skull profile with *Rhizomys* and other features of the basicranium and palate, plus traits related to burrowing.

Because it is closely related to living *Rhizomys* species, but distinct, *Brachyrhizomys shansius* is treated appropriately as a subgenus within *Rhizomys*. Living forms are all relatively close, distinguished by shared advanced features, and I classify them as *Rhizomys (Rhizomys)*. Features distinguishing *Rhizomys (Rhizomys)* are correlated with the more elevated cranium, which yields dorsoventrally extended orbital structures and a high occiput. The occiput is further exaggerated as a large flat surface area for attachment of musculature used in burrowing.

Among the dozen or so named forms of extant *Rhizomys* (mostly subspecies), systematists consistently recognize three species, *R. pruinosus*, *R. sinensis*, and the larger *R. sumatrensis*. Wang (2003) adds *R. wardi* at the species level. Dental morphology perhaps distinguishes some of the subspecies, for example, the large M3 of *Rhizomys sinensis vestitutus*. *R. shansius* is about the size of small individuals of *R. pruinosus* or *R. sinensis*, but its features do not argue for special affinity with any living species (its M3 size is moderate, judgment made difficult by incomplete eruption). Some authors have placed the large species *R. sumatrensis* in its own subgenus *Nyctocleptes*, but Musser and Carleton (2005) do not follow this; distinctions of this species are largely allometric.

There are also named forms of *Rhizomys* from the Pleistocene fossil record of China. All of these are clearly modern in grade, some assignable to living species, and all can be classified as *Rhizomys (Rhizomys)*. *Rhizomys troglodytes* is like living *R. sinensis* in size, and was compared with the latter by Matthew and Granger (1923). *R. ultimus* Young and Liu (1950) was synonymized with *R. sinensis* by Zheng (1993). Zheng (1993, 2004) conserved *R. troglodytes* and added the small form *Rhizomys brachyrhizomysoides* as extinct bamboo rats from eastern Sichuan Province and from Hubei Province. Wei et al. (2004) named *Rhizomys fanchangensis* from Anhui Province, assigning it to the living genus based on similar dentition, which is consistent with incisor orthodonty of the fossil material. This oldest described *Rhizomys (Rhizomys)* dates to the early Matuyama magnetic chron, greater than 2 Ma.

Brachyrhizomys shansius is known for remains from Yushe Basin. The species name is applied by Zheng (1993) to fossils said to be from the Zhoukoudian Cap Travertine, but I have not seen these specimens. The Yushe fossils are all Pliocene in age. Flynn (1993) added a new, small species to the Yushe fossil record, *Rhizomys (Brachyrhizomys) shajius*, based on a single dentary from Late Miocene deposits. Like *B. shansius*, this species is primitive in its unshortened diastema, moderate crown height, m2 longer than wide, and termination of the masseteric crest under m1 (not more anteriorly). A recalibrated paleomagnetic age for *Brachyrhizomys shajius* is 5.9 Ma. This species is significantly older than *B. shansius* and much smaller (estimated m1–m3 length, 9.3 mm).

Flynn (1982) applied the name *Brachyrhizomys* to large, fossorial bamboo rats from the Siwalik deposits of the Indian subcontinent. The several Siwalik species share a number of features with *B. shansius* (and living *Rhizomys*), and are distinct from other large fossil bamboo rats, such as *Rhizomyides sivalensis*. However, the Late Miocene Rhizomyini, as exemplified by GSP 8362 (Flynn, 1982, pl. 2), do not show the derived closure of the ventral slit of the infraorbital foramen of *B. shansius*. Also, GSP 8362 is a low skull and not as broad and wedge shaped as

AMNH 117337. These Siwalik bamboo rats and Miocene age representatives from southern China cannot be maintained in the taxon *Brachyrhizomys*, and require a new generic level name.

Miorhizomys, new genus

TYPE SPECIES: *Miorhizomys nagrii* (Hinton, 1933); illustrated in Flynn (1982).

INCLUDED SPECIES: *Miorhizomys blacki* (Flynn, 1982), *Miorhizomys choristos* (Flynn, 1982), *Miorhizomys harii* (Prasad, 1968), *Miorhizomys micrus* (Flynn, 1982), *Miorhizomys nagrii* (Hinton, 1933), *Miorhizomys pilgrimi* (Hinton, 1933), *Miorhizomys tetracharax* (Flynn, 1982).

DIAGNOSIS: (after Flynn, 1982, characteristics for ''*Brachyrhizomys,*'' which were drawn mainly from these fossil species) Rhizomyini with moderately deep dentaries and a masseteric crest lacking a strong anterior extension, lower crest not inflated; lower incisor usually with flattened enamel and no median ridge; molars relatively small and of moderate crown height, with unilateral hypsodonty; M1 rounded anteriorly, without anterolingual flexus; m3 with small posterolingual enamel lake and often a deep buccal reentrant; incomplete closure of ventral slit of the infraorbital foramen; pronounced fossorial adaptations. In addition, *Miorhizomys* shows low elevation of the skull, m2 with three roots and strong mesolophid, and a longitudinal connection (mure) on m2 and m3.

AGE AND GEOGRAPHIC RANGE: Late Miocene of southern Asia, from Pakistan to Yunnan.

ETYMOLOGY: *Mio-* (prefix derived from the epoch during which this bamboo rat genus thrived) plus *rhizomys* (''root rat'').

DISCUSSION: *Miorhizomys* is a rhizomyine genus showing fossorial adaptations, but is not as derived as either *Rhizomys* or *Cannomys*. The Siwalik fossil genus *Rhizomyides* Bohlin, 1946, is a large tachyoryctine, and more distantly related. *Anepsirhizomys* Flynn, 1982, is another large genus of unclear affinity to which Flynn (1990) transferred the species *A. pinjoricus* (Hinton, 1933). *Miorhizomys* shows remarkable diversity shortly after its appearance in the fossil record of the Indian subcontinent. Oldest records date to about 9.6 Ma, with age of actual appearance likely to be no greater than 9.9 Ma (Barry et al., 2002). By about 9 Ma, four species were present. The genus continued to be diverse through at least 8 Ma, probably later, and is well represented in the Late Miocene of northern India. Flynn (1985) pointed out that high diversity and cladogenesis are not unexpected for a fossorial rodent. Flynn and Qi (1982) noted broad distribution of rhizomyines across southern Asia into Southeast Asia, and cited some of the same species at Lufeng, Yunnan Province, as in the Siwaliks. Recent reexamination of original, large samples of the Lufeng material (personal observation) confirms that the Lufeng species are very close to, but not all identical with the Siwalik species. They are certainly congeneric.

Tribe Rhizomyini, all members of which show fossorial adaptations, appeared during Late Miocene time around 10 Ma. The early genus *Miorhizomys* ranged throughout southern Asia, from Pakistan to Yunnan, and was successful as measured by high species richness. The species of *Miorhizomys* are the ecological precursors to modern *Rhizomys*, which appeared about 6 Ma in China and became established during the Pliocene. Given late fossil occurrences for a group considered to be of remote common ancestry with other muroids (Steppan et al., 2004; Jansa and Weksler, 2004), it is important to review the record of older rats potentially related to them.

KEY CONSTRAINTS FROM THE FOSSIL RECORD

As so eloquently stated by Musser and Carleton (2005, above) the fossorial habits of *Rhizomys*, *Spalax,* and *Myospalax* have led to skeletal modifications that overprint the features primitively characterizing each clade. The similar adaptations across the genera, but lack of these in early members of each clade, makes diagnosis of rhizomyines, spalacines, and myospalacines difficult. Review of the fossils attributed to each group places in context not only the antiquity of each, but allows a judgment of the likelihood of their interrelationships and focuses on any direct

evidence for burrowing adaptations in these lineages. The analysis below suggests that each group acquired full fossoriality independently.

SUBFAMILY RHIZOMYINAE

Flynn (1982) revised knowledge of the evolution of rhizomyines, benefiting from a greatly expanded fossil record, primarily from the Siwaliks of Pakistan. His diagnosis for the higher taxon (his Family Rhizomyidae) including extant *Rhizomys*, *Cannomys,* and *Tachyoryctes* noted the muroid condition of three cheek teeth, the advanced muroid condition of myomorphy, proodonty (some forms orthodont), lophodonty (transverse crests as high as cusps), and differential hypsodonty, with upper molars markedly higher crowned internally than externally. There is also a strong molar wear gradient in all rhizomyines: first molars are always much more worn than posterior molars. Musser and Carleton (2005) cautiously regard *Tachyoryctes* as potentially independent of *Rhizomys* and *Cannomys.* However, some South Asian fossils, such as *Eicooryctes* argue that tachyoryctines were widespread in the Late Miocene (Flynn, 1982), and not an independent African group.

MORPHOLOGY: An important feature in tracing the evolution of muroids is the character state of the anterior part of the zygomatic arch, and the muscle scar of the masseter. In hystricomorphs, the deep part of the masseter penetrates the enlarged infraorbital foramen and originates on the snout; the lateral part of the masseter is confined to the ventral border of the arch. Muroids show progressive myomorphy in which the lateral masseter extends anteriorly on an expanded zygomatic plate. This plate rises anteriorly, constricting the infraorbital foramen ventrally, but leaving a slit behind. Advanced myomorphs extend the origin of the lateral masseter anteriorly by adding a projecting flange onto the plate. Lindsay (1977) hypothesized gradational transformation of hystricomorphy to myomorphy in muroids, early taxa (Oligocene) being hystricomorphous (barely any expansion of the lateral masseter

origination) or showing low inclination of the zygomatic plate.

