

Miocene Small Mammals from Jalalpur, Pakistan, and Their Biochronologic Implications

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Abstract Isolated deposits near Jalalpur, Potwar Plateau, northern Pakistan, yield a diverse small mammal fossil assemblage. The fossil locality, JAL-101, contains a particularly good sample of a primitive species of the early murid *Progonomys*, which is named herein. This and other elements of the fauna (particularly Cricetidae and Rhizomyidae) argue for an age younger than that of typical Chinji Formation sites. Consequently JAL-101 is important because it improves the sample of fossils representing early late Miocene time in the Siwaliks (time encompassing deposition of upper portions of the Chinji Formation and lower portions of the Nagri Formation). The fauna of 13 small mammal species can be used to make an age estimate for JAL-101 by correlation to the Potwar biostratigraphic sequence. Temporal ranges of rodent species, as presently known, constrain JAL-101 to about 11 Ma, possibly as young as 10 Ma.

Key words: Pakistan, Miocene, Siwaliks, rodents, systematic paleontology.

Introduction

The rodent material described here was collected from isolated redbeds considered correlative to the upper part of the Chinji Formation or the lower part of the Nagri Formation. The fossil deposit is an isolated outcrop of steeply dipping redbeds northeast of Jalalpur, called locality JAL-101 (Figs. 1, 2). It was investigated during two field excursions in 1982 and 1984, during which bulk samples were quarried for later screening of microfossils. On the basis of the field work carried out in 1982, preliminary results were published by Cheema *et al.* (1983), but most of the determinations were incomplete due to small sample size, and no species were recognized with certainty. The muroids were apparently new, but too poorly represented to be

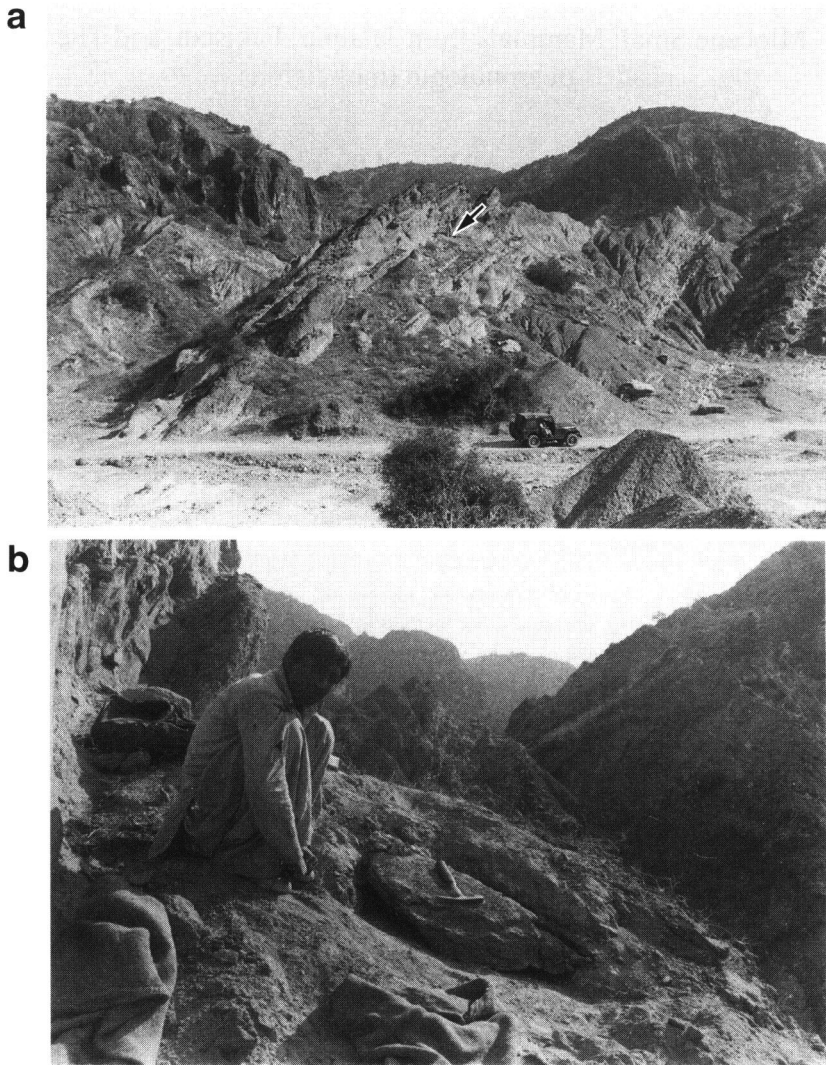


Fig. 1. a: General view of the Miocene rocks exposed near the Jalalpur area; arrow shows the location of JAL-101. b: closer view of the locality JAL-101.

characterized. Faunal comparison was also difficult because of the incomplete small mammal fauna record then known from upper Chinji horizons. Field work in 1984 improved samples, permitting a more informed discussion of the fauna, including diagnosis of a new species. Meanwhile, the biostratigraphy of the type areas of the Chinji and Nagri formations became more refined, and with its magnetostratigraphy (Flynn *et al.* 1995) we can estimate the age of JAL-101.

