A comparative analysis of the molars of *Mus booduga*, *Mus dunni* 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 dunni* (chromosome type-I) show slightly derived features compared to those of *Mus booduga* collected from Mysore and *Mus dunni* (chromosome type-II). *Mus auctor*, *Mus elegans*, *Mus flynni*, *Mus* sp. indet., *Mus jacobsi*, *Mus* sp., *Mus booduga* and *Mus dunni* are closely related to each other in having moderately elongated and rather strongly distorted M^1s and moderately reduced M^3s (except for *Mus elegans*, *Mus* sp. and *Mus jacobsi*). 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, M^1 (first upper molar) is relatively longer than M^2 (second upper molar), which in turn is longer than M^3 (third upper molar). According to Misonne[1] lengthening of M^1 in a forward direction accompanied by reduction of M^3, brings the whole series forward and occupies the place left by P^4 (fourth upper premolar). The length of M^1 and M^3 is given in relation to M^2, which has a standard relative length of 100% (ref. 1). Generally ancient murids have broad molars, thus Misonne[1] suggested that broad molars correspond to the more generalized types. Jacobs[2] proposed that in primitive murids, labial cingulum on lower molars are poorly developed and anterostyle on M^1 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 mice[3], most closely. In the light of evolutionary trends of murids suggested by Misonne[1] and generalized dental characters of murids proposed by Jacobs[2] an attempt has been made here to study *Mus booduga* (extant taxon, collected from Varanasi and Mysore), *Mus dunni* (extant taxon, chromosome types I, II and III), *Mus auctor* and *Mus* sp. reported from Late Miocene and Early Pleistocene Siwalik deposits, respectively[2], *Mus flynni* and *Mus* sp. indet. recovered from Late Pliocene (around 2.5 m.y.) Siwalik sediments

of India[4], *Mus jacobsi* discovered from Late Pliocene (around 2.4 m.y.) deposits of Karewas (Kashmir, India)[5] and *Mus elegans* reported from Pliocene deposits of Paul-I-Charkhi, Afghanistan[6].

Eleven skulls (with 132 teeth) each of adult *Mus booduga* and *Mus dunni* 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[2] is followed here.

Matthey and Petter[7] were first to distinguish between *Mus booduga* and *Mus dunni* 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 dunni*, 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 dunni* is distinct due to presence of composite submetacentric *X* and large acrcocentric *Y* chromosomes. The works carried out in the Cytogenetics Laboratory of BHU over the last several years have revealed that *Mus dunni* is in active phase of speciation. In sharp contrast to the extreme conservation observed in the karyotype of *Mus booduga* throughout India, *Mus dunni* 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[8]. 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[9]. The stable karyotypic difference among the three chromosomes types of *Mus dunni* has been achieved by establishing homozygosity for heterochromatin variation at the centromeric regions and as prominent short arms of the autosome pairs 1, 3 and 6. The chromosome types are incipient biological species.

Marshall[10] examined specimens of *Mus booduga* collected from Utter Pradesh, Madhya Pradesh, Karnataka and Tamil Nadu states, and of *Mus dunni* collected from Haryana, Uttar Pradesh, Madhya Pradesh, Maharastra 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) surmounted 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 M^1 and lacked a prestyle (Figure 1 *a*, *b*).

Incisive foramina of *Mus booduga* collected from Varanasi penetrate deeper (reaching between antero-style and enterostyle of the M^1) compared to those of *Mus booduga* collected from Mysore and *Mus dunni* (chromosome types I, II and III), where it reaches the level of anterostyle of M^1 (Figure 1 *f–j*). Upper incisors of *Mus booduga* collected from Mysore are more curved compared to those of *Mus booduga* (Varanasi) and *Mus dunni* (types I, II and III) (Figure 1 *k–o*).