Flynn et al. (1985) found rhizomyines to cluster among derived muroids in their myomorphy—they were not a part of the early radiation of muroids that were typically hystricomorphous. The myomorphous condition of Rhizomyinae is modified further with respect to many living muroids by a degree of closure of the ventral part of the keyhole-shaped infraorbital foramen. In later rhizomyini, the ventral notch of the keyhole opening is totally eliminated, leaving only a dorsal hole in *Rhizomys* and *Cannomys* (autapomorphy for this pair of genera). Less modified rhizomyines are represented by *Tachyoryctes* and 9 Ma *Miorhizomys* and *Kanisamys*, which show abbreviated ventral notches. These taxa can be reinterpreted as showing an early stage in the transformation of myomorphy from hystricomorphy, while *Rhizomys* and *Cannomys* show secondarily reduced myomorphy. They are a product of muroid evolution at a time when the myomorphous condition had not reached full development of an expanded, high-angle zygomatic plate with deep ventral slit.

Rhizomyinae are derived with respect to many Paleogene muroids in loss of the archaic posterior connection of the protoconid and metaconid on m1. The posterior connection runs directly from the protoconid, or from its posterior arm, transversely to the metaconid. Early rhizomyines may display an ephemeral posterior connection, but also lack an anterior connection. A firm connection of the anterior arm of the protoconid to the metaconid developed in later *Kanisamys* (Flynn, 1982) in parallel to that trend in other Miocene muroids. This observation agrees with the early stage of myomorphy in plotting rhizomyines among derived, but not modern muroids.

Rhizomyines possess persistent longitudinal ornamentation on the enamel of the lower incisor. As in many late Oligocene to Early Miocene muroids, a double ridge occurs on the incisor in early species. By the Late Miocene this is a single ridge, which persists throughout Tribe Tachyoryctini. This condition is transformed again in Tribe Rhizomyini in which ridges are totally absent.

These features imply origin of rhizomyines (and spalacids in general) from Late Oligocene muroids that already displayed a degree of myomorphy, suppression of the archaic posterior connection between metaconid and protoconid of m1, and the then widespread occurrence of persistent ridges along the midline of the enamel of the lower incisor. Muridae and Cricetidae are Miocene derivatives of a more advanced stock of muroids.

FOSSIL RECORD: The Siwalik Group deposits, primarily in Pakistan, contain a relatively complete series of bamboo rat fossils, filling the gap between standard muroids and living rhizomyines. Small Miocene species of the genera *Prokanisamys* and *Kanisamys* are abundantly preserved in successive horizons spanning > 20 to 8 Ma (de Bruijn et al., 1981; Flynn, 1986; Wessels and de Bruijn, 2001). Postcrania show that these species were not obligate fossorial rodents. There are some digging modifications in the humerus of *Kanisamys sivalensis* (about 9 Ma), but they are not striking. In contrast, beginning after 10 Ma, other large-body species do show fossorial adaptations in the skull and forelimb. These have been gathered under the names *Rhizomyides* and "*Brachyrhizomys*" (now *Miorhizomys*). Flynn (1985) saw the Late Miocene species-rich pattern of occurrence of large-bodied *Miorhizomys* as consistent with fossorial lifestyle (underground habitus promoting isolation and splitting). Apparently, bamboo rats were initially terrestrial scratch diggers; commitment to subterranean life came later and independently in different groups.

The fossil record of rhizomyines is substantially older than the first evidence for fossoriality, but just how old is this lineage? The emerging pre-Siwalik fossil record shows greater antiquity for the group than previously in evidence. Lindsay (1996) described the oldest rodent attributable at present to the bamboo rat lineage. Under the name *Eumyarion kowalskii* (in earlier works he mentioned this as an unnamed species of *Eucricetodon*), he showed the beginnings of the lophodont rhizomyine dentition, modified from the basic cricetid plan, and preserving, variably, the archaic posterior connection between protoconid and metaconid on the m1. Its elevated crown height is barely advanced over that of typical muroids. The studied sample is from the Zinda Pir Dome, western Pakistan, locality Z113. Isolated incisors from Z113 show a double ridge on the enamel. The age of this site is demonstrably younger than the classic Bugti Oligocene sites of Paali Nala (Welcomme et al., 1999) and Z108 and Y417 (Flynn and Cheema, 1994), and older than Early Miocene sites in the area. Analysis of the magnetic polarity stratigraphy of the Zinda Pir Dome (Lindsay et al., 2005) allows two reasonable correlations to the geomagnetic polarity time scale, which place the site at about 24 or 27 Ma (near the Oligocene-Miocene boundary or during the Late Oligocene). Thus, the oldest rhizomyines appear to antedate other spalacid muroids.

SUBFAMILY SPALACINAE

In summarizing the spalacine fossil record, Ünay (1999) noted that rhizomyines, spalacines and other lineages of burrowers appear to be distinctive throughout most of their histories, at least in dental characteristics (fig. 5), although all converge in adaptations to fossorial lifestyle. Potapova and Vorontsov (2004) agreed and noted convergence in auditory structures correlated with subterranean life. Paleontologists, therefore, have considered the spalacines to be distinct at the family level from other muroid groups. Three morphological features have tended to support the apparently remote ancestry of *Spalax*: (1) The expanded infraorbital foramen is round (but not reduced and dorsal in position) and lacks an inclined myomorphous zygomatic plate; the lateral masseter origin is clearly defined, but restricted to the ventral border of the zygoma, close to the condition seen in hystricomorphs. (2) The lower first molar lacks the anteriorly placed connection between the protoconid and metaconid (the posterior metalophid is generally lost as well). (3) The lower incisor shows very weak if any longitudinal ornamentation, unlike most Late Oligocene–Miocene muroids. Given the data then at hand, Flynn et al. (1985) concluded that spalacines were of ancient origin from hystricomorphous muroids that lacked advanced molar structure and incisor ridges. It
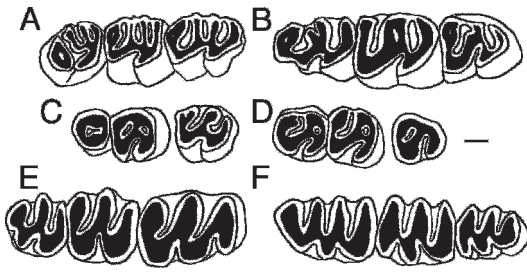
Fig. 5. Comparisons of upper and lower molars of a generalized rhizomyine (A, B), spalacine (C, D), and myospalacine (E, F). Molar rows are composites of fossils, except E and F, which are associated. Seen left to right, A (right M3 to M1) and B (left m1 to m3) are based on *Kanisamys sivalensis* from Flynn (1982). C (worn right M3–M2 and separate M1) and D (left m1 and m2 and worn m3) are based on *Pliospalax macoveii* from Şen (1977). E (right M3 to M1) and F (left m1 to m3) are based on *Mesosiphneus praetingi* from Teilhard de Chardin (1942). Scale is 1 mm.

appeared that rhizomyines were more derived in these features.

The spalacines have a modern distribution from the Mediterranean area throughout eastern Europe to western Asia, with extinct species of *Spalax* and *Pliospalax* recorded widely in Eurasia, but not the Far East. The fossil record is Early Miocene and younger. The Oligocene *Rhizospalax* is a beaver (Hugueney and Mein, 1993). The late Early Miocene *Heramys* Klein Hofmeijer and de Bruijn (1985) shows several spalacine features (lophodonty, high molar crowns, loss of metalophid on m1), but retains a large m3. Ünay (1996) added to the fossil record the more primitive, lower-crowned genus *Debruijnia*, which shows a variable metalophid connection on m1. The age of the earliest species of this genus is ca. 20 Ma. Neither *Heramys* nor *Debruijnia* indicate fossoriality, but postcrania are unknown.

Sarica and Şen (2003) added key fossil remains from the early Late Miocene Sinap Formation of Turkey. These revealed important anatomical details of spalacines in the 11 to 9 Ma age range. Sarica and Şen (2003) named *Sinapospalax* for an array of species that share robust dentaries, lophodont molars, and incisors bearing multiple

longitudinal ridges. *Sinapospalax* showed that ridges were indeed present on early spalacine incisors. Further, the robust dentaries suggest that these muroids were proodont burrowers.

Generally considered separate but closely related are the extinct anomalomyines, characterized primarily by *Anomalomys* and *Prospalax* (Fejfar, 1972). These have a similar age range as spalacines, but are confined to Europe. Bolliger (1999) reviewed the group and noted the presumed fossorial habitus of later species. Following de Bruijn and Saraç (1991), he further drew comparison to the Early Miocene muroid *Eumyarion*, based on molar similarities and the double ridge of enamel along the length of the lower incisor. *Eumyarion* is known from the Early Miocene of Turkey (Ünay-Bayraktar, 1989), as well as Pakistan (above), older than *Anomalomys* or *Debruijnia*. If anomalomyines and spalacines are closely related, Late Oligocene origin of this group would be probable.

Despite the projected Oligocene origin for spalacines and their apparently primitive morphology, the oldest clear spalacine fossils are younger than the earliest rhizomyines. Still, given that spalacines and *Anomalomys* may share common ancestry with a morphotype resembling *Eumyarion*, one can hypothesize close relationship to the earliest rhizomyines, a hypothesis consistent with molecular data. The features of early spalacines are now better known, and may be reinterpreted as similar to those of early rhizomyines, not more primitive. Early members of both groups show enamel ornamentation and similar m1 morphology. The undeveloped zygomatic plate of *Spalax* and *Pliospalax*, possibly a reversal, does differ from the stronger plate of early rhizomyines.

