Lawrence J. Flynn
Peabody Museum, Harvard University, Cambridge

# Small mammal indicators of forest paleo-environment in the Siwalik deposits of the Potwar Plateau, Pakistan

The Siwalik Group comprises a thick sequence of terrestrial deposits in the northern part of the Indian Subcontinent, with a relatively high degree of completeness over most of Neogene time. Derived from highlands to the north, the Siwaliks were deposited by river systems that preserved many superposed fossil assemblages that are well dated. In the Potwar Plateau of northern Pakistan, the fossil record is good for the interval of 18 to 6 Ma; deposits elsewhere and in India complement it. The record as a whole shows historical trends that test interpretations of paleoenvironments. Principle conclusions are these: (1) high mid-Miocene faunal diversity persisted until 10 Ma; (2) decreasing diversity is a sustained trend through the late Miocene; (3) mid-Miocene small mammal elements indicate considerable arboreal habitat; (4) forest elements decline slightly in diversity through 11 Ma, with return to higher proportions by 8 Ma; (5) open/grass adapted elements begin to appear in the interval of 9 - 8 Ma, and arboreal elements show turnover, with decline to a lower proportion by 7 Ma. The trends indicate sustained change that is not abrupt, and there is no major restructuring of the fauna until about 8 Ma. Late Miocene faunal change indicates changing arboreal habitat, which likely corresponds to increasing seasonality and fragmentation of formerly widespread forest. In general, modern mammalian analogues appear to be useful for interpreting habitat preferences of Miocene fossil rodents, but an apparent exception is the gundi *Sayimys*, which may have been a subtropical element unlike arid-adapted modern relatives.

Correspondence: Lawrence J. Flynn, Peabody Museum, Harvard University, Cambridge, MA 02138, USA

## INTRODUCTION

The Siwalik Group of the Indian Subcontinent comprises a thick sequence of fluvial deposits outcropping south of the spectacular mountain chains along the interface with the Tibetan highlands. Its successive formations represent continuous, rapid deposition of sediment shed from these highlands throughout Neogene time. The deposits contain multiple, superposed assemblages, spanning approximately 20 million years. These successive faunas are snapshots of past life, superposed unambiguously and readable like an epic volume of natural history.

