

CRICETID RODENTS FROM SIWALIK DEPOSITS NEAR CHINJI VILLAGE. PART I: MEGACRICETODONTINAE, MYOCRICETODONTINAE AND DENDROMURINAE.

by

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Mots-clés: Rongeurs, Siwalik, Miocène moyen, Megacricetodontinae, Myocricetodontinae, Dendromurinae.

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ABSTRACT

Seventeen species of cricetid rodent are recognized and described from lower and middle Siwalik deposits in the Potwar Plateau of Pakistan. These species are grouped in three categories, characterized as subfamilies (e.g., Megacricetodontinae, Myocricetodontinae, and Dendromurinae); an additional and more abundant category of rodents from these deposits, the Democricetodontinae, is excluded from this study, and will be described in a later study. Fifteen of the species are new, and four new genera are described. The Siwalik cricetid taxa are : *Megacricetodon aquilari*, n. sp.; *Megacricetodon sivalensis*, n. sp.; *Megacricetodon daamsi*, n. sp.; *Megacricetodon mythikos*, n. sp.; *Punjabemys downsi*, n. gen. & n. sp.; *Punjabemys leptos*, n. gen. & n. sp.; *Punjabemys mikros*, n. gen. & n. sp.; *Myocricetodon sivalensis*, n. sp.; *Myocricetodon* sp.; *Dakkamyoides lavocati*, n. gen. & n. sp.; *Dakkamyoides perplexus*, n. gen. & n. sp.; *Dakkamys asiaticus*, n. sp.; *Dakkamys barryi*, n. sp.; *Dakkamys* sp.; *Paradakkamys chinjiensis*, n. gen. & n. sp.; *Potwarmus primitivus*, n. gen.; and *Potwarmus minimus*, n. gen. & n. sp.

This diverse record of middle Miocene small mammals illuminates a profound radiation of cricetid rodents in southern Asia, the effects of which were felt in Europe and Africa as well as the rest of Asia.

INTRODUCTION

Sedimentary rocks of the Siwalik Group are well exposed in the Potwar Plateau of northern Pakistan. These rocks have been under study for almost two decades and have produced a wealth of new paleontologic and chronologic data (for example, Pilbeam *et al.* 1977, 1979; Jacobs, 1978; Moonen *et al.* 1978; Opdyke *et al.* 1979; Badgley & Behrensmeyer, 1980; de Bruijn *et al.* 1981; Johnson *et al.* 1982; Barry *et al.* 1982, 1985; Flynn & Jacobs, 1982; Pilbeam, 1984). It seems likely that Siwalik sediments of the Potwar Plateau are among the most productive and best calibrated terrestrial sediments that span the last 18 million years. These deposits have yielded a good record of cricetid rodents for only about half (9-18 million year) of the Siwalik interval of deposition, being replaced by murid rodents during much of the latter half of Siwalik deposition.

Most of the cricetid rodents included in this study were collected from lower Siwalik deposits (Kamlial and Chinji Formations) in the vicinity of Chinji village, about 120 km south of Islamabad (the capitol) where the Potwar Plateau meets the Salt Range, and are tied to stratigraphic sections published by Johnson *et al.* (1985) and by Barry *et al.* (1985). Geographic location of this area is shown in Figure 1 (from Flynn & Jacobs, 1982). Stratigraphic location of fossil sites is given in Figure 2 (from Johnson *et al.* 1985). Any geographic/stratigraphic or curatorial questions should be addressed to the author or the Harvard-Geological Survey of Pakistan Project, Peabody Museum, Department of Anthropology, Harvard University, Cambridge, MA 02138.

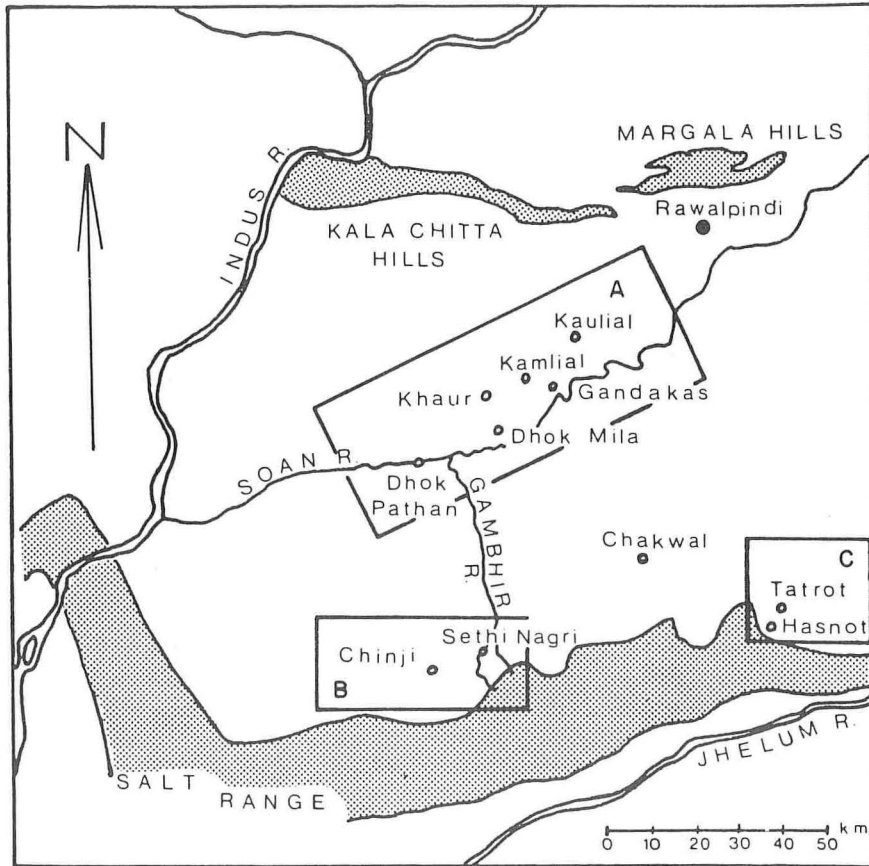


Figure 1. Map of Potwar Plateau, Pakistan, showing location of principal fossil collecting areas in Siwalik deposits. A=Dhok Pathan-Khaur area; B=Chinji-Nagri area; C=Tatrot-Hasnot Area. (From Flynn and Jacobs, 1982, Figure 1).

Cricetid rodents had not been reported from Siwalik deposits prior to 1977 (Pilbeam *et al.* 1977). Barry *et al.* (1982) reported cricetid rodents from the "*Hipparion s.l.*"/*Selenoportax lydekkeri* interval zone, and in older deposits. Following that study, more emphasis was placed on the collection of older Siwalik deposits, and many of the fossils included in this study were collected after 1982 by screen washing Lower Siwalik sediments in the vicinity of Chinji Village. Jacobs *et al.* (in press) reviewed the Neogene record of rodents in southern Asia, noting that cricetids are common members of lower and middle Siwalik assemblages. This study is a description and taxonomic assessment of cricetid fossils from those lower and middle Siwalik deposits. Four lineages of cricetid rodents are presently recognized from Siwalik deposits, and only three of those lineages (e.g., Megacricetodontinae, Myocricetodontinae, and Dendromurinae) are included in this report. The largest lineage (Democricetodontinae) will be reported later.

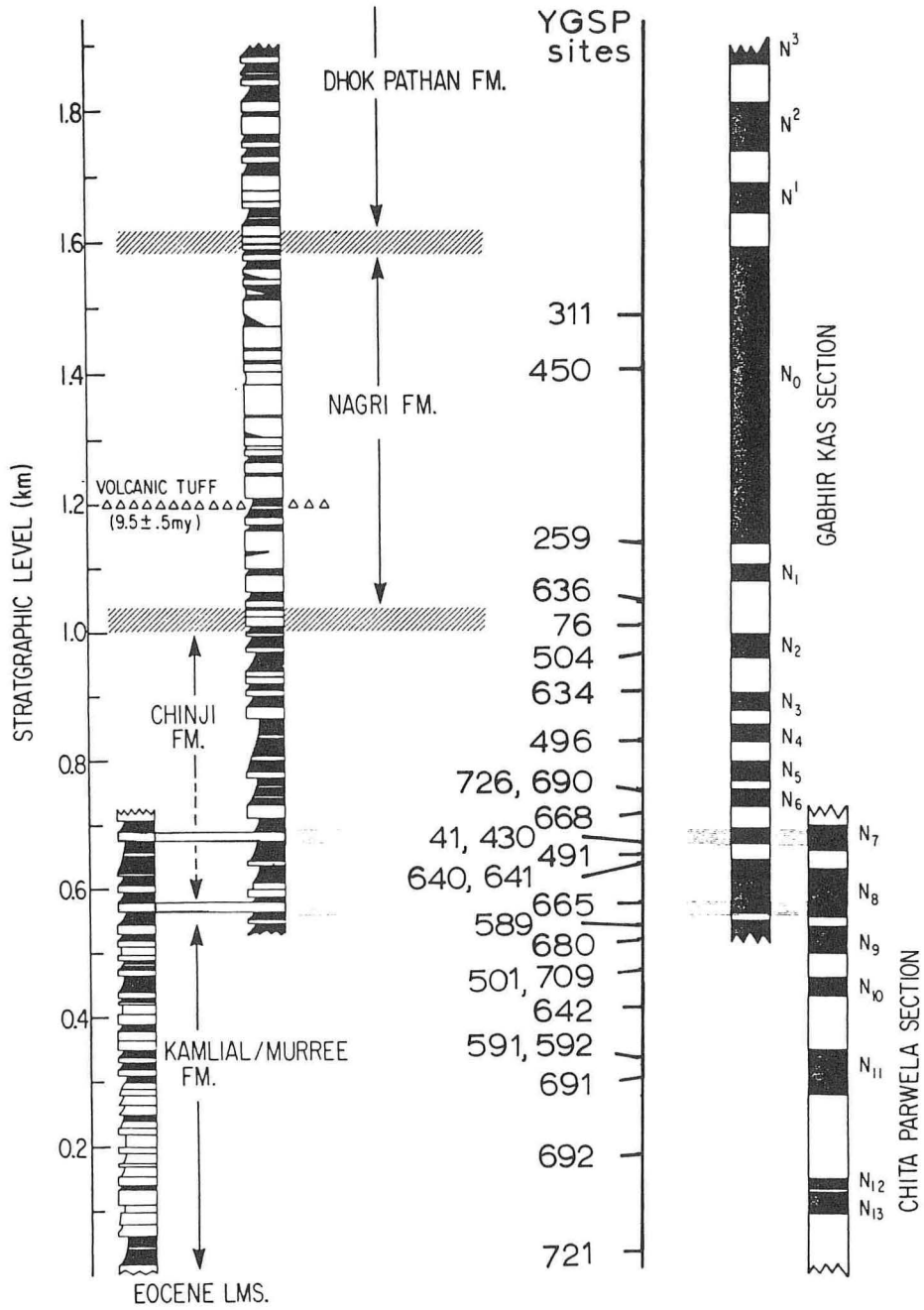


Figure 2. Composite stratigraphic sequence of lower and middle Siwalik deposits with YGSP fossil sites yielding cricetid rodents. (Modified from Johnson and others, 1985, Figure 4).

SYSTEMATICS

A comprehensive systematic revision of the Cricetidae is badly needed, but is beyond the limits of this study. The most recent review of European fossil cricetids was by Mein & Freudenthal (1971), in which seven cricetid subfamilies were recognized. Most of the Siwalik cricetids in this study would be included in the Cricetodontinae and Cricetinae of Mein & Freudenthal (1971). Lavocat (1961) identified a group of African Miocene cricetids that he named Myocricetodontinae; myocricetodontines are now known from Asia and are included in this study. The last group included in this study is the Dendromurinae, or African tree mice. Dendromurinae have often grouped with the Muridae (*e.g.*, Walker, 1968) rather than Cricetidae; they were considered ancestral to the Muridae by Lavocat (1959) and by Petter (1966). This study supports the conclusion of Lavocat (1959) and Petter (1966), that Dendromurinae were probably ancestral to the Muridae; however, it appears the Dendromurinae are better placed among the Cricetidae, and the Siwalik record supports the interpretation (in conflict with the conclusions of Lavocat, 1959, and Petter, 1966) that Asian dendromurines gave rise to the earliest Muridae.

The four lineages of Siwalik cricetids are characterized below as subfamilies (*e.g.*, Megacricetodontinae, Democricetodontinae, Myocricetodontinae, and Dendromurinae). However, with more extensive review these lineages might be reduced to tribes within one or two subfamilies. In this study they are characterized as subfamilies for convenience; they are diagnosed to facilitate comparison and later revision, if necessary. This report includes only three of the four Siwalik cricetid lineages; the Myocricetodontinae and Dendromurinae seem closely related to, and derived from, the Megacricetodontinae. In contrast, the Democricetodontinae appear a more distinct lineage, evolving in a different direction relative to the Megacricetodontinae. For clarification, the Copemyinae of Jacobs and others (in press) are identical the Democricetodontinae in this study. As presently recognized, *Copemys* is a North American democricetodontine and *Democricetodon* is an Old World democricetodontine; these two "genera" are so similar, especially in the middle Miocene, they can be considered subgenera, as expressed by Fahlbusch (1967). The terms *Democricetodon* and Democricetodontinae are applied in this study for internal consistency, following convention for the Old World taxon.

CRICETID DENTAL TERMINOLOGY

Terms used in the description of these taxa are illustrated in Figure 3. Unless stated otherwise, the Siwalik cricetid teeth are characterized by the following dental features : M1/ has 5 cusps (anterocone, paracone, protocone, metacone, and hypocone), M2/ has four cusps (paracone, protocone, metacone, and hypocone), and M3/ has 2 or 3 cusps (paracone, protocone, and sometimes a hypocone), M/1 has five cusps (anteroconid, protoconid, metaconid, hypoconid, and entoconid), M/2 has four cusps (protoconid, metaconid, hypoconid, and entoconid), and M/3 has three cusps (protoconid, metaconid, and hypoconid). The protocone and hypocone are lingual in upper molars and labial in lower molars (as protoconid and hypoconid). In general, M1/1 is longer than but approximates the width of M2/2; M3/3 is always shorter and commonly more narrow than anterior molars. Upper molars have three prominent roots and lower molars have two prominent roots; accessory rootlets are unknown in these species.

Most of the terms applied in these descriptions have been applied previously (e.g., Fahlbusch, 1964; Engesser, 1972; and Lindsay, 1972); however, some terms are new and in other instances the limits of terms have been re-defined; these are illustrated (Figure 3) for clarification.

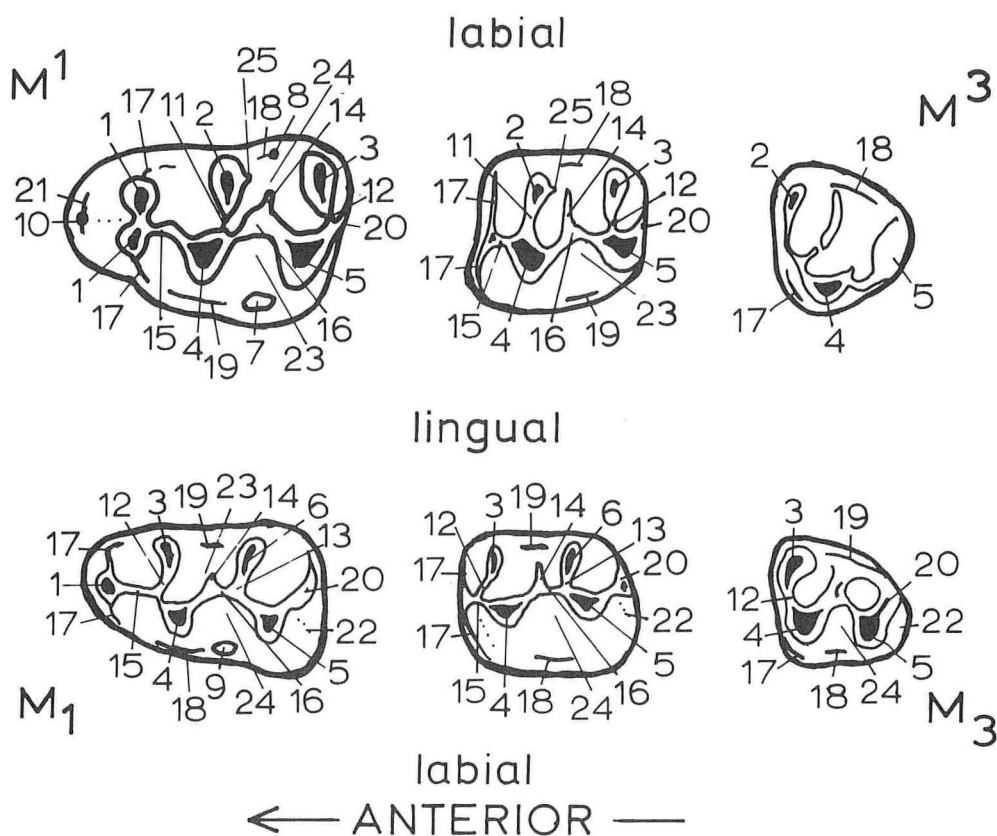


Figure 3. Cricetid dental terminology.

| | | |
|---------------------|------------------------|---|
| 1- Anterocone (-id) | 11- Protoloph | 21- Anterior styler shelf |
| 2- Paracone | 12- Metaloph (-id) | 22- Posterolabial shelf (or sulcus) |
| 3- Metacone (-id) | 13- Hypolophid | 23- Lingual transverse valley (or sinus) |
| 4- Protocone (-id) | 14- Mesoloph (-id) | 24- Labial transverse valley (or sinusid) |
| 5- Hypocone(-id) | 15- Anterior mure | 25- Posteriorly-directed spur |
| 6- Entoconid | 16- Posterior mure | |
| 7- Enterostyle | 17- Anterior cingulum | |
| 8- Mesostyle (-id) | 18- Labial cingulum | |
| 9- Ectostylid | 19- Lingual cingulum | |
| 10- Anterostyle | 20- Posterior cingulum | |

A brief discussion of some of the terms follows. The term *mure* is used for the anteroposterior wall that divides the tooth into unequal internal and external halves; it is called an "ectoloph" (or "ectolophid") by Mein & Freudenthal (1971). This structure is often incomplete or even absent, especially in Myocricetodontinae and Dendromurinae. Therefore the anterior part, comprising the anteroloph (or anterolophid) that may join the anterocone (or anteroconid) with the protocone or paracone (or protoconid or metaconid) is termed the *anterior mure*. The posterior part, comprising the ridge that

may join the protocone, hypocone, and protoloph (or protoconid, hypoconid, and entolophid) is termed the *posterior mure*. The same structure (*e.g.*, the posterior mure) is termed the "langsglat" (= longitudinal crest) by Fahlbusch (1964), and Engesser (1972). The entire structure, both anterior and posterior mure, is also called the *longitudinal crest* in some descriptions.

In Siwalik cricetids the *enterostyle* and *ectostylid* are important dental structures. Usually the corresponding enteroloph or ectolophid is very short or absent. The "ectomesolophid" of Wessels *et al.* (1982) is called an ectostylid in these descriptions.

The *labial branch of the anteroloph* is a common feature of some Democricetodontinae but is rare in Megacricetodontinae. This structure is termed the "vordere quersporn" in descriptions by Fahlbusch (1964) and Engesser (1972), and the "labial anteroloph" or the "labial spur of the anterolophule" in descriptions by many French paleontologists; it is termed the "labial spur on the anterior arm of the protocone" by Wessels and others (1982). The *labial anterior cingulum* in the following descriptions was termed the "labial branch of the anterolophid" by Wessels *et al.* (1982).

The *lingual sinus* of upper molars and *labial sinusid* of lower molars have frequently been called, respectively, the "sinus" and "sinusid" or "innenbucht" and "aussehbucht" in descriptions by European paleontologists. If both lingual and labial sinuses (or inflections) on both sides of the same tooth are involved, they are called the *transverse valley*.

Another term used in these descriptions is the *posterolabial sulcus* or *posterolabial shelf* that develops between the hypoconid and posterior cingulum of lower cheek teeth, especially M/2. The posterolabial sulcus or shelf results from development of a "labial posterolophid", as described by R. Daams in Whybrow and others (1982, p. 114) for the genus *Shamalina*. The labial posterolophid is poorly developed in Siwalik cricetids, compared to its development in *Shamalina*; however, a posterolabial sulcus is common in many species of Siwalik cricetids.

The *protoloph* and *metaloph* (or *metalophid* and *hypolophid*) in the following descriptions are termed the "vorjochkante" and "nachjochkante" in descriptions by many German paleontologists, or "protolophule" and "metalophule" (or "metalophulid" and "hypolopholid") in descriptions by many French paleontologists, and by Wessels *et al.* (1982).

Specimens illustrated in Plates 1-10 are Siwalik cricetids, photographed by a scanning electron microscope. Magnification of each photograph varies by as much as 5 percent. In order to facilitate comparison of those figures, a horizontal line scaled to one millimeter at the magnification of the accompanying specimen underlies each illustration.

MEGACRICETODONTINAE

The Siwalik Megacricetodontinae are characterized by having a strongly bilobed anterocone on M1/; on upper molars the anterior arms of the protocone and hypocone are more robust than the posterior arms, a mesoloph is usually present but rarely long, and a small spur may be directed posteriorly on the paracone; the anteroconid is long, narrow, and single cusped although twinning of the anteroconid may be incipient (*e.g.* in *M. sivalensis*) on M/1; the anterior arms of the protoconid and hypoconid are commonly shorter than the posterior arms and a mesolophid is commonly present but rarely long; accessory cusps (lingual in upper molars, labial in lower molars) are usually absent or very small.

