



## PHYLOGENY OF SIWALIK MURINE RODENTS: IMPLICATIONS FOR *MUS-RATTUS* DIVERGENCE TIME

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### ABSTRACT

The freshwater Siwalik deposits of the Indian subcontinent, ranging in age from ~18 Ma to ~.5 Ma, have yielded over 28 murine species belonging to 14 genera, most of them showing an *in situ* evolution. In the present work, a cladistic analysis (using PAUP) based on 26 derived and generalized dental characters distributed among Siwalik fossil murines of the Indian subcontinent and their extant counterparts has been carried out. The cricetids, *Potwarmus* and *Myocricetodon* were used as the out-group taxa to the in-group murine rodents. The results support monophyly of murines. The basal most murine taxon *Antemus* shares a common ancestry with rest of the murines. *Progonomys* was next to diverge, followed by the split leading to two clades, one comprising *Karnimata* and *Parapelomys* and the other having mostly modern murine taxa, with *Mus* occupying the basal-most position. Rest of the taxa of the latter clade form another clade comprising *Millardia*, *Cremnomys*, *Dilatomys*, *Golunda*, *Hadromys*, *Rattus*, *Bandicota* and *Nesokia*. The cladogram has been calibrated using the Siwalik chronostratigraphical data. Presently, *Mus-Rattus* divergence date is placed between 10-12 Ma based either on the first occurrence of *Progonomys* or on the *Progonomys-Karnimata* split date. The cladogram presented here suggest a rather different scenario indicating that the first appearance datum of *Mus* in the geological record, which at the moment is 7.3 Ma, appears to denote the divergence date of *Mus* and several rat genera including the genus *Rattus*. Further, this younger date of *Mus-Rattus* split validates younger first appearance dates of fossil *Millardia*, *Cremnomys*, *Dilatomys*, *Golunda*, *Hadromys*, *Rattus*, *Bandicota* and *Nesokia*.

**Keywords:** Fossil murines, Siwaliks, dental characters, cladistics, phylogeny

### INTRODUCTION

Murines (old world rats and mice) with 584 species and 129 genera is the most diverse mammalian subfamily today (Musser and Carlton, 2005). Although, they are usually regarded as pests and carriers of deadly diseases, they have been of great value in biomedical research. In recent years, a lot of efforts have been made to understand their molecular phylogenetics (Steppan *et al.*, 2004; 2005; Jansa and Weksler, 2004; Rowe *et al.*, 2008; Lecompte *et al.*, 2008; Michaux *et al.*, 2001; Chevret *et al.*, 2005). However, fossil based phylogenetic studies have so far been limited to particular regions (Chaimanee, 1998; Denys *et al.*, 1992; López Martínez *et al.*, 1998; Lecompte *et al.*, 2002; López Antanonzas, 2009). This could be due to the fact that murine dental elements (molars), although widely used for taxonomy of modern as well as fossil forms, have been known to show some level of convergence (homoplasy), as they are functionally adapted to particular diet (see for example Lecompte *et al.*, 2002; López Martínez *et al.*, 1998).

Today, the Indian sub-region which includes, India, Pakistan, Afghanistan and most of the Himalayan foothills is occupied by around 53 murine species (Agarwal, 2000; Srinivasulu and Pradhan, 2003). Northeastern states, particularly Assam and Manipur are fairly rich in murine rodents. Around 25 murine species occur in Assam (Kurup, 1975), whereas Manipur has around 15 murine species (Musser, 1987). Western Ghats has around 12 murine species (Mishra and Dhanda, 1975; Chandrashekar-Rao and Sunquist, 1996; Shanker and Sukumar, 1999), while the Himalayan foothills are home to around 16 murine species.

The fossil murine record of the Indian subcontinent (India, Pakistan and Afghanistan) is deep rooted and is fairly rich (Table 1), distributed mainly along the Himalayan foothills, where the

Neogene and Quaternary Siwalik deposits are exposed. The oldest murine rodent *Antemus* (Jacobs, 1978) appears at around 16 Ma in the Lower Manchar Formation of Pakistan, where both *Potwarmus* and *Antemus mancharensis* occur at about the same time (Wessels, 2009). *Antemus chinjiensis* appears around 13.8 Ma in the Chinji Formation (Jacobs, 1978; Wessels *et al.*, 1982; Jacobs and Flynn, 2005). This is followed by the appearance of *Progonomys*, for the first time at 12.2 Ma (Jacobs and Flynn, 2005). By 11.1 Ma, *Progonomys* gave rise to *Karnimata* lineage which in turn produces *Parapelomys* by ~ 8.1 Ma on one hand and on the other, *Progonomys* evolves anagenetically into *Mus auctor* by 6.4 Ma (Jacobs and Downs, 1994). The oldest occurrence of *Mus* in the Siwaliks is now dated to 7.3 Ma (Jacobs and Flynn, 2005). *Parapodemus*, which is considered to be an immigrant from the west appears in 9.2 Ma sediments of Pakistan (Jacobs and Flynn, 2005). It has also been reported from Indian Siwaliks in ~ 9 Ma deposits at Haritalyangar (Vasishat, 1985) and in Middle Siwalik sediments exposed near Mohand (Tiwari and Bhandari, 2014). Indian fossil *Mus* are known to occur in 2.5 to ~ 30,000 years deposits (Table 1). By ~3.5-4.5 Ma modern murine taxa such as *Golunda*, *Cremnomys* and *Millardia* appear (Patnaik, 1997). The Gauss-Matuyama transition at 2.5 Ma saw a diversification in murine species (Patnaik, 2001; Gupta and Prasad, 2001). At this time *Bandicota* makes its first appearance (Patnaik, 2001), which is followed by the appearance of *Nesokia* sometime around 2 Ma (Raghavan, 1990). Hypsodont murine *Hadromys* appear around 3 Ma in Pakistan (Cheema *et al.*, 1997; Musser, 1987). *Dilatomys* and *Hadromys* are known from the Indian Siwaliks from ~3.5-4.5 Ma and ~2 Ma deposits, respectively (Patnaik, 2001; 1997). Gaur (1986) mention the presence of *Rattus* from the Pinjor Formation, but its identification was later refuted by Musser (1987).

Table 1. Locality and age of fossil murine taxa of the Indian subcontinent.