The paleo-Indus River of Pakistan occupied a vast flood plain with local variation in relief and, presumably, habitats. Since at least Early Miocene time (Downing *et al.* 1993), it drained the rising hills of the highlands to the north, depositing sediments in its flood plain, layer upon layer, and entombing fossiliferous horizons in succession. These deposits are differentiated today as formations of the Chitarwata and Siwalik groups, which yield
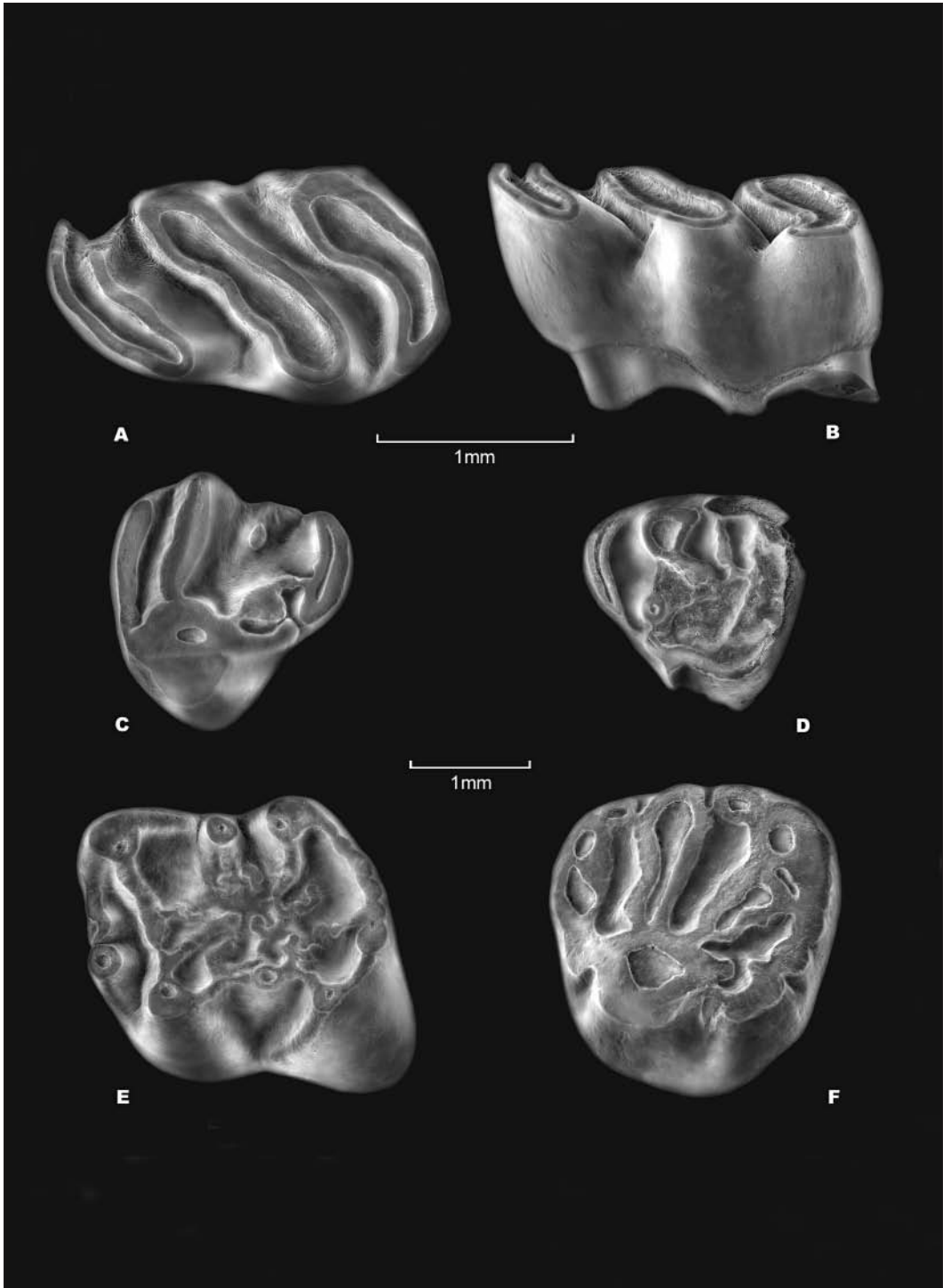
Figure 1  Images of selected arboreal taxa discussed in the text. **A** & **B**: Platacanthomyidae, occlusal and labial views of YGSP 36144. **C**: *Callosciurus* sp., left M3, YGSP 21682. **D** & **E**: *Ratufa sylva*, YGSP 17260 and 17269, m1 and P4. **F**: *Ratufa* sp., YGSP 48043, upper molar. Scale bars equal 1 mm; A and B, above, at same scale; scale bars below for C-F.

fossils throughout the country, from the Murree Hills in the north, to the distal reaches of Sind in the south. The Siwaliks (shorthand for most of these units) have been known to westerners to produce fossils for the last two centuries, and to local peoples for many centuries before that (see Colbert 1935). Many scholars have found and described Siwalik fossils (e.g., Dehm & zu Oettingen-Spielberg 1958; Pilbeam *et al*. 1980; de Vos *et al.* 1987; van der Made & Hussain 1992).

Despite early work on small mammals (Hinton 1933; Wood 1937) it was not until late last century that the techniques of wet sieving of large quantities of fossiliferous sediment began to fill out the rich rodent record of the Siwaliks (see e.g., Jacobs 1978). Teams under Hans de Bruijn, Utrecht University, led at the forefront of the developing small mammal record in Pakistan. Key papers summarize important work in various regions of the country (De Bruijn *et al*. 1981; De Bruijn *et al.* 1989; Wessels 1996; Wessels *et al.* 1982).

The Potwar Plateau of northern Pakistan contains a particularly well exposed and fossiliferous sequence of the Middle to Late Miocene Kamlial, Chinji, Nagri, and Dhok Pathan formations. This area has been studied by a group of colleagues from Harvard, Yale, University of Arizona, and other institutions working with the Geological Survey of Pakistan. Given relatively continuous and complete sedimentation, paleomagnetic techniques have been applied successfully to date the sequence. In the Potwar Plateau, Siwalik Group sedimentation began before 18 Ma with the Kamlial Formation. Its varied sands and reddish overbank deposits yield a moderately productive fossil record. A changed sedimentation regime at about 14 Ma, dominated by red fine-grained units, deposited the Chinji Formation, which is rich in fossils. The superposed Nagri Formation is time transgressive at its contacts, is characterized by dominance of thick, multistoried sands, usually blue-gray in hue, and is of sporadic

fossil productivity. The base of the unit is >11 Ma locally, and its upper contact is usually <10 Ma. The overlying Dhok Pathan Formation represents Late Miocene time and is characterized by fossiliferous overbank deposits and smaller buff-colored sand units representing other stream systems (Barry *et al.* 1980). Local thin conglomerates increase in occurrence at higher stratigraphic levels. The fossil record for the Potwar Plateau has been developed especially in three regions: the Khaur area, the Chinji area 40 km to the south, and the Hasnot area 70 km to the east (see Barry *et al.* 1990, 1995, 2002). The small mammal record is, of course, dominated by screen-wash sites. Surface remains are important, but rodent diversity has emerged in large collections screened from bulk samples of fossiliferous sediment. Over 60 small mammal sites have been intensively screened by wet-sieving, yielding numerous records of species throughout the 18 to 6 Ma interval (Flynn *et al.* 1995).