Transverse valleys in Megacricetodontinae are usually oriented transverse to the longitudinal axis of teeth, although the lingual sinus and sinusid are commonly located

slightly anterior relative to the labial sinus and sinusid. The posterior mure is well developed in *Megacricetodontinae*, which separates the labial and lingual sinuses (and sinusids) near the midline. In contrast, the transverse valleys of *Myocricetodontinae* and *Dendromurinae* are more continuous than in *Megacricetodontinae* and may be oriented more oblique relative to the longitudinal axis, or offset with the lingual sinus and sinusid anterior relative to the labial sinus and sinusid. Alignment and continuity of the transverse valley is a guide to distinguishing *Megacricetodontinae*, *Myocricetodontinae* and *Dendromurinae*.

A dental feature of Siwalik *Megacricetodontinae*, and some of their descendants, was to develop "pillar-like" cusps by steepening one side of the cusps (especially noticeable on the labial cusps of upper molars and the lingual cusps of lower molars). Steepening one side of cusps also creates the illusion that the cusps are inclined, especially when the non-vertical side slopes farther from the vertical axis of the cusp. These features are also developed in many European cricetids such as in *Megacricetodon similis* and *Megacricetodon collongensis*, and in lower dentitions of *Democricetodon minor* and *Democricetodon bavaricus*. Upper dentitions of *Democricetodon* (from both the Siwaliks and Europe) rarely have the posterior side of cusps steepened.

In general, the illusion of inclined cusps is greater in some *Myocricetodontinae* and *Dendromurinae* than in *Megacricetodontinae* (or *Democricetodontinae*) because the base of cusps in members of those lineages is commonly lengthened anteriorly in upper molars and posteriorly in lower molars. *Dendromurids* are the only group of cricetids in which cusps of some taxa are really inclined.

MEGACRICETODON FAHLBUSCH, 1964

The genus *Megacricetodon* is very diverse in Europe where 12 species have been recognized (see Aguilar 1980 & 1981, Daams, personal communication, 1985) in the middle Miocene (e.g., MN zones 4-9). Evolutionary trends seen in these species include a general change in size, development of a posteriorly-directed spur on the paracone, reduction of the mesoloph and mesolophid, anteroconid of M/1 bilobed, and lingual sinus of upper cheek teeth pinched anteriorly, labial sinusid of lower cheek teeth becoming pinched posteriorly. In general, European species of *Megacricetodon* lack (or develop to a lesser degree) many of the trends seen in southern Asian species of *Megacricetodon*, such as steepening one side of cusps, reduction of the mure, shortening posterior arms of lingual cusps in upper molars, and shortening anterior arms of labial usps in lower molars.

Megacricetodon sp. was reported from Siwalik deposits by Wessels *et al.* (1982), based on 15 isolated cheek teeth from the Chinji Fm. near Banda Daud Shah, Kohat District, Pakistan. Those specimens are considered most similar to *Megacricetodon mythikos*, n. sp., described below. Wessels *et al.* (1982) also recognized a zapodid, genus and species indeterminate, from the same site, based on a jaw fragment with M/2-3 and three isolated M/2. These latter specimens are also regarded as *Megacricetodontinae* (rather than *Zapodidae*) and are probably closely related to *Megacricetodon mythikos*.

Megacricetodon has also been reported from the Xiacaowan Formation of Jiangsu Province (Li *et al.* 1983), and from the Chetougou Formation of Qinghai Province (Li & Qiu, 1980; Qiu, Li, and Wang, 1981) in China. The Xiacaowan Fm. has yielded 68 isolated cheek teeth of *Megacricetodon* that were compared to *M. collongensis* of Europe in having similar size and cusp morphology, although it was

noted the M/1 of the Xiacaowan fauna is smaller and lacks a twinned anteroconid that is developed in some specimens of *M. collongensis* (Li *et al.* 1983; translated by Will Downs). Qiu *et al.* (1981) described *Megacricetodon sinensis* from the Chetougou Fm. at Danshuilu as an extremely small and brachydont species with a short wedge-shaped outline and a simple, untwinned anteroconid in M/1, plus a relatively broad M/2. Another isolated M1/ from Pijiagoukou, considered more or less equivalent to that at Danshuilu, was described as *Megacricetodon cf. sinensis*. Casts of these Chinese specimens show numerous similarities with the Siwalik specimens.

Dental characters of Siwalik *Megacricetodon*

Cheek teeth are low crowned, with M1/ unequally bilobed (lingual lobe always smaller than labial lobe) and four prominent cusps about the same size as the labial lobe of the anterocone; M/1 with narrow, single-cusped anteroconid located slightly labial to the midline; cusps of upper molars steepened on the posterior side, cusps of lower molars steepened on the anterior side; labial cusps elongated transversely in upper molars, and located opposite (more or less) lingual cusps; lingual cusps elongated transversely in lower molars, and located slightly anterior relative to labial cusps; anterior arms of lingual cusps in upper molars relatively long, straight or robust with posterior arms of same cusps short and usually oriented more transverse than the anterior arms; posterior arms of labial cusps in lower molars relatively long, straight or robust with anterior arms of same cusps shorter; posterior cingulum relatively short in upper molars, usually joining the posterior base of the metacone to enclose a narrow, shallow posterolabial valley; posterior cingulum relatively long in lower molars, high medially, descending lingually to usually join the posterior base of the entoconid and enclose a long, shallow posterolingual basin, commonly descending labially to form a posterolabial sulcus or valley; transverse valleys are closed medially by the posterior mure and are usually oriented transversely or slightly oblique to the longitudinal axis in upper molars, usually offset or oriented oblique to the longitudinal axis in lower molars; upper molars with three prominent roots, lower molars with two prominent roots; accessory rootlets unknown.

Megacricetodon aguilari new species

(Plate 1 a-i)

Type : YGSP 19562, isolated left M1/ from locality YGSP 592, Potwar Plateau, Pakistan.

Diagnosis : Small rodent, slightly larger and lower crowned than *Megacricetodon sivalensis*, n. sp.; M1/ with unequally bilobed anterocone and a low lingual cingulum that ascends the hypocone; M2/ lacks an anterior mure, with the posterior mure poorly developed; M/1 with narrow single-cusped anteroconid located slightly labial to the midline; M/1-2 with posterolabial sulcus well developed; M/2 with short anterior mure; upper molars with labial cusps located more or less opposite lingual cusps.

Etymology : Named for Jean-Pierre Aguilar, a modern student of *Megacricetodontinae*.

Hypodigm : Type, plus 35 isolated cheek teeth, including five M1/, six M2/, four M3/, nine M/1, eight M/2, and four M/3.

Age and distribution: Middle Miocene of southeast Asia; localities YGSP 642, 591 and 592 in the Kamliak Fm., 640, 641, and 680 in the Chinji Fm., Potwar Plateau, Pakistan.

Description : Molars are low crowned and the posterior mure is well developed and relatively straight in both upper and lower molars.

M1/: Occlusal outline longer than wide, slightly wider posteriorly, with a sharp increase in width posterior to the anterocone; anterocone wide, unequally bilobed with lobes of anterocone convex anteriorly in 4 of 5 specimens, separated by a relatively deep groove; labial cusps join the posterior arms of lingual cusps by short, transverse protoloph and metaloph; protolophule II absent; posteriorly-directed spur on paracone absent; anterior mure relatively short, joining anterior arm of protocone with middle of anterocone near the midline; posterior mure joining anterior arm of hypocone with junction of protoloph and posterior arm of protocone; mesoloph very short; labial and lingual anterior cingula directed posteriorly from anterocone, with labial side slightly higher; posterior cingulum joining base of the metacone; lingual cingulum high, almost cuspsate before ascending lingual side of the hypocone; lingual sinus not pinched anteriorly.

M2/: Occlusal outline subquadrate, narrow posteriorly; protoloph joins central part of protocone, metaloph joins the anterior hypocone; protolophule II absent; posteriorly-directed spur on paracone absent; anterior mure short, lingual to midline of tooth; posterior mure relatively straight, joining anterior arm of hypocone and posterior arm of protocone; mesoloph absent; anterior cingulum continuous from the labial to the lingual side of tooth, forming a narrow and shallow shelf anterior to the paracone, and a curved, shallow shelf anterior to the protocone; posterior cingulum high and robust medially where it joins the posterior arm of the hypocone, descending labially to join the posterior base of the metacone; lingual sinus relatively wide, not pinched anteriorly; lingual cingulum low.

M3/: Occlusal outline subtriangular, with rounded corners; the protocone and smaller paracone (oriented transversely) prominent, with a minute hypocone near the posterior midline; protoloph long and narrow, joining the anterior arm of the protocone; posterior arm of the protocone weakly joins the hypocone; posterior arm of hypocone forms a high posterior cingulum that continues as the labial cingulum; anterior arm of hypocone directed anterolabially, weakly joins labial cingulum; anterior cingulum continuous from anterior base of paracone to lingual side of protocone, enclosing a narrow shelf or basin anterior to the paracone, terminating on the posterolingual side of the protocone; a broad, shallow basin located posterior to the protoloph, and partially divided by a median loph.

M/1: Occlusal outline much longer than wide, with greatest width posteriorly; anteroconid high, narrow, single-cusped, located on labial side of midline; anterior mure formed by union of the anterior arm of protoconid with the long, posteriorly-directed anterolophid and the short, transversely-directed metalophid; posterior mure developed by union of the posterior arm of protoconid with the anterior arm of the hypoconid and the short, transversely-directed hypolophid; mesolophid long and low, reaching the labial margin of the tooth; anterior cingula low, distinct, directed posteriorly from both labial and lingual sides of the anteroconid, labial side longer, almost cuspsate; posterior cingulum long, joining posterior base of the hypoconid; posterolabial sulcus shallow; transverse valleys slightly closed by low cingula; labial

sinusid not pinched posteriorly.

M/2: Occlusal outline subrectangular, longer than wide; anterior mure very short, joining the anterior cingulum with junction of the anterior arm of protoconid and the short, transverse metalophid; posterior mure long, joining the posterior arm of the protoconid and the short, transverse hypolophid; mesolophid variable, long in 3 specimens, short in 3 specimens, and absent in 2 specimens; anterior cingulum continuous from anterior base of the metaconid to base of the protoconid, high lingually, low labially, forming a rather broad anterolabial shelf; posterior cingulum relatively heavy, joining posterior base of the entoconid; posterolabial sulcus sharp and deep; lingual sinusid curved posteriorly, not pinched, partly closed by lingual cingulum.

M/3: Occlusal outline longer than wide, with a straight anterior margin and gently rounded posterior margin; three cusps present, entoconid absent; posterior arm of the protoconid robust, continuing across midline of tooth as a relatively high mesolophid, joining the lingual cingulum; anterior arm of protoconid and the short metalophid join the high anterior cingulum slightly lingual to the midline; anterior cingulum develops a narrow shelf anterior to the metaconid, much reduced labial to the midline; posterior cingulum robust, continuing around posterolingual corner as a high lingual cingulum that joins the posterior side of the metaconid to enclose a large, curved anterior basin and a smaller, shallow and oblong posterior basin; labial sinusid narrow, partly closed by low labial cingulum. Measurements are given in Table 1.

Discussion: *Megacricetodon aguilari*, n. sp., resembles a number of European species of *Megacricetodon* in cusp morphology, especially *M. primitivus*, *M. collongensis*, *M. minor*; *M. bavaricus*, and *M. similis*. Cusps in *M. aguilari* are lower crowned than in the European species, plus the anteroconid of M/1 is relatively smaller and the hypoconid of M/3 is relatively larger in *M. aguilari*. *M. aguilari* is larger than *M. primitivus*, *M. collongensis*, *M. minor*, and *M. similis*; it is smaller than *M. bavaricus*.

Megacricetodon aguilari is larger and lower crowned than *Megacricetodon sivalensis*, n. sp., and *Megacricetodon daamsi*, n. sp., from Siwalik deposits; it is smaller than *Megacricetodon mythikos*, n. sp., also from Siwalik deposits.

Megacricetodon aguilari is larger than *M. sinensis* from the Chetougou Fm. in the Xining Basin of China. *M. cf. sinensis* near Lierbao in the Xining Basin is similar to *M. aguilari* in both size and height of crown; lobes of the anterocone in *M. cf. sinensis* are less inflated and more separated than in the anterocone of *M. sivalensis* (the anterior edge of the anterocone is broken off in *M. cf. sinensis*); the lingual cingulum is better developed on *M. aguilari* (Qiu, Li & Wang, 1981, translated by Will Downs, 1986). *M. aguilari* is larger than *Megacricetodon* aff. *collongensis* reported from the Xiacaowan Fm. in China by Li *et al.* (1983).

M. aguilari also shares many dental characters with *Shamalina tuberculata* known from early Miocene deposits in Saudi Arabia (Whybrow *et al.*, 1982). *Shamalina tuberculata* is lower crowned than *M. aguilari* and the cusps (especially the anterocone) are more inflated in *M. aguilari*. They are similar in steepening posterior side of cusps in upper molars and anterior side of cusps in lower molars; the posterolabial sinus is better developed in lower molars of *Shamalina*, and cingula with incipient cuspules are better developed in both upper and lower molars of *Megacricetodon*. *Shamalina* is a very plausible ancestor for *Megacricetodon*; however, details of this possible ancestry have never been worked out. One possible scenario is for *Shamalina tuberculata* to gain height of crown and a wider, more inflated anterocone on M1/. It would then be

indistinguishable from *Megacricetodon cf. sinensis* from the Xining Basin of China.

Megacricetodon sivalensis, new species

(Plate 1 j-o and Plate 2 a-c)

Type: YGSP 19231, isolated left M1/ from YGSP locality 491, Potwar Plateau, Pakistan.

Diagnosis: Small rodent with wide, unequally bilobed anterocone on M1/; M2/ with short anterior mure, protoloph tending to join anterior side of protocone, and metaloph joining the anterior or central side of hypocone; M2/ and M3/ with small anterolingual shelf; M1/ with a single-cusped anteroconid, located slightly labial to midline; M1/ and M2/ with posterolabial sulcus relatively well developed; M2/ tends to lack an anterior mure, with a small anterolabial shelf.

Etymology: *sival* + *ensis* in reference to the occurrence of this species in the lower Siwalik deposits of Pakistan.

Hypodigm: Type, plus 105 isolated cheek teeth, including 25 M1/, 23 M2/, two M3/, 23 M1/, 25 M2/, and seven M3/.

Age and distribution: Middle Miocene of southern Asia; YGSP localities 41, 430, 491, 640, 641, 665 & 668 in the Chinji Formatio, Potwar Plateau, Pakistan.

Description: Molars are relatively low crowned and the posterior mure is well developed, relatively straight, near the midline.

M1/: Occlusal outline longer than wide, with greatest width near the middle of the tooth; anterocone very wide, unequally bilobed, with the lingual lobe distinctly smaller than the labial lobe; a deep groove separates the anterocone lobes to their base; anterior styler shelf developed at the base of the anterocone in 10 of 22 specimens; anterocone generally more inflated in specimens lacking the anterior styler shelf; labial cusps join the posterior arm of lingual cusps by short, transversely-directed protoloph and metaloph; protolophule II absent or indistinct in 21 of 22 specimens; posteriorly-directed spur absent on the paracone in 18 of 22 specimens; anterior arm of the hypocone heavier and oriented more oblique than the anterior arm of the protocone; anterior and posterior mure short, oriented anteroposteriorly; anterior mure joins lingual lobe of anterocone lingual to midline, posterior mure joins protoloph near the midline, labial relative to location of the anterior mure; mesoloph distinct but usually short (in 11 of 20 specimens); anterior cingulum low on both sides of the anterocone, limiting the anterior labial and lingual valleys; posterior cingulum short and low, merging with posterior side of the metacone; lingual cingulum prominent, ascends the hypocone, nearly continuous with the anterior cingulum in three specimens (YGSP 19160, 19499, and 24601), almost cuspsate in 3 of 20 specimens; labial cingulum low or indistinct; labial sinus wide; lingual sinus slightly "pinched" anteriorly.

M2/: Occlusal outline subquadrate, slightly more narrow posteriorly; union of the protoloph and metaloph with the protocone and hypocone more variable than in M1/; protoloph joins the anterior side of the protocone in 17 of 21 specimens; metaloph joins anterior part (8 specimens) or central part (13 specimens) of hypocone; protolophule II usually absent, short and discontinuous in 3 of 21 specimens; posteriorly-directed spur developed on the paracone in 14 of 21 specimens; mesoloph relatively long and low, reaching the labial margin in 5 of 21 specimens; anterior cingulum wide, high labially, low lingually, terminating at the labial and lingual margins; posterior cingulum high and

relatively long, joining the posterior metacone; lingual sinus not pinched anteriorly, partly closed in 18 of 21 specimens; lingual cingulum incipiently cusped in 3 of 21 specimens.

M3/: Occlusal outline triangular, with rounded corners and a relatively straight anterior margin; paracone transversely elongate, larger than the protocone; hypocone indistinct, continuous with the relatively high posterior cingulum that joins the posterior arm of the protocone in 1 of 2 specimens; metacone absent; anterior cingulum high labially, low lingually, forming a high and narrow shelf anterior to the paracone, and a low, slightly wider shelf anterior to the protocone; posterior cingulum continues anteriorly on the labial margin, and joins posterior side of the paracone in 1 of 2 specimens, to enclose a wide, shallow central basin; a low, multi-armed loph occupies the central basin.

M/1: Occlusal outline much longer than wide, with greatest width posteriorly; anteroconid large, single-lobed, relatively broad at the base, symmetrical (although the tip of the anteroconid is located slightly labial to the midline in 7 of 11 specimens), incipiently twinned in two specimens (YGSP 19193 & 19654); anterior mure relatively long, located labial to midline in 9 of 18 specimens; posterior mure relatively long and straight, located on or near the midline; mesolophid short in 19 of 22 specimens; anterior cingula short, descending posteriorly from the anteroconid on labial and lingual sides; posterior cingulum long and robust, joining posterior side of entoconid; posterolabial sulcus shallow; labial sinusid not "pinched" posteriorly.

M/2: Occlusal outline subrectangular, longer than wide; anterior mure absent or indistinct (metalophid and anterior arm of the protoconid join the anterior cingulum near the midline); posterior mure relatively long, oriented anteroposteriorly; mesolophid short or indistinct in 17 specimens, absent in 4 specimens; anterior cingulum high medially, descending labially to develop a wide anterolabial shelf, descending lingually as a very narrow anterolingual shelf; posterior cingulum prominent, joining posterior base of the entoconid; posterolabial sulcus well developed, deep in 3 of 22 specimens; labial sinusid angular in 21 of 25 specimens, slightly pinched posteriorly; labial cingulum low, partly closing the labial sinusid in 7 of 18 specimens.

M/3: Occlusal outline longer than wide, with a straight anterior margin and a narrower, gently rounded posterior margin; three prominent cusps, the entoconid absent or indistinct; posterior arm of the protoconid long and robust, forming an oblique transverse wall that joins the high lingual cingulum to separate a long, narrow anterior basin and a rounded, smaller posterior basin; anterior arm of the hypoconid joins the oblique transverse wall to close the labial side of the posterior basin; posterior cingulum continues lingually and anteriorly as the high lingual wall; anterior cingulum high medially, continuing lingually as a short, narrow shelf anterior to metaconid, descending labially as a low, curved anterolabial shelf; labial sinusid relatively deep, bounded by a low labial cingulum in 4 of 7 specimens. Measurements are given in Table 1.

Discussion: Teeth of *Megacricetodon sivalensis*, n. sp. are slightly smaller and higher crowned than *Megacricetodon aguilari*. Cusps are steeper on one side and are generally more narrow at the base relative to cusps of *M. aguilari*; the mesolophid tends to be shorter, more reduced in *M. sivalensis*. In comparison with European species of *Megacricetodon*, *M. sivalensis* is most similar in size to *Megacricetodon collongensis*.

In fact, if isolated specimens of *M. collongensis* were accidentally grouped with specimens of *M. sivalensis* they would be separated with great difficulty, except for the M3/.

Specimens of *M. collongensis* provided for comparison by P. Mein show that M3/ of *M. collongensis* is much smaller and more circular in occlusal outline than M3/ of *M. sivalensis*. Unfortunately, all of the Siwalik specimens of *Megacricetodon* are isolated, and the smallest specimens (e.g., M3/) are least abundant and are identified with the least confidence. Other differences noted between *M. sivalensis* and *M. collongensis* are: (1) the lobes of the anterocone on M1/ are less equal in *M. sivalensis*; (2) the anterior cingular shelf on M1/ is usually better developed (in 10 of 22 specimens) in *M. sivalensis*; (3) the anterior arms of lingual cusps are usually more robust in upper molars of *M. sivalensis*; (4) the posterior mure is better developed in lower molars of *M. sivalensis*; (5) the anteroconid of M/1 is usually more robust in *M. sivalensis*; (6) the posterior cingulum of M/1 and M/2 is usually more robust in *M. sivalensis*; and (7) M/3 appears slightly shorter with the hypocone more reduced in *M. sivalensis*. Similarity of these species is striking; differences are subtle and incomplete. Large samples are required to recognize differences between these species. While it is biologically improbable that the European and southern Asia populations of these small mice were continuous or genetically homogeneous, it is paleontologically probable that these species were closely related, and that the French Vieux Collonges fauna (= MN 4b zone) is a close biochronologic correlative of the lower Chinji faunal interval of the Potwar Plateau where *Megacricetodon sivalensis* thrived. *M. sivalensis* is the only Siwalik species of *Megacricetodon* that tends to develop a bilobed anteroconid on M/1; both *M. bavaricus* and *M. similus* of Europe, which are larger than *M. sivalensis*, tend to develop a bilobed anteroconid on M/1.