Skull and postcranial remains, rare before the Late Miocene, show that *Pliospalax* was an active burrower (Şen, 1977). The robust, proodont dentary of *Sinapospalax* also suggests burrowing. However, there is no evidence for fossoriality in early spalacines, and the conservative dentitions of *Heramys* and *Debruijnia* suggest that these were not obligate burrowers. Present evidence indicates independent acquisition by the early

Late Miocene of the subterranean lifestyle in rhizomyines and spalacines.

SUBFAMILY MYOSPALACINAE

Whereas spalacines and anomalomyines are European-Mediterranean and western Asian rodents, and rhizomyines are primarily South Asian–East African, myospalacines (zokors) are common eastern Asian burrowers, typical of much of northern China and Mongolia and ranging into southern Siberia, the Altai Mountains, and eastern Kazakhstan. Living species, up to about 250 grams in body mass, are highly derived subterranean small mammals that dig with their forelimbs (Nevo, 1999). They have adopted, therefore, a different strategy than rhizomyines and spalacines, which utilize the incisors extensively in burrowing.

Living myospalacines comprise at least seven species (Musser and Carleton, 2005), which can be assigned to two genera, *Myospalax* and *Eospalax*. The fossil record of myospalacines in China is extraordinarily rich, and appears to show geographic differences, with different species as contemporaries in eastern and central China. Most researchers acknowledge broad morphological diversity among the array of fossil zokor species. Zheng (1997) recently rearticulated his rationale for diagnoses of generic and higher level groupings (here, tribes). In Prosiphneini Leroy, 1940, he groups *Prosiphneus* Teilhard, 1926, *Myotalpavus* Miller, 1927, *Pliosiphneus* Zheng, 1994, *Eospalax* Allen, 1938, *Allosiphneus* Kretzoi, 1961; in Mesosiphneini Zheng, 1994, he places *Chardina* Zheng, 1994, *Mesosiphneus* Kretzoi, 1961, *Yangia* Zheng, 1997 (= *Youngia* Zheng, 1994); in Myospalacini Lilljeborg, 1866, are *Episiphneus* Kretzoi, 1961, and *Myospalax*, Laxmann, 1769. This diversity reflects a high degree of cladogenesis, likely promoted by isolating mechanisms correlated with solitary lifestyle and small home ranges.

Structural characteristics of myospalacines include a zygoma interpreted as myomorphous, although the infraorbital foramen is not strongly keyhole shaped and the zygomatic plate is not expansive or greatly inclined, a forelimb highly derived for burrowing, and superficially prismatic molars. It is clear that their prismatic (*omega form* is a better term used by Carleton and Musser, 1984) condition is derived convergently with respect to the much more complex molar shapes of arvicolines. The lower first molar presents an anterior connection between the anterior arm of the protoconid and the metaconid, which appears to be the derived muroid condition. It could have been constructed independently, much the same way as it developed in rhizomyines. Also like earlier rhizomyines and various muroids, the lower incisor is always characterized by a single longitudinal ridge. These morphological features suggest that myospalacines evolved from later muroids more derived than the ancestral stock for spalacines.

The fossil record demonstrates rapid diversification of zokors, with most of the splitting during the past 10 million years. The oldest species attributed to early *Prosiphneus* date to over 11 Ma according to Zheng et al. (2004). As research has developed in China, scientists have traced the origin of the myospalacines to the Middle Miocene muroids *Plesiodipus* Young, 1927, or *Gobicricetodon* Qiu, 1996, both in excess of 12 Ma (see Wang et al., 2003). It seems logical to transfer these genera to the Myospalacinae. However, *Plesiodipus* is comparable to generalized cricetids, the family in which Qiu (1996) classifies it, and *Gobicricetodon* is low crowned, although robust. Probably these earliest myospalacines were not truly fossorial. More likely, myospalacines acquired fossoriality independently about 11 Ma, an independence consistent with characteristic forelimb-digging in contrast to chisel-tooth digging in rhizomyines and spalacines.

Conclusions based on morphology and the fossil record are: (1) Zokors show derived features (myomorphy, anterior metaconid-protoconid connection, incisor ridge) suggesting derivation from Miocene muroids. (2) Zokors evolved forelimb burrowing independently about the beginning of the Late Miocene. (3) Zokor origin appears to be Middle Miocene; the common ancestor of *Myospalax* and *Spalax* must be much older than the known range of myospalacines, and more basal among murids. The Middle Miocene zokor origin conflicts with a Plio-

cene estimate by Michaux and Catzeflis (2000). Norris et al. (2004) discounted a Pliocene split based on molecular grounds, and found that mitochondrial genes place *Myospalax* basal to *Spalax* and *Rhizomys*. Jansa and Weksler (2004) reanalyzed the von Willebrand Factor (vWF) gene results of Michaux and Catzeflis (2000) and also placed *Myospalax* outside the other spalacids. However, a maximum-likelihood analysis of the first exon of the IRBP gene placed *Myospalax* somewhat closer to rhizomyines (Jansa and Weksler, 2004) and showed that the geometry of the three taxa is not yet understood robustly. A monophyletic relationship with *Spalax* and *Rhizomys,* in which *Myospalax* is the most basal form, is unexpected from morphology and the fossil record. This relationship disrupts character distributions and calls for a zokor lineage back to the end of the Oligocene, which is nowhere in evidence. As noted below, nesting of zokors within Miocene rhizomyines seems more conceivable.

OTHER CHINESE FOSSIL MUROIDS

The enigmatic *Pararhizomys* and *Tachyoryctoides* have been implicated in the evolution of bamboo rats. *Pararhizomys hipparionum* is a Late Miocene species from Mongolia and North China that presents rhizomyine-like features with some exceptions. Dentition is lophodont and rather high crowned, and skull material shows modified myomorphy (reduced ventral slit of the infraorbital foramen), as in late Neogene rhizomyines. Unlike rhizomyines the molar wear gradient is even (not markedly stronger anteriorly). Unlike most rhizomyines but like spalacines, third molars are reduced, and m1 lacks a metalophid. The lower second molar has two buccal reentrants, the anterior one bounded by a strong buccal extension of the anterolophid. This buccal anterolophid is normally suppressed in rhizomyines, but present in early species, and conserved in myospalacines. Unlike *Rhizomys* but like *Tachyoryctes*, the near-flat incisor of *Pararhizomys* shows a single longitudinal ridge. Myospalacines conserve the ridge as well. The skull of *Pararhizomys* is strongly built, but not wedge shaped like a committed

fossorial rodent. It is rather low and elongate (Kowalski, 1968), comparable perhaps to that of a small *Marmota*.

Pararhizomys is known from several Late Miocene sites of North China (Zhang et al., 2005). The genus may also be recorded from the Late Miocene of Tibet. *Brachyrhizomys hehoensis* Zheng, 1980, from Biru, Bulong Basin, is unusual for rhizomyines (small m3, even molar wear) and may be a member of the genus *Pararhizomys* (Jacobs et al., 1985).

Zhang et al. (2005) evaluated proposed *Pararhizomys* relationships to rhizomyines, spalacines, myospalacines, and tachyoryctoidines, and found two most probable scenarios: *Pararhizomys* is a primitive rhizomyine or a derivative of independent early muroid origin. I cannot improve on this suggestion at present other than to emphasize that if *Pararhizomys* is a rhizomyine, it is not closely related to living bamboo rats. The odd m2 reentrant and retention of the incisor ridge would be primitive structures modified in Rhizomyini. The elevated molar crown height reminiscent of spalacines and Tribe Tachyoryctini likely evolved independently. In building a hypothesis of sister-taxon status for spalacines and rhizomyines, it is conceivable to include *Pararhizomys* as a member of that clade, outside Tribe Rhizomyini. Further, if myospalacines are indeed part of the spalacine-rhizomyine radiation, then *Pararhizomys* could root close to the origin of Myospalacinae, possibly among Middle Miocene rhizomyines.

Oligocene to Early Miocene *Tachyoryctoides* shows no special features to align it with either rhizomyines or spalacines. Its characteristics illustrate primitive muroid features. The cheek teeth are rather low crowned. The crests are not transformed as sweeping lophs, but rather, in early wear, as thin interconnections with deep reentrants. The primitive muroid buccal arm of the anterolophid is well developed on m2 and m3. Reminiscent of the spalacine condition of m1, there is no direct connection of the protoconid and metaconid. *Tachyoryctoides* has almost no mesolophid on lower molars; upper molars have a very short mesoloph, but are four-crested due to a long posteroloph emanating from the hypocone. In the absence of cranial material, the masseteric

condition may be inferred from the mandible. The masseteric crest is quite heavy, flaring laterally and terminating opposite m2, although a weak portion of the scar extends below m1. Probably a heavy lateral masseter originated from the bottom of the zygoma. The lower incisor is heavy and distinctly flattened, lacking a ridge, but with low thickenings of enamel along both the medial and lateral borders. The chisel-like incisor is consistent with digging, but until postcrania or skull material are described, fossorial adaptation for *Tachyoryctoides* is poorly supported.