Localities in the field are tied unambiguously to composite sections, with demonstrable superposition. Their sequence is observed; their ages are interpolated from magnetostratigraphy, according to the Cande & Kent (1995) time scale. This time scale is more useful than others, but the actual age of sites is irrelevant for many discussions - it is the superposition and known difference in age of successive sites that are important.

The fine data base of Siwalik mammal occurrences has been utilized to track changes in standing diversity and faunal turnover in the fossil record (Barry *et al.* 1995). Middle Miocene species richness climbed and built to a maximum at about 14 Ma, declined gradually and then more rapidly after about 10 Ma. The small mammal record demonstrates a remarkably high level of species richness (higher than expected of modern analogues) during the Middle Miocene, paralleling apparent trends in Europe (Flynn *et al.* 1998). Turnover was ongoing throughout the Miocene, but also concentrated in peaks. Other work has shown that vegetation changed

in the late Miocene after 8 Ma (Cerling *et al.* 1997), although recent study indicates that this change was set in motion earlier (Morgan *et al.* 1994; Jacobs *et al.* 1999). Some clusters of mammal events in the late Miocene may reflect the vegetation revolution (Barry *et al.* 2002).

Larger numbers of specimens recovered from single sites (generally > 200 teeth) are considered to represent local Siwalik paleo-communities reasonably well for two reasons. First, they record greater proportions of past biotas and show relative stability in composition of taxa through time. Second, taphonomic processes, as far as we can ascertain, are comparable for almost all sites (see Badgley *et al.* 1998); those that are distinctive can be excluded from analysis. Sites are individual bedding sets of homogeneous depositional origin (flood plain near channels), and formed on the scale of years (not millennia). Fluvial processes tend to scatter elements, not concentrate them; richer concentrations are local, representing no more than the ranges of predators. Badgley *et al.* (1998) noted that Chinji Formation collecting sites represent mainly flood plain habitat, and are primary accumulations; the preserved assemblages vary little and composition is not affected by lithology. Flynn *et al.* (1998) felt that these observations pertain to the entire section, although there is some evidence that environment of deposition changes to more aquatic conditions in the upper levels of the Dhok Pathan Formation.

## INTERPRETING PALEOENVIRONMENT
Given advances in recognizing and specifying faunal turnover, it is time to turn to interpreting significance of the observed changes. Many analyses of vertebrate paleo-habitats focus on rodents. The approach herein is similar, but with notation of changes among other small mammals. Given that most Siwalik small mammal taxa have no associated osteological remains to indicate adaptation, with the exception of some rhizo-

myids (Flynn 1982), the principle means of inferring paleohabitat from small mammals is through actualism - assumption that the habitat preferred by modern analogues is that of fossil relatives. This assumption is a big one given the time depth, 6 to 18 Ma, and given that most genera are not extant. Yet it is reasonable to suppose similar paleohabitat for conservative groups, e.g., families whose modern members dominantly prefer certain habitats. Examples include slow lorises and tree shrews that today prefer arboreal habitat, or hares (Leporidae), many of which are adapted to open country.

However, this approach is very risky, particularly when based upon single taxa. One can cite apparent exceptions, such as *Caprolagus* that likes bushy cover unlike most leporids that prefer open country, or the dry-adapted *Galago senegalensis* that does not need closed canopy as lorises do. For this reason, previously I have avoided conclusions about paleohabitat. Yet as the Siwalik data base grows, the validity of paleohabitat reconstruction becomes firmer. By using whole assemblages and judging consistency through time, trends become meaningful. In the following, I start to analyze paleohabitat by considering preferences of whole groups.