Genus	Species	Fossil Site	Age	References	
<i>Antemus</i>	<i>A. mancharensis</i>	Seh 8224 Pakistan	13.3 – 16.2	Wessels,2009	
		Seh 8114 Pakistan	13.3 – 16.2	Wessels,2009	
		Seh 82247 Pakistan	13.3 – 16.2	Wessels,2009	
		Seh 8425 Pakistan	13.3 – 16.2	Wessels,2009	
	<i>A. chinjiensis</i>	Y491		13.8 Ma	Jacobs and Flynn (2005)
		Y665		13.7 Ma	Jacobs and Flynn (2005)
		Y59,640		13.6 Ma	Jacobs and Flynn (2005)
		HGSP 107		Middle Miocene	Wessels et al 1982
		Y430,651		13.5 Ma	Jacobs and Flynn (2005)
		Y668		13.3 Ma	Jacobs and Flynn (2005)
		Y718,690-1		13.0 Ma	Jacobs and Flynn (2005)
		Y714		12.7 Ma	Jacobs and Flynn (2005)
		Ramnagar		~13 Ma	Sehgal and Patnaik (2012)
<i>Progonomys</i>	<i>P. sp.</i>	Y634	12.2 Ma	Jacobs and Flynn (2005)	
	<i>P. hussaini</i>	Y504	11.5 Ma	Jacobs and Flynn (2005)	
		Y76	11.3 Ma	Jacobs and Flynn (2005)	
		JAL-101	Early Late Miocene	Cheema et al., (2000)	
		Y797	11.1 Ma	Sen, 1993 Jacobs and Flynn (2005)	
		Bharil	Lower Siwaliks	Joshi, 2008	
	<i>P. sp.</i>	Y259	10.4 Ma	Jacobs and Flynn (2005)	
		Y450	10.2 Ma	Jacobs and Flynn (2005)	
		Y311	10.0 Ma	Jacobs and Flynn (2005)	
	<i>P. debruijni</i>	Y410	9.3 Ma	Jacobs and Flynn (2005)	
		Y182	9.2 Ma	Jacobs and Flynn (2005)	
		Y367 Ladhyani	8.9 Ma ~8.9 Ma	Jacobs and Flynn (2005) Tiwari, 1996	
	<i>P. sp.</i>	Y388	8.7 Ma	Jacobs and Flynn (2005)	
		Y24	8.1 Ma	Jacobs and Flynn (2005)	
	<i>Karnimata</i>	<i>K. sp.</i>	Y388	8.7 Ma	Jacobs and Flynn (2005)
Y24			8.1 Ma	Jacobs and Flynn (2005)	
Y457			7.3 Ma	Jacobs and Flynn (2005)	
	Large <i>Karnimata</i>	Y931	7.2 Ma	Jacobs and Flynn (2005)	
		Y182	9.2 Ma	Jacobs and Flynn (2005)	
		Y367	8.9 Ma	Jacobs and Flynn (2005)	
		Y388	8.7 Ma	Jacobs and Flynn (2005)	
	<i>K. darwini</i>	Y410	9.3 Ma	Jacobs and Flynn (2005)	
		Y182	9.2 Ma	Jacobs and Flynn (2005)	
		Y367 Ladhyani	8.9 Ma ~8.9 Ma	Jacobs and Flynn (2005) Tiwari, 1996	
		Bharil	Lower Siwaliks	Joshi, 2008	
	<i>K. Cf. intermedia</i>	Haritalyangar, India	~7 Ma	Flynn et al.,1990	
	<i>K. intermedia</i>	Ghazgay, Afghanistan	~6.7 Ma	Brandy et al.,1980	
	<i>K. minima</i>	Sherullah, Afghanistan	~9.2 Ma	Brandy et al.,1980	
	<i>K. sp.</i>	Y797	11.1 Ma	Jacobs and Flynn (2005)	
		Y259	10.4 Ma	Jacobs and Flynn (2005)	
		Y450	10.2 Ma	Jacobs and Flynn (2005)	
		Y311	10.0 Ma	Jacobs and Flynn (2005)	
	<i>K. huxleyi</i>	DP13	6.4 Ma	Jacobs and Flynn (2005)	
	<i>Parapelomys</i>	<i>P. sp.</i>	Y24	8.1 Ma	Jacobs and Flynn (2005)
Cf. <i>P. robertsi</i>			Y457	7.3 Ma	Jacobs and Flynn (2005)
<i>P. robertsi</i>		Y931	7.2 Ma	Jacobs and Flynn (2005)	
		DP13	6.4 Ma	Jacobs and Flynn (2005)	
		Dhammi/Bali	~2.5 Ma	Gupta and Prasad, 2001	
		Kanthro	~2.5 Ma	Patnaik, 2001	
		Ladhyani	~8.9 Ma	Tiwari, 1996	

	<i>P. charkhensis</i>	Pul-e Charkhi	~5 Ma	Sen, 1983	
<i>Pelomys</i>	<i>Pelomys/Parapelmomys orientalis</i>	Sarobi, Kabul, Afghanistan	~3 Ma	Sen, et al., 1979, Brandy et al., 1980	
? <i>Mastomys</i>	<i>M. Colberti</i>	Bilaspur, H.P.	? Late Miocene	Lewis, 1939	
<i>Parapodemus</i>	<i>P. sp.</i>	Y182	9.2 Ma	Jacobs and Flynn (2005)	
		Haritalyangar	~9 Ma	Vasishat, 1985, Pillans et al., 2005	
		Mohand	Middle Siwaliks	Tiwari and Bhandari, 2014	
Murinae indet A.	Murinae indet A	Y311	10.0 Ma	Jacobs and Flynn (2005)	
<i>Saidomys</i>	<i>S. afghanensis</i>	Pul-e Charkhi	~5 Ma	Sen, 1983	
	<i>S. transversus</i>	Pul-e Charkhi	~5 Ma	Sen, 1983	
Murinae indet Y.	Murinae indet Y	Moginand	3.5-4.5 Ma	Patnaik, 1997	
		Kanthro	~2.5 Ma	Patnaik, 1997	
Murinae indet X.	Murinae indet X	Kanthro	~2.5 Ma	Patnaik, 1997	
<i>Mus</i>	<i>Mus sp.</i>	Y457	7.3 Ma	Jacobs and Flynn (2005)	
	<i>M. auctor</i>	DP 13	6.4 Ma	Jacobs, 1978	
	<i>M. jacobsi</i>	Khaigam, Karewas	2.4 Ma	Kotlia, 1992	
	<i>M. linnaeusi</i>	Ghaggar, Pinjor Fm.	2 Ma	Patnaik, 1997	
	<i>M. elegans</i>	Kabul, Afghanistan	~5 Ma	Sen, 1983	
	<i>M. flynni</i>	Dhammi/Bali	Kanthro	~2.5 Ma	Gupta and Prasad, 2001
			Kanthro	~2.5 Ma	Patnaik, 2001
			Nadah	1.8-2 Ma	Patnaik, 2001
	<i>M. dhailai</i>	Bhimtal	45-52,000 yrs. BP	Kotlia, 1996	
	<i>Mus sp.</i>	Devakachar	40,000 yrs BP	Patnaik, 1995	
<i>M. dulamensis</i>	Dulam, Uttarakhand	30,000	Kotlia, 2008		
<i>Golunda</i>	<i>G. tatrocticus</i>	Moginand	3.5-4.5 Ma	Patnaik, 1997	
	<i>G. kelleri</i>	Lehri	2 Ma	Cheema et al., 2003	
		Kanthro	~2.5 Ma	Patnaik, 2001	
		PMNH 8802 Mirpur	~ 3 Ma	Cheema et al., 1997	
	<i>G. dulamensis</i>	Dulam	31,000 yrs BP	Kotlia and Sanwal, 2004	
	<i>G. sp.</i>	Dhammi/Bali	~2.5 Ma	Gupta and Prasad, 2001	
	<i>G. sp.</i>	Kanthro	~2.5 Ma	Patnaik, 2001	
<i>Dilatomys</i>	<i>D. magnus</i>	Sarobi, Kabul, Afghanistan	~3 Ma	Sen, 1983	
	<i>D. moginandensis</i>	Moginand	3.5-4.5 Ma	Patnaik, 1997	
	<i>D. pilgrimi</i>	Dhammi/Bali	~2.5 Ma	Gupta and Prasad, 2001	
	<i>D. sp.</i>	Nadah	1.8-2 Ma	Patnaik, 1997	
<i>Millardia</i>	<i>M. sp.</i>	Dhammi/Bali	~2.5 Ma	Gupta and Prasad, 2001	
		Moginand	3.5-4.5 Ma	Patnaik, 1997	
		Kanthro	~2.5 Ma	Patnaik, 2001	
	<i>M. meltada</i>	Devakachar	40,000 yrs BP	Patnaik, 1995	
	<i>M. kathalene</i>	Kurnool Caves	16,000 yrs. BP	Patnaik et al., in Press	
<i>Cremnomys</i>	<i>C. Cf. cutchicus</i>	Moginand	3.5-4.5 Ma	Patnaik, 1997	
		Kanthro	~2.5 Ma	Patnaik, 1997	
	<i>C. blanfordi</i>	Kurnool Caves	16,000 yrs. BP	Murty, 1975	
	<i>C. sp.</i>	Lehri	2 Ma	Cheema et al., 2003	
<i>Raghadodemus</i>	<i>R. hansdebruijini</i>	Khaigam, Karewas	2.4 Ma	Kotlia et al., 1998	
<i>Apodemus</i>	<i>Apodemus dominans</i>	Pul-e Charkhi	~5 Ma	Sen, 1983	
<i>Hadromys</i>	<i>H. loujacobsi</i>	Pabbi Hills	1.7 ma	Musser, 1987	
		Lehri	2 Ma	Cheema et al., 2003	
	<i>H. sp.</i>	PMNH 8802 Mirpur	~ 3 Ma	Cheema et al., 1997	
<i>Bandicota</i>	<i>Bandicota sivalensis</i>	Kanthro	~2.5 Ma	Patnaik, 1997	
	<i>B. Cf. bengalensis</i>	Devakachar	40,000 yrs BP	Patnaik, 1995	
	<i>B. Cf. bengalensis</i>	Kurnool Caves	16,000 yrs. BP	Patnaik et al., 2008	
<i>Nesokia</i>	<i>N. hardwiki</i>	Unknown locality Upper Siwaliks	? Plio=Pleistocene	Lydekker, 1884	
	<i>N. panchkulaensis</i>	Ghaggar	~ 2 Ma	Raghavan, 1990	

