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AN UNUSUAL DIATOMYID RODENT FROM AN INFREQUENTLY SAMPLED LATE MIOCENE INTERVAL IN THE SIWALIKS OF PAKISTAN

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ABSTRACT

The Siwalik deposits of Pakistan yield numerous superposed assemblages that record the small mammal fauna throughout the middle and late Miocene on the Indian subcontinent. A few stratigraphic intervals are poorly represented by microfaunas. Between older, rich Chinji Formation assemblages and fossiliferous levels high in the Nagri Formation, few fossil localities yield abundant rodents between about 11.3 and 10.4 Ma. Locality Y797, predating the first local appearance of hipparionine equids, is notable for presence of a new large diatomyid rodent, *Willmus maximus* gen. et sp. nov., recorded nowhere else. *Willmus* has affinity with *Diatomys* from China and Thailand and with predecessors such as *Fallomus* from the pre-Siwalik formations of Bugti and the Zinda Pir Dome, Pakistan. *Willmus* is derived in its large size, absence of accessory cusps, and extreme bilophodonty, and is by far the latest and rarest member of its group. Faunal similarity indices between Y797 and well-sampled older Chinji and younger Nagri rodent faunas are very high at the species level. Large mammal faunas are also similar. Fauna and lithology suggest nothing unusual about this locality and offer no compelling evidence for a unique microhabitat. *Willmus* is a derived end member in a distinct rodent group of low taxonomic diversity. This unusual family reappears in the Siwalik record at Y797 after a long absence from the fossil record. It is perhaps the derived features of *Willmus* that contributed to the survival of this group.

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INTRODUCTION

Will Downs was one of the grand old men of the Siwaliks. His knowledge of Siwalik fossils, localities, and stratigraphy was extensive and, due mainly to his tenacity and drive, the biostratigraphy of Siwalik microfauna was built as arguably the finest long sequence of superposed microfaunas in the world. One hundred screenwash localities span the 18 to 6 Ma Potwar Plateau sequence in northern Pakistan. Will also added other sites, notably those from the older Zinda Pir Dome in western Pakistan. Ten thousand small mammal specimens document this composite sequence. Some portions of the record are represented by about 10 fossil sites per million years; of these, some sites are separated by less than 100,000 years. Elsewhere, the record is poorly documented with gaps approaching a million years. Ten years ago, our primary small mammal collecting agenda was to reduce the number of substantial gaps in the fossil record by targeting specific intervals. One of us (MEM) had the good fortune to find a rich microsite in the lower part of the Nagri Formation, an interval otherwise poorly known by only a few sparse large mammal localities. Will enthusiastically returned to Y797 the following year to recover more material. Among the abundant small mammal teeth in this site are two specimens of an odd, large rodent. Our purpose is to describe this rodent and its provenance, and discuss both with respect to their Siwalik context.

Biostratigraphic Sequence

The following discussion of the fossiliferous sequence of the Potwar Plateau considers major collection localities, both those yielding large mammals and/or small mammals. The Chinji Formation of the Potwar Plateau produces many classic Siwalik fossils from well-known horizons (Colbert 1935). In our experience (Barry et al. 1995), the Chinji Formation, comprised predominantly of reddish mudstones, is densely fossiliferous in its middle part, and becomes less fossiliferous upwards. The superposed Nagri Formation, dominated by thick sandstones, has a low density of localities, although near the top the famous Sethi Nagri locality complex (our site Y311) is highly productive. Above this are the many localities of the Dhok Pathan Formation.

Whereas the density of small mammal fossil horizons is on the order of one per 100,000 years in the middle Chinji Formation (Flynn et al. 1998), that frequency declines upward. There was a gap of about a million years between upper Chinji and younger Nagri sites when Barry et al. (1990) analyzed the overall rodent record. In that analysis, the gap centered around 10 Ma; current paleomagnetic time scales make it older.

The youngest well-sampled small mammal localities of the Chinji Formation in the Gabhir Section east of Chinji and Bhilomar are Y504 and Y76, 11.5 and 11.3 Ma, respectively, using the Cande and Kent (1995) time scale. Y311 is much younger, at 10.0 Ma. In the Kaulial Kas section, approximately 50 km to the northwest from the Gabhir Section, locality Y259 is a productive small mammal site lower in the Nagri Formation at 10.4 Ma. We attempted explicitly to fill this gap of nearly one million years by intensive field surveys in 1989. We screened previously identified sites and found several new localities in the lower part of the Nagri Formation.

