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Late Oligocene and Early Miocene Muroidea of the Zinda Pir Dome

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A series of Oligocene through Early Miocene terrestrial deposits preserved in the foothills of the Zinda Pir Dome of western Pakistan produce multiple, superposed fossil mammal localities. These include small mammal assemblages that shed light on the evolution of rodent lineages, especially Muroidea, in South Asia. Nine small mammal localities span approximately 28–19 Ma, an interval encompassing the Oligocene–Miocene boundary. The Early Miocene rodent fossil assemblages are dominated by muroid rodents, but muroids are uncommon and archaic in earlier Oligocene horizons. The Zinda Pir sequence includes the evolutionary transition to modern Muroidea at about the Oligocene–Miocene boundary. We review the muroid record for the Zinda Pir Dome, which includes the early radiation of primitive bamboo rats (Rhizomyinae) and early members of the modern muroid radiation, which lie near crown Cricetidae and Muridae. The Zinda Pir record dates diversification of modern muroids in the Indian Subcontinent and establishment by 19 Ma of muroid assemblages characteristic of the later Siwaliks.

Keywords: Cricetidae; Muroidea; Pakistan; Oligocene; Miocene

Introduction

Profound changes occur in muroid rodents during the Oligocene Epoch. Morphologic features in muroids of cricetid grade from Eocene and Oligocene deposits differ markedly from those of modern Cricetidae from Miocene and younger deposits (Flynn et al. 1985). Changes of modern grade include (1) incisors with thin enamel, rounding half way around the labial side, to flat incisors with thicker enamel and an angular labial shoulder; (2) transformation of the zygoma (Vianey-Liaud 1974, 1979, 1985) from rodents with a large infraorbital foramen and hystricomorphous structure, or with a basally constricted infraorbital foramen and slightly upturned zygomatic plate, to myomorphous rodents with a narrow, slit-like and near-vertical zygomatic plate constricting the lower infraorbital foramen, and the lateral masseter muscle expanded onto the anterior surface of the zygomatic plate and (3) rodents with low crowned, cuspate molars replaced by genera with lophate and high crowned to ever-growing molars. Herein, muroids showing primitive character states are considered 'archaic'; muroids with derived conditions are 'modern'.

Unfortunately the patterns of these changes are poorly documented, in part due to lack of research on incisors, because the zygomatic structure of Oligocene and earlier rodent skulls are rarely preserved, and due to limited sample sizes. Development of new research techniques primarily by Wighart von Koenigswald and colleagues (e.g. von Koenigswald 1985; Kalthoff 2000) has provided detailed knowledge of the evolution of enamel 'schmelzmuster' in mammalian teeth including incisors. While rare, early rodent skulls clearly show that the primitive zygoma of cricetid rodents was hystricomorphous with a large infraorbital foramen and a flat zygomatic plate. Small sample sizes limit observations that can be made on key taxa, for example the Early Miocene *Spanocricetodon ningensis* based on a single dentary with m1–3 (Li 1977). Key work in the Murree Formation, northern Pakistan, yielded for de Bruijn et al. (1981) 24 isolated teeth of the primitive cricetid *Primus microps*, along with *Spanocricetodon lii* (14 teeth) and *S. khani* (46 isolated teeth). Small sample sizes have made it difficult to evaluate what features are stable and therefore characteristic of Oligocene and Early Miocene rodents.

In contrast, Fahlbusch (1964) published a thorough analysis of Miocene cricetids from Bavaria with a sample of 1019 teeth, listing two new genera (*Democricetodon* and *Megacricetodon*) and eight new species (including three subspecies that were later raised to species). Knowledge of Oligocene rodents continues to improve rapidly, primarily because of the collection of large fossil samples. Maridet et al. (2011) made a thorough analysis of the genus *Spanocricetodon* Li (1977) in characterizing *Democricetodon sui* and clarifying the stratigraphic appearance of the well-known genus *Democricetodon* Fahlbusch (1964).

Another phenomenon characterizes the transition between primitive and modern cricetid rodents: changes in the loph (ridge of enamel) that connects the anterior main cusps in first molars. In primitive cricetid rodents the loph uniting the protoconid and the metaconid in the lower first molar has its origin on the posterior part of the protoconid,

and in modern cricetid rodents the loph uniting the protoconid and metaconid has its origin anteriorly on the protoconid (see Flynn et al. 1985). The morphological change, involving loss of a strong connection between two salient cusps, followed by a new connection between these same two cusps was a long and tedious process, involving multiple trials spanning millions of generations of rodents. This transition, recognized in the Late Oligocene/Early Miocene record of fossil cricetid rodents, can be identified by the presence of two lophs directed transversely between the paracone and metacone in upper cheek teeth and between the metaconid and entoconid in lower cheek teeth (Figure 1). In Europe this transition is seen in *Para-cricetodon* and *Heterocricetodon*; in Asia it is seen in *Eucricetodon*; in North America it is seen in *Leidymys*. The transition is nearly completed with the appearance of

Democricetodon in Eurasia and *Copemys* in North America; *Primus* is part of that transition. If two lophs occur in the middle of the molar, the anterior one can be identified as a spur from the posterior arm of the protocone (upper tooth) or protoconid (lower tooth) and the posterior loph can be identified as a true mesoloph (upper tooth) or mesolophid (lower tooth). This can be complex, leading Maridet et al. (2009) to recognize a 'second mesoloph' and 'second mesolophid,' a rare feature characteristic of the transition.

Herein we describe and characterize Oligocene and Early Miocene muroid fossils including 44 new teeth of *Primus microps,* a new species of *Primus* based on 153 specimens, and 68 molars of *Democricetodon khani*. The new samples come from the Zinda Pir Dome, western Pakistan (map: Figure 1 of Lindsay et al. 2005, 2015),
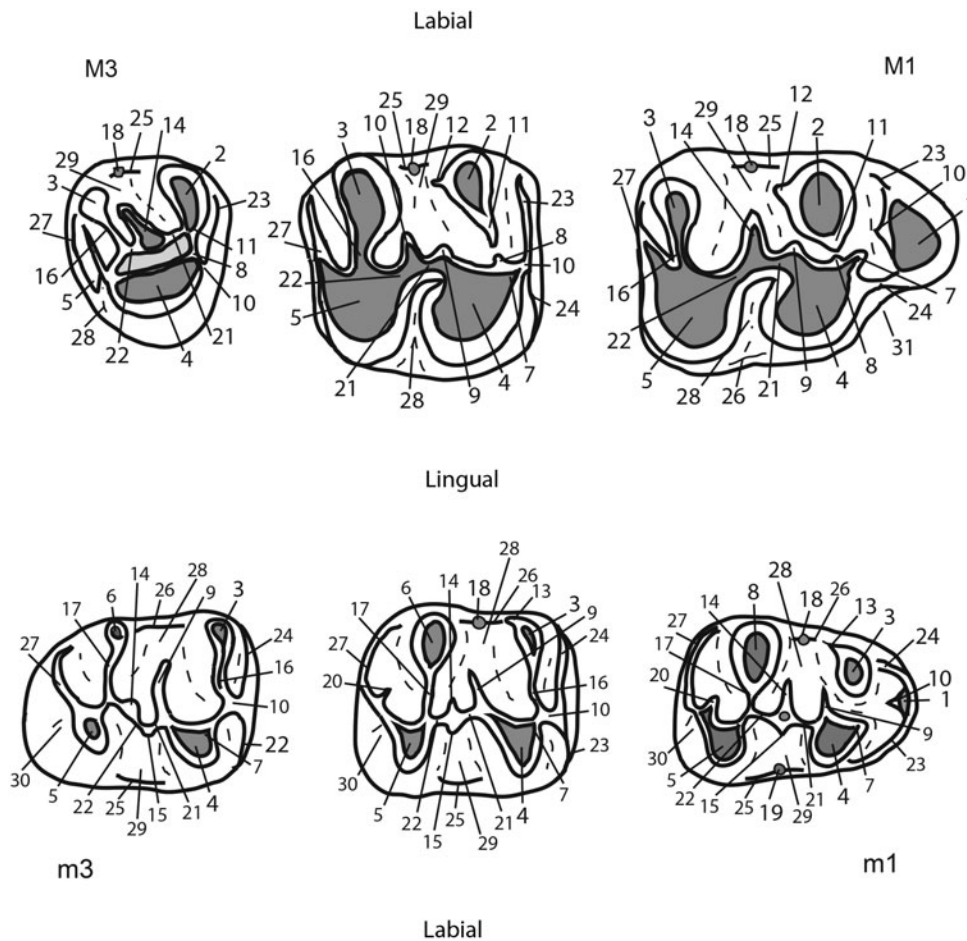

Figure 1.   Dental terminology for muroid rodents, upper molars (M1-M3) above and lower molars (m1-m3) below. Anterior to right; lingual and labial directions indicated. (1) Anterocone (-id), (2) Paracone, (3) Metacone (-id), (4) Protocone (-id), (5) Hypocone (-id), (6) Entoconid, (7) Protocone (-id) anterior arm, (8) Protoloph I, (9) Protoloph (-id) II or protoconid posterior arm, (10) Anteroloph (-id), (11) Paraloph, (12) Paracone posterior spur, (13) Metaconid lingual spur, (14) Mesoloph (-id), (15) Ectolophid, (16) Metaloph (-id), (17) Entolophid , (18) Mesostyle (-id), (19) Ectostyle (-id), (20) Hypoloph (-id), (21) Anterior mure, (22) posterior mure, (23) Anterior labial cingulum, (24) Anterior lingual cingulum, (25) Labial cingulum, (26) Lingual cingulum, (27) Posterior cingulum, (28) Lingual sinus or lingual transverse valley, (29) Sinusid or labial transverse valley, (30) Posterior labial sulcus, (31) Anterolingual notch.

collected over the years 1988–2000 in collaboration with the Pakistan Museum of Natural History (PMNH). The Zinda Pir Dome area stratigraphy and paleomagnetic dating has been presented in Lindsay et al. (2005) and Flynn et al. (2013). Zinda Pir localities span the Oligocene – Miocene boundary (Figure 2). Our descriptions take advantage of Maridet et al. (2011) thorough review of *Democricetodon* and *Spanocricetodon*, and casts of *Primus microps, Spanocricetodon lii* and *S. khani,* kindly provided by Hans de Bruijn.

Methods

Complete lists of specimens referred to taxa are available as Supplemental Online Material. Supplemental Tables 1– 5 include specimen numbers and localities with maximum

length and width measurements in occlusal view (see measuring scheme in Figure 6.2 of Wessels 2009). Fossil material, currently under study at the University of Arizona, Tucson AZ, USA, is on loan from the Pakistan Museum of Natural History (PMNH), Islamabad, Pakistan. We also cite specimens collected previously by the Howard University-Geological Survey of Pakistan (H-GSP) collaborative team.

Muroids are exceedingly rare in the older part of the Zinda Pir and Bugti sections (Cocu et al. 1999). They dominate assemblages from the upper part of the Chitarwata Formation and Vihowa Formation (Lindsay et al. 2005). We use the Superfamily Muroidea to designate those rodents with cheek dentition reduced to molars only. Diverse Muroidea of modern grade (three
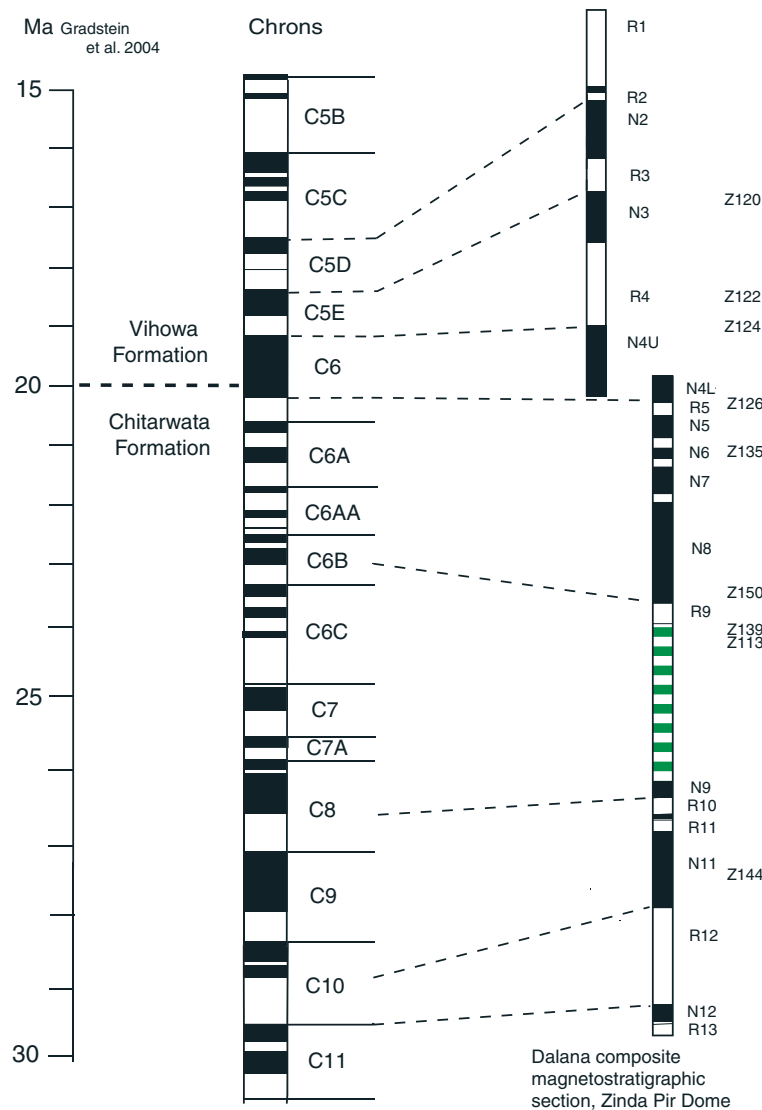