Tachyoryctoides is distributed throughout northern China and Mongolia, and westward to the Aral Sea region, as a common component of Oligocene and Early Miocene assemblages. It is thus a contemporary of the basal rhizomyine *Eumyarion kowalskii*. The differences in the structures of these taxa show that *Tachyoryctoides* is not a rhizomyine. Flynn (1982) agreed with Fejfar (1972) that the genus could be a primitive spalacine, but that idea comes from the similar m1 structure. Otherwise, there are no special features shared with *Heramys* or with *Anomalomys*. Consequently, *Tachyoryctoides* is not readily associated with either rhizomyines or spalacines, and at present its sister status with rhizomyines + spalacines cannot be defended.

DISCUSSION

The Tribe Rhizomyini arose late in bamboo rat evolution, after 10 Ma, and all fossil members show burrowing adaptations. Likely their success reflects radiation into the subterranean niche, and exploitation of available underground resources. Early species lack some of the advanced fossorial traits of extant taxa, and cranial fossils demonstrate that they are not assignable to *Rhizomys* or *Cannomys*. The new generic name, *Miorhizomys,* is created for the Late Miocene radiation of subterranean bamboo rats. It is characterized among other features by retaining an abbreviated ventral portion of the myomorphous infraorbital foramen. *Miorhizomys* was distributed across southern Asia from Pakistan in the west to Yunnan Province in the east. The oldest known

Rhizomys is from the Late Miocene of northern China, 5.9 Ma, but the oldest well-represented species is *Rhizomys (Brachyrhizomys) shansius* from the early Pliocene of Yushe Basin, Shanxi Province. Osteological material consisting of the skull and anterior parts of the axial skeleton, parts of both forelimbs, and a partial hindlimb shows that by the Pliocene, Chinese bamboo rats were fully modern with advanced burrowing adaptations and derived skull structure, especially the modified, high and round, infraorbital foramen of living species.

The pattern of evolution of burrowing rodents appears to be linked to opportunities to exploit available subterranean ecological space (Nevo, 1999; Cook et al., 2000). Controlling factors would include availability of underground food sources and quality of the soil (including rockiness and moisture). One hypothesis sees radiation of subterranean rodents and emergence of hominids as phenomena connected to the evolution by plants of underground nutrient-storing organs, which would be highly desirable food sources (Laden and Wrangham, 2005). The data to test these ideas come from the fossil record, and for rodents include constraining the timing of acquisition of fossorial traits across lineages. How muroids, in particular, acquired subterranean lifestyles is relevant to testing whether burrowing evolved in this group due to availability of a new food source. If bamboo rats, the blind mole rat (*Spalax*), and zokors are confamilial (Steppan et al., 2004; Jansa and Weksler, 2004), then early acquisition of burrowing traits might be proposed as a synapomorphy uniting them (Norris et al., 2004). It turns out that the pattern of evolution of fossoriality in these muroids shows late and independent commitment to subterranean lifestyles. Fossorial features cannot be used to define Spalacidae cladistically, and probably evolved in the early Late Miocene to exploit new food sources.

Rhizomyines have the longest known fossil record of the three subfamilies. Early forms (Late Oligocene and younger) clearly were not obligate subterranean dwellers. Full fossoriality appears only after 10 Ma. The known time depth of spalacines rivals that of rhizomyines, but osteological evidence for

burrowing is rather young. Dental remains indicate lack of features, like high-crowned, lophodont teeth, that are correlated with burrowing. In contrast, the known time range of zokors is hardly half of the other groups, and morphological features suggest that zokors represent a later radiation. Middle Miocene zokor species show no evidence of fossoriality, but fossil representatives of the radiation after 11 Ma include humeri modified for burrowing. Independent acquisition of full burrowing adaptations in each muroid group appears to be the pattern. Independence is underscored by the forelimb burrowing in zokors that contrasts with the chisel-tooth digging of bamboo rats and blind mole rats.

Despite independent and divergent means of solving the problems of subterranean life, the three groups may have evolved from generalized muroid scratch-diggers that lived in burrows, but were not fully subterranean. The fossil record should be consistent with such a hypothesis, and is relevant for constraining the timescale of evolution. The oldest known spalacids are Late Oligocene, 27 Ma at most. Under this scenario, the spalacid group would have originated in the Late Oligocene and the three lineages would have adopted fully subterranean lifestyles later, probably not before the Late Miocene.

Given that molecular and morphological data place Spalacidae as a basal group among all other (studied) living muroids, origination dates for all other muroid groups would be younger than 27 Ma, which is a maximum estimate for the earliest known spalacid fossil. A younger, Miocene, age for the appearance of other extant muroid families would be expected.

Herein, morphological features used to evaluate relationships have been reinterpreted given the molecular hypothesis of spalacid monophyly. Impressed by differences between spalacines and rhizomyines, Flynn (1982) had considered the former as primitive and to have originated significantly earlier. The zygoma of *Spalax* was interpreted as hystricomorphous, instead of myomorphous with a weakly inclined plate, the smooth incisor enamel was taken as primitive (not as secondary loss of ornamentation), and molar

lophs were considered underived (which they are, as are early rhizomyines, relative to most Miocene taxa).

The constructive challenge of new molecular data leads to reappraisal of character states, which properly entails a survey of the extant muroids (since spalacids are basal), plus well-known key fossil taxa (appendix 1). This survey makes use of the mammal collections of the AMNH and MCZ and of available casts of fossil material. There are far too few character states for the 400 living and fossil muroid genera to allow informative phylogenetic analysis using parsimony, but a tree can be generated as a testable hypothesis (fig. 6) using the relationships of living families established on molecular grounds. Injecting fossil taxa into a tree generated by molecular data is provocative in stimulating a hard look at both character definition and polarity on the one hand, and assumptions about molecular evolution on the other. It is hoped that this hypothesis will stimulate a deep and extended search for characters and a new survey of fossil taxa to generate a more rigorous test.

A tree (fig. 6) showing both living and fossil groups allows reanalysis of character distributions. Salient morphological features that can be observed on the tree include: early muroids are hystricomorphous and later genera show modifications of the zygoma, including progressive inclination and expansion of the plate, the posterior connection of m1 is lost, followed by construction of an anterior connection, and incisor ornamentation is a conservative feature that appears among muroids and then is lost. Other features of the dentition are overlain on the tree (fig. 6) with polarity proposed by outgroup comparison.

Character states for stem spalacids may be reinterpreted as follows: (1) The common ancestor had a zygomatic structure advanced over hystricomorphy but incompletely myomorphous, with moderately inclined zygomatic plate not defining a narrow ventral slit and without an anteriorly expanded flange. (2) The first lower molar had lost its posterior connection but variably showed a remnant of a protoconid-metaconid bridge, and lacked a new anterior connection. (3) The lower incisor was ornamented with a pair of
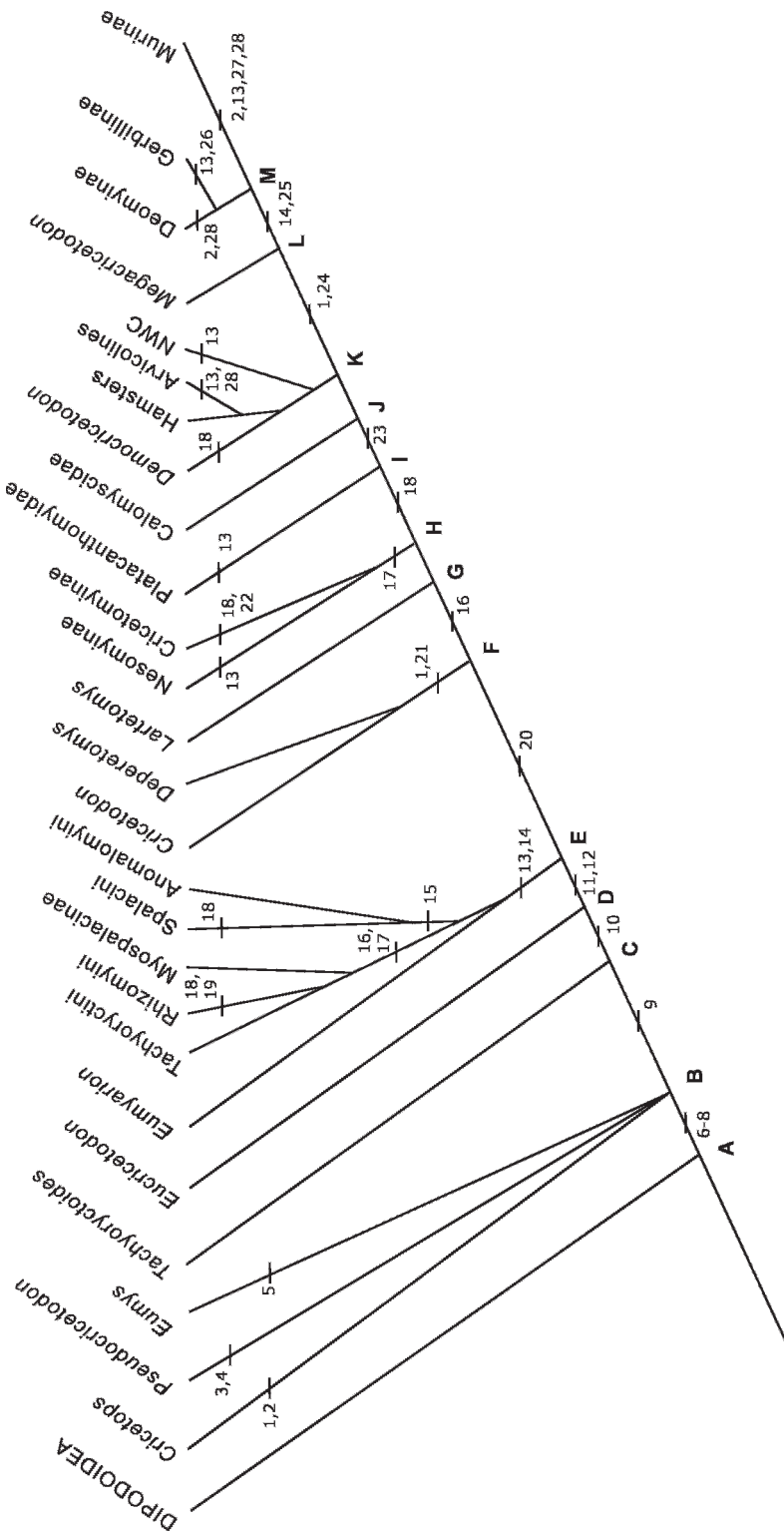
Fig. 6. Phylogenetic tree depicting arrangement of major living groups of muroids plus key fossil taxa, with Dipodoidea as outgroup. This hypothesis depends on molecular data to arrange the living groups, and uses a set of characters (appendix 1) with proposed polarities to plot the fossil taxa. Homoplasy is clear and there are far too few characters to run an analysis based on parsimony. Note that under this analysis, certain higher taxa in occasional usage such as Cricetodontidae need significant revision or abandonment.
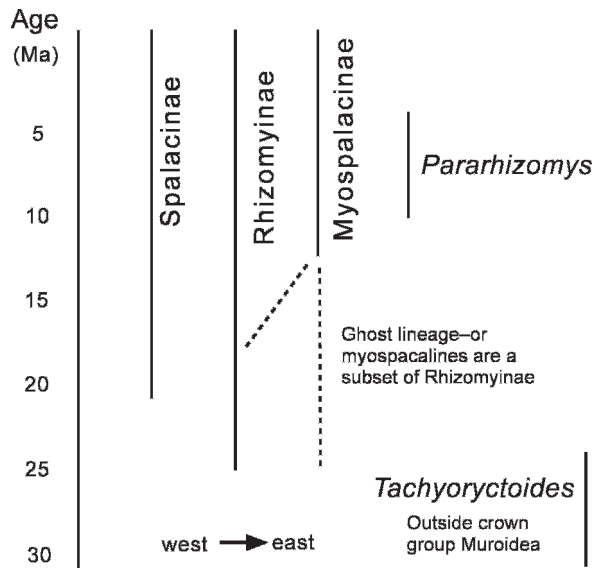
Fig. 7.   Known age ranges of the three spalacid subfamilies and key taxa discussed in the text. These are arranged, west to east, according to geographic range, although rhizomyines extend as far eastward (but to the south) as do myospalacines. Rhizomyinae have the longest known age range. Known myospalacines, beginning with *Gobicricetodon* at about 13 Ma, have a much shorter age range. This implies two hypotheses (dashed): either the group has a long ghost lineage, or it is in fact a derivative (infrafamily) of Subfamily Rhizomyinae. *Pararhizomys* may also be a member of Rhizomyinae. *Tachyoryctoides*, on the other hand, does not show spalacid synapomorphies and is excluded from Spalacidae.

