A comparative analysis of the molars of *Mus booduga*, *Mus dunnii* and fossil *Mus* of the Indian subcontinent: Phylogenetic and palaeobiogeographic implications

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Upper molars of *Mus booduga* collected from Varanasi and *Mus dunnii* (chromosome type-I) show slightly derived features compared to those of *Mus booduga* collected from Mysore and *Mus dunnii* (chromosome type-II). *Mus auctor, Mus elegans, Mus flynni, Mus sp. indet., Mus jacobi*, *Mus sp., Mus booduga* and *Mus dunnii* are closely related to each other in having moderately elongated and rather strongly distorted M3s and moderately reduced M3s (except for *Mus elegans, Mus sp.* and *Mus jacobi*). Representation of *Mus*, both in terms of taxonomic diversity and considerable numbers, in the Plio—Pleistocene deposits of the Indian subcontinent is indicative of an early diversification event in the history of *Mus*.

In all murids, M1 (first upper molar) is relatively longer than M2 (second upper molar), which in turn is longer than M3 (third upper molar). According to Misonne1 lengthening of M1 in a forward direction accompanied by reduction of M3, brings the whole series forward and occupies the place left by P4 (fourth upper premolar). The length of M1 and M3 is given in relation to M2, which has a standard relative length of 100% (ref. 1). Generally ancient murids have broad molars, thus Misonne1 suggested that broad molars correspond to the more generalized types. Jacobs2 proposed that in primitive murids, tabial cingulum on lower molars are poorly developed and anterostyle on M1 relative to lingual anterocone, but not on the posterior extremity.

During the preliminary studies on Late Pliocene *Mus*, it was observed that it resembles *Mus booduga*, the Indian Pigmy Field mice3, most closely. In the light of evolutionary trends of murids suggested by Misonne1 and generalized dental characters of murids proposed by Jacobs2 an attempt has been made here to study *Mus booduga* (extant taxon, collected from Varanasi and Mysore), *Mus dunnii* (extant taxon, chromosome types I, II and III), *Mus auctor* and *Mus sp.* reported from Late Miocene and Early Pleistocene Siwalik deposits, respectively2, *Mus flynni* and *Mus sp.* indet. recovered from Late Pliocene (around 2.5 m.y.) Siwalik sediments.
of India, *Mus jacobsi* discovered from Late Pliocene (around 2.4 m.y.) deposits of Karezas (Kashmir, India) and *Mus elegans* reported from Pliocene deposits of Paul-I-Charkhi, Afghanistan.

Eleven skulls (with 132 teeth) each of adult *Mus booduga* and *Mus dunnii* housed at Cytogenetics Laboratory, Centre of Advanced Study in Zoology, Banaras Hindu University, were examined. Forty isolated teeth of fossil *Mus* housed at Vertebrate Palaeontology Laboratory, Centre of Advanced Study in Geology, Panjab University have been used here for comparison.

Measurements were made using a microscope fixed with a reticule. Dental terminology of murid molars proposed by Jacobs is followed here.

Matthey and Petter were first to distinguish between *Mus booduga* and *Mus dunnii* on the basis of divergent karyotypes but they also observed a slight difference in shape of molar and colour of underparts. The colour of underparts however is at times misleading. The pygmy field mice *Mus booduga* and *Mus dunnii*, which are endemic to the Indian subcontinent, are morphologically very similar and they inhabit the same ecological fields.

The diploid number of chromosomes is 40 in them but while the karyotype of *Mus booduga* with all acrocentric chromosomes is identical to *Mus musculus*, that of *Mus dunnii* is distinct due to presence of composite submetacentric X and large acrocentric Y chromosomes. The works carried out in the Cytogenetics Laboratory of BHU over the last several years have revealed that *Mus dunnii* is in active phase of speciation. In sharp contrast to the extreme conservation observed in the karyotype of *Mus booduga* throughout India, *Mus dunnii* populations of different places have divergent karyotypes. Three chromosome types (I, II and III), which are apparently parapatric in distribution, have been found so far, and on conducting mate-preference behaviour in them have shown some degree of ethological isolation. Recently, on hybridization between chromosome types I and III, it has been observed that they are also to some extent reproductively isolated since varying conditions of hybrid sterility of males and inviability of hybrid females have been observed. The stable karyotypic difference among the three chromosomes types of *Mus dunnii* has been achieved by establishing homoygosity for heterochromatin variation at the centromeric regions and as prominent short arms of the autosomes pairs 1, 3 and 6. The chromosome types are incipient biological species.

Marshall examined specimens of *Mus booduga* collected from Uttar Pradesh, Madhya Pradesh, Karnataka and Tamil Nadu states, and of *Mus dunnii* collected from Haryana, Uttar Pradesh, Madhya Pradesh, Maharashtra and Tamil Nadu states of India. According to him, *Mus booduga* has a long and slender first upper molar with a long anterior cusp (lingual anterocone) surrounded by an accessory cusp (prestyle) and an inconspicuous antero-external cusp (labial anterocone). During the present investigation, the above-mentioned features were clearly observed on *Mus booduga* collected from Varanasi but specimens of *Mus booduga* collected from Mysore have relatively shorter lingual anterocones on M1 and lacked a prestyle (Figure 1a, b).

Incisive foramina of *Mus booduga* collected from Varanasi penetrate deeper (reaching between antero- and ento-styles of the M1) compared to those of *Mus booduga* collected from Mysore and *Mus dunnii* (chromosome types I, II and III), where it reaches the level of antero-style of M1 (Figure 1f-e). Upper incisors of *Mus booduga* collected from Mysore are more curved compared to those of *Mus booduga* (Varanasi) and *Mus dunnii* (types I, II and III) (Figure 1k-o).