Locality Y799 produces one of the oldest local occurrences of a hipparionine horse. Its age is 10.7 Ma (Pilbeam et al. 1996). Lower still are two localities, Y791 at 11.2 Ma and Y797 at 11.1 Ma. The former has few fossils, but does yield interesting tree shrew material. The latter proved to be one of our richest small mammal localities, currently about 330 catalogued specimens. Although not squarely in the middle of the long "small mammal gap," Y797 provides a large enough sample (Flynn et al. 1998) to offer an informative view of the Siwalik small mammal fauna in the early late Miocene.

Geological Setting

Locality Y797 is located in the lower portion of the Nagri Formation, a formation dominated by large sandstones. In this region the beds dip at approximately 15 degrees to the northwest. The sandstone locally referred to as GB2 is superposed over the locality and is a complex, multi-storied sand more than 15 m thick that can be traced laterally for several kilometers (Willis 1992). Beneath Y797 is the sandstone GB1.5, locally several meters thick. The lithology of Y797 consists of lenses of red silt and gray sand with pockets of a sandy clay and calcium carbonate nodule conglomerate that are part of a small-scale floodplain channel sandwiched between GB1.5 and GB2. The eastern edge of the channel was observed clearly, but a convincing western edge was not identified in the field. We presume that the western edge was cut out by an adjacent channel to the west. The locality and capping and underlying sandstones are illustrated in Figure 1.

This floodplain channel, measuring approximately 75 m wide and 3 m thick, is comprised primarily of coarse to mixed sand and silt with preserved bedding. The upper portion (1 to 1.5 m)

Figure 1. Photo by Will Downs, 1990, looking northeast from outcrop of the GB1.5 sandstone. Y797 is marked by an arrow pointing to full sacks of matrix about 1 m tall. GB1.5 can be seen to thin to the east. The more dominant sandstone GB2 can be seen immediately above Y797.

is mostly red silt and is not very fossiliferous. The underlying 2 m of section are comprised of red silt and gray sand lenses, with a sandy clay and calcium carbonate nodule conglomerate, which could represent a small-scale splay deposit. Small bone is densest in the conglomerate, which appears to thicken and become coarser and less sandy to the west. The small mammals were sampled from two places within this lower layer (see Figure 2). One sampling location is visible in the photo. The second place is stratigraphically slightly higher and is on the south side of the hill. Surface collected large mammal bone is generally quite weathered and white in color, in contrast to better fossil preservation at most localities of similar lithology in the Gabhir Kas section.

SYSTEMATICS

Family DIATOMYIDAE Mein and Ginsburg, 1997
Genus *WILLMUS*, new

Diagnosis: Large diatomyid, most high crowned absolutely and relative to size, strongly bilophodont with lophs closely positioned and cusps suppressed, lophs nearly straight (except anterior loph of dp4), no accessory cuspules, no hint of posterior cingulum on dp4.

Type Species: (only known species): *Willmus maximus*, new species.

Etymology: Named for famed fossil hunter Will Downs, plus *mus*, Latin for mouse.

Willmus maximus, new species

Figure 2. Photo by Will Downs, 1990, looking southeast from top of portion of the multi-storied sandstone locally named GB2. Arrow denotes one of two sampling locations for small mammals. The white bags of matrix each measure about a half meter across. The second sampling location is on the south side of the small mound and is obscured from view. The local topography of the region and the northern dip of the beds are well illustrated.

Holotype: GSP 33100, right dp4.

Hypodigm: GSP 33100, plus GSP 36161, left M3.

Type Locality: (only known occurrence): Y797, lower part of Nagri Formation, Gabhir section of the Potwar Plateau, 11.1 Ma.

Diagnosis: As for genus, only member of the genus.

Etymology: *maximus*, Latin for greatest, invoking the greatest member of this mouse lineage, and the greatest mouse hunter, Will Downs, or, if you will, "mighty mouse."