It is also probable that *Megacricetodon* aff. *collongensis* from the Xiaocaowan fauna of China may be identical to *M. sivalensis*. Li and others (1983, translation by Will Downs, 1985) reported size morphology of the undescribed Xiaocaowan specimens of *Megacricetodon* are similar to *M. collongensis*, but the M/1 is comparatively smaller and lacks a bilobed anteroconid. *Megacricetodon sinensis* from the Chetougou Fm. in the Xining Basin of China has a shorter M/1 than *M. sivalensis* and the anteroconid is asymmetrical, labial to the midline in *M. sinensis*; size of M/2-3 is comparable to *M. sivalensis* (Qiu and others, 1981, translated by Will Downs, 1986). *M. sinensis* is known from three teeth (isolated M/1 and associated M/2-3); an isolated M1/ (*Megacricetodon* cf. *sinensis*, V6013) was also reported from another site (near Lierbao) in the Xining Basin by Qiu and others (1981). As reported above, *M. cf. sinensis* is more similar to *M. aguilari*.

Megacricetodon daamsi, n. sp.

(Plate 2 d-k)

Type: YGSP 19525, isolated left M1/ from locality YGSP 41, Potwar Plateau, Pakistan.

Diagnosis: Small size; cusps narrower at the base than in other Siwalik species of *Megacricetodon*; anterocone of M1/ narrow, unequally bilobed, slightly inflated, lacking anterior styler shelf; anteroconid of M/1 long and narrow, single-cusped, located slightly labial to midline; transverse valleys slightly offset in lower molars.

Etymology: Named for Remmert Daams, a modern student of Megacricetodontinae.

Hypodigm: Type and 24 isolated cheek teeth, including: Six M1/, two M2/, four M3/, seven M/1, four M/2 and two M/3.

Age and distribution: Middle Miocene of southern Asia; localities YGSP 41, 76, 491, 589, 634 and 641 in the Chinji Formation, Potwar Plateau, Pakistan.

Description: Molars low crowned and small although molars of *M. daamsi* teeth broadly overlap size of *M. sivalensis* molars; cusps of *M. daamsi* are relatively slender at the base and more vertical on one side (posterior side in upper molars, and anterior side in lower molars). Roots of upper cheek teeth have not been observed in *M. daamsi*.

M1/: Occlusal outline longer than wide, with greatest width in mid-length; anterocone unequally bilobed, slightly inflated, lobes of anterocone separated by very shallow groove that disappears before reaching base of enamel; anterior cingular shelf absent; labial cusps join lingual cusps by short protoloph and metaloph; protolophule II absent; posteriorly-directed spur on paracone absent in 5 of 6 specimens; anterior mure short, formed by anterior arm of protocone joining lingual lobe of anterocone slightly lingual to midline; posterior mure short, variable in orientation; mesoloph long and low, disappearing at labial margin; mesostyle absent; anterior cingulum descending to base of paracone and protocone, partly closing labial and lingual anterior valleys; posterior cingulum high and narrow, joining posterior base of metacone; lingual cingulum ascends hypocone, partly closing lingual sinus; lingual sinus not "pinched" anteriorly.

M2/: Occlusal outline subquadrate, much narrower and more rounded posteriorly; protoloph short, joining the anterior protocone; metaloph short, weakly joining the anterior or center of the hypocone; anterior mure short, joining the anterior cingulum with the junction of protoloph and anterior arm of protocone; posterior mure short, joining posterior arm of protocone and anterior arm of hypocone; mesoloph long and low; mesostyle absent; anterior cingulum high where it joins the anterior arm of protocone lingual to the midline, descending labially to join paracone, and descending lingually to join base of the protocone, forming a narrow anterior shelf; posterior cingulum high near midline, joining posterior hypocone; lingual sinus rounded medially, not "pinched" anteriorly; lingual cingulum noncuspsate, ascending the hypocone.

M3/: Occlusal outline subtriangular, with rounded corners and a relatively straight anterior margin; two large cusps present (a larger protocone and smaller transversely-oriented paracone); an indistinct hypocone located near the posterior midline; protoloph narrow, joining anterior arm of the protocone near the midline; posterior arm of protocone joining the hypocone; arms of the hypocone directed labially as a "mesoloph" and "posterior cingulum"; anterior cingulum narrow, continuous from anterior base of the paracone to lingual base of the protocone, developing a narrow anterior shelf; labial cingulum indistinct; central basin large and open; transverse posterior basin small and shallow.

M/1: Occlusal outline much longer than wide, with greatest width posteriorly; anteroconid single-cusped, relatively narrow, symmetrical, located well in advance of metaconid slightly labial to the midline; lingual cusps join labial cusps by short metalophid and hypolophid; anterior mure long and narrow, labial to midline, developed by union of anterior arm of the protoconid with the anterolophid and metalophid;

posterior mure relatively long, joining posterior arm of protoconid and the hypolophid with anterior arm of the hypoconid; mesolophid short and low; anterior cingula long on lingual side, short on labial side, partly closing the anterior labial valley; posterior cingulum high near midline, descending labially to posterior base of the entoconid; posterolabial sulcus shallow and broad; transverse valleys slightly offset, with lingual sinusid anterior to labial sinusid; labial sinusid relatively angular medially, incipiently "pinched" posteriorly in 3 of 6 specimens; labial and lingual cingula indistinct or absent.

M/2: Occlusal outline subrectangular, longer than wide; lingual cusps join anterior arms of labial cusps by a short metalophid and hypolophid; anterior mure absent; posterior mure relatively long, joining posterior arm of protoconid with anterior arm of hypoconid and the hypolophid; anterior cingulum high near midline, descending lingually as a narrow shelf to join the anterior metaconid, descending labially as a curved anterolingual shelf and joining anterior base of the protoconid; posterior cingulum high and robust near midline, joining posterior base of the entoconid; posterolabial sulcus relatively shallow in 3 of 4 specimens, forming a narrow posterolabial shelf in 2 of 4 specimens; transverse valleys slightly offset; labial sinusid angular, not "pinched" posteriorly; labial cingulum low, slightly closing the labial sinusid.

M/3: Occlusal outline longer than wide, with a straight anterior margin and a more narrow, gently rounded posterior margin; three prominent cusps, the entoconid absent; posterior arm of protoconid long and robust, forming an oblique transverse wall that joins the high lingual cingulum to separate a narrow, transversely-elongate anterior basin and a rounded, smaller posterior basin; anterior arm of hypoconid joins the oblique transverse wall to close the labial side of the posterior basin; posterior cingulum continues lingually and anteriorly as a high lingual wall; anterior cingulum high medially, continuing lingually as a short, narrow shelf anterior to metaconid, descending labially to join base of the protoconid and form a low, curved anterolabial shelf; labial sinusid relatively deep and steep sided. Measurements are given in Table 1.

Discussion: *Megacricetodon daamsi*, n. sp., is the smallest species of *Megacricetodon* known from Siwalik deposits; however, its size overlaps that of *Megacricetodon sivalensis*. *M. daamsi* is distinguished from *M. sivalensis* by having a more narrow and smaller anterocone in M1/, a relatively longer and more narrow anteroconid in M/1. Cusps in *M. daamsi* tend to be steeper on one side and more narrow at the base than in *M. sivalensis*, and the posterior mure is better developed in *M. daamsi*.

M. daamsi is similar in size and cusp morphology to *Megacricetodon sinensis* from the Chetougou Fm. in the Xining Basin of China and *Megacricetodon collongensis* from the Vieux Collonges fauna in France. It is smaller than those species and differs in having the anterocone of M1/ narrower, less divided, and the anteroconid of M/1 is relatively longer and more narrow in *M. daamsi*. *M. daamsi* is also similar in cusp morphology to *M. primitivus* and *M. minor* of Europe; it differs from those species in having better development of the mure. *M. daamsi* is smaller than all other known European species of *Megacricetodon*.

Megacricetodon mythikos, new species

(Plate 3 a-e)

Type: YGSP 19556, isolated right M1/ from locality YGSP 501, Potwar Plateau,

Pakistan.

Diagnosis: Medium size, low crowned rodent with M1/ anterocone very wide and strongly bilobed, descending to a long, anterior cingular shelf; M/1 with large, asymmetrical anteroconid; hypocone and hypoconid relatively large; posterior mure well developed, relatively short.

Etymology: *mythikos* (Gr.) for fable of a mythical murid ancestor.

Referred specimens: Type, and ten isolated cheek teeth, including four M1/, one M2/, two M3/, one M/1, and two M/2.

Age and distribution: Middle Miocene of southern Asia; localities YGSP 592, 642, and 680 in the Kamlial Fm., localities YGSP 491, 501, 589 and 668 in the Chinji Formation, Potwar Plateau, Pakistan.

Description: Molars are low crowned, comparatively large, with cusps very slightly inflated; posterior mure well developed but short.

M1/: Occlusal outline longer than wide with greatest width posterior to middle of tooth; anterocone wide, strongly bilobed, with lobes separated by a deep and narrow groove that descends to a relatively long and prominent anterior cingular shelf; hypocone, the largest cusp, slightly wider than the protocone; labial cusps join posterior arms of lingual cusps by short protoloph and metaloph; protolophule II absent; posteriorly-directed spur on paracone absent, but a similar spur occurs on the labial anterocone in 1 of 2 specimens; anterior mure developed by anterior arm of protocone joining lingual lobe of anterocone lingual to midline; posterior mure short, oriented anteroposteriorly, joining oblique posterior arm of protocone with mesoloph and oblique anterior arm of hypocone; posterior arm of hypocone directed labially to join metaloph and posterior cingulum; mesoloph relatively long, terminating short of the labial margin in 3 of 4 specimens; mesostyle minute, in 3 of 5 specimens; anterior cingulum low, partly closing labial and lingual anterior valleys; posterior cingulum short and narrow, descending from midline to join posterior base of metacone; lingual cingulum well developed, discontinuous lingual to protocone, with minute entostyle; labial cingulum low, almost cuspsate; lingual sinus slightly pinched anteriorly.

M2/: Occlusal outline subrectangular, slightly longer than wide; hypocone slightly wider than the protocone; protoloph long, joining anterior arm of protocone; metaloph bifurcating near midline, with posterior branch joining posterior arm of the hypocone, and anterior branch directed toward anterior arm of hypocone; protolophule II short; anterior mure relatively long, joining anterior cingulum lingual to midline; posterior mure joining posterior arm of protocone with mesoloph and anterior arm of hypocone; mesoloph long, terminating short of labial margin; mesostyle absent; anterior cingulum high and narrow, well separated from paracone, joining anterior base of paracone and lingual base of protocone to form a double anterior basin, wider labially; posterior cingulum high and narrow, joining posterior metacone; lingual cingulum well developed, almost continuous with lingual anterior cingulum; labial cingulum low; lingual sinus narrow, not "pinched" anteriorly.

M3/: Occlusal outline subtriangular, with rounded corners; paracone (oriented transversely) and protocone prominent, hypocone minute, metacone absent; posterior arm of protocone joins anterolingual side of hypocone; hypocone with anterior arm directed labially into central basin, posterior arm continuous with posterior cingulum; protoloph long, joining anterior arm of protocone and anterior cingulum, lingual to midline; anterior cingulum high near union with protoloph and protocone, descending labially to form a relatively shallow basin anterior to paracone; descending lingually to form a curved anterolingual basin; posterior cingulum descending to posterolabial

corner then curving anteriorly as the low labial cingulum, slightly closing a broad, shallow central basin.

M/1: Occlusal outline much longer than wide, with greatest width posteriorly; anteroconid large, single-cusped, asymmetrical, located slightly labial to midline; lingual cusps opposite the anterior side of labial cusps, joining labial cusps by short metalophid and hypolophid; anterolophid very low, joining metaconid lingual to midline; mesolophid short, inflated at base; posterior mure well developed; labial anterior cingulum prominent, descending posteriorly from anteroconid; lingual anterior cingulum concentrated as a minute cuspule at the lingual base of the anteroconid; posterior cingulum high near midline, descending to posterior base of entoconid; anterior valleys relatively wide, partly closed by anterior cingulum; transverse valleys relatively wide, oriented oblique to longitudinal axis, closed medially; labial sinusid slightly "pinched" posteriorly; posterolabial sulcus broad and shallow.

M/2: Occlusal outline subrectangular, longer than wide; labial cusps slightly larger than lingual cusps; posterior arm of protoconid long, directed toward entoconid; posterior arm of hypoconid long, directed toward midline; metalophid and hypolophid short, joining anterior and posterior mure; mesolophid relatively long, not reaching lingual margin; posterior mure oriented anteroposteriorly, joining hypolophid and hypoconid with protoconid and mesolophid; anterior cingulum high near midline, restricted to labial side in 1 of 2 specimens, descending labially as a curved anterolabial shelf; posterior cingulum high near midline, descending to posterior base of entoconid; posterolabial sulcus shallow and broad; transverse valleys oriented slightly oblique to longitudinal axis; labial sinusid slightly "pinched" posteriorly in 1 of 2 specimens. Measurements are given in Table 1.

Discussion: *Megacricetodon mythikos*, n. sp., is the largest species of *Megacricetodon* recorded from Siwalik deposits. Tooth dimensions of *M. mythikos* are generally wider and longer than other specimens assigned to *Megacricetodon*. Specimens assigned to *Megacricetodon* sp. from Banda Daud Shah by Wessels et al. (1982) are comparable in size and cusp morphology to *M. mythikos* and should probably be assigned to the same species; however, both samples should be compared directly to resolve this possible synonymy.

Megacricetodon mythikos is comparable in size to *Megacricetodon germanicus* of Europe. *M. mythikos* differs from *M. germanicus* in having better development of the lingual cingulum in upper molars and labial cingula in lower molars; the mure also appears higher and more persistent in *M. bavaricus* than in *M. mythikos*.

PUNJABEMYS new genus

Type: *Punjabemys downsi*, new genus and new species.

Diagnosis: Medium size rodents whose cusps are robust and inflated; anterocone of M1/ strongly bilobed, with anterior arm of protocone joining lingual lobe of anterocone, usually lingual to midline; anteroconid of M/1 single-cusped, relatively narrow; lingual sinus constricted anteriorly in upper molars, forming a distinctive anterior flexure in M2/; labial sinusid commonly angular or constricted posteriorly in M/1, always constricted posteriorly or with a posterior flexure in M/2.

Dental characters of *Punjabemys*

The inflation of cusps in these species is very distinctive; in addition, posterior side of cusps in upper molars are more vertical than anterior sides and anterior side of cusps in lower molars are more vertical than posterior sides; labial cusps in upper molars elongated transversely, located slightly anterior relative to more rounded lingual cusp; lingual cusps in lower molars elongated transversely, located slightly anterior relative to more rounded labial cusps; lingual cusps in upper molars with anterior arm robust, with posterior arm reduced or absent; labial cusps in lower molars with posterior arm robust, with anterior arm reduced or absent; posterior cingulum very reduced in M1-2/, enclosing a minute posterolabial valley posterior to the metacone; posterior cingulum long and heavy in M/1-2, descending lingually to join posterior base of entoconid, usually descending labially to form a shallow posterolabial sulcus; transverse valleys narrow and steep-sided, usually closed medially by posterior mure, oriented transverse or slightly oblique to longitudinal axis in upper molars, oriented oblique or slightly offset in lower molars; upper molars with three prominent roots, lower molars with two prominent roots; accessory rootlets unseen.

Included species: *P. downsi*, n. sp.; *P. leptos*, n. sp.; *P. mikros*, n. sp.

Etymology: *Punjab*-for the province of Pakistan where this taxon was collected, and *mys* (Gr.) for mouse.

Punjabemys downsi new genus and new species

(Plate 3 f-j, Plate 4 a-f, and Plate 5 i)

Type: YGSP 19119, isolated right M/1 from locality YGSP 430, Potwar Plateau, Pakistan.

Diagnosis: Large size (for the genus); anterocone large, subequally bilobed; enterostyle small, usually present on M1/, usually absent on M2/; M3/ with a small hypocone; M/1 with a relatively narrow, single-cusped anteroconid, usually with a short anterolophid, and mesolophid with a swollen base (an indistinct mesoconid); mesolophid base less swollen in M/2; lingual sinus narrow, slightly constricted anteriorly in M1/, with long and wider anterior flexure in M2/; labial sinusid narrow, constricted posteriorly in M/1, slightly curved posteriorly and wider in M/2-3.

Hypodigm: Type, plus 105 isolated cheek teeth, including 16 M1/, 21 M2/, 14 M3/, 17 M/1, 18 M/2 and 20 M/3.

Etymology: Named for Mr. William R. Downs, for his diligence and enthusiasm in collecting small mammals from Punjab.

Age and distribution: Middle Miocene of southern Asia; localities YGSP 430, 491 and 589 in the Chinji Formation, Potwar Plateau, Pakistan.

Description: Cusps of cheek teeth are robust and steep-sided; posterior mure commonly short and distinct from anterior arm of hypocone in upper molars, distinct from posterior arm of protoconid in lower molars.

M1/: Occlusal outline oval, longer than wide; anterocone large and wide, with shallow to deep groove separating lobes of anterocone in 10 of 11 specimens, a minute cuspule at base of the labial lobe, near the groove, in 3 of 11 specimens; protocone markedly circular, with the robust anterior arm joining lingual lobe of the anterocone, a short posterior arm (absent in 3 of 12 specimens) directed labially to join the protoloph near the midline; hypocone with a long, robust anterior arm directed toward the paracone, joining the protoloph near the midline; posterior arm of hypocone short, directed labially

to join the posterior cingulum; short protoloph and metaloph, metaloph directed posteriorly to join short posterior cingulum; paracone with posteriorly-directed loph absent in 10 of 13 specimens, short in 3 specimens; enterostyle small, isolated on short labial cingulum in 11 of 13 specimens; labial and lingual anterior cingula directed posteriorly to join protocone and paracone, mesoloph absent or indistinct in 8 of 13 specimens, short in 5 specimens; posterior cingulum narrow and short.

M2/: Occlusal outline subquadrate, with rounded corners, more narrow posteriorly; anterior arm of protocone joins narrow labial anterior cingulum at the midline; short lingual anterior cingulum present in 15 of 19 specimens, anterior to protocone; anterior arm of hypocone joins the paracone in 18 of 19 specimens, flexed labially to join mesoloph in 12 of 19 specimens; mesoloph short in 10 specimens, long in 2 specimens; protoloph and metaloph short; posteriorly-directed loph on paracone absent in 15 specimens, short in 4 specimens; lingual cingulum low and non-cusped in 6 of 19 specimens, with minute and isolated enterostyle in 4 specimens.

M3/: Occlusal outline subtriangular, with straight anterior margin; protocone large and robust; paracone large, transversely elongate; hypocone small, distinct; metacone absent in 9 specimens, small in 4 specimens; anterior arm of protocone robust and short; anterior arm of hypocone short and narrow, usually joining the protoloph; mesoloph long and low, joining posterior arm of protocone near center of the tooth; labial anterior cingulum long, joining anterior arm of protocone near the midline; lingual anterior cingulum low, distinct in 4 of 13 specimens.

M/1: Occlusal outline long and narrow, tapering anteriorly; anteroconid narrow, with a short anterolophid in 10 of 11 specimens, that joins the metaconid in 7 of 10 specimens; labial cusps relatively circular, join lingual cusps by short metalophid and hypolophid; base of mesolophid swollen, resembling a small mesoconid in 11 of 14 specimens; anterior arm of protoconid absent or indistinct in 9 of 11 specimens; anterior arm of hypoconid short; metalophid short, isolated from the protoconid in 12 of 15 specimens hypolophid short, joining the hypoconid and mesoconid; mesolophid short; mesostylid usually absent, small in 3 of 12 specimens; ectostylid absent; labial cingulum low in 7 of 11 specimens; labial and lingual sides of anterior cingulum directed posteriorly, slightly longer on labial side; posterolabial sulcus very shallow or indistinct; transverse valley oriented slightly oblique to longitudinal axis.

M/2: Occlusal outline subrectangular, longer than wide, slightly more narrow anteriorly; anterior arm of protoconid joins metalophid near the midline in 15 of 16 specimens; anterior arm of hypoconid joins the hypolophid; posterior arm of protoconid long, joins the mesoconid; posterior arm of hypoconid short, joins the posterior cingulum labial to the midline; mesolophid short, swollen at the base (as a mesoconid) in 14 of 18 specimens; mesostylid absent in 14 of 16 specimens; ectostylid absent; labial anterior cingulum low, continuing posteriorly to base of the protoconid; lingual anterior cingulum reduced, distinct in only 2 of 16 specimens; labial and lingual cingula low or absent; posterior cingulum high and swollen near midline; posterolabial sulcus shallow and broad.