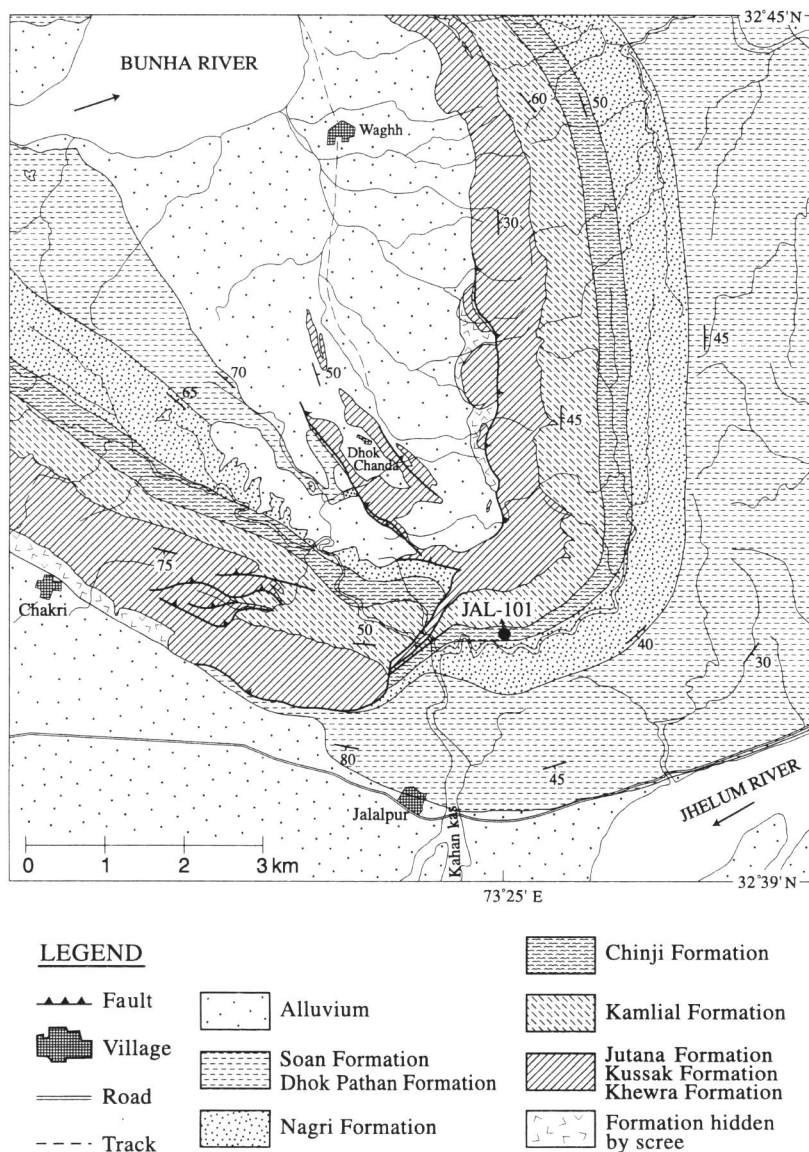


Fig. 2. Geologic map of the Jalalpur area showing the location of JAL-101 (modified from Gee, 1981).

The present work considers all small mammal fossils from the 1982 and 1984 collections, but detailed comments are restricted to those taxa for which better representatives are now available. The 1984 collection yielded a surprisingly abundant assemblage of murid teeth, which can now be considered at the species level. Other ro-

dent groups such as Cricetidae, Rhizomyidae, and Sciuridae are not significantly improved by the 1984 collection, but comments on these taxa are revised in light of other recent work.

Thus, the purpose of this paper is to formally describe the new murid, and to review the biochronological significance of the fauna, based on the new work. Since many of the specimens were figured in Cheema *et al.* (1983), we concentrate mainly on figuring new material relevant to these goals. In our approach, we use standard dental nomenclature (molar and premolar designated by "M" and "P" respectively, and upper and lower teeth by superscript or subscript). Measurements are in millimeters. All specimens bear the prefix PMNH (Pakistan Museum of Natural History), and are properly housed at that institution.

Systematic Paleontology

Order Erinaceomorpha Gregory, 1910

Family Erinaceidae Fischer de Waldheim, 1817

Genus *Galerix* Pomel, 1848

Galerix* cf. *G. rutlandae Munthe and West, 1980

Material: PMNH 5001, lower molar fragment.

Description: The Jalalpur fauna includes two insectivore-like molars. A single fragmentary lower molar (PMNH 5001) is appropriate in size and morphology for *Galerix rutlandae* (see Munthe & West, 1980). The other tribosphenic specimen (PMNH 5002) is too large to pertain to this species. Neither identification figures importantly in the biochronological record.

Order Scandentia Wagner, 1855

Family Tupaiidae Gray, 1825

Tupaiidae gen. et sp. indet.

Material: PMNH 5002, damaged trigonid of left $M_{1\text{ or }2}$.

Description: The specimen is cracked and fragmented, but shows a weak buccal cingulum. At the main cusp, the protoconid, the trigonid wall is high. The paraconid diverges widely from the metaconid. The much greater size of PMNH 5002 (trigonid width=1.6 mm) than that of PMNH 5001 and open trigonid basin confirm comparison with Tupaiidae. Further identification requires more material.

Order Rodentia Bowdich, 1821

Suborder Sciuromorpha Brandt, 1855

Family Sciuridae Gray, 1821

Eleven teeth in the total Jalalpur collection represent this family. Sciuridae are

an old group of rodents with distinctive masseteric musculature (sciuromorphy; see McKenna and Bell, 1997, for discussion on the logic of subordinal divisions of the Order). Sciuridae include terrestrial to arboreal squirrels, and occur throughout the Siwalik sequence, but always in low abundance. Numerically, the dominant rodents of higher category in the Siwalik record are the myomorphs (see below).

Sciuridae are represented in the Siwalik record mainly by chipmunks, indicating vegetational cover (but not necessarily closed canopy), by a few ground squirrels, and by flying squirrels (usually indicating trees). Cheema *et al.* (1983) indicated that two taxa were represented in the Jalalpur collection, a smaller gracile and a robust form. The gracile form corresponds to the type material of the chipmunk *Eutamias uralis*.

Subfamily Sciurinae Baird, 1857
Genus *Eutamias* Trouessart, 1880
Eutamias uralis Munthe, 1980

Fig. 3a, b

“Cf. *Eutamias uralis*,” in part; Cheema *et al.*, 1983, p. 277–278, fig. 8.

Material: Four isolated teeth, PMNH 5003 (M^{1-2}), 5004 (damaged M_{1-2}), 5005 (DP_4 fragment), and 5006 (M_3).

Description: The upper molar has high, thin crests (protoloph, metaloph, and anteroloph). The straight, transverse protoloph shows a minute protoconule. The metaloph, with strong metaconule, is incomplete. An indistinct hypocone is partially merged with the sloping posterior wall of the protocone.

The lower molars show well separated protoconid and hypoconid, which are joined by a thin, longitudinal crest. The anterolophid is thin, as is the posterolingual wall, which incorporates an indistinct entoconid. The short posterior arm of the protoconid is low and terminates abruptly.

Discussion: The morphology of the specimens corresponds closely to that of the hypodigm for this species (Munthe, 1980). Measurements are also consistent, although at the upper end of the range for the hypodigm (for example, PMNH 5003 length (1.5) and width (1.8) are near the upper limits observed by Munthe, 1980). JAL-101 is likely younger than Daud Khel, type locality for the species, and larger observed size is consistent.

Eutamias uralis is the only formally named squirrel of the Lower and Middle Siwaliks. Other taxa, and probably younger chipmunks can be described in the future, but at present the limiting parameter is lack of good comparative material. Because squirrels are always uncommon, the stratigraphic range of *E. uralis* could be extended upward. Consequently, this species, by itself, does not constrain precisely the age of JAL-101.