Figure 2. Magnetostratigraphy and timescale for the Zinda Pir Dome, with correlation of key small mammal fossil localities. Magnetozones for the Vihowa and Chitarwata Formations, with fossil localities (Z numbers) are plotted on the right, with correlation to the Geomagnetic Polarity Time Scale on the left. Figure adapted from Flynn et al. 2013.
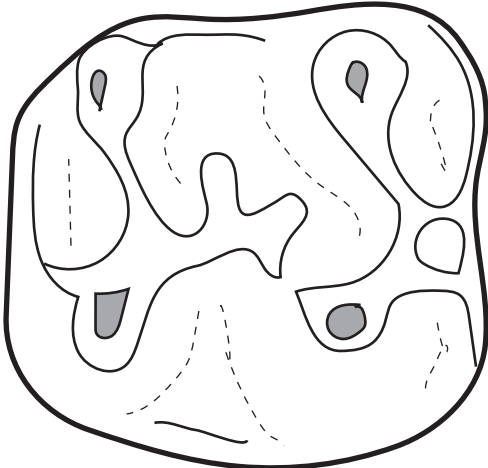
Figure 3. Line drawing of PMNH specimen 2127, *Atavocricetodon* sp., upper molar from locality Z144. Anterior to right; scale bar is 1 mm.

features specified above) dominate the younger Siwalik assemblages, and we see the origin of Siwalik faunas in the Zinda Pir record. Modern muroids include extant families, but the assignment of many Early Miocene genera to crown groups remains controversial, largely because they are stem taxa. We present the alpha taxonomy of the Zinda Pir muroids as a necessary first step prior to resolving higher level systematics.

Systematic paleontology
Rodentia Bowdich 1821
Eucricetodontinae Mein and Freudenthal 1971
Atavocricetodon Freudenthal 1996

Atavocricetodon sp. right M2, PMNH 2127 from locality Z144, Oligocene, lower part of the Chitarwata Formation (Figure 3).

Description. Occlusal outline squared, with length (0.96 mm) nearly equal to width (1.02) and cusps rather high and slender; lingual cusps slightly larger than labial cusps, and labial cusp positions are opposite the anterior side of lingual cusps (little offset of cusps). Long protocone arm continuous with the narrow paraloph that descends from the paracone. Protocone posterior arm is relatively short, bifurcating to form a short protocone spur and the anterior mure. Long hypocone anterior arm is directed labially to join the posterior mure and the narrow mesoloph near the midline. Short hypocone posterior arm continues labially at the posterior midline as a high and narrow posterior cingulum joining the metacone. The short anteroloph is located well lingual to the midline on the narrow and low anterior cingulum. The medium length metaloph is directed posteriorly from the mure it descends lingually from the metacone to join the posterior mure and the hypocone arm near the midline. The lingual cingulum is moderately high; labial cingulum low and moderately long, ascending the anterior metacone where it terminates. The lingual sinus, squared near the midline, expands near the lingual margin. Lingual anterior cingulum is long, curves posteriorly and continues to join the protocone base. The long labial anterior cingulum curves gently posteriorly from the midline to terminate near the labial margin and enclose a shallow, narrow anterolabial atoll. Roots are not preserved.

Comment. Assignment to tooth locus is tentative, but the single tooth is consistent with M2 of *Atavocricetodon paaliense* Cocu et al. 1999 This molar represents a rare element in the early to mid-Oligocene assemblages of the Indian Subcontinent. It is the only muroid tooth from locality Z144, which occurs in a long normal magneto-zone, possibly correlated with Chron 9, although Chron 8 or Chron 10 cannot be ruled out. Cocu et al. (1999) brought attention to the rare occurrence of primitive muroids in their study of the Early Oligocene fauna of Paali, Bugti, to the southwest of the Zinda Pir Dome, in Baluchistan. The rarity of archaic muroids stands in stark contrast to the diverse and dominant Muroidea of the Indian subcontinent at the debut of the Miocene.

Rhizomyinae Winge 1887
Prokanisamys De Bruijn, Hussain, Leinders 1981

Included species. *Prokanisamys arifi* de Bruijn et al. 1981 (type species), *Prokanisamys major* Wessels and de Bruijn 2001, *Prokanisamys benjavuni* (Mein and Ginsburg 1985), *Prokanisamys kowalskii* (Lindsay 1996).

Comment. De Bruijn et al. (1981) created this genus for primitive bamboo rats from Early Miocene deposits in Pakistan. Since then, the genus has been recognized in the Potwar Plateau, Pakistan, and in Thailand, where *P. benjavuni* was first named as a species of *Kanisamys* (Mein and Ginsburg 1985). Family level systematics for Rhizomyinae are controversial because molecular data indicate relationship with spalacine rodents. For the present, we follow de Bruijn et al. (in press) who withhold judgement on family designation. We also agree with Wessels and de Bruijn (2001) that *Eumyarion kowalskii* should be transferred to *Prokanisamys* and new materials here inform us of the extent of variation within the species.

Prokanisamys kowalskii (Lindsay 1996)
Material. From Z113, PMNH 679–716, 718–744 1096–1098, 2443 (16 M1, 17 M2, 9 M3, 8 m1, 10 m2, 11 m3); from Z135, PMNH 716, 799, 2250, 2252–2256

(M1, M3, m1, three M2, two m2); from Z139, 2208, 2216–2218 (M2, m3, two m2); from Z150, PMNH 2165, 2167–2171, 2176, 2179, 2182, 2184, 2192 (M3, two M1, five m1, three m3).

Discussion. Here we report more specimens from more localities than previously available. The species is low crowned with weak lophodonty, and it is a large species for the genus. M1 (mean length 2.29 mm in Lindsay 1996) has inflated paracone and metacone, and a prominent anterolingual sulcus. There is a thin posteroloph and the mesoloph is minute to short, although in one specimen it touches the swollen metacone. The anterocone is weakly bifurcated and asymmetrical. There are three roots, although the large lingual root tends to be split. M2 is similar except in lacking the anterocone and its mesoloph is relatively stronger; tooth length is often greater than width. M3 is rounded due to the reduced hypocone and metacone, and the mesoloph is relatively longer than in M1–2. The lingual sinus, almost eliminated in some specimens, is closed after wear by a continuous wall. Lower m1 has a short mesolophid and variable connection between metaconid and protoconid; a thin loph from the metaconid (rather than the anterolophid) intersects the anteroconid directly. This two-rooted tooth is longer than m2 or m3, but narrower than m2. The latter tooth has a strong anterior cingulum elevated to the height of other crests. Its mesolophid is short and well separated from the hypolophid. The lower third molar is relatively short, rounded posterolingually due to its reduced entoconid and its anterior cingulum is thinner than in m2. The m3 mesolophid is longer than in other lower molars, directed posterolingually, and is separated from the hypolophid.

Prokanisamys kowalskii is the only representative of its genus in the latest Oligocene site Z113, and it is the least lophodont rhizomyine recognized. Like other *Prokanisamys, P. kowalskii* is low crowned and m3 is small relative to the other molars (m3 is large in most rhizomyines). In addition, m1 is shortened relative to other Oligocene muroids, and this feature is shared by later rhizomyines. *P. kowalskii* presents features primitive for rhizomyines: generally undeveloped mesoloph (-id) in anterior molars, strong anterior cingulum in m2–3, mesolophid separate from hypolophid, weak and variable metaconid-protoconid connection in m1. *P. kowalskii* is considerably larger than the younger *P. arifi*, which may argue against ancestor-descendant relationship, but close affinity is indicated by the analysis of López-Antoñanzas et al. (2013).

Prokanisamys arifi De Bruin et al. 1981

Holotype. H-GSP 22, right m1 from Banda Daud Shah, Murree Formation, northern Pakistan

Additional Material. From Z124, PMNH 600, 694 (two M1) and 2003, 2315 (two m1); from Z126, PMNH 746

(m1), 747–748 (two m3), 749 (M3); from Z120, PMNH 591, 2416, 2417 (three M1), 2418, 2420 (two M2), 2422, 2423 (two m1), 320, 2424–2427 (five m2), 2428, 2429 (two m3); from Z122, PMNH 2317, 2318, 2320, 2323 (four M1), 596, 2325, 2326, 2328, 2407 (five M2), 583, 2331, 2332, 2408 (four M3), 331, 2334, 2352, 2409, 2410 (five m1), 784, 2341, 2342, 2346, 2411, 2412 (six m2), 2349, m3.

Comment. The specimens from the older sites (Z126, Z124; 20–19 Ma) match well the hypodigm of *Prokanisamys arifi* from the Murree Formation at Banda Daud Shah. *P. arifi* co-occurs with *P. major* at the younger sites, Z 122 and Z 120, where some of the *P. arifi* specimens seem to be a little larger than the original sample from Banda Daud Shah. Still, these are considerably smaller than *P. major*. If the samples are indicative of the paleocommunity, then *Prokanisamys arifi* was more abundant than *P. major*.

Prokanisamys major Wessels and de Bruin 2001

Holotype. H-GSP 4522, left M1 from Lower Manchar Formation, Sind, Pakistan

Additional Material. From Z120, PMNH 382 (m3) and 2419 (M2); from Z122, PMNH 2319, 2322 (two M1), 2327, 2329 (two M2), 2430 (M3), 2333, 2337 (two m1), 2324, 2335, 2336, 2338, 2339, 2343, 2413, 2432 (eight m2), 2347, 2350, 2351 (three m3). All Early Miocene.

Comment. This species is considerably larger than *P. arifi*. Named for fossils from the Manchar Formation (Wessels and de Bruijn 2001), it appears in the Vihowa Formation and persists into the lower part of the Kamlial Formation in the Potwar Plateau.

Prokanisamys sp

Material. From Z120, PMNH 543 (m3) and 2415 (m2); from Z122 PMNH 2340, 2414 (two m2) and 2348 (m3), Early Miocene.

Comment. These teeth are smaller than the lower end of the size range reported for *P. arifi* by Wessels and de Bruijn (2001). For example, well-preserved m3 PMNH 2348 length × width = 1.2 × 0.95 mm. These teeth are too small for inclusion in *P. arifi*, but interestingly co-occur with specimens listed above under *P. arifi*.

Unnamed rhizomyine

Material. From Z122 PMNH 2433, left m3, 2344 (m2 or m3), 2345 (m1), PMNH 2431 (M3 fragment), 2330 (M2), 2321 (M1); also from Z135, PMNH 2251, partial m1. Early Miocene, Zinda Pir Dome, western Pakistan (Figure 4).

Description. M1 (~2.9 × 2.4 mm) is represented by a single heavily worn tooth. Features are nearly obliterated,
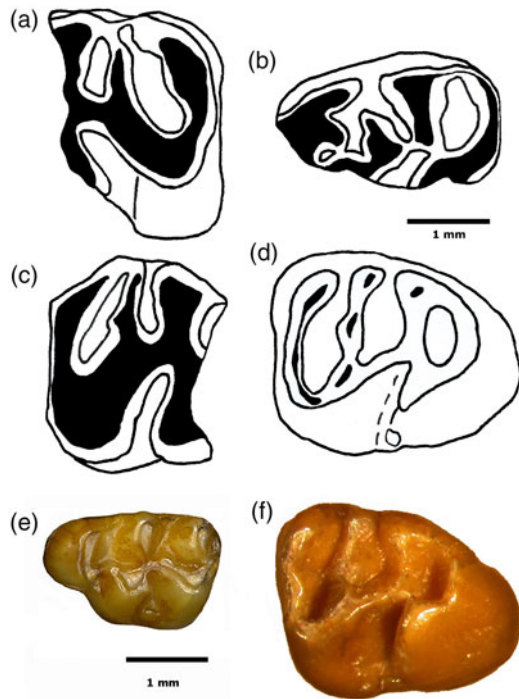
Figure 4. Early Rhizomyinae. Line drawings (a-d) of large body-size species from locality Z122: (a) M2 PMNH 2330, (b) m1 PMNH 2345, (c) m3 or m2 PMNH 2344, (d) m3 PMNH 2433. Lophodonty of *P. kowalskii* M1 PMNH 678 (e) compared to that of larger m3 PMNH 2433, (f) anterior to left.

but the anteroloph with broad anterocone, and the metaloph including metacone are distinguishable. A median transverse loph represents a broad paraloph and probably a long mesoloph fused with it. There is a distinct anterolingual sulcus. There are three roots, including a large, longitudinally expanded, lingual root. M2 ($>$2.4 × 2.7 mm), broken, has length under-represented. Its long, separate mesoloph terminates short of the buccal wall of the tooth. Metacone is merged into the relatively narrow posteroloph. Likely there were four roots. The fragmentary M3 has a distinct mesoloph and small metacone.