Outside Siwaliks, *Progonomys* is known from China, where *Progonomys cathalai* is known to occur in the Bahe fauna (Baodean, Early Late Miocene ~10 Ma; Qiu and Li, 2003; Qiu *et al.*, 2003). The first Northern African *Progonomys* sp. is from Egypt (Vallesian, Heissig, 1982) and Algeria in deposits younger than 11 Ma (Bernor *et al.*, 1988; Aneur, 1984). In Anatolia and Europe the first *Progonomys* species appear at around 10 Ma (Dam *et al.*, 2006; Sen, 2003). Further, in 9-10 Ma old sediments of Namibia and East Africa, there is indication of presence of *Karnimata* and Cf. *Parapelomys* (Conroy *et al.*, 1992; Senut *et al.*, 1992; Gerrads, 2001). *Mus* is also known from Late Miocene of Afghanistan (Sen, 1983) and Early Pliocene (4.5 Ma) of Kenya, Africa (Winkler, 2002). *Dilatomys* has been found in ~3 Ma deposits in Afghanistan (Sen, 1983). *Golunda* and *Millardia* are also known from several African sites of Mio-Pliocene age (Sabatier, 1982; WoldeGabriel *et al.*, 1994; Benammi *et al.*, 1996; Wynn *et al.*, 2006). However, Musser (1987) has argued that the African fossil *Golunda gurai* (Sabatier, 1982) has been misidentified as *Golunda*.

Missone (1969) in his classic work, distinguished the subfamily Murinae from Cricetinae based on the presence of three cusps in the first and second tooth row of each upper molars (Fig.1). Jacobs *et al.* (1989) defined Murinae by the presence of two extra lingual cusps on M1 (first upper molar), with the anterostyle (t1) connected to the lingual anterocone (t2) and enterostyle (t4) isolated or connected to protocone (t5). Musser and Carleton (2005) have used derived molar characters such as presence of t1 and t4 on the lingual border of M1 and M2, forming two chevron shaped lamina, lack of longitudinal crests between the lamina in both upper and lower molars and cusps situated opposite to each other on the lower molars, to define murinae. However, Wessels (2009) argues against such a classification of murinae and cites the exceptional case of *Acomys* which in spite of the presence of typical murine molar pattern of having t1 and t4 on M1, is not a murine, rather is related to Gerbillinae based on molecular phylogenetic studies (see Denys and Michaux, 1992; Chevret *et al.*, 1993). Wessels (2009) is of the opinion that *Potwarmus* is also a murine, whereas, Jaeger *et al.* (1985) have argued against the inclusion of *Antemus* in Murinae. The general consensus is that *Antemus* is the oldest murine (Musser and Carleton, 2005).

The only cladistic study where Siwalik murines (*Antemus* and *Progonomys*) have been used is by López Antanonzas (2009). The present work is the first attempt to construct a phylogenetic relationship among extinct murines of the Siwaliks and their extant counterparts using the cladistic software PAUP (Swafford, 2001). Further, the results have been compared with previous evolutionary studies based on dental morphology and molecular phylogeny, and some aspects of palaeobiogeography of Siwalik murines have also been discussed herein.

## MATERIAL AND METHODS

Fossil murine dental elements from the Siwaliks described

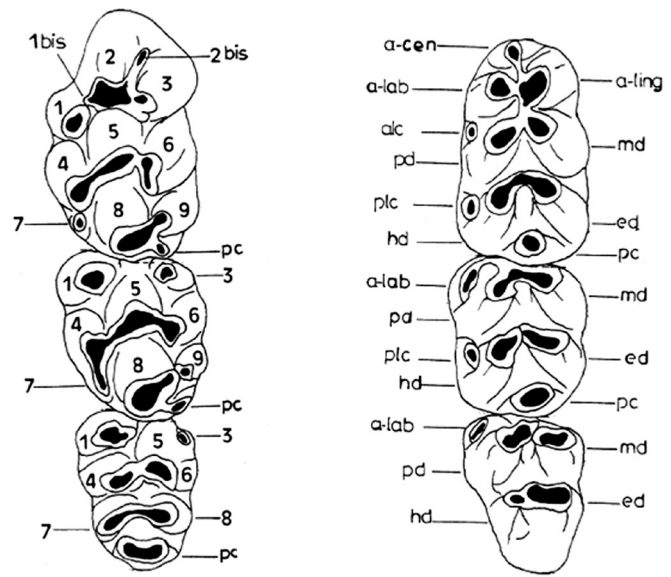


Fig. 1. Murid dental terminology (from Miller, 1912 and Wreed, 1976). pc, posterior cingulum; a- cen, anterocentral cusp; a-lab, anterolabial cusp; a-ling, anterolingual cusp; alc, anterolingual cusplet; md, metaconid; pd, protoconid; plc, posterolabial cusplet; hd, hypoconid; ed, entoconid.

in literature, have been analysed using generalized and derived dental characters following the works of Missone, (1969); Jacobs, (1978); Jacobs *et al.* (1989); Musser, (1981); Musser and Newcomb, (1983); Chaimanee, (1998); López Martínez *et al.* (1998) and López Antanonzas (2009).