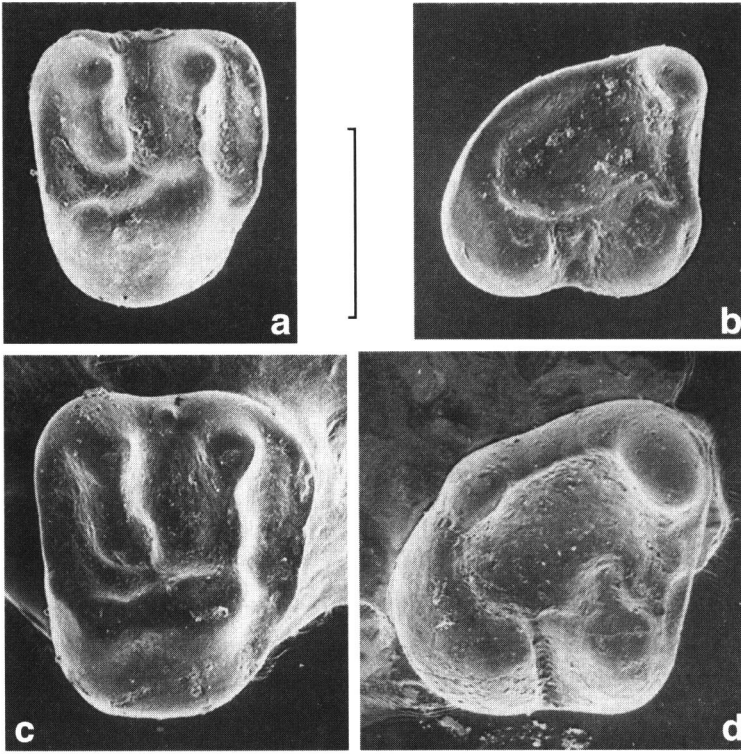


Fig. 3. *Eutamias urialis* (a–b) and Sciurinae gen. et sp. indet. (c–d). a: PMNH 5003, R M^{1-2} ; b: PMNH 5006, R M_3 ; c: PMNH 5007, R M^{1-2} ; d: PMNH 5013, R M_3 . Scale bar represents 1 mm.

Sciurinae gen. et sp. indet.

Fig. 3c, d

Material: PMNH 5007 (P_4), 5008 (M^{1-2}), 5009–5012 (M_{1-2}), 5013 (M_3).

Description: Compared to *Eutamias urialis*, these cheek teeth are larger, higher crowned, and with major cusps more inflated and relatively closer. Crests joining cusps are correspondingly less sharp (more inflated) than those of *Eutamias urialis*. The conules are undeveloped; the metaloph thins near the protocone, but is complete. The protocone is near the center of the internal side of the tooth; its lingual wall slopes strongly. The hypocone is well developed. On lower molars, the bulbous protoconid and hypoconid nearly touch. Entoconids are variably developed. M_3 is triangular in shape.

Discussion: Because so few sciurid taxa from the Siwaliks have been adequately described, with range of variation characterized, it is not possible to determine the

affinities of this larger squirrel precisely, or even to ascertain whether more than one species is represented. For comparison, dimensions of PMNH 5008 are 1.75 mm long, 2.3 wide. Because this record cannot effect the biochronology until squirrel biostratigraphy is better understood, it is not considered further here.

Suborder Hystricomorpha Brandt, 1855
 Superfamily Ctenodactyloidea Tullberg, 1899
 Family Ctenodactylidae Zittel, 1893
 Genus *Sayimys* Wood, 1937
Sayimys chinjiensis Baskin, 1996

“Cf. *Sayimys* sp.”; Cheema *et al.*, 1983, p. 279.

Material: PMNH 5014, DP⁴ fragment; 5015, well preserved M¹⁻²; 5016, worn M¹⁻²; 5017 and 5018, two lower molar fragments.

Description: The lingual flexus of the single complete upper molar extends almost to the base of the crown, while the buccal flexus is very deep in the center of the tooth but relatively shallow at the buccal margin. Unilateral hypsodonty of the lingual part of the molar has developed to the same degree as in *Sayimys obliquidens* (Bohlin, 1946), and wear is relatively even on the lingual surface. The protoloph is simple, without a distinct anteroloph. The protoloph and metaloph unite centrally very early in wear. The metaloph comprises the hypocone and metacone and a small posteroloph which are quickly fused with wear. The protoloph is slightly wider than the metaloph. Measurements of M¹⁻² (PMNH 5015): Length×Posterior width×Anterior width=2.04×2.13×2.22 mm.

Discussion: These specimens compare well with *Sayimys* of Chinji and Nagri formations and resemble morphologically the type material of *S. sivalensis*. Like the Daud Khel locality (H-GSP 247) sample of Munthe (1980), the Jalalpur material is somewhat larger than this genotypic species. *S. sivalensis* is reported from the Chinji Formation at Banda Daud Shah by Wessels *et al.* (1982) who cite comparable measurements. We place the Jalalpur specimens in Baskin's (1996) new species because it falls squarely into the appropriate size range, which is greater than that of *S. sivalensis*, especially for third molars. De Bruijin *et al.* (1989) note that morphologic change in *Sayimys* is complex, but they see the evolution of the *S. sivalensis* group as a continuum, as do we.

Like Sciuridae, *Sayimys* is a usual but minor component of the Lower to Middle Siwalik rodent community. However, Baskin (1996) was able to advance the systematics of this ctenodactylid by utilizing all Chinji and Nagri formation samples in the same analysis. He established biostratigraphic ranges at the species level. His work restricts *Sayimys sivalensis* to the temporal interval of about 12.5 to 15 Ma. He places the range of *Sayimys chinjiensis* observed elsewhere on the Potwar Plateau in the interval 12.5 to about 9.6 Ma.

Suborder Myomorpha Brandt, 1855
 Family Myoxidae Gray, 1821
 Genus *Myomimus* Ognev, 1924
Myomimus sumbalenwalicus Munthe, 1980

Fig. 4a

Material: PMNH 5019, an upper molar fragment.

Description: The specimen agrees with the holotype of this species in morphology and size (width=1.2 mm). It shows a low, hooked accessory crest posterolingual to the paracone; the anteroloph is isolated.

Discussion: This dormouse indicates significant vegetation cover, if not forest. Myoxids (formerly, glirids) are a usual, but rare component of the Siwalik rodent fauna. Their systematics are not advanced, so conclusions about temporal limits to the range of *Myomimus sumbalenwalicus* are not possible at present. The significant observation here is that myoxids are not known in the Indian Subcontinent prior to about 14 Ma.

Family Rhizomyidae Miller and Gidley, 1918
 Subfamily Tachyoryctinae Miller and Gidley, 1918
 Genus *Kanisamys* Wood, 1937
Kanisamys nagrii Prasad, 1968

Kanisamys nagrii; Flynn, 1982, p. 341–343, fig. 9-G, H.

Kanisamys sp.; Cheema *et al.*, 1983, p. 272–273, fig. 4.