M/3: Occlusal outline oval, wider and more straight anteriorly, gently rounded posteriorly; metaconid and protoconid large, hypoconid small, entoconid absent or indistinct (represented by a posterolingual swelling on posterior cingulum in 2 of 15 specimens); posterior arm of protoconid long and robust, continuing across the midline as a mesolophid that reaches the lingual margin; posterior arm of hypoconid robust,

continues around the posterolingual margin to join the narrow lingual cingulum; labial anterior cingulum short and low in 13 of 15 specimens; lingual anterior cingulum short, distinct in only 4 of 15 specimens; lingual cingulum high and narrow, closing the narrow lingual sinusid; labial cingulum low in 13 of 15 specimens; posterolabial sulcus indistinct. Measurements are given in Table 2.

Discussion: *Punjabemys* has the most robust dentition of any Siwalik cricetids, and *P. downsi*, n. sp., is larger than any other species of the Siwalik Megacricetodontinae. The cricetid most similar to *Punjabemys* is *Collongomys*, especially *Collongomys lappi* from Vieux Collonges in France. *P. downsi* differs from *C. lappi* in being more robust, in having a small lingual styler cusp on M1/, and the metalophid of *P. downsi* joins the posterior cingulum rather than the hypoconid in M2/. The mesolophid is better developed in lower molars of *P. downsi*, the anteroconid of M1/ is shorter and broader, and the hypoconid of M3/ is wider, less reduced, compared to *C. lappi*.

Punjabemys leptos new species

(Plate 4 g-i and Plate 5 a-h)

Type: YGSP 19517, isolated right M1/ from locality YGSP 430, Potwar Plateau, Pakistan.

Diagnosis: Smaller than *Punjabemys downsi*, n. sp. and larger than *Punjabemys mikros*, n. sp.; M1/ with wide, unequally bilobed anterocone, lobes of anterocone separated by a shallow vertical groove; M2/ with anterior arm of lingual cusps swollen distally; paracone of M1-2/ lacks a posteriorly-directed spur; enterostyle minute or absent on M1/, absent on M2/; M1/ with single-cusped, symmetrical anteroconid, usually lacking an anterolophid, base of mesolophid not swollen (lacking the mesoconid); lingual sinus narrow, slightly flexed anteriorly in M1/, strongly flexed anteriorly in M2/; labial sinusid narrow, slightly flexed posteriorly.

Etymology: *leptos* (Gr.) - thin, referring to reduction of breadth in this species.

Hypodigm: Type, plus 42 isolated cheek teeth, including 12 M1/, eight M2/, four M3/, six M1/, eight M2/ and five M3/.

Age and distribution: Middle Miocene of southern Asia; YGSP localities 430, 491, 640, 665 and 668 in the Chinji Formation, localities 642 and 680 in the Kamli Formation, Potwar Plateau, Pakistan.

Description: Cusps of cheek teeth are inflated and relatively robust; posterior mure relatively short; transverse valleys closed medially by posterior mure, oriented transversely in upper molars, oriented slightly oblique to longitudinal axis in lower molars.

M1/: Occlusal outline oval, longer than wide, with a pronounced lingual inflection between the anterocone and protocone; anterocone large, with lobes separated by a shallow vertical groove that disappears before reaching the base of the crown; short protoloph and metaloph; anterior arm of protocone joins lingual lobe of anterocone near the midline; anterior arm of hypocone directed more transverse than arm of protocone, weakly joins the protoloph labial to the midline in 10 of 11 specimens; posterior arms of lingual cusps short; enterostyle minute or indistinct near base of hypocone on labial cingulum; labial and lingual anterior cingula short and low, directed posteriorly from the anterocone; mesoloph very short or indistinct; posterior cingulum low and narrow.

M2/: Occlusal outline subquadrate, with rounded corners and more narrow posteriorly; metacone smaller than other cusps; short protoloph; anterior arm of protocone swollen

distally and bifurcating to join the anterior cingulum (in 6 of 7 specimens) and the protoloph; anterior arm of hypocone swollen distally at the base of the mesoloph, with a narrow spur joining the protoloph; posterior arm of protocone absent; posterior arm of hypocone short and narrow, weakly joining metaloph near the midline; mesoloph long and low (5 specimens) or indistinct (2 specimens); anterior cingulum high labially, forming a narrow transverse shelf anterior to the paracone, low lingually, forming a low shelf anterior to the protocone; enterostyle minute (4 specimens) or indistinct (3 specimens) on labial cingulum; posterior cingulum low and narrow (6 specimens) or indistinct (1 specimen).

M3/: Occlusal outline subtriangular, with rounded corners and straight anterior margin; large subequal protocone and paracone, joined by a relatively long transverse protoloph; hypocone small or indistinct; metacone indistinct (swelling at posterolabial corner of tooth); anterior arm of protocone short and robust, joining anterior cingulum near midline; posterior arm of protocone absent; hypocone with weak anterior and posterior arms, the anterior arm directed toward the paracone but usually not reaching that cusp, the posterior arm directed labially as a posterior cingulum; anterior cingulum restricted to labial side, enclosing a shallow transverse basin anterior to the paracone; central basin shallow and narrow, partially divided by anterior arm of the hypocone, open labially.

M/1: Occlusal outline long and narrow, tapering anteriorly; anteroconid large, symmetrical on midline; labial cusps relatively round; anterolophid usually absent, distinct on YGSP 19644; anterior arm of protoconid absent in 3 of 4 specimens; anterior arm of hypoconid very narrow, joining hypolophid near midline; posterior arm of protoconid robust, directed toward entoconid, joining the posterior mure at midline; posterior arm of hypoconid relatively short, joining posterior cingulum at midline; metalophid and hypolophid short or indistinct; mesolophid short (2 specimens) or indistinct (2 specimens); mesostylid and ectostylid absent; anterior cingulum descending posteriorly from labial and lingual sides of anteroconid, longer on labial side, partly closing labial and lingual anterior valleys; labial cingulum low and narrow, partly closing labial sinusid; lingual cingulum indistinct (3 specimens) or low (1 specimen); posterior cingulum long; posterolabial sulcus indistinct.

M/2: Occlusal outline subrectangular, narrow anteriorly; anterior arm of labial cusps very short, posterior arm of labial cusps long; metalophid and hypolophid short; mesolophid short or absent; mesostylid and ectostylid absent; anterior cingulum restricted to labial side, descending from midline to form narrow shelf anterior to the protoconid; labial cingulum low; lingual cingulum absent; posterior cingulum long, joining posterior base of the entoconid; posterolabial sulcus broad and very shallow.

M/3: Occlusal outline oval, wider anteriorly, with straight anterior margin and gently rounded posterior margin; three large cusps, entoconid absent; anterior arm of protoconid short, joining the anterior cingulum near the midline; anterior arm of hypoconid short, joining posterior arm of the protoconid near the midline; posterior arm of protoconid long and robust, continuing across the midline to join the lingual cingulum; posterior arm of hypoconid continues lingually around the posterior margin as a high posterior cingulum, joining the lingual cingulum to enclose a small steep-sided posterior basin; anterior cingulum subdued, indistinct; lingual cingulum joins posterior side of the metaconid, the posterior arm of the protoconid (and the posterior cingulum) to enclose a deep oblique central basin; labial sinusid partly closed by labial cingulum (2 specimens) or open (2 specimens); posterolabial sulcus absent. Measurements are given in Table 2.

Discussion: *Punjabemys leptos*, n. sp., is smaller than *Punjabemys downsi*, and differs from *P. downsi* in having a more reduced enterostyle in upper molars, greater distal expansion of anterior arms of lingual cusps in M2/, and the base of the mesolophid is not swollen in lower molars of *P. leptos*. Stratigraphic range of *P. leptos* overlaps and is lower than that of *P. downsi*.

Punjabemys mikros new species

(Plate 6 a-f)

Type: YGSP 19524, isolated left M/1 from locality YGSP 501, Potwar Plateau, Pakistan.

Diagnosis: Smallest known species of the genus; M1/ with large, wide anterocone, and strong lingual inflection between anterocone and protocone; lingual cingulum prominent in M1-2/, lacking a distinct enterostyle; M/1 with large, asymmetrical anteroconid (higher lingually), located labial to midline; paracone of M1-2/ lacks a posteriorly-directed spur; mesolophid not swollen at base, long on M/1, short or indistinct on M/2; lingual sinus weakly constricted or unconstricted anteriorly in M1/, strongly flexed anteriorly in M2/; labial sinusid narrow, slightly constricted posteriorly.

Etymology: *mikros* (Gr.) - minute size.

Hypodigm: Type, plus 18 isolated cheek teeth, including five M1/, four M2/, two M3/, one M/1, two M/2 and five M/3.

Age and distribution : Middle Miocene of southern Asia; localities YGSP 430, 640, 641 and 668 in the Chinji Formation; and localities YGSP 501, 592, 642 and 680 in the Kamli Formation, Potwar Plateau, Pakistan.

Description: Cusps of cheek teeth are robust and steep-sided; posterior cingulum short, usually distinct relative to arms of adjacent cusps; transverse valleys closed medially, oriented slightly oblique to longitudinal axis in upper molars, slightly offset medially in lower molars;

M1/ : Occlusal outline oval, much longer than wide, with a pronounced lingual inflection between anterocone and protocone; anterocone large, with shallow and narrow vertical groove weakly separating lobes; labial cusps relatively circular, lingual cusps more oval due to expansion of anterior arms; posterior arm of lingual cusps short and narrow; protoloph and metaloph very short, weakly joining posterior arms of lingual cusps; mesoloph low and long (YGSP 19601) or absent (YGSP 19602); enterostyle indistinct (a swelling) on the posterior half of the lingual cingulum; anterior cingulum low on labial and lingual sides, partly closing the anterior valleys; labial and lingual cingula well developed, partly closing transverse valleys; posterior cingulum narrow, joining posterior side of metacone.

M2/ : Occlusal outline subrectangular, with rounded corners and more narrow posteriorly; labial cusps slightly smaller than lingual cusps; posterior arm of lingual cusps short and narrow, or absent (YGSP 19606); protoloph narrow, directed lingually, flexed anteriorly near midline to join anterior arm of protocone; metaloph narrow, directed lingually toward the midline where it joins the posterior arm of the hypocone; mesoloph long and narrow (YGSP 19605) or indistinct; enterostyle indistinct or absent on lingual cingulum; anterior cingulum high near the midline, continuing labially as a low anterior shelf, descending lingually and flexing posteriorly to join lingual side of the protocone (YGSP 19606), or continuing around protocone to join the lingual cingulum (YGSP 19605); posterior cingulum short and narrow, joining posterior side of metacone.

M3/ : Occlusal outline subrectangular with rounded corners and straight anterior margin; paracone and protocone joined by long transverse protoloph, hypocone minute, metacone indistinct; anterior arm of protocone joins anterior cingulum lingual to the midline; posterior arm of protocone continuous with hypocone, continuing around the posterior margin (as the posterior cingulum) to the labial margin; anterior arm of hypocone directed labially toward the paracone, flexed posteriorly near center of central basin, terminating short of labial margin; anterior cingulum high near the midline, descending labially to form a low anterior shelf, descending lingually as a less distinct shelf; central basin elongated transversely, closed lingually by union of protocone and hypocone, slightly closed labially by low labial cingulum.

M/1 : Occlusal outline long and narrow, tapering anteriorly; anteroconid large, single-cusped, asymmetrical with lingual side slightly higher and more steep, located labial to midline; anterolophid low, directed toward the protoconid, joining metalophid or anterior arm of protoconid labial to the midline; anterior arms of labial cusps short and narrow; metalophid and hypolophid short, directed labially to join anterior and posterior mure, respectively; mesolophid long and low, lacking a swollen base; ectostylid absent; anterior cingulum partly closing anterior valleys, longer and higher on labial side; labial and lingual cingula low, partly closing transverse valleys; posterolabial sulcus shallow and broad.

M/2 : Occlusal outline subrectangular with rounded corners; entoconid slightly smaller than other principal cusps; metalophid and hypolophid short, directed anterolabially to join anterior cingulum and posterior mure, respectively; mesolophid short or indistinct; mesostylid and ectostylid absent; anterior cingulum restricted to labial side, high at midline, descending to labial base of protoconid, nearly continuous with labial cingulum in YGSP 19609; labial and lingual cingula low, partly closing transverse valleys; posterior cingulum massive, forms a minute "hypoconulid" on YGSP 19610; posterolabial sulcus very shallow.

M/3 : Occlusal outline oval, narrow posteriorly, with straight anterior margin and gently rounded posterior margin; three large cusps with the entoconid absent; anterior arms of labial cusps indistinct, protoconid appressed against anterior cingulum at midline and hypoconid appressed against long posterior arm of protoconid; posterior arm of protoconid long and robust, directed toward center of tooth where it bifurcates (3 specimens) or is flexed lingually (2 specimens) to join the lingual cingulum; posterior branch of posterior arm of the protoconid very short, weakly joining the hypolophid as the posterior mure; posterior arm of hypoconid directed lingually as a posterior cingulum, continuing as the lingual cingulum; anterior cingulum indistinct or absent (3 specimens), or descending from the midline to labial side of the protoconid (2 specimens); labial cingulum low, partly closing labial sinusid; lingual cingulum high, closing anterior and posterior basins; posterior basin very narrow and steep-sided; anterior basin long and deep; posterolabial sulcus absent or indistinct; labial sinusid very deep, continues to lingual cingulum in 2 of 5 specimens. Measurements are given in Table 2.

Discussion : *Punjabemys mikros* n. sp., is smaller than *Punjabemys downsi* and *Punjabemys leptos*. In addition to size, *P. mikros* differs from *P. downsi* in lacking a distinct enterostyle in upper molars, and lacking a swollen base of the mesolophid in lower molars. In addition to smaller size, *P. mikros* differs from *P. leptos* in having a relatively larger, asymmetrical anteroconid on M/1. *P. mikros* is more similar to species of *Megacricetodon* than other species of *Punjabemys*; it shares about as many dental

features with *Megacricetodon collongensis* from France (e.g., size and shape of M1/ and M3/) as it does with *Megacricetodon sivalensis* (e.g., size and shape of M/1 and M/2) from Siwalik deposits.

MYOCRICETODONTINAE

The genus *Myocricetodon* was named and described by Lavocat (1952), based on the most common small mammal from the fauna of Beni-Mellal in Morocco, *Myocricetodon cherifiensis*. In a later study, Lavocat (1961) named and described more cricetids (*Cricetodon atlas* and *Cricetodon parvus*) from the same fauna, and erected the subfamily Myocricetodontinae, with *M. cherifiensis* as the only known genus. Lavocat (1961) characterized the Myocricetodontinae as cricetids whose longitudinal crest (=mure) is greatly reduced or absent, and in which an accessory lingual tubercle (=enterostyle) is weakly developed or absent in upper molars.

In a later study of the Beni-Mellal fauna, with additional material, Jaeger (1977a) expanded the characterization of Myocricetodontinae, and redefined the diagnosis of *Myocricetodon* as (free translation) : "Myocricetodontinae of small to medium size whose dentition is characterized by reduction of M3/ and reduction of the longitudinal crest (mure), plus a cranium with elongate posterior palatal foramina". Jaeger (1977a) transferred *Cricetodon parvus* to the newly revised genus *Myocricetodon* (e.g., *Myocricetodon parvus*), and erected two new genera and one new species (e.g., *Dakkamys zaini*, n. gen. & n. sp., and *Mellalomys atlasi*, n. gen.), both included in the Myocricetodontinae. *Dakkamys* was characterized as a large species having on M1/ and M2/ a strong lingual accessory cusp (= enterostyle), joining the posterior arm of the protocone by a narrow loph, plus normal development of the mure and a deep lingual sinus on M2/. *Mellalomys* (= *Cricetodon atlasi* of Lavocat) was characterized as a cricetid of medium size, with small posterior palatal foramina, M3/3 little reduced, anterocone of M1/ incompletely divided, mure of normal development (not reduced), anteroconid of M/1 slightly elongate with incipient development of an accessory cuspule on the lingual anterior cingulum, and with two (divided) anterior roots on M/2 and M/3.

Jaeger (1977a, p. 111-112) noted several morphological features shared by *Mellalomys atlasi* and *Dakkamys zaini*, pointing out that some of these features are also shared with, but are more advanced in, *Myocricetodon*. He suggested that *Mellalomys*, *Dakkamys* and *Myocricetodon* form a relatively isolated but closely related phyletic lineage within the Myocricetodontinae.

Jaeger (1977b) described seven middle and late Miocene rodent faunas from the Maghreb area, north Africa, in which he identified *Myocricetodon* cf. *cherifiensis* and *Myocricetodon parvus intermedius*, plus seven new species of *Myocricetodon* (*M. irhoudi*, *M. magnus*, *M. seboui*, *M. ouedi*, *M. trerki*, *M. ouaichi* and *M. ultimus*), plus four new species of *Zramys* (*Z. dubius*, *Z. semmeninsis*, *Z. selemi* and *Z. hamamai*) along with the genotypic species *Zramys haichai* in an indeterminate subfamily of Cricetidae. He also named and described a new genus and species of gerbillid (*Protatera algeriensis*), interpreted as a descendant of the Myocricetodontinae of north Africa.

Robinson *et al.* (1982) described small mammal fossils from late Miocene deposits (Kechabta Fm.) of northwestern Tunisia, including Myocricetodontinae (*Myocricetodon* cf. *seboui*), plus the cricetid *Zramys* and the murid *Progonomys*. In their discussion of *Zramys*, Robinson *et al.* (op. cit.) noted the significance of 4 or 5 roots on M1/ of cricetids in the tribe Cricetodontini and only 3 roots on M1/ of Megacricetodontinae, Myocricetodontinae, plus *Zramys* and *Mellalomys*. All of the rodents described in this report are consistent with the interpretation of Robinson *et al.*

(1982) in having only 3 roots in upper molars of Megacricetodontinae, Myocricetodontinae (and Dendromurinae).

Myocricetodontinae are redefined (below) to distinguish these rodents from another Miocene to Recent offshoot of cricetids, the Dendromurinae. Dendromurines are characterized by reduction of the mure (as in Myocricetodontinae) plus development of a single lingual accessory cuspule on M1-2/, and occasionally developing a labial cuspule (= ectostylid) on M/1. According to this re-definition, several of the species assigned to *Myocricetodon* from Maghreb by Jaeger (1977b) (e.g., *M. seboui* and *M. ouaichi*, and taxa questionably assigned to them), and the genus *Dakkamys* are transferred to the Dendromurinae. Provisionally, the species *M. seboui* and *M. ouaichi* of Jaeger (1977b) are considered species of the genus *Dakkamys*, although these taxa are not included in this study. This revised diagnosis of Myocricetodontinae and Dendromurinae distinguishes members of these two lineages in the middle Miocene, and emphasizes autapomorphic features of Dendromurinae that place them closer to the Muridae.

Revised diagnosis of the Myocricetodontinae

The Myocricetodontinae are characterized by absence of a mesoloph and mesolophid, reduction of the longitudinal crest or mure, absence or incipient development of accessory cusps, transverse valleys of both upper and lower molars tends to be oriented oblique to the longitudinal axis of the tooth, and posterior molars are reduced in size. Four myocricetodon taxa are presently recognized from lower Siwalik deposits near Chinji village.

Dental characters in Myocricetodontinae

Myocricetodontinae share the "pillar-like" cusps exhibited by Megacricetodontinae, but develop a greater illusion of sloping cusps (than in Megacricetodontinae) by lengthening the anterior base of cusps in upper molars and the posterior base of cusps in lower molars. However, the posterior side of cusps in upper molars and the anterior side of cusps in lower molars are vertical (or near-vertical) in most of the Megacricetodontinae and the Myocricetodontinae. Several members of the Dendromurinae (among Siwalik cricetids) exhibit true inclination of cusps (e.g., inclined posteriorly in upper molars and anteriorly in lower molars). As the base of the cusps was lengthened in Myocricetodontinae, the width of transverse valleys in those teeth was correspondingly decreased.

Myocricetodontinae also resemble Megacricetodontinae in having labial cusps in upper molars and lingual cusps in lower molars elongated transversely. Similarly, anterior arms of lingual cusps in upper molars and posterior arms in lower molars are longer, more prominent than opposing arms (posterior arms on lingual cusps of upper molars, anterior arms on labial cusps of lower molars) of the same tooth in both Myocricetodontinae and Megacricetodontinae.

When the cusps are opposite in position (as they tend to be in Siwalik Megacricetodontinae), the transverse valleys are oriented transversely; however, when cusps are alternate in position, the transverse valleys also become alternate, shifting along with the cusps. As the lingual cusps are shifted slightly anteriorly relative to the lingual cusps, the transverse valleys in Myocricetodontinae become oriented more oblique to the longitudinal axis of the tooth, or in lower molars may be offset. Reducing the height of the posterior mure in Myocricetodontinae brings continuity and orientation of the transverse valley into sharper focus. In some Siwalik Myocricetodontinae cusps are shifted no more than in Megacricetodontinae; however, orientation of transverse

valleys in Siwalik *Myocricetodontinae* is more conspicuous because the reduced posterior mure makes the transverse valleys appear more continuous. Anterior shifting of lingual cusps is more pronounced in some *Dendromurinae*, resulting in greater offset of the transverse valley; however, not all *Dendromurinae* have alternation of cusps in upper molars.