## Taxa preferring moist forest/arboreal habitat
Small mammals recovered by screening methods from Siwalik sediments are dominantly rodents. Chiroptera are relatively few, although they must have been an abundant component of the Miocene biota. There are some erinaceids and fewer lagomorphs, shrews, tree shrews, and lorises. Certain rodents seem to indicate subtropical to tropical wet conditions, including closed canopy forest. These stand out as the clearest signal of habitat throughout the Siwalik sequence. Habitat preferences are less readily hypothesized for most taxa, however, because surviving relatives show varied specializations. In the following, a simplistic approach is taken to evaluate habitat. I simply note that fraction

of taxa (not abundance) in successive assemblages that indicate subtropical forest. The approach is conservative in that only those taxa likely to indicate forest are emphasized; probably the proportion of forest habitat elements is underestimated. The Appendix lists assemblages in million year time slices (a slice is centered at the Ma unit, +/- 100,000 yrs). Forest elements are flagged by an asterisk.

Among Siwalik assemblages, squirrels (Sciuridae) are never a dominant element. Many of the squirrel teeth recovered are ground squirrel or chipmunk relatives (*Eutamias*), which could reflect open to dry habitat as readily as forest, so these are not tagged as indicators of dense cover. However, the arboreal flying squirrels (Petauristinae) occur in various localities. These are few in number at any given site, and Bouwens & De Bruijn (1986) have pointed out difficulties in identification. The nomen *Hylopetes* is applied presently for small flying squirrels in the fossil record. Although the unfortunate bias against preservation of flying squirrels has led to their under-representation, the issue is occurrence rather than abundance, which means that the analysis depends on larger samples (see Flynn *et al.* 1998). There are other arboreal squirrels in the Siwalik record (see below).

Most rhizomyid rodents are scored as subtropical forest indicators. Living taxa require moist conditions, Asian bamboo rats being restricted to areas of dense growth. That African *Tachyoryctes* occupies more open habitat is likely a derived condition, correlated to hypsodonty of the cheek teeth. Therefore, the advanced Siwalik tachyoryctine *Eicooryctes* is not scored as dependent on forests.

I judge fossil thryonomyoids (*Paraulacodus*, *Kochalia*) as indicators of dense growth, although the living species *Thryonomys gregorianus* lives in moist, tropical savanna (Kingdon 1974). Probably the enigmatic *Diatomys* is a tropical indicator, given its occurrence in the middle Miocene of

Thailand and China (Mein & Ginsburg 1985; Li 1974), but its younger Siwalik relative at 11 Ma is high crowned, likely more open-adapted.

Dormice are typically forest dwellers, although some species are terrestrial. I assign forest habitat for species of *Myomimus*, which occur throughout the 8-13+ Ma interval.

Dendromurine rodents dominantly prefer dense growth today, but are problematic because some living forms are arid-adapted. Only a few living species are actually arboreal. Some Siwalik genera have been considered dendromurines (e.g. Lindsay 1988), but Wessels (1996) argues for gerbilline relationship for *Dakkamys* and *Paradakkamys*. In any case, assumption of forest habitat is not supported for these taxa. The genus *Potwarmus* may be a primitive dendromurine, and is considered forest-dwelling based on occurrence elsewhere in the Oriental Realm, the Middle Miocene of Thailand. One might suspect that the true mouse *Antemus*, conceivably derived from *Potwarmus* (Lindsay 1988), preferred tropical forest, too, but mice have radiated throughout the globe, displaying wide variance in habitat preference. Cladistic treatment of fossil and living taxa might help to trace the pattern of radiation into varied habitats.

## Platacanthomyidae

This small group of muroids is frugivorous and prefers moist, arboreal habitat exclusively. Up to now unknown in the fossil record of the Indian Subcontinent, one specimen (Fig. 1a, b) indicates the presence of this group in the early Middle Miocene Lower Siwaliks. YGSP 36144 is a right lower third molar from locality Y802, which dates to about 17 Ma. Measurements are 2.0 mm long, 1.3 mm wide. The molar is reduced and narrow posteriorly as in early platacanthomyids (see Fejfar & Kalthoff 1999). It has three oblique, transverse lophs, which are gently inclined posteriorly. The two valleys between lophs, corresponding to synclines II and III (see Fejfar

1999), are open both lingually and labially, but the labial outlet is constricted slightly (Fig. 1b). The enamel of the anterior loop is worn anterolabially; anterolingually the enamel wall is thickened, but there is no hint of expansion of the anterolophid as occurs in this region in all known platacanthomyids.

YGSP 36144 is most similar to, but larger than, *Typhlomys cinereus chapensis* among living forms. It is much larger than fossil *Typhlomys* from the late Miocene of Lufeng, Yunnan (Qiu 1989), but only somewhat larger than *T. macrurus*, ZHENG 1991, from the late Pliocene Longgupo fauna, south bank of the Yangtze River. The Siwalik specimen is closer to some species of the fossil genus *Neocometes* in that the oblique valleys are open labially. It is much larger than *Neocometes orientalis* MEIN *et al.* 1990, from Li, early Middle Miocene of Thailand.