### Description of molar character states

Generalized or ancestral states are marked as (0) and derived states are marked as (1) or (2). Four of the total five multistate characters (1,5,7 and 24) chosen here, usually show evolutionary change in one direction (morphocline) in particular lineages and do not reverse or appear more than once in the geological history. States 1 and 2 of character number 12, could have evolved independently.

### Upper molars

In general, murine molars are low crowned or brachydont, therefore increase in their crown height is a derived state. In the Siwaliks, Miocene murines such as *Antemus*, *Progonomys*, *Karnimata* etc., were brachydont and the first evidence of crown height increase comes in the form of Early Pliocene *Dilatomys* and Middle Pliocene *Hadromys* (Plate II and b). Both these taxa were semi-hypsodont, whereas later forms such as *Nesokia* and *Bandicota* (Plate II and b) e and f) became fully hypsodont.

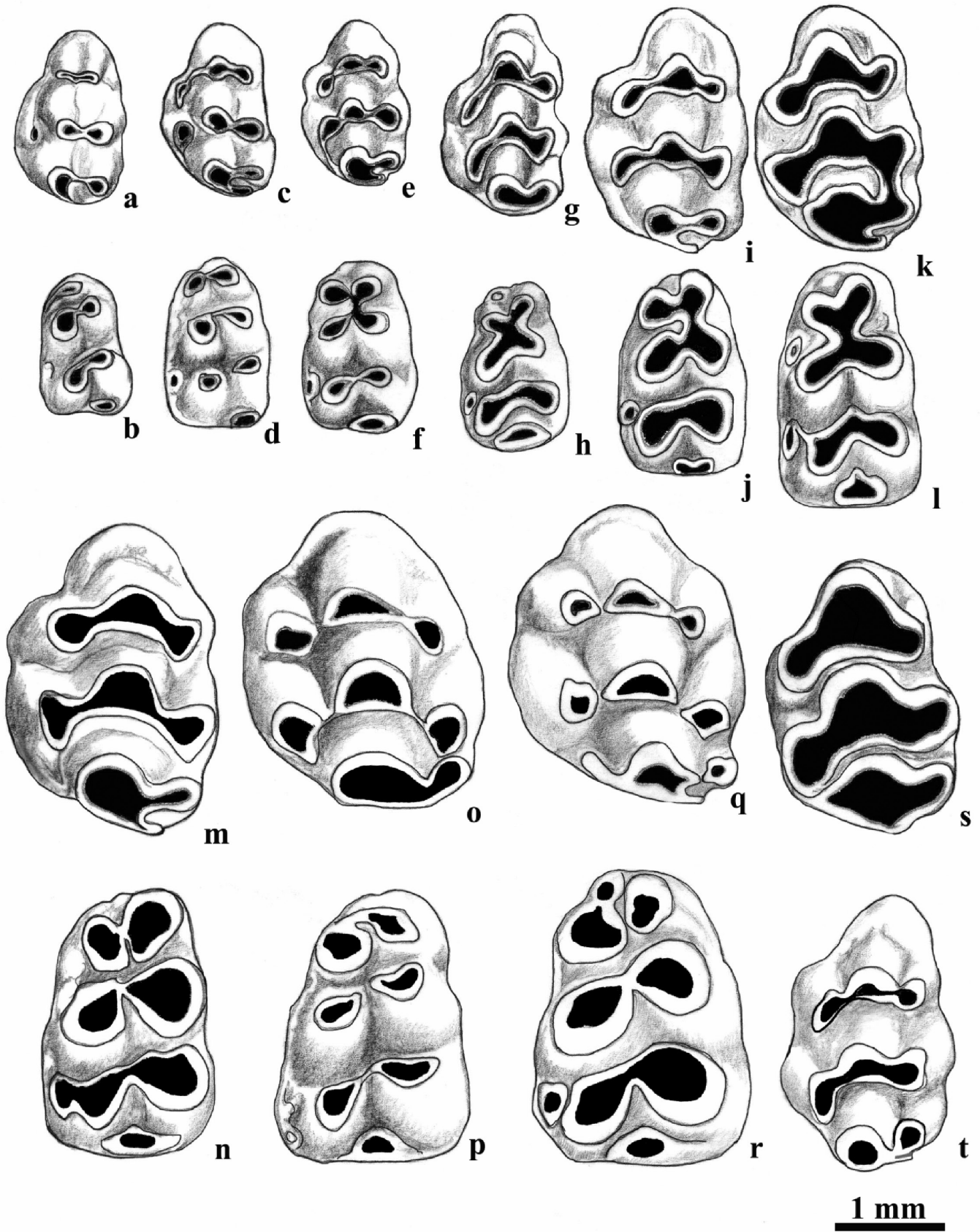
1. Brachydont (0); semi-hypsodont (1); hypsodont (2).

Generally murine molars are cuspidate and the chevrons are arcuate in shape, therefore, a strong connection between cusps leading to formation of straight laminae such as in the case of *Nesokia* is a derived state (Plate II f).

2. Union of cusps: cuspidate (0); laminated (1).

## EXPLANATION OF PLATE I

I. Occlusal views of various fossil cricetid and murine molars. a & b, M1 and m1 of *Potwarmus primitives* respectively; c & d, M1 and m1 of *Antemus chinjiensis* respectively; e & f, M1 and m1 of *Progonomys hussaini* respectively; g & h, M1 and m1 of *Mus auctor* respectively; i & j, M1 and m1 of *Karnimata darwini* respectively; k & l, M1 and m1 of *Parapodemus* sp. respectively; m & n, M1 and m1 of *Parapelomys robertsi* respectively; o, M1 of *Golunda tatroticus*; p, m1 of *Golunda kelleri*; q & r, M1 and m1 of *Saidomys natrunensis* respectively; s, M1 of *Cremnomys cf. C. Cutchicus*; t, M1 of *Millardia* sp. Source: Lindsay (1988); Jacobs *et al.* (1989); Cheema *et al.* (2000); Jacobs (1978); Patnaik (1997); Slaughter and James (1979); Gupta and Prasad (2001). In order to maintain symmetry, some right M1 and m1 figures redrawn from the above sources, have been flipped horizontally to make them appear as left molars.



3. Cusp rows: Chevrons are arcuate in shape (0); straight (1).

It is generally accepted that the murine dental feature of three longitudinal rows of cusps on upper molars evolved from two rows of the cricetid upper molars and the addition of cusps took place from the lingual side. In *Potwarmus* and *Myocricetodon* anterostyle (t1) is absent (Lindsay, 1988) (Plate Ia). In primitive (ancient) murines, such as *Antemus* and *Progonomys*, the cusp t1 is displaced well posterior to t2. In *Antemus* this cusp is often ridge-like and is very weakly connected to t2 (Jacobs *et al.*, 1989; Wessels, 2009). Misonne (1969: page 57) also notes that the “liaison between t1 and t2 does not seem to be strong in primitive forms”. To begin with t1 was either labio-lingually or antero-posteriorly compressed as in the case of *Antemus* and *Progonomys* (Plate I c, e). Later, it acquired a rather circular or arcuate outline, as in *Karnimata* and *Parapelomys*, but remained individualized (Plate I i, m). In highly hypsodont taxa such as *Bandicota* and *Nesokia* this cusp becomes laminated and merges with t2 (Plate II f). Usually, the cusp t3 is little smaller or as large as t1 and is placed posterior to t2. In the derived state, this cusp gets reduced and is placed at the level of t2, making the first chevron narrower compared to the second one as seen in *Cremnomys* and *Millardia* (Plate I s,t).

