

**CRICETID RODENTS OF LOWER SIWALIK DEPOSITS,
POTWAR PLATEAU, PAKISTAN
AND MIOCENE MAMMAL DISPERSAL EVENTS**

by

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Siwalik deposits in Pakistan record a 17 Ma interval of vertebrate history in southern Asia. This record includes the evolutionary appearance and radiation of murid rodents, the most successful group of terrestrial mammals; the radiation of bovids in Asia; the Miocene appearance of the three-toed horse *Hipparion* and the Pliocene appearance of the one-toed horse *Equus* from North America; plus the radiation, and extinction of many other groups of mammals. Siwalik deposits have provided one of the best known records of mammalian evolution. Knowledge of the Siwalik vertebrate record has increased markedly during the last ten years. It was fueled by the quest for knowledge about hominoids that are part of the Siwalik record; it has resulted in a precise chronologic framework based on biostratigraphy and magnetostratigraphy (BARRY et al., 1982; JOHNSON et al., 1982).

The Siwalik fossil record is important to European Neogene stratigraphy because many of the mammals recorded from the Siwaliks are also recorded from deposits in Europe. The Siwalik record, with fossils placed in superposed biostratigraphic sequence and calibrated by magnetostratigraphy, can serve as a test for the European fossil record where superposition and magnetostratigraphy are less frequently available. This paper focuses on the oldest Siwalik deposits to illustrate the radiation and dispersal history of cricetid rodents in those deposits. The Siwalik record of cricetid rodents and their derivatives, support the interpretation that small mammals dispersed between continents during at least two separate intervals during the Miocene. These dispersal intervals are broadly defined at the present time; however, their precise chronologic resolution can very likely be attained with a better fossil record. The intervals I wish to emphasize are at 8–10 Ma and 15–17 Ma. These intervals are represented in the Siwalik stratigraphic sequence in the Nagri and Kamli formations, respectively, illustrated in Fig. 1 (from BARRY et al., 1985).

Two discrete lineages of Miocene cricetid rodents, the *Democricetodontini* and the *Megacricetodontini*, were identified by FAHLBUSCH (1964) and were further exemplified by MEIN and FREUDENTHAL (1971). The *Megacricetodont* lineage is represented in Siwalik deposits by *Megacricetodontini* and its presumed derivatives, the *Dendromurini* and *Myocricetodontini*. *Megacricetodont* cricetids can be characterized by an M_1 with a strongly bilobed anterocone, upper molars that tend to have a single loph joining the paracone and protocone, and M_1 that is usually long with a relatively narrow anteroconid. The *Dendromurini* differ from the *Megacricetodontini* primarily in development of lingual cingula and cusps on the upper molars. The *Myocricetodontini* differ from the *Megacricetodontini* primarily in reducing the longitudinal connection between cusps (the mure) in both upper and lower molars. Murid rodents are believed derived from *Megacricetodonts* by developing a lingual cingulum and accessory cusps on the upper molars and reducing the longitudinal connection of cusps, in order to derive the distinctive chevron folds of upper murid dentitions.