The first lower molar represented by PMNH 2345 is abraded and missing anterior enamel, so that its length of 2.8 mm is underestimated. The anteroconid and metaconid (with posterolingual spur) are worn and fused. The protoconid connects anteriorly to this complex; a direct metaconid-protoconid bridge is incomplete. The irregular mesolophid is midway between the protoconid and broad hypolophid, and terminates well short of the lingual wall. A lingual spur running posteriorly from the hypolophid is continuous with the posterolophid. An anterior m1 fragment from Z135, PMNH 2251, attests to earlier Miocene presence of the species. This tooth shows an incomplete metaconid-protoconid bridge and a short mesolophid.

PMNH 2344 is heavily worn and broken ($>$2.5 × 2.75 mm). It most likely represents m3 because it

appears to have had an expanded posterior root. Although worn, it shows no evidence of an anterior cingulum. The complete mesolophid with an anterior spur is located about midway between metalophid and hypolophid. A distinctive feature is the deep sinus that crosses half the tooth. PMNH 2433, slightly worn m3 (2.95 × 2.55 mm) would be bigger than m1 if preserved teeth are representative of the species. It has narrow, high lophs, no indication of anterior cingulum, a narrow, complete mesolophid and a hypolophid confluent with the posterolophid. The mesolophid is anterior in position, midway between the metalophid and hypolophid. The sinus is deep, with a small cuspule at its outlet.

Discussion. This large rodent is low crowned but with lophodont molars, m3 lacks an anterior cingulum and its mesolophid is long and separate, and m1 has a weak metaconid-protoconid connection. Wessels (2009) also saw diversity in early rhizomyines, noting a large *Prokanisamys*, but its size is considerably less than seen here. These large species underscore Early Miocene diversity and the major role played by rhizomyines in the younger Siwalik faunas.

Discovery of this large rhizomyine in the Early Miocene of the Zinda Pir Dome is unexpected. Nothing as large is known prior to the Middle Miocene Chinji Formation *Kanisamys potwarensis* Flynn (1982). It is also strongly lophodont, more lophodont than *Prokanisamys*. Figure 4(f) contrasts the most complete tooth with an unworn molar of the smaller, less lophodont *Prokanisamys kowalskii* (Figure 4e). Crown height is, however, as low as that of *Prokanisamys*; the ratio of height to length of the unworn m3 PMNH 2433 is 0.56, much in line with its contemporaries. The anterior position of the mesolophid, not shifted toward the hypolophid and the lack of connection from the anterior arm of the protoconid to the metaconid are primitive for rhizomyines. Although difficult to judge given the sample size, the species does not display the reduced m3 characteristic of *Prokanisamys*, and the derived suppression of the anterior cingulum on m3 makes generic assignment problematic.

Cricetidae Rochebrune 1883

Primus de Bruijn, Hussain, Leinders 1981

Included species. *Primus microps* (type species) and *Primus cheemai* sp. nov.

Primus microps de Bruijn, Hussain, Leinders 1981

Holotype. H-GSP 135, left m1 from Banda Daud Shah, Murree Formation, northern Pakistan.

Distribution and age. Murree Formation in the Trans-Indus region plus the Chitarwata and Vihowa Formations in

western Pakistan; localities considered latest Oligocene and Early Miocene. Zinda Pir fossils from localities Z113, Z135, Z139 and Z150 in the Chitarwata Formation and locality Z120, Z122 in the Vihowa Formation.

Diagnosis (emended). *Primus microps* is a small cricetid (Supplementary Table 1) with simple dental pattern; upper cusps usually have little or no offset between lingual and labial cusps, lower cusps have slight offset, with lingual cusps opposite to the anterior margin of labial cusps. The anterocone is relatively large and broad; the anteroconid is small, low and wide, located on the continuous anterior cingulum. A mesoloph is usually present, with variable length; metaloph is long and joins the hypocone; protolophid II is short or absent; metalophid usually joins the protoconid; long entolophid joins the posterior mure and/or hypocone arm. Occlusal outline of M3 is transversely oval, wider than long.

Description. M1: Occlusal outline is lozenge shape, longer than wide, slightly wider near middle length. The anterocone is relatively large, about the size of the hypocone, which is slightly larger than the protocone and subequal metacone; the paracone is the smallest cusp. Labial cusps are placed opposite to the posterior side of lingual cusps. The anterocone is broad, with dual (right and left) wear facets on the steep posterior side while the inflated anterior surface has only a slight depression. Protocone anterior arm is medium length, directed anteriorly toward (commonly joining) the lingual end of the anterocone. Protocone posterior arm is short, joining the paraloph and anterior mure near the midline. The long paraloph descends lingually to join the posterior arm of the protocone. Paracone posterior spur is indistinct, located near the labial margin. Hypocone anterior arm is medium length, directed toward the paracone and joins (or continues as) the posterior mure near the midline. Short hypocone posterior arm descends toward the posterior midline and joins the low posterior cingulum near the midline. Anteroloph and protoloph I are absent, protoloph II is absent or indistinct. The mesoloph is medium length, low, directed toward the anterior metacone and terminates freely. Mesostyle, ectoloph and ectostyle are all absent. Metaloph I is long, it descends lingually and curves slightly anteriorly to join the minute hypoloph at either the anterior hypocone (2/3) or its center. Metaloph II is absent. The central mure is short and straight. Lingual anterior cingulum, very short and low, joins the protocone anterior arm near the midline. Labial anterior cingulum is medium length it is relatively high and encloses a large basin anterior to the paracone. Transverse shelves are offset with lingual shelf anterior; labial shelf is wide and high, lingual shelf narrow and low. The lingual sinus is narrow and deep. Short lingual cingulum descends anteriorly from the hypocone to terminate at the posterior base of the protocone. Labial cingulum is low, continuous between the metacone and paracone. Low posterior cingulum descends and terminates at the posterior base of the metacone. There are three well developed roots: a large lingual root and small anterolabial and posterolabial roots (Figure 5).

M2: Occlusal outline is subrectangular, longer than wide, slightly wider anteriorly. Protocone and hypocone are larger than the paracone and metacone. Labial cusps are located opposite to the anterior side of lingual cusps as in M1; union of lophs with cusps follow the pattern of M1 except that the paraloph joins the anterior arm of the protocone rather than the posterior arm. Protocone anterior arm is short, directed anteriorly to join the anteroloph lingual to the midline. The paracone posterior spur is usually (6/7) minute, descending posteriorly to terminate near the labial margin. Arms of the hypocone are as in M1. Anteroloph is short and high, located slightly lingual to the midline and joins the protocone anterior arm. Protoloph I is minute or indistinct; protoloph II is usually (4/7) minute or short (3/7). The mesoloph is usually short and free (3/7), or medium length and free (2/7), or long (2/7), terminating near the labial margin. The central mure is very short, located near the midline and joins the protocone posterior arm at the base of the mesoloph and the hypocone anterior arm. Lingual anterior cingulum is medium length, it descends lingually from the anteroloph and curves posteriorly to terminate at the base of the protocone (5/7) or continues as the lingual cingulum. Labial anterior cingulum is long and relatively high, directed from the anteroloph toward the labial margin and curves slightly posteriorly to terminate at the anterior base of the paracone. Transverse shelves and lingual sinus as in M1. Lingual cingulum is usually (6/7) low and indistinct, or continuous and slightly ascends the lingual hypocone (1/7). Labial cingulum is low. Posterior cingulum follows the pattern of M1. There are three roots, as in M1.

M3: Occlusal outline is oval, wider than long, with a relatively straight anterior side and a gently rounded posterior side. The protocone and paracone are subequal, larger than the small hypocone; the metacone is absent or indistinct. Protocone-paraloph union is similar to that of M2. The long protocone posterior arm is directed toward the posterior midline, weakly joining the minute hypocone anterior arm. Hypocone posterior arm joins the robust posterior cingulum. Anteroloph is similar to that of M2, and mesoloph, mesostyle, ectoloph and ectostyle, metaloph I and II and central mure are all absent. A short lingual anterior cingulum descends from the anteroloph and curves posteriorly to terminate anterior to the protocone; labial anterior cingulum is usually long and high, directed toward the labial margin to join the paracone base and enclose a narrow anterior basin. Transverse shelves and the lingual sinus are short and narrow; lingual cingulum is indistinct; labial cingulum is short and low; posterior cingulum is robust but short,

directed toward the labial margin and gently curving anteriorly to terminate at the posterior base of the paracone. Roots are as in M1 and M2.

m1: Occlusal outline is lozenge shape, longer than wide, slightly wider posteriorly. Labial cusps (protoconid and hypoconid) are slightly larger than lingual cusps (metaconid and entoconid), and the anteroconid, although wide, is much smaller. Lingual cusps are located opposite to the anterior margin of labial cusps. Arms of the protoconid are short to medium length, directed toward the anteroconid to join the anterolophid and toward the lingual margin to join (sometimes) the metaconid. Metaconid posterior spur is usually (3/5) low or indistinct, near the lingual margin. Arms of the hypoconid are short, directed toward the metaconid to join the posterior mure and entolophid near the midline or directed toward the posterior midline to join the posterior cingulum. Anterolophid is short, directed toward (usually joining) the protoconid anterior arm. Metalophid I is usually (5/6) absent, or medium length and directed toward the anteroconid. Metalophid II is medium length, directed toward the protoconid and may (2/4) join it. Mesolophid is short (2/4) or absent. Mesostylid, ectolophid, ectostylid and hypolophid are all absent. Entolophid is medium length, directed toward the hypoconid and usually joins the minute hypolophid and posterior mure near the midline. The central mure is medium length, very narrow and straight, placed slightly labial to the midline; it is distinct relative to the arms of the protoconid and hypoconid. Labial anterior cingulum descends from the anteroconid and curves posteriorly to terminate near the base of the protoconid. Lingual anterior cingulum, is high and narrow, curves posteriorly to join the metaconid and enclose a small anterolingual basin. The transverse shelves are not offset; they are low, wide and synclinal (lower near the midpoint). The labial sinusid is rather wide, almost rectangular. Lingual cingulum is low; labial cingulum is low or indistinct; the low posterior cingulum curves anteriorly and slightly ascends the posterior entoconid. Posterior labial sulcus is relatively deep until late wear. Two transversely wide roots, anterior and posterior, are present.

m2: Occlusal outline is subrectangular, longer than wide, slightly wider posteriorly. The protoconid and hypoconid are slightly larger than the metaconid and entoconid as in m1. Lingual cusps are placed opposite to the anterior side of labial cusps. Protoconid and hypoconid arms follow the pattern seen on m1. Protoconid posterior spur or mesolophid is usually absent (7/12), or short (5/12) or long (1/12); both a protoconid posterior spur and mesolophid are present on only one m2. The mesolophid is usually short or indistinct; it is always directly opposite an ectolophid if an ectolophid is present. Metaconid posterior spur is usually absent or weakly developed. The anterolophid is short, high and near the midline, joining the protoconid anterior arm and sometimes metalophid I. Metalophid I is medium length, and descends anterolabially from the apex to join the protoconid anterior arm and the anterolophid near the midline. An ectostylid is usually absent (11/12) or minute. The entolophid follows the pattern of m1. The central mure is short and straight, it joins the protoconid posterior arm and the hypoconid anterior arm (and the entolophid) near the midline. Labial anterior cingulum descends from the anterolophid and curves posteriorly to terminate near the labial margin of the protoconid. Lingual anterior cingulum is directed from the anterolophid and merges with the anterior metaconid short of the lingual margin. Labial sinusid is usually broad (8/12) or narrow and steep (4/12). Lingual and labial cingula are low or indistinct; posterior cingulum descends lingually from the midline and curves anteriorly to terminate near the posterior base of the entoconid. Posterior labial sulcus is weakly developed or absent. Roots are as in m1.

m3: Occlusal outline is subtriangular with a relatively straight anterior margin and narrow, rounded posterior margin. The protoconid is slightly larger than the metaconid, the hypoconid is much smaller and the entoconid is absent or indistinct. The protoconid is almost opposite (slightly posterior) to the metaconid. Protoconid arms are similar to those of m2, although the anterior arm is shorter, and the posterior arm is long or medium length, directed toward the posterolingual corner of the tooth to join the hypoconid anterior arm and the entolophid near the midline. Protoconid posterior spur is absent. Hypoconid arms are long anteriorly, joining the mure (posterior arm of protoconid) near the midline, and short posteriorly to merge with the robust posterior cingulum. The minute anterolophid, placed near the midline, joins the protoconid anterior arm and the metalophid. Metalophid I descends labially from the apex to join the protoconid anterior arm and the anterolophid. Metalophid II, short and low, descends labially from the metaconid (2/3) or is absent. The mesolophid is absent or indistinct. Hypolophid I and central mure are indistinct; hypolophid II is absent. The long labial anterior cingulum descends from the anterolophid and curves posteriorly to terminate near the labial margin of the protoconid. The lingual anterior cingulum is short, directed lingually from the anterolophid to merge with the anterior metaconid short of the labial margin. Transverse shelves are indistinct. Labial sinusid is narrow and steep. Low lingual cingulum is continuous between the metaconid and hypoconid; labial cingulum is low or indistinct; posterior cingulum is short and robust, continuous with the lingual cingulum. Posterior labial sulcus is absent. Roots are as in m1 and m2.

