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Received 18 July 2001
Revision received
26 November 2001 and
accepted 11 December 2001

Keywords: hominoids,
micromammals, Neogene,
Yuanmou, Yunnan.


The micromammalian fauna from the Leilao, Yuanmou hominoid locality: Implications for biochronology and paleoecology

The discovery of *Lufengpithecus* at Yuanmou, in Yunnan Province, China, provides important clues to understanding the evolution of early hominoids in eastern Asia. However, the age and paleoecology of the fauna remain to be established. An assemblage of micromammalian fossils, collected recently by screenwashing at Leilao, one of the hominoid-bearing localities at Yuanmou, contains 41 species belonging to 16 families and 4 orders, and represents the most diverse Neogene micromammalian fauna known from southwestern China. This paper presents an analysis of the taxonomy, age, and paleoecology of the micromammalian fauna. The Yuanmou hominoid fauna is now considered older than the Lufeng fauna, and is currently thought to correspond to an age of about 9 Ma. The micromammalian fauna indicates a predominantly forested habitat, with marginal environments consisting of bush-grassland.

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Journal of Human Evolution (2002) 42, 535–546

doi:10.1006/jhev.2001.0540

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Introduction

The Yuanmou Basin, a lower Cenozoic sedimentary basin in Yunnan Province, China, lies on the northern edge of the Yunnan–Guizhou Plateau. Following the discovery of *Lufengpithecus* in the basin in 1986 (Zheng & Zhang, 1997), a series of excavations was conducted at the sites of Zhupeng, Xiaohe and Leilao of Wumau District, northwest of the county seat of Yuanmou (Figure 1). Among the numerous mammal remains, a cranial fragment of a juvenile individual, several pieces of upper and lower jaws, and more than one thousand isolated teeth of hominoids have been recovered from these localities. The assemblages from Zhupeng and Xiaohe have been designated as the Yuanmou hominoid fauna or Yuanmou fauna (Jiang, 1996; Cai, 1997; Gao & Ma, 1997; Ji & Zhang, 1997; Pan, 1997; Zheng & Zhang, 1997; Zong, 1997a). The collections provide important material

for the study of hominoid and mammalian evolution in eastern Asia. However, the age and paleoecology of the Yuanmou fauna are the subject of continuing debate (Jiang *et al.*, 1987; Ji & Zhang, 1997; Qian, 1997; Zong, 1997b).

The rapid evolution and the degree of specialization of small mammals make them especially valuable for chronological correlation in the absence of other dating methods. Moreover, the narrow habitat preferences of many small mammals makes them useful for the reconstruction of paleoecology. To date, however, the majority of the fossil remains collected in the Yuanmou Basin was of large mammals; only about a dozen teeth representing six insectivore and rodent species have been described previously (Cai, 1994). In the winters of 1999 and 2000, we excavated and screenwashed more than 10 tons of sediment at Leilao, with the aim of resolving the age of the Yuanmou hominoid fauna. To date, one

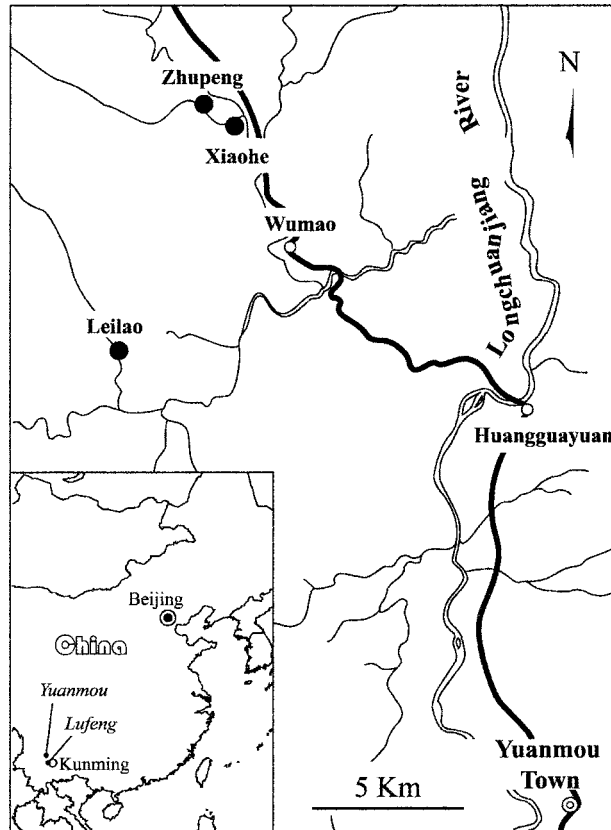


Figure 1. Location of the Yuanmou fossil localities.

half of the concentrate has produced more than 400 small mammal specimens.