4. Anterostyle (t1) absent from upper M1 (0); present (1).

5. Anterostyle (t1) is displaced well posterior to t2 (0); t1 is relatively placed anteriorly (1); placed almost at the level of t2 (2).

6. Anterostyle (t1) is very weakly connected to t2 (0); moderate to strongly connected to t2 (1).

7. Cusp t1 is anteroposteriorly or labio-lingually compressed (0); round to arcuate (1) laminated (2).

8. Cusp t3 on M1/: as large as t1 (0); reduced or merged with t2 losing its individuality (1).

Cusps of the central row are generally of the same shape as those of the lingual and labial rows. In derived states as seen in *Dilatormys* they become wider (Plate II b). In all or most of the samples of primitive murines, cusp t3 is present on the second and often on the third upper molars. This cusp is absent from the second and third molars in all or most specimens of advanced murine molars (Musser and Newcomb, 1993). Although this cusp is absent from M2 of extant *Bandicota*, but is retained on one specimen of fossil *Bandicota* (Plate II c). In fact, a fossil *Nesokia* even had t1 present on M2 (Plate II d).

9. Labial anterocone (t3) present in M2 and M3 (0); absent (1).

10. Normal central cusps (0); wide central cusps (1).

The valleys between cusps are normal to start with as is the case in *Antemus* and *Progonomys*. They become shallow in high crowned and laminated teeth (ex. *Bandicota*) or become very deep separating adjacent cusps completely (ex. *Golunda*). Cusps t4 and t6 of the central chevron are usually distal to t5. In advanced case they are situated at the level of t5. Connection of cusp t4 to the cusps of the third chevron is considered as a derivation. The cusp t7 is not present in the murine fossils so far recovered from the Siwaliks, but it occurs in the *Rhagapodemus* from the Pliocene of Karewas of Kashmir and *Apodemus*, recovered from the Pliocene of Kabul, Afghanistan (Kotlia *et al.*, 1998; Sen, 1983). In *Antemus* t4 is not connected to t5. Therefore

presence of this connection is a derived state (Plate Ic).

11. Valleys between cusps, normal (0); shallow (1); deep (2).

12. Cusp t4 slightly distal to t5 (0); lies at the same level (1).

13. Cusp t4 not connected to t5 (0); connected (1).

Longitudinal connection between transverse chevrons particularly between the second and the third chevrons due to formation of crests connecting t6 to t9 or t4 to t8 or t7 leads to stephanodonty, which is a derived state and is not seen in primitive murines (Michaux, 1967). Normally cusp t9 is a large and discrete cusp on first upper molars, situated next to t8. In derived state it becomes reduced losing its individuality, or is displaced mesially. In very advanced forms t9 merges with t8 (Misonne, 1969). Normally each first upper molar is three rooted, or sometimes four rooted. Presence of five or more roots is derived (Musser and Newcomb, 1993; Bienvenu *et al.*, 2008). A ridge-like posterior cingulum is present in *Antemus* and *Progonomys*. In most recent forms this is absent (Plate I c).

14. Cusp t9 as large as t6 (0); reduced losing its individuality or absent (1).

15. Cusp t6-t9 connection: absent (0) present (1)

16. Cusp t9 situated at the level of t8 (0); closer to t6 (1).

17. Number of roots on M1/: less than 5 (0); 5 or more (1).

18. Posterior cingulum on M1/: present (0); absent (1).

As per Misonne (1969: page 49) “species showing strong interlocking of the molars is most certainly advanced on that character than species with poor interlocking”. There is slight slanting of cusps in general leading to no overlap of molars as such. In derived state the molars show strong overlapping (Musser and Newcomb, 1993).

In primitive murines the difference of M1 length and M2 length is less compared to that in the advanced murines, where M1 is elongated and M3 is highly reduced, such as in *Mus*.

On the M3's of primitive forms the t9 is usually not reduced, but in derived forms this cusp is reduced or even absent.

19. No overlapping of molars (0); overlapping or interlocking (1).

20. M3, Metacone (t9): not reduced (0); reduced or absent (1).

#### Lower molars

In derived forms the lower molars show widening of the anterior loph, comprising anterolabial and anterolingual cusps. A strong connection between labial and lingual cusps, presence of longitudinal connection among the transverse rows, absence of anterolabial cusp in second and third molars, reduction of posterior cingulum, increase in the number of roots (Bienvenu *et al.*, 2008) are considered as derived features. Anteroconid in *Potwarmus* and *Myocricetodon* is single cuspid (Plate Ib). In *Antemus* anteroconid cusp is absent. In *Progonomys* anterolabial and anterolingual cusps are almost of equal size (Plate If).

21. Anteroconid unicuspid (0); have two cusps (1).

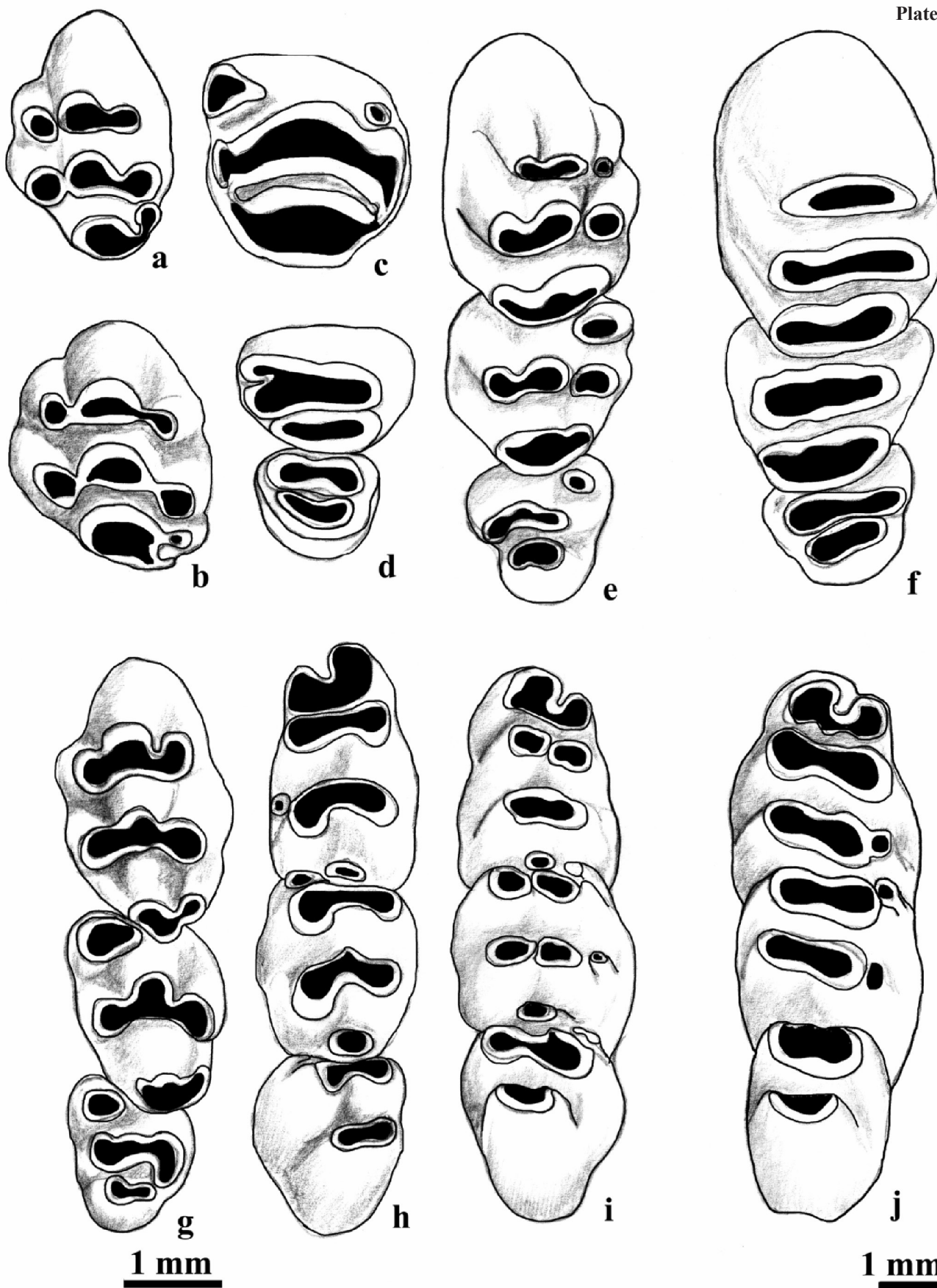
22. Anteroconid cusp absent (0); present (1)