Discussion. In *Primus* we see the reduction but frequent presence of the protoconid (and the protocone) posterior spur and its replacement by the mesolophid and mesoloph. This dental change is also witnessed in the genus

Eucricetodon (and possibly other genera) recorded from Oligocene deposits in Asia and Europe, and in *Leidymys* and *Paciculus* in North America (see Lindsay et al. 2015). Given the generally modern grade of the dentition, *Primus* may have exhibited the advanced cranial and incisor characters of modern muroids, as well.

The reduction and loss of the protoconid posterior spur and its replacement in the muroid dentition is widely recognized among vertebrate paleontologists but is poorly documented, primarily because of the absence or lack of study of large samples among Oligocene cricetid rodents. Also, it is difficult to distinguish the protocone posterior spur from the mesoloph in many rodent teeth. Figures of *Primus* reveal some clues. Note in Figure 5(b) there are two lophs directed labially between the paracone and metacone. The smaller and more anterior loph would be the protocone posterior spur and the longer, posterior loph would be the mesoloph. On Figure 5(c) there is a single loph between the paracone and metacone and this small loph is closer to the metacone than the paracone; therefore, it should be the mesoloph. In Figure 5(e) of two lophs in this position, the anterior is directed toward the metaconid and should be the protoconid posterior spur, and the posterior loph, directed toward the entoconid should be the mesolophid. In Figure 5(f), there is a single loph in this position, clearly coming from the protoconid, so this is interpreted as a protoconid posterior spur.

Primus cheemai, new species

Holotype. PMNH 2001, isolated right m1 from locality Z113, Chitarwata Formation, Zinda Pir Dome.
Additional Material. All localities: 33 M1, 28 M2, 5 M3, 21 m1, 22 m2, 9 m3 (Supplementary Table 2, Figure 6).
Distribution. PMNH localities Z113, Z135, Z139, Z150 and Z126 in the Chitarwata Formation, and localities
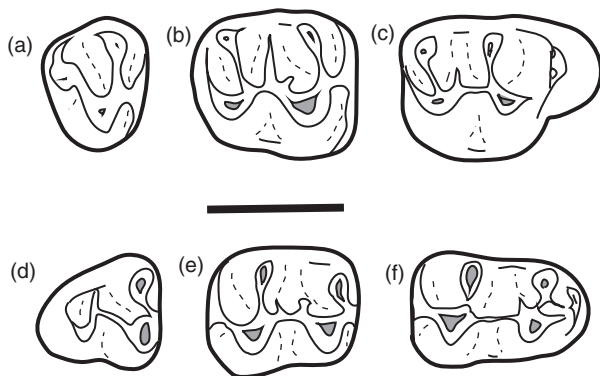

Figure 5. *Primus microps.* Anterior is to the right. (a) PMNH 788, left M3 (reversed); (b) PMNH 665, left M2 (reversed); (c) PMNH 662, right M1; (d) PMNH 625, right m3; (e) PMNH 2160, left m2 (reversed); (f) PMNH 677, right m1. Scale barh = 1 mm.
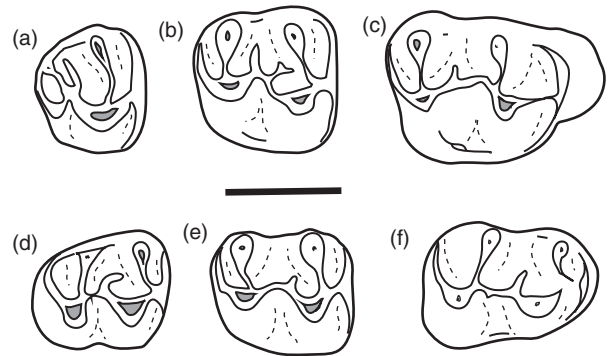

Figure 6. *Primus cheemai.* Anterior is to the right. (a) PMNH 622, right M3; (b) PMNH 793, right M2; (c) PMNH 631, right M1; (d) PMNH 1061, left m3 (reversed); (e) PMNH 1058, right m2; (f) PMNH 2001, right m1 (type). Scale bar = 1 mm.

Z120, 122 and Z124 in the Vihowa Formation, Zinda Pir Dome, Late Oligocene to Early Miocene.
Etymology. Named for Iqbal Umer Cheema, formerly of the Pakistan Museum of Natural History, for his contributions to the study of cricetid fossils from Pakistan and for initiating paleontological work in deposits of the Zinda Pir Dome.
Diagnosis. A small rodent with lingual cusps slightly offset (lingual cusps opposite to anterior margin of labial cusps). The anterocone is large and wide, single-cusped but slightly asymmetrical with the labial side descending more steeply than the lingual side; anteroconid is small or minute, located on the anterior cingulum that joins the metaconid near mid-height and the protoconid base. Mesolophs and mesolophids are usually short or absent; protoloph II and protolophid II are usually short or absent; metaloph is long, usually joining the hypocone; entolophid is usually long and joins the posterior mure and hypoconid arm; ectoloph and ectolophid are usually minute or absent.
Differential diagnosis. *Primus cheemai* resembles *Primus microps*, but differs in larger size (Supplementary Table 2), more robust and distinctly wider cheek teeth, especially M3 and m3. Among the cricetid species of the Chitarwata and Vihowa formations the anterocone of *P. cheemai* M1 is not bilobed in contrast to a smaller anterocone with two wear surfaces on M1 of *P. primus*, and a bilobed anterocone on *Democricetodon khani*, *Myocricetodon tomidai* n. sp. and *Potwarmus mahmoodi* n. sp.. Also, the anteroconid on m1 of *Primus cheemai* is larger, wider and more symmetrical than the anteroconid of *P. microps;* the anteroconid on m1 of *P. cheemai* is smaller than the anteroconid of *Democricetodon khani*, narrower than the anteroconid of *M. tomidai* and wider than the anteroconid of *P. mahmoodi*.
Description. M1: Occlusal outline is lozenge shape, longer than wide and slightly wider posteriorly. Largest cusp is the anterocone which is slightly larger than the hypocone, which is slightly larger than the protocone, which is about

the size of the metacone, which is slightly larger than the paracone. Labial cusps are placed opposite to the anterior margin of lingual cusps, with slight transverse offset of lingual cusps. The anterocone is asymmetrical with a high apex labial to the midline and the lingual side descends less steeply than the labial side; the protocone anterior arm is long and joins the lingual anterocone near its termination. Paraloph is long, descending lingually from the apex to join either the anterior mure-protoloph II near the midline (24/26) or the protoloph I (2/26). A paracone posterior spur is usually (9/13) weakly developed, terminating near the labial margin or minute. Hypocone anterior arm is medium length, directed toward the paracone to join the posterior mure (and the metaloph). Hypocone posterior arm is short, directed toward the posterior midline to merge with the posterior cingulum. The anteroloph is minute or indistinct, descending posteriorly from the lingual side of the anterocone. Protoloph I is usually minute and free (22/33) or it joins the paraloph (2/33), or is absent (9/33). Protoloph II is minute, commonly joining the paraloph (30/32) or indistinct. The mesoloph is usually short (22/26) or long (2/26), directed labially from the middle of the posterior mure or it is indistinct (2/26). A mesostyle, ectoloph and ectostyle are all absent. Metaloph I is long, it descends lingually from the apex to join a minute hypoloph, usually near the middle (19/27), or the posterior (6/27) or the anterior (2/27) area of the hypocone. Metaloph II is absent. The central mure is long and straight, located near the midline. Lingual anterior cingulum is low, directed posteriorly from the junction of the protocone anterior arm with the anterocone (17/20), or it continues posteriorly as the lingual cingulum (3/20) lingual to the protoconid. Labial anterior cingulum, relatively high, joins the labial anterocone and the anterior paracone to enclose a shallow anterolabial basin. Transverse shelves are relatively equal in height, with a distinct offset (labial side posterior to lingual side), with the labial shelf slightly wider than the lingual shelf. The lingual sinus is narrow and straight. Both the lingual and labial cingula are low; the posterior cingulum descends labially from the midline, thins distally and curves anteriorly to terminate at the posterior base of the metacone. There are three roots, a large root below the anterocone, a large lingual root below the protocone and hypocone and a smaller labial root below the metacone.

M2: Occlusal outline is subrectangular, slightly longer than wide and wider anteriorly. The protocone is the largest cusp, with the hypocone, paracone and metacone of successively decreasing size. Labial cusps are almost opposite lingual cusps (with little or no transverse offset). Protocone anterior arm is short, joining the anteroloph and the paraloph lingual to the midline. The long paraloph descends anterolingually from the apex to join the minute protoloph I near the midline. A neoloph (new term) is formed between the protocone and paracone by union of protoloph II with a posterior spur from the paraloph; it is present in 2/28 specimens. Paracone posterior spur descends near the labial margin as in M1; usually weakly developed (18/28), or well developed (10/28). Hypocone anterior arm follows the pattern seen on M1. The anteroloph is short and high, located lingual to the midline. Protoloph I joins the paraloph near the midline. Protoloph II is usually directed labially between the paracone and the metacone, and the mesoloph is always posterior relative to protoloph II; usually both lophs are present (26/33) with the mesoloph usually longer or better developed (24/26). If only a single loph is present (6/33) between the paracone and metacone, it is interpreted the protoloph II based on its position closer to the paracone; rarely (1/33) both lophs are absent. The mesoloph is short or medium length, extending from the junction of the posterior mure with the hypocone anterior arm. Mesostyle, ectoloph and ectostyle are all absent. Metaloph I joins the hypocone as in M1; metaloph II is absent. The short central mure joins protoloph II and the hypocone anterior arm, and is often oriented slightly oblique on the tooth. Lingual anterior cingulum follows the pattern seen on M1; labial anterior cingulum is long, flexed posteriorly near the labial tooth margin and may thicken (cusplike) to join the anterior paracone and enclose a narrow anterolabial basin. Transverse shelves are relatively broad, slightly higher labially and not as offset transversely as seen in M1. The lingual sinus is steep and narrows internally. Both lingual and labial cingula are low; the posterior cingulum descends slightly, thins labially and curves gently to terminate at the base of the metacone. There a large lingual root plus two small anterolabial and posterolabial roots (posterolabial root tends to merge with the lingual root).

M3: Occlusal outline is a rounded triangle with a straight anterior face and a narrower, gently rounded posterior margin. The protocone is larger than the paracone with a minute hypocone and indistinct metacone. Protocone arms are short and follow the pattern of M1 and M2, with the posterior arm trifurcating distally as three narrow spurs; the long and most anterior spur is free and resembles the mesoloph, the middle short spur resembles the metaloph and joins the labial cingulum (or ghost metacone) and the short posterior spur is directed toward and joins the hypocone. Paraloph is long and narrow, descending to join a minute protoloph (and the protocone arm). Hypocone arms are short, merging with the trifurcating posterior spur of the protocone arm (the longest loph of the trifurcation is the mesoloph). Posterior arm of the hypocone is short and merges with the narrow posterior cingulum. The anteroloph is minute, located lingual to the midline. Metaloph I is interpreted the middle loph of the trifurcation. Lingual, and labial anterior cingula are as in M1 and M2. The labial cingulum is moderately high and continues posteriorly from the

paracone to join the posterior cingulum. Roots are as in M2.

m1: Occlusal outline is lozenge shape, longer than wide and wider posteriorly. The hypoconid is usually (14/19) slightly larger than the protoconid, about equal in size to the entoconid and larger than the metaconid. The anteroconid is minute, representing a broad expansion of the anterior cingulum near the midline. Lingual cusps are offset transversely, placed slightly anterior to the margin of labial cusps. Protoconid anterior arm (= protolophid I) is short or medium length, directed toward the anterior midline, usually weakly joining metalophid l (17/19), or anterolophid (2/19). Protolophid II is usually short (17/18) or absent; it joins the metaconid (6/17), the protoconid posterior arm (5/17) or terminates freely. Six m1 have two lophs (both anterior protolophid II and posterior mesolophid). Metaconid posterior spur is either well developed (16/23) and descends near the lingual margin to constrict the lingual transverse valley, or is weakly developed (7/23). Hypoconid anterior arm is short, directed toward the lingual margin to join the entolophid and posterior mure near the midline. Hypoconid posterior arm is short, directed toward the posterior midline and slightly robust (12/24), or narrow (12/24), always merging with the posterior cingulum. The anterolophid is short, directed posteriorly to join only the metalophid (7/14), or both the metalophid and the protoconid anterior arm (4/14), or it is indistinct (3/14). Metalophid I is medium length, it descends anterolabially from the apex and curves anteriorly to join the anterolophid (7/19); metalophid II may descend labially from the metaconid and recurve to join the middle or posterior protoconid (6/19); metalophid I and II are both present in (6/19). The mesolophid is usually absent (15/23) or short (8/23), directed lingually from the junction of the anterior mure with the hypoconid anterior arm. An ectolophid is usually absent (17/27), or short (5/27), directed labially from the central mure. Mesostylid and ectostylid are both absent. The long entolophid descends labially from the apex to join the hypoconid anterior arm and the posterior mure near the midline. The central mure is medium length and straight, joining the protoconid posterior arm and the hypoconid anterior arm near the midline. Labial anterior cingulum is, medium length, it descends from the anteroconid and curves posteriorly to terminate anterior to the base of the protoconid. Lingual anterior cingulum, is short and high, it joins the anterolophid and curves posteriorly to join the metaconid near the midline and enclose a shallow anterolingual basin. The transverse shelves are slightly offset (lingual side anterior to labial side) and higher lingually, especially if protolophid II or an ectolophid is present. Labial sinus is broad and relatively flat. Lingual cingulum and labial cingulum are both low, the lingual cingulum is slightly shorter than the labial cingulum. Posterior cingulum descends lingually from the posterior

midline and then curves gently toward and ascends the posterior entoconid to enclose a shallow posterolingual basin. Posterior labial sulcus is distinct with little or no wear, or becoming indistinct with moderate wear. The two transversely wide roots are located anterior and posterior, with the posterior root slightly wider.