The fossil sites at Leilao are located about 7 km southwest of Zhupeng and Xiaohe, and are inferred to be associated with the same depositional setting. Sediments are mainly diluvial-alluvial deposits, principally comprising a series of brownish-red sandy clays and argillaceous siltstones, with some intercalations (sometimes small lenticular bodies) of grayish-yellow and grayish-green pebbly sandstone. These sediments are lithologically similar to those of the Xiaohe Formation in the neighboring Xiaohe section (Zheng *et al.*, 1997). The excavation sites are located on a slope to the east of the village of Leilao (N25°50'48.9",

E101°44'9.4"). The grayish-yellow bands of sandstone are fossiliferous, and the fossil-bearing beds are about 30 m thick, representing at least five layers. Sediments for screenwashing came from sites 9903, 9904, 9906, 9905 and 9905T0. These sites represent three different horizons, with the first three being higher in the sequence, and 9905T0 the lowest (Figure 2). All of these sites have produced hominoid remains. Preliminary study shows that the hominoids and larger mammals from Leilao are identical to those from Zhupeng and Xiaohe (Q. Qi, W. Liu & L. Zhao, personal communication). There is no doubt that the micro-mammalian assemblage from Leilao can be attributed to the Yuanmou Fauna.

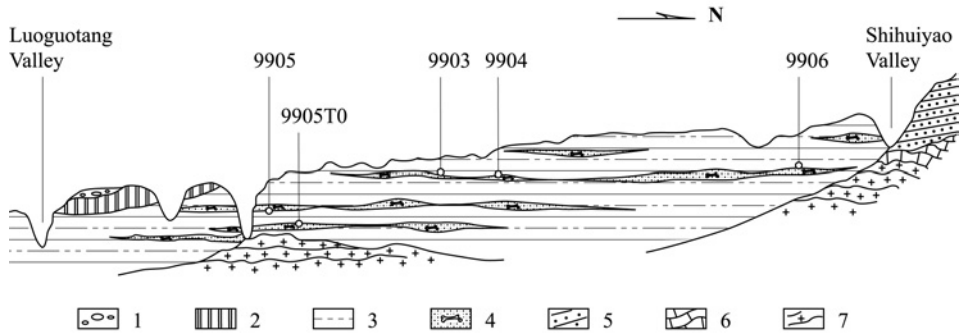


Figure 2. Section of the fossil sites at Leilao, Yuanmou. 1. Quaternary deposits; 2. Sandstone with calcareous and manganese nodules belonging to the Tulin Formation; 3. Sandy mudstone of the Xiaohe Formation; 4. Fossiliferous bands of pebbly sandstone of the Xiaohe Formation; 5. Sandstone of the Jiangdihe Formation; 6. Metamorphic limestone of Kunyang Group; 7. Metamorphic granite of the Kunyang Group.

Faunal composition

The 41 taxa collected, including 36 genera, 16 families and four orders, represent the most diverse Neogene micromammalian fauna so far known from southwestern China (Table 1).

Scandentia: A mandible fragment with p4 and m1, and nine isolated teeth are referred to the Tupaiidae (tree shrews). Two taxa of tree shrews can be readily distinguished by size and morphology. The smaller species can be identified as *Proden-drogale*, which is also known from Shihuiba, Lufeng (Qiu, 1986). The larger form is similar to the extant *Ptilocercus lowii* from Borneo and Sumatra (Wilson, 1993), in having a heavily built mandible, less molarized p4, well developed entoconid, and high and narrow entocristid on m1. Further study may lead to the recognition of a new genus and species, perhaps representing the first fossil record of Ptilocercinae.

Insectivora: Three families of Insectivora, Erinaceidae (hedgehogs), Talpidae (moles), and Soricidae (shrews), can be identified in the assemblage. The 25 teeth of Erinaceidae are identical in size and morphology to the hairy hedgehog (or moon rat) *Hylomys* aff. *suillus* of Shihuiba. There are only eight cheek teeth of moles in the collec-

tion, all referred to *Yunoscaptor scalprum*, also known from Shihuiba. Shrews are rare, but five species, representing the subfamilies Heterosoricinae and Soricinae, are recognized. Heterosoricinae are apparently represented by a single taxon, *Heterosorex wangi*. Among the soricines, only *Anourosorex oblongus* is positively identified.