Material: PMNH 5020, left M₂; 5021 and 5022, M₁ fragments; 5023–5025, three upper molar fragments.

Description: The small sample of *Kanisamys* includes only one complete tooth, PMNH 5020, M₂ figured and described by Cheema *et al.* (1983). We note here its moderately well developed mesolophid located close to the hypolophid. Being worn, its width dimension is slightly greater than length (length, 2.1, width, 2.25). One M₁ fragment shows its metaconid to be isolated, except anteriorly, where it joins the anterolophid. A labial fragment of upper molar is unworn and measures ca. 2 mm high, suggesting a lingual crown height of near 3 mm.

Discussion: Flynn (1982) revised rhizomyid systematics, clarifying the status of *Kanisamys nagrii*, whose relationship to *K. indicus* and *K. sivalensis* named by Wood (1937) had been in question. The closeness of the mesolophid to the hypolophid on PMNH 5020 is an advanced feature, characteristic of *K. nagrii* and *K. sivalensis*, in contrast to the older *K. indicus*. So, too, the anterior connection of the metaconid on M₁ separates the species from *K. indicus*. Flynn (1986) applied metric data to diagnose *K. nagrii*, as well. The dimensions of PMNH 5020, and the crown height of the upper molars are all characteristic of *K. nagrii*. The temporal range of *K. indicus*

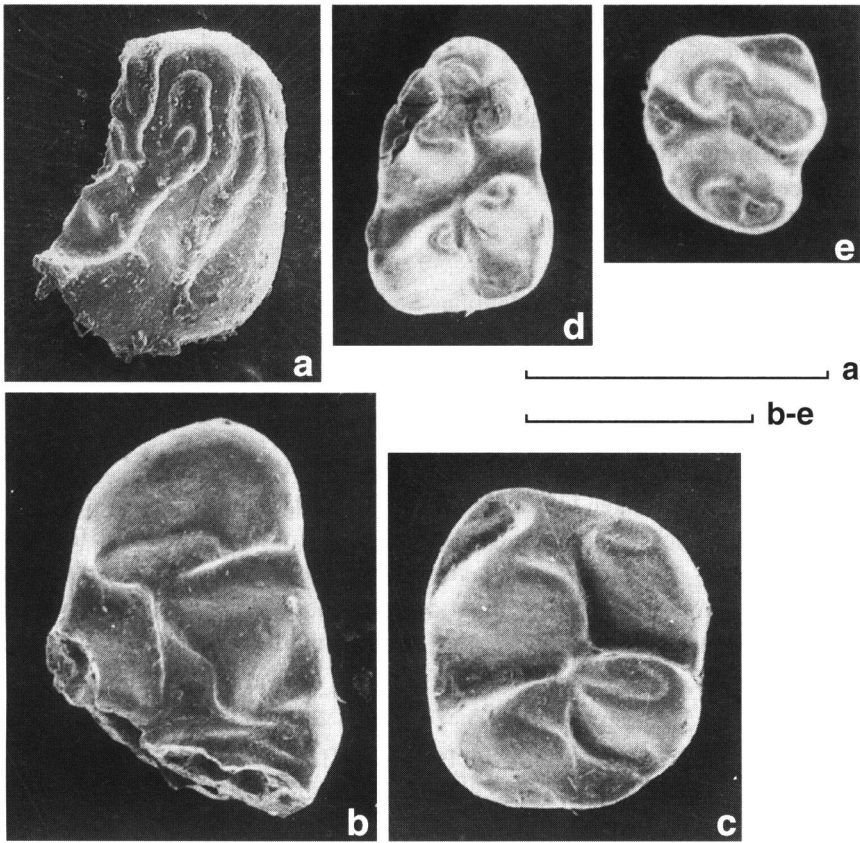


Fig. 4. *Myomimus sumbalanwalicus* (a), *Dakkamys asiaticus* (b-c), and *Paradakkamys chinjienensis* (d-e). a: PMNH 5019, R M²; b: PMNH 5052, R M¹; c: PMNH 5056, L M₂; d: PMNH 5057, L M₁; e: PMNH 5061, R M₂. Scale bar represents 1 mm.

overlaps slightly with *K. nagrii*. *K. indicus* persists in the Potwar Plateau up to about 11 Ma, and *K. nagrii* appears at 11.1 Ma, an age which is tightly constrained (see Flynn *et al.*, 1995).

Superfamily Muroidea Miller and Gidley, 1918
Family Cricetidae Rochebrune, 1883

The Cricetidae are characterized by presence of only three molars in each cheek tooth row. Molar crown pattern is conservative, basically four cusps and connecting crests, but some species possess extra cusps and ridges. None have the extra row of cusps on upper molars so distinctive of Muridae. Cricetids have a strong anterocone or anteroconid on the first molar. The cricetids collected in 1984 improved the sample

previously available, and confirmed our suspicion that more than one species of *Democricetodon* was present at JAL-101. Much of our ambivalence in Cheema *et al.* (1983) was due to the fact that most of the specimens then known did not compare well to *D. kohatensis*, the only other Siwalik *Democricetodon* then described. We saw two Jalalpur forms, one apparently like *D. kohatensis*, and one much larger. Now molars of three sizes and morphologies can be distinguished, the smallest one comparing well with *D. kohatensis*.

Subfamily Cricetodontinae Stehlin and Schaub, 1951
Genus *Democricetodon* Fahlbusch, 1964
***Democricetodon kohatensis* Wessels *et al.*, 1982**

Democricetodon cf. *kohatensis*; Cheema *et al.*, 1983, p. 273–274, fig. 5.

Material: PMNH 5026, left M¹; 5027, left M²; 5028, right M³, 5029, left M₁; 5030, right M₁; 5031, broken left M₁; 5032, left M₂; 5033, left M₂.

Description: These specimens agree in size with the type material from Banda Daud Shah. On M¹, the anterocone is doubled and the mesoloph is short. On M² the protolophule is double. On M₁ the anteroconid is short, its labial arm is low, and its lingual arm is high. Measurements (Table 1) are within the range of variation cited by Wessels *et al.* (1982).

***Democricetodon* sp. B–C sensu Lindsay, 1994**

Democricetodon cf. *gaillardi*, in part; Cheema *et al.*, 1983, p. 275–276, fig. 6.