m2: Occlusal outline is subrectangular, longer than wide and wider anteriorly. Cusps are nearly equal in size with the metaconid or entoconid slightly smaller. Protoconid anterior arm is short, directed toward the anterior midline to join the minute anterolophid and metalophid I. Usually a single loph is directed lingually between the metaconid and entoconid (18/22); it is interpreted protolophid II if located anteriorly (15/18), or a mesolophid; if located posteriorly (3/18), closer to the entoconid; rarely two lophids are present (2/22). Metaconid posterior spur is usually well developed near the lingual tooth margin. Hypoconid anterior arm is short, directed toward (21/22) the lingual margin or the metaconid; it joins the entolophid and posterior mure (21/22), or only the entolophid. Hypoconid posterior arm follows the pattern seen in m1. Anterolophid is short and high, usually placed near the anterior midline (12/20) or slightly labial to the midline (8/20). Metalophid I is medium length, descending anterolingually from the apex and curving anteriorly to join the anterolophid near the midline. Metalophid II is absent. Mesolophid is usually absent (18/22), or minute (4/22), located at the junction of the posterior mure with the hypoconid anterior arm. Ectolophid is usually absent (22/25), or minute (3/25). The mesostylid and ectostylid are absent. Entolophid is medium length (7/12), it descends labially from the apex and then ascends to join the hypolophid near the midline. The central mure is short and straight, following the pattern of m1. Labial anterior cingulum terminates at the labial protoconid (19/23), or continues posteriorly as the labial cingulum (4/23). Lingual anterior cingulum follows the pattern seen on m1 to merge with the anterior metaconid short of the lingual margin. Transverse shelves are virtually opposite with little or no offset, although the lingual side is noticeably wider. The labial sinusid is wide and straight. Both lingual and labial cingula are low. The posterior cingulum follows the pattern of m1. The posterior labial sulcus is distinct with little or no wear, becoming indistinct after moderate wear. Two transversely wide roots are as in m1.

m3: Occlusal outline is lozenge shape, nearly rectangular but slightly wider anteriorly. The protoconid is larger than the metaconid which is about the size of the hypoconid; the entoconid is absent, although a worn remnant of a minute entoconid is present on 1/6. Metaconid is opposite the anterior side of the protoconid (very slight offset). Protoconid and hypoconid arms follow the pattern seen on m2, with posterior arms relatively more robust. Protoconid posterior spur

(= protolophid II) is usually absent (5/6) or short and thin. Anterolophid is usually absent (5/6) or short, located slightly labial to the midline. Metalophid I and II are as in m2, and the mesolophid is usually absent or indistinct (5/6), or short and narrow, directed anterolingually from the protoconid anterior arm. Mesostylid, ectolophid and ectostylid are all absent. The entolophid is long and narrow; it joins the lingual cingulum and the hypoconid anterior arm (5/6), or is absent. The central mure is indistinct relative to the protoconid anterior arm and usually joins the hypoconid anterior arm. Labial and lingual anterior cingula follow the pattern seen in m2. Transverse shelves are indistinct. Labial sinusid is deep and narrow. Lingual cingulum is continuous from the hypoconid to the posterior metaconid. Labial cingulum is low or indistinct; posterior cingulum is robust, continuous with the lingual cingulum. Posterior labial sulcus is absent. Two roots are developed, as in m2.

Discussion. As for *Primus microps* the dentition of *Primus cheemai* demonstrates the reduction of the protocone posterior spur and its replacement by the mesoloph in upper teeth and reduction of the protoconid posterior spur (and its replacement by the mesolophid in lower teeth). Between the paracone and metacone in Figure 6(b), we interpret the short anterior loph as the protocone posterior spur and the long posterior loph as the mesoloph. Note that the anterior loph is closer to the paracone and the posterior loph is closer to the metacone. Figure 6(c) shows only one loph between the paracone and metacone located closer to the metacone, so we interpret this as a mesoloph. On both Figure 6(e) and 6(f) the single loph between the metaconid and entoconid is closer to the metaconid, and we interpret it as a protoconid posterior spur. Note on Figure 6(f) a minute ectolophid between the protoconid and the hypoconid, is posterior in position. Usually on a lower molar an ectolophid is opposed by the mesolophid when present. In upper molars an entoloph is opposed by a mesoloph when present.

Democricetodon Fahlbusch 1964

Democricetodon khani (de Bruijn, Hussain, Leinders 1981)

Holotype. H-GSP 221, right m2 from the Murree Formation, Banda Daud Shah.

Additional Material. Locality Z135, Chitarwata Formation, and Z124, Z120, Z122, Vihowa Formation, Early Miocene. Damaged specimens questionably referred from Z113, Z150 (Supplementary Table 3, Figure 7).

Features. M1 has a large, bilobed anterocone, m1 has a small and wide anteroconid located on a gently rounded anterior cingulum; opposing cusps are slightly alternating, with labial cusps opposite posterior margin of lingual cusps in upper molars, and lingual cusps opposite posterior margin of labial cusps in lower molars; mesolophs and
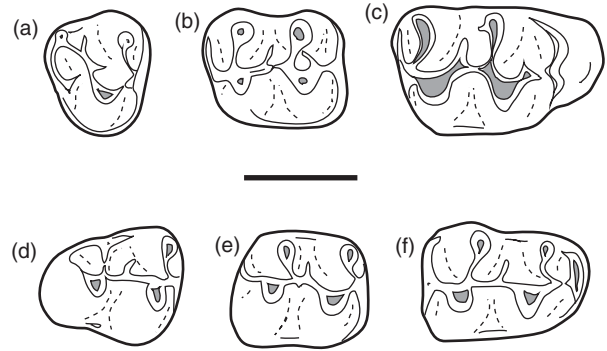

Figure 7.   *Democricetodon khani.* Anterior is to the right. (a) PMNH 538, right M3; (b) PMNH 355, right M2; (c) PMNH 349, left M1 (reversed); (d) PMNH 496, right m3; (e) PMNH 358, right m2; (f) PMNH 376, right m1. Scale bar = 1 mm.

mesolophid are usually short and terminate freely; the entoconid on m3 is minute or indistinct.

Comparisons. *Democricetodon khani* is distinguished by its primitive retention of extra transverse crests (posterior protocone/protoconid spur) in some teeth, these being distinct from true mesolophs (-ids). The bilobed anterocone of M1 is deeply divided anteriorly, sometimes with a low shelf at the anterior margin of the tooth; the lower first molar is relatively short, with a broad, blunt anteroconid. M1 of *Democricetodon khani* resembles that of the Middle Miocene *D. kohatensis* Wessels et al. (1982) from Pakistan, but differs in its much smaller size and less elongated m1 (Supplementary Table 3). Both species have (variably) a second loph directed labially between the paracone and metacone on M2 in distinction from several Middle Miocene European species. The small size of *D. khani* distinguishes it from many species of the genus, but it is slightly larger than *D. sui* Maridet et al. (2011) from the Junggar Basin, China. The latter has an undivided anterocone on M1 and m1 is less blunt, more tapered anteriorly.

D. khani is larger than the Early Miocene *D. anatolicus* Theocaropoulos (2000) from Anatolia and Greece, but is about the same size as *D. doukasi* of the same author. *D. anatolicus*, possibly the oldest *Democricetodon*, has a lower first molar with variable (primitive) loph structures and resembles *D. khani* in this and in its short, blunt anterolophid. The upper first molar is also primitive; its simple anterocone contrasts greatly with that of *D. khani*. *D. doukasi* also has a simple, undivided anterocone, but its lower molar structures are stable and derived and the anteroconid is larger with a longer anterolophid.

Description. M1: Occlusal outline lozenge shape with cusps usually slightly offset, labial cusps located opposite the posterior margin of lingual cusps (slightly offset). Anterocone is the largest cusp, slightly larger than the protocone and hypocone, which are larger than the paracone and slightly smaller metacone. The large

anterocone is unequally bilobed with the labial lobe larger than the lingual lobe, and its anterior surface is grooved between the lobes, usually deeply; a low anterior basal shelf is well developed (3/9), or weak (2/9) or absent (4/9). Protocone anterior arm is short or medium length, directed anteriorly to weakly join the anteroloph on the lingual lobe of the anterocone; protocone posterior arm is short, directed posterolabially to join the paraloph and the anterior mure. Hypocone anterior arm is medium length, directed toward the paracone to join the posterior mure at the base of the mesoloph near the midline; hypocone posterior arm is short, directed toward the posterior midline to merge with the posterior cingulum. A minute anteroloph is directed posteriorly from the lingual lobe of the anterocone and joins the protocone anterior arm; one specimen has a longer but low anteroloph directed posteriorly from the lingual anterocone, terminating freely. Paraloph is medium length, it descends lingually from the apex to join the protocone posterior arm and mure; protoloph I is usually (9/13) short or indistinct, directed labially and terminates freely (7/9) or joins the paracone; protoloph II is minute, it joins the paraloph as the protocone posterior spur. The paracone posterior spur is usually poorly developed (10/12), located near the labial margin or central paracone. The mesoloph is, usually short (9/13) or absent, it descends labially and terminates freely. A mesostyle is usually absent (11/12) or minute; the ectoloph is absent, and an ectostyle is usually absent (8/12) or minute. Metaloph is medium length, it descends from the apex to join the hypocone posteriorly (8/12) or centrally (3/12) or anteriorly (1/12); metaloph II is absent. The central mure is short and straight, it joins the arms of the protocone and hypocone. The lingual anterior cingulum descends from the anterocone, curves posteriorly and continues as the lingual cingulum (7/12), or terminates at the base of the protocone (5/12); the labial anterior cingulum is short and high, it continues from the anteroloph and curves posteriorly to terminate at the anterior base of the metacone. Transverse shelves are slightly offset with lingual shelf anterior to labial shelf; both are narrow and synclinal. The lingual sinus is usually narrow and moderately deep. Both lingual and labial cingula are low; the lingual cingulum being shorter. The posterior cingulum is directed labially from the posterior midline, it curves anteriorly near the labial margin and terminates at the posterior base of the metacone to enclose a wide posterior basin. Three roots: a large median root longitudinally elongated, a large and round anterior root and a small, round posterolabial root.

M2: Occlusal outline is trapezoidal, longer than wide, with nearly straight but oblique anterior and lingual margins; it is longer than wide and slightly wider anteriorly. Lingual cusps (protocone and hypocone) are slightly larger than labial cusps (paracone and metacone) and located slightly anterior to the centre of labial cusps (slight offset). Protocone anterior arm is short, directed toward the anterior midline to join the anteroloph; a protocone posterior spur is variably directed labially toward the paracone, which it would join with wear. Protocone posterior arm is medium length, directed toward the metacone to join the paraloph and mure near the midline. Hypocone anterior arm is medium length and slightly robust (9/13) or short (4/13); hypocone posterior arm is short, directed toward the posterior midline, merging with the posterior cingulum. The high anteroloph, is usually short (7/13) or medium length (6/13), located near the midline to join the protocone arm. The paraloph is medium length and descends posterolingually from the apex to join the protocone arm and the mure near the midline. Protoloph I is usually absent or short and very narrow, directed toward the paracone and rarely joins it; protoloph II is short and free (8/13) or absent (3/13) or joins the base of the paracone. The paracone posterior spur, is usually weakly developed (12/15) well developed (3/15), it descends posteriorly from the centre of the paracone and terminates near the labial tooth margin. The mesoloph is usually short (8/14) or absent (5/14), or long in one case and terminates freely; a mesostyle and ectoloph are absent; a rare ectostyle (2/13) is minute. Metaloph is medium length, it descends lingually from the apex to join the hypocone anteriorly (10/13), or centrally (2/15), or it terminates freely; metaloph II is absent. The short central mure is slightly oblique to the tooth axis, located near the midline (10/13) or slightly lingual to the midline (3/13). The lingual anterior cingulum is high near the anteroloph, it descends lingually and curves posteriorly to terminate at the protocone (6/13), or continues as the lingual cingulum (7/13); the labial anterior cingulum is directed labially from the anteroloph close to the paracone, it curves posteriorly and terminates at the base of the paracone. The transverse shelves are usually slightly offset (8/14) with lingual shelf anterior, or are opposite one another (6/14). The lingual sinus is wide near the tooth margin, narrow near the midline. Lingual cingulum is low and may be continuous (4/15); labial cingulum is also low and usually shorter than the lingual cingulum (11/12), or subequal in length. Posterior cingulum as in M1. There is a large median root and small anterolabial and posterolabial roots.