MYOCRICETODON LAVOCAT, 1952

As noted above, *Myocricetodon* is best known from northern Africa. Teeth of *Myocricetodon* are low crowned with the posterior mure reduced (usually represented by a longitudinal line or low ridge near the midline). In addition, the M1/ has an unequally bilobed anterocone, anterior arm of protocone joins the lingual lobe of the anterocone, usually lingual to the midline; the M/1 has a narrow, single-cusped anteroconid; and accessory cuspules (entostyle and ectostylid) are absent or incipient in both upper and lower molars. Upper molars have the posterior side of cusps near-vertical, and lower molars have the anterior side of cusps near-vertical. Base of the cusps are lengthened anteriorly in upper molars, and base of the cusps are lengthened posteriorly in lower molars. Mesoloph and mesolophid are absent; lingual cingula are prominent, non-cusped in upper molars, labial cingula are prominent, non-cusped in lower molars. Transverse valleys are weakly closed medially, and are usually oriented oblique to the longitudinal axis in both upper and lower molars. Posterior cingula are short in upper molars, joining the posterior side of the metacone to enclose a shallow posterolabial basin; posterior cingula are long in lower molars, high near the midline, descending lingually to join the base of the entoconid and enclosing a long curved posterolingual valley, usually descending labially to form a posterolabial sulcus or valley. Posterior molars are reduced in size. Upper molars have three prominent cusps, lower molars have two prominent roots; accessory rootlets are unknown.

Myocricetodon sivalensis new species

(Plate 6 g-m)

Type : YGSP 19576, isolated left M1/ from locality YGSP 592, Potwar Plateau, Pakistan.

Diagnosis : M1/ with large and inflated anterocone, unequally bilobed; anteroconid of M/1 relatively small, single cusped; posterior mure reduced, barely separating slightly oblique transverse valleys; lingual cingulum prominent, non-cusped in upper molars; labial cingulum well developed, non-cusped in lower molars.

Etymology : *sival* = Siwalik, *ensis* = in the place of, referring to the occurrence of this species in Siwalik deposits of Pakistan.

Hypodigm : Type and 35 isolated specimens, including eight M1/, six M2/, eight M/1 and 14 M/2.

Age and distribution : Middle Miocene, localities YGSP 591 and 592 in the Kamlial formation, Potwar Plateau, Pakistan.

Description : Medium size, low crowned rodent with posterior mure reduced.

M1/ : Occlusal outline longer than wide, with greatest width near midlength; anterocone large, inflated, unequally bilobed, with labial lobe larger and higher than lingual lobe; opposite cusps weakly joined medially by short protoloph (contacting posterior side of protocone) and short metaloph (contacting posterior or anterior [in YGSP 19576] side of hypocone); paracone with posteriorly-directed spur indistinct (4 specimens) or small

(3 specimens); anterior cingulum low on both labial and lingual sides, partially closing wide labial and narrow lingual anterior valleys; lingual cingulum slightly ascending anterior side of hypocone; labial cingulum low; posterior cingulum short, joining posterior side of the metacone; transverse valleys partially closed distally by cingula, especially on lingual side.

M2/ : Occlusal outline subrectangular, longer than wide, more narrow and rounded posteriorly; metacone slightly smaller than other prominent cusps; anterior arms of lingual cusps directed anteriorly; posterior arms of lingual cusps short, directed posterolabially; metaloph joins anterior (4 specimens) or middle (2 specimens) side of protocone; hypoloph joins middle of hypocone in 4 of 6 specimens; paracone with minute posteriorly-directed spur in 4 of 6 specimens; anterior cingulum long and straight, forming a narrow shelf anterior to the paracone, descending lingually to the protocone, continuous with lingual cingulum (around protocone) in 4 of 6 specimens; lingual cingulum ascends the anterior hypocone; labial cingulum low or indistinct.

M/1 : Occlusal outline much longer than wide, narrow anteriorly; anteroconid small, single cusp, relatively robust, usually located on midline, (labial to midline in 2 specimens, lingual to midline in 2 specimens); anteroconid smaller than metaconid, which is usually smaller than other prominent cusps; anterior arm of protoconid joins short metalophid and short anterolophid at midline; anterior arm of hypoconid joins hypolophid and posterior mure (posterior arm of protoconid) near midline; labial anterior cingulum descends to base of protocone; lingual anterior cingulum indistinct, with anteroconid and metaconid joined at base; lingual and labial cingula low, slightly closing broad transverse valley; posterolabial sulcus shallow but persistent in 5 of 8 specimens; transverse valleys slightly oblique; labial sinusid slightly rounded, narrow internally.

M/2 : Occlusal outline subrectangular, longer than wide, slightly wider posteriorly in 5 of 14 specimens; metalophid joins short anterior mure and anterior arm of protoconid at midline in 9 of 12 specimens; posterior arm of protoconid long and straight, joins anterior arm of hypoconid (as the posterior mure) and hypolophid on midline; anterior cingulum high at midline, descends lingually to unite with metaconid and enclose a very narrow and short anterolingual valley, descends labially and rounds corner as a prominent anterolabial shelf; labial and lingual cingula low, partially closing transverse valley; posterolingual basin relatively wide, curved; posterolabial valley well developed in 10 of 14 specimens; transverse valleys wide; labial sinusid relatively angular, not "pinched" posteriorly. Measurements are given in Table 3.

Discussion : *Myocricetodon sivalensis* new species, is similar in size to both *Myocricetodon cherifiensis* and *Myocricetodon parvus* from Beni-Mellal in Morocco. *M. sivalensis* is slightly smaller than *M. cherifiensis* and slightly larger than *M. parvus*. Jaeger (1977a, p. 99) noted a strong lingual cingulum with an accessory tubercle in 19% of the M1/ specimens of *M. parvus* from Beni-Mellal. Lavocat (1952) had characterized *M. cherifiensis* as having a small tubercle on the lingual cingulum of M1-2/, but Jaeger (1977a) assigned M1/ specimens with a tubercle on the lingual cingulum to *M. parvus*. In this respect *M. sivalensis* is more like *M. cherifiensis*. In addition to size, *M. sivalensis* differs from *M. cherifiensis* in having a more inflated and more equally lobed anterocone on M1/, anteroconid of M/1 is smaller and broader, and cusps are more erect. In addition to size, *M. sivalensis* differs from *M. parvus* in better development of the lingual lobe of the anterocone on M1/, absence of a lingual tubercle and more anterior union of the metaloph with the hypocone on M1/, and more anterior

union of the protoloph with the protocone on M2/. *M. sivalensis* differs from *M. parvus intermedius* from Pataniak 6 in having larger size, and a smaller, broader anteroconid on M1/. *M. sivalensis* differs from *M. ouedi* from Oued Zra and *M. irhoudi* from Pataniak 6 in having smaller size; plus the anterocone of M1/ is more divided, and the anteroconid of M1/ is not bilobed. *M. ouedi* and *M. irhoudi* also have the base of cusps more lengthened (anteriorly in upper molars, posteriorly in lower molars) compared to *M. sivalensis*. M3/3 of *M. sivalensis* have not been identified, so these teeth cannot be used presently to distinguish this species.

The development of a lingual tubercle on some of the M1-2/ specimens of *M. parvus* is interpreted as a trend that led eventually to the Dendromurinae. *M. parvus* is probably close to the ancestry of Dendromurinae. Similarity of *M. sivalensis* with *M. parvus* and *M. cherifiensis* from Beni-Mellal also suggests a close temporal correlation of the Beni-Mellal fauna with the restricted range of *M. sivalensis*, about 16 Ma. Jaeger (1977b) considered the Beni-Mellal fauna about two m.y. younger (close to 14 Ma).

Hussain *et al.* (1977) reported but did not describe cricetid fossils in the Daud Khel fauna of the Trans-Indus area of Pakistan, with some material identified as *Myocricetodon*. Casts of this material indicate *M. sivalensis* might be included in the Daud Khel sample, however, most of the Daud Khel specimens appear to be dendromurines, as re-defined below. Cheema *et al.* (1983) also reported remains of *Myocricetodon* from Siwalik deposits near Jalalpur on the Potwar Plateau of Pakistan. Casts of the Jalalpur specimens include *Myocricetodon*, possibly including *M. sivalensis*.

Myocricetodon sp.

(Plate 7 i)

Two isolated M1/ (YGSP 24648 & 24649) from locality YGSP 592 in the Kamliak Formation have a large, inflated, bilobed anterocone; they appear significantly larger than molars of *Myocricetodon sivalensis* and are considered a second species of that genus. The specimens lack a mesoloph, excluding them from the Megacricetodontinae; they lack a lingual enterostyle, excluding them from the Dendromurinae. In addition to larger size, *Myocricetodon* sp. differs from *Myocricetodon sivalensis* in having a larger, almost equally lobed and more inflated anterocone. Formal description and naming of this species is withheld until it is represented by more material. *Myocricetodon* sp. from the Kamliak Formation appears most similar to *M. irhoudi* from the Pataniak 6 fauna of north Africa in size and other dental features.

DAKKAMYOIDES new genus

Type : *Dakkamyoides lavocati* new genus and new species.

Included species : Type and *D. perplexus* new species.

Diagnosis: Medium size, low crowned rodents; M1/ with unequally bilobed anterocone and long, relatively straight arms of lingual cusps; M1 with single-cusped, short anteroconid located on midline, and long, relatively straight arms of labial cusps; base of cusps lengthened anteriorly in upper molars, lengthened posteriorly in lower molars; lingual accessory cusps absent or incipient on M1/ and M2/, absent on lower molars; posterior molars reduced in size.

Other dental characters of *Dakkamyoides*

Teeth of *Dakkamyoides* are low crowned, with the posterior mure reduced but persistent. Upper molars have the posterior side of cusps near-vertical and anterior side of cusps lengthened significantly; lower molars have anterior side of cusps near-vertical and posterior side of cusps lengthened significantly. Labial cusps in upper molars are elongated transversely, located opposite the posterior side of lingual cusps; lingual cusps in lower molars are elongated transversely, located opposite the anterior side of labial cusps. Mesoloph and mesolophid are absent; the posterior mure is reduced, relatively straight. Paracone with posteriorly-directed spur present on M1/, absent or indistinct on M2/. The metacone of M2/ is slightly smaller than other cusps.

Lingual cingula are well developed in upper molars, discontinuous around the protocone of M1/, usually continuous in M2/. The anterior cingulum is long on M2/, forming both lingual and labial anterior shelves. Transverse valleys are weakly closed medially by the posterior mure, oriented oblique to the longitudinal axis in upper molars, slightly offset (lingual side anterior) in lower molars. Posterior cusps are slightly smaller than anterior cusps in M/2-3. Posterior cingula are very short in upper molars, descending labially, usually leaving short posterolabial valley incompletely closed; posterior cingula are long in lower molars, high medially, descending lingually to join posterior entoconid and enclose long, shallow posterolingual basin, descending labially to form posterolabial sulcus. Upper molars have three prominent roots, lower molars have two prominent roots; accessory rootlets are unknown.

Dakkamyoides lavocati new genus and new species

(Plate 7 a-h)

Type: YGSP 19229, isolated right M1/ from locality YGSP 491, Potwar Plateau, Pakistan.

Diagnosis: M1/ with relatively narrow, unequally bilobed and uninflated anterocone; M1/ and M2/ with anterior arm of protocone long, directed anteriorly near midline; M1/ and M2/ with posterior arm of protoconid long, directed posteriorly, near midline; M1-2/ with large hypocone, slightly medial relative to position of protocone.

Hypodigm: Type, plus 17 isolated cheek teeth, including four M1/, four M2/, four M1, four M2 and two M3.

Etymology: *lavocati*, patronym for Professor R. Lavocat in recognition of his numerous contributions to the history of rodents.

Age and distribution: Middle Miocene; localities YGSP 430, 491 and 665 in the Chinji formation, Potwar Plateau, and possibly H-GSP locality 107 in the Chinji formation near Banda Daud Shah, Trans-Indus, Pakistan.

Description: Medium size, low crowned rodent with anterior base of cusps lengthened in upper molars and posterior base of cusps lengthened in lower molars; M/3 reduced in size; posterior mure reduced, weakly joining adjacent cusps.

M1/: Occlusal outline longer than wide, with greatest width posterior to mid-length; anterocone relatively narrow, not inflated, shallow furrow divides lobes of anterocone anteriorly and disappears before reaching small, anterior stylar shelf (restricted to lingual half of anterocone in YGSP 19229); metacone slightly smaller than other cusps; protoloph and metaloph very short, joining posterior side of protocone and hypocone, respectively; paracone with small posteriorly-directed spur; anterior arm of protocone long, narrowing anteriorly (as the anterior mure) to join lingual lobe of anterocone lingual to midline; anterior arm of hypocone long, joining protoloph and posterior arm

of protocone (as the posterior mure); anterior cingulum descending posteriorly on lingual and labial sides of anterocone, partially closing relatively wide anterior lingual and labial valleys; lingual cingulum incipiently cusped; labial cingulum indistinct or absent; labial sinus rounded, relatively narrow internally.

M2/: Occlusal outline subrectangular, longer than wide, narrow posteriorly; hypocone relatively large, and metacone relatively small compared to anterior cusps; anterior arm of protocone long, joining anterior cingulum lingual to midline; anterior arm of hypocone long, joining posterior arm of protocone (as posterior mure); paracone with posteriorly-directed spur absent or indistinct; protoloph short, joins middle of protocone; metaloph very short, weakly joins anterior side of hypocone; anterior cingulum long and straight, expanded (almost cusped) on labial side, high medially where it joins anterior arm of protocone, descending lingually around base of protocone (in 2 of 3 specimens) as a prominent lingual cingulum; lingual cingulum incipiently cusped, ascending anterior side of hypocone; labial cingulum absent (or low in 1 of 3 specimens).

M1/: Occlusal outline much longer than wide, with greatest width posteriorly; anteroconid large, robust, single-lobed, on midline; anterolophid very short or indistinct; metalophid short and narrow, weakly joining anterior arm of protoconid; hypolophid short and relatively broad, weakly joining posterior mure; labial anterior cingulum long, descending to anterior base of protoconid; lingual anterior cingulum short, partially enclosing small, shallow, anterolingual valley; lingual and labial cingula low; labial sinusid wide, not pinched posteriorly; posterolabial sulcus shallow and narrow.

M2/: Occlusal outline subrectangular, longer than wide, slightly more narrow posteriorly; posterior cusps slightly smaller than anterior cusps; anterior arm of protoconid indistinct; metalophid short and narrow, weakly joining anterior side of protoconid; hypolophid short, relatively wide, weakly joining anterior side of hypoconid; labial anterior cingulum long, descending from midline to anterolabial side of protoconid to form a narrow anterolabial shelf; lingual anterior cingulum short and high, joining anterior side of metaconid; labial cingulum low, partially closing relatively wide labial sinusid; lingual cingulum short and low; transverse valleys oriented oblique to longitudinal axis, almost offset; labial sinusid wide, subangular, not pinched posteriorly; posterolabial sulcus shallow and narrow.

M3/: Occlusal outline subtriangular, with straight anterior side and broadly rounded posterior margin; protoconid and metaconid subequal, larger than hypoconid; entoconid minute, joined at base with hypoconid; arms of labial cusps short or indistinct, a short, narrow loph (vestige of posterior mure) weakly joins the protoconid and hypoconid near the midline; metalophid short, weakly joining posterior or center of protoconid; anterior cingulum high near midline, continues lingually to join anterior side of the metaconid and enclose a shallow anterolingual basin, descending labially to anterior base of protoconid, forming a narrow anterolabial shelf; lingual cingulum short and high, joins the entoconid and metaconid, partially enclosing a narrow and shallow lingual basin; labial cingulum absent; posterior cingulum indistinct. Measurements are given in Table 4.

Discussion: *Dakkamyoides lavocati* n. sp., is similar to *Mellalomys atlasi* from Beni-Mellal in Morocco, especially in having a slightly larger hypocone in upper molars and slightly smaller posterior cusps in M/2-3. *D. lavocati* differs from *Mellalomys* in

having a longer, more prominent anterior mure on M1-2/, and better development of cingula in upper molars (e.g., anterior styler shelf at base of the anterocone in M1/, plus lingual and labial cingula in M1-2/). Also, *D. lavocati* has a small but distinct entoconid on M/3 that is indistinct or absent in *Mellalomys*. Size ranges of *D. lavocati* and *M. atlasi* overlap, but the mean of *D. lavocati* is smaller.

Specimens assigned to *Dakkamys* sp. by Wessels *et al.* (1982) from the Chinji formation near Banda Daud Shah appear very similar to *Dakkamyoides lavocati*, and possibly some specimens (other than M1/) assigned to *Dakkamys* sp. from Banda Daud Shah might be assigned to *Dakkamyoides*. The M1/ fragment from Banda Daud Shah (Wessels *et al.* 1982, plate 2, fig. 16) appears larger and with a broader anterocone, plus the posteriorly-directed spur on the paracone is more reduced than in specimens of *D. lavocati* from the Potwar Plateau. These differences suggest that another species of *Dakkamyoides* might be present at Banda Daud Shah. The specimens from Banda Daud Shah are excluded from *Dakkamys* because the enterostyle is much smaller than in specimens of *Dakkamys* on the Potwar Plateau. *Dakkamys asiaticus* is larger and *Dakkamys perplexus* is smaller than specimens assigned to *Dakkamys* by Wessels *et al.* (1982).

D. lavocati differs from *Myocricetodon sivalensis* in larger size. In addition, *D. lavocati* differs from species of *Myocricetodon* in having the base of cusps lengthened more (anteriorly in upper molars, posteriorly in lower molars), plus the anterocone is relatively smaller and more narrow on M1/ of *D. lavocati*.

Dakkamyoides perplexus new species

(Plate 8 a-c)

Type: YGSP 24651, isolated left M1/ from locality YGSP 668.

Diagnosis: Smaller than *Dakkamyoides lavocati*; M1/ with broad, uninflated anterocone and lacking the enterostyle; M/1 with small, broad, single-cusped anteroconid, located on the midline; hypocone relatively large on M1/, metacone relatively small on M2/.

Hypodigm: Type, plus five isolated cheek teeth, including four M1/, one M2/ and one M/1.

Etymology: *perplexus* (L.) = intricate or involved, in reference to characters associated with this species.

Age and distribution: Middle Miocene; localities YGSP 491, 641, 668 and 726 in the Chinji Formation, Potwar Plateau, Pakistan.

Description Medium size, low crowned rodent with base of cusps expanded anteriorly in upper molars, base of cusps expanded posteriorly in lower molars; posterior mure reduced; hypocone relatively large in M1-2/; upper cheek teeth with three well developed rooth that may be strongly inclined anteriorly, with a distal expansion in some roots.

M1/: Occlusal outline longer than wide, with greatest width posterior to mid-length; anterocone not inflated, relatively wide, unequally bilobed, with lobes divided anteriorly by a shallow furrow terminationg above a small, transverse anterior styler shelf; hypocone slightly larger and higher than protocone; short protoloph and metaloph join posterior side of lingual cusps; paracone with very short posteriorly-directed spur that weakly joins a "mesoloph" in late wear; anterior arm of protocone long and low, joining anterocone lingual to midline; anterior arm of hypocone long, sloping, and weakly joining posterior arm of protocone near midline; posterior arms of labial cusps short; anterior cingulum indistinct; lingual cingulum low, non-cusplate; labial cingulum minute

or indistinct; posterior cingulum narrow and short; transverse valleys relatively wide, oriented slightly oblique, separated medially by remnant of the mure, partially closed laterally, especially on lingual side; lingual sinus relatively short; three prominent roots preserved on YGSP 24651, with strong anterior inclination of all three roots, and distal expansion of anterior root.

M2/: Occlusal outline subrectangular, more narrow and rounded posteriorly; metacone slightly smaller than other cusps; anterior arm of protocone short, joining anterior cingulum lingual to midline; posterior arms of lingual cusps very short; protoloph joins anterior side of protocone; metaloph joins posterior side of hypocone; paracone lacks posteriorly-directed spur; anterior cingulum long, high near midline, descending lingually to join anterior protocone, descending labially to join anterior paracone; lingual cingulum short and low; labial cingulum indistinct; posterior cingulum short; lingual sinus long, curved anteriorly; lingual root very large, with distal expansion.

M1/: Occlusal outline much longer than wide, narrow anteriorly; anteroconid broad, single-cusped, on midline; cusps greatly reduced; posterior arms of labial cusps directed posteriorly toward the midline; anterolophid short and bifurcated, with lingual branch continuing lingual to midline to join the metaconid; metalophid and hypolophid indistinct; labial and lingual anterior cingula short, descending to join anterior base of the protoconid and metaconid, weakly closing narrow anterior labial and lingual valleys; posterior cingulum joining posterior base of entoconid; transverse valleys relatively wide; labial sinus narrow, not pinched posteriorly; posterolabial sulcus broad and shallow. Measurements are given in Table 4.

Discussion: *Dakkamyoides perplexus* new species, is smaller than *D. lavocati*, and the shelf at the anterior base of the anterocone is better developed in *D. perplexus*. *D. perplexus* is about the same size as *Myocricetodon* sp. from the Kamlial Fm., but differs from that species in having a less robust anterocone and a more prominent anterior styler shelf on M1/. *D. perplexus* is slightly larger than *Myocricetodon sivalensis*; in addition to size, it differs from that species in having the base of cusps lengthened more (anteriorly in upper molars, posteriorly in lower molars), the anterior mure is longer and more prominent, and the anterocone is less robust on M1/ of *D. perplexus*.