Material: PMNH 5034, right M¹; 5035, right M²; 5036, broken left M²; 5037,

Table 1. Measurements for complete molars of species of *Democricetodon* from Jalalpur locality JAL-101 (length, width in mm.).

| Element | <i>D. kohatensis</i> | <i>Democricetodon</i> sp. B–C | <i>Democricetodon</i> sp. G |
|----------------|------------------------|-------------------------------|-----------------------------|
| M ¹ | 1.90×1.20 | 2.30×1.45 | 2.50×1.80 2.40×1.60 |
| M ² | 1.25×1.30 | 1.70×1.55 | 1.80×1.60 1.60×1.55 |
| M ³ | 1.05×1.15 | 1.20×1.35 | 1.35×1.50 1.30×1.45 |
| M ₁ | 1.60×1.15 1.60×1.20 | 2.05×1.30 | 1.95×1.30 |
| M ₂ | 1.40×1.20 1.45×1.15 | 1.70×1.60 | 1.75×1.65 |
| M ₃ | | | 1.65×1.40 |

left M³; 5038, left M₁; 5039, broken right M₁, 5040, right M₂.

Description: The specimens of this large *Democricetodon* are relatively low-cusped and the crown height is brachyodont. The molars are relatively slender, and their cusps show some oblique offset, rather than directly opposite position. The anterocone of M¹ is weakly doubled. The M₁ anteroconid is elongate with moderately developed labial and lingual arms. The teeth agree in morphology and size (see Table 1) with Potwar Plateau samples that have been designated *Democricetodon* sp. B–C (Lindsay, 1994). See discussion below.

***Democricetodon* sp. G sensu Lindsay, 1994**

Democricetodon cf. *gaillardi*, in part; Cheema *et al.*, 1983, p. 275–276, fig. 6.

Material: PMNH 5041, right M¹; 5042, right M¹; 5043, broken right M¹; 5044, left M²; 5045, right M²; 5046 right M³; 5047, left M³; 5048, right M₁; 5049, right M₁ fragment; 5050, right M₂; 5051, right M₃.

Description: This material, mainly described by Cheema *et al.* (1983), consists of stout molars (width relatively great; see Table 1). Crown height and cusp height are robust, and the enamel on the major cusps is somewhat wrinkled. M¹ has a doubled anterocone. Mesoloph and mesolophids are always present, but usually do not cross the teeth. The anteroconid on M₁ is relatively blunt. The material corresponds to *Democricetodon* sp. G of Lindsay (1994).

Discussion: *Democricetodon* is a diverse genus in the Siwaliks of Pakistan. Up to six species have been recognized at a single horizon (Lindsay, 1994). At JAL-101, *D. kohatensis* is distinctive by its small size. That there are two larger species became evident when larger samples were attained. *Democricetodon* sp. B–C is the informal name for a single species that is nearly as large as *Democricetodon* sp. G (sensu, Lindsay, 1994). Teeth of the latter are more robust, however, and show other morphological differences. Lindsay (1994) provides the temporal ranges of these three species.

Subfamily Dendromurinae Lindsay, 1988

Genus *Dakkamys* Jaeger, 1977

***Dakkamys asiaticus* Lindsay, 1988**

Fig. 4b, c

Dakkamys sp.; Cheema *et al.*, 1983, p. 276–277, fig. 7a.

Material: PMNH 5052, partial right M¹; 5053, upper molar fragment; 5054, right M₁; 5055 and 5056, right and left M₂.

Description: M¹ shows a broad anterocone with central mure joining the protocone and a short crest from the protocone to the paracone; the lingual enterostyle

joins the protocone posteriorly. The cusps of M_1 (2.2×1.4 mm), except for the anteroconid, are strongly inclined; the labial arm of the anteroconid has a small cusp and the lingual arm is short. The cusps of M_1 are alternate, the mure is low, there is no mesolophid, and there are minute cusplets between the major cusps, both lingually and labially. The cusps of M_2 (1.8×1.5 mm) are alternate, and joined longitudinally by a sloping central mure. M_2 has a strong anterolabial cingulum and posterolophid that expands in a terminal cusp; no mesolophid is present.

Discussion: This taxon includes PMNH 5054, the M_1 described and figured by Cheema *et al.* (1983; fig. 7a) under the name *Dakkamys* sp. The specimens are the same size and morphology as for the sample named *D. asiaticus* by Lindsay (1988). All of the characters observed on the newly recovered teeth agree with that taxon. The range of *D. asiaticus* as determined on the Potwar Plateau is from about 13 to 10 Ma.

Genus *Paradakkamys* Lindsay, 1988
Paradakkamys chinjiensis Lindsay, 1988

Fig. 4d, e

Myocricetodon sp.; Cheema *et al.*, 1983, p. 277, fig. 7b, c.

Material: PMNH 5057, left M^2 ; 5058, left M_1 ; 5059, fragmentary M_1 ; 5060 and 5061, two right M_2 .

Description: This small muroid is characterized by offset cusps that make oblique pairs, and weak longitudinal crests. On M^2 the metacone and hypocone are closely appressed, there is a strong anterolingual cingulum, and the small enterostyle is low and isolated. On M_2 the mure joins cusp pairs only after advanced wear, and the anterolabial cingulum is strong. M_1 is represented by a fresh, well preserved specimen, and by a worn fragment that is damaged anteriorly. The former measures 1.55 mm in length and 0.95 mm in width. The metaconid and entoconid are anterior to the protoconid and hypoconid, respectively, yielding oblique cusp pairs that are weakly joined by transverse ridges. The protoconid and hypoconid are asymmetricaly pinched. The metaconid is close to the simple, conical anteroconid. The mure is only emergent after advanced wear. The posterior arm of the hypoconid is a strong posterolingual cingulum. There is a labial cingulum anterior and posterior to the protoconid. Unlike this tooth, which lacks a mesolophid, the damaged specimen allocated here has a short mesolophid.

Discussion: The JAL-101 M^2 and M_2 of this species were described and figured by Cheema *et al.* (1983) under the name "*Myocricetodon* sp." We report here their major features, and discuss in some detail the new M_1 , PMNH 5058. PMNH 5059, a worn specimen with a mesolophid, is questionably assigned here since it is too slender to pertain to *Democricetodon*. Otherwise this sample compares well with Chinji

area specimens described and named *Paradakkamys chinjiensis* by Lindsay (1988), except that the present M_1 lacks an ectostylid. The temporal range of this species in the Potwar Plateau is nearly the same as for *Dakkamys asiaticus*.

Family Muridae Gray, 1821
Genus *Progonomys* Schaub, 1938
***Progonomys hussaini* sp. nov.**

Figs. 5, 6

Holotype: PMNH 5062, left M^1 (Fig. 5a).

Hypodigm: PMNH 5062–5118, fifty-seven isolated molars representing M^{1-3} and M_{1-3} (see Table 2) and thirty unnumbered molar fragments.

Type locality: JAL-101, upper part of the Chinji Formation of the Jalalpur area, District Chakwal, Potwar Plateau, Punjab, Pakistan.

Etymology: Named for Prof. Syed Taseer Hussain, in recognition for his promotion of scientific research in Pakistan, and especially for his work on Siwalik fossils.