Description: Both specimens are strongly bilophodont and high crowned (Figures 3, 4). GSP 33100 is well preserved, moderately worn, and the enamel is light brown in color. GSP 36161 is less worn, but the enamel is corroded. It is possible, although improbable, that the two teeth represent the same individual. Many rodents, including rhizomyids, have delayed eruption of last molars such that anterior dentition is considerably worn before M3 erupts.

The lower premolar is narrow anteriorly, as is characteristic for the family (see below), with inclined lophs. The leading crest has a rounded V-shape derived from a linked protoconid-anteroconid-metaconid. The protoconid portion of the V is slightly thicker and the posterior cleft of the V is lingual to the midline of the tooth. The posterior loph is nearly straight and slightly oblique (ento-

Figure 3. Digital images of premolar (left) and molar (right) of *Willmus maximus,* in occlusal (above) and side views. GSP 33100 on the left in occlusal and labial views; GSP 36161 on the right in occlusal and lingual views, scale bar in mm. See Figure 4.

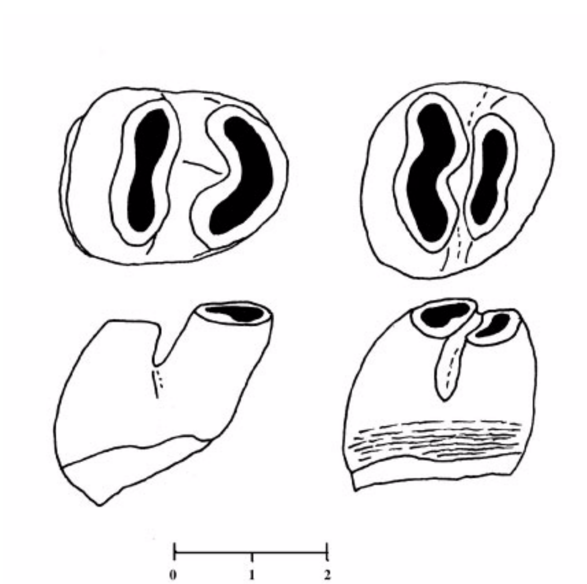

Figure 4. Interpretive line drawing with 2 mm scale of photos in Figure 3: GSP 33100 on the left in occlusal and labial views; GSP 36161 on the right in occlusal and lingual views.

conid end slightly anterior to hypoconid), and with gently invaginated anterior wall. There are no stylids or cingula. The valley between transverse lophs is equally open on each side, descending to about 0.9 mm above the base of the enamel on each side. The base of the enamel undulates slightly. In lateral view, loph inclination is clear, and the occlusal wear planes on each loph slope anteriorly. Holding the tooth in anatomical position with the base of the enamel horizontal, the dimensions are 2.95 mm long and 2.33 mm wide (length would be slightly greater in an unworn tooth, due to the inclination of the crown). Root structure is unknown, but the base of the crown suggests two posterior roots. It is unknown whether GSP 33100 is p4 or dp4.

M3 appears slightly inclined posteriorly, with a vertical posterior loph and slanted anterior wall of the first loph. The base of the enamel undulates slightly and length equals width (2.43 mm). The first and larger loph has a gently convex anterior wall and posterior wall invaginated at the midline of the tooth. This loph represents the joined protocone-paracone of equal size. The second loph is a shorter figure-8 representing the smaller, fused hypocone-metacone. The base of the metacone appears to be larger than the base of the hypocone and is probably supported by an independent root. The hypocone is labial with respect to the protocone. The lophs are tightly appressed, but valleys at each end are open and rise to within 0.8 mm of the enamel-dentine junction. The two lophs in early attrition appear to share a common wear plane with some unevenness suggesting oblique power strokes; observed crown height, greater anteriorly, is 2.0 mm. At high magnification fine perikymata representing enamel prism decussation are visible on both sides of the M3, although they are more pronounced on the lingual side where the enamel surface is somewhat corroded.

Discussion: This unique taxon is distinguished by derived features of large size, considerable crown height, extreme bilophodonty, and absence of accessory cusps or cingula. It is derived with respect to *Diatomys* from the late early and early middle Miocene of China, Thailand, and Pakistan. It is also derived with respect to the more bunodont *Fallomus* and unnamed related Oligo-Miocene forms from Pakistan and India. These genera constitute the known record of this enigmatic Asian family of rodents.