DENDROMURINAE

The Dendromurinae are characterized by M1/ with a strongly bilobed anterocone; absence of a mesoloph and mesolophid; reduction of the posterior mure; presence of a single lingual accessory cuspule (the enterostyle) on M1-2/ and occasionally developing a single labial cuspule (the ectostylid) on M1; posterior molars reduced in size. Some dendromurines have the base of cusps lengthened (e.g., *Dakkamys* and *Paradakkamys*), other dendromurines have only a slight swelling at the base of cusps (e.g., *Potwarmus*). These differences are also reflected in width of the transverse valleys which are usually continuous or weakly closed medially in Dendromurinae. Transverse valleys are usually oriented slightly oblique to the longitudinal axis in upper molars, oriented oblique or offset at the midline in lower molars of dendromurines.

At least six dendromurine taxa are recognized from lower Siwalik deposits near Chinji village. Until recently the Dendromurinae were considered primarily an African group, where they presently reside; a number of dendromurines have been reported from southern Asia since 1985 (Jaeger *et al.* 1985, Mein & Ginsburg, 1985) and Aguilar *et al.* (1984) reported the first European dendromurine (*Dendromus*) from late

Miocene deposits in southern Spain. As discussed below, *Antemus primitivus* described by Wessels *et al.* (1982) from Pakistan is included in the Dendromurinae, rather than the Muridae.

DAKKAMYS JAEGER 1977a

Dakkamys was characterized by Jaeger (1977a) as a Myocricetodontinae with a strong lingual accessory cuspule that joins the posterior arm of the protocone on M1-2/; plus normal development of the mure, and a wide lingual sinus on M2/. Presence of the lingual accessory cuspule in *Dakkamys* places it among the Dendromurinae in this study.

Dakkamys has been reported from Daud Khel and Banda Daud Shah in the Trans-Indus area (Hussain *et al.* 1979; Munthe, 1980; Dehm *et al.* 1982; Wessels *et al.* 1982), and from the Potwar Plateau (Cheema *et al.* 1983). However, none of these species have been named, and the only *Dakkamys* material described from Pakistan is from Banda Daud Shah. As noted above, some of the specimens referred to *Dakkamys* sp. by Wessels *et al.* (1982) are considered *Dakkamyoides*, a myocricetodont, in this study. *Dakkamys* is also known from Morocco (Jaeger, 1977a) and Turkey (Sickenburg *et al.* 1975). Casts of representative specimens from Daud Khel, Banda Daud Shah, and Jalalpur have been provided by J. Munthe, H. de Bruijn, and L. Flynn.

Dental characters of Siwalik *Dakkamys*

Molars of *Dakkamys* are low crowned; they have an unequally bilobed anterocone and slight lingual inflection on M1/, a single-cusped anteroconid on M/1. Posterior molars are small. The lingual cingulum has an enterostyle on M1-2/ and may be continuous around the protocone in M1/; the lingual cingulum is low, non-cusped but usually continuous in lower molars. The posterior mure is weak or poorly defined in anterior molars, usually better developed in M2/2. Anterior base of cusps is lengthened in upper molars and posterior base of cusps is lengthened in lower molars. Cusps of molars are slightly inclined (posteriorly in upper molars, anteriorly in lower molars). Labial cusps in upper molars are elongated transversely and are located slightly posterior relative to lingual cusps; lingual cusps in lower molars are elongated transversely and are located slightly anterior relative to labial cusps. In upper molars lingual cusps have long and straight anterior arms, short posterior arms; in lower molars labial cusps have short posterior arms, very short or indistinct anterior arms. Transverse valleys are commonly weakly closed medially by the posterior mure, and are oriented oblique to the longitudinal axis in upper molars, slightly offset (lingual side anterior) in lower molars. The posterior cingulum is short and narrow in upper molars, usually free from the posterior base of the metacone; it is long in lower molars, high medially, descending lingually to join the posterior base of the entoconid, descending labially as a relatively shallow and wide posterolabial sulcus or valley. Upper molars have three prominent roots, lower molars have two prominent roots; accessory rootlets are unknown.

Dakkamys asiaticus new species

(Plate 9 a-c)

Type: YGSP 19541, isolated left M1/ from locality YGSP 76, Chinji fm., Pakistan.

Diagnosis: Relatively large size; M1/ with very large lingual enterostyle, joining protocone by a narrow loph; anterocone bilobed, wide, not inflated; posterior mure relatively weakly developed in upper and lower molars.

Hypodigm: Type, and six isolated cheek teeth, including three M1/, one M2/, and two M3/. Cast of *Dakkamys* sp. from Jalalpar (Cheema *et al.* 1983, fig. 7a) is included as the only known M1/.

Etymology: *asiaticus*, for continent inhabited by this species.

Age and distribution: Middle Miocene; localities YGSP 76 in the Chinji formation, locality YGSP 259 in the lower Nagri formation; and Pakistan Museum of Natural History locality 2 km NE of Jalalpur village, Potwar Plateau, Pakistan.

Description: A relatively large, low crowned rodent with tall, broad, slightly inclined cusps; posterior mure weakly developed and posterior molars greatly reduced in size.

M1/: Occlusal outline longer than wide, with relatively straight labial side and broadly rounded lingual side; greatest width slightly posterior to mid-length; anterocone wide, not inflated, unequally bilobed, with labial lobe larger and higher; a deep furrow separates lobes of the anterocone, persisting to the transverse anterior styler shelf; short protoloph and metaloph; lingual enterostyle slightly smaller than prominent cusps, joins posterior side of the protocone by a low, short loph; anterior arm of protocone long and high, continuing anteriorly to join the posterior anterocone near the midline; anterior arm of hypocone high, joins protoloph near the midline; posterior arm of lingual cusps very short; paracone with posteriorly-directed spur that becomes more pronounced with wear; anterior cingulum indistinct; anterior labial and lingual valleys open; lingual cingulum low, continuous around protocone, weakly joining the enterostyle; labial cingulum short and low; lingual sinus blocked by large enterostyle.

M2/: Occlusal outline subrectangular, more narrow and rounded posteriorly; anterior cusps slightly larger than posterior cusps; protoloph and metaloph narrow, weakly joining center of protocone and hypocone, respectively; enterostyle prominent, smaller than metacone, joins posterior side of protocone by short loph; anterior arm of lingual cusps long, high, directed anteriorly; posterior arm of lingual cusps short; paracone lacks posteriorly-directed spur; labial anterior cingulum high, joining anterolabial side of paracone to enclose a small anterolabial valley; lingual anterior cingulum indistinct; lingual cingulum low, discontinuous at base of protocone; labial cingulum indistinct; lingual sinus relatively long and narrow, closed by large enterostyle.

M3/: Occlusal outline subtriangular, with straight anterior side; three large and slightly inflated cusps, metacone indistinct as a slight expansion on labial side of hypocone; paracone and protocone join anterior cingulum near midline; anterior cingulum restricted to labial side, separated from paracone by narrow anterolabial valley; transverse valleys narrow, separated medially by weak posterior mure.

M1/: Occlusal outline longer than wide, narrow anteriorly; anteroconid small, single-cusped, located slightly labial to midline; protoconid and entoconid slightly larger than metaconid and hypoconid; metalophid and hypolophid broad; labial anterior cingulum low and short, lingual anterior cingulum indistinct, forming a low shelf anterior to metaconid; labial and lingual cingula low, with minute (labial) ectostylid and (lingual) mesostylid; posterolabial sulcus shallow; transverse valleys closed medially by weak posterior mure, partially closed laterally by minute ectostylid and mesostylid; labial sinus narrow medially. Measurements are given in table 5.

Discussion: *Dakkamys asiaticus* n. sp., is very similar to *Dakkamys zaiani* from

Beni-Mellal, Morocco (Jaeger, 1977a). Size range of these species overlap broadly, although the mean of *D. asiaticus* is larger than *D. zaiani*. *D. asiaticus* differs from *D. zaiani* in having a more prominent anterior shelf at the base of the anterocone on M1/ and the lingual accessory cusp is larger and more isolated on M1-2/. The anteroconid on M/1 is smaller and not as long in *D. asiaticus*, and M3/ of *D. asiaticus* has a more medial hypocone, with the anterior arm joining the protoloph as a median longitudinal crest. *D. asiaticus* differs from *Mellalomys atlati* from Beni-Mellal, Morocco, in having larger size and a prominent enterostyle on M1-2/.

Dakkamys has also been reported from Yeni Eskihisar, Turkey (Sickenburg and others, 1975) but hasn't been described. Casts of *Dakkamys* and cf. *Dakkamys* specimens from Yeni Eskihisar appear smaller than known Siwalik species of *Dakkamys*.

Dakkamys barryi new species

(Plate 9 d-h)

Type: YGSP 24717, right maxilla fragment with M1-3/ from locality YGSP 726, Potwar Plateau, Pakistan.

Diagnosis: Medium size, with enterostyle prominent on M1/, present on M2/; anterocone on M1/ large and wide, slightly inflated; M2/ with long anterior cingulum (on labial as well as lingual side), continuous with well developed lingual cingulum; M3/ small, with a labial anterior cingulum and indistinct metacone; M/1 with a large, robust, single-lobed anteroconid and a thick posterior cingulum lingual to the midline; M/3 small, with a narrow posterior mure medial to the midline and indistinct entoconid; posterior mure reduced in upper and lower molars; lower molars lack an ectostylid.

Hypodigm: Type, plus a right maxilla fragment bearing M1-2/, (YGSP 24721); left maxilla fragment bearing M1-3/, (YGSP 24722); left dentary fragment bearing M/1-3, (YGSP 24719); an isolated left M/1, (YGSP 24720); an isolated left M/2 (YGSP 19252).

Etymology: *barryi* for John C. Barry who collected most of the specimens included in the hypodigm of this taxon.

Age and distribution: Middle Miocene, localities YGSP 491 and 726 in the Chinji Formation, Potwar Plateau, Pakistan.

Description: A medium size, low crowned rodent with enterostyle on M1-2/; posterior mure weakly developed; cusps slightly inflated, especially the anterocone on M1/ and anteroconid on M/1; posterior molars reduced in size.

M1/: Occlusal outline longer than wide, with greatest width slightly posterior to mid-length and shallow lingual inflection between the anterocone and protocone; anterocone large, slightly inflated, unequally bilobed with labial lobe larger and higher than lingual lobe; lobes of anterocone separated by a relatively deep vertical furrow that terminates above a small anterior stylar shelf; hypocone slightly larger than other cusps; enterostyle prominent but smaller than other cusps, joining posterior side of protocone by a narrow and low loph, located directly opposite paracone; labial and lingual cusps joined medially by a short protoloph to posterior side of protocone, and by a metaloph to posterior side (3 specimens) or middle (1 specimen) of hypocone; anterior arms of labial cusps high and long, directed anteriorly along midline; posterior arms of labial cusps very short, directed transversely; paracone lacks posteriorly-directed spur; anterior cingulum low, continuous lingually with lingual cingulum in 1 of 3 specimens, reduced labially to an indistinct cingulum; lingual cingulum well developed anterior to enterostyle; labial cingulum low, almost stylar in 2 of 3 specimens.

M2/: Occlusal outline subrectangular, longer than wide, narrow and more rounded posteriorly; hypocone slightly larger and metacone slightly smaller than other cusps; enterostyle small, isolated from protocone, on posterior end of lingual cingulum; labial cusps joining lingual cusps by short protoloph (to middle of the protocone) and metaloph (to anterior side of the hypocone); anterior arms of lingual cusps directed anteriorly along or slightly lingual to midline; anterior arm of protocone short, joining anterior cingulum (as short anterior mure) at midline (2 specimens) or lingual to midline (1 specimen); posterior arm of lingual cusps very short; paracone with posteriorly-directed spur weakly developed in 2 of 3 specimens; anterior cingulum long, flexed at anterolabial corner to join base of paracone and enclose a shallow anterolabial valley, expanded as an incipient parastyle in 1 of 3 specimens; anterior cingulum descends lingually and continues to the enterostyle as the lingual cingulum; labial cingulum low; transverse valley oriented obliquely, closed medially by posterior mure; lingual sinus partly blocked by lingual cingulum and enterostyle.

M3/: Occlusal outline subtriangular, with straight anterior side and rounded posterior margin; paracone larger than protocone, protocone larger than hypocone, metacone indistinct; paracone elongated transversely and joining anterior cingulum at midline by narrow protoloph; minute metaloph joins middle of hypocone; arms of lingual cusps indistinct, although protocone and hypocone may join (as a posterior mure) lingual to midline in late wear; anterior cingulum high labially, almost cuspsate, separated from paracone by shallow anterolabial valley, descending lingually as an indistinct anterolingual shelf; lingual and labial cingula absent; posterior cingulum high, continuous with hypocone; transverse valley curved (convex anteriorly) and narrow, weakly closed medially by posterior mure.

M/1: Occlusal outline much longer than wide, narrowing anteriorly; anteroconid large, robust, single-cusped, on midline; hypoconid larger and metaconid smaller than other principal cusps; metalophid and hypolophid indistinct, with lingual and labial cusps joining medially in mid to late wear; arms of labial cusps short; anterolophid short, directed posteriorly along midline to join metaconid (and secondarily the anterior arm of protoconid); labial anterior cingulum long, almost continuous with labial cingulum near protoconid; lingual anterior cingulum short, partially closing narrow and shallow anterolingual valley; labial cingulum long and low, non-cuspsate although slightly swollen in 1 of 2 specimens; lingual cingulum absent; posterolabial sulcus short and very shallow; transverse valley offset with wide labial sinusid posterior relative to narrow lingual sinusid.

M/2: Occlusal outline subrectangular, longer than wide; protoconid slightly larger than other cusps; lingual cusps joining anterior side of labial cusps by short protolophid and hypolophid; anterior cingulum high near midline where it joins the short anterior mure, descending labially and flexed around protoconid to continue as the labial cingulum in 1 of 2 specimens; labial cingulum relatively long, non-cuspsate; lingual cingulum short and low; posterolabial sulcus very shallow, forming a small posterolabial shelf; transverse valleys offset, with labial sinusid posterior relative to lingual sinusid.

M/3: Occlusal outline subtriangular, with straight anterior side; hypoconid much smaller than protoconid and metaconid, entoconid indistinct; metaconid elongated transversely, located directly opposite and joining middle of protoconid by narrow metalophid; anterior arm of protoconid indistinct, posterior arm of protoconid very narrow, directed posterolingually to join posterior cingulum in position of indistinct entoconid; hypoconid oriented transversely and gently rounded, continuing lingually as posterior cingulum-lingual cingulum that partially closes narrow and shallow lingual basin; anterior cingulum narrow, high near midline, descending labially as a small anterolabial

shelf that joins the base of the protoconid; labial cingulum short and low; labial sinusid very narrow and short. Measurements are given in Table 5.

Discussion: *Dakkamys barryi* n. sp., is smaller than *D. asiaticus* and *D. zaian* in Addition to size, *D. barryi* differs from *D. asiaticus* in having a smaller enterostyle and better development of the shelf at the anterior base of the anterocone in M1/, better development of the lingual cingulum in M2/, and greater separation of the indistinct metacone from the hypocone in M3/. The anteroconid in M/1 of *D. barryi* is larger and the labial cingulum is better developed in *D. barryi* relative to *D. asiaticus*. *D. barryi* differs from *Mellalomys atlasi* of Beni-Mellal, Morocco, in having an enterostyle on M1-2/. *Dakkamys* material from Yeni Eskihisar, Turkey, appears noticeably smaller than *D. barryi*.

Specimens described as *Dakkamys* sp. from Banda Daud Shah by Wessels *et al.* (1982) are very similar to *D. barryi* and some of that material might be assigned to *D. barryi*. However, it appears that the lingual accessory cusp is smaller and the size of many of the *Dakkamys* specimens from Banda Daud Shah may be smaller relative to *D. barryi*.

Dakkamys species indeterminate

(Plate 9 i)

Five isolated M/1 from the Chinji and Nagri Formations (localities YGSP 259, 634 and 726) are assigned to the genus *Dakkamys*, but no species is designated. These specimens are smaller than *Dakkamys asiaticus* and *Dakkamys barryi* (see Table 5); in addition, the posterior mure is very reduced, the anteroconid is small and narrow, base of the cusps are expanded anteriorly, the metaconid is almost alternate relative to location of the labial cusps, and the posterior cingulum is short. These five specimens are close in size (slightly smaller) and share several other morphological features with *Paradakkamys chinjiensis*, n. gen. and n. sp. described below, but lack the ectostylid that characterizes M/1 of *Paradakkamys*. This taxon might be close to the ancestry of *Paradakkamys* but is too poorly represented to be characterized.

?*Dakkamys* species

(Plate 9 j)

Six isolated lower molars (one M/1, four M/2 and one M/3) from locality YGSP 491 in the Chinji Formation and locality YGSP 259 in the Nagri Formation are questionably assigned to *Dakkamys*. An alternative interpretation is that these specimens might represent the unrecognized lower dentition of the myocricetodont *Dakkamyoides perplexus*. The alternative interpretation is rejected, because these specimens seem large relative to the size expected in *Dakkamyoides perplexus*, and the posterior mure is more reduced in these specimens than in *Dakkamyoides perplexus*. The small and narrow anteroconid on M/1, and the alternation of cusps on M/2 suggest affinity with *Paradakkamys*. Assignment of this taxon to *Dakkamys* is questioned until more material can be evaluated.

PARADAKKAMYS new genus

Type: Type and only species is *Paradakkamys chinjiensis*, new species.

Diagnosis: Relatively small, low crowned rodent with posterior mure very reduced; a prominent enterostyle present on M1-2/, and a small ectostylid present on M/1, absent

on M/2; M1/ long and narrow, with a very wide, slightly inflated, unequally bilobed anterocone having a broad, shallow sulcus anteriorly; M2/ with a short, lingual anterior cingulum; M/1 relatively long and narrow, with a small anteroconid located close to the metaconid; M/1-2 with a short, almost isolated posterior cingulum resembling a posteroconid.

Etymology: *Para-* for similarity to *Dakkamys*, which lacks accessory cusps on lower cheek teeth.

Dental characters of *Paradakkamys*

Molars of *Paradakkamys* are very similar to those of *Dakkamys*, differing primarily in having a prominent ectostylid on M/1. In addition, molars are low crowned, having a very wide unequally bilobed anterocone and smooth lingual margin, lacking an inflection on M1/, and with a small single-cusped anteroconid on M/1. The lingual cingulum is low, with a prominent enterostyle on M1-2/. The posterior mure is weak or discontinuous on M1/1, continuous on M2/2. As in *Dakkamys*, anterior base of cusps is lengthened in upper molars and posterior base of cusps is lengthened in lower molars; labial cusps of upper molars are elongated transversely and are located opposite the posterior side of lingual cusps; lingual cusps of lower molars are elongated transversely and are located opposite the anterior side of labial cusps; the mesoloph and mesolophid are absent; and posterior molars are reduced. In upper molars lingual cusps have long and straight arms, posterior arms are minute or indistinct; in lower molars labial cusps have short posterior arms, anterior arms are minute or indistinct. Transverse valleys are weakly closed or continuous medially, and oriented oblique to the longitudinal axis in upper molars, oriented oblique or offset in lower molars. The posterior cingulum is short in both upper and lower molars, tending to be isolated as a "hypoconulid" or posteroconid in M/1-2. The posterolabial sulcus is generally broad and shallow in M/1-2. Upper cusps have three prominent roots, lower molars have two prominent roots; accessory rootlets are unknown.

Paradakkamys chinjiensis new species

(Plate 8 d-k)

Type: YGSP 24656, isolated right M1/ from locality YGSP 76, Potwar Plateau, Pakistan.

Diagnosis: As for the genus (above).

Hypodigm: Type and 22 isolated cheek teeth, including three M1/, three M2/, six M/1, nine M/2 and Two M/3.

Etymology: *chinjiensis*, ensis = "in the place of" Chinji village, in reference to the general area where this taxon was initially collected.

Age and distribution: Middle Miocene; localities YGSP 76, 491, 504, 634, 636 and 726 in the Chinji formation; and locality YGSP 259 in the Nagri formation, Potwar Plateau, Pakistan.

Description: A relatively small, low crowned rodent with relatively long and narrow cheek teeth; posterior mure greatly reduced; metacone smaller than other cusps in upper molars.

M1/: Occlusal outline oval, much longer than wide, with greatest width slightly posterior to mid-length; lingual margin gently rounded, lacking an inflection between the anterocone and protocone; anterocone very wide, slightly inflated, unequally bilobed, with labial lobe larger and higher than lingual lobe; lobes of anterocone separated by a broad and shallow sulcus, terminating at a minute anterostyle near the midline in 1 of 2 specimens; protocone located slightly lingual relative to the hypocone;

labial cusps join posterior side of lingual cusps by short protoloph and metaloph; enterostyle prominent, joining posterior side of protocone by a low, short loph; anterior arm of protocone long, directed anteriorly (as the anterior mure) to join anterocone near the midline; paracone with small posteriorly-directed spur; mesostyle and parastyle minute; anterior lingual cingulum short; anterior labial cingulum absent; lingual cingulum short and low anterior to enterostyle; labial cingulum absent; posterior cingulum short and narrow; transverse valleys weakly closed medially by short posterior mure; lingual sinus short and broad, blocked by enterostyle.

M2/: Occlusal outline subtriangular, longer than wide, more narrow and rounded posteriorly, with greatest width at anterior base of enterostyle; protoloph relatively wide, joins middle or anterior side of protocone; metaloph very short, joins anterior side of hypocone; enterostyle small, joins posterior protocone by short loph in 2 of 3 specimens; paracone with minute posteriorly-directed spur; mesostyle and parastyle absent; labial anterior cingulum high, enclosing narrow anterolabial valley; lingual anterior cingulum absent in 2 of 3 specimens; lingual cingulum low anterior to enterostyle; posterolabial basin very shallow; transverse valley narrow, curved (convex anteriorly) incompletely closed medially by remnant of posterior mure; labial sinus narrow, partly blocked by enterostyle.