Chiroptera: Specimens of bats are too few to allow identification below the family level, but at least three families are present.

Rodentia: Nine families of rodents are represented in the collections. Twelve species of Sciuridae (squirrels) are recognized based on 58 cheek teeth. Sciurids are the most diverse rodents in the fauna, and they represent a number of adaptive types. Seven species found at Leilao co-occur at Shihuiba.

Only three teeth belong to Castoridae. They are identical in size and morphology to the beaver reported as "*Monosaulax*" sp. from Shihuiba, Lufeng and Xiaohe, Yuanmou (Cai, 1994). Nevertheless, the specimens do not correspond morphologically to the diagnosis of *Monosaulax* and their identification remains in doubt. Fifty-nine molars are identified as Platacanthomyidae (spiny dormouse and Chinese pygmy dormouse), and these can be assigned to *Platacanthomys dianensis*, *Typhlomys primitivus*

Eighteen specimens, including a maxilla with complete upper molar dentition, represent four species of Rhizomyidae (bamboo rats), of which three are assigned to *Brachyrhizomys*. The maxillary fragment and five teeth are similar in size and structure to *B. nagrii* from the Siwaliks, South Asia, but differ in having four roots on M1. The lower molars are similar to the corresponding teeth of “*B. nagrii*” from Shihuiba. All of these specimens probably represent a new species of *Brachyrhizomys*. *B. blacki* is known from the Siwaliks and Xiaohe, Yuanmou (Flynn, 1982; Cai, 1994), but not from Shihuiba, Lufeng (Qi, 1986). Another three upper molars of rhizomyids, distinguishable from those of *Brachyrhizomys*, share some characters with *Kanisamys*. Further study may show these specimens to represent a new species of tachyoryctine.

Cricetidae are relatively common. Almost all of the specimens ($n=48$ molars) can be referred to *Kowalskia hanae*, also known from Shihuiba. Minor differences between the Leilao and Shihuiba specimens include the root numbers and morphology of M1. The M1 in all five specimens with preserved roots is three-rooted and lacks a vertical groove on the lingual face of the inner root, while in the Shihuiba sample 13 of 24 specimens are four-rooted and a vertical groove is present in eight of 11 three-rooted molars (Qiu, 1995). Another M1 from Leilao differs from that of *K. hanae* and is assigned to an indeterminate hamster, based on its larger size, relatively higher crown, and more robust cusps and crests.

Murids are the most abundant rodent family in the collection ($n=159$ molars). Most of the specimens are identified as “*Progonomys*” *yunnanensis* as from Shihuiba. The Leilao population is less derived than that from Shihuiba in such characters as total absence of t7 in all 35 M1 specimens, while an incipient t7 is present in 20% of the corresponding specimens from Shihuiba (Qiu & Storch, 1990), a wider separation of

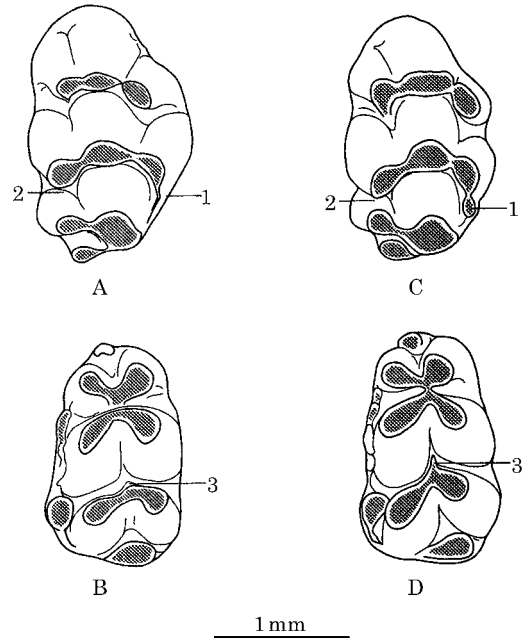


Figure 3. Molars of “*Progonomys*” *yunnanensis*, indicating the differences between Leilao population and Shihuiba population. Leilao population: A (M1, V13120.1), B (m1, V13120.11); Shihuiba population: C (M1, V9494.197), D (m1, V9494.59). Compared with Shihuiba the molars from Leilao have: (1) a less well-developed t4-t8 connection and without t7; (2) a wider separation of t6 and t9; and (3) anterior spur on the hypoconid-entoconid chevron absent or faintly developed.