Li (1974) described *Diatomys shantungensis* for a nearly complete, but deteriorated skeleton preserved in diatomites at Shanwang, a key reference locality for the early middle Miocene of China. In view of the transversely lophodont cheek teeth, Li (1974) considered geomyoid and pedetoid affinity of this form but was not satisfied with familial identification. The skull was too poorly preserved to indicate higher taxon relationships; the teeth were clearly advanced in being quadrate, bilophodont, and multirooted. *D. shantungensis* dentition is comparable in size to that of *Willmus maximus* (see table in Li 1974). The M3 (length, width = 2.65, 2.8 mm) is larger than that of *Willmus,* but the premolar (length, width = 2.6, 1.9 mm) is smaller.

Flynn et al. (1986) named another bilophodont rodent, this one from the Bugti assemblage of Baluchistan, Pakistan. *Fallomus razae* was so named, being mouse like in transverse arrangement of cusps, but obviously not a murine, being derived from a generalized ctenodactyloid dental pattern. Affinity with the more derived *Diatomys* was recognized. Hypothesized membership of *Fallomus* in the ctenodactyloid Chapattimyidae led Flynn et al. (1986) to support affinity to Pedetidae within Hystricognathi for these genera.

Mein and Ginsburg (1985) explicitly supported a pedetid relationship for diatomyids when they named *Diatomys liensis* for material from the early Miocene of Thailand. They demonstrated diversity in the generic content of *Diatomys*. They also noted that similar unnamed forms had been found in at least two sites in Pakistan (see de Bruijn et al. 1981; de Bruijn and Hussain 1984). Later, Mein and Ginsburg (1997) described the variation present in a large sample of *D. liensis* and formally named Family Diatomyidae under Superfamily Ctenodactyloidea. *D. liensis* was distinguished by smaller size and frequent presence of an ectostylid in m1 and by a reduced anterior cingulum on DP4 and posterior cingulum on dp4. This species, although smaller than *Willmus maximus*, (M3 average length, width: 2.02, 2.18 mm; dp4: 2.00, 1.44) shows relative crown height rivaling that of *Willmus* (height of unworn M3 about 1.5 mm).

By the end of the millennium, additional fossils known from various sites of the Indian subcontinent began to place *Fallomus* in temporal context with *Diatomys*. Kumar et al. (1996) found diverse and high crowned *Fallomus* in the late Oligocene or early Miocene Kargil Formation, Ladakh, India, as well as a new rodent, *Wakkamys hartenbergeri*. The latter, a primitive cricetid, tends to support Oligocene age of the locality. This fauna argues for considerable antiquity of *Fallomus* predating *Diatomys*. Nanda and Sahni (1998) formally named the Kargil species as *Fallomus ladakhensis* to emphasize its advanced nature over *Fallomus razae*.

Marivaux and Welcomme (2003) demonstrated Oligocene age of basal Bugti assemblages and recognized diversity in their large sample of *Fallomus* from Paali, Bugti. The pre-Siwalik early Miocene Zinda Pir sequence (Downing et al. 1993) yielded undescribed material from several sites intermediate in morphology and age between *Fallomus* and *Diatomys*. The Siwaliks of the Potwar Plateau also produced additional material of *Diatomys* from locality Y747 near the base of the Kamlial Formation.

Evolution of the Diatomyidae on the Indian subcontinent involves suppression of the ctenodactyloid crown pattern by bilophodonty, through fusion of cusps, and increasing crown height. The bunodont ctenodactyloid pattern, with low ridges connecting cusps, is evident in *Fallomus*. *Fallomus* has deciduous and permanent fourth premolars, as well as P3. Third molars are large, premolars are the smallest cheek teeth and primitively replaced, and lower teeth have a characteristic hypoconulid. In addition, upper molars (and P4 of *Fallomus*) show an extra internal cusp, the entostyle, while lower teeth have an external ectostylid. The p4 and dp4 show three cusps in the anterior arcuate or V-shaped loph: the protoconid, anteroconid, and metaconid.

