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Rodents of the Miocene Daud Khel Local Fauna, Mianwali District, Pakistan. Part 1. Sciuridae, Gliridae, Ctenodactylidae, and Rhizomyidae

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Abstract: Approximately 1,000 rodent cheek teeth were recovered from a single Miocene locality ten meters stratigraphically below the local top of the Chinji Formation. Four of the fossil rodent taxa represented in this collection are described here. *Eutamias (Eutamias) urialis* n. sp. is the first chipmunk known from South Asia and the earliest known from Asia. The P^3 of *E. urialis* was a functional tooth and much larger relative to the other cheek teeth than in living chipmunks. A glirid, *Myomimus sumbalenwalicus* n. sp., is the first South Asian fossil representative of its family to be described. *Myomimus sumbalenwalicus* is similar to living *M. personatus* in the small size of its P^4, but appears more closely related to the European Miocene species *M. dehmi.* A large sample of the ctenodactylid *Sayimys sivalensis* has been recovered at Daud Khel. As the largest sample of a Miocene ctenodactylid yet known, it provides useful information on variability within a population. All described South Asian ctenodactylids are considered to represent *S. sivalensis,* which is distinct at the generic level from the African *Metasayimys* and *Africanomys* and the central Asian *"Sayimys" obliquidens. Sayimys sivalensis* may be a descendant of *"Sayimys" obliquidens* and ancestral to *Metasayimys.* A rhizomyid, *Kanisamys indicus,* is well-represented at Daud Khel. Although similar to the later *K. sivalensis* in its range of occlusal morphology, *K. indicus* is significantly smaller.

INTRODUCTION

Neogene fluvial sedimentary rocks of the Siwalik Group near Daud Khel, at the western edge of Pakistan's Potwar Plateau, have been studied by the Howard University-Geological Survey of Pakistan project since 1976. Previous reports have discussed the area's stratigraphy and presented faunal lists of the fossil vertebrates recovered from various levels (Munthe *et al.*, 1979; Hussain *et al.*, 1979). A vertebrate assemblage from sites near the local top of the Chinji Formation northeast of Daud

Khel has been designated the Daud Khel local fauna (Hussain *et al.*, 1977), and a new species of artiodactyl from this fauna has recently been described (West, 1980). Some of the fossil rodents of the Daud Khel local fauna are described here. A second paper will consider the Cricetidae and Muridae and the biostratigraphic, paleoecologic and paleozoogeographic implications of the rodent fauna. The Insectivora of this fauna will be discussed in a separate paper.

Despite numerous earlier studies, the fossil rodents of the Siwalik Group are poorly known. Rodents have been described and discussed by Colbert (1933, 1935), Hinton (1933), Wood (1937, 1977), Lewis (1939), Prasad (1970), Black (1972a), Jacobs (1977, 1978), Hussain *et al.* (1977), Vasishat (1978), and Pilbeam *et al.* (1979). Earlier work was summarized by Black (1972a). Jacobs' ongoing studies of the rodents of the classic Siwalik Group sections on the Potwar Plateau are reflected in his discussions of the Rhizomyidae and Muridae (Jacobs, 1977, 1978) and in the faunal lists presented by Pilbeam *et al.* (1979), which give the first indication of the succession of rodent faunas within the Siwaliks.

Only the rodent faunas being studied by Jacobs and the Daud Khel rodent fauna described below are based on large numbers of specimens. The Daud Khel sample comprises by far the largest number of rodent specimens yet recovered from a single Siwaliks locality. It therefore represents relatively completely the rodent fauna living at one time in one place. Six families and at least nine species of rodents are represented at Daud Khel. The sciurid, glirid, ctenodactylid and rhizomyid from Daud Khel are described here.

GEOLOGIC SETTING

The stratigraphy of the Daud Khel Siwalik Group section has been discussed in detail elsewhere (Munthe *et al.*, 1979; Hussain *et al.*, 1979), and the regional setting of the Daud Khel local fauna has been briefly described (Hussain *et al.*, 1977). The vertebrate taxa from Howard-Geological Survey of Pakistan localities 17, 18, 19, 130, 131 and 134 (Hussain *et al.*, 1979, Fig. 2) are included in the local fauna. Most of the taxa and specimens of the Daud Khel local fauna were recovered from localities 17 and 18. All the large vertebrates listed by Hussain *et al.* (1977) are represented at locality 17, while all the small vertebrates, including *Dorcatherium minimus* (West, 1980), are from locality 18.

The Daud Khel local fauna sites are in the upper part of unit 59 of the Daud Khel section (Hussain *et al.*, 1979), which is the uppermost red mudstone bed of the Chinji Formation. This unit is 34 meters thick and consists of massive claystone to siltstone with occasional lenses of very fine-grained sandstone up to one meter thick. Locality 17 is 15 meters below the top of unit 59, which is the local Chinji Formation-Nagri

Formation contact (Munthe *et al.*, 1979). Fossils at locality 17 were recovered from both a thin sandstone bed and the surrounding siltstone beds. Locality 18 is 700 meters south-southeast of locality 17 and five meters higher in unit 59.

Locality 18 consists of a single resistant ledge which is approximately 40 centimeters thick and extends for less than ten meters along strike (Hussain *et al.*, 1977, Fig. 5). It is eroded away at the south end of the exposure and merges abruptly into siltstone at the north end. Approximately 30 square meters of the fossil-producing bed is exposed.

The lithology of locality 18 is unique in the Daud Khel section. The rock is a bright red granular calclithite with silt to fine-grained sand matrix and granule clasts. The calcareous cementation is irregular, tending to unite grains in resistant pellets and stringers. The clasts are frequently well-preserved fossils, including fish, amphibian and reptile remains in addition to abundant mammal teeth and rare charophytes.

MATERIALS AND METHODS

All the fossils described below were recovered from Howard University-Geological Survey of Pakistan locality 18 at 32°55′45″N and 71°39′20″E, approximately one kilometer northeast of the village of Sumbalenwala, Mianwali District, Pakistan. The sample comprises approximately 1,000 rodent specimens, most of which are isolated cheek teeth recovered during screen-washing of 1,000 kilograms of sediment by Howard-Geological Survey of Pakistan personnel during 1976 and 1977. The repository for these specimens is the National Museum of Natural History, Islamabad, Pakistan. Epoxy casts of type and figured specimens are at the Milwaukee Public Museum, Milwaukee, Wisconsin.

Acronyms used herein are: H-GSP = Howard University-Geological Survey of Pakistan, MPM = Milwaukee Public Museum, FMNH = Field Museum of Natural History, GSI = Geological Survey of India, YPM = Yale Peabody Museum.

All measurements indicated in tables are in millimeters. Abbreviations used in the tables are: N = sample size, OR = observed range, X = sample mean, s = sample standard deviation, V = sample coefficient of variation.

For tooth cusp terminology of sciurids see Black (1963, Fig. 3) and for method of measuring sciurid teeth see Van de Weerd (1976, Fig. 27). For tooth cusp terminology of glirids see Storch (1978, Fig. 43). Tooth terminology of Miocene ctenodactylids is that generally applied to morphologically simple rodents. For tooth terminology of rhizomyids see Jacobs (1978, Figs. 3, 4). Measurements of the hypsodont ctenodactylids and rhizomyids are maxima, rather than highly variable occlusal measurements, and were taken as nearly as possible parallel to or perpendicular to the long axis of the tooth row.

SYSTEMATIC PALEONTOLOGY

Family Sciuridae Gray, 1821
Subfamily Sciurinae Baird, 1857
Genus *Eutamias* Trouessart, 1880
Subgenus *Eutamias (Eutamias)* Trouessart, 1880
***Eutamias urialis* new species**
(Figures 1-3; Table 1)

Holotype: H-GSP 2013, left mandible fragment with M_1-M_2, from H-GSP locality 18, upper Chinji Formation, Miocene.

Paratypes: G-HSP 2026-2027, P^3; 1992-1993, DP^4; 1994-1996 and 2329, P^4; 1997-1998, 2002-2011, and 2330, M^{1-2}; 1999-2001, M^3; 2012, P_4; 2015-2025, M_{1-2}; 2014, M_3.

Etymology: Named for the Salt Range urial, *Ovis orientalis punjabiensis,* whose only remaining viable population lives on and around H-GSP locality 18.

Diagnosis: Parastyle small and closely appressed to paracone or lacking on P^4, P^3 large, mesostyles lacking, mesostylids and mesoconids lacking, metalophid ridge from protoconid present.

Differential diagnosis: Eutamias urialis differs from *E. sibiricus* in having larger P^3, small or no parastyle on P^4, and in lacking mesostyles and mesoconids; from *E. orlovi* in having smaller parastyles on all upper teeth, and in lacking mesostyles, mesostylids and mesoconids; and from *Tamias wimani* in having smaller parastyle on P^4, better-developed posterior lobe on M^3, and in lacking mesoconids. *Eutamias urialis* differs from all described Eurasian species of *Eutamias,* and other specimens which may be assignable to this genus, in having generally smaller, lower cusps and better-developed ridges.