Mus is characterized by having a reduced M_3 and M^3, anterostyle on M^1 anteroposteriorly compressed and

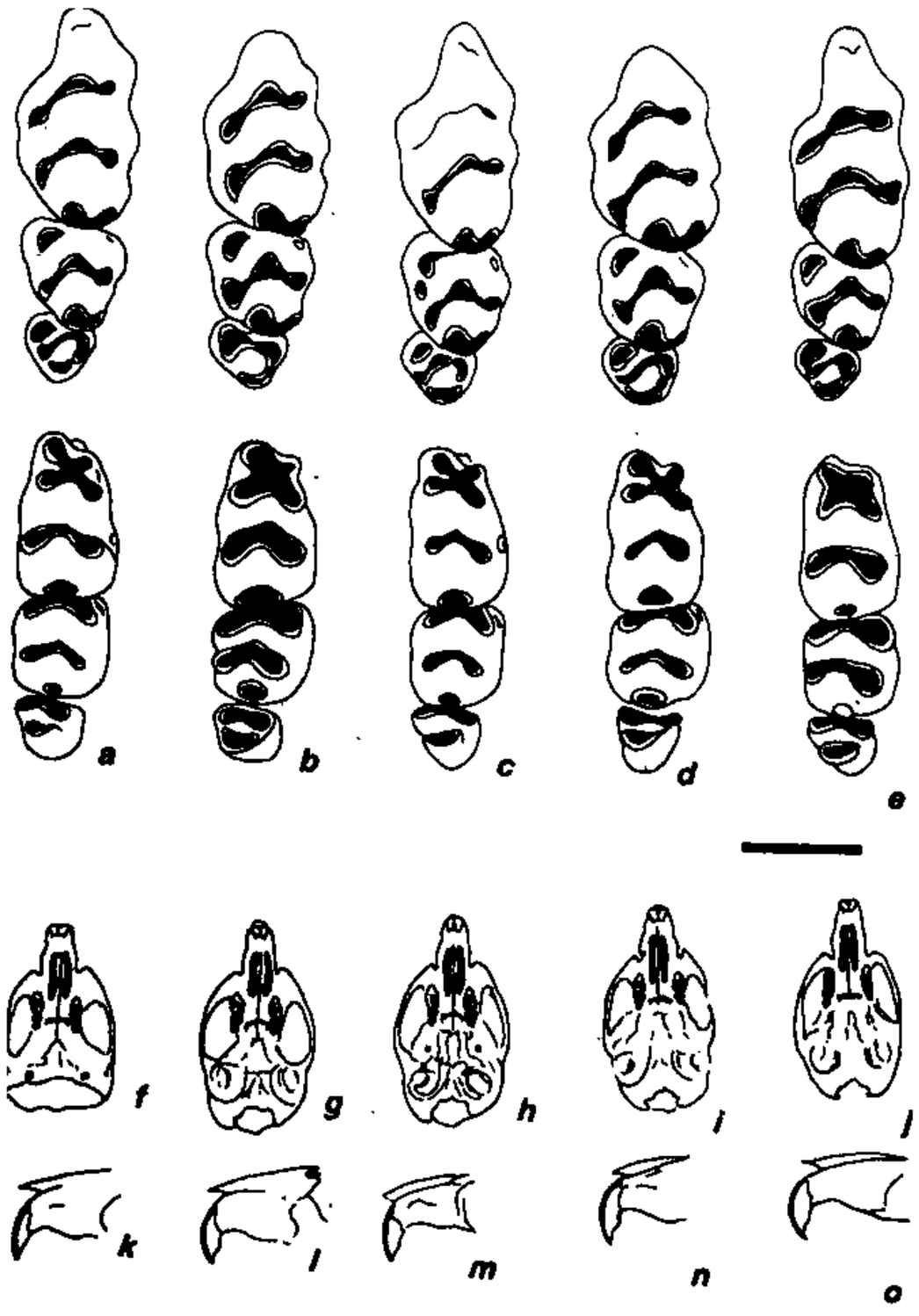

Figure 1. Occlusal views of upper and lower molars of *a*, *Mus booduga*, (Varanasi specimen no. Mbv-3); *b*, *Mus booduga* (Mysore sp. no. M3); *c*, *Mus dunni* (type I, sp. no. Mdv-4), *d*, *Mus dunni* (type II, sp. no M6); *e*, *Mus dunni* (type III, sp no. Mdm-1); *f j* and *k-o*, skulls showing position of incisive foramia and curvature of upper incisors (sp. nos. Nbv 3, M3, Mdv-4, M6 and Mdm-1 respectively). Bar = 1 mm.