Diatomys joins opposite cusps in transverse lophs. Teeth are quadrate, and there is no indication of premolar replacement, meaning that the deciduous premolar is retained throughout life. Because *Willmus* is derived with respect to *Diatomys*, we interpret its single premolar as deciduous. Hypoconulids are lost but evidenced in some specimens by a posterior cingulum. Crown height is somewhat increased. An intermediate stage is present in fossils from Zinda Pir locality Z113, and from the Murree Formation equivalent site HGSP 116 (de Bruijn et al. 1981). Lower premolars from each (Flynn 2000) show retention of the ectostylid and hypoconulid. Unpublished specimens from Z113 suggest that the entostyle is lost in upper teeth, but show two premolar morphologies, indicating replacement in this intermediate, pre-*Diatomys* form.

Willmus continues the trend of simplification. Lower premolars have a straight posterior loph and a V-shaped leading crest. No ectostylid or posterior cingulum is in evidence. The posterior wall of the tooth slants steeply and drops almost vertically near the base of the crown. The upper molar of *Willmus* is simply bilophodont, with no indication of an entostyle. Both teeth are high crowned and large. Crown height appears to have been achieved to an equal extent on both the lingual and labial sides of the teeth; there is no unilateral development of hypsodonty. This interesting element of the Middle Siwalik fauna is the latest and most derived of its small group. A taxon of archaic origin, it persisted through the middle Miocene, evidently at low abundance in the Siwaliks.

COMPARISON OF FAUNAS

Y797, situated in the lower part of the Nagri Formation, provides an opportunity to evaluate to what extent the facies change between the Chinji and Nagri Formations is associated with faunal change, with particular emphasis on small mammals. There are at least 38 mammal taxa present in the recovered sample of 528 specimens from Y797, comprising 21 rodents, three other small mammals, and 14 larger mammals (Table 1). In addition, ostracods, fish, amphibians, turtles, lizards, snakes, crocodiles, and a bird are documented; *Acrochordus* snake vertebrae are abundant.

Dense sampling at levels dating from 11.3 to 11.5 Ma and 10 to10.4 Ma, with extensive prospecting in between, have allowed for detailed faunal comparisons across these horizons (e.g., Barry et al. 1995). Among large mammals, there is substantial change in faunal composition, including the appearance of hipparionine equids at 10.7 Ma (Pilbeam et al. 1996). A significant cluster of taxa that persists for nearly four million years has last appearances at 10.3 Ma. These include the giraffid, *Giraffokeryx punjabiensis*, and two suoids, *Listriodon pentapotamiae* and *Conohyus sindiensis*. Notable first appearances between from 10.2 and 10.3 Ma include the larger giraffid, *Bramatherium megacephalum*, the larger suoid, *Hippopotamodon sivalense*, and the first large bovid, *Selenoportax vexillarius* (Barry et al. 2002). In addition, three tragulid species have last appearances between 10.4 and 10.7 Ma, and three other tragulid species have first appearances between 10.3 and 10.4 Ma. The bovids also show marked species change during this 0.9 m.y. interval, with last appearances of several dominant Chinji taxa (Barry, personal commun. June 2004). Most of the large mammal faunal change between 10 and 11.5 Ma appears to occur in the younger half of this interval. The Y797 large mammal fauna, though currently represented by only 14 taxa, supports this interpretation with faunal composition similar to upper Chinji localities. *Giraffokeryx punjabiensis*, *Listriodon pentapotamiae*, and *Conohyus sindiensis* are all recorded at Y797. However, Y797 does record the first appearance of an unnamed tragulid species.

Rodents support the same conclusion of overall close similarity to Chinji faunas and difference from younger Nagri assemblages. The small mammal record, previously nearly unknown between Chinji locality Y76 at 11.3 Ma and Y259 at 10.4 Ma, is enhanced for various rodent groups, e.g., cricetids, murids, ctenodactylids (Lindsay 1988; Jacobs and Downs 1994; Baskin 1996), by data from Y797 and other smaller assemblages (Cheema et al. 2000). Ongoing taxonomic revision of Siwalik microfauna, e.g., Lopez-Antoñanzas and Sen (2003) tends to alter taxon names, but numbers of taxa and lineages are stable, lending support to our conclusions.