Description: Both P^3s here assigned to *E. urialis* are single-rooted and have nearly round occlusal outlines. They have single transverse ridges which are slightly worn on both specimens. H-GSP 2026 has minute accessory cusps both behind and in front of the transverse ridge (Fig. 1).

The parastyle, paracone, metacone and protocone of the *E. urialis* DP^4 (Fig. 2A) are nearly equal in size and height. There is a small metaconule, but no protoconule.

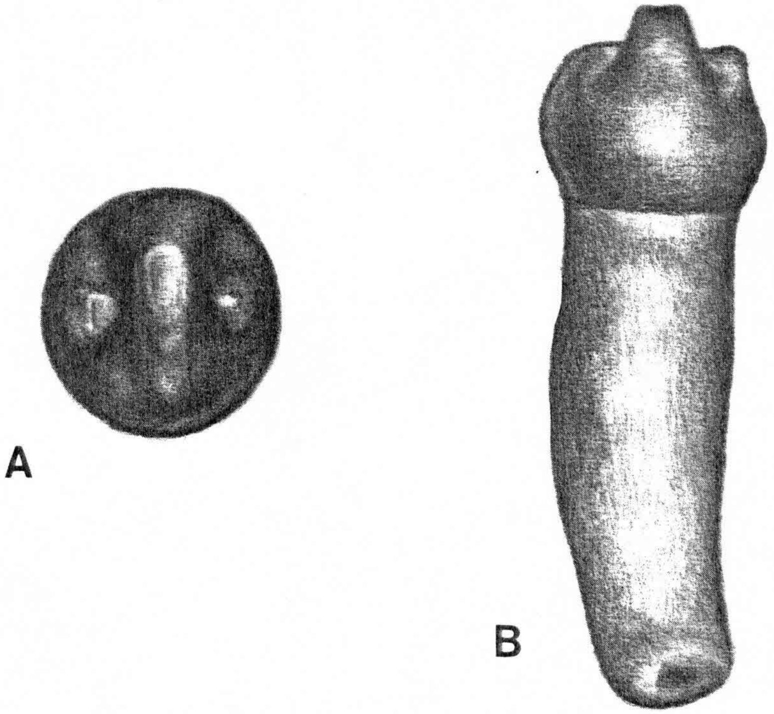

Fig. 1. P^3 of *Eutamias urialis* n. sp., H-GSP 2026. A—Occlusal view. B—Lateral view.

The P^4 completely lacks a parastyle on three of the four H-GSP specimens. H-GSP 1996 has a small parastyle closely appressed to the paracone. This specimen and H-GSP 1994 (Fig. 2B) have a small accessory cusp near the center of the anterior cingulum. H-GSP 1995, 1996 and 2238 have small metaconules, but none of the *E. urialis* P^4s have protoconules. The weak parastyle of the *E. urialis* P^4 gives this tooth nearly the same U-shaped occlusal outline seen in M^{1-2}.

The parastyle seldom forms a cusp distinct from the anterior cingulum of M^{1-2} (Fig. 2C). These teeth lack protoconules and mesostyles in all cases, and the hypocone is seldom differentiable as a distinct cusp. A small metaconule is usually present. The protoloph and metaloph are continuous in most cases, with no interruption buccal to the protocone. The protocone is neither as bulbous nor as hypsodont as is generally true of Eurasian *Eutamias*.

The only cusps consistently developed on *E. urialis* M^3 are the paracone and protocone. One specimen has a small protoconule and another

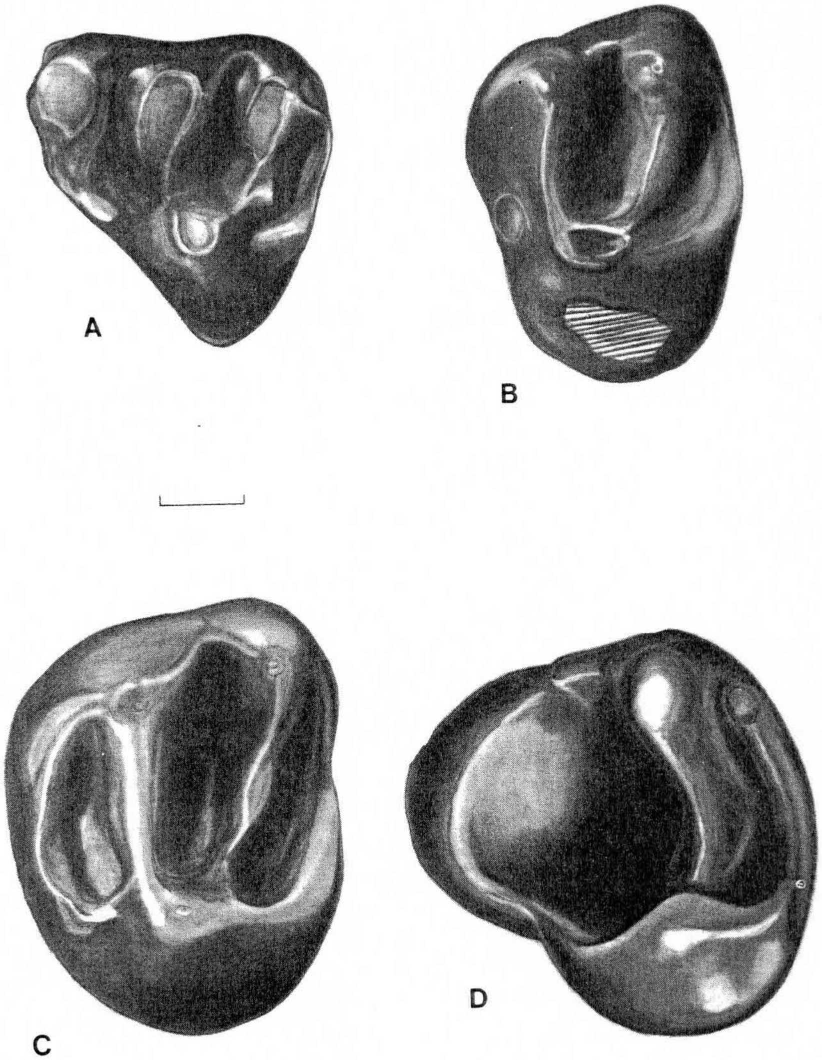

Fig. 2. Upper teeth of *Eutamias urialis* n. sp. A—Left DP^4, H-GSP 1992. B—Left P^4, H-GSP 1994. C—Left M^1 or M^2, H-GSP 1998. D—Right M^3, H-GSP 1999. Scale bar equals 0.5 millimeter.

a minute cusp on the anterior cingulum (Fig. 2D), but M^3 morphology is typically very simple. The posterior lobe of M^3 is well-developed.

The anterior part of P_4 (Fig. 3B) is wider relative to the posterolophid than is typical of Eurasian *Eutamias*, producing a squarer, less triangular occlusal outline in *E. urialis*. The metaconid, protoconid, hypoconid and a small entoconid are the only cusps on the *E. urialis* P_4 at the stage of wear of the only specimen known.

The M_2 is larger and proportionately shorter than the M_1 in the *E. urialis* holotype (Fig. 3A), but size and occlusal shape are sufficiently variable in the isolated lower molars that I have not attempted to differentiate these as M_1 and M_2. Only the metaconid, protoconid and hypoconid are developed on M_{1-2}. Mesostylids, entoconids and mesoconids are lacking. A slight swelling frequently occurs on the buccal end of the anterior cingulum. This, together with the posterolingual ridge from the protoconid and posterobuccal ridge of the metaconid, tends to enclose a small fossette. The metalophid ridge is frequently nearly complete between metaconid and protoconid, and a sharp ridge connects the protoconid and hypoconid.

There is only one M_3 in the H-GSP *E. urialis* sample (Fig. 3C). This specimen is the only *E. urialis* tooth to possess a small mesoconid. It is otherwise morphologically similar to M_{1-2}, but much longer and with a narrower talonid.

Discussion: Eutamias urialis is the first chipmunk to be recognized in Asia south of the Himalaya. It is also the earliest chipmunk yet known in Asia. Therefore, it is of considerable interest with respect to the evolution and distribution of the Eurasian chipmunks.

Discussions of chipmunk taxonomy, at the tribe, genus and subgenus level, can be found in Howell (1929), Ellerman (1940), Bryant (1945), White (1953), and Shotwell (1970). This literature is all North American, reflecting the modern distribution of the group, with most of the species being North American. A current consensus, supported by White's (1953) meticulous study and recent immunological evidence (Ellis and Maxson, 1979), regards the chipmunks as assignable to the genera *Tamias* and *Eutamias*. *Tamias* is represented only by the species *T. striatus* of eastern North America. *Eutamias* is divided into the subgenera *Eutamias (Neotamias)*, with approximately 16 species in western North America, and *Eutamias (Eutamias)*, represented today only by *Eutamias sibiricus* of northeastern Asia.