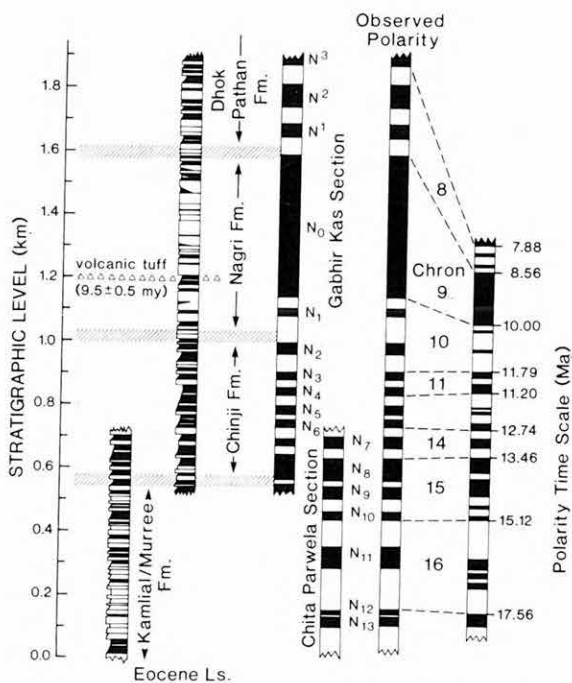


Fig. 1. Lower Siwalik stratigraphic and magnetostratigraphic sequence

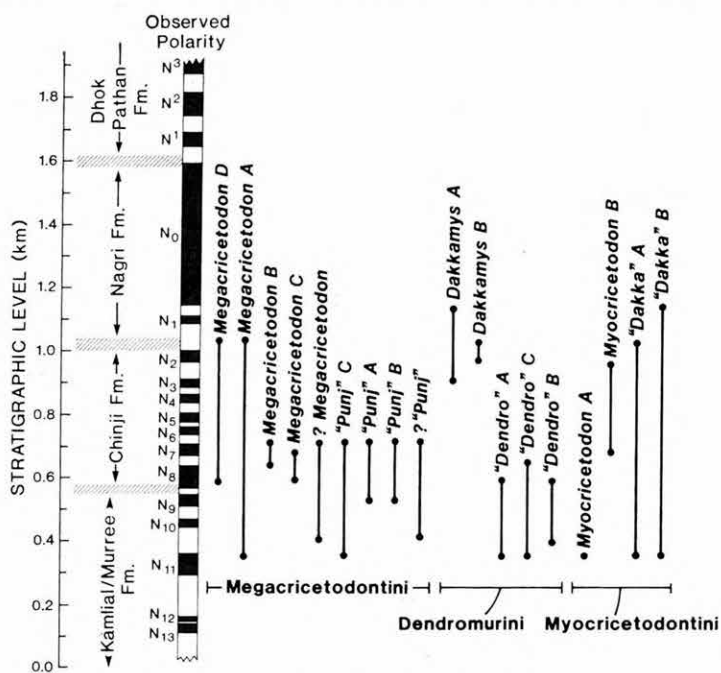


Fig. 2. Stratigraphic ranges of Megacricetodontinae

The Siwalik record of Megacricetodont rodents in the Potwar plateau is illustrated in Fig. 2. It should be pointed out that several of these taxa have never been published, although a relatively large sample has been studied. Also, the sample is being expanded, so some of the identifications are likely to be changed. In spite of this, the sample is presently adequate to characterize most of the species and further taxonomic changes are expected to be minor. Note that Megacricetodontini, Dendromurini and Myocricetodontini are all known from the oldest Siwalik faunas with cricetids considered about 16 Ma. This suggests that all of these rodents were thriving in southern Asia just prior to 16 Ma or they underwent an explosive radiation in southern Asia about that time. JAEGER et al. (1985) described a similar dendromurid (*Antemus thailandicus*) and an Asian rodent *Diatomys*, but none of the other cricetid groups, from middle Miocene deposits in Thailand.

The highest diversity, as well as maximum abundance, of these megacricetodont rodents occurs in the Lower Chinji Formation, about 13–14 Ma. Surprisingly, the Megacricetodonts had virtually disappeared from the Potwar plateau by the time the Nagri Formation was deposited about 10–11 Ma.

The second lineage of cricetids in these deposits is the Democricetodontini. Democricetodonts are characterized by M_1 having a wide and weakly bilobed anterocone (medial lobe much smaller than labial lobe); upper molars commonly have more than one loph directed toward and frequently joining the opposing cusp; posterior molars are slightly reduced in size especially in the lower dentition. In addition, the longitudinal crest (mure) is very persistent and the mesoloph (mesolophid) is commonly present but short in all molars. Democricetodonts probably gave rise to the Rhizomyidae in southern Asia, although an ancestral species has not been identified.

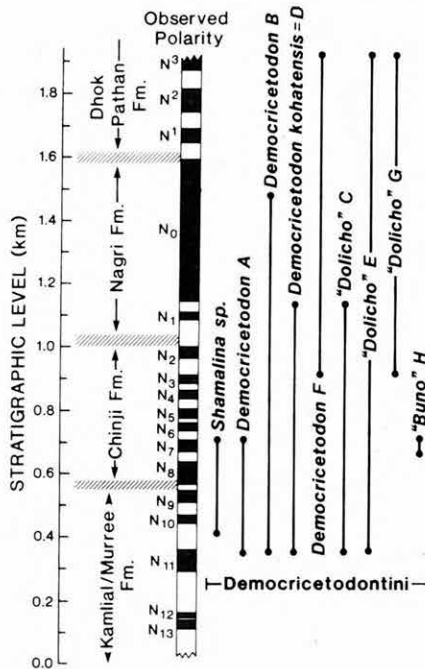


Fig. 3. Stratigraphic ranges of Democricetodontinae

Shamalina, a small cricetid from early Miocene deposits of Saudi Arabia is also recorded from the Potwar Plateau; *Shamalina* appears closely related to both cricetid lineages.