t6 and t9 on M1, and absent or only faintly developed anterior spur on the hypoconid-entoconid chevron of m1 (Figure 3). Mein *et al.* (1993) doubt whether *Progonomys* occurs in Asia. It seems reasonable to exclude the Shihuiba “*Progonomys*” from the genus on the basis of the possession of a distinct connection between t4 and t8, an incipient t7 in some M1, and well developed tma on m1. Further study of this taxon from Shihuiba and Leilao is under way by Storch and Ni. Another 28 molars from Leilao probably represent a new genus and species of Muridae. These teeth are comparable in size to those of *Yunomys wui* from Shihuiba, but the crowns are lower and there are differences in occlusal morphology.

Hystriidae are represented by only three cheek teeth, belonging to *Hystrix* (porcupine) and *Atherurus* (brush-tailed porcupine). Previously, the fossil record of *Atherurus* extended to only the Quaternary (Zheng, 1993). A p4 resembling that of the springhare would represent the first record of the Pedetidae in eastern Asia. Morphologically the specimen differs from *Megapedetes* from the Miocene of Africa and Anatolia (MacInnes, 1957; Sen, 1977), but it is similar to extant *Pedetes capensis*, apart from its distinctly smaller size and much more rounded pre-lobe of p4.

Table 1 shows the occurrence of micro-mammal taxa at the different Leilao sites. Site 9905T0, the basal fossiliferous horizon, has produced only *Atherurus* sp. and “*Progonomys*” *yunnanensis*. The former occurs in site 9905 (middle horizon), and the latter appears in all sites. The topmost horizon yielded nearly all of the same taxa as the middle horizon, with minor differences probably due to sampling given the smaller amount of sediment processed. Judging from the dominant cricetids and murids, no distinct difference in morphology can be detected in the material from the top and middle horizon. Furthermore, there is no evident depositional hiatus among the three horizons. Thus, the taxa from these localities are treated here as a single faunal unit.

Biochronology

The micromammalian composition from Leilao, Yuanmou, is very similar to that from Shihuiba, Lufeng. Based on the study of Rhizomyidae, Muridae and Cricetidae, the Lufeng Fauna is generally assigned to the late Miocene (=Baodean Chinese Land Mammal Age), which corresponds to an age of about 8–9 Ma (Flynn & Qi, 1982; Qi, 1986; Qiu & Qiu, 1995, and see below). The similarities of the two micromammalian faunas makes it reasonable to conclude

that the Yuanmou Fauna could also be considered Baodean.

Among the 41 species of small mammals in the Yuanmou Fauna, 25 are shared with Lufeng (Table 1). It is notable that Leilao and Shihuiba share some significant bio-chronological index taxa, including those characterized by relative rapid evolution, such as *Kowalskia hanae*, “*Progonomys*” *yunnanensis*, and some species of Rhizomyidae. Essential differences are: the presence of a *Ptilocercus*-like tree shrew, a springhare, *Atherurus*, and undescribed hamsters and mice; the greater diversity of squirrels and bamboo rats; and the absence of *Lanthanotherium*, *Yunomys* and *Alilepus*. These differences might indicate a time gap between the two faunas.

An increase in the number of roots is an evolutionary trend in several rodent lineages, including *Kowalskia*. The higher proportion of four-rooted M1s in *Kowalskia hanae* from Shihuiba suggests that it is more derived than *K. hanae* of Leilao. Evolutionary change in many lineages of murids includes a tendency towards progressive development of t7, approach of t6 and t9, and strengthening of anterior spur of hypoconid-entoconid chevron on m1. The absence of t7, the wider separation of t6 and t9 and the faint development of anterior spur of hypoconid-entoconid chevron in the “*Progonomys*” *yunnanensis* from Leilao, and the presence of t7 in some specimens, the distinct closeness of t6 and t9 and the strong development of the anterior spur of hypoconid-entoconid chevron on m1 from Shihuiba indicate such a change (Figure 3). Both *Kowalskia* and “*Progonomys*” in the Yuanmou fauna seem to retain more primitive features than those from the Lufeng fauna, and this suggests an older age for the fauna.