parallel, raised ridges. Later derived transformations included: (1) elimination of the ventral portion of the infraorbital foramen in later rhizomyines, but restriction of the lateral masseter to the zygomatic arch in spalacines, (2) neomorphic establishment of a connection to the metaconid from the anterior arm of the protoconid in rhizomyines and myospalacines, (3) loss of incisor ridges in later spalacines and successive reduction from two to one to none in rhizomyines, a single ridge conserved in myospalacines.

Myospalacines present features derived with respect to stem spalacids, but consistent with earlier rhizomyines. Muroids more derived than spalacids adopt the advanced anterior connection for m1, lose incisor ridges, and progressively build the modern myomorphous zygoma, including a strongly inclined plate, usually with ventral slit, and often expanded anteriorly with a flange to offer greater origination area for the lateral masseter muscle.

The scenario favored here, given molecular constraints that unite these muroids, is that Spalacidae originated during the late Oligo-

cene, and that Spalacinae and Rhizomyinae are sister taxa that split shortly thereafter (fig. 7). Myospalacinae are more derived and a younger group that would be closer to Rhizomyinae than to Spalacinae. Character distributions are most consistent when myospalacines are considered as derived from Early Miocene rhizomyines. This also reduces the apparently long ghost lineage leading to the first zokor fossils (fig. 7). If this hypothesis is maintained, myospalacines may be reconsidered as a taxon of lower rank within Subfamily Rhizomyinae.

Among enigmatic Asian fossil taxa, some may have been part of the spalacid radiation. Possibly *Pararhizomys* from the late Neogene of Mongolia and northern China is an early rhizomyine-zokor derivative. The archaic Asian *Tachyoryctoides*, however, is distinguished as a primitive muroid excluded from Spalacidae.

CONCLUSION

There is irony in the maturing analysis of basal muroid groups. It is those scientists

studying morphology (and paleontologists necessarily emphasize morphology) who conclude independence of bamboo rats, blind mole rats, and zokors, and suspect that similar degrees of fossoriality and the attendant "panoply of adaptations . . . obscure[s] phylogenetic connections" (after Musser and Carleton, 2005). It is molecular biologists (e.g., Jansa and Weksler, 2004; Norris et al., 2004) who indicate that these lineages are actually closely related, and imply shared predisposition to subterranean life. While not falsified by morphology or the fossil record, this scenario is constrained by the distribution of features and by paleontology. There is no evidence for subterranean lifestyle among early members of any of the groups. Each group developed fossoriality in Middle to Late Miocene and younger members, and burrowing features cannot be used to diagnose Spalacidae cladistically. Of the three groups, zokors present more derived conditions in dentition and skull morphology, and they have the shortest fossil record.

The origin and radiation of *Rhizomys* is a late event in muroid evolution. Fossil representatives close to extant species occur throughout much of China and Southeast Asia during the Pleistocene. Early Pliocene fossils show the derived conditions of living *Rhizomys*, especially the ventrally constricted infraorbital foramen and features of the skull and humerus associated with a subterranean mode of life. Skull features are, however, generally less derived than those of living species. The best represented Pliocene bamboo rat is from strata of Yushe Basin, Shanxi Province, dating to around 3.5 Ma, and is distinguished at the subgenus level as *Rhizomys (Brachyrhizomys) shansius*. The oldest known *Rhizomys* at 5.9 Ma is also from Yushe. Earlier during the Late Miocene, more primitive bamboo rats were distributed across southern Asia, from Pakistan to Yunnan. Diverse species, many gathered under the new name *Miorhizomys,* show fossorial characteristics but are less derived than *Rhizomys*. Still older nonfossorial Rhizomyinae can be traced to the late Oligocene cricetid-like species *Eumyarion kowalskii*.

Molecular data strongly argue for closer relationships of Spalacinae, Rhizomyinae, and Myospalacinae with each other than with any other living muroids, but do not yet demonstrate which two of the three subfamilies are most closely related. Morphology and the fossil record appear to argue against myospalacines being more basal than the others. Zokors share more features with Rhizomyinae than with Spalacinae, but are not part of the modern bamboo rat tribe. It is reasonable to consider zokors and fossil *Pararhizomys* as derivatives of early rhizomyine evolution.

It is important to continue testing the hypothesis of monophyly of *Spalax + Rhizomys + Myospalax*. More genetic evidence is likely to clarify the interrelationships of the three taxa from a molecular point of view. This will help to focus reanalysis of polarity of morphological features and the pattern of evolution of these structures. Clearly the demands of a fossorial lifestyle encourage morphological convergence. Could the evolution of some molecules be channeled by selection? Studying more genes is welcome, but also expanding the data set to capture other distantly related burrowing muroids might help. *Ellobius* is perhaps the most fossorial of several burrowing arvicolines, and based on morphology, would not group with spalacids. Inclusion of this and other taxa in the muroid genetic sampling serves as a test of observed relationships. It is the integration of molecular, morphological, and natural history data, and continual testing of hypotheses of relationship and pattern of evolution that promise to advance understanding of the course of muroid evolution. This is what Guy Musser knows so well.

ACKNOWLEDGMENTS

sion of molecular data. Michèle Morgan, Alexa Weingarden, John Barry, and David Pilbeam of the Peabody Museum at Harvard, provided vigorous discussions of various aspects of this work. Reviewers Louis Jacobs and Şevket Şen offered constructive comments that improved the manuscript. Many thanks to Rob Voss and Mary Knight for their help and patience.

REFERENCES

Allen, G.M. 1938. The mammals of China and Mongolia. Natural History of Central Asia, vol. 11 (1): 1–620. New York: American Museum of Natural History.

Barry, J.C., M.E. Morgan, L.J. Flynn, D. Pilbeam, A.K. Behrensmeyer, S.M. Raza, I.A. Khan, C. Badgley, J. Hicks, and J. Kelley. 2002. Faunal and environmental change in the Late Miocene Siwaliks of northern Pakistan. Paleobiology Memoirs 3, Suppl. 28:1–71.

Black, C.C. 1972. Review of fossil rodents from the Neogene Siwalik Beds of India and Pakistan. Palaeontology 15 (2): 238–266.

Bohlin, B. 1946. The fossil mammals from the Tertiary deposit of Taben-buluk, western Kansu. Part II: Simplicidentata, Carnivora, Artiodactyla, Perissodactyla, and Primates. Sino-Swedish Expedition Publication 28, 6 (4): 1–259, 9 pls.