23. Anterior loph narrow cuspidate (0); wider and laminated (1).

24. Labial and lingual cusps: isolated or weakly connected (0); moderately connected (1) pressed against each other to form a lamina (2).

#### EXPLANATION OF PLATE II

Occlusal surface of some fossil and recent murine molars. a, M1 *Hadromys loujacobsi* (flipped horizontally); b, M1 *Dilatormys moginandensis*; c, M2 *Bandicota* sp., d, *Nesokia panchkulaensis*; e & f, *Bandicota indica*; g & h, *Rattus rattus*; f & j, *Nesokia indica*. Redrawn from: Musser (1987); Patnaik (1997; 2001); Raghavan (1990); Musser (1981); Musser and Brothers (1994).



25. Anterior mure on m1: present (0); first lamina isolated from the second one (1).

26. Roots on m1: Two or 3 (0); four or more (1).

*Potwarmus* and *Myocricetodon* were selected as the outgroup taxa, which are distinct from the ingroup murines in lacking a t1 on M1 and having an unicuspid anteroconid on m1. Beside Pakistan, *Potwarmus* is known from Thailand in the east to Saudi Arabia and Libya in the west. *Potwarmus* has been considered very close to *Antemus* (Lindsay, 1988; Wessels, *et al.*, 2003; Wessels, 2009), but a recent cladistic work on early murine phylogeny (López Antanonzas, 2009), suggest *Myocricetodon* to be a sister taxon of *Antemus*.

**Analyses**

The data set as NEXUS file (Table 2) was analysed using PAUP 4.1 software (Swafford, 2001). The following is the settings.

- Data matrix has 15 taxa, 26 characters
- Valid character-state symbols: 012
- Missing data identified by '?'
- Processing of file "C:\Users\rajeev\Desktop\Final2.nex" completed.
- Branch-and-bound search settings:
- Optimality criterion = parsimony
- Character-status summary:
- Of 26 total characters:
- All characters are of type 'unord'
- All characters have equal weight
- 1 character is parsimony-uninformative
- Number of parsimony-informative characters = 25
- Initial upper bound: unknown (compute heuristically)
- Addition sequence: furthest
- Initial 'MaxTrees' setting = 100
- Branches collapsed (creating polytomies) if maximum branch length is zero
- 'MulTrees' option in effect
- Topological constraints not enforced
- Trees are unrooted
- Branch-and-bound search completed:
- Score of best tree found = 48
- Number of trees retained = 4

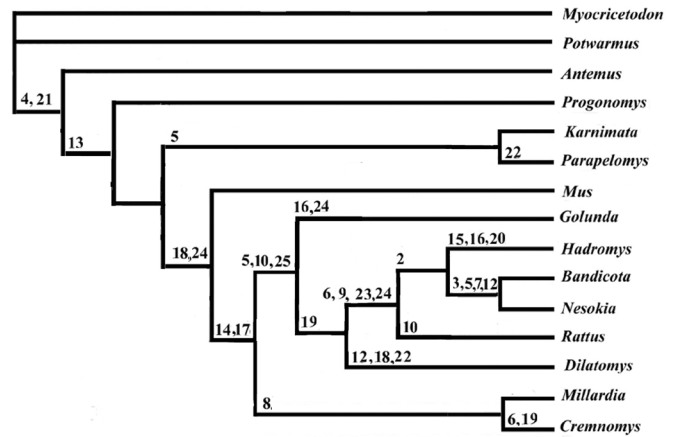


Fig. 2. Cladogram illustrating the relationships among fossil murine taxa and their extant counterparts. Numbers at various nodes and branches denote derived characters.

Time used = 0.00 sec  
 Tree description:  
 Unrooted tree(s) rooted using outgroup method  
 Character-state optimization: Accelerated transformation (ACCTRAN)  
 Tree number 1 (rooted using default outgroup)  
 Tree length = 48  
 Consistency index (CI) = 0.6458  
 Homoplasy index (HI) = 0.3542  
 Retention index (RI) = 0.7976  
 Rescaled consistency index (RC) = 0.5151  
 A heuristic search also yielded identical consensus tree of length 48 steps with the same CI, HI, and RI as above.

**RESULTS**

**Phylogeny**

The BandB search yielded 4 most parsimonious trees with a length of 48 steps. The strict consensus tree obtained is shown in Figure. 2, has a Consistency index (CI) = 0.6458 Homoplasy index (HI) = 0.3542 and Retention index (RI) = 0.7976

**Table 2. Matrix of character codings used in the analysis of relationships among fossil Siwalik murine rodents and their extant counter parts. *Myocricetodon* and *Potwarmus* are used as the out-group.**

Character										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2
Taxa	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
<i>Myocricetodon</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Potwarmus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Antemus</i>	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Progonomys</i>	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Karnimata</i>	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Parapelomys</i>	0	0	0	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	0	0
<i>Mus</i>	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	1	0	0
<i>Golunda</i>	0	0	0	1	1	0	1	0	0	1	2	0	1	1	0	1	1	1	0	1	1	0	0	0	1	0
<i>Dilatomys</i>	1	0	0	1	1	0	1	0	0	1	1	1	1	1	0	0	1	0	1	0	1	1	0	1	1	1
<i>Millardia</i>	0	0	0	1	0	0	1	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	1	0	1
<i>Cremnomys</i>	0	0	0	1	0	1	1	1	0	0	0	0	1	1	0	0	1	1	1	1	1	0	0	1	0	1
<i>Hadromys</i>	1	1	0	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	2	1	1
<i>Bandicota</i>	2	1	1	1	2	1	2	0	1	1	1	1	1	0	0	0	1	1	1	0	1	0	1	2	1	1
<i>Nesokia</i>	2	1	1	1	2	1	2	0	1	1	1	1	1	0	0	0	1	1	1	0	1	0	1	2	1	1
<i>Rattus</i>	0	0	0	1	2	1	1	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	1	2	1	1