Because they are distinguished primarily on anatomical characters seldom or never preserved in the fossil record, *Eutamias* and *Tamias* have proven difficult to recognize as fossils. *Eutamias* has P^3, whereas *Tamias* does not, but most samples of fossil chipmunks are inadequate

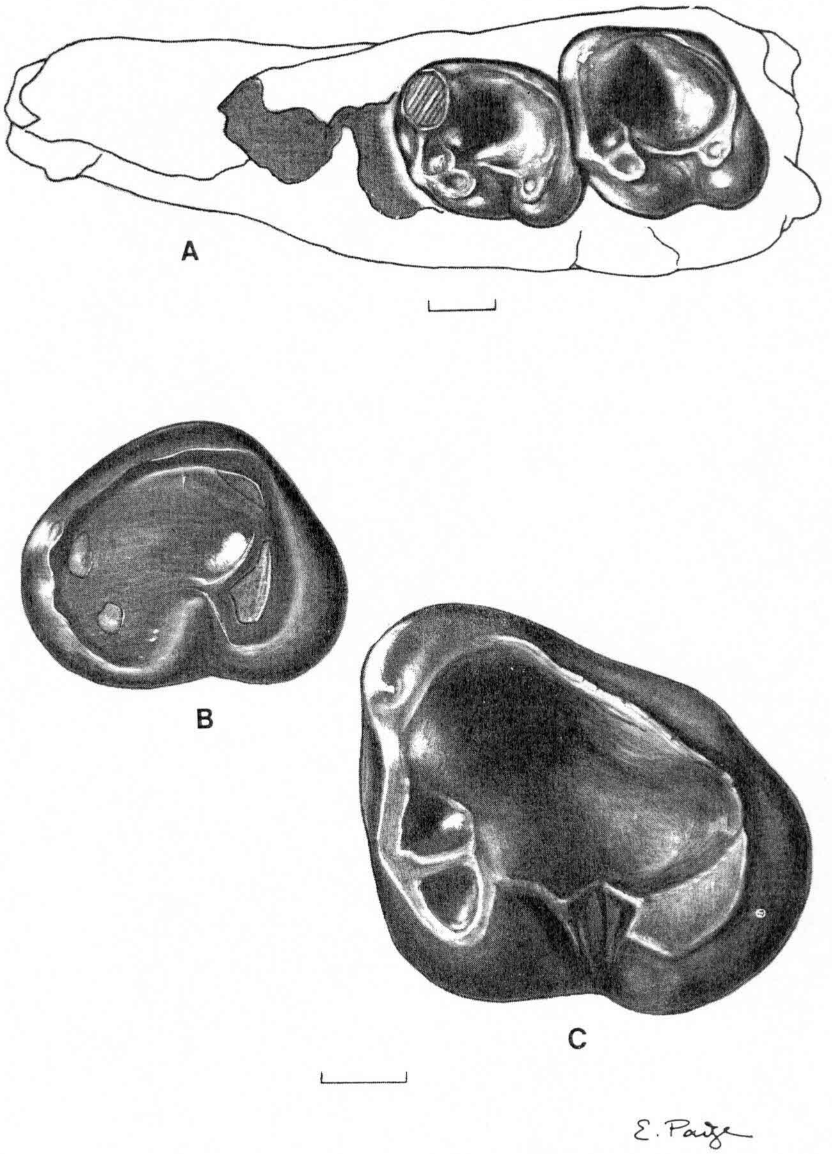

Fig. 3. Lower teeth of *Eutamias urialis* n. sp. A—Left mandible fragment with M_1-M_2, H-GSP 2013, holotype. B—Left P_4, H-GSP 2012. C—Left M_3, H-GSP 2014. Anterior to left. Scale bars equal 0.5 millimeter.

to definitely establish the presence or absence of P^3. This tooth is small and can be lost even in screen-washing. Further, P^3 does not leave an interdentinal wear facet on the anterior surface of P^4 in the samples of *E. sibiricus* I have examined, so absence of this wear facet cannot be used to identify *Tamias.*

Two teeth in the locality 18 sample are identical in root structure and occlusal morphology to P^3 of an *E. sibiricus* sample from Mongolia. However, they are proportionately much larger than *E. sibiricus* P^3, and they are moderately worn. The P^3 and P^4 erupt simultaneously in *E. sibiricus,* after M^3 is in occlusion, as demonstrated by FMNH 43499 (female, Hei-lung-chiang Province, Manchuria), in which DP^3, DP^4, P^3 and P^4 are all present. However, the occlusal surface of P^3 stays well above that of P^4 and P^3 only rarely comes into occlusion. Although morphologically simple, P^3 of *E. urialis* seems to have been a more functional tooth. I suggest that the *Eutamias* P^3 became less important in mastication between the Miocene and Holocene, and that as it was proportionately reduced in size its function was increasingly taken over by the parastyle of P^4. This would account for the large size and moderate wear of P^3 and the lack of a P^4 parastyle in *E. urialis.*

In addition to the character of P^3, a complex of features involving emphasis of ridges over cusps in the dentition separates *E. urialis* from other species of its subgenus. *Eutamias sibiricus* is rather variable in occlusal morphology, with some populations being much more hypsodont than *E. urialis* (e.g., FMNH 25576-25583 from north of Urga, Mongolia), but *E. sibiricus* always possesses a well-developed parastyle on P^4 as well as mesostyles and mesoconids on the molars. *Eutamias orlovi* (Sulimski, 1964) is even more extreme in the development of accessory cusps, with the lower molars possessing distinct mesostylids. *Tamias wimani* (Young, 1927; Bohlin, 1946) appears closest to *E. urialis* in dental morphology, but it too possesses mesoconids and an expanded parastyle on P^4. The ridges of *E. urialis* teeth are sharp and continuous in comparison to other Eurasian *Eutamias* species. In particular, the metalophid ridge of *E. urialis* is better-developed than in other *Eutamias* samples.

Eutamias urialis appears to be slightly smaller than the other Eurasian *Eutamias* species. However, the observed differences are not statistically significant and I do not use size to recognize any of these species. Measurements of upper teeth of a Mongolian *E. sibiricus* sample are given in Table 1 along with measurements of the *E. urialis* hypodigm for comparison. See also the measurements of the *E. orlovi* type series (Sulimski, 1964, Table 5).

Chipmunks are known from fairly abundant material in Hemingfordian (middle Miocene) faunas of the United States (e.g. Black, 1963). Definite published records of chipmunks in Eurasia begin only with the

Pliocene (Black, 1972b), although De Bruijn and Van der Meulen (1979) list *Tamias* in a Greek fauna which may be earlier than the Daud Khel fauna. Based largely on this fossil record, Black (1972b) suggested that chipmunks may have originated in North America and migrated to Eurasia *via* Beringia. This suggestion received some support from Ellis and Maxson (1979), and the timing for this event was hypothesized to be more recent than ten million years ago based on Hopkins' (1967) evidence concerning ecological conditions in Beringia. *Eutamias urialis* belongs to a pre-*Hipparion* fauna, which, by comparison with faunas and stratigraphic sections reported by Pilbeam *et al.* (1979), is probably approximately 11 million years old. Although this indicates that chipmunks were established in Eurasia prior to the migration event suggested by Black (1972b) and Ellis and Maxson (1979), records of chipmunks still go back at least six million years earlier in North America than in Eurasia. There is at present no compelling evidence concerning the time or place of origin of chipmunks.

Table 1. Measurements of *Eutamias urialis* cheek teeth. Upper tooth measurement of a *Eutamias sibiricus* sample from north of Urga, Mongolia, FMNH 25576-25583, are given for comparison.

Eutamias urialis holotype, H-GSP 2013: M_1 length - 1.40 width - 1.46 M_2 length - 1.48 width - 1.72

	Length					Width				
	N	OR	X	s	V	N	OR	X	s	V
				Eutamias urialis						
P_4	1	1.8	—	—	—	1	1.0	—	—	—
M_{1-2}	13	1.28-1.56	1.43	.09	6.3	13	1.40-1.84	1.61	.13	8.1
M_3	1	1.76	—	—	—	1	1.64	—	—	—
P^3	2	.74-.76	.75	.01	1.3	2	.76-.82	.79	.04	5.1
DP^4	2	1.24-1.26	1.25	.01	0.8	2	1.22-1.30	1.26	.06	4.8
P^4	4	1.06-1.18	1.12	.06	5.4	4	1.34-1.48	1.38	.07	5.1
M^{1-2}	13	1.26-1.44	1.35	.05	3.7	13	1.48-1.80	1.71	.08	4.7
M^3	3	1.60-1.70	1.66	.05	3.0	3	1.60-1.76	1.68	.08	4.8
				Eutamias sibiricus						
P^3	8	.40-.45	.42	.03	7.1	8	.35-.50	.45	.05	11.1
P^4	8	1.15-1.30	1.21	.05	4.1	8	1.20-1.45	1.36	.08	5.9
M^1	8	1.40-1.45	1.43	.03	2.1	8	1.65-1.80	1.71	.06	3.5
M^2	8	1.40-1.50	1.48	.04	2.7	8	1.80-1.90	1.83	.05	2.7
M^3	8	1.60-1.75	1.66	.06	3.6	8	1.65-1.80	1.77	.06	3.4

Family Gliridae Thomas, 1897
Subfamily Glirinae Thomas, 1897
Genus *Myomimus* Ognev, 1924
Myomimus sumbalenwalicus new species

(Figures 4-5; Table 2)

Holotype: H-GSP 1986, M^1, from H-GSP locality 18, upper Chinji Formation, Miocene.