Bolliger, T. 1999. Family Anomalomyidae. *In* G.E. Rössner and K. Heissig (editors), The Miocene Land Mammals of Europe: 389–394. München: Verlag Dr. Friederich Pfeil.

Cande, S.C., and D.V. Kent. 1995. Revised calibration of the geomagnetic polarity time-scale for the Late Cretaceous and Cenozoic. Journal of Geophysical Research 100B: 6093–6095.

Carleton, M.D., and G.G. Musser. 1984. Muroid rodents. *In* S. Anderson and J.K. Jones, Jr (editors), Orders and families of Recent mammals of the world: 289–379. New York: Wiley.

Cook, J.A., E.P. Lessa, and E.H. Hadly. 2000. Paleontology, phylogenetic patterns, and macroevolutionary processes in uubterranean rodents. *In* E.A. Lacey, J.L. Patton, and G.N. Cameron (editors), Life underground: the biology of subterranean rodents: 332–369. Chicago: University of Chicago Press.

de Bruijn, H., and G. Saraç. 1991. Early Miocene rodent faunas from the eastern Mediterranean area. Part 1. The genus *Eumyarion*. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 94 (1): 1–36.

de Bruijn, H., S. Taseer Hussain, and J.J.M. Leinders. 1981. Fossil rodents from the Murree formation near Banda Daud Shah, Kohat, Pakistan. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B Physical Sciences, 84: 71–99.

Fejfar, O. 1972. Ein Neuer Vertreter der Gattung *Anomalomys* Gaillard, 1900 (Rodentia, Mammalia) aus dem europäischen Miozän (Karpat). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 141 (2): 168–193.

Flynn, L.J. 1982. Systematic revision of Siwalik Rhizomyidae (Rodentia). Géobios 15: 327–389.

Flynn, L.J. 1985. Evolutionary patterns and rates in Siwalik Rhizomyidae. Acta Zoologica Fennica 170: 141–144.

Flynn, L.J. 1986. Species longevity, stasis, and stairsteps in rhizomyid rodents. *In* K.M. Flanagan and J.A. Lillegraven (editors), Vertebrates, phylogeny, and philosophy (Contributions to Geology Special Paper 3): 273–285. Laramie: University of Wyoming.

Flynn, L.J. 1990. The natural history of rhizomyid rodents. *In* E. Nevo and O.A. Reig (editors), Evolution of subterranean mammals at the organismal and molecular levels: 155–183. New York: Wiley-Liss.

Flynn, L.J. 1993. A new bamboo rat from the Late Miocene of Yushe Basin. Vertebrata Palasiatica 31: 95–101.

Flynn, L.J., and I.U. Cheema. 1994. Baluchimyine rodents from the Zinda Pir Dome, western Pakistan: systematic and biochronologic implications. *In* Y. Tomida, C. Li, and T. Setoguchi (editors), Rodent and lagomorph families of Asian origins and diversification. Tokyo National Science Museum Monograph 8: 115–129.

Flynn, L.J., L.L. Jacobs, and E.H. Lindsay. 1985. Problems in muroid phylogeny. *In* W.P. Luckett and J.L. Hartenberger (editors), Evolutionary relationships among rodents: a multidisciplinary analysis: 589–616. New York: Plenum.

Flynn, L.J., and G. Qi. 1982. Age of the Lufeng, China, hominoid locality. Nature 298: 746–747.

Gray, J.R. 1831. Characters of three new genera, including two new species of Mammalia from China. Proceedings of the Zoological Society of London 1: 94–96.

Hartenberger, J.-L. 1967. Contribution à l'étude de l'anatomie cranienne des rongeurs. I. Principaux types de Cricetodontinés. Palaeovertebrata 1: 47–64.

Hinton, M.A.C. 1933. Diagnoses of new genera and species of rodents from Indian Tertiary deposits. Annals and Magazine of Natural History Series 10, 12: 620–622.

Hugueney, M., and P. Mein. 1993. A comment on the earliest Spalacinae (Rodentia: Muroidea). Journal of Mammalian Evolution 1 (3): 215–223.

Jacobs, L.L., and L.J. Flynn. 2005. Of mice… again: the Siwalik rodent record, murine distribution, and molecular clocks. In D.E. Lieberman, R.J. Smith, and J. Kelley (editors), Interpreting the past, essays on human, primate, and mammal evolution in honor of David Pilbeam: 63–80. Boston: Brill.

Jacobs, L.L., L.J. Flynn, and C. Li. 1985. Comments on rodents from the Chinese Neogene. Bulletin of the Geological Institutions of the University of Uppsala New Series 11: 59–78.

Jaeger, J.J. 1977. Les rongeurs du Miocène moyen et supérieur du Maghreb. Palaeovertebrata 8 (1): 1–166, 7 pls.

Jansa, S.A., F.K. Barker, and L.R. Heaney. 2006. The pattern and timing of diversification of Philippine endemic rodents: evidence from mitochondrial and nuclear gene sequences. Systematic Biology 55 (1): 73–88.

Jansa, S.A., and M. Weksler. 2004. Phylogeny of muroid rodents: relationships within and among major lineages as determined by IRBP gene sequences. Molecular Phylogenetics and Evolution 31: 256–276.

Kalthoff, D. 2000. Die Schmelzmikrostruktur in den Incisiven der hamsterartigen Nagetiere und anderer Myomorpha (Rodentia, Mammalia). Palaeontographica Abteilung A Palaeozoologie-Stratigraphie 259: 1–193.

Klein Hofmeijer, G., and H. de Bruijn. 1985. The mammals from the lower Miocene of Aliveri (Island of Evia, Greece) – the Spalacidae and Anomalomyidae. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen Series B Physical Sciences 88: 185–198.

Kowalski, K. 1968. Pararhizomys hipparionum Teilhard and Young, 1931 (Rodentia) from the Pliocene of Altan Teli, western Mongolia. Palaeontologia Polonica 19: 163–168.

Kretzoi, M. 1961. Zwei Myospalaxiden aus dem Nordchina. Vertebrata Hungarica 3 (1–2): 123–136.

Laden, G., and R. Wrangham. 2005. The rise of the hominids as an adaptive shift in fallback foods: plant underground storage organs (USOs) and australopith origins. Journal of Human Evolution 49: 482–498.

Laxmann, M.E. 1769. Sibirische Briefe: 74–77. Göttingen: Gotha.

Lazzari, V., and J.P. Aguilar. 2007. First occurrence in Europe of Myocricetodontinae (Rodentia, Gerbillidae) during the lower Middle Miocene in the karstic locality of Blanquetère1 (southern France): implications.

Journal of Vertebrate Paleontology 27 (4): 1062–1065.

Lazzari, V., J. Michaux, and J.P. Aguilar. 2008. Les Megacricetodon du gisement karstique Miocène moyen de Blanquetère1 (Pyrénées-Orientales, Sud de la France): nouvelles espèces, implications biochronologiques et phylogéniques. Géobios 40: 91–111.

Leroy, P. 1940. Observations on living Chinese mole-rats. Bulletin of the Fan Memorial Institute of Biology. Zoology 10: 167–193.

Lilljeborg, W. 1866. Systematisk Öfversigt af de Gnagande Däggdjuren, Glires. 59pp. Kongliga Akademiska Boktryckeriet, Uppsala.

Lindsay, E.H. 1977. Simimys and origin of the Cricetidae (Rodentia: Muroidea). Géobios 10 (4): 597–623.

Lindsay, E.H. 1988. Cricetid rodents from Siwalik deposits near Chinji Village. Part I: Megacricetodontinae, Myocricetodontinae and Dendromurinae. Palaeovertebrata 18 (2): 95–154.

Lindsay, E.H. 1996. A new eumyarionine cricetid from Pakistan. Acta Zoologica Cracoviensia 39: 279–288.

Lindsay, E.H., L.J. Flynn, I.U. Cheema, J.C. Barry, K.F. Downing, A.R. Rajpar, and S.M. Raza. 2005. Will Downs and the Zinda Pir Dome. Palaeontologia Electronica 8 (1) 19A: 1–19 (available at http://palaeo-electronica.org/toc.htm).

Matthew, W.D., and W. Granger. 1923. New fossil mammals from the Pliocene of Sze-Chuan, China. Bulletin of the American Museum of Natural History 48 (17): 563–598.

McKenna, M.C., and S.K. Bell. 1997. Classification of mammals above the species level. New York: Columbia University Press.

Michaux, J., and F. Catzeflis. 2000. The bushlike radiation of muroid rodents is exemplified by the molecular phylogeny of the LCAT nuclear gene. Molecular Phylogenetics and Evolution 17: 280–293.

Miller, G.S. 1927. Revised determinations of some Tertiary mammals from Mongolia. Palaeontologia Sinica C Series 5 (2): 1–20.

Miller, G.S., and J.W. Gidley. 1918. Synopsis of the supergeneric groups of rodents. Journal of the Washington Academy of Science 8: 431–448.

Musser, G.G., and M.D. Carleton. 2005. Superfamily Muroidea. In D.E. Wilson and D.M. Reeder (editors), Mammal species of the world: a taxonomic and geographic reference, 3rd ed.: 894–1531. Baltimore, MD: Johns Hopkins University Press.

Musser, G.G., A.L. Smith, M.F. Robinson, and D.P. Lunde. 2005. Description of a new genus and species of rodent (Murinae, Muridae, Rodentia) from the Khammouan Limestone

National Biodiversity Conservation Area in Lao PDR. American Museum Novitates 3497: 1–31.

Nevo, E. 1999. Mosaic evolution of subterranean mammals: regression, progression, and global convergence. Oxford: Oxford University Press.