The affinities of the taxon represented by this single specimen are far from clear. It is closest to different platacanthomyid species in different respects, and I do not attempt to assign it to a known genus. Yet, for the purposes of environmental reconstruction, its lophate pattern is consistent with frugivory.

## Arboreal squirrels

Several specimens throughout the Lower to Middle Siwaliks represent arboreal squirrels other than volant Petauristinae. Currently under study, some can be attributed to frugivorous genera living in Southeast Asia and islands of the Indian Ocean.

Genus *Callosciurus* GRAY 1867
*Callosciurus* sp.

One molar from locality Y589 at 14 Ma attests to the presence of this squirrel in the Siwaliks. YGSP 21682 (L = 2.1, W = 2.2 mm; Fig. 1c) is a left upper third molar that conforms to the proportions of living *Callosciurus*. Its major cusps and crests show planar wear. There is no hypocone, but the expanded posterolabial portion of the tooth bears a large metaconule. The protoloph is

narrow, without hint of a paraconule. A thin anterior cingulum joins the protocone. There is a distinctive, transversely elongate mesostyle, and a crest posterior to the metacone, which joins the protocone by means of a cingulum. There are three roots.

Genus *Ratufa* GRAY 1867
*Ratufa sylva* sp. nov.

**Holotype:** YGSP 17260, left m1 (Fig. 1d).
**Hypodigm:** YGSP 17260, 17259 (left P4), 17306 (anterior portion of a right lower molar).
**Measurements:** YGSP 17260, m1: L = 2.6, W = 2.6 mm; YGSP 17306, m 1 or 2: anterior W = 2.5 mm; YGSP 17259, P4: L = 1.9, W = 1.9 mm.
**Etymology:** Latin for forest, in reference to its probable habitat.
**Type locality:** Y259, Nagri Formation, Kaulial Kas, Potwar Plateau, Pakistan (10.5 Ma). YGSP 17259 is also from this locality. YGSP 17306 is from Y410 (9.4 Ma).
**Diagnosis:** Smallest known species of the genus.
**Description:** YGSP 17260 represents a large squirrel with bulbous cusps and numerous crenelations typical of *Ratufa*. It is somewhat wider posteriorly than anteriorly. The trigonid is a narrow valley with small anteroconid on its border, anterolingual to the protoconid. The metaconid is high; the metalophid is complete, but very low at its midpoint. The tooth is dominated by a large basin. A strong mesoconid lies internal to, and is connected to both protoconid and hypoconid. A lingual mesostylid is isolated. The posterior wall of the tooth is a continuous, beaded crest. YGSP 17306 agrees in all preserved details, but its anteroconid projects more anteriorly.

YGSP 17259 (Fig. 1e) is somewhat smaller than might be expected based on size of the lower molar, if these single teeth can be taken as representative for the fossil species. However, it is damaged and missing enamel posteriorly and lingually. It is triangular due to the anterolabially projecting anterocone.

The paracone is bigger than the metacone. The enamel is crenelated (one fold in the position of the mesostyle). There are both paraconule and metaconule. There is no hint of a hypocone from what is preserved.

### cf. *Ratufa* sp.

An additional specimen (Fig. 1f) may be referred to *Ratufa*, although its identity with *R. sylva* is doubtful. YGSP 48043 is a left upper molar from locality Y802 (17 Ma). It appears to be more heavily built, perhaps higher crowned than *R. sylva*, although its size (L = 2.3, W = 2.55 mm) is comparable. The specimen is worn, but shows a prominent anterolabial cingulum, protoloph with small paraconule, metaloph with large metaconule, and a hypocone close to and smaller than the protocone. Both protoloph and metaloph become narrow near the protocone. There is a small mesostyle and the tooth has three roots, the largest located internally.

### Discussion

*Ratufa* or close relatives are present in the Siwaliks from at least from 17 to 9.4 Ma. Samples are inadequate to judge whether these might represent a single lineage throughout this time. The older Y802 specimen is worn, and does not show the expected crenelations. If it is representative of the entire Siwalik lineage, then it shows that this Miocene species is characterized by hypocone size smaller than the protocone. Dimensions alone do not rule out referral of the Y802 specimen to *Ratufa sylva*. The Siwalik *Ratufa* are clearly smaller than any known species including the fossil *Ratufa maelongensis* MEIN *et al.*, 1990, from Thailand. The Y802 molar is much less complicated than the holotype of *R. maelongensis*. The freshness of the holotype of *R. sylva* lends to a gracile appearance relative to living species.