The rodent fauna of Y259 differs moderately in species composition from that of Y76, with five first appearances at Y259 and seven last appearances at Y76. Two *Democricetodon* species are not present at Y76 but extend into rocks younger than Y259. Y797 affords a look at the small mammal record during the lower portion of this interval. Percent similarity comparisons of the rodent taxa at Y259, Y797, Y76, and Y504 range from 63% to 84% (Table 2). This percent similarity is calculated by taking the number of common species, divided by the lesser of the two species richnesses. Y797 is taxonomically close to all; Y259 differs more from the Chinji localities than it does from Y797. Y797 extends downward from Y259 the range of

Table 1. List of all recovered specimens from locality Y797 with current taxonomic attributions.

HIGHER TAXON	GENUS	SPECIES	SPECIMENS
Ampullariidae	*Pila*	species	1
Vertebrata	Indet. genus	indet. species	4
Osteichthyes	Indet. genus	indet. species	28
Amphibia	Indet. genus	indet. species	1
Chelonia	Indet. genus	indet. species	2
Lacertilia	Indet. genus	indet. species	2
Ophidea	Indet. genus	indet. species	98
Crocodylia	Indet. genus	indet. species	3
Mammalia	Indet. genus	indet. species	9
Erinaceidae	*Galerix*	*rutlandae*	2
Soricidae	Indet. genus	indet. species	3
Chiroptera	Indet. genus	indet. species	1
Sciurinae	cf. *Heteroxerus*	species	2
Tamiini	*Eutamias*	urialis	3
Petauristinae	cf. *Hylopetes*	species	1
Petauristinae	cf. *Hylopetes*	big species	1
Cricetidae	Indet. genus	indet. species	8
Copemyinae	*Democricetodon*	indet. species	9
Copemyinae	*Democricetodon*	species D	3
Copemyinae	*Democricetodon*	species E	9
Copemyinae	*Democricetodon*	species B-C	2
Copemyinae	*Democricetodon*	species F	1
Copemyinae	*Democricetodon*	species G	3
Copemyinae	*Democricetodon*	species H	11
Myocricetodontinae	*Myocricetodon*	indet. species	2
Dendromurinae	*Dakkamyoides*	*perplexus*	1
Dendromurinae	*Dakkamys*	*asiaticus*	3
Dendromurinae	*Paradakkamys*	*chinjiensis*	11
Tachyoryctinae	*Kanisamys*	*nagrii*	117

one species, the murid, *Karnimata* sp. A; it does not record the other four newly appearing taxa present at Y259, *Ratufa sylva*, *Eutamias new sp., Rhizomyides punjabiensis*, and an unnamed murid species. Y797 extends the range upward of four of the seven taxa previously last found at Y76, *Eutamias urialis*, cf. *Hylopetes* big sp., *Dakkamyoides perplexus*, and *Myocricetodon* sp. Two other taxa, *Kanisamys indicus,* and *Megacricetodon daamsi* have last appearances at Y76, although *M. daamsi* is rare enough that this could be a sampling issue. The seventh taxon is a unique undescribed murid currently only known from Y76. Thus, both Y76 and Y259 record unique murid species currently unidentified elsewhere, and Y797 preserves two rodent species not found elsewhere, *Willmus maximus* and an additional species of *Sayimys* (sp. B of Baskin 1996). In addition, Y797 extends the known ranges of five taxa in the fossil record, including one first and four last appearances of taxa. The relative abundance of rodent taxa at Y797 also indicates general comparability with most well sampled lower and middle Siwalik localities. Murines and tachyoryctines are dominant. Together these two subfamilies comprise more than 70% of all recovered specimens at Y797 and are distributed among three species. Cricetids, which dominate the lower and middle Chinji For-

Table 1 (continued).