The record of democricetodont rodents in the Potwar Plateau is shown in Figure 3. Democricetodonts are less diverse but have a longer record than the megacricetodonts; however their maximum abundance is in the Lower Chinji Formation, about the same time as the "blooming" of Megacricetodonts. Probably the decline of cricetid rodents in Middle Siwalik deposits results from competition with the murids, their descendants. It is only the larger cricetids that continue into the Dhok Pathan Formation. By about 8–10 Ma all of the smaller cricetids had been replaced by small murids.

With this stratigraphic—taxonomic framework in mind, we can postulate the intercontinental dispersal history of these rodents. The oldest dispersal interval, 15–17 Ma, is illustrated in Fig. 4. This interval precedes the appearance of murids; it also records the presence of both Megacricetodontini and Democricetodontini in Europe (e.g., La Grive and Sansan), and in China (the Xining Basin (*Megacricetodon* and *Plesiodipus*)). In the Siwalik deposits, Megacricetodontini, Democricetodontini, Dendromurini, and Myocricetodontini all occur together in the same site. Southern Asia probably records a higher diversity of cricetid rodents during this interval than anywhere else in the world. In Africa both Dendromurini (e.g. *Dakkamys*) and Myocricetodontini (e.g. *Myocricetodon*) are recorded during this interval (e.g., at Beni Mellal, and Ngorora).

The second interval of intercontinental dispersal that I emphasize is the 8 to 10 Ma interval, illustrated in Fig. 5. This interval occurs later than the evolutionary appearance of murids in southern Asia (about 14 Ma), and the appearance (by dispersal) of *Hipparion* into Eurasia. It also approximates the youngest known record of hominoid primates in southern Asia as well as the dispersal appearance of murid rodents in Europe (Can Llobateres) and Africa (Bou Hanifia). Note that the Megacricetodontini cricetids had become extinct in SE Asia by 10 Ma although some Democricetodontini cricetids persisted with Muridae in Europe (Can Llobateres), in China (Lufeng), and in the Siwaliks as noted above.

AGUILAR and others (1984) have reported the Myocricetodontini *Myocricetodon* and the Dendromyini *Dendromus* along with murids (*Apodemus*, *Stephanomys*, *Occitanomys*, *Castillomys* and *Parathomys*), Democricetodontini (*Cricetus* and *Calomyscus*) and the gerbilline *Protatera* from deposits near Salobrena in southern Spain. These authors note that the assemblage from Salobrena correlates best with latest Miocene or early Pliocene; that is near 5 Ma rather than 8–10 Ma. These are the only known records of *Myocricetodon* and *Dendromus* from Europe. These genera are well-known from the southern shores of the Mediterranean and perhaps the Salobrena record indicates a shift of southern Mediterranean mammals toward the north at the end of the Miocene. At the least, the Salobrena Spain record indicates that populations of Myocricetodontini and Dendromurini in the Mediterranean long after their extinction in SE Asia.

Myocricetodontini (and Dendromurini?) cricetids occur with murids in North African faunas associated with the 8–10 Ma dispersal interval (e.g. at Oued Zra and Bou Hanifia). Thus this interval of dispersal is best described as the radiation and dispersal of murid rodents associated with "relict" Democricetodontini in Eurasia and with "relict"; Myocricetodontini and Dendromurini in Africa.