The occurrence of Rhizomyidae in the Siwaliks, in association with paleomagnetic data, affords an opportunity to correlate the Lufeng and Yuanmou faunas with the

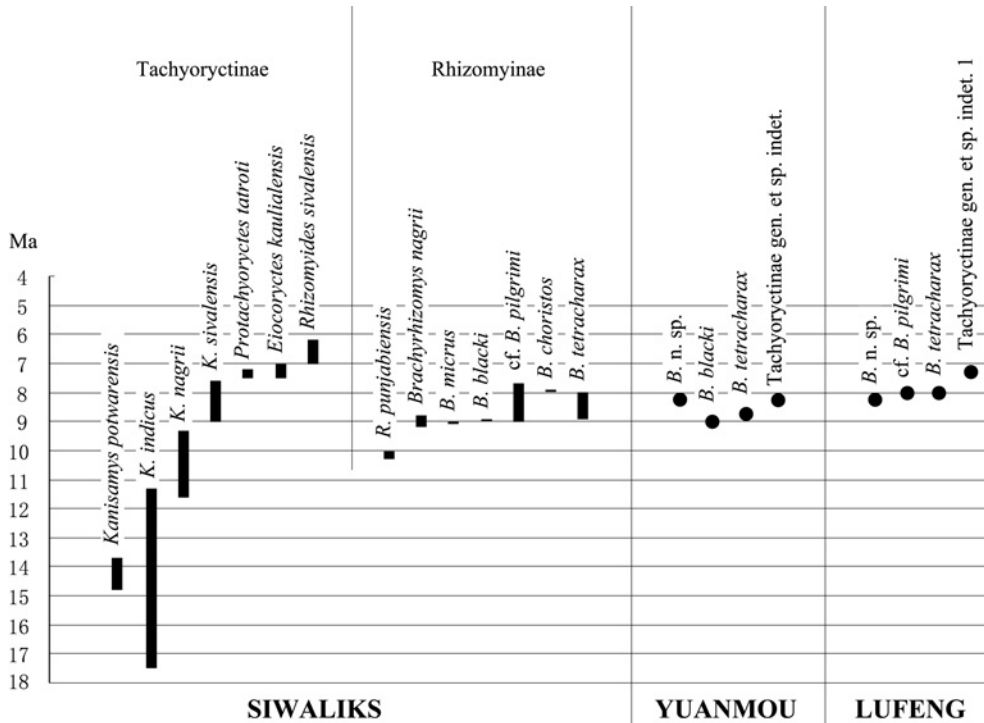


Figure 4. Chart showing the age ranges of rhizomyids from the Siwaliks and the correlation of rhizomyids from Yuanmou and Lufeng.

well-documented Siwalik biochronology. According to Flynn (1982), *Brachyrhizomys blacki* is a small species with relatively primitive characters in the *Brachyrhizomys* lineage. It occurs in the Yuanmou Fauna, but is absent in the Lufeng Fauna. *Brachyrhizomys tetracharax* and *B. cf. pilgrimi* are more derived species of the genus. The former occurs more commonly at Shihuiba than at Leilao, whereas the latter is only known from Shihuiba. An indeterminate rhizomyid, represented by M1 at Shihuiba (Qi, 1986), is comparable with the tachyoryctine from Leilao. The Shihuiba specimen is obviously more derived in being much larger in size and higher crowned. Flynn & Qi (1982) gave an age of 8 Ma for Lufeng, although this was considered a maximum estimate. Subsequent revision of the magnetic time scale (see Flynn *et al.*, 1998) adjusts this estimate to about 9 Ma. On the basis of

rhizomyid biostratigraphy and Siwalik magnetostratigraphy, a date of about 9 Ma can be inferred for the Yuanmou Fauna, while the Lufeng Fauna may be dated to as young as 8 Ma. These data include the co-occurrence of *Brachyrhizomys tetracharax*, *B. blacki*, a new species similar to *B. nagrii*, but with four-rooted M1, and a tachyoryctine at the corresponding evolutionary level of *Kanisamys sivalensis* in its middle and late stages (Figure 4).