## ANALYSIS

Assemblages contain a sizable minority of taxa that can be classified as indicating moist forest. Tracking occurrences of the taxa noted above, the proportion of small mammal species indicating forest is about one fourth to one third at most localities. The Appendix shows species lists for rodents for each million-year interval from 18 through 7 Ma. The table includes all records at each time slice (centered at the million year mark, +/- 100,000 years), not just the most productive localities that Flynn *et al.* (1998) used to study species richness. The Appendix provides notation of how many localities contribute to each time slice and the approximate number of specimens on which each faunal list is based. The slices do not sample some of the richer localities between m.y. intervals in the sequence. Fluctuation through time in total species richness seems to be an insignificant factor for the overall pattern (Flynn *et al.* 1998). Despite the late Miocene decline in species richness demonstrated by previous studies, the proportion of moist forest indicators remains roughly stable through the Miocene (Fig. 2). There is some suggestion that forest elements decline slowly in taxonomic richness through 11 Ma, recover to higher proportions thereafter, and then turn downward at the end of the study interval. The reality of these underlying trends needs to be tested.

The more robust observation is simply that forest habitat persisted as a component of Siwalik environments through 7 Ma. However, the taxa contributing to the proportion undergo extinction, particularly later in the Miocene. They are replaced by other forest indicators. Nelson (2003) is studying Siwalik paleohabitats with reference to local extinction of *Sivapithecus* at about 8.4 Ma. Her analysis of oxygen isotopes indicates that the seasonal precipitation pattern of the Siwaliks changed mainly by decreasing total annual precipitation, with the likely result that expanses of forest became increasingly fragmented. Under this scenario, even after
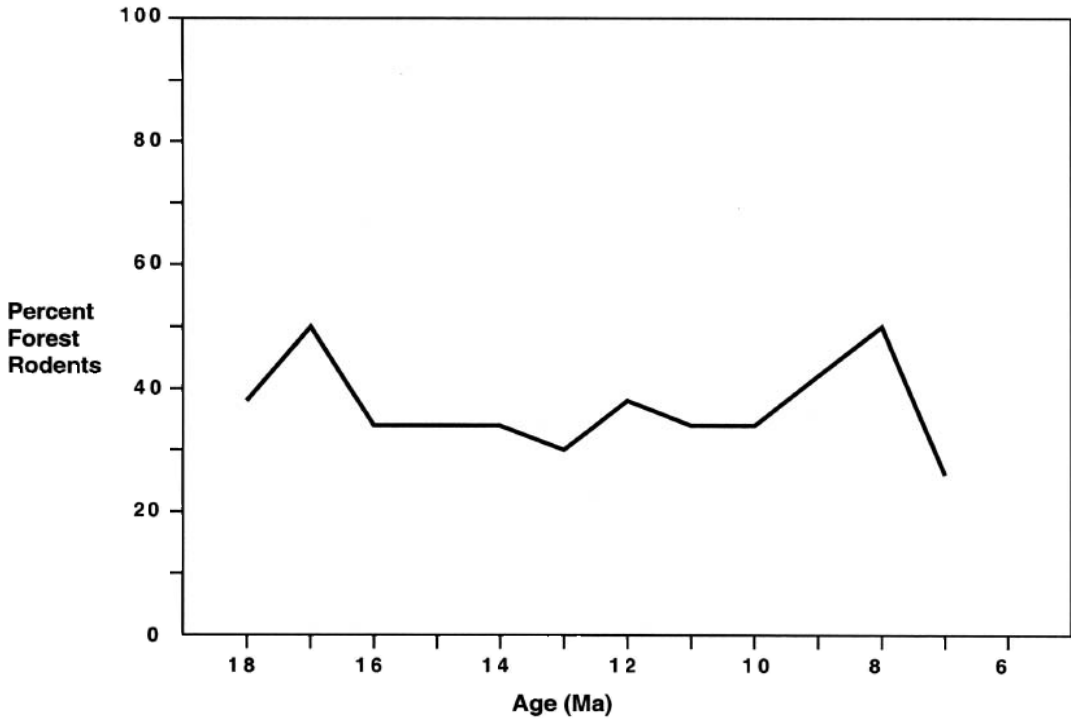
Figure 2  Rodent assemblages analyzed in million year time slices (centered at the million years, +/- 100,000 yrs). Percent species indicating forest habitat is tracked through time, 18 through 7 Ma, left to right. The data indicate presence of forest throughout this time, although trends of decreasing forest, followed by recovery at 8 Ma and late Miocene decline, are suggested; their validity remains to be tested.

large hominoids could no longer be supported by remaining forest, certain small mammals, needing fewer resources, could persist.