M3: Occlusal outline is subtriangular, wider than long, narrower lingually. Largest cusp is the protocone, with a smaller paracone, a minute hypocone and minute but distinct metacone. The anteroloph is lingual to the midline; the paraloph is narrow and joins the anterior cingulum labial to the anteroloph. Posterior arm of the protocone is long and narrow, with a minute spur directed anteriorly toward the paracone base and a short mesoloph directed labially toward the labial margin, and joins the short metaloph descending from the metacone. The tiny hypocone has a short, free anterior arm and the posterior

arm is long and narrow, continuing labially to join the metacone. The anterolingual cingulum descends and continues posteriorly around the protocone to terminate at the base of the hypocone; the anterolabial cingulum merges labially with the paracone. A short labial cingulum terminates posterior to the paracone. No roots are preserved.

m1: Occlusal outline is lozenge shape, longer than wide and slightly wider posteriorly. Posterior cusps (hypoconid and entoconid) are slightly larger than anterior cusps, with lingual cusps placed slightly anterior to centre of labial cusps (slight offset). The small anteroconid is broad transversely, located on the continuous anterior cingulum. Protoconid anterior arm is short or medium length, directed toward the anterior midline to join the metalophid (and sometimes the anterolophid) near the midline; protoconid posterior arm is medium length, directed posteriorly to merge with the anterior mure. Hypoconid anterior arm is short, directed toward the metaconid or the lingual margin, it joins the entolophid and posterior mure near the midline; hypoconid posterior arm is short, directed toward the posterior midline to merge with the posterior cingulum. The metaconid posterior spur is well developed (3/5), or weak, descending near the lingual margin posterior to the metaconid. Protolophid I and protolophid II are absent. Metalophid I descends anterolabially from the apex to join the protoconid anterior arm (and sometimes the anterolophid); metalophid II is usually absent (3/5), or minute, directed toward the posterior protoconid. The mesolophid is absent (3/5), short (1/5) or long (1/5). Mesostylid, ectolophid and ectostylid are absent. The long entolophid descends anterolabially from the apex to join the hypolophid (and hypoconid) and the posterior mure near the midline. Central mure is long and straight, near the midline. Labial anterior cingulum descends labially from the anterolophid, it curves posteriorly and terminates short of the protoconid; lingual anterior cingulum is short, directed lingually from the anterolophid, it curves posteriorly to join the metaconid near the tooth margin. Transverse shelves are slightly offset, with the lingual shelf anterior and usually (4/5) higher than the labial shelf. Labial sinusid is wide, oriented slightly oblique internally. Lingual cingulum is low and narrow; labial cingulum is usually slightly longer than the lingual cingulum; posterior cingulum descends lingually from the midline and curves anteriorly near the lingual margin to terminate at the base of the entoconid. A posterior labial sulcus remains until late wear. There is a rounded anterior root and a wide posterior root.

m2: Occlusal outline is subrectangular, longer than wide, slightly wider posteriorly. Protoconid and hypoconid are subequal, larger than the entoconid, which is slightly larger than the metaconid. Lingual cusps (metaconid and entoconid) are located opposite to the anterior side of labial cusps (slight offset). Protoconid and hypoconid arms follow the pattern seen on m1. A protoconid posterior spur (closer to the metaconid than the entoconid) is usually present (16/19) and directed lingually from the mure. The mesolophid (closer to the entoconid than the metaconid) is usually absent (17/19) or short (2/19). The minute anterolophid is located near the midline. A short metalophid I descends anterolabially from the apex to join the anterior cingulum (14/18) or protoconid arm (4/18); metalophid II is absent. A mesostylid is usually absent, present only on PMNH 552. An ectolophid, usually absent, is faint on PMNH 552 and 556. An ectostylid is absent (16/19), or minute (3/19). The entolophid descends anterolabially from the apex to join the posterior mure and hypoconid arm. The central mure is short and usually transversely broad (16/18). The labial anterior cingulum descends from the anteroloph and curves posteriorly to terminate at the labial base of the protoconid. The lingual anterior cingulum merges with the metaconid short of the lingual margin. Transverse shelves are slightly offset with the lingual shelf anterior to the labial shelf. The lingual cingulum and shorter labial cingulum are both low. The posterior cingulum is as in m1. A well-developed posterior labial sulcus persists until late wear. There are transverse anterior and posterior roots.

m3: Occlusal outline is a rounded triangle, longer than wide, wider anteriorly. The protoconid is slightly larger than the hypoconid, which is slightly larger than the metaconid; the entoconid is minute or indistinct. The metaconid is placed opposite to the anterior margin of the protoconid with very slight transverse offset. Protoconid and hypoconid arms developed as in m1 and m2. A protoconid posterior spur (or mesolophid) is short, directed anterolabially and usually terminates freely. The anterolophid is minute, located near the midline. Orientation and union of cusps follow the pattern seen on m2, except for a rare minute ectostylid (Figure 7). A central mure is long or medium length, straight and located near the midline. The anterior cingulum and labial sinusid have similar features as seen on m2. The lingual cingulum is high and continuous between the metaconid and robust posterior cingulum; labial cingulum is low and short. There is a shallow posterolabial sulcus. Roots are similar to those on m2.

Discussion. Democricetodon khani was originally attributed to *Spanocricetodon,* but we agree with Maridet et al. (2011) that the species is not consistent with the genus. Like other Early Miocene species of *Democricetodon*, *D. khani* displays a mix of archaic and modern muroid features. As in *Primus* the transition in development of lophs on cheek teeth (the protocone-protoconid posterior spur vs. the mesoloph or mesolophid) occurs in early species of *Democricetodon*. For *Democricetodon khani* (Figure 7a) the single loph between the paracone and metacone is closer to the hypocone than the protocone, so we interpret it as a mesoloph. On Figure 7(b) the single

loph between the paracone and the metacone is equidistant between them, but distal to the posterior arm of the protocone, so it is not derived from the protocone; we interpret it as a mesoloph. The small loph (Figure 7c) between the paracone and the metacone is slightly closer to the metacone, and the posterior arm of the protocone is weak, so we consider this a mesoloph. On Figure 7(e) the small loph is clearly closer to the entoconid than the metaconid but it is anterior to what appears to be a minute entolophid; it is indistinguishable as a protoconid posterior spur or a mesolophid. Similarly problematic is identifying the small loph between the metaconid and entoconid on Figure 7(f). Hypothetically these are a protoconid posterior spur and a mesolophid, respectively. The protocone (-id) posterior spur is virtually lost in later Miocene species of *Democricetodon*, which have meso-lophs (-ids).

The appearance of *Democricetodon* in the Indian subcontinent by 22 Ma, possibly earlier, rivals the antiquity of the genus in Turkey and China. *Democrice-todon* appears without a likely ancestral predecessor, so it is considered an immigrant. *D. khani* is the first representative of the diverse and long-lived *Democriceto-don* group that is characteristic of later Siwalik faunas.

<div align="center">

Myocricetodon Lavocat 1952

Myocricetodon tomidai, new species

</div>

Holotype. PMNH 394, left M1 from locality Z120, Vihowa Formation.

Referred material. Isolated cheek teeth 3 M1, 16 M2, 1 M3, 14 m1, 14 m2 and 6 m3 (Supplementary Table 4).

Distribution and age. Localities Z120, Z122, Z124 and Z135 in the lower part of the Vihowa Formation and upper part of the Chitarwata Formation, Zinda Pir Dome, central Pakistan, Early Miocene.

Etymology. Named in honor of Dr. Yukimitsu Tomida, who advanced the National Museum of Nature and Science as a centre for paleontology, and conducted landmark research on fossils of Asia, especially small mammals, and including fieldwork in the Siwaliks.

Diagnosis. Small muroid with *Myocricetodon* features of double anterocone on M1 and variable enterostyle, m1 with metalophid I joining metaconid to anterior arm of protoconid, low longitudinal crests and reduced third molars (Figure 8). Cusp locations and sizes similar to those of the larger *M. sivalensis* Lindsay (1988), but more lophodont with evident longitudinal crest and transverse connections (Supplementary Table 4).

Differential diagnosis: *Myocricetodon tomidai* is larger than *M. sivalensis* and its anterocone on M1 is equal to or larger than the other cusps on M1, with lobes of the anterocone not differing greatly in size. Features resemble *Myocricetodon* sp. from Kamlial Fm. Y592 (Lindsay 1988), but the latter is considerably larger (M1
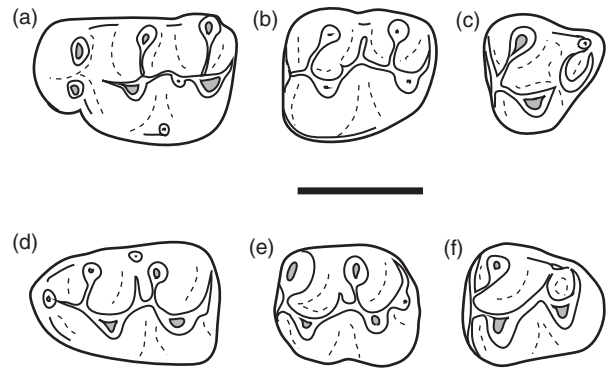

Figure 8. *Myocricetodon tomidai*. Anterior is to the left. (a) PMNH 394, left M1 (type); (b) PMNH 456, left M2; (c) PMNH 489, left M3; (d) PMNH 413, right m1 (reversed); (e) PMNH 452, left m2; (f) PMNH 407, left m3. Length of scale bar is 1 mm.

length = 1.83 mm). Close in size to *M. seboui* Jaeger (1977) from Morocco, but that species has a prominent enterostyle connected to the protocone.

M. tomidai differs from *Megacricetodon* in having a more reduced (lower and narrower) longitudinal crest or mure, less reduced M3/m3, and occasional presence of an enterostyle which is rare in *Megacricetodon*. *M. tomidai* differs from the larger *Megacricetodon mythikos* in having a lower and narrower longitudinal crest and occasional enterostyle on M1 and M2. *M. tomidai* differs from *Punjabemys* in having a low and thin longitudinal crest, less transverse offset of longitudinal valleys in upper molars and more reduced last molars. *M. tomidai* differs from *Dakkamys* and *Potwarmus* in having a smaller and more divided bilobed anterocone on M1, less developed enterostyle on M1 and especially M2. *M. tomidai* also differs from *Sindemys sehwanensis* Wessels (1996), which has a less frequent enterostyle, a deeper sinus (sinusid) and weak posterobuccal connection of the protocone.

Description. M1: Occlusal outline is lozenge shape, longer than wide, with a sharp increase of width posterior to the anterocone. The largest cusp is the unequally bilobed anterocone, larger than the primary cusps, which are subequal. Labial cusps slightly posterior to lingual cusps, with slight transverse offset of opposing cusps. The unequally bilobed anterocone has the labial cusp slightly larger than the lingual cusp, usually (2/3) with a shallow to deep anterior groove and no anterior shelf. Protocone anterior arm is medium length, directed toward the centre of the anterocone; protocone posterior arm is short, directed toward the metacone to join the anterior mure. Paraloph descends posterolingually from the apex to join the anterior mure and protocone posterior arm. A paracone posterior spur is absent. Hypocone anterior arm is medium length, directed toward the paracone and joins the protocone posterior arm (=mure) near the midline; hypocone posterior arm is short, directed toward the

posterior midline to merge with the posterior cingulum. Anteroloph is usually absent, or indistinct; short protoloph I is low or indistinct; short protoloph II joins the paraloph and anterior mure near the midline. Mesoloph is usually absent (3/4) or short and low. Mesostyle, and entoloph are both absent; the entostyle is usually absent, or small and isolated on the lingual tooth margin. Long metaloph I descends lingually from the apex and joins the anterior side of the hypocone; metaloph II is absent. The central mure is long, flexed lingually (as the protocone posterior arm) and weakly joins the hypocone anterior arm at its lowest point near the midline. A minute swelling marks termination of the posterior mure on Z-394 (Figure 8a). Short and low lingual anterior cingulum terminates freely at the lingual margin. Labial anterior cingulum is medium length, it descends posteriorly from the labial lobe of the anterocone and terminates at the anterior base of the protocone. Transverse shelves are approximatyely opposite, with broad synclinal floors; lingual sinus is wide and deep. Lingual cingulum is low or indistinct; labial cingulum, also low, joins the bases of paracone and metacone. Posterior cingulum descends labially from the posterior midline and ascends slightly to terminate at the posterior base of the metacone. Roots are unknown.