Age: Early Late Miocene.

Diagnosis: *Progonomys* with cusps relatively low and not strongly inclined; cusps of upper molars joined by low crests in chevrons, and the second and third chevrons of M^1 are weakly connected lingually; anterostyle of M^1 variable in degree of posterior position and lateral pinching; M_1 with centrally connected anteroconids.

Description: M^1 is oval but varies in degree of elongation in occlusal outline. It is low crowned and the cusps are slightly inclined posteriorly. The anterostyles vary in degree of anteroposterior pinching. Although the anterostyle and enterostyle are generally located posteriorly, their position is observed to be variable. In one specimen, the anteriorly placed enterostyle makes the second chevron almost straight. In another, the anterostyle is anterior and conical (Fig. 5b). The enterostyle is joined by a low crest to the hypocone; the metacone and paracone are well separated. The posterior cingulum is well developed. The precingulum is absent to weak; a minute prestyle is present in two of eight teeth.

M^2 varies continuously in size and robusticity. The enterostyle is always firmly linked with the protocone, and joins the hypocone by means of a low crest. The metacone and paracone are well separated. The posterior cingulum is well developed. The two M^3 differ greatly in overall size and in development of the anterostyle.

The anteroconids of M_1 are always double and closely appressed. They vary from equal in size to strongly asymmetrical, and join near the midline of the tooth. They always connect posteriorly via a low to well developed anterior mure to the protoconid and metaconid. In only one specimen is there a minute anterior prestylid. The posterior cingulum varies in size of its cusp. The labial cingulum varies greatly in its development and the number of cusps present on it, but C_1 (classic murid terminology; see Jacobs, 1978) appears to be developed to some degree in all cases. One very

Table 2. Measurements of the molars of *Progonomys hussaini* sp. nov. from Jalalpur locality JAL-101 (in mm.).

| Element | Catalogue No. | Length | Width | Remarks |
|----------------|----------------|--------|-------|-------------------|
| M ¹ | 5062 | 1.80 | 1.10 | Holotype, fig. 5a |
| | 5063 | 1.85 | 1.15 | Fig. 5b |
| | 5064 | 1.80 | 1.20 | |
| | 5065 | 2.00 | 1.20 | |
| | 5066 | 2.05 | 1.15 | |
| | 5067 | 2.20 | 1.25 | |
| | 5068 | 2.00 | 1.30 | |
| | 5069 | 2.05 | 1.20 | |
| | M ² | 5070 | 1.30 | 1.25 |
| 5071 | | 1.35 | 1.30 | Fig. 5d |
| 5072 | | 1.20 | 1.10 | |
| 5073 | | 1.20 | 1.20 | |
| 5074 | | 1.20 | 1.15 | |
| 5075 | | 1.20 | 1.05 | |
| 5076 | | 1.40 | 1.20 | |
| 5077 | | 1.25 | 1.15 | |
| 5078 | | 1.20 | 1.20 | |
| 5079 | | 1.40 | 1.25 | |
| 5080 | | 1.35 | 1.20 | |
| 5081 | | 1.40 | 1.20 | |
| 5082 | | 1.15 | 1.30 | |
| M ³ | 5083 | 0.95 | 0.95 | Fig. 6a |
| | 5084 | 0.75 | 0.80 | |
| M ₁ | 5085 | 1.60 | 0.95 | Fig. 5e |
| | 5086 | 1.45 | 0.95 | Fig. 5f |
| | 5087 | 1.70 | 1.05 | |
| | 5088 | 1.70 | 1.00 | |
| | 5089 | 1.50 | 0.95 | |
| | 5090 | 1.80 | 1.10 | |
| | 5091 | 1.75 | 1.15 | |
| | 5092 | 1.60 | 1.10 | |
| M ₂ | 5093 | 1.50 | 0.95 | |
| | 5094 | 1.25 | 1.10 | Fig. 5g |
| | 5095 | 1.25 | 1.15 | Fig. 5h |
| | 5096 | 1.15 | 1.10 | Fig. 5i |
| | 5097 | 1.20 | 1.10 | |
| | 5098 | 1.30 | 1.05 | |
| | 5099 | 1.25 | 1.05 | |
| | 5100 | 1.30 | 1.05 | |
| | 5101 | 1.35 | 1.05 | |
| 5102 | 1.25 | 1.05 | | |
| 5103 | 1.20 | 1.05 | | |

Table 2. Continued.

| Element | Catalogue No. | Length | Width | Remarks | |
|----------------|----------------|--------|-------|---------|---------|
| M ₂ | 5104 | 1.45 | 1.15 | | |
| | 5105 | 1.35 | 1.15 | | |
| | 5106 | 1.30 | 1.15 | | |
| | 5107 | 1.40 | 1.15 | | |
| | 5108 | 1.30 | 1.10 | | |
| | 5109 | 1.30 | 1.20 | | |
| | 5110 | 1.30 | 1.15 | | |
| | 5111 | 1.30 | 1.15 | | |
| | 5112 | 1.35 | 1.10 | | |
| | 5113 | 1.30 | 1.15 | | |
| | 5114 | 1.35 | 1.15 | | |
| | M ₃ | 5115 | 1.00 | 0.90 | Fig. 6b |
| | | 5116 | 1.20 | 0.95 | Fig. 6c |
| 5117 | | 0.95 | 0.85 | | |
| 5118 | | 1.10 | 0.90 | | |

small M₁ lacks well developed labial and posterior cingula, and the anterior mure; it may be missing enamel due to corrosion from digestive processes of a predator.

M₂ shows a broad, continuous range of sizes. The labial anteroconid is moderately to well developed. The labial and posterior cingula and cingular cusps vary also. M₃ size variation is about 20%. The labial anteroconid is small, the labial cingulum weak. One specimen (Fig. 6c) shows a swelling on the lingual arm of the hypoconid, which may be an entoconid homologue.

Discussion: This new species is assigned to *Progonomys* based on the shared features of the genus, including the enterostyles linked to the protocones, and the anteroconids stable in twinning (in distinction from *Antemus*), and anterostyle posteriorly shifted (usually) and posterior cingulum well developed (in distinction from other murids).

Progonomys hussaini sp. nov. is primitive in low crown height without strong inclination of cusps, in weak cusp connections, and in the broad posterior lobe of M₃, which may indicate an incorporated entoconid. It is smaller than *P. woelferi*, about the size of *P. cathalai*. In contrast to *P. cathalai*, the anterostyle is usually more posterior and the anterior mure on M₁ is less developed. *P. hispanicus* is somewhat smaller, with higher and more inclined cusps (Michaux, 1971). *P. yunnanensis* (also somewhat smaller) is more stephanodont, with anterior posterostyle, higher cusps, and other advanced features (Qiu & Storch, 1990).