Figure 2. Occlusal views of upper and lower molars of *a*, *Mus auctor* (sp. nos. M^1-DP210, M^2-DP325, M^3-DP 326, M_1 DP294, M_2-DP 335, M_3-DP 337) redrawn from Jacobs[2]; *b*, *Mus flynni* (all VPL/RP numbers. M^1SM-2, M^2-Sm, -32, M^3-Sm-45, M_1SM-10, M_2&M_3-SM-38), redrawn from Patnaik[4]; *c*, *Mus* sp. indet. (all VPL-RP nos. M^1-SM-5, M^2-SM-33, M^3-SM-44, M_1-M-6-A), redrawn from Patnaik[4]; *d*, *Mus jacobsi* (M^1-KHM/11, M^2-KHM/104, M_1-KHM/37, M_3-KHM/85, M_3-KHM/120, redrawn from Kotlia[5]; *e*, *Mus elegans* (M^1-AFG 932, M^2-AFG-936, M_1, AFG-415, M_2-AFG-421), redrawn from Sen[6]; *f*, *Mus* sp. (M^1-DP-210, M_1-DP-202), redrawn from Jacobs[2]. Bar = 1 mm.

posterior relative to the lingual anterocone and posterior cingulum reduced or absent. Further, M_1 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 jacobsi*, *Mus elegans*, *Mus* sp., *Mus booduga* and *Mus dunni* in having a reduced M^1 with distinct precingulum, M^2 with a conspicuous labial anterocone and a reduced posterior cingulum and M^3 with a labial anterocone (Figure 2*a*). Possible phylogenetic relationships between *Mus flynni* and *Mus auctor* and *Mus jacobsi* and *Mus auctor* have been suggested[4, 5].

Molars of *Mus dunni* (type-II), *Mus booduga* (Mysore) and *Mus flynni* resemble each other in having moderately elongated lingual anterocones and M_1s lacking labial cingulum (Figure 1*b*, *d* and 2*b*). On the other hand, molars of *Mus dunni* (type I and III), *Mus booduga* (Varanasi), *Mus* sp. indet. and *Mus jacobsi* are quite similar to each other in having considerably elongated lingual anterocones, prestyles (variably present) M_1s with distinct labial cingulum and medial anteroconids (Figure 1*a*, *c*, *e*, 2*c* and *d*).

Misonne[1] suggested that in advanced murids, M^1 is extremely elongated relative to M^2 and M^3 and some

Table 1. Measurements (in mm) of upper molars of various *Mus* species examined Mean lengths of *Mus auctor*, *Mus flynni*, *Mus elegans*, *Mus jacobsi* and *Mus* sp. indet. taken from Jacobs[2], Patnaik[4], Sen[6], Kotlia[5], and Patnaik[4], respectively. Length of M^2 has been taken here as a standard

Species	Element	Mean length	Percentage
Mus auctor	M^1	1.699	162
	M^2	1.047	100
	M^3	0.63	60 17
Mus flynni	M^1	1.83	179
	M^2	1.02	100
	M^3	0.66	64
Mus elegans	M^1	1.876	179
	M^2	1.044	100
Mus jacobsi	M^1	2.149	200 27
	M^2	1 073	100
Mus sp. indet.	M^1	2.13	206
	M^2	1.03	100
	M^3	0.56	54 36
Mus booduga (Mysore)	M^1	1.75	190.21
	M^2	0.92	100
	M^3	0.52	56.52
Mus booduga (Varanasi)	M^1	1 93	198 96
	M^2	0 97	100
	M^3	0 58	59.79
Mus dunni (type I)	M^1	1.84	197 84
	M^2	0.93	100
	M^3	0.56	60 21
Mus dunni (type-II)	M^1	1.78	189.36
	M^2	0.94	100
	M^3	0.58	61.70
Mus dunni (type-III)	M^1	1.87	190 80
	M^2	0.98	100
	M^3	0.55	56.12