Norris, R.W., K. Zhou, C. Zhou, G. Yang, C.W. Kilpatrick, and R.L. Honeycutt. 2004. The phylogenetic position of the zokors (Myospalacinae) and comments on the families of muroids (Rodentia). Molecular Phylogenetics and Evolution 31: 972–978.

Potapova, E.G., and N.N. Vorontsov. 2004. Taxonomic position of the genus *Tachyoryctes* and mutual relations between Rhizomyidae and Spalacidae families (Rodentia). Zoologicheskiĭ Zhurnal 83 (8): 1044–1058. [in Russian]

Prasad, K.N. 1968. The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh, India. Palaeontologia Indica New Series 39: 1–56.

Qiu, Z.-d. 1996. Middle Miocene micromammalian fauna from Tunggur, Nei Mongol. Beijing: Academic Press. [in Chinese, English summary]

Rummel, M. 1999. Tribe Cricetodontini. *In* G.E. Rössner and K. Heissig (editors), The Miocene land mammals of Europe: 359–364. Munich: Pfeil.

Sarich, V.M. 1985. Rodent macromolecular systematics. *In* W.P. Luckett and J.-L. Hartenberger (editors), Evolutionary relationships among rodents: a multidisciplinary analysis: 423–452. New York: Plenum.

Sarica, N., and Ş. Şen. 2003. Spalacidae (Rodentia). *In* M. Fortelius, J. Kappelman, Ş. Şen, and R.L. Bernor (editors), Geology and Paleontology of the Miocene Sinap Formation, Turkey: 141–162. New York: Columbia University Press.

Şen, Ş. 1977. La faune de Rongeurs pliocènes de Çalta (Ankara, Turquie). Bulletin du Muséum National d'Histoire Naturelle Série 3, 465: 89–171.

Steppan, S.J., R.M. Adkins, and J. Anderson. 2004. Phylogeny and divergence-date estimates of rapid radiations in muroid rodents based on multiple nuclear genes. Systematic Biology 53 (4): 533–553.

Teilhard de Chardin, P. 1926. Mammifères tertiaires de Chine et de Mongolie. Annales de Paléontologie 15: 1–51.

Teilhard de Chardin, P. 1942. New rodents of the Pliocene and lower Pleistocene of north China. Publications of the Institut Géo-biologie 9: 1–101.

Ünay, E. 1996. On fossil Spalacidae (Rodentia). *In* R.L. Bernor, V. Fahlbusch, and H.W. Mittmann (editors), The evolution of Western Eurasian neogene mammal faunas: 246–252. New York: Columbia University Press.

Ünay, E. 1999. Family Spalacidae. *In* G.E. Rössner and K. Heissig (editors), The Miocene land mammals of Europe: 389–394. Munich: Pfeil.

Ünay-Bayraktar, E. 1989. Rodents from the Middle Oligocene of Turkish Thrace. Utrecht Micropaleontological Bulletins Special Publication 5: 389–394. Netherlands.

Vianey-Liaud, M. 1985. Possible evolutionary relationships among Eocene to lower Oligocene rodents of Asia, Europe, and North America. *In* W.P. Luckett and J.L. Hartenberger (editors), Evolutionary relationships among rodents: a multidisciplinary analysis: 277–309. New York: Plenum.

Wahlert, J.H. 1985. Skull morphology and relationships of geomyoid rodents. American Museum Novitates 2812: 1–20.

Wang, X., Z.-d. Qiu, and N.D. Opdyke. 2003. Litho-, bio-, and magnetostratigraphy and paleoenvironment of Tunggur Formation (Middle Miocene) in central Inner Mongolia, China. American Museum Novitates 3411: 1–31.

Wang, Y.-x. 2003. A complete checklist of mammal species and subspecies in China: a taxonomic and geographic reference. Beijing: China Forestry Publishing House. [in Chinese and English].

Wei, G., Y. Kowamura, and C. Jin. 2004. A new bamboo rat from the Early Pleistocene of Renzidong Cave in Fanchang, Anhui, central China. Quaternary Research 43 (1): 49–62.

Welcomme, J.-L., L. Marivaux, P.-O. Antoine, and M. Bennami. 1999. Mammifères fossiles des collines Bugti (Balochistan, Pakistan): nouvelles données. Bulletin de la Societé d'Histoire Naturelle de Toulouse 135: 135–139.

Wessels, W. 1996. Myocricetodontinae from the Miocene of Pakistan. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen 99: 253–312.

Wessels, W. 1999. Family Gerbillidae. *In* G.E. Rössner and K. Heissig (editors), The Miocene land mammals of Europe: 395–400. Munich: Pfeil.

Wessels, W., and H. de Bruijn. 2001. Rhizomyidae from the Lower Manchar Formation (Miocene, Pakistan). Annals of Carnegie Museum 70: 143–168.

Winge, H. 1887. Jordfundne og nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien. E Museo Lundii, University of Copenhagen 1: 1–178.

Young, C.C. 1927. Fossile Naetiere aus Nord-China. Palaeontologia Sinica Series C 5 (3): 1–82, + 3 pls.

Young, C.C., and Liu, P.T. 1950. On the mammalian fauna at Koloshan near Chung-

king, Szechuan. Bulletin of the Geological Society of China 30: 43–90.

Zhang, Z.-q., L.J. Flynn, and Z.-d. Qiu. 2005. New materials of *Pararhizomys* from northern China. Palaeontologia Electronica 8 (1) 5A: 1–9 (available at http://palaeo-electronica.org/toc.htm).

Zheng, S.-h. 1980. The *Hipparion* fauna from the Bulong Basin of Biru County, Tibet. Paleontology of Tibet 1: 33–47. Beijing: Science Press. [in Chinese, English summary]

Zheng, S.-h. 1993. Quaternary rodents of Sichuan-Guizhou area, China. Beijing: Kexue Chubanshe. [in Chinese, English summary]

Zheng, S.-h. 1994. Classification and evolution of the Siphneidae. *In* Y. Tomida, C.K. Li, and T. Setoguchi (editors), Rodent and lagomorph families of Asian origins and diversification. Tokyo National Science Museum Monographs 8: 57–76.

Zheng, S.-h. 1997. Evolution of the Mesosiphneinae (Siphneidae, Rodentia) and environmental change. *In* Y. Tong, Y. Zhang, W. Wu, J. Li, and L. Shi (editors), Evidence for evolution—essays in honor of Prof. Chungchien Young on the hundredth anniversary of his birth: 137–150. Beijing: China Ocean Press. [in Chinese with English summary]

Zheng, S.-h. 2004. Mammalia: Rodentia. *In* S.-h. Zheng (editor), Jianshi hominid site—state key project of the 9th five year plan—origin of early humans and environmental background. Series monograph 1: 121–181. Beijing: Science Press. [in Chinese, English summary]

Zheng, S.-h., Z.-q. Zhang, and N. Cui. 2004. On some species of *Prosiphneus* (Siphneidae, Rodentia) and the origin of Siphneidae. Vertebrata Palasiatica 42 (4): 297–315. [in Chinese, English summary]

APPENDIX 1

NOTES FOR CLADISTIC RELATIONSHIPS OF SELECTED MUROIDEA[2]

NODES:

A. As outgroup to Muroidea, Dipodoidea illustrate character polarity (P4 present, hystricomorphy, poorly developed anterior cusps on first molars). These two superfamilies constitute a well-defended infraorder Myodonta Schaub (see, e.g., Vianey-Liaud, 1985).

B. This polytomy does not differentiate between *Cricetops*, *Pseudocricetodon*, or the American taxon *Eumys*. All three lack derived character states in m1 morphology, zygomasseteric structure, and incisor ornamentation, which are tracked in more derived taxa. *Cricetops* appears to conserve the primitive zygomasseteric condition of hystricomorphy; *Pseudocricetodon* has a weakly inclined masseteric plate (Lindsay, 1977), and *Eumys-Leidymys* show a plate inclined toward a very high infraorbital foramen (the height seems to be an autapomorphy, Hartenberger, 1967).

C. *Tachyoryctoides* shows low zygomatic plate inclination, hence weak myomorphy. Its flat incisor has no median ridges. These features are taken to indicate a more basal position than *Eucricetodon*, but it is also conceivable that these character states are overprinted by modifications and the position could be reversed with that of *Eucricetodon*.

D. *Eucricetodon* presents moderate zygomatic plate inclination, and is thus modernized; this is also the first taxon to show the widespread double ridges on lower incisors.

E. *Eumyarion* plots as the immediate sister taxon to all living spalacids; here I extend the strong case of de Bruijin and Saraç (1991) for affinity of *Eumyarion* with anomalomyines, to affinity with all spalacids. Within Spalacidae, anomalomyines are close to spalacines, and myospalacines share features with rhizomyines.

F. *Cricetodon* and the closely allied *Deperetomys* show a more modern zygoma than do *Eucricetodon* or *Eumyarion*: more inclined plate with a ventral trough or slit. This condition is observed in nesomyids. The double ridge on the incisor is retained.

G. *Lartetomys* is placed here to signify stable presence of the new anterior connection of m1; that is, a crest running from the anterior arm of the protoconid to the metaconid.

H. Nesomyids present the modern m1, but variably developed myomorphy. Here the primitive character states for the group are interpreted to be m1 anterior connection present, one incisor ridge retained, moderate myomorpy. The Malagasy nesomyines retain the incisor ridge, but develop myomorphy variably, some genera showing a strongly inclined plate; continental cricetomyines lost the incisor ridge (a very weak ridge is sometimes observed), but do not develop myomorphy (some are nearly "hystricomorphous").