M/1: Occlusal outline longer than wide, more narrow anteriorly; anteroconid small, single-cusped, symmetrical on midline; metaconid slightly smaller than other cusps; short metalophid and hypolophid; ectostylid prominent, at posterior end of labial cingulum; anterior arms of labial cusps short, protoconid weakly joins short anterolophid (as the anterior mure); posterior arms of labial cusps very short; labial anterior cingulum long, forming an anterolabial shelf, almost continuous with labial cingulum at base of protoconid; lingual anterior cingulum indistinct or absent; labial cingulum low; lingual cingulum absent; posterior cingulum short, almost isolated (joining hypoconid only after mid-wear); transverse valley with strong oblique orientation relative to longitudinal axis, closed medially in late wear by short posterior mure; labial sinusid narrow, partially blocked by ectostylid.

M/2: Occlusal outline subrectangular, longer than wide, more narrow posteriorly; posterior cusps slightly smaller than anterior cusps; ectostylid absent or incipient on 8 specimens; metalophid and hypolophid short, joining anterior side of labial cusps; anterior cingulum restricted to labial side, high at midline, descending and curving posteriorly to join base of protoconid and form anterolabial shelf, continuous with labial cingulum in 2 of 9 specimens; labial cingulum long and low; lingual cingulum absent; posterior cingulum short and thick, resembling a posteroconid; transverse valley narrow, oriented oblique relative to longitudinal axis, closed medially by short posterior mure; labial sinusid long, narrow medially.

M/3: Occlusal outline subtriangular, with straight anterior side and broadly rounded posterior margin; hypoconid smaller than anterior cusps; entoconid absent; metaconid elongated transversely, located directly opposite and joining middle of protoconid by narrow metalophid; anterior arm of protoconid short, joining anterior cingulum labial to midline; posterior arm of protoconid long, directed posteriorly and joining hypoconid lingual to the midline; arms of hypoconid indistinct; hypoconid merges with high posterior cingulum that curves anteriorly as the lingual cingulum and joins the posterior base of the metaconid, enclosing a small posterolingual basin; anterior cingulum high near midline, joining anterior side of metaconid to enclose a minute anterior basin, descending labially as a small anterolabial shelf; labial sinusid short and narrow, steep sided. Measurements are given in table 6.

Discussion: *Paradakkamys chinjiensis* n. sp., is smaller than *Dakkamys asiaticus* and *Dakkamys barryi*; it differs from species of *Dakkamys* in development of a prominent labial accessory cusp on M/1. *P. chinjiensis* is comparable in size to *Dakkamys* sp. from Yeni Eskihisar, Turkey, and shares many morphological similarities with the Turkish specimens. However, the only M/1 available (on a cast) of the Turkish material is slightly smaller and lacks the labial accessory cusp of *P. chinjiensis*.

POTWARMUS new genus

Wessels *et al.* (1982) described a new species, *Antemus primitivus*, from the Chinji formation near Banda Daud Shah, Northwest Frontier Province, west of the Indus River in Pakistan. They assigned this taxon to *Antemus*, a murid, and considered it the most primitive murid known, but closely related to *Antemus chinjiensis* Jacobs 1977, from the Chinji formation in the Potwar Plateau in Pakistan. Subsequently, additional fossils have been collected from Siwalik deposits near Chinji village and have forced re-evaluation of the genus and of *Antemus primitivus*. Based on the evaluation of Jacobs *et al.* (in press) and a larger fossil sample, *A. primitivus* is hereby removed from the genus *Antemus* (and the Muridae) because it lacks three cusps on the anterior chevron (or equivalent structure) of M1/. The lingual cusp on M1/ of "*A.*" *primitivus* (*sensu* Wessels and others) is connected to the anterior cingulum in some specimens; however, this cusp must be the enterostyle (equivalent to T/4) because it is always located between the protocone and hypocone. This taxonomic re-assignment requires erecting a new taxon, *Potwarmus*, n. gen., for "*A.*" *primitivus*, which we place in the Dendromurinae of the Cricetidae, a subfamily whose members are characterized by having a bilobed anterocone, and a single lingual cusp (enterostyle) on M1/.

Recently another species from southeast Asia ("*Antemus*" *thailandicus*) has been assigned to *Antemus* (Jaeger *et al.* 1985, Mein and Ginsburg, 1985). "*A.*" *thailandicus* is clearly closely related to "*A.*" *primitivus* and is transferred to *Potwarmus* for the same reasons. "*A.*" *thailandicus* was considered more primitive than "*A.*" *primitivus* by Jaeger *et al.* (1985) and by Mein & Ginsburg (1985). All of the researchers who have studied these rodents agree that *Potwarmus primitivus* is probably ancestral to *Antemus chinjiensis*, the most primitive member of the Muridae.

Included species : *Potwarmus primitivus*, *Potwarmus thailandicus* and *Potwarmus minimus*, new species.

Diagnosis: Small size, low crowned rodents with a symmetrical bilobed anterocone and lingual enterostyle on M1/; small single lobed anteroconid on M1/; cusps of upper molars and labial cusps of lower molars relatively circular, slightly inflated at the base; posterior mure reduced, with transverse valleys continuous (or nearly so) medially until mid or late wear (except in M/2).

Etymology: Named for the Potwar Plateau of Pakistan, inhabited by this rodent during the Miocene.

Dental characters of *Potwarmus*

Molars of *Potwarmus* are relatively short and fat, the bilobed anterocone is relatively large and symmetrical on an M1/ that is expanded at the "waist" by a large enterostyle, and the anteroconid of M/1 is short, close to the metaconid. The lingual cingulum of upper molars is well developed, bearing an enterostyle, and usually continuous with the anterior cingulum in M1-2/. Upper molars have almost lost the posterior mure; it is retained better in lower molars, especially M/2. Cusps of molars are relatively round, except for the labial cusps in upper molars and lingual cusps in lower molars which are elongated transversely. Roundness of cusps results primarily from

reduction of anterior and posterior arms of lingual cusps in upper molars and of labial cusps in lower molars, and slight inflation at the base of cusps. Labial cusps of upper molars are located opposite the posterior side of lingual cusps and join those cusps medially by short protoloph and metaloph; lingual cusps of lower molars are located opposite the anterior side of labial cusps and join those cusps medially by short metalophid and hypolophid. As in other dendromurids, the mesoloph and mesolophid are absent and posterior molars are probably reduced. Transverse valleys of upper molars are open medially until late wear and are oriented transverse to the longitudinal axis; transverse valleys of lower molars are closed medially after early wear and are commonly oriented oblique to the longitudinal axis. The posterior cingulum is short in both upper and lower molars, with short posterolabial valley usually open in upper molars and with posterolingual valley usually open in lower molars. The posterolabial sulcus is relatively broad in M/1-2. Upper molars have three prominent roots, lower molars have two prominent roots; accessory rootlets are unknown.

Potwarmus primitivus (WESSELS, de BRUIJN, HUSSAIN & LEINDERS 1982)

(Plate 10 a-e)

Type: HGSP 5521, isolated left M1/ from locality HGSP 107, Banda Daud Shah, Pakistan.

Diagnosis of Wessels et al. (1982): "*Antemus primitivus* has small molars with an incipient murid pattern. Longitudinal connections between the cusps are weak or absent. The anteroconid of M/1 consists of only one cusp. The labial cingulum of the M/1 runs from the anteroconid to the hypoconid and may reach the posterolophid. The t/2 and the t/3 in the M1/ are separated by a shallow furrow, the t/1 may be a small cusp or ridge. The t/12 is a small ridge."

Emended diagnosis: M/1 with a small, single-cusped anteroconid located on the midline; M1/ with a wide, moderately inflated, symmetrical, bilobed anterocone, and lingual cingulum that may join the anterocone with a prominent enterostyle; M2/ with a long anterior cingulum, continuous from the anterolabial corner to a prominent lingual enterostyle; posterior mure reduced, weakly closing transverse valleys; lower molars with a well developed labial cingulum that lacks an ectostylid.

Referred specimens: Thirteen isolated cheek teeth, including three M1/, one M2/, four M/1, two M/2 and three M/3.

Age and distribution: Middle Miocene; localities HGSP 107, YGSP 589 and 709 in the Chinji formation, and localities YGSP 591 and 592 in the Kamli formation, Pakistan.

Description: A small, low crowned rodent with cusps relatively rounded, slightly inflated at the base, and posterior mure very reduced.

M1/: Occlusal outline longer than wide, with greatest width posterior to mid-length, and lingual inflection between anterocone and protocone; anterocone wide, moderately inflated, symmetrical, subequally bilobed, with lobes separated by a very shallow furrow; anterior base of the anterocone with a weak anterior styler shelf in 2 of 3 specimens; enterostyle (t/4) small (about the size of the lingual lobe of anterocone), isolated from the protocone; labial cusps join lingual cusps by short, narrow protoloph and metaloph; low ridge (vestige of the posterior mure) near the midline; paracone with a weakly developed posteriorly-directed spur; labial anterior cingulum short or indistinct; lingual cingulum long, continuous with enterostyle in 2 of 3 specimens; posterior cingulum narrow, short, weakly joining posterior metacone; transverse valley slightly closed medially, oriented transverse or slightly oblique to longitudinal axis; lingual sinus relatively narrow, blocked by enterostyle.

M2/: Occlusal outline subrectangular, longer than wide, more narrow and rounded posteriorly; labial cusps slightly smaller than lingual cusps, joining lingual cusps medially by short, narrow protoloph and metaloph; paracone lacks a posteriorly-directed spur; anterior cingulum long, swollen labially as an incipient parastyle, enclosing a narrow anterolabial valley, descending lingually and continuing posteriorly as the lingual cingulum that joins the enterostyle; posterior cingulum narrow and short, approaching but free from the metacone; transverse valley slightly closed medially, oriented transverse to longitudinal axis.

M1/: Occlusal outline longer than wide, more narrow and rounded anteriorly; anteroconid small, slightly asymmetrical, located near midline; lingual cusps join labial cusps medially by short, narrow metalophid and hypolophid; anterior arms of labial cusps very short; posterior arms of labial cusps comparatively long and low; anterolophid very short, weakly joining metalophid in 1 of 2 specimens; ectostylid absent; labial anterior cingulum long, terminating anterior to protoconid; lingual anterior cingulum absent; labial cingulum low; posterolabial shelf shallow; transverse valley weakly closed medially, oriented slightly oblique to longitudinal axis; labial sinusid relatively wide.

M2/: Occlusal outline subrectangular, wider posteriorly; lingual cusps slightly smaller than labial cusps, joining labial cusps medially by short metalophid and hypolophid; anterior arms of labial cusps short; posterior arms of labial cusps relatively long; ectostylid absent; anterior cingulum high near midline where it joins the metalophid and anterior arm of the protoconid, descending lingually to form a very narrow shelf, descending labially to form a prominent anterolabial shelf anterior to the protoconid; labial cingulum low and long; lingual cingulum low and short; transverse valley weakly closed medially, oriented slightly oblique to longitudinal axis; labial sinusid relatively wide.

M3/: Occlusal outline subtriangular with straight anterior margin and rounded posterior margin; protoconid and metaconid subequal, hypoconid smaller, located lingual relative to position of protoconid; entoconid absent; metaconid elongated transversely, located directly opposite protoconid, joining posterior (2 specimens) or anterior (1 specimen) protoconid by short metalophid; anterior arm of protoconid short, directed anteriorly and joining anterior cingulum at midline; posterior arm of protoconid long, directed posterolabially, crossing midline, terminating short of high lingual cingulum in 2 of 3 specimens; anterior arm of hypoconid short, joining posterior arm of protoconid in 2 of 3 specimens; posterior arm of hypoconid continues as the posterior cingulum that curves anteriorly (the lingual cingulum) and joins the metaconid; anterior cingulum long, high medially, descending lingually to join base of anterior metaconid, descending labially and curving posteriorly to form anterolabial shelf and join base of the protoconid; labial cingulum low and short; labial sinusid narrow, relatively deep. Measurements are given in table 7.

Discussion: *Potwarmus primitivus* is assigned to the new genus *Potwarmus* because it lacks an anterolingual cingular cusp (t/1) that is characteristic of *Antemus* and other murids. *Potwarmus* is included in the Dendromurinae of the Cricetidae, and considered a possible ancestor of *Antemus* and other murids through development of the anterolingual cingular cusp on M1/ and other features. It is not known whether the lingual enterostyle (t/4), which is always isolated in *Antemus* (Jacobs *et al.*, in press) and may be connected to the lingual cingulum in *Potwarmus*, moved anteriorly to become the t/1 (with subsequent development of a new t/4); or whether the lingual cingulum separated from the enterostyle (t/4) and shortened, to develop a new cusp (t/1) at the shortened end of the lingual anterior cingulum. The latter scenario seems more

likely; however, transitional stages have not been identified in the excellent sample of fossils from the Chinji area that span the stratigraphic interval where those transitional stages would be expected.

Potwarmus primitivus is very similar to *Potwarmus thailandicus* from Miocene deposits in the Li basin of Thailand. Size of *P. thailandicus* is identical to that of *P. primitivus*, based on measurements given by Jaeger *et al.* (1985); measurements of *P. primitivus* from Banda Daud Shah appear slightly smaller (Wessels *et al.* 1982). *P. primitivus* differs from *P. thailandicus* in having a more prominent enterostyle on M1-2/ and less reduction of the longitudinal crest in both upper and lower molars. Jaeger *et al.* (1985) noted absence of a notch in the lingual margin of M1/ between the anterocone and protocone of *P. thailandicus*. That notch is variable in *P. primitivus*, as seen in Plate 2 of Wessels *et al.* (1982) and on Plate 10. The M/1 of *P. primitivus* has a small, single cusped anteroconid; the anteroconid appears to be bilobed (Figure in Jaeger *et al.* 1985) or broad with numerous cuspules (Figures in Mein & Ginsburg, 1985) in *P. thailandicus*. The anteroconid is usually bilobed in *Antemus* (Jacobs and others, in press). *P. primitivus* differs from *Megacriceton mythikos* in having smaller size, absence of a mesoloph (and mesolophid), reduction of the longitudinal crest, and better development of the enterostyle. *M. mythikos* occurs at the same and higher stratigraphic levels as *Potwarmus* and parallels some dental features seen in *Potwarmus*.

Potwarmus minimus n. sp.

(Plate 10 f-m)

Type: YGSP 19555, isolated left M/1 from locality YGSP 589, Chinji formation, Potwar Plateau, Pakistan.

Diagnosis: Small size, low crowned rodent with posterior mure reduced, a small enterostyle present on M1/ and usually present on M2/; M/1 with a small asymmetrical single-cusped anteroconid; cusps of upper molars less rounded than in *P. primitivus*; smaller than *P. primitivus*.

Hypodigm: Type plus ten isolated cheek teeth, including two M1/, four M2/, two M/1 and three M/2.

Etymology: *minimus*, (L.) = least, in reference to small size.

Age and distribution: Middle Miocene; locality YGSP 642 in the Kamliyal formation, and locality YGSP 589 in the Chinji formation, Potwar Plateau; also, possibly HGSP localities in the Chinji formation at Banda Daud Shah, Northwest Frontier Province, Pakistan.

Description: A small, low crowned rodent with cusps of both upper and lower molars inflated at the base and slightly rounded.

M1/: Occlusal outline longer than wide, with greatest width posterior to mid-length; anterocone missing on all known specimens; labial cusps elongated transversely, located opposite posterior side of lingual cusps; protoloph and metaloph short and narrow, joining posterior side of the protocone and middle of the hypocone; enterostyle small, joining anterolingual base of the hypocone, and continuous with lingual cingulum; anterior arms of lingual cusps comparatively long and low, directed anteriorly; posterior arms of lingual cusps very short; paracone lacks a posteriorly-directed spur; anterior cingulum indeterminate; lingual cingulum well developed, continuous around protocone; labial cingulum short and low; posterior cingulum descending labially to posterior side of metacone; transverse valley weakly closed

medially, oriented transverse to longitudinal axis; lingual sinus narrow, partly blocked by enterostyle.

M2/: Occlusal outline subtriangular, more narrow and rounded posteriorly; labial cusps elongated transversely; protoloph narrow, joining middle of protocone; metaloph narrow, joining middle (3 specimens) or anterior (1 specimen) hypocone; enterostyle (t/4) minute on lingual cingulum in 2 of 4 specimens; anterior and posterior arms of lingual cusps relatively short and low, with posterior arm of protocone (= posterior mure) most persistent arm; paracone with minute posteriorly-directed spur on 2 of 4 specimens; anterior cingulum long, slightly swollen labially, forming a narrow anterolabial shelf, continuing lingually as the lingual cingulum; lingual cingulum prominent, continuous around protocone in 3 of 4 specimens; labial cingulum low and narrow in 3 of 4 specimens; posterior cingulum narrow, short, weakly joining metacone; transverse valley weakly closed medially, oriented transverse to longitudinal axis; lingual sinus short.

M/1: Occlusal outline much longer than wide, more narrow and rounded anteriorly; anteroconid very small, slightly asymmetrical with lingual wing reduced, located slightly lingual to midline and very close to metaconid; lingual cusps joining labial cusps by short, narrow metalophid and hypolophid; anterior arms of labial cusps very short; posterior arm of protoconid long and low; posterior arm of hypoconid short or absent; labial anterior cingulum long, descends to join base of protoconid; lingual anterior cingulum indistinct; labial cingulum long and low, non-cusped; lingual cingulum short and low; posterior cingulum low; posterolabial shelf shallow; transverse valley weakly closed medially, oriented oblique to longitudinal axis; labial sinusid broad.

M/2: Occlusal outline subrectangular, longer than wide; lingual cusps slightly smaller than labial cusps, joined medially by short, narrow metalophid and hypolophid to anterior side of protoconid and hypoconid; anterior arms of labial cusps short; posterior arms of labial cusps comparatively long, especially the protoconid; anterior cingulum high near midline where joined by metalophid and anterior arm of the protoconid, descending labially and curving posteriorly to form anterolabial shelf anterior to the protoconid; labial cingulum long and low; lingual cingulum short and low; posterior cingulum weakly joining posterior arm of the hypoconid; posterolabial sulcus broad; transverse valley weakly closed medially, oriented slightly oblique to longitudinal axis; labial sinusid wide. Measurements are given in table 7.

Discussion: *Potwarmus minimus* n. sp., differs from *P. primitivus* in smaller size, the enterostyle is smaller, and the longitudinal crest is less reduced. Lingual cingula in upper molars, and labial cingula in lower molars are less continuous or prominent in *P. minimus*, compared to *P. primitivus*.

P. minimus differs from *P. thailandicus* in smaller size; less reduction of the longitudinal crest; better development of the lingual cingulum in upper molars; in having a single-cusped anteroconid in M/1; and less continuous labial cingulum in lower molars.

P. minimus seems more primitive than *P. primitivus* and *P. thailandicus* because it has the longitudinal crest less reduced and smaller size; it may represent the "stem" of the Dendromurinae, possibly derived from a small myocricetodont.

GENERAL CONCLUSIONS

Cricetid rodents were an important component of the south Asian small mammal fauna during the middle Miocene. They are well represented in sediments of the Chinji Formation on the Potwar Plateau of Pakistan, and several Asian species of cricetid show marked similarity to European and African species. In addition, four of the seven cricetid genera included in this study are endemic to southern Asia, as presently understood. Thus, Siwalik cricetids were diverse and abundant during the middle Miocene. They were surely related to cricetids living in Europe and Africa as well as other parts of Asia during the Miocene. However, zoogeographic relationships and phylogenetic affinities of cricetid species from all of these continents need comparison and further study before definitive relationships can be concluded.

Perhaps the most significant biological conclusions about the south Asian cricetid record are ancestry of the Muridae and the subsequent replacement of cricetids by their descendants. These relationships are alluded to but are beyond the main focus of this study. It is hoped the morphologic-descriptive framework utilized in this study is clear and straight forward, so that the data will prove useful and will help to clarify systematic relationships of these small mammals. A further hope is that this study will stimulate additional analyses, that will generate new data for more reliable interpretations of vertebrate evolution.