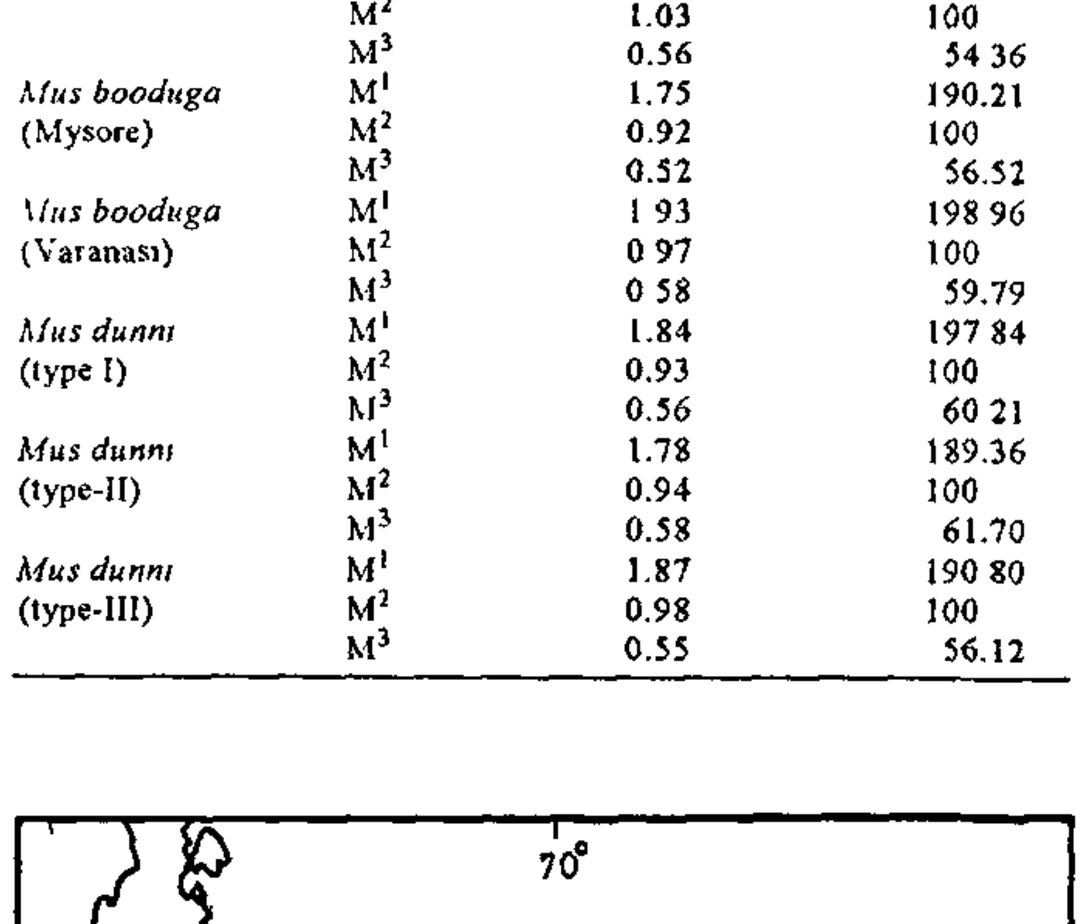

Figure 3. Plio–Pleistocene biogeographic province based on the fossil *Mus* occurrences in the Indian subcontinent. *A*, Paul-I-Charkhi, Afghanistan; *B*, Pabbi Hills, Pakistan; *C*, Kashmir Valley, India; *D*, Saketi Village (Himachal Pradesh, India)

forms of *Mus* even have M^1 with length over 240% of M^2 and M^3 arouhd 40%; this gives a total of