HIGHER TAXON	GENUS	SPECIES	SPECIMENS
Murinae	Unidentified genus	unident. species	61
Murinae	*Progonomys*	*hussaini*	16
Murinae	*Karnimata*	species A	32
Myoxidae	*Myomimus*	*sumbalenwalicus*	3
Ctenodactylidae	*Sayimys*	*chinjiensis*	14
Ctenodactylidae	*Sayimys*	species B	6
Diatomyidae	*Willmus*	*maximus*	2
Carnivora	Indet. genus	indet. species	5
Viverridae	Indet. genus	indet. species	1
Paradoxurinae	*Paradoxurus*	new species	1
Elephantoidea	Indet. genus	indet. species	1
Artiodactyla	Indet. genus	indet. species	6
Suidae	Indet. genus	indet. species	14
Listriodontinae	*Listriodon*	*pentapotamiae*	1
Tetraconodontinae	*Conohyus*	*sindiensis*	1
Suinae	*Hippopotamodon*	new species	4
Tragulidae	Indet. genus	indet. species	1
Tragulidae	*Dorcabune*	*anthracotherioides*	1
Tragulidae	*Dorcatherium*	new species	2
Tragulidae	*Dorcatherium*	*majus*	2
Sivatheriinae	*Giraffokeryx*	*punjabiensis*	1
Bovidae	Indet. genus	indet. species	9
Chalicotheriini	*Chalicotherium*	*salinum*	1
Rhinocerotidae	Indet. genus	indet. species	1
Rallidae	Indet. genus	indet. species	1
Total number specimens:			528

mation, are progressively less common, although interestingly they remain diverse throughout the Chinji and into the lower part of the Nagri Formation, with six taxa represented at Y797. The sciurids and ctenodactylids are stable members of Siwalik faunas at relatively low abundances. Thus, in patterns of abundance as well as species composition, Y797 is similar to upper Chinji Formation microfaunas, except for the presence of the diatomyid, *Willmus maximus*.

Willmus is represented by two teeth from among the 321 rodent specimens recovered. *Willmus* is large, with a body mass exceeding 250 g by reference to larger tachyoryctine rhizomyids, and there should be minimal collecting bias against its recovery. Possibly there was taphonomic bias against its preservation if it was not on the menu of preferred prey by predatory concentrators. *Willmus* is among the largest of the Siwalik rodents, exceeded in size by large *Brachyrhizomys* and *Hystrix* of the upper Siwaliks. It is truly a unique, rare taxon amongst a fairly typical "Chinji" fossil assemblage in the lower Nagri Formation that precedes the larger scale faunal and climatic changes of the upper middle Siwaliks.

CONCLUSIONS

The rare, large diatomyid *Willmus maximus* occurs only at locality Y797 in the Nagri Formation of the Potwar Plateau. There is no evidence of a precursor to this species in the Chinji Formation and no successor known anywhere. Like Will Downs, this taxon is unique, a fascinating character mixed in with a fairly typical group of suspects. Because the depositional context is common for the Siwaliks, that is, a floodplain setting near major streams, and because the faunal composition is so

Table 2. Percent similarity indices of rodent faunas from Y797 and adjacent rich localities, Y259, Y76, and Y504. Percent similarity is a ratio of the number of shared taxa between two localities to the number of taxa at the locality with fewer species.

	Y504 (N=18)	**Y76 (N=19)**	**Y797 (N=21)**	**Y259 (N=19)**
Y504 (11.5 Ma)	-			
Y76 (11.3 Ma)	83%	-		
Y797 (11.1 Ma)	83%	84%	-	
Y259 (10.4 Ma)	72%	63%	79%	-

similar to older Chinji assemblages, we do not attribute the record of *Willmus* to unusual conditions of preservation. What conditions in the fossil record are required to assert that a taxon is "rare?" If any taxon can be called rare, *Willmus* can; its fossils are few in number and encountered at a single locality exhibiting usual taphonomic conditions.

Additional circumstances remain a mystery. *Willmus maximus* is the youngest (by far) and most derived of the diatomyids. It is high crowned, truly bilophodont, and simplified in loss of accessory cusps. This may correlate with specialized diet or habitat. It may have been subterranean (at a time before rhizomyines radiated into this niche), but this is conjecture. Was *Willmus* preserved in the Siwaliks because the family had evolved to succeed in a niche not previously exploited? Possibly the group survived through the middle Miocene in Southeast Asia and reappeared in the Siwaliks in a transformed state in the late Miocene, or a temporary shift toward preferred habitat allowed its return to the Potwar. Whatever influenced its preservation, *Willmus* was not long-lived in the Siwaliks; the rich assemblages from upper parts of the Nagri Formation and the U-level of the Dhok Pathan Formation yield no trace of Diatomyidae.

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