Other faunal data support this view of changing habitat and forest fragmentation. Late in the small mammal record, taxa apparently preferring open habitat begin to appear. The spread of open habitat taxa is heralded by the unique record of the gerbil *Abudhabia pakistanensis* FLYNN & JACOBS, 1999, at about 8.6 Ma. Later, around 8 Ma, the porcupine *Hystrix* and hares appear. By 7.8 Ma, rhizomyids undergo significant turnover, including appearance of the high crowned tachyoryctine *Eicooryctes*. Coinciding with these events are the last records of forest-adapted tree shrews and lorises at about 8 Ma.

During later Miocene time, forest habitat did not decrease monotonically to zero. Some small scale trends are suggested, including decline and recovery by 8 Ma, but these remain to be tested, and this study has not addressed changes in abundance or ecomorphology. The drop in forest elements from 8 to 7 Ma could reflect small sample numbers at 7 Ma, or the beginning of late Miocene loss of forest. Also, forest habitat thinning could have been a long process involving changes in its mosaic aspect (Jacobs *et al.* 1999). Still, riparian forest could have continued as a food source, particularly for small mammals, long after 7 Ma.

Forest habitat persisted as a component of the Siwalik environmental mosaic through 7 Ma. Although data are insufficient currently to reflect the fate of the forests in the latest Miocene, future work on fossiliferous rocks in the 6 to 5 Ma range in the Indian Subcontinent should show how the landscape

reflected changing floral patterns during this critical time. Future approaches to understanding habitat might involve ecomorphology of all taxa. The present study surveyed only forest elements. More diverse habitat preferences could be postulated for more taxa.

One final note concerns Ctenodactylidae. Apparently counter to the trend of loss of moist habitat is the disappearance of the ctenodactylid *Sayimys* at 10 Ma. Living ctenodactylids, or gundis, are arid-adapted and confined to Africa, yet the group was widespread and diverse throughout the Old World during the Neogene. I suspect that Ctenodactylidae present a case where attribution of modern habitat to fossil genera is erroneous. The living forms may have survived <u>because</u> they radiated into arid niches. *Sayimys* and other genera may have preferred moist environment, and competition with other forms, notably murids, possibly led to their decline.

## ACKNOWLEDGMENTS

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**APPENDIX** Rodent species recorded in million year intervals for the Potwar Plateau Siwaliks. Sources include Flynn *et al*. (1995) and citations therein plus Baskin (1996), Wessels (1996), Cheema *et al*. (2000).  * = taxa hypothesized to prefer forest habitat.

| **18 Ma** | **17 Ma** | **16 Ma** |
|---|---|---|
| 2 localities, 300 specimens | 1 loc. 75 specimens | 2 locs. 170 specimens |
| Sciuridae | cf. *Ratufa* sp.* | Sciurid A |
| *Sayimys minor* | *Sayimys intermedius* | *Sayimys intermedius* |
| *Prokanisamys* sp.* | Platacanthomyidae* | *Kochalia geespei*\* |
| *Potwarmus primitivus*\* | *Prokanisamys* sp.* | *Prokanisamys* sp.* |
| *Myocricetodon sivalensis* | *Kanisamys* sp.* | *Kanisamys indicus*\* |
| *Sindemys aguilari* | *Potwarmus primitivus*\* | *Potwarmus primitivus*\* |
| *Democricetodon* A | *Myocricetodon sivalensis* | *Myocricetodon sivalensis* |
| *Diatomys* sp.* | *Sindemys aguilari* | *Punjabemys mikros* |
| | *Democricetodon* A | *Sindemys aguilari* |
| | *Democricetodon* B | *Democricetodon* A |
| | | *Democricetodon* B |
| | | *D. kohatensis* |