Paratypes: H-GSP 1985, P^4; 1988, M_1; 1989-1990, M_2; 1991, M_3.

Questionably referred specimen: H-GSP 1987, M^2.

Etymology: Named for the village of Sumbalenwala, which is one kilometer southwest of H-GSP locality 18.

Diagnosis: Three-rooted lower molars, M_3 large and P^4 very small in proportion to the other cheek teeth.

Differential diagnosis: Myomimus sumbalenwalicus differs from *M. roachi* and *M. personatus* in being smaller, having a simpler P^4, having better-developed centrolophs, centrolophids and posterior accessory ridges, and in its more lingual endolophs; from *M. judaicus* in its much smaller and simpler P^4, and its more complex molars; from *M. maritsensis* in its much smaller P^4, better-developed posterior centrolophs, centrolophids and posterior accessory ridges, and in its more lingual endolophs; from *Peridyromys compositus* in its smaller upper dentition with very small and simple P^4, its much simpler upper molar morphology, and in its more lingual centroloph; and from *P. dehmi* in its much smaller and simpler P^4, and larger M_3.

Description: The single *Myomimus sumbalenwalicus* P^4 (Fig. 4A) is morphologically very simple for the genus. It has only a protoloph, metaloph and short posteroloph. There is no anteroloph. This tooth is no larger in proportion to the upper molars than in Recent *Myomimus personatus.*

The holotype (Fig. 4B) is an M^1 or M^2, probably M^1 based on its relatively great width. The anteroloph is separated from the protoloph at both its lingual and buccal extremities. The protoloph is long and straight. It extends to the lingual margin and turns sharply posteriorly, forming an anteroposteriorly straight endoloph. Both the anterior and posterior centrolophs are well-developed. They unite at the center of the tooth and continue as a single crest toward the endoloph. The metaloph and posteroloph are both straight. The metacone is separated from the posterior centroloph by a valley as deep as any on the tooth.

Another M^1 or M^2, probably M^2, is here tentatively referred to *M. sumbalenwalicus.* It is quite different from the holotype in occlusal morphology, but in size, concavity and height of lophs it appears

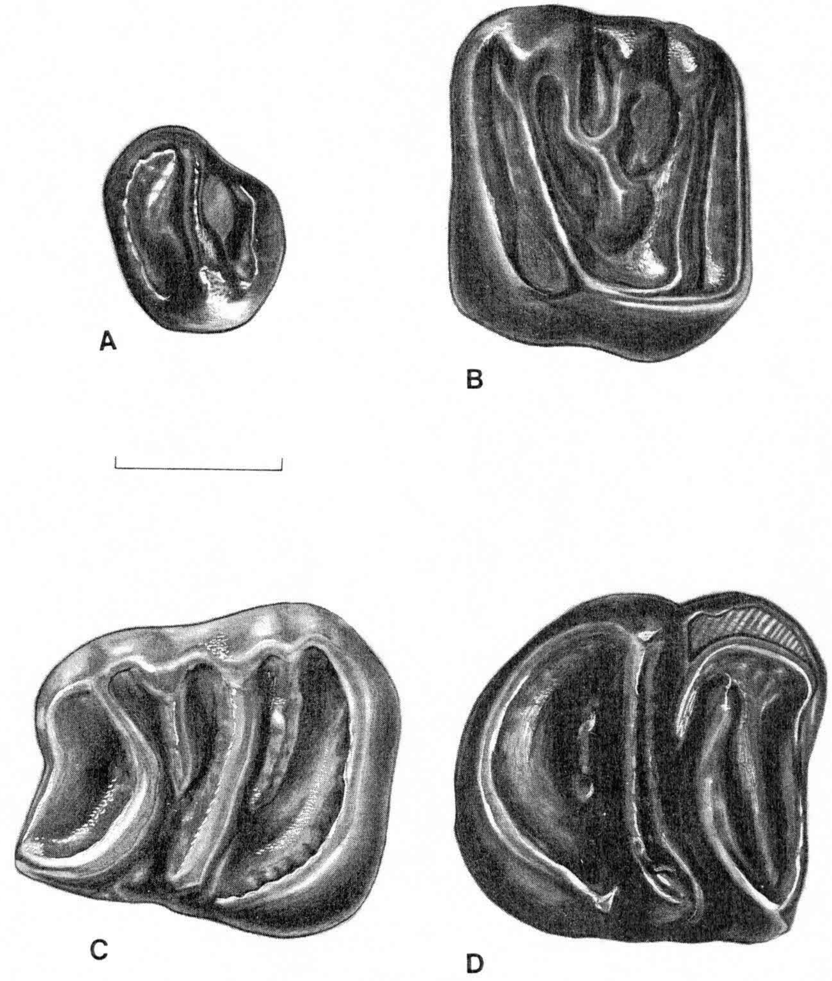

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Fig. 4. Teeth of *Myomimus sumbalenwalicus* n. sp. A—Right P^4, H-GSP 1985. B—Left M^1, H-GSP 1986, holotype. C—Left M_1, H-GSP 1988. D—Right M_3, H-GSP 1991. Scale bar equals 0.5 millimeter.

assignable to the same taxon (Fig. 5). The protoloph and anteroloph seem to have merged lingually in this specimen, and the anterior centroloph has been extended lingually to join the endoloph. The resulting pattern has the same number of ridges in approximately the same position as on the holotype, but the arrangement and connections of these ridges are quite different.

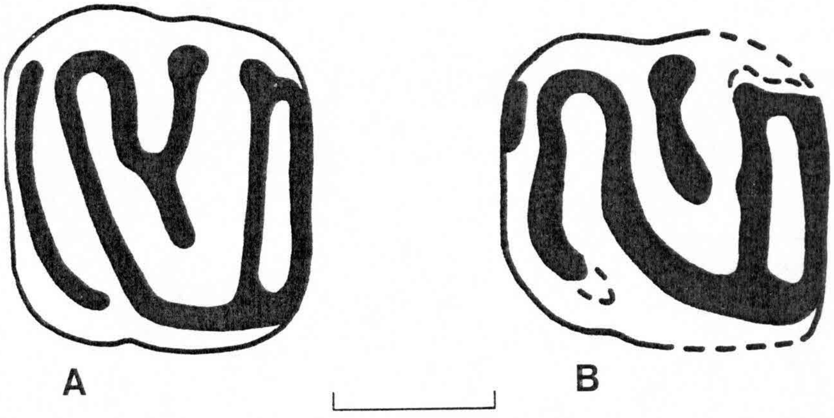

Fig. 5. Upper molars of *Myomimus sumbalenwalicus* n. sp. for comparison of occlusal morphology. A—Left M^1, H-GSP 1986, holotype. B—Left M^2, H-GSP 1987. Anterior to left. Scale bar equals 0.5 millimeter.

No glirid lower premolars have yet been recovered from locality 18. The lower molars are all three-rooted. In M_1 (Fig. 4C) the metalophid joins the anterolophid lingually to form a loop. The centrolophid is separated from this loop by a valley and extends buccally across more than half the width of the tooth. The hypoconid is large, forming a high and wide part of the posterolophid. The posterior accessory ridge is long and almost as high and wide as the ridges surrounding it.

The M_2 is identical to M_1 in occlusal morphology, except that the metalophid does not reach the metaconid to unite with the anterolophid. The M_3 (Fig. 4D) is almost as large as M_2, but its occlusal pattern is somewhat simpler. The centrolophid is much shorter on M_3 than on M_1 and M_2, and there are only two small, low cusps in the position of the posterior accessory ridge.

Discussion: Myomimus sumbalenwalicus is the first fossil glirid to be described from South Asia. Examination of even the small locality 18 sample is sufficient to demonstrate that occlusal pattern is variable in this species. I follow Engesser (1972) and others here in considering number of roots, concavity of occlusal surface, and size, particularly relative sizes of adjacent teeth in the dentition, to be more important characters for glirid taxonomy than occlusal pattern.

In size and occlusal morphology, the locality 18 glirid is similar only to some species of *Myomimus, Peridyromys,* and *Microdyromys.* De Bruijn synonymized *Myomimus* and *Peridyromys* in 1970 (in De Bruijn *et al.,* 1970) because of the great dental similarities between their type species, but now considers it possible that they may be distinct genera which arrived in Europe during successive immigration events (personal communication, 1979). *Peridyromys,* with two-rooted lower molars, disappears from the European record in the Aragonian. Following a brief hiatus, three-rooted *Myomimus* appears in the Vallesian (Remmert Daams, personal communication, 1979). All the species of both genera are rather similar in size and occlusal morphology, but I do not consider the early and middle Miocene two-rooted species here for comparison with the Daud Khel glirid.