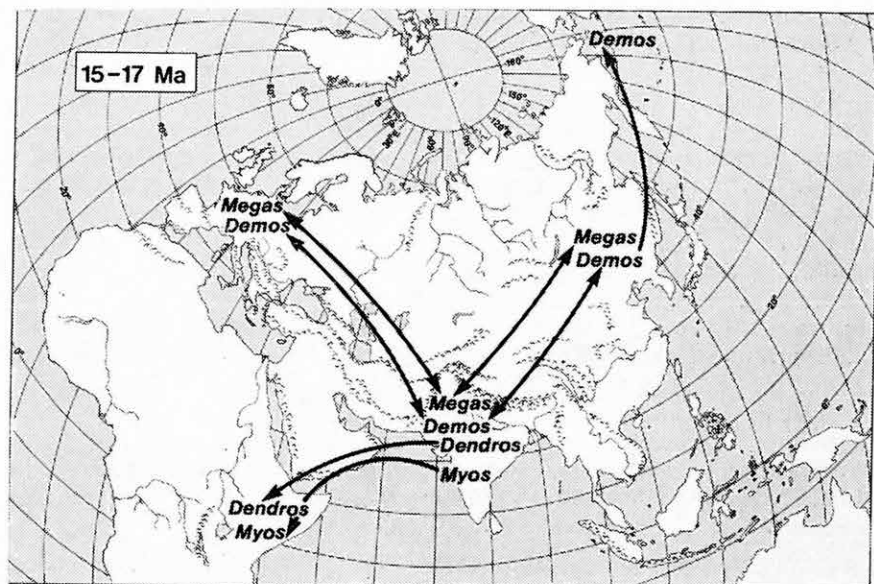


Fig. 4. The 15–17 Ma dispersal interval

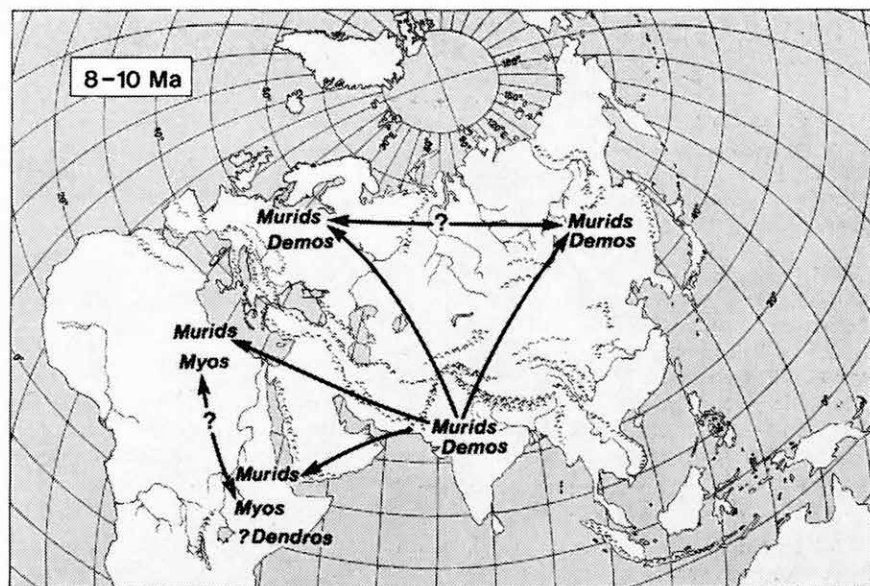


Fig. 5. The 8–10 Ma dispersal interval

To summarize, muroid rodents are small, rapidly evolving, locally abundant and widely distributed. They are good travelers and have provided a good fossil record. They are proving extremely useful for biostratigraphic and biochronologic subdivisions. They also promise to clarify the timing and direction of intercontinental mammal dispersal events during the Miocene. These muroid rodents suggest intercontinental dispersal between Asia, Europe and Africa during two broadly defined intervals 15–17 Ma and 8–10 Ma. The first interval (15–17 Ma) probably brought muroids from Europe and Africa to Asia. However, the records of muroid rodents in Asia prior to 17 Ma is poor, so the direction of dispersal cannot be determined with confidence. The later dispersal interval (8–10 Ma) is more clear. This interval appears dominated by dispersal of murids from Asia into Europe and Africa.

In drawing the conclusions present here, I have borrowed from the work of a large consortium of colleagues associated with the Geological Survey of Pakistan and Peshawar University in Pakistan plus Dartmouth College, Harvard University, Yale University, Columbia University, the University of Arizona, Southern Methodist University and the Smithsonian Institution in the United States. I particularly wish to acknowledge my colleagues Larry FLYNN (American Museum of Natural History) plus Louis JACOBS and Will DOWNS (Southern Methodist University) for sharing their knowledge of Siwalik small mammals with me.

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