I. Based on AMNH specimens of *Typhlomys cinereus*, the inclined zygomatic plate is not developed in keyhole fashion; the ventral slit is not compressed and there is no flange of the plate expanded anteriorly. Neither fossil nor living genera are known to show incisor enamel ornamentation (Kalthoff, 2000; personal commun.). Tentatively placed in a position more derived than nesomyids, but lower than calomyscids, platacanthomyids have not yet been evalu-

---

[2] Letters refer to comments for nodes and chosen taxa, and numerals represent key characters plotted on the cladogram. This tree presents an explicit hypothesis for testing; it is not an attempt at full phylogenetic analysis of the superfamily (see fig. 6).

ated with other muroids on the basis of molecular data; they could lie outside nesomyids. The group displays extreme lophodonty.

J. Calomyscidae is represented by *Calomyscus*, which is of modern cricetid-murid grade. It is modern in zygomasseteric structure (strongly inclined plate, with ventral slit), in m1 morphology (anterior protoconid connection to metaconid; metaconid relatively anterior in position), and in suppression of the incisor enamel ornamentation (there remains a faint striation on *C. baluchi*). Wessels (1999) lists Late Miocene records for the genus, based primarily on small third molars and lack of mesoloph/-id, and argues for gerbil relationship. However, the simple anterocone/-id and strong longitudinal crest of these fossils are not consistent with gerbil relationship. Placement of Calomyscidae here follows Jansa et al. (2006) and Steppan et al (2004).

K. Fossil *Democricetodon* represents stem cricetids. Its myomorphy is advanced, with the ventral slit of the infraorbital foramen pinched in keyhole fashion, and the M1 has an expanded anterocone. Relationships of groups of cricetids are informed by both the fossil record and molecular data. NWC (New World cricetids) have a late Early Miocene record, younger than the oldest *Democricetodon* (Jacobs and Flynn, 2005).

L. *Megacricetodon* is a derived muroid showing a double anterocone on M1, an elongated anteroconid on m1, and reduced mesoloph/-ids. Third molars are generally reduced. These features place *Megacricetodon* close to murid ancestry (Flynn et al., 1985), and as outgroup to murines plus deomyines, could reasonably be seen as a basal murid, not assigned to a subfamily. This hypothesis seemed weak in 1985, but Lazzari and Aguilar (2007) have documented high variability in large samples of Middle Miocene (ca. 16 Ma) *Megacricetodon*, including occasional presence of accessory cusps in the positions of the classic murid morphology (anterostyle on M1 lingual to double anterocone, enterostyle adjacent to protocone), which makes this genus a reasonable murid outgroup. *Potwarmus* Lindsay (1988) shows M1 morphology near that of murids with stable presence of the enterostyle, but m1 is conservative; the genus would fall near node M on the cladogram.

M. Jaeger (1977) laid the morphological groundwork for realization that gerbils had something to do with murid origination. Inclusion of extinct myocricetodontines among gerbils provided a deep fossil record to envision close relationship. Wessels (1996) documented the richness of myocricetodontine diversity, including taxa with accessory cusps; this Early and Middle Miocene radiation is consistent with closeness of true gerbils and the small Deomyinae group, including very murinelike genera. Sister status of Deomyinae and Gerbillinae was found by Steppan et al. (2004) and Jansa et al. (2006). Sarich (1985) had discovered 20 years earlier that the deomyine *Acomys* plotted outside murines.

Myocricetodontines and gerbils present a characteristic pattern of alternating cusps in m1. Special features of murines (and some gerbils and deomyines) include reduction of longitudinal crests and realignment of the power stroke in chewing (Lazzari et al., 2008). Distinctive murine molar morphology with stable accessory cusp pattern and propalinal mastication either appeared independently among certain deomyines, or this complex suite of features was simplified secondarily in gerbils (and some deomyines).

CHARACTERS:

1. Double anterocone on M1. Some muroids have transversely twinned anterocone cusps. This derived condition is found in isolated genera, plus a radiation of advanced muroids, including Muridae.

2. Double anteroconid on m1. This feature does not occur without presence of character 1. However, not all muroids with a double anterocone have a double anteroconid.

3. Pinnate incisor ornamentation. Autapomorphy for *Pseudocricetodon* among genera surveyed here.

4. Low inclination of zygomatic plate. Lindsay (1977) cites a measure of 10 degrees, barely advanced over hystricomorphy.

5. Zygomatic plate inclined to high infraorbital foramen. Hartenberger (1967) shows that the precociously inclined zygomatic plate of Oligocene North American genera reflects the high position of the infraorbital foramen.

6. Central anterocone on M1. All muroids share a distinct anterocone that is near the midline of the tooth (not in extreme buccal position).

7. Expanded anteroconid on m1. Dipodoids have a small anteroconid (if any).

8. P4 absent. Correlated with characters 6 and 7, muroids lack the small, peglike P4 of dipodoids.

9. Moderate zygomatic plate inclination. Lindsay (1977) measures 29° and higher for *Eucricetodon* and other Miocene genera.

10. Double longitudinal ridge on the enamel of the lower incisor (present through node F).

11. Anterocone on M1 expanded in transverse anteroloph.

12. Posterior connection on m1 weak or absent. The widespread primitive condition of a crest joining the metaconid directly to the protoconid or its posterior arm is reduced and lost in Early Miocene lineages. Later changes include anterior shift of the metaconid cusp and construction of a new connection from the anterior arm of the protoconid to the metaconid. This new connection is not the same as linkage to the metaconid from the lingual side of the anteroconid.

13. Lophodonty. This condition unites spalacids, but arose independently in other groups, including arvicolines, gerbils, platacanthomyids, some murines, and some New World cricetids; it is widespread but not universal in nesomyines, and occurs in cricetomyines.

14. Reduced anterior cingulum on M2 and M3. The primitive cingulum is suppressed in many genera. Its suppression unites spalacids and is usual in later muroids.

15. Infraorbital foramen expanded and origin of lateral masseter confined to ventral border of zygomatic arch. This condition appears to be a reversal from the trend of developing full myomorphy, and characterizes Spalacinae (unknown in Anomalomyini) and several other living genera, e.g., *Deomys*.

16. Anterior connection on m1 from the anterior arm of the protoconid to the metaconid. This condition characterizes derived muroids after Node F, and appears to have been developed independently in Rhizomyinae + Myospalacinae.

17. Single ridge on lower incisor enamel. Reduction from two ridges to one is observed within the genus *Kanisamys* (Flynn, 1982) and is evident in Nesomyinae.

18. Absence of ridges on lower incisor. This trait evolved in parallel in Spalacinae, Rhizomyini, and Cricetomyinae. It would characterize all higher muroids, except that some south Asian *Democricetodon* show the double ridge.

19. Infraorbital foramen transformed as a high, rounded opening in the anterior root of the zygoma.

20. Zygomatic plate large and inclined. *Cricetodon* and later muroids are clearly more derived in myomorphy (relative size, anterior expansion, inclination) than any spalacid. Although zygomatic plate size is difficult to evaluate given allometric scaling (*Cricetodon* is larger than *Eucricetodon*) its prominent zygomatic plate resembles that of nesomyines.

21. Thick, wrinkled enamel on molars links the clade of cricetodontine genera (Rummel, 1999).

22. Reduced inclination of the zygomatic plate. Molecular data link nesomyines and cricetomyines. Whereas nesomyines generally retain the zygomatic plate, it is reduced in most cricetomyines, greatly so in some, such as *Steatomys*.

23. Full myomorphy. Full myomorphy means presence of a keyhole infraobital foramen, the upper part of which transmits the medial masseter muscle onto the side of the snout, and the lower part of which is compressed by anterior expansion of the lateral masseter onto an expanded zygomatic plate; this plate is often built anteriorly as a flange of bone lateral to the foramen. This condition is plotted for muroids based on widespread distribution. It is important to note the high frequency of variant zygomatic structures, some of which represent character reversals. The feature is not distributed consistently even within small, well-defined clades. Within cricetines (hamsters) for example, *Cricetus* shows rather typical myomorphy, but *Cricetulus* lacks the zygomatic flange.

24. Prominent, elongated anteroconid on m1. Whereas the anterocone of M1 is expanded and prominent along much of this tree, the anteroconid is often small, and its longitudinal extent is not great. All murids have a prominent anteroconid and most have twinned cusps (character 2).

25. Frequent accessory lingual cusps on upper molars, and buccal shelf with cusps on lower molars. This appears occasionally in *Megacricetodon* and *Sindemys* as a variable trait.

26. Anterocone on M1 and accessory cusps simplified. In gerbils the M1 is simplified by variable reduction of the doubled anterocone and loss of lingual cusps.

27. Murine plan for first molars: M1 with lingual cusps stable in position (anterostyle linked with double anterocone, enterostyle always adjacent to protocone) and m1 with X-shaped double anteroconid-protoconid-metaconid). These features are present in some deomyines (e.g., *Acomys*).

28. Anteroposterior power stroke in chewing. Most rodents, including many muroids, have an oblique component to mastication, and chew preferentially with alternate jaws. A few lineages of rodents develop fully propalinal mastication, nearly perfectly anteroposterior in direction. This feature characterizes true murines, and deomyines for the most part, but gerbils preserve an oblique chewing component (Lazarri et al., 2008). Although propalinal mastication arises in parallel among distantly related rodents, the character serves as a derived condition for murids.