Microdyromys is common in the Miocene of Europe and is at least superficially similar to the locality 18 glirid. However, *Microdyromys* has two-rooted lower molars and a fundamentally different type of occlusal morphology. Most *Microdyromys* species have more complex crest patterns than *Myomimus sumbalenwalicus,* but even those with simple patterns, such as *M. koenigswaldi,* have proportionately shorter and wider teeth than *M. sumbalenwalicus. Microdyromys* typically has anterior accessory ridges developed on its molars, whereas *M. sumbalenwalicus* lacks these and tends to develop posterior accessory crests.

The only *Myomimus* species from which *M. sumbalenwalicus* can be easily distinguished on the basis of size are *M. personatus* and *M. roachi.* These species have been synonymized by Corbet and Morris (1967), but Storch (1978) and others consider them both valid. In either case, these Pleistocene and Recent animals are significantly larger than *Myomimus sumbalenwalicus.* The Pleistocene and Recent species of *Myomimus* are the simplest in occlusal pattern; this too serves to distinguish them from *M. sumbalenwalicus. Myomimus judaicus* (Tchernov, 1968) has the simplest occlusal morphology of any *Myomimus* species. It lacks centrolophs, centrolophids and all accessory ridges.

The European Miocene and Pliocene species of *Myomimus* are all close to *M. sumbalenwalicus* in size. However, all these species differ from *M. sumbalenwalicus* in having much larger and more complex P^4, proportionately smaller M_3, and endolophs which are positioned more buccally on the upper molars. *Myomimus maritsensis* (De Bruijn *et al.,* 1970) appears to be simpler in molar morphology than *M. sumbalenwalicus,* while *Peridyromys* (= *Myomimus*) *compositus* (Bachmeyer and Wilson, 1970) is more complex, particularly in the upper molars. *Peridyromys* (= *Myomimus*) *dehmi* (De Bruijn, 1966) is very similar to *M. sumbalenwalicus* in molar morphology.

If we accept the separation of *Peridyromys* and *Myomimus* based on the number of roots in the lower molars, *M. sumbalenwalicus* is perhaps the earliest representative of its genus. No potential ancestral forms are known in Asia, and derivation of *M. sumbalenwalicus* from a European glirid such as *Peridyromys murinus,* while possible, is not clear. The small P^4 and large M_3 of *M. sumbalenwalicus,* as well as certain peculiarities of its molar morphology such as its lingual endoloph, set it rather far apart from all European glirids. *Myomimus personatus* resembles *M. sumbalenwalicus* in P^4 size, but this may be a case of reduction from the typically larger P^4 of earlier *Myomimus* species and does not appear to indicate close relationship with *M. sumbalenwalicus.* The present isolation in time and space, together with the variable morphology in the small Daud Khel sample, make it impossible to evaluate the relationships of *M. sumbalenwalicus.*

Table 2. Measurements of *Myomimus sumbalenwalicus* cheek teeth.

H-GSP Number	Length	Width
1985, P^4	.48	.60
1986, M^1 (holotype)	.94	1.02
1987, M^2	.98	1.00
1988, M_1	1.04	.96
1989, M_2	1.10	1.04
1990, M_2	1.04	1.02
1991, M_3	1.04	1.00

Family Ctenodactylidae Zittel, 1893
Genus *Sayimys* Wood, 1937
Sayimys sivalensis (Hinton, 1933)
(Figures 6-8, Table 3)

Pectinator sivalensis Hinton, 1933, Ann. Mag. Nat. Hist., ser. 10, v. 12, p. 622.

Sayimys perplexus Wood, 1937, Amer. Jour. Sci., ser. 5, v. 34, pp. 73-76, figs. 6, 14.

Sayimys perplexus Prasad, 1970, Palaeontologia Indica, n. ser., v. 39, p. 15, pl. 22.

Sayimys sivalensis Black, 1972, Palaeontology, v. 15, pp. 241-243, fig. 1.

Sayimys sivalensis De Bruijn and Rumke, 1974, Akad. Weten. Koninkl. Ned. Proc., ser. B, v. 77, pl. 2, fig. 5, pl. 3, fig. 4.

Sayimys sp. Hussain *et al.*, 1977, Milwaukee Pub. Mus. Contrib. Biol. Geol., no. 16, pp. 3-4, fig. 6.

Africanomys sivalensis Wood, 1977, Jour. Palaeontol. Soc. India, v. 20, pp. 129-130, figs. 2J, 3G, 3L.

Sayimys perplexus Vasishat, 1978, Curr. Sci., v. 47, pp. 859-860, fig. 1.

Holotype: GSI D284, mandible fragment with M_2-M_3.

Emended diagnosis: P^4 larger relative to molars than in *Metasayimys;* protolophs and metalophids with only two cusps; DP_4 with anteroconid which is joined to metalophid by ridge; posterobuccal cingulum present on DP_4 and P_4, usually present on M_1 and M_2, usually absent on M_3; lower crowned than *Metasayimys;* lacking cement.

Stratigraphic and geographic distribution: Chinji and Nagri Formations of northeastern Pakistan and northwestern India.

Referred material from Daud Khel: H-GSP 247, maxillary fragment with P^4-M^3; 2039, maxillary fragment with DP^3-DP^4; 2040, palate fragment with right P^4 and broken M^1-M^2, left M^2; 2053, maxillary fragment with M^1-M^2; 2080, maxillary fragment with M^2-M^3; 2199, mandible fragment with M_2 and broken M_3; 2233, possibly associated DP_4 and M_1; and isolated teeth as follows: DP^4—234, 2028-2038, and 2236; P^4—2041-2052; M^1—237 and 2054-2079; M^2—241 and 2081-2107; M^3—2108-2125 and 2237; DP_4—243, 256, and 2126-2134; P_4—2135-2159; M_1—239 and 2160-2190; M_2—242, 246, 2191-2214, and 2234-2235; M_3—2215-2232.

Description: A single *Sayimys sivalensis* DP^3 is present in the Daud Khel collection (Fig. 6A). Were it not associated with a DP^4, this peg-like tooth could not have been assigned to *Sayimys* as its morphology suggests nothing concerning its affinities. No isolated *Sayimys* DP^3s are represented in the Daud Khel sample, despite the fact that similar and even smaller teeth of other taxa, such as *Eutamias* P^3 and *Myomimus* P^4, have been recovered. Because this tooth was in occlusion at the same time as a well-worn DP^4 and has not been found associated with P^4, I regard it as DP^3 rather than P^3 (see Jaeger, 1971, p. 124).

The DP^4 has a nearly symmetrical candelabra-shaped occlusal outline when well-worn (Fig. 6A). The protocone and hypocone are equally developed, as are the smaller paracone and metacone. A large anteroloph is well-separated from the paracone and joined to the protocone by an oblique ridge. The posteroloph is positioned relatively close to the metacone. This ridge is connected to the center of the metaloph by a curving ridge. The three buccal flexi are approximately equal in depth below the occlusal surface and all are shallower than the lingual flexus.