At least seven genera in the Yuanmou Fauna—*Heterosorex*, *Sorex*, *Albanensis*, *Forsythia*, *Leptodontomys*, *Kowalskia*, and *Hystrix*—are congeneric with or closely related to European Miocene taxa, but no precise biochronological correlation to the European sequence can be justified at the present. However, *Kowalskia* and “*Progonomys*” from the Yuanmou fauna show similar evolutionary stages to representatives from

Table 2 Supposed habitat selection types of micromammals from Leilao and Shihuiba hominoid localities

Habitat selection types	Taxa
Restricted to forest habitats	<i>Prodendrogale yunnanica</i> ; Ptilocercinae gen. et. sp. nov.†; <i>Hylomys</i> aff. <i>suillus</i> ; <i>Lanthanotherium</i> sp.*; <i>Hylopetes</i> sp.; <i>Albanensia</i> sp.; <i>Forsythia</i> sp.; Petauristinae gen. et sp. indet. 1†; Petauristinae gen. et sp. indet. 2†; <i>Ratufa</i> sp.†; <i>Dremomys</i> sp 1.; <i>D.</i> sp. 2†; <i>Leptodontomys</i> sp.; Eomyidae gen. et sp. indet.; <i>Platacanthomys dianensis</i> ; <i>Typhlomys primitivus</i> ; <i>T. hipparionum</i> ; <i>Brachyrhizomys</i> sp. nov; <i>B. tetrecharax</i> ; <i>B. blacki</i> †; <i>B. cf. pilgrimi</i> *
Inhabiting forest and relatively humid shrub at forest edges	<i>Yunosceptor scalprum</i> ; Talpinae gen. et sp. indet.*; <i>Heterosorex wangi</i> ; <i>Anourosorex oblongus</i> ; <i>Blarinella</i> sp.*; <i>Sorex</i> sp. 1; S. sp. 2†; Sorecinae gen. et sp. indet.†; Sorecinae gen. et sp. indet. 1*; <i>Atherurus</i> sp.†
Adapted to forest or bush habitats	<i>Callosciurus</i> sp.; <i>Tamiops</i> sp.; <i>Sciurotamias</i> sp.; Sciurinae gen. et sp. indet.†; <i>Hystrix</i> sp.
Preferring waterways at forest edges	“ <i>Monosaulax</i> ” sp.
Living in bush and grassland	Tachyoryctinae gen. et. sp. indet.†; Tachyoryctinae gen. et. sp. indet. 1*; Pedetidae gen. et sp. indet.†
Adapted to various habitats including forest, bush or grassland	<i>Kowalskia hanae</i> ; Cricetidae gen. et sp. indet.†; “ <i>Progonomys</i> ” <i>yunnanensis</i> ; <i>Yunomys wui</i> *; Muridae gen. et sp. nov.†; <i>Alilepus longisinuosus</i> *

†Only found from Leilao locality; *Only found from Shihuiba locality.

European late Vallesian or early Turolian faunas (upper MN10 or lower MN11).

Paleoecology

Fossil micromammalian assemblages are extremely useful for paleoecological reconstructions. The most common method is to assume that habitat preferences are correlated with taxonomic affinity and morphological characteristics, and to assign the fossil species to various ecological groups (e.g., Daams & van der Meulen, 1984; van Dam, 1997). In the micromammalian fauna of Yuanmou (excluding bats), 14 out of 34 genera and 12 out of 13 families have extant representatives, so it is possible to deduce habitat preferences of fossil taxa based on the premise that they are adapted to similar ecological niches as their recent close relatives. On this basis, the Yuanmou species can be assigned to six overlapping habitat types (Table 2). This present analysis also includes the Lufeng micromammalian fauna for comparison with that from Leilao,

because the paleoecology of the Shihuiba hominoid locality has been studied in some detail previously (e.g., Badgley *et al.*, 1988; Qi, 1993).

Among the fossil taxa, two species of tree shrews, two species of moonrats, all the flying squirrels, all species of spiny dormice, some tree squirrels and bamboo rats are considered to prefer forest environments since their extant congeners are typically forest dwellers (Walker *et al.*, 1968; Corbet & Hill, 1991). *Prodendrogale* and *Lanthanotherium* in the Lufeng micromammalian fauna are assumed to be closely related to *Dendrogale* and *Hylomys* respectively (Qiu, 1986; Storch & Qiu, 1991). *Dendrogale* and *Hylomys* are strictly arboreal insectivores, and they are distributed today in forested areas of eastern Asia (Corbet & Hill, 1991; Wilson, 1993). *Ptilocercus lowi* is distributed in southeastern Asia and is confined to forested environments (Corbet & Hill, 1991; Wilson, 1993). We assume that the fossil ptilocerine from Leilao shared similar habitats with the recent species. Eomyids are

extinct, but they are inferred to the forest dwellers, preferring dense vegetation (Daams & van der Meulen, 1984; van Dam, 1997). A complete skeleton of an eomyid, preserving soft tissue and hair, had been discovered and reconstructed as a glider, similar to modern flying squirrels (Storch *et al.*, 1996). *Brachyrhizomys* already possessed many derived rhizomyine characters and it can be assumed to have been similar to recent burrowing *Rhizomys* (Flynn, 1982, 1985), which mainly inhabits montane bamboo forests.