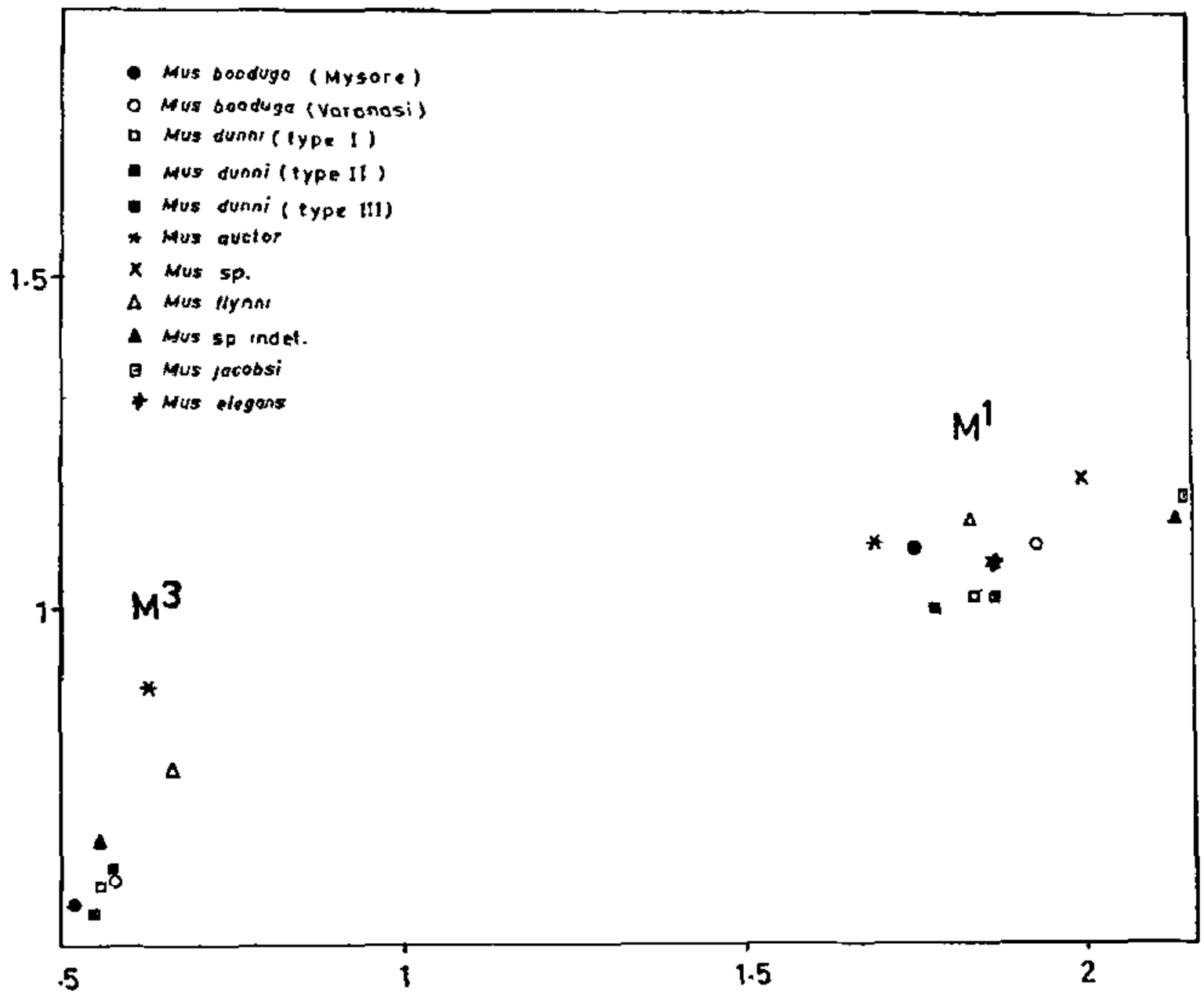

Figure 4. Scatter diagram of length and width of M^1 and M^3s of various *Mus* species examined. Here plots are made by taking mean values of length and width of *Mus auctor* and *Mus* sp. (from Jacobs[2]) *Mus flynni* and *Mus* sp. indet. (from Patnaik[4]) *Mus jacobsi* (from Kotlia[5]) and *Mus elegans* (from Sen[6]).

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 1). *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 dunni* (type II) are generalized in this character compared to *Mus booduga* (Varanasi) and *Mus dunni* (type-I), whereas *Mus dunni* (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[2]. Forty-three specimens of *Mus jacobsi* come from Late Pliocene deposits of Karewa, Kashmir[5]. 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[4]. 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)[11] and Lake Turkana, Kenya (represented by six molars)[12]. As this collection from Africa lacks M^1s, 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 M^1s and M^3s of all the *Mus* specimens fall in one domain. This observation encourages us to propose that on the whole *Mus booduga*, *Mus dunni*, *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*.

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