Progonomys hussaini is an early representative of the genus, and is correspondingly primitive. The sample from JAL-101 shows considerable variation, leading to the suspicion that more than one taxon could be present. Some teeth seem unusual in

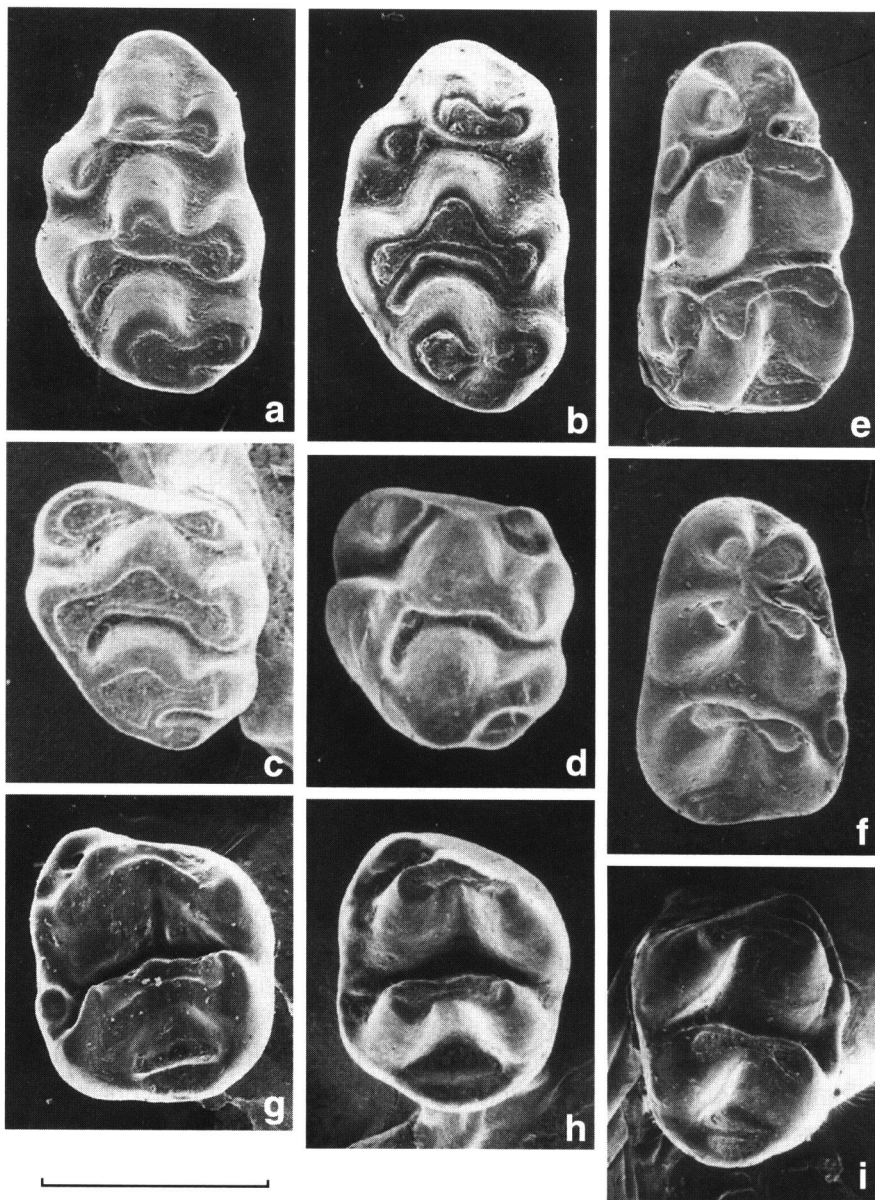


Fig. 5. *Progonomys hussaini*, sp. nov. a: PMNH 5062, L M¹ (holotype); b: PMNH 5063, L M¹; c: PMNH 5070, L M²; d: PMNH 5071, L M²; e: PMNH 5085, L M₁; f: PMNH 5086, R M₁; g: PMNH 5094, L M₂; h: PMNH 5095, L M₂; i: PMNH 5096, R M₂. Scale bar represents 1 mm.

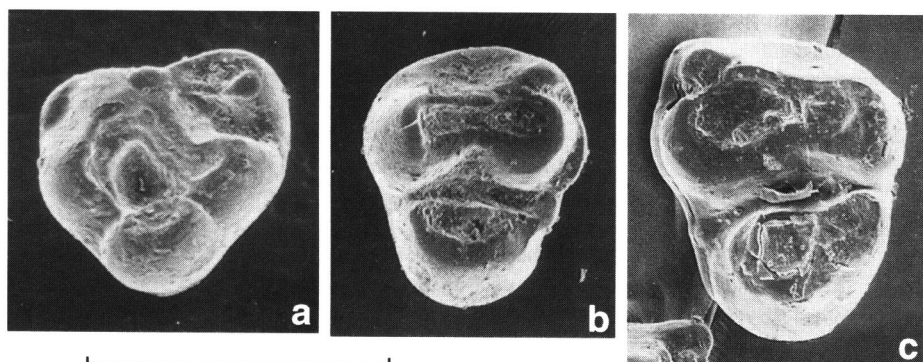


Fig. 6. *Progonomys hussaini*, sp. nov. a: PMNH 5083, R M³; b: PMNH 5115, R M₃; c: PMNH 5116, L M₃. Scale bar represents 1 mm.

size (contrast the two M³). Morphology also varies, but not in a way congruent with size. Indeed, the odd M¹ (Fig. 5b) seems incongruent with the usual *Progonomys* morphology (posterior and lophate anterostyle), and Cheema *et al.* (1983) felt that it might represent a primitive *Karnimata* described by Jacobs (1978). Despite considerable size variation, the samples do not indicate two clusters. Given larger samples now, the murid variations appear to intergrade and we take the conservative view that only one species is present. Consequently, we assign all murid specimens from JAL-101 to *P. hussaini*, and observe a broad range of variation for the species.

McKenna and Bell (1997) submerged *Karnimata* with *Progonomys* without justification. Clearly the type species differ at the generic rank, and they were distinct at 9 Ma (Jacobs, 1978). One question for the Siwaliks is “what is the earliest record of each genus?” The origin of *Karnimata* is a somewhat different question. The Jalalpur assemblage shows considerable variation. That variation could encompass the origins of both *P. debruijni* and *Karnimata*, as implied by Jacobs *et al.* (1990). Alternatively, *Karnimata* could indeed be present at JAL-101 in low abundance, but we cannot defend this at present. Earlier *Progonomys* and *Karnimata* were close in size, and later *Progonomys* likely was smaller, converging on *Mus* size (Jacobs, 1978). Early *Karnimata* would be difficult to recognize on the basis of size.