The results support monophyly of the subfamily murinae which is characterized by the presence t1 and t4 on M1 and a bicuspid anteroconid on m1. The basal-most taxon *Antemus* shared a common ancestry with rest of the murines, which in turn are characterized by having an M1 with t4 connected to t5. *Progonomys*, the most widespread Miocene murine, diverges next. This is followed by the split leading to two clades, one comprising *Karnimata* and *Parapelomys*, which is supported by the presence of an anteriorly placed t1. The second clade is supported by the absence of a posterior cingulum on M1 (except for *Dilatomys*) and moderate to strongly connected labial and lingual cups of m1. *Mus* occupying the basal most position of this clade, with mostly modern murine taxa (except for *Dilatomys*), including *Rattus*. This is followed by a split of a clade consisting of *Millardia* and *Cremnomys* based on a reduced t3 on M3. *Cremnomys* is derived compared to *Millardia* in having a stronger t1-t2 connection and overlapping molars. The next clade comprises *Golunda*, *Dilatomys*, *Hadromys*, *Rattus*, *Bandicota* and *Nesokia*. These clades are united by a reduced t9 and four or more roots on m1. The clade comprising *Golunda*, *Dilatomys*, *Hadromys*, *Rattus*, *Bandicota* and *Nesokia* is strongly supported by synapomorphies such as anteriorly placed t1, wide central cusps, moderate to deep valley between cusps and absence of anterior mure on m1. Further, there is a strong support for *Hadromys*, *Rattus*, *Bandicota* and *Nesokia* lineage by synapomorphies such as moderate to strong t1-t2 connection, absence of t3 on M2 and M3, a wide and laminated anterior loph on m1. The union of sister taxa *Bandicota* and *Nesokia* is supported by having highly hypsodont molars with straight, laminated chevrons and t4 lying at the level of t5 on M1.

## DISCUSSION

### Phylogenetic relationships

A dental character based cladistic analysis by López Antanonzas (2009) clearly demonstrate that *Antemus* and *Progonomys* are sister taxa characterised by having a t1 on M1 and a bi-lobed anteroconid on m1. They form a clade with *Potwarmus* spp. and *Myocricetodon liui*. Close relationship between *Karnimata* and *Parapelomys* has already been recognized on dental morphology (Jacobs, 1978; Jacobs and Downs, 1994). The Asian *Golunda* has recently been shown to share common ancestry with the African Arvicanthines by recent molecular phylogenetic study (Lecompte *et al.*, 2008). Earlier Michaux *et al.* (2007) and Ducroz *et al.* (2001) have also indicated closeness of *Golunda* to Arvicanthines. Based on dental characters Misonne (1969) grouped *Golunda* in *Arvicanthis* Division, which was also approved by Musser (1987). *Dilatomys* shows close affinity to *Golunda* supported by four synapomorphies (Fig.2). In fact, *Dilatomys magnus* from Afghanistan (Sen, 1983) was initially identified as *Arvicanthis magnus* (Sen *et al.*, 1979). *Saidomys*, the widely distributed Arvicanthine genus from Egypt, Kenya, Afghanistan and Thailand (Slaughter and James, 1979; Winkler, 2002; Sen, 1983; Chaimanee, 1998) (Plate I, q & r), forms a sister taxon to *Golunda*, when included in the present matrix and analysed. *Millardia-Cremnomys* have been shown to share common ancestry with Arvicanthines (Lecompte *et al.*, 2008), which is also reflected in the present cladogram. *Rattus*, *Hadromys*, *Bandicota* and *Nesokia* form a clade which is strongly supported by four synapomorphies. The status of *Hadromys* is not clear

as it has not yet been included in any molecular phylogenetic study. Misonne (1969) included it in the *Arvicanthis* Division, but Musser (1987) has strongly argued against its inclusion in this division. *Rattus*, *Bandicota* and *Nesokia* are strongly related at the molecular level (Verneau *et al.*, 1998; Michaux *et al.*, 2007; Suzuki *et al.*, 2001; Lecompte *et al.*, 2008). They are here united by two shared derived characters. Further, the sister taxa, *Bandicota* and *Nesokia* are strongly supported by four synapomorphies.

The present molar morphology based phylogeny showing closer relationship of *Golunda* and *Millardia* to *Rattus* and allies is fundamentally different from that based on the molecular phylogeny (Lecompte *et al.*, 2008), exhibiting closer relationship of *Golunda* and *Millardia* to *Mus*.

### *Mus-Rattus* divergence date

The oldest evidence of fossil *Mus* comes from 7.3 Ma Siwaliks locality Y457 (Jacobs and Flynn 2005). On the other hand, the oldest fossils of *Rattus* are known only from ~ 3 Ma deposits of Thailand (Chaimanee *et al.*, 1996) and China (Zheng, 1993). As mentioned earlier, though *Rattus* sp. is reported from Upper Siwaliks of India (Gaur, 1986), its identification based on just one first lower molar is doubtful (Musser, 1987). However, *Bandicota* grouped within *Rattus sensu stricto* (Verneau *et al.*, 1998) does occur in 2.5-2 Ma old Siwalik deposits (Patnaik, 1997; 2001).

Based on evolutionary changes observed on Siwalik murine molars, Jacobs (1978) proposed anagenesis of *Antemus* to *Progonomys* to *Mus*. It was observed by Jacobs (1978), that *Mus* dental features appeared to have evolved from those of *Progonomys*, whereas, the dental characters of extant *Rattus* reflect evolution from those of *Karnimata*. Jacobs and Pilbeam (1980) provided a window of 14- 8 Ma for the *Mus-Rattus* divergence based on the Siwalik murine record. The maximum split date was further reduced to 12 Ma, primarily based on the first appearance of *Progonomys* (Jaeger *et al.*, 1986) and the split between *Progonomys* and *Karnimata* (Jacobs and Downs, 1994). The divergence date between *Progonomys* and *Karnimata* has been interpreted to represent *Mus-Rattus* split (Jacobs and Downs, 1994). This divergence date (maximum) has been estimated to be between 10.4 to 11.1 Ma (Jacobs and Flynn, 2005, figure 5.2).

Molecular phylogenetic trees have been calibrated based on very well constrained fossil finds (12-10 Ma). However, molecular divergence times between various lineages have been found to vary because of difference in the taxa sampled, methods used and selection of calibration points. Nevertheless, one thing has come out quite clearly that *Mus-Rattus* divergence took place deep in the evolutionary history of murines (Steppan *et al.*, 2004; Michaux *et al.*, 2001; Chevret *et al.*, 2005). Steppan *et al.* (2004) came up with an estimate of 10.3-8.8 Ma as the *Mus-Rattus* divergence date. They found their dates to be less compared to those estimated (based on 12 and 14 Ma calibration) by some previous workers (Robinson *et al.*, 1997; Ruedas and Kirsch, 1997; Ducroz *et al.*, 1998; Verneau *et al.*, 1998; Dubois *et al.*, 1999; Barome *et al.*, 2000; Huchon *et al.*, 2002; Michaux *et al.*, 2001; Salazar-Bravo *et al.*, 2001), but quite compatible with the dates interpreted by others (She *et al.*, 1990; Smith and Patton, 1999), based on a 10 Ma calibration point. Recently, Lecompte *et al.* (2008, Fig.2) based on a Bayesian molecular clock set (10-12 Ma) calibrated using the fossil record (Jacobs and Downs, 1994; Jacobs and Flynn, 2005; Jaeger *et al.*, 1986) found their *Mus-Rattus* split date to be about 11.3 +/- .5 Ma.