M2: Occlusal outline is trapezoidal with anterior, posterior and labial margins nearly perpendicular or parallel to each other but lingual margin is oblique to the other margins, length greater than width. Lingual cusps (protocone and hypocone) are larger than labial cusps (paracone and metacone). Labial cusps are placed opposite to the anterior side of lingual cusps with slight transverse offset. Protocone anterior arm is directed toward the anterior margin to join the paraloph and anteroloph near the midline; protocone posterior arm is medium length, directed toward the metacone (12/18) or labial margin (6/18), it joins the anterior mure near the midline. Paraloph descends anterolingually from the apex to join the protocone anterior arm near the midline. Paracone posterior spur is usually (9/16) weakly developed, descending posteriorly toward the labial margin, or is absent (6/16), or is well developed (1/16). Hypocone anterior arm is short, directed toward the paracone to join the mure and metaloph near the midline; hypocone posterior arm is short, directed toward the posterior midline to merge with the posterior cingulum. Anteroloph is short and medium height, usually located near the midline (14/18) or slightly lingual to the midline (4/18). Minute protoloph 1 joins the paraloph; protoloph II is usually absent (15/18) or minute (3/18). A mesoloph is usually absent (7/18) or minute (7/18), or short and free (4/18). A mesostyle and entoloph, are absent; an entostyle is usually absent (15/18) or small (3/18). Metaloph I joins the hypocone anterior (12/18) or posterior (6/18) to the centre; metaloph II is absent. Central mure is usually short (15/18) or medium length (3/18) and slightly oblique to

orientation of the tooth. Lingual anterior cingulum is prominent, descends lingually from the anteroloph, curves posteriorly, and continues (12/17) as the lingual cingulum, or terminates (5/17) at the lingual base of the paracone. Labial anterior cingulum is prominent, directed lingually from the anteroloph, curved gently posteriorly to terminate at the base of the paracone. The transverse shelves are wide with a synclinal base and show little or no overlap. Lingual sinus is wide and deep, blocked by the low lingual cingulum. Lingual cingulum is usually (12/17) continuous, long and ascends (slightly) the anterior hypocone or terminates (5/17) lingual to the protocone. Labial cingulum is low and short. Posterior cingulum follows the pattern seen on M1. There are a broad median root, plus smaller anterolabial and posterolabial roots.

M3: Occlusal outline is subtriangular with a narrow curved posterior margin. The largest cusp is the paracone, high and slender, the protocone is large and broad, the hypocone is small and the metacone is minute but distinct. Protocone arms are similar to those on M2 except the posterior arm usually terminates short of the hypocone. The paraloph is developed as in M2. Hypocone arms are short and narrow, directed toward the metacone, and terminate to enclose a narrow posterior basin and complete the posterior boundary of a large central basin. Anteroloph is minute but high, located on the anterior cinglulum slightly labial to the anterior midline. The protolophs, mesoloph, mesostyle, entoloph, entostyle, metaloph II and central mure are all absent. Metaloph I is minute and narrow, it descends anterolabially to join the hypocone anterior arm posterior to the large central basin; metaloph II and central mure are absent. Lingual and labial anterior cingulum as in M2. Lingual cingulum is short and low; labial cingulum is low, continuous between the paracone and metacone. Posterior cingulum is short and narrow, it joins the hypocone and metacone. Roots as in M2.

m1: Occlusal outline is lozenge shape, longer than wide, wider posteriorly, with a well-rounded anterior margin. Labial cusps (protoconid and hypoconid) are slightly larger than the lingual cusps (metaconid and entoconid) and the anteroconid. Lingual cusps are located opposite to the anterior margin of labial cusps, with slight transverse offset of cusps. Tall anteroconid is single-cusped and slightly smaller than the other cusps, usually on the midline, with prominent wings that descend and curve posteriorly. Protoconid anterior arm is medium length, usually (3/4) directed toward the lingual side or centre of the anteroconid; it joins the anterolophid and/or the metalophid near the midline. Protoconid posterior arm is medium length, directed toward the posterolingual corner of the tooth to join the anterior mure near the midline. Protolophid I is minute; protolophid II is absent. Short hypoconid anterior arm is directed toward the lingual margin to join the posterior mure and entolophid. A metaconid posterior spur is absent. The short to

medium-length anterolophid, descends posteriorly from the anteroconid to join the metalophid and protoconid arm near the midline. Metalophid I is medium length, it descends anterolabially from the apex to join the anterolophid and protoconid arm near the midline; metalophid II is usually absent (14/15) or short; if present it descends posterolabially from the metaconid to join the protoconid base. A mesolophid is usually (10/15) absent, or long (3/15) or minute (2/15). Ectolophid and ectostylid are absent. Entolophid is medium length or short, it descends labially from the apex to join the posterior mure and hypoconid arm near the midline. Central mure is short and low or indistinct. If present it joins the protoconid arm at the base of the mesolophid, with the entolophid and hypoconid arm near the midline. Long labial anterior cingulum descends posteriorly as the labial wing of the anteroconid and terminates at the anterior base of the protoconid; lingual anterior cingulum is shorter and descends posteriorly to terminate at the anterior base of the metaconid. Transverse shelves overlap significantly, the lingual shelf is anterior to the labial shelf. Labial sinusid is wide and deep, oriented slightly oblique relative to the tooth orientation. Lingual cingulum low or indistinct; labial cingulum is higher and slightly longer than the lingual cingulum. Posterior cingulum is prominent and narrow, it descends lingually and curves anteriorly to terminate at the posterior base of the entoconid. Posterior labial sulcus is well-developed, distinct until late wear. Two roots are present, a prominent rounded anterior root and a transversely wide posterior root.

m2: Occlusal outline is a rounded rectangle, longer than wide and usually slightly wider posteriorly. Lingual cusps are slightly larger than labial cusps and are located opposite to the anterior margin of labial cusps (with significant transverse offset). Protoconid and hypoconid arms follow the pattern seen in m1. Metaconid posterior spur is absent or indistinct. Minute anterolophid usually located near (13/15) or slightly lingual to the midline. Short metalophid descends from the apex to join the protoconid anterior arm (9/14) or anterolophid (5/14). Mesolophid is usually absent (9/13) or minute and free (4/13). Short entolophid descends labially from the apex to join the posterior mure and hypoconid arm near the midline. Short central mure is located near the midline. Labial anterior cingulum is short and descends from the anterolophid and curves gently posteriorly to terminate at the base of the protoconid; lingual anterior cingulum is high and short, close to and merging with the metaconid short of the lingual margin. Transverse shelves are offset significantly with the lingual shelf anterior to the labial shelf. Labial sinusid is moderately deep, it expands internally. Lingual and labial cingula are short and low. Posterior cingulum has an incipient posteroconid at its base, the cingulum descends labially from the posteroconid and curves gently anteriorly near the labial margin

to terminate at the posterior base of the entoconid. Posterolabial sulcus is usually deep and distinct until late wear. Two roots are similar to those of m1.

m3: Occlusal outline is subtriangular with the long axis equal to tooth length and with a well-rounded posterior margin. Protoconid is larger than the metaconid, which is larger than the small hypoconid, the entoconid is represented by a minute thickening on the lingual cingulum. The metaconid is opposite to the centre of the protoconid – little or no transverse offset of cusps. Protoconid and hypoconid arms follow the pattern seen in m2, but the protoconid posterior arm is long, the posterior cingulum lacks a posteroconid, and it is robust. Anterolophid is minute, located near the anterior midline or slightly lingual to the midline. Short metalophid descends anteriorly from the apex to join the anterior cingulum slightly lingual to the midline. Entolophid is short, directed labially from the ghost entoconid and joins the arms of the protoconid and hypoconid slightly lingual to the midline. Central mure is indistinct, represented by the protoconid posterior arm. Labial and lingual anterior cingula as in m2. Labial sinusid is deep and usually (5/6) narrow. Lingual cingulum is high and continuous between the metaconid and posterior cingulum; labial cingulum is usually low and narrow (5/6), or indistinct. Posterior cingulum is robust and continuous with the lingual cingulum. Posterior labial sulcus is usually (5/6) indistinct, or shallow. Two heavy roots are present, a round posterior root and a transverse anterior root.

Discussion. *Myocricetodon* is a characteristic component of the small mammal fauna of the lower to middle Siwaliks. In the Potwar area, it is recorded from the Kamlial Formation and Chinji Formation up to about 13 Ma (Flynn et al. 1995). The common species through this range is *M. sivalensis*, which differs from *M. tomidai* in showing more derived features of reduced lophodonty and a weaker longitudinal crest. The apparent immigration of Myocricetodon as recorded in the Vihowa Formation is a familiar feature of Siwalik small mammal assemblages.

Potwarmus Lindsay 1988

Included species. *Potwarmus primitivus* Wessels et al. 1982, *P. minimus* Lindsay 1988, *P. thailandicus* Jaeger et al. 1985, *P. mahmoodi*, new species.

Potwarmus mahmoodi, new species

Holotype. PMNH 515, isolated left m1 from locality Z122, Vihowa Formation.
Referred material. Isolated cheek teeth 16 M1, 12 M2, 1 M3, 16 m1, 12 m2 and 2 m3 (Supplementary Table 5, Figure 9).
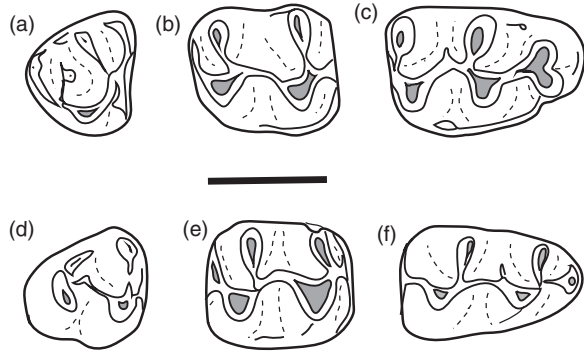
Figure 9. *Potwarmus mahmoodi.* Anterior is to the right. (a) PMNH 491, left M3 (reversed); (b) PMNH 479, right M2; (c) PMNH 397, right M1; (d) PMNH 410, right m3; (e) PMNH 511, right m2; (f) PMNH 515, left m1 (reversed; type). Scale bar = 1 mm.

Distribution and age. Localities Z120, Z122, and Z124 in the lower part of the Vihowa Formation, Zinda Pir Dome, central Pakistan, occurring in and below strata correlated to Chron C5En, approximately 19 Ma, Early Miocene.

Etymology. Named in honour of Dr. S. Mahmood Raza who supported Siwalik paleontological work for many years, first at the Geological Survey of Pakistan and later through the Higher Education Committee, and who inspired our work in the Zinda Pir Dome.

Diagnosis. Small muroid with M1 having a large asymmetrical anterocone (larger labially) and a lingual cingulum from the lingual anterocone to the hypocone (frequently incomplete near the protocone), commonly with a small or indistinct enterostyle. On M1 the paraloph and metaloph tend to join the protocone and hypocone posteriorly, but on M2 the paraloph and metaloph tend to join the protocone and hypocone anteriorly, enhancing formation of transverse parallel lophs rather than oblique lophs. For lower molars union of lophs with cusps is always anterior. Junction of the mure with adjacent cusps is weak anteriorly in upper molars and weak posteriorly in lower molars.

Differential diagnosis. *Potwarmus mahmoodi* is near the size of *P. primitivus*, but larger than either *P. minimus* or *P. thailandicus* (Supplementary Table 5) and has less massive cusps. The anterocone of *P. mahmoodi* is more deeply furrowed and less symmetrical than that of *P. primitivus* or *P. thailandicus* (see Mein and Ginsburg 1997). The lingual cingulum and its accessory enterostyle on M1–M2 are less well developed in *P. mahmoodi*. *P. mahmoodi* differs from *Potwarmus primitivus* and *P. minimus* as follows: (1) the mure (longitudinal crest) is higher and more prominent; (2) M1 anterocone is asymmetrical with a deep anterior sulcus and often a small anterior shelf; (3) M2 paraloph joins the protocone rather than the anteroloph; (4) m2 metalophid joins the anterolophid rather than the protolophid.

Description. M1: Occlusal outline is lozenge shape, longer than wide and slightly wider in the middle of the tooth. The anterocone is the largest cusp, followed in size by the protocone, the hypocone, the paracone and the metacone. Labial cusps are placed opposite the posterior margin of lingual cusps; lingual cusps are slightly inclined and elongated anteroposteriorly, whereas labial cusps are usually less inclined but more elongated transversely. A large anterocone is unequally bilobed with the labial cusp larger than the lingual cusp; the anterior surface of the anterocone has a deep sulcus between the lobes and commonly (9/15) a small shelf on the anterior base of the anterocone. Protocone anterior arm is long, directed anteriorly to join the anteroloph near the midline; protocone posterior arm is short, directed toward the labial margin to join the paraloph and posterior mure. Paracone posterior spur is rare (1/26) or minute. Long hypocone anterior arm is directed toward the paracone to join the posterior mure near the midline; hypocone posterior arm is short, directed toward the posterior midline to merge with the posterior cingulum. Anteroloph is indistinguishable; protoloph I is usually absent (15/16) or short and free; protoloph II (=protocone posterior arm) is short and joins the paraloph and posterior mure. A mesoloph is absent (7/14), or of medium length. An entoloph, rarely present (1/14) is medium length and free; a small entostyle is usually located at the posterior termination of the lingual cingulum (12/14) and may ascend the anterior hypocone (9/13). The mure is short and low and joins the protocone posterior arm and the hypocone anterior arm near the mesoloph. The lingual cingulum is long and low, usually (8/13) continuous between the anterocone and the hypocone; the labial cingulum is low between the anterocone and paracone and may (1/13) have a small labial anterostyle. Transverse shelves are offset (lingual side anterior to labial side), with slight overlap of area. The lingual sinus is usually blocked by the lingual cingulum and the enterostyle. The lingual cingulum is long and low, continuous to the hypocone (8/13); the labial cingulum is short and low; the medium length posterior cingulum is narrow and descends labially from the posterior midline to join the posterior metacone and enclose a narrow posterolabial atoll. Transverse shelves are offset (lingual side anterior to labial side), with slight overlap of area. The lingual sinus is usually blocked by the lingual cingulum and the enterostyle. There are three roots: a round anterior root, a large medial root that is elongated antero-posteriorly and a small round posterolingual root.