A morphometric approach to analyzing successive samples of Siwalik murids could clarify this problem.

Conclusion

The Jalalpur locality JAL-101 is important because it represents heretofore poorly sampled strata correlative to the upper part of the Chinji Formation or the lower part of the Nagri Formation. Its mammal fauna is diverse, the 148 numbered specimens representing 13 species. More identifiable specimens would likely increase

Table 3. Faunal list of the micromammal assemblage from JAL-101 and number of specimens identified.

| | TAXA | No. specimens |
|-----------------|---|---------------|
| Erinaceidae | <i>Galerix</i> sp. cf <i>G. rutlandae</i> | 1 |
| Tupaiidae | Gen. et sp. indet. | 1 |
| Sciuridae | <i>Eutamias urialis</i> | 4 |
| | Sciurinae gen. et sp. indet. | 7 |
| Ctenodactylidae | <i>Sayimys chinjiensis</i> | 5 |
| Myoxidae | <i>Myomimus sumbalenwalicus</i> | 1 |
| Rhizomyidae | <i>Kanisamys nagrii</i> | 6 |
| Cricetidae | <i>Democricetodon kohatensis</i> | 8 |
| | <i>Democricetodon</i> sp. B–C | 7 |
| | <i>Democricetodon</i> sp. G | 11 |
| | <i>Dakkamys asiaticus</i> | 5 |
| | <i>Paradakkamys chinjiensis</i> | 5 |
| Muridae | <i>Progonomys hussaini</i> sp. nov. | 87 |

the faunal list. Almost all of the material consists of isolated teeth (dominantly molars), but five postcranial elements, a rib and four podial fragments, were also retrieved. Taxa identified so far from the micromammal assemblage from JAL-101 are listed in Table 3.

The enhanced rodent fauna of JAL-101 confirms the earlier appearance of the *Progonomys* lineage than was known when Jacobs (1978) conducted his pioneering study. Since then, Jacobs *et al.* (1989, 1990) argued that *Progonomys* and *Karnimata* appeared much earlier than previously recognized in the Indian Subcontinent. *Karnimata* is not clearly represented in the fauna, but some specimens suggest that this lineage possibly had differentiated by this time. The cricetid species resemble those reported from elsewhere in the Chinji Formation of the southern Potwar and Kohat area (Dehm *et al.*, 1982; Wessels *et al.*, 1982). However, the co-occurrence of *Progonomys* with a species of *Kanisamys* advanced over *K. indicus* of the lower Chinji Formation and with typical upper Chinji/lower Nagri formation cricetids suggests an early late Miocene age for the fauna. The earlier assertion (Cheema *et al.*, 1983) of early Vallesian equivalence is consistent with these results.

The 1984 collection helps to refine faunal correlation to the Potwar Plateau sequence. Flynn *et al.* (1995) plot the known temporal ranges of all Potwar species, which are dated paleomagnetically. They show the first occurrence of *Myomimus* at 13.8 Ma and the last occurrence of *Eutamias urialis* at 10.6 Ma, although as noted above, these chipmunks may well have persisted later in time. *Megacricetodon*, distinctive by its absence from JAL-101, last occurs at 12.5 Ma elsewhere on the Potwar Plateau. *Kanisamys nagrii* is known from 11.1 to 8.8 Ma. *Dakkamys asiaticus* and

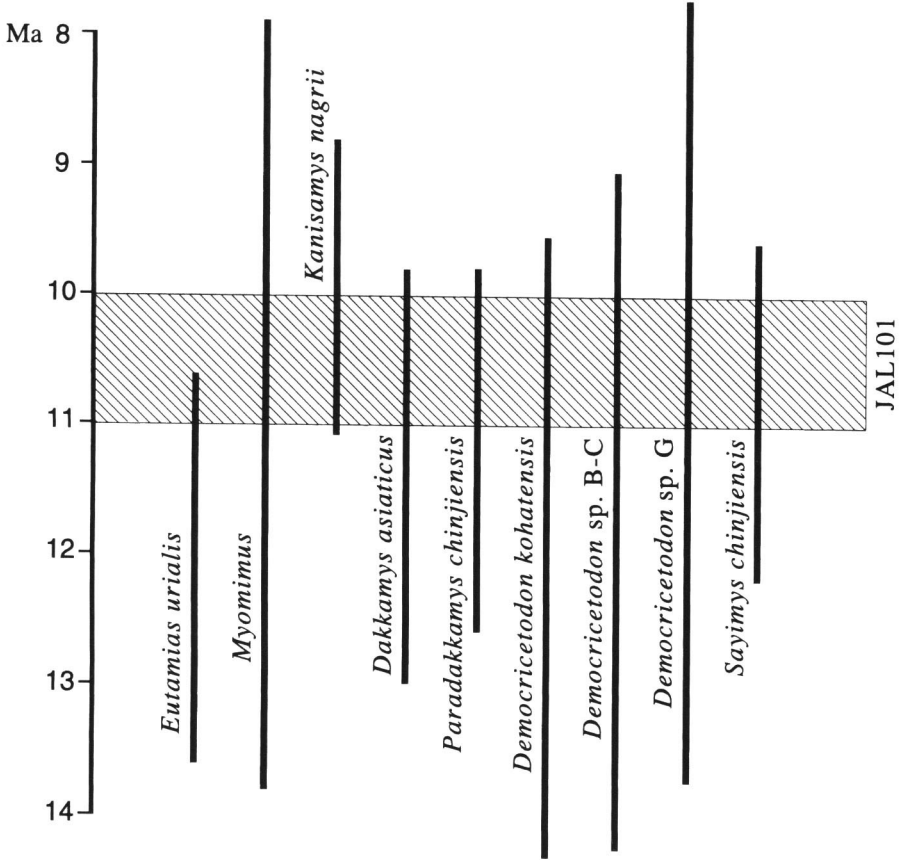


Fig. 7. Stratigraphic ranges for rodent species found at JAL-101, based on their occurrences in Siwalik rocks of the Potwar Plateau (see Flynn *et al.*, 1995). The age of JAL-101 is approximated to 11 to 10 Ma, and likely lies toward the older part of this range (see text).

Paradakkamys chinjiensis are known in excess of 12 Ma to about 10 Ma. *Karnimata* becomes recognizable in murid samples around 10 Ma, possibly as old as 10.6 Ma. *Sayimys chinjiensis* is confined to ca. 12 to 9.5 Ma. In summary, the likely age of JAL-101 is constrained to circa 11 Ma to perhaps as young as 10 Ma (Fig. 7), which corresponds to the uppermost part of the Chinji Formation in its type area.

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