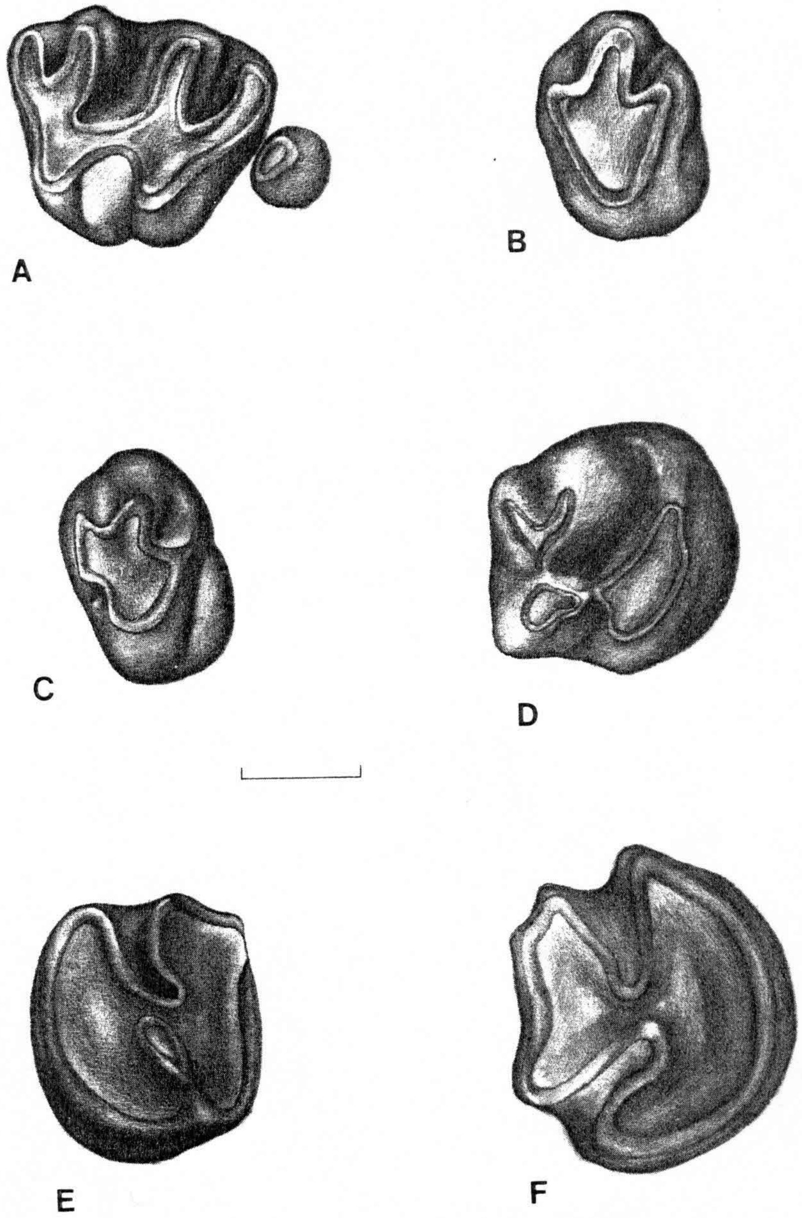

Fig. 6. Upper teeth of *Sayimys sivalensis*. A—Right DP^3-DP^4, H-GSP 2039. B—Left P^4, H-GSP 2041. C—Right P^4, H-GSP 2044. D—Right M^1, H-GSP 2054. E—Left M^1, H-GSP 2066. F—Right M^3, H-GSP 2108. Scale bar equals 1.0 millimeter.

When unworn, this tooth bears a strong resemblance to some molars of more complex Miocene ctenodactylids such as *Africanomys* and *"Sayimys" obliquidens*. This has resulted in its misidentification as M^1 or M^2 by De Bruijn and Rumke (1974) before the entire *Sayimys sivalensis* dentition was known.

The P^4 is large relative to the molars, as in *"Sayimys" obliquidens* (Bohlin, 1946, Fig. 30a, d), and morphologically simple. In most Daud Khel specimens, the only distinct cusp is at the center of the buccal margin of the tooth, flanked by equally developed anterobuccal and posterobuccal crests (Fig. 6B). Comparison with M^1 and M^2 suggests that this central cusp of the P^4 is the metacone. In three Daud Khel specimens the lingual portion of the P^4 transverse crest is offset anteriorly (e.g., Fig. 6C), giving the tooth the same appearance as the *"Sayimys" obliquidens* P^4s illustrated by Bohlin (1946, Fig. 30 a''', d').

As shown by H-GSP 247 (Fig. 7) and the measurements presented in Table 3, M^1 (Fig. 6D, E) is significantly smaller than M^2 or M^3 (Fig. 6 F), and M^2 and M^3 are approximately the same size. The lingual flexus extends almost to the base of the crown, while the buccal flexus is very deep in the center of the tooth but relatively shallow at the buccal margin. However, unilateral hypsodonty of the lingual part of the upper molars has developed to the same degree as in *"Sayimys" obliquidens* (Bohlin, 1946, Fig. 35) and wear is disproportionately great on the lingual surface. Therefore, the only two specimens in the Daud Khel collection so worn as to have developed fossettes through closure of the flexi have closed the deeper lingual flexus first (Fig. 6E). The protoloph is simple, without a distinct anteroloph. A slight anterobuccal swelling, suggestive of an anteroloph, is present in 21 of 81 upper molars, but it is never better-developed than in H-GSP 247 (Fig. 7) or 2054 (Fig. 6D). This stands in marked contrast to the more complex protolophs in

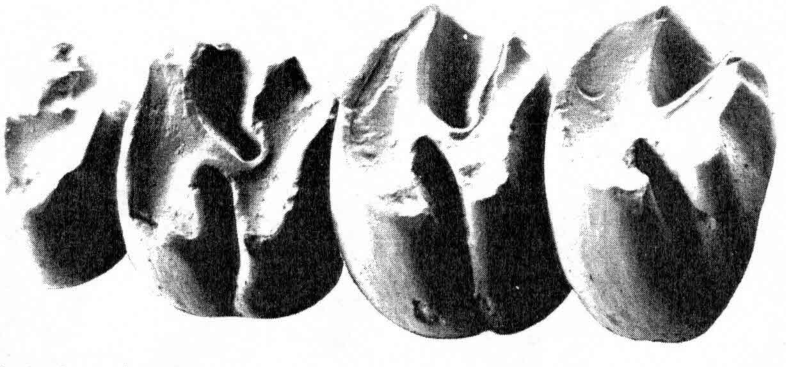

Fig. 7. Scanning electron micrograph of *Sayimys sivalensis* left maxillary fragment with P^4-M^3, H-GSP 247.

Africanomys (Jaeger, 1971, 1977) and *"Sayimys" obliquidens* (Bohlin, 1946). The protoloph and metaloph unite centrally very early in wear. Only four specimens are so slightly worn as to have unfused lophs (e.g., Fig. 6D). The metaloph comprises the hypocone and both metacone and metastyle, which are quickly fused with wear. Metacone and posteroloph remain distinct longest in M^1, the flexus between them being as deep as the buccal flexus between the lophs in this tooth. Fusion is earlier in M^2 and the metacone and metastyle are distinctly separated only on completely unworn specimens of M^3. The metaloph joins the protoloph by an anterobuccal spur of the hypocone. Protoloph and metaloph are approximately equally wide in M^1, giving the tooth an almost square occlusal outline. The protoloph tends to be wider than the metaloph in M^2 and it is much wider than the reduced metaloph of M^3.

The occlusal morphology of the *Sayimys sivalensis*'DP_4 is so similar to that of the lower molars that its cusp homologies are clear. In addition to large protoconid, hypoconid, metaconid and entoconid, DP_4 has a prominent, centrally positioned anteroconid and a large hypoconulid. A well-developed posterobuccal cingulum is also present, although it is not always so prominent as to render the posterior occlusal outline as square as in H-GSP 2126 (Fig. 8A). The anteroconid is not isolated from the metalophid as in *Metasayimys curvidens* (Jaeger, 1971, Pl. 2, Fig. 7), even when the tooth is quite unworn, but the anteroconid-metalophid ridge is very narrow and sharp. The DP_4, like DP^4, was evidently functional for a long time during ontogeny in *S. sivalensis.* While not so hypsodont as P_4 or the molars, it is quite hypsodont for a deciduous premolar among mammals generally, and several of the Daud Khel specimens were worn nearly to the base of the lingual flexids before being replaced.

The P_4 (Fig. 8B) comprises a prominent ridge connecting the hypoconid and hypoconulid, a posterobuccal cingulum which is invariably present but not as well-developed as in most DP_4s, and an anterolingual cusp which is probably the entoconid. Only the Y-shaped hypoconid-hypoconulid-entoconid ridge was in occlusion on even the most heavily worn Daud Khel specimens. This tooth is very similar to the *"Sayimys" obliquidens* P_4 (Bohlin, 1946) in size relative to the molars, occlusal morphology, and hypsodonty.

The lower molars (Fig. 8C-F) are variable in overall size, relative dimensions of the trigonids and talonids, positioning of the buccal cusps relative to the lingual cusps, and the development of the posterobuccal cingulum. The metalophid always consists of metaconid and protoconid only, with no suggestion of the additional anterolingual cusp which occurs in *"Sayimys" obliquidens.* The anterior-posterior positioning of the metaconid relative to the protoconid is highly varia-