Fossil moles, shrews, and brush-tailed porcupine are inferred to have inhabited forest and relatively humid shrub at forest edges. Moles occur typically in environments with moist, friable soils. According to Storch & Qiu (1991), the humerus of *Yunosaptor scalprum* from Shihuiba is similar to that of *Scapanulus oweni* (Gansu mole), which lives today in forests and humid shrubland at forest edges in Yunnan, Sichuan and Gansu Provinces. Shrews occur in various habitats, but their distribution is principally determined by moist conditions, so they tend to be most abundant in mesic forest habitats (Churchfield, 1990). *Sorex* may also occur in moist shrub and grassland, but most species are adapted to forested environments. *Anourosorex* and *Blarinella* (found at Shihuiba) are restricted today to montane forest areas in South China, northern Thailand and Burma. In sum, one can assume that the soricids from Leilao and Shihuiba are predominantly forest dwellers or that they occurred in humid shrub habitats at forest edges.

Modern *Atherurus* only occurs in forested areas in Africa and southern Asia, especially favoring forest edges near waterways (Walker *et al.*, 1958). *Callosciurus*, *Tamiops* and *Sciurotamias* mainly live today in various kinds of forests, including tropical rainforest and forest scrub, throughout most of the Oriental Region. Modern *Hystrix* is highly adaptable, but in Asia it is most common in

forest or bush in the south. The fossil hystriid is assumed to indicate similar habitats. Beavers inhabit waterways, preferring forest edge habitats. “*Monosaulax*” in the Yuanmou and Lufeng faunas would require similar aquatic environments. Incidentally, the occurrence of this type of habitat is corroborated by the presence of fish remains in the fossil collections.

Recent tachyoryctines are distributed in uplands regions of northeastern Africa, and prefer open grassland, sparsely wooded savanna, moorland, and cultivated areas. Pedetids mainly occur in semi-arid grasslands in eastern and southwestern Africa (Kingdon, 1974). We presume that fossil tachyoryctines and pedetids preferred similar environments.

Recent murids and cricetids show broad ecological tolerances. Fossil cricetids with relatively high-crowned molars, and murids with well developed stephanodontology, indicate open and arid environment (van Dam, 1997). However, all the cricetids and murids from Leilao and Shihuiba have low-crowned molars without stephanodontology. We recognize them, therefore, as groups that may have lived in a diversity of habitats ranging from forest to grassland. Fossil *Alilepus* is recorded from both southern and northern China, and also Europe (Qiu & Han, 1986; de Bruijn, 1995), and was probably adapted to living in various habitats.

Half of the small mammals from Leilao locality are reasonably inferred to prefer forest habitats, while 18.4% tend to be associated with forested habitats and humid forest edges. Only 5.3% possibly indicate grassland, bush, and open woodland environments (Figure 5). There is no statistically significant difference between the composition of habitat types based on the Yuanmou and Lufeng micromammalian faunas ($\chi^2=0.4037$; $P=0.9952$), indicating that the paleoecological conditions were similar. The paleoenvironment of the Shihuiba hominoid locality is interpreted as