*Mus* is characterized by having a reduced M3 and M4, antero-style on M1 anteroposteriorly compressed and

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**Figure 1.** Occlusal views of upper and lower molars of a, *Mus booduga* (Varanasi specimen no. Mbw-3); b, *Mus booduga* (Mysore sp. no. M33); c, *Mus dunnii* (type I, sp. no. Mdv-4); d, *Mus dunnii* (type II, sp. no. M6); e, *Mus dunnii* (type III, sp. no. Mdn-1); f-j and k-o, skulls showing position of incisive lamina and curvature of upper incisors (sp. nos. Mbw 3, M3, Mdv-4, M6 and Mdn-1 respectively). Bar = 1 mm.
posterior relative to the lingual anterocone and posterior cingulum reduced or absent. Further, M₁ has an 'X' pattern formed by the joining of labial and lingual anteroconids, protoconid and metaconid. *Mus auctor* is considered to be the most primitive form of *Mus* recovered so far. It differs from *Mus flynni*, *Mus sp. indet.*, *Mus jacobisi*, *Mus elegans*, *Mus sp.*, *Mus booduga* and *Mus dumi* in having a reduced M₁ with distinct precingulum, M₂ with a conspicuous labial anterocone and a reduced posterior cingulum and M₃ with a labial anterocone (Figure 2a). Possible phylogenetic relationships between *Mus flynni* and *Mus auctor* and *Mus jacobisi* and *Mus auctor* have been suggested. Molars of *Mus dumi* (type-II), *Mus booduga* (Mysore) and *Mus flynni* resemble each other in having moderately elongated lingual anterocones and M₃s lacking labial cingulum (Figure 1b, d and 2b). On the other hand, molars of *Mus dumi* (type I and III), *Mus booduga* (Varanasi), *Mus sp. indet.* and *Mus jacobisi* are quite similar to each other in having considerably elongated lingual anterocones, prestyles (variably present) M₃s with distinct labial cingulum and medial anteroconids (Figure 1a, c, e, 2c and d).

Misonne suggested that in advanced murids, M₁ is extremely elongated relative to M₂ and M₃ and some forms of *Mus* even have M₁ with length over 240% of M₂ and M₃ around 40%: this gives a total of

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**Table 1.** Measurements (in mm) of upper molars of various *Mus* species examined. Mean lengths of *Mus auctor*, *Mus flynni*, *Mus elegans*, *Mus jacobisi* and *Mus sp. indet.* taken from Jacobs², Patnaik³, Sen⁴, Kollia⁵ and Patnaik⁶, respectively. Length of M₁ has been taken here as a standard.

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<th>Species</th>
<th>Element</th>
<th>Mean length</th>
<th>Percentage</th>
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<td>M₁</td>
<td>1.699</td>
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<td></td>
<td>M₂</td>
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<td></td>
<td>M₃</td>
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<td>M₃</td>
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**Figure 3.** Plio-Pleistocene biogeographic province based on the fossil *Mus* occurrences in the Indian subcontinent. A, Pauri-Charkhi, Afghanistan; B, Pahari Hills, Pakistan; C, Kashmir Valley, India; D, Saketi Village (Himachal Pradesh, India).
240 + 100 + 40 = 380% which implies that in spite of having three teeth, such specimens would have a surface equal to that of four teeth of dental series of primitive rodents. Such calculations were carried out on fossil and extant taxon compared herein. The results show that *Mus auctor* should be most generalized of all in this character followed by *Mus flynni* and *Mus elegans* (Table I). *Mus* sp. indet. and *Mus jacobsi* are considered here to be relatively derived in this character. Among the extant forms, *Mus booduga* (Mysore) and *Mus dunnii* (type II) are generalized in this character compared to *Mus booduga* (Varanasi) and *Mus dunnii* (type-I), whereas *Mus dunnii* (type-III) falls somewhere in between these two types.

Three specimens of *Mus* sp. have been reported from the Early Pleistocene Siwalik deposits, near Pabbi Hills, Pakistan. Forty-three specimens of *Mus jacobsi* come from Late Pliocene deposits of Karcwa, Kashmir. Twenty-nine specimens of *Mus flynni* and 11 specimens of *Mus* sp. indet. have been collected from Late Pliocene, Siwalik sediments, near Saketi Village, Himachal Pradesh, India. Such a representation of *Mus* species may suggest an early diversification in the history of *Mus*. On the basis of occurrences of *Mus* in Pliocene and Pleistocene deposits, a palaeobiogeographic province has been constructed (Figure 3).

Apart from the Indian subcontinent, Plio-Pleistocene *Mus* is known from Hadar Formation, Ethiopia (represented by four molars) and Lake Turkana, Kenya (represented by six molars). As this collection from Africa lacks M1's, it is at the moment difficult to compare it with that of the Indian subcontinent from the phylogenetic point of view.

In Figure 4, values (length and width) of M1's and M2's of all the *Mus* specimens fall in one domain. This observation encourages us to propose that on the whole *Mus booduga, Mus dunnii, Mus flynni, Mus auctor, Mus elegans, Mus* sp. indet., *Mus jacobsi* and *Mus* sp. are very close to each other and further recovery of fossil material, particularly from Pleistocene deposits may provide a better picture on the evolutionary lineages of *Mus*.

9 Bahadur, M and Sharma, T., Abstracts of the XVI All India Cell Biology Congress and Symposium, Varanasi, 1993, pp. 1–83.

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