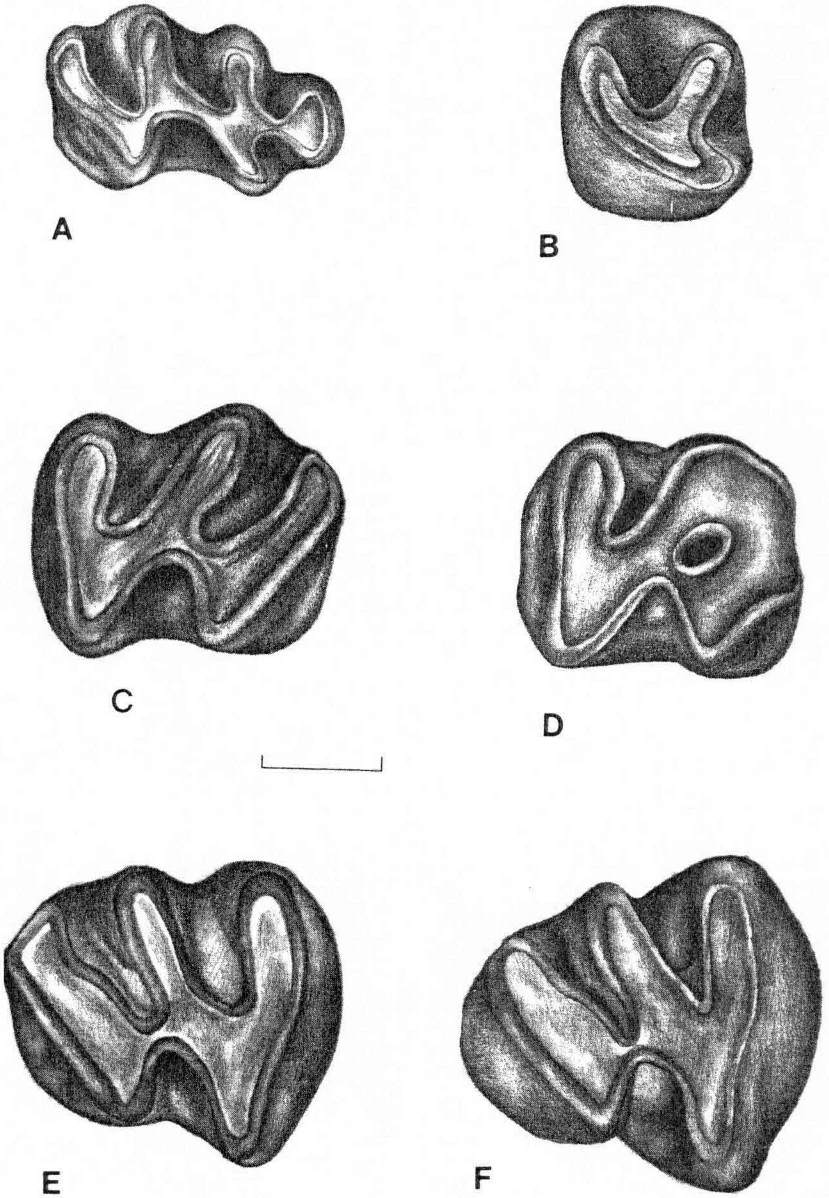

Fig. 8. Lower teeth of *Sayimys sivalensis.* A—Right DP$_4$, H-GSP 2126. B—Right P$_4$, H-GSP 2135. C—Left M$_1$, H-GSP 2160. D—Left M$_1$, H-GSP 2165. E—Right M$_2$, H-GSP 2191. F—Right M$_3$, H-GSP 2215. Scale bar equals 1.0 millimeter.

ble, with the metaconid ranging from slightly anterior to slightly posterior of the protoconid. Since the lingual part of the metalophid slopes first anteriorly and then posteriorly as wear proceeds through the crown, this metaconid-protoconid relationship depends in part on stage of wear. In this feature of the metalophid, as well as in the relative positioning of the metaconid and entoconid, the Daud Khel sample shows diagnostic features of both *Sayimys perplexus* and *S. sivalensis* (Black, 1972a). The hypoconulid is joined to the middle of the protoconid-entoconid ridge by a narrow spur; there is no gap at this junction even in the least worn of the Daud Khel lower molars. Relative to the metalophid, the hypoconid-hypoconulid ridge is best-developed in M_1, frequently being wide enough to give the tooth a rectangular occlusal outline (Fig. 8D). This ridge tends to be somewhat reduced in M_2 and quite reduced in M_3, but this is so variable in M_3 (see M_3 posterior width data in Table 3) that M_3 frequently can be distinguished from M_2 only by its backward-sloping posterior root. See, for example, the close similarity between H-GSP 2191, M_2 (Fig. 8E) and 2215, M_3 (Fig. 8F). The development of the posterobuccal cingulum is also quite variable. A distinct cingulum is present in 30 of 33 M_1s, 21 of 28 M_2s, and 2 of 18 M_3s. Despite the fact that Black's illustration does not indicate a posterobuccal cingulum on the *S. sivalensis* M_2 (1972a, Fig. 1c, e), a cast of the holotype shows that this cingulum is developed to an extent typical of the Daud Khel M_2s.

Discussion: The Daud Khel material described above is the largest sample of Miocene ctenodactylids studied to date. It therefore gives an approximation of the range of variation which can be expected in a Miocene population. The variation within the Daud Khel sample indicates that the holotypes of *Sayimys sivalensis* and *S. perplexus* represent the same species. This range of variation also suggests that such nominal taxa as *Metasayimys curvidens (M. jebeli* of Jaeger, 1971) and *Testouromys solignaci* (Robinson and Black, 1973) are members of at least the same genus and possibly the same species. New names for Miocene ctenodactylids should probably be proposed only if based on large samples or very distinctive morphologic characters.

I consider all described South Asian ctenodactylids to represent a single species. This species has a varied taxonomic history, as indicated by the synonymy above. I believe this multiplicity of names for the Siwalik ctenodactylids results from three factors: 1) Descriptions have previously been based on very small samples; the eight papers which have discussed Siwalik ctenodactylids have dealt with only eight specimens. 2) *Sayimys sivalensis* is highly variable in dental size and occlusal morphology, as demonstrated by the Daud Khel sample. That such a range of morphology is encompassed in a single population was unknown to earlier workers. 3) De Bruijn and Rumke (1974) misidentified a *S. sivalensis* DP^4 as M^1 or M^2, leading Wood (1977) to conclude that *Africanomys* was present in South Asia.

The type mandible fragments of *Pectinator sivalensis* (Hinton, 1933) and *Sayimys perplexus* (Wood, 1937) were the only ctenodactylid specimens available to Black for his review of the Siwalik rodents (1972a). He was unaware of Prasad's (1970) specimen from Haritalyangar. Black recognized that the two mandibles belonged to the same genus, but separated them at the species level because he believed them to be significantly different in size and lower molar morphology. His distinction between *Sayimys sivalensis* and *S. perplexus* has been followed by all later authors. De Bruijn and Rumke (1974) described the first ctenodactylid upper tooth from the Siwaliks, but, having nothing with which to compare their specimen, they misidentified a DP^4 as M^1 or M^2. Assuming their identification to be correct, Wood (1977) proposed that *Sayimys sivalensis* belongs in the genus *Africanomys*. Neglecting this error, Black's concept of a smaller Chinji species and a larger Nagri species of *Sayimys* has been accepted.

The Daud Khel ctenodactylid sample is highly variable in size (Table 3). It spans the previously known size range from *S. sivalensis* to *S. perplexus*, except that no Daud Khel specimens quite match the *S. perplexus* type mandible in metalophid width. No bimodality is apparent in any of the measurements; the Daud Khel sample appears to represent a single population. This is equally true of the features of lower molar occlusal morphology. The angulation of the metalophid ranges from the transverse condition considered diagnostic of *S. sivalensis* by Black (e.g., H-GSP 2160, Fig. 8C) to the more oblique condition diagnostic of *S. perplexus* (e.g., H-GSP 2191, Fig. 8E). The metaconid and entoconid are as closely appressed as in the type of *S. sivalensis* (e.g., H-GSP 2194) or as widely separated as in the type of *S. perplexus* (e.g., H-GSP 2199). Perhaps the most variable character of the Daud Khel lower molars is the development of the posterobuccal cingulum. Always present on DP_4 and P_4, although in some cases constituting only a minor swelling rather than the more common shelf, this cingulum is occasionally absent on M_1 (e.g., H-GSP 2163) and often absent on M_2. Most M_3s have no posterobuccal cingulum, but this feature is very well-developed on H-GSP 2223.

The Daud Khel sample is apparently intermediate in stratigraphic position, and therefore possibly in age, between the previously described Chinji and Nagri ctenodactylids. Additional discoveries may demonstrate a clinal distribution of character states within these ctenodactylids, ranging from smaller Chinji samples to larger Nagri samples and with accompanying shifts in occlusal features, but such evolution is not indicated by the present evidence.

Table 3. Measurements of *Sayimys sivalensis* cheek teeth from Daud Khel. If no posterior width is indicated, the anterior width data reflects maximum figures for that tooth.