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TABLES

Table 1. Measurements of *Megacricetodon* species

| <i>Megacricetodon aguilari</i> n. sp. | | | | | | | |
|---|--------|----|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 5 | 1.686 | .063 | 1.60-1.76 | 3.74 | .028 |
| | width | 5 | 1.094 | .060 | 1.05-1.17 | 5.48 | .027 |
| M2/ | length | 6 | 1.180 | .061 | 1.12-1.28 | 5.17 | .025 |
| | width | 8 | 1.054 | .041 | 1.00-1.11 | 3.89 | .014 |
| M3/ | length | 2 | 0.90 | | 0.88-0.92 | | |
| | width | 2 | 1.02 | | 1.01-1.03 | | |
| M/1 | length | 3 | 1.493 | .032 | 1.47-1.53 | | |
| | width | 7 | 0.959 | .078 | 0.84-1.10 | 8.13 | .029 |
| M/2 | length | 7 | 1.224 | .026 | 1.20-1.27 | 2.12 | .010 |
| | width | 8 | 1.015 | .051 | 0.92-1.08 | 5.02 | .018 |
| M/3 | length | 6 | 1.052 | .042 | 1.00-1.10 | 3.99 | .017 |
| | width | 7 | 0.916 | .037 | 0.85-0.96 | 4.04 | .014 |
| <i>Megacricetodon sivalensis</i> n. sp. | | | | | | | |
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 21 | 1.588 | .056 | 1.48-1.69 | 3.53 | .012 |
| | width | 20 | 1.007 | .040 | 0.92-1.08 | 3.97 | .009 |
| M2/ | length | 22 | 1.087 | .059 | 1.00-1.22 | 5.43 | .013 |
| | width | 22 | 0.982 | .047 | 0.90-1.08 | 4.79 | .010 |
| M3/ | length | 2 | 0.905 | | 0.84-0.97 | | |
| | width | 2 | 1.08 | | 1.08 | | |
| M/1 | length | 15 | 1.393 | .056 | 1.30-1.50 | 4.02 | .014 |
| | width | 22 | 0.888 | .026 | 0.82-0.93 | 2.93 | .006 |
| M/2 | length | 24 | 1.119 | .063 | 0.88-1.18 | 5.63 | .013 |
| | width | 24 | 0.935 | .048 | 0.79-1.01 | 5.13 | .010 |
| M/3 | length | 6 | 0.930 | .049 | 0.85-0.99 | 5.27 | .020 |
| | width | 7 | 0.796 | .039 | 0.73-0.85 | 4.90 | .015 |

Table 1. (continued)

| | | <i>Megacricetodon daamsi</i> n. sp. | | | | | |
|-----|--------|---------------------------------------|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 2 | 1.525 | | 1.52-1.53 | | |
| | width | 5 | 0.958 | .039 | 0.90-1.00 | 4.07 | .017 |
| M2/ | length | 2 | 0.995 | | 0.97-1.02 | | |
| | width | 2 | 0.895 | | 0.86-0.93 | | |
| M3/ | length | 4 | 0.858 | .043 | 0.80-0.90 | 5.01 | |
| | width | 4 | 1.015 | .068 | 0.92-1.08 | 6.70 | |
| M1/ | length | 6 | 1.375 | .053 | 1.28-1.42 | 3.85 | .022 |
| | width | 7 | 0.834 | .042 | 0.77-0.88 | 5.00 | .016 |
| M2/ | length | 4 | 1.023 | .048 | 0.97-1.08 | 4.69 | |
| | width | 4 | 0.863 | .068 | 0.79-0.93 | 7.88 | |
| M3/ | length | 2 | 0.815 | | 0.77-0.86 | | |
| | width | 2 | 0.705 | | 0.69-0.72 | | |
| | | <i>Megacricetodon mythikos</i> n. sp. | | | | | |
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 1 | 1.92 | | | | |
| | width | 5 | 1.162 | .112 | 1.02-1.29 | 9.60 | .050 |
| M2/ | length | 1 | 1.47 | | | | |
| | width | 1 | 1.40 | | | | |
| M3/ | length | 2 | 0.95 | | 0.94-0.96 | | |
| | width | 2 | 1.12 | | 1.08-1.16 | | |
| M1/ | length | 1 | 1.76 | | | | |
| | width | 1 | 1.09 | | | | |
| M2/ | length | 1 | 1.44 | | | | |
| | width | 1 | 1.32 | | | | |

Table 2. Measurements of *Punjabemys* species

| <i>Punjabemys downsi</i> n. gen. & n. sp. | | | | | | | |
|---|--------|----|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 12 | 2.053 | .087 | 1.89-2.17 | 4.25 | .025 |
| | width | 14 | 1.392 | .056 | 1.27-1.50 | 4.02 | .015 |
| M2/ | length | 19 | 1.379 | .083 | 1.23-1.51 | 6.02 | .019 |
| | width | 20 | 1.392 | .083 | 1.22-1.52 | 5.96 | .019 |
| M3/ | length | 13 | 1.045 | .087 | 0.85-1.13 | 8.30 | .024 |
| | width | 12 | 1.149 | .063 | 1.02-1.25 | 5.48 | .018 |
| M1/ | length | 9 | 1.884 | .117 | 1.67-2.00 | 6.20 | .039 |
| | width | 11 | 1.275 | .050 | 1.21-1.35 | 3.92 | .015 |
| M2/ | length | 18 | 1.490 | .079 | 1.32-1.58 | 5.30 | .019 |
| | width | 15 | 1.317 | .061 | 1.15-1.38 | 4.63 | .016 |
| M3/ | length | 19 | 1.258 | .068 | 1.12-1.38 | 5.40 | .016 |
| | width | 19 | 1.119 | .069 | 0.97-1.20 | 6.17 | .016 |
| <i>Punjabemys leptos</i> n. gen. & n. sp. | | | | | | | |
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 8 | 1.840 | .120 | 1.58-1.99 | 6.52 | .042 |
| | width | 10 | 1.257 | .066 | 1.12-1.36 | 5.25 | .021 |
| M2/ | length | 7 | 1.299 | .055 | 1.23-1.38 | 4.23 | .021 |
| | width | 7 | 1.244 | .064 | 1.16-1.33 | 5.14 | .024 |
| M3/ | length | 3 | 0.98 | .020 | 0.96-1.00 | | |
| | width | 3 | 1.083 | .029 | 1.05-1.10 | | |
| M1/ | length | 4 | 1.678 | .054 | 1.62-1.75 | 3.22 | |
| | width | 4 | 1.10 | .059 | 1.04-1.18 | 5.36 | |
| M2/ | length | 5 | 1.366 | .038 | 1.31-1.41 | 2.78 | .017 |
| | width | 6 | 1.162 | .091 | 1.04-1.30 | 7.80 | .037 |
| M3/ | length | 3 | 1.15 | .030 | 1.12-1.18 | | |
| | width | 3 | 0.977 | .049 | 0.92-1.01 | | |

Table 2 (continued)

| <i>Punjabemys mikros</i> n. gen. & n. sp. | | | | | | | |
|---|--------|---|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 2 | 1.63 | | 1.60-1.66 | | |
| | width | 3 | 1.03 | .062 | 0.98-1.10 | 6.02 | |
| M2/ | length | 4 | 1.13 | .055 | 1.07-1.19 | 4.87 | |
| | width | 3 | 1.067 | .023 | 1.04-1.08 | | |
| M3/ | length | 2 | 0.94 | | 0.90-0.98 | | |
| | width | 2 | 0.98 | | 0.96-1.00 | | |
| M/1 | length | 1 | 1.50 | | | | |
| | width | 1 | 0.96 | | | | |
| M/2 | length | 2 | 1.28 | | 1.25-1.31 | | |
| | width | 2 | 1.105 | | 1.07-1.14 | | |
| M/3 | length | 4 | 1.043 | .061 | 0.97-1.12 | 5.87 | |
| | width | 4 | 0.933 | .075 | 0.82-0.98 | 8.04 | |

Table 3. Measurements of *Myocricetodon* species

| <i>Myocricetodon sivalensis</i> n. gen. & n. sp. | | | | | | | |
|--|--------|----|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 4 | 1.658 | .059 | 1.58-1.72 | 3.56 | .030 |
| | width | 8 | 0.994 | .072 | 0.93-1.15 | 7.24 | .025 |
| M2/ | length | 6 | 1.208 | .028 | 1.18-1.25 | 2.32 | .011 |
| | width | 6 | 1.075 | .058 | 0.96-1.12 | 5.40 | .024 |
| M/1 | length | 8 | 1.424 | .059 | 1.33-1.49 | 4.14 | .021 |
| | width | 8 | 0.943 | .047 | 0.84-1.00 | 5.03 | .017 |
| M/2 | length | 12 | 1.252 | .031 | 1.20-1.31 | 2.48 | .009 |
| | width | 13 | 1.03 | .037 | 0.95-1.08 | 3.59 | .010 |

| <i>Myocricetodon</i> sp. A | | | | | | | |
|----------------------------|--------|---|-----------|--|-----------|--|--|
| | | N | \bar{X} | | O.R. | | |
| M1/ | length | 1 | 1.83 | | | | |
| | width | 2 | 1.075 | | 1.07-1.08 | | |

Table 4. Measurements of *Dakkamyoides* species

| | | <i>Dakkamyoides lavocati</i> n. gen. & n. sp. | | | | | |
|-----|--------|--|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 2 | 2.00 | | 1.92-2.08 | | |
| | width | 4 | 1.235 | .034 | 1.20-1.28 | 2.77 | |
| M2/ | length | 4 | 1.34 | .041 | 1.31-1.40 | 3.06 | |
| | width | 4 | 1.193 | .034 | 1.16-1.24 | 2.85 | |
| M/1 | length | 3 | 1.707 | .064 | 1.66-1.78 | | |
| | width | 4 | 1.098 | .071 | 1.00-1.16 | 6.50 | |
| M/2 | length | 3 | 1.31 | .066 | 1.24-1.37 | | |
| | width | 4 | 1.105 | .044 | 1.04-1.13 | 3.94 | |
| M/3 | length | 2 | 1.02 | | 1.00-1.04 | | |
| | width | 2 | 0.965 | | 0.96-0.97 | | |
| | | <i>Dakkamyoides perplexus</i> n. gen. & n. sp. | | | | | |
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 1 | 1.84 | | | | |
| | width | 3 | 1.037 | .051 | 0.98-1.08 | | |
| M2/ | length | 1 | 1.21 | | | | |
| | width | 1 | 1.12 | | | | |
| M/1 | length | 1 | 1.68 | | | | |
| | width | 1 | 1.12 | | | | |

Table 5. Measurements of *Dakkamys* species

| | | <i>Dakkamys asiaticus</i> n. gen. & n. sp. | | | | | |
|-----|--------|--|-----------|------|-----------|---|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 2 | 2.45 | | 2.42-2.48 | | |
| | width | 3 | 1.527 | .076 | 1.44-1.58 | | |
| M2/ | length | 1 | 1.67 | | | | |
| | width | 1 | 1.56 | | | | |
| M3/ | length | 2 | 0.95 | | 0.92-0.98 | | |
| | width | 2 | 1.03 | | 0.98-1.08 | | |

Table 5. (continued)

| | | <i>Dakkamys barryi</i> n. gen. & n. sp. | | | | | |
|-----|--------|---|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | 3 | 2.34 | .036 | 2.31-2.38 | | |
| | width | 3 | 1.477 | .076 | 1.39-1.53 | | |
| M2/ | length | 3 | 1.633 | .112 | 1.55-1.76 | | |
| | width | 3 | 1.42 | .044 | 1.39-1.47 | | |
| M3/ | length | 2 | 0.87 | | 0.84-0.90 | | |
| | width | 2 | 1.005 | | 0.98-1.03 | | |
| M/1 | length | 2 | 1.985 | | 1.93-2.04 | | |
| | width | 2 | 1.25 | | 1.25 | | |
| M/2 | length | 1 | 1.43 | | | | |
| | width | 1 | 1.26 | | | | |
| M/3 | length | 1 | 0.98 | | | | |
| | width | 1 | 1.02 | | | | |
| | | <i>Dakkamys</i> sp. indet. | | | | | |
| | | N | \bar{X} | S | O.R. | V | S_x |
| M/1 | length | 2 | 1.41 | | 1.37-1.45 | | |
| | width | 3 | 0.897 | .059 | 0.83-0.94 | | |
| | | <i>?Dakkamys</i> sp. | | | | | |
| | | N | \bar{X} | S | O.R. | V | S_x |
| M/1 | length | 1 | 1.60 | | | | |
| M/2 | length | 4 | 1.345 | .019 | 1.32-1.36 | 1.41 | |
| | width | 3 | 1.113 | .025 | 1.09-1.14 | | |
| M/3 | length | 1 | 0.97 | | | | |
| | width | 1 | 0.82 | | | | |

Table 6. Measurements of *Paradakkamys chinjiensis* n. gen. & n. sp.

| | | N | \bar{X} | S | O.R. | V | S_x |
|-----|--------|---|-----------|------|-----------|------|-------|
| M1/ | length | 2 | 1.79 | | 1.70-1.88 | | |
| | width | 3 | 1.017 | .055 | 0.98-1.08 | | |
| M2/ | length | 3 | 1.11 | .056 | 1.05-1.16 | | |
| | width | 3 | 0.923 | .006 | 0.92-0.93 | | |
| M/1 | length | 3 | 1.473 | .012 | 1.46-1.48 | | |
| | width | 3 | 0.873 | .050 | 0.82-0.92 | | |
| M/2 | length | 8 | 1.166 | .064 | 1.12-1.29 | 5.49 | .023 |
| | width | 9 | 0.984 | .055 | 0.92-1.08 | 5.59 | .018 |
| M/3 | length | 2 | 0.945 | | 0.89-1.00 | | |
| | width | 2 | 0.98 | | 0.94-1.02 | | |

Table 7. Measurements of *Potwarmus* species

| <i>Potwarmus primitivus</i> n. gen. | | | | | | | |
|-------------------------------------|--------|---|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M/1 | length | 2 | 1.56 | | 1.56 | | |
| | width | 3 | 1.023 | .059 | 0.98-1.09 | | |
| M2/ | length | 1 | 1.18 | | | | |
| | width | 1 | 1.08 | | | | |
| M/1 | length | 4 | 1.338 | .033 | 1.30-1.37 | 2.47 | |
| | width | 4 | 0.903 | .026 | 0.88-0.94 | 2.91 | |
| M/2 | length | 1 | 1.21 | | | | |
| | width | 2 | 1.005 | | 0.97-1.04 | | |
| M/3 | length | 2 | 0.88 | | 0.84-0.92 | | |
| | width | 3 | 0.857 | .051 | 0.80-0.90 | | |

Table 7. (continued)

| | | <i>Potwarmus minimus</i> n. gen. & n. sp. | | | | | |
|-----|--------|---|-----------|------|-----------|------|-------|
| | | N | \bar{X} | S | O.R. | V | S_x |
| M1/ | length | | | | | | |
| | width | 2 | 0.955 | | 0.93-0.98 | | |
| M2/ | length | 4 | 1.06 | .063 | 0.99-1.14 | 5.92 | |
| | width | 4 | 0.95 | .035 | 0.92-1.00 | 3.64 | |
| M/1 | length | 2 | 1.185 | | 1.16-1.21 | | |
| | width | 2 | 0.785 | | 0.76-0.81 | | |
| M/2 | length | 2 | 1.10 | | 1.08-1.12 | | |
| | width | 3 | 0.92 | .040 | 0.88-0.96 | | |

LEGENDS OF PLATES

PLATE 1

Fig. a-i: *Megacricetodon aguilari* new species

- | | |
|-------------------------------|-------------------------------|
| a. left M1/ 592/19563 (37X); | f. left M/3 591/19582 (37X); |
| b. left M2/ 592/19671 (37X); | g. right M/2 642/24613 (40X); |
| c. right M3/ 680/24567 (39X); | h. left M/1 592/19513 (36X); |
| d. left M1/ 592/19562 (35X); | i. left M/3 642/24592 (37X). |
| e. left M/1 642/24569 (37X); | |

Fig. j-o: *Megacricetodon sivalensis* new species

- | | |
|------------------------------|------------------------------|
| j. left M1: 491/19168 (34X); | m. left M/1 491/19200 (37X); |
| k. left M2/ 491/19177 (36X); | n. left M/2 491/19510 (37X); |
| l. left M/2 491/19511 (38X); | o. left M/3 491/19223 (35X). |

PLATE 2

Fig. a-c: *Megacricetodon sivalensis* new species

- | |
|-------------------------------|
| a. left M1/ 491/19231 (40X); |
| b. left M/1 491/19196 (48X); |
| c. right M/3 491/19224 (38X). |

Fig. d-k: *Megacricetodon daamsi* new species

- | | |
|-------------------------------|-------------------------------|
| d. left M1/ 668/24600 (36X); | h. right M/1 491/19529 (38X); |
| e. left M1/ 41/19525 (34X); | i. left M/2 641/19664 (39X); |
| f. right M2/ 491/19528 (37X); | j. right M/3 491/19221 (37X); |
| g. left M3/ 491/19240 (34X); | k. right M/1 491/19507 (38X). |

PLATE 3

Fig. a-e: *Megacricetodon mythikos* new species

- | | |
|-------------------------------|-------------------------------|
| a. right M2/ 491/19557 (40X); | d. left M/2 668/19350 (41X); |
| b. right M1/ 501/19556 (38X); | e. right M/1 589/19570 (37X). |
| c. left M3/ 491/19189 (36X); | |

Fig. f-j: *Punjabemys downsi* new genus and new species

- | | |
|-------------------------------|-------------------------------|
| f. left M/1 430/19120 (38X); | i. left M/2 430/19132 (34X); |
| g. right M/1 430/19119 (34X); | j. right M/3 430/19145 (39X). |
| h. left M/2 430/19127 (39X); | |

PLATE 4

Fig. a-f: *Punjabemys downsi* new genus and new species

- | | |
|------------------------------|-------------------------------|
| a. left M1/ 430/19078 (36X); | d. right M2/ 430/19102 (41X); |
| b. left M1/ 430/19074 (37X); | e. left M3/ 430/19097 (38X); |
| c. left M2/ 430/19085 (39X); | f. left M3/ 430/19114 (39X). |

Fig. g-i: *Punjabemys leptos* new genus and new species

- g. right M/1 430/19517 (36X);
 h. left M/2 641/19639 (39X);
 i. right M/1 680/19644 (39X).

PLATE 5

Fig. a-h: *Punjabemys leptos* new genus and new species

- | | |
|-------------------------------|-------------------------------|
| a. left M1/ 668/19620 (39X); | e. left M3/ 668/19629 (39X); |
| b. right M1/ 665/19588 (36X); | f. right M3/ 665/19632 (47X); |
| c. left M2/ 668/19622 (41X); | g. left M/2 665/19636 (39X); |
| d. left M2/ 665/19628 (39X); | h. right M/3 668/19612 (41X). |

Fig. i: *Punjabemys downsi* new genus and new species

- i. left M/3 430/19151 (37X).

PLATE 6

Fig. a-f: *Punjabemys mikros* new genus and new species

- | | |
|-------------------------------|------------------------------|
| a. right M3/ 640/24560 (37X); | d. left M/1 501/19524 (37X); |
| b. right M2/ 642/19606 (46X); | e. left M/2 640/19609 (38X); |
| c. right M1/ 592/19601 (39X); | f. left M/3 668/19642 (39X). |

Fig. g-m: *Myocricetodon sivalensis* new species

- | | |
|-------------------------------|-------------------------------|
| g. left M1/ 592/19566 (39X); | k. left M/2 592/24636 (38X); |
| h. left M2/ 592/24627 (41X); | l. right M/1 591/24616 (32X); |
| i. right M2/ 592/19569 (37X); | m. right M/1 592/24632 (35X). |
| j. right M1/ 592/19576 (36X); | |

PLATE 7

Fig. a-h: *Dakkamyoides lavocati* new genus and new species

- | | |
|-------------------------------|-------------------------------|
| a. right M1/ 491/19227 (36X); | e. right M2/ 491/19236 (39X); |
| b. right M1/ 491/19229 (39X); | f. left M/1 491/19534 (38X); |
| c. right M2/ 491/19237 (39X); | g. right M/1 491/19244 (36X); |
| d. right M/2 491/19254 (38X); | h. left M/3 491/19256 (37X). |

Fig. i: *Myocricetodon* sp.

- i. right M1/ 592/24648 (40X).

PLATE 8

Fig. a-c: *Dakkamyoides perplexus* new genus and new species

- a. left M1/ 668/24651 (39X);
 b. left M2/ 641/24556 (38X);
 c. left M/1 668/24599 (39X).

Fig. d-k: *Paradakkamys chinjiensis* new genus and new species

- | | |
|-------------------------------|------------------------------|
| d. right M/1 504/24659 (39X); | h. right M1/ 76/24656 (39X); |
| e. right M2/ 504/24657 (40X); | i. left M/1 504/24658 (35X); |
| f. right M1/ 504/24667 (37X); | j. left M/2 504/24661 (40X); |
| g. right M2/ 636/19539 (35X); | k. left M/3 76/24663 (38X). |

PLATE 9

Fig. a-c: *Dakkamys asiaticus* new species

- a. left M1/ 76/19541 (35X);
 b. left M2/ 259/24665 (38X);
 c. left M3/ 259/19543 (36X).

Fig. d-h: *Dakkamys barryi* new species

d. left M1-3/ 726/24722 (21X);
 e. left M/1-3 726/24719 (20X);
 f. right M1-3/ 726/24717 (20X);

g. left M/1 726/24720 (39X);
 h. left M/2 491/19252 (35X).

Fig. i: *Dakkamys* sp.

i. left M/1 259/19247 (38X).

Fig. j: ?*Dakkamys* sp.

j. left M/3 259/19257 (35X).

PLATE 10

Fig. a-e: *Potwarmus primitivus* new genus

a. right M1/ 589/19546 (38X);
 b. left M2/ 709/24718 (35X);
 c. left M1/ 589/19549 (38X);

d. right M/2 592/19577 (36X);
 e. right M/1 589/19552 (36X).

Fig. f-m: *Potwarmus minimus* new genus and new species

f. right M2/ 642/24614 (35X);
 g. right M1/ 642/24608 (37X);
 h. right M/1 642/24610 (37X);
 i. left M1/ 709/24723 (32X);

j. left M2/ 589/19550 (35X);
 k. right M/2 642/24605 (35X);
 l. left M/1 589/19555 (37X);
 m. left M/2 642/24603 (38X).