| **15 Ma** | **14 Ma** | **13 Ma** |
|---|---|---|
| 2 localities 140 specimens | 4 localities 1200 specimens | 3 localities 950 specimens |
| Sciurid A | Large Sciurid | Sciurid B |
| Petauristinae* | *Eutamias* sp. | *Eutamias* sp. |
| *Sayimys sivalensis* | *Callosciurus* sp.* | *Heteroxerus* sp. |
| *Kochalia geespei*\* | Petauristine* | Petauristine* |
| *Prokanisamys* sp.* | *Sayimys sivalensis* | *Myomimus* sp.* |
| *Kanisamys indicus*\* | *Kochalia geespei*\* | *Sayimys sivalensis* |
| *Potwarmus primitivus*\* | *Prokanisamys* sp.* | *Kochalia geespei*\* |
| *Myocricetodon sivalensis* | *Kanisamys indicus*\* | *Paraulacodus indicus*\* |
| *Mellalomys lavocati* | *Kanisamys potwarensis*\* | *Prokanisamys* sp.* |
| *Punjabemys mikros* | cf. *Potwarmus* sp.* | *Kanisamys indicus*\* |
| *Sindemys aguilari* | *Myocricetodon sivalensis* | *Antemus chinjiensis* |
| *Sindemys mythikos* | *Myocricetodon* sp. | *Myocricetodon sivalensis* |
| *Democricetodon* A | *Mellalomys lavocati* | *Dakkamys barryi* |
| *Democricetodon* B | *Punjabemys mikros* | *Dakkamys asiaticus* |
| *D. kohatensis* | *Punjabemys downsi* | *Mellalomys lavocati* |
| | *Sindemys aguilari* | *Mellalomys perplexus* |
| | *Sindemys mythikos* | *Punjabemys mikros* |
| | *Democricetodon* A | *Punjabemys downsi* |
| | *Democricetodon* B | *Sindemys sivalensis* |
| | *D. kohatensis* | *Sindemys mythikos* |
| | *Democricetodon* E | *Democricetodon* B |
| | | *D. kohatensis* |
| | | *Democricetodon* E |
| | | *Democricetodon* F |
| | | *Democricetodon* G |
| | | *Democricetodon* H |

## APPENDIX (continued)

| 12 Ma | 11 Ma | 10 Ma |
|---|---|---|
| 2 localities 300 specimens | 1 locality 320 specimens | 1 locality 200 specimens |
| Petauristine* | cf. *Hylopetes* sp.* | *Eutamias* sp. |
| *Eutamias urialis* | *Eutamias urialis* | *Ratufa* sp.* |
| *Myomimus* sp.* | *Myomimus* sp.* | cf. *Hylopetes* sp.* |
| *Sayimys* sp. | *Sayimys* sp. | *Myomimus* sp.* |
| *Sayimys chinjiensis* | *Sayimys chinjiensis* | *Sayimys chinjiensis* |
| *Kochalia geespei** | cf. *Diatomys* sp. | *Kanisamys nagrii** |
| *Prokanisamys* sp.* | *Kanisamys indicus** | *Progonomys hussaini* |
| *Kanisamys indicus** | *Kanisamys nagrii** | *Karnimata* sp. |
| *Progonomys hussaini* | *Progonomys hussaini* | new murine |
| *Dakkamys asiaticus* | *Dakkamys asiaticus* | *Democricetodon* B |
| *Paradakkamys chinjiensis* | *Paradakkamys chinjiensis* | *Democricetodon* F |
| *Mellalomys perplexus* | *Mellalomys perplexus* | *Democricetodon* G |
| *Democricetodon* B | *Democricetodon* B | |
| *D. kohatensis* | *D. kohatensis* | |
| *Democricetodon* E | *Democricetodon* E | |
| *Democricetodon* F | *Democricetodon* F | |
| *Democricetodon* G | *Democricetodon* G | |
| *Democricetodon* H | *Democricetodon* H | |

| 9 Ma | 8 Ma | 7 Ma |
|---|---|---|
| 3 localities 500 specimens | 3 localities 400 specimens | 2 localities 300 specimens |
| *Eutamias* sp. | cf. *Eutamias* sp. | Sciuridae undet. |
| *Hylopetes* sp.* | *Hylopetes* sp.* | *Hystrix* sp. |
| *Myomimus* sp.* | *Myomimus* sp.* | *Eicooryctes kaulialensis* |
| *Kanisamys sivalensis** | *Hystrix* sp. | *Protachyoryctes tatroti** |
| *Brachyrhizomys tetracharax** | *Kanisamys sivalensis** | *Rhizomyides sivalensis** |
| *Brachyrhizomys pilgrimi** | *Rhizomyides* sp.* | cf. *Mus* sp. |
| *Progonomys debruijni* | *Brachyrhizo. pilgrimi** | *Karnimata huxleyi* |
| *Karnimata darwini* | *Progonomys* sp. | *Parapelomys robertsi* |
| Large murine | *Karnimata* sp. | |
| *Parapodemus* sp. | *Parapelomys* sp. | |
| *Democricetodon* F | | |
| *Democricetodon* G | | |