M2: Occlusal outline is trapezoidal, longer than wide, with the posterior width much less than the anterior width. Lingual cusps are larger than labial cusps, with labial cusps located opposite to the centres of lingual cusps (virtually no transverse offset of cusps). Protocone anterior arm is short, merging with the anteroloph lingual to or near the midline. Protocone posterior arm of medium length is directed toward the metacone and joins the anterior mure

near the midline (point of flexure). Protocone posterior spur is absent. Paracone posterior spur is usually absent (8/12), or weakly developed. Hypocone anterior arm is usually short (8/12) or medium length, directed toward the paracone to join the posterior mure near the midline. Hypocone posterior arm is short, directed toward the posterior midline to merge with the posterior cingulum. The high anteroloph is located lingual to the midline, directed posteriorly to join the protocone arm. A minute protoloph joins the paraloph near the midline; protoloph II is absent. The mesoloph is variable: usually absent or minute (8/12), or medium length (2/12), or long (2/12). The medium length metaloph descends lingually from the apex to join the hypocone anteriorly (5/10), or centrally (3/10), or posteriorly (2/10). An enterostyle is small (5/10), minute (3/10) or indistinct (2/10) on the lingual cingulum. The mure is short or medium length, variable in both height and orientation. The lingual anterior cingulum descends from the anteroloph, curves posteriorly and is very thin, usually continuous to the base of the hypocone; the labial anterior cingulum is high, descends from the anteroloph and curves posteriorly near the labial margin and may swell in height (4/12) before terminating at the paracone. Transverse shelves are wide and synclinal, with little or no offset. The lingual sinus is wide and deep. Lingual cingulum is continuous but very thin from the anteroloph to the hypocone; labial cingulum is low and short; posterior cingulum is medium length and thin, it descends labially from the posterior midline and terminates at the posterior base of the metacone. There are there three roots: a large and elongated medial root, plus small anterolabial and posterolabial roots.

M3: Occlusal outline is subtriangular, with rounded apices, almost equilateral. Largest cusp is the protocone followed by the slender paracone; the hypocone is virtually absent and a metacone is minute. The large central basin has a small 'island' posterior to its centre, joining a thin loph directed labially from the posterior arm of the protocone. There is a very small anterolingual shelf produced by the lingual anterior cingulum. The labial anterior cingulum is long and high, terminating at the anterolingual margin of the tooth. A thin posterior cingulum joins the minute metacone with the posterior protocone. A low discontinuous labial cingulum occurs between the paracone and metacone. Roots are not preserved.

m1: Occlusal outline is lozenge shape, longer than wide with greatest width near the posterior margin. Labial cusps (protoconid and hypoconid) are slightly larger than lingual cusps (metaconid and entoconid) which are larger than the anteroconid. Lingual cusps are placed opposite the anterior margin of labial cusps, with greater offset than in upper molars and lingual cusps are transversely elongated more than labial cusps. The anteroconid is small and single with wide tapering transverse 'wings;' position is usually (10/13) slightly labial to or on the midline. Protoconid anterior arm is usually (10/13) short, directed labially to join the metalophid and occasionally the anterolophid. Protoconid posterior arm is short, directed toward the entoconid to join the posterior mure near the midline. A protoconid posterior spur is absent; a metaconid posterior spur is usually absent (10/13) or weakly developed. Hypoconid anterior arm is short, directed toward the labial margin to join the entolophid or posterior spur near the midline; hypoconid posterior arm is short, directed toward the posterior midline to join the posterior cingulum. The anterolophid is medium length and narrow, descending posteriorly from the anteroconid to join the metalophid and protoconid arm near the midline. Short metalophid I descends labially from the metaconid to join the anterolophid and protoconid arm near the midline. A mesolophid is absent (7/13) or small. Entolophid is medium length, it descends posterolabially from the apex to weakly join the posterior mure and hypoconid arm near the midline. The mure is short, joining the protoconid posterior arm and the hypoconid arm near the midline. The labial anterior cingulum is short or medium length, it descends from the anterocone, curves posteriorly and terminates at the anterior base of the protoconid. The lingual anterior cingulum is short, it descends from the anterocone and terminates at the anterior base of the metaconid. The transverse shelves are slightly offset, with the lingual shelf more anterior and wider than the labial shelf; they are closed medially by the mure. Labial sinusid is wide and deep, slightly oblique relative to the tooth axis. Lingual and labial cingula are low; posterior cingulum is high and narrow, descending lingually from the midline, it curves or flexes anteriorly near the tooth margin to terminate at the posterior base of the entoconid. A posterolabially sulcus is usually deep (9/12) and persists until late wear. There is a small, round anterior root and a large, transversely wide posterior root.

m2: Occlusal outline is subrectangular, longer than wide, slightly wider posteriorly. Anterior cusps (protoconid and metaconid) are slightly larger than posterior cusps (hypoconid and entoconid), with lingual cusps more elongated transversely and located opposite the anterior side of labial cusps (slight anterior offset of lingual cusps). Protoconid and hypoconid arms follow the pattern seen on m1. There is a minute protoconid posterior spur in 4/13 specimens. The metaconid posterior spur is usually absent (10/13) or weakly developed. Anterolophid is short (6/11) or minute, located slightly lingual to the midline. The short metalophid descends anterolabially from the apex to weakly join the anterolophid (10/11) or the protoconid anterior arm. A mesolophid is usually absent (7/12) or minute (5/12) and terminates freely. An ectostylid is absent or indistinct. The entolophid is short (5/11), or medium length (5/11) or long, it descends labially from the apex to join the anterior hypoconid. The mure is medium length, it is moderately high and joins the arms of the protoconid and hypoconid. Labial anterior cingulum descends from the anterolophid and

continues (7/12) thinly around the protoconid arm or terminates (5/12) at the anterior protoconid. Lingual anterior cingulum, is high near the anterolophid, it descends and merges with the metaconid short of the lingual tooth margin. The transverse shelves are slightly offset (lingual side anterior) and relatively flat centrally, grading into a gently inclined anterior surface and steeply inclined posterior surface; transverse shelves are separated medially by the mure, and the lingual margin is slightly higher than the labial margin. Labial sinusid is wide and straight. The low labial cingulum is usually (7/12) continuous; lingual cingulum is low; posterior cingulum, is high near the midline, it descends and thins lingually to terminate at the posterior base of the entoconid. The posterior labial sulcus is well developed, diminishing with wear. There are two transversely wide roots, the anterior root is slightly narrower than the posterior root.

m3: Occlusal outline is a rounded triangle with a wide posterior margin. Three cusps are present: large protoconid, smaller hypoconid and metaconid; the entoconid is an indistinct thickening on the lingual cingulum. The protoconid weakly joins the minute anterolophid labial to the midline; the protolophid is minute, directed toward the short metalophid, and the protoconid posterior arm is long and narrow. Anterior arm of the hypoconid is minute or indistinct; posterior arm of the hypoconid is short and robust. Lingual cingulum is high, joining the metaconid and hypoconid with wear. Roots are unknown.

Discussion. *P. mahmoodi* is less derived than other species of *Potwarmus*. Its anterocone is more deeply divided and asymmetrical, the longitudinal crest is less reduced and the and on upper molars the enterostyle is less prominent on the lingual cingulum. Cusp arrangement of *Potwarmus* is similar to *Dakkamys*, but species of the latter genus are larger, with more stable lingual cingulum and more prominent enterostyle. *P. mahmoodi* differs from *Myocricetodon tomidai* in having a smaller anterocone and more continuous lingual cingulum on M1.

The Zinda Pir biostratigraphy shows the appearance of *Potwarmus*, a derived member of later Siwalik small mammal communities, at about 19 Ma. Like *Myocricetodon*, it is a modern muroid with affinity to Muridae. Both genera appear to be immigrants of the Early Miocene.

Conclusions

At the outset of this study we noted profound changes that occurred in the fossil record of muroid rodents during the Oligocene Epoch, and attempted to illustrate some of the morphological transformations observed in southern Asia, one of the centres of mid-Cenozoic mammalian evolution. Muroid rodents have a well-known historical biology and importantly have short life spans and enormous reproductive potential, with females capable of sexual maturity shortly after one month. If a female muroid lives for 12 months she will probably have had three or four litters, and will die of starvation, because her cheek teeth will have worn down to rooted pegs, unable to process her food. They also represent an enormous source of protein for numerous avian and mammalian predators.

Dentally, muroid rodents from the Zinda Pir Dome in Pakistan illustrate the reduction and loss of a spur from the protocone (protoconid) and its replacement by a transverse mesoloph (mesolophid) on the longitudinal crest in upper and lower cheek teeth; they also illustrate the enlargement of the anterior cusp, the protocone on M1 and the development of a continuous lingual cingulum, frequently with a cusp (the enterostyle), on upper molars. This contribution documents a part of that evolution; the conclusion remains to be documented.

The Muroidea of Bugti and the Zinda Pir Dome are rare (only *Atavocricetodon* at locality Z144) until the end of the Oligocene as shown by Cocu et al. (1999). In the Zinda Pir area, the terminal Oligocene is represented by localities Z113 and Z139. Muroids of this age, low in the upper part of the Chitarwata Formation, are stem representatives of later groups, *Prokanisamys kowalskii,* a rhizomyine, and species of *Primus*. These muroids are abundant in latest Oligocene assemblages, but do not show stable, derived molar morphology.

A low crowned but lophodont and much larger rhizomyine (the unnamed rhizomyine) accompanies *P. kowalskii* at Z135, debut of the Miocene. Also at this time, modern muroids appear: *Democricetodon khani* and *Myocricetodon tomidai*. This Early Miocene assemblage is distinct from Oligocene associations, but still not close to the microfauna characteristic of the later Siwaliks. The assemblage corresponds to 'Assemblage A' in the analysis of Antoine et al. (2013).

At the top of the Chitarwata Formation, locality Z126 (~20 Ma), and low in the overlying Vihowa Formation (Z124, ~19.5 Ma) more derived species appear (*Prokanisamys arifi* and *Potwarmus mahmoodi*). Somewhat higher in the Vihowa Formation (~19 Ma) rhizomyines have become diverse, with several co-occurring species of the genus *Prokanisamys*. Complementing fossils from the Bugti Hills, this microfauna corresponds to 'Assemblage B' of Antoine et al. (2013). By this time, muroids dominate the small mammal fauna in diversity and abundance, heralding the Siwalik muroid faunas of the middle to late Miocene.

Following is a synopsis.

Species at locality Z144: *Atavocricetodon* sp.

Z113–Z139: *Prokanisamys kowalskii*, *Primus microps*, *Primus cheemai*

Z150: *Prokanisamys kowalskii*, *Primus microps*, *Primus cheemai*

Z135: *Prokanisamys kowalskii*, large rhizomyine, *Primus microps*, *Primus cheemai, Myocricetodon tomidai*

Z126: *Prokanisamys arifi, Primus cheemai*

Z124: *Prokanisamys arifi, Primus cheemai, Potwarmus mahmoodi, Myocricetodon tomidai*

Z122: *Prokanisamys arifi, P. major, P.* minute sp., large rhizomyine, *Primus microps, Primus cheemai, Democricetodon khani, Potwarmus mahmoodi, Myocricetodon tomidai*

Z120: *Prokanisamys arifi, P. major, P.* minute sp., *Primus cheemai, Democricetodon khani, Potwarmus mahmoodi, Myocricetodon tomidai*

From the earliest Miocene, muroids are a major element of the small mammal fauna, and if the Zinda Pir record may be taken as indicative for the Indian Subcontinent, then Early Miocene assemblages retain archaic taxa until about 20 Ma. Thereafter, muroids become abundant and diverse, with increasingly advanced species, and representatives of living families. By 19 Ma, the Zinda Pir small mammal fauna had taken on aspects typical of the subsequent Siwalik small mammal assemblages. The Zinda Pir ranges of *Prokanisamys arifi, Primus microps* and *Democricetodon khani* may be used to estimate indirectly the age of the Murree assemblage at Banda Daud Shah (de Bruijn et al. 1981) at about 20 Ma.

Supplementary materials

Supplementary material related to this articles is available online http://dx.doi.org/10.1080/08912963.2015.1027888.

Disclosure statement

The authors receive no financial benefit from this research.

Note

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