The present cladogram when calibrated with the first appearance of various murine taxa in the Siwalik record (Figure 3), indicates a different picture. Although *Progonomys* shares ancestry with rest of the murines, it is *Karnimata* that has a closer relationship to *Mus* and its allies, including *Rattus*. Therefore, neither *Progonomys-Karnimata* split, nor the first appearance of *Progonomys* appear to represent *Mus-Rattus* divergence, as per the present cladogram. Rather, it is the earliest fossil evidence of *Mus*, that at present is 7.3 Ma (Jacobs and Flynn, 2005) constraints the maximum date for the *Mus-Rattus* split. But this record has the potential of going back up to 10.4 Ma, when the first confirmed record of *Karnimata* is recognized in the Siwaliks (Jacobs and Flynn, 2005). Further, the oldest record of *Mus* would also determine the age estimates of divergence between *Arvicanthis-Golunda* and *Mus*, which is at present estimated to be 11+/- .5 Ma by Lecompte *et al.* (2008, Figure 2), following a 10-12 Ma calibration. Steppan *et al.* (2004) estimated *Arvicanthis-Mus* split at 9.7 Ma. The *Millardia-Golunda* split as per Lecompte *et al.* (2008) happened 10.2 +/- .6 Ma ago. This split as per figure 3, occurred sometime around 4 Ma, which would be quite consistent with a younger *Mus-Rattus* split date proposed here. Molecular phylogeny within *Rattus Sensu Stricto*, which includes the split of *Bandicota bengalensis* and other *Rattus* species occurred ~3 Ma ago as per Verneau *et al.* (1998). The *Rattus* and *Bandicota+Nesokia* split as shown in

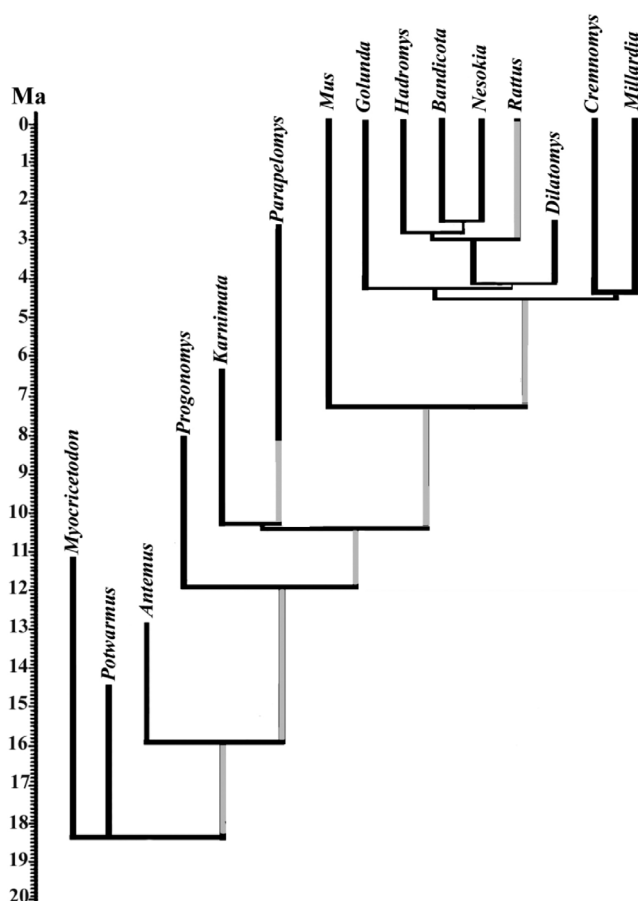


Fig. 3. Phylogeny calibrated based on the cladistic relationships presented in Fig. 4. The recorded temporal ranges are in black. The bars in grey represent missing ranges and missing ancestral lineages. Source of chronostratigraphical data: Barry *et al.* (2002); Jacobs and Flynn, (2005), Patnaik, 1997; 2001; Wessels (2009); Cheema *et al.*, (2003); Raghavan, (1990).

figure 3, appears at 2.5 Ma. However, presence of *Rattus*, which is basically a south-east Asian phenomenon (Chaimanee *et al.*, 1996) is yet to be confirmed in the Siwalik fossil record.

### Biogeographic implications

From an *Antemus* stock, *Progonomys* diverges and probably spreads towards west and north west appearing in Africa by 12 Ma (Winkler, 1994; Jacobs, 1985; Gerrads, 2001), Europe by 11 Ma (Aguilar and Mixhau, 1996; Renaud *et al.*, 1999) and China, by 10 Ma (Qiu *et al.*, 2003). Murine dispersal beginning around 11.8 Ma through Arabia has been postulated by Jacobs *et al.* (1990). This is attested by the sudden appearance of the equid *Hipparion* in Africa around 11 Ma (Bernor *et al.*, 1987;1990; Garces *et al.*, 1997). *Karnimata* sp. and cf. *Parapelomys* appear in Namibia and East Africa by 9-10 Ma ago (Conroy *et al.*, 1992; Senut *et al.*, 1992; Gerrads, 2001). Around this time *Parapodemus* might have migrated in the opposite direction to appear in the Siwaliks. This corridor may have remained active between 9-7 Ma as indicated by dispersal of bovids (Thomas, 1994), elephantoids (Tassy, 1986) and other rodents (Wynn *et al.*, 2006) from Eurasia to Africa. However, it may be noted that Middle East witnessed high aridity between 7-8 Ma as evidenced by the rise of gerbils (Tchernov, 1992; Pickford, 1991). This may have caused hindrance in faunal exchange between Africa and Eurasia through the Arabian corridor. The corridor may have again got activated by the terminal Miocene and Early Pliocene, and used by the Asian genera *Mus*, followed by *Golunda* and *Millardia* to migrate westward to Africa, and African *Saidomys* to disperse eastwards to appear in Afghanistan and Thailand. This may explain polyphyletic origin of African murines (Lecompte *et al.*, 2008).

### CONCLUSIONS

The present phylogeny reveals that the murinae is a monophyletic group and is deeply rooted in the geological history of the Indian subcontinent. The cladogram obtained here differ from previous studies based on dental morphological evolution and indicates that *Progonomys* is unlikely to be the direct ancestor of *Mus*. This implies that the *Progonomys-Karnimata* split or the first occurrence of *Progonomys* may no longer be taken as to represent *Mus-Rattus* split. *Mus* occupies a basal position in the clade leading to most of the modern murine taxa, including *Rattus*. This has implications for a possible younger *Mus-Rattus* divergence date which at the moment is 7.3 Ma. A younger *Mus-Rattus* divergence date justifies younger first appearance dates of *Millardia*, *Crennomys*, *Dilatomys*, *Hadromys*, *Bandicota* and *Nesokia* in the Siwaliks. Siwaliks murines between ~4 and ~7.5 Ma are poorly represented. Future work should focus on this interval in order to understand the phylogenetic origin of several modern taxa.

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