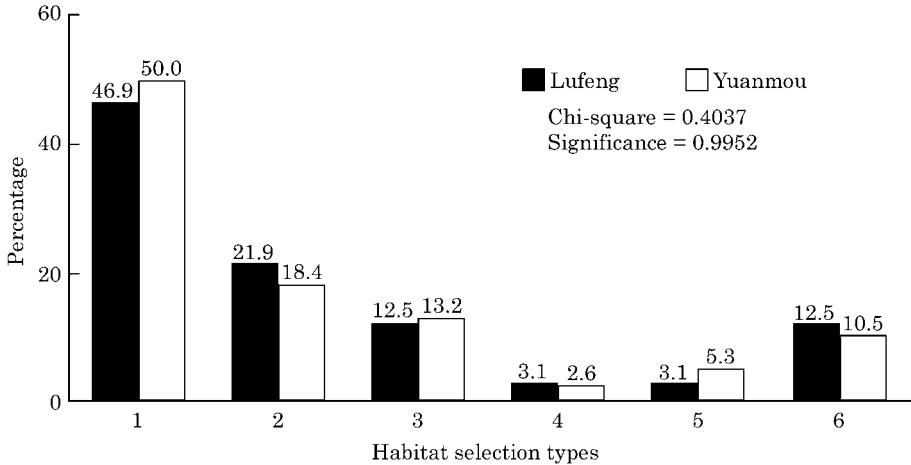


Figure 5. The composition of various habitat selection types of micromammals in Yuanmou and Lufeng faunas. (1) Restricted to forest habitats; (2) inhabiting forest and relatively humid shrub at forest edges; (3) adapted to forest or bush habitats; (4) preferring waterways at forest edges; (5) living in bush and grassland; and (6) adapted to various habitats, including forest, bush or grassland.

forested, with the presence of forest-edge shrub, patches of shrub–grasslands, and riparian habitats. This scenario is based on evidence from faunal analysis, mineralogy and palynology (Sun & Wu, 1980; Chen *et al.*, 1986; Badgley *et al.*, 1988; Qiu *et al.*, 1985; Qiu, 1986, 1989; Qi, 1993). The paleoenvironment of the Leilao hominoid locality can be visualized as a landscape of montane forest, with luxuriant shrubs, patches of open bush and grassland, located in a wide flat valley with nearby rivers.

Since the early Miocene, the micromammalian faunas of China have been characterized by distinct provinciality and latitudinal ecological variation. Those from southern and northern China are quite different in taxonomic composition, especially the faunas from Yunnan and those from the Mongolia-Xinjiang Plateau in the north (Qiu, 1996; Qiu & Wang, 1999). This difference in distribution is evidently the result of differences in environment. All of the orders and families in the Lufeng and Yuanmou faunas, except the Eomyidae, are extant today. Aside from the eurytopic families (i.e., Talpidae, Soricidae, Vespertilioni-

dae, Sciuridae and Muridae), Galericinae, Platanthomyidae and Scandentia are restricted to the Oriental Region, Rhizomyidae, Hipposideridae and Hystricidae are confined to or mainly distributed over the tropical or subtropical areas of the Old World, Castoridae are found in the Holarctic Region, and the Cricetidae have mainly a Palearctic distribution. All the small mammal families, except Castoridae, Cricetidae, and Pedetidae persist to the present-day in Yunnan. Thus, the Lufeng and Yuanmou hominoid faunas are predominantly Oriental in character, but differ slightly from the present day fauna of Yunnan. The occurrence of the large-sized tree shrew, the tropical sciurines and petauristines, and abundant platanthomyids indicate that the climate in Yunnan was warmer and more humid than today, and was probably more similar to that of Southeast Asia.

Mammalian faunal changes in central Europe indicate that grasslands began to replace tropical and subtropical forests during MN Zone 11–13, with similar changes occurring during the same period in southwestern Asia (Fortelius *et al.*, 1996). A

widespread increase in the biomass of C₄ grasses, as indicated by changes in the carbon isotope ratios of fossil tooth enamel in Pakistan, East Africa, North America and South America, also began around 8 Ma (Cerling *et al.*, 1997). However, it would appear that forest was still the predominant habitat type in southwestern China around 9–8 Ma.

Conclusion

The assemblage of micromammalian fossils from the Leilao hominoid locality, Yuanmou, collected recently by screenwashing, contains 41 species belonging to 16 families and four orders, and it represents the most diverse Neogene micromammalian fauna known from southwestern China. The composition of the micromammalian fauna indicates that the Yuanmou hominoid fauna is slightly older than that of the Lufeng Fauna, currently estimated to be about 9 Ma and 8 Ma respectively. The Yuanmou Fauna suggests a climate and habitat similar to that inferred for Lufeng. Both localities had landscapes dominated by montane forests, with humid and luxuriant shrub, patches of open bush and grassland, located in wide valleys with rivers nearby.

Acknowledgements

Many thanks are given to the Yunnan team members of Pandeng Project who assisted in the field work. The authors would like to express their gratitude to Dr L. J. Flynn (Harvard University), Professor T. Harrison (New York University), and Dr Louis H. Taylor (Denver Museum of Nature and Science) for critiquing the manuscript and improving the English. The research is supported by Pandeng Project (95-special 01) and Major Basic Research Projects of Ministry of Science and Technology, China (G2000077700).

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