	Length					Anterior Width					Posterior Width				
	N	OR	X	s	V	N	OR	X	s	V	N	OR	X	s	V
DP^3	1	.60	—	—	—	1	.68	—	—	—					
DP^4	14	2.00-2.16	2.08	.05	2.4	14	1.52-1.96	1.76	.12	6.8					
P^4	14	1.32-1.64	1.49	.10	6.7	14	1.72-2.28	1.93	.15	7.8					
M^1	29	1.84-2.24	2.08	.08	3.8	29	1.68-2.36	2.02	.19	9.4	29	1.68-2.20	1.92	.14	7.3
M^2	31	1.96-2.60	2.33	.15	6.4	31	2.12-2.80	2.46	.16	6.5	31	1.92-2.56	2.20	.17	7.7
M^3	21	1.96-2.64	2.28	.13	5.7	21	2.28-2.72	2.50	.13	5.2	21	1.56-1.96	1.77	.10	5.7
DP$_4$	12	2.24-2.52	2.36	.09	3.8	12	1.36-1.56	1.45	.07	4.8					
P$_4$	25	1.40-1.60	1.52	.06	3.9	25	1.40-1.68	1.56	.07	4.5					
M$_1$	33	2.00-2.60	2.24	.14	6.3	33	1.56-2.08	1.90	.11	5.8	33	1.60-2.08	1.85	.20	10.8
M$_2$	28	2.32-2.80	2.61	.12	4.6	28	2.24-2.64	2.48	.12	4.8	28	1.80-2.68	2.20	.16	7.3
M$_3$	18	2.48-2.92	2.67	.12	4.5	18	2.32-2.84	2.56	.15	5.9	18	1.80-2.20	2.02	.13	6.4

Maglio (1973, p. 14) has discussed the practical difficulties of dealing with the paleontologic species concept when an apparent morphologic discontinuity is bridged by the discovery of a morphologically transitional form in what was previously a temporal gap. He notes, correctly I believe, that the taxonomic nomenclature applied to such cases is unimportant so long as the evolutionary continuity which has been demonstrated is clear. The Daud Khel ctenodactylid initially appears to be a morphologically "transitional form" which also bridges the temporal "gap" between the earlier, smaller *Sayimys sivalensis* and the later, larger *S. perplexus.* Closer study, however, reveals that the Daud Khel ctenodactylid is more than this. Because of its variability and the limited sample sizes of the nominal species involved, the Daud Khel sample spans the entire morphologic range seen in these species. Thus, we can not be sure of the direction of the morphologic gradient. Under these circumstances, I propose the synonymy of *Sayimys sivalensis* and *S. perplexus,* with *S. sivalensis* the senior synonym, as the nomenclatorial solution least likely to imply that the nature of evolutionary change in Chinji-Nagri ctenodactylids is known.

The genus *Sayimys* is here considered to be monotypic. I believe Jaeger (1971) to be correct in transferring *Sayimys jebeli* (Lavocat, 1961) to *Metasayimys,* and *"Sayimys" obliquidens* (Bohlin, 1946) does not appear to be congeneric with the Siwalik ctenodactylids. Therefore, since the name *Sayimys* was validly proposed for a South Asian species and all South Asian specimens are here placed in a single species, I recognize only one species of *Sayimys.* The earliest available name for this species is *S. sivalensis.* Although Hinton (1933) did not illustrate the holotype of his *Pectinator sivalensis,* he did provide "a statement that purports to give characters differentiating the taxon" (International Code of Zoological Nomenclature, Article 13a [i]). The specimen was subsequently transferred to *Sayimys,* illustrated, and described in detail (Black, 1972a). Despite the fact that *Sayimys perplexus* is here considered a junior synonym of *S. sivalensis, S. perplexus* must remain the nominal type-species of *Sayimys. Sayimys sivalensis* could replace *S. perplexus* as the type-species only in the case of objective synonymy; the present rules of zoological nomenclature do not provide for replacement of the type-species in cases of subjective synonymy.

Sayimys differs from the other Miocene African, Arabian and central Asian ctenodactylids in the features compared in Table 4. The insular Mediterranean Miocene ctenodactylids are not considered here, as they differ radically from the other Miocene taxa in size and other aspects of morphology. This is perhaps related to insular development. For the purposes of the comparisons in Table 4, *Africanomys* includes *A. pulcher* (Jaeger, 1971), *A. minor, A. major* and *A. ketterati* (Jaeger, 1977), *"Sayimys" obliquidens* includes the Taben-buluk material of Bohlin (1946), *Sayimys* includes only *S. sivalensis* (this paper), and

Metasayimys includes *M. curvidens* (*M. jebeli* of Jaeger, 1971; see discussion in Wood, 1977, p. 128) and *Testouromys solignaci* (Robinson and Black, 1973). I have not yet seen the type mandible of *Metasayimys intermedius* (Sen and Thomas, 1979). This species may be referrable to *Sayimys* (see below).

Table 4. Morphologic comparison of four Miocene ctenodactylid genera.

	Africanomys	"*Sayimys*" *obliquidens*	*Sayimys*	*Metasayimys*
size of P^4_4 relative to molars	small-medium	large	large	small
complex/protoloph/metalophid	yes	yes	no	no
isolated metacone	yes	no	no	no
anteroconid on DP_4	no	—	yes	yes
transverse or oblique lophids	transverse	oblique	variable	variable
posterobuccal cingulum on DP_4-M_2	no	yes	yes	no
cement	no	no	no	variable

Considered within the framework of the morphology and relative ages of the Oligocene ctenodactylids *Tataromys* and *Karakoromys*, and the post-Miocene genera *Irhoudia, Pellegrinia, Ctenodactylus, Pectinator, Massouteria* and *Felovia*, I interpret the general structural trends within the Miocene ctenodactylids as follows: 1) The deciduous lower premolars trend toward acquisition of a distinct anteroconid. 2) The permanent premolars tend to become reduced. 3) The upper and lower molars tend to become simpler in occlusal morphology, particularly anteriorly. 4) The lophids of the lower molars tend to become more oblique. 5) There is a trend toward deposition of cement.

Given these trends, *Africanomys* is the least derived of the Miocene ctenodactylids. *Africanomys* is progressive only in the relatively small premolars of some species. The frequently isolated metacone in *African-*

omys also suggests that it is more distantly related to the other three Miocene genera then they are to each other. An independent origin for *Africanomys,* possibly extending as far back as *Terrarboreus* (e.g., Wood, 1977, Fig. 2), seem plausible. Because of its frequently small premolars, isolated metacone, and apparent contemporaneity, *Africanomys* is not likely to be ancestral to *Sayimys.*

Sayimys sivalensis and *"Sayimys" obliquidens* are more closely related to each other than either is to *Africanomys* or *Metasayimys,* although the much greater complexity of the *"Sayimys" obliquidens* molars appears to separate them at the generic level. If simplicity of occlusal morphology is indeed the derived condition here, *"Sayimys" obliquidens* could well be directly ancestral to *S. sivalensis.* Little modification of the lower premolars or molars would be necessary to derive *S. sivalensis* from the Taben-buluk animal, particularly considering the very similar posterobuccal cingula in the two taxa. The buccal portions of the upper molars, however, are considerably more complex in *"Sayimys" obliquidens.*

A logical continuation of the structural trend from *"Sayimys" obliquidens* to *S. sivalensis* suggests that *S. sivalensis* could be ancestral to *Metasayimys.* Certainly the reverse cannot be true and the simplified morphology and small premolars of *Metasayimys* could easily be derived from *S. sivalensis* through reduction. *Metasayimys intermedius* may represent an intermediate stage in such a transition. Although Sen and Thomas (1979) did not compare this Arabian specimen with the Siwalik *Sayimys* material, it is clearly more similar to *S. sivalensis* than to *"Sayimys" obliquidens,* with which they did compare it. The lower molars of *M. intermedius* have simple metalophids, as in *S. sivalensis* and unlike *"Sayimys" obliquidens.* There appear to be posterobuccal cingula on DP_4 and M_1, and the DP_4 anteroconid is joined to the metalophid, both of which suggest relationship to *S. sivalensis* rather than *Metasayimys curvidens.*

The hypothesis outlined above, in which there may be a phylogenetic sequence proceeding from *"Sayimys" obliquidens* through *Sayimys sivalensis* to *Metasayimys,* with *Africanomys* not involved in the ancestry of these genera, has implications for the biostratigraphic and, particularly, paleozoogeographic interpretation of the Daud Khel local fauna. These implications will be considered in part II of this study.

Family Rhizomyidae Miller and Gidley, 1918
Genus *Kanisamys* Wood, 1937
Kanisamys indicus Wood, 1937
(Figure 9, Table 5)

Theridomys sp. Hinton, 1933, Ann. Mag. Nat. Hist., ser. 10, v. 12, p. 621.

Kanisamys indicus Wood, 1937, Amer. Jour. Sci., ser. 5, v. 34, pp. 68-70, figs. 5, 7, 11.

Kanisamys indicus Black, 1972, Palaeontology, v. 15, pp. 258-259, fig. 9.

Rhizomyidae indet. Jacobs, 1978, Bull. Mus. No. Arizona, no. 52, p. 22, fig. 11.

Holotype: YPM 13810, mandible fragment with I and M_1-M_3.

Stratigraphic and geographic distribution: Chinji Formation of northeastern Pakistan.

Referred material from Daud Khel: H-GSP 2275, mandible fragment with broken M_2, and isolated teeth as follows: M^1—2238-2254, M^2—2255-2261, M^3—2262-2274, M_1—2276-2285, M_2—2286-2299, 2301-2306 and 2328, M_3—2307-2327.

Description: The *Kanisamys* dental morphology has been described in detail by Jacobs (1978); he illustrated a rather wide range of variation in morphology within a single population (1978, Figs. 6-9). Although Jacobs' material was from the Dhok Pathan Formation and referred to *K. sivalensis,* rather than *K. indicus,* most of his observations, particularly with respect to the great morphological variability of *Kanisamys* samples, apply equally well to the Daud Khel sample.

The basic plan of the Daud Khel upper molars consists of strong protoloph and metaloph with variably developed anteroloph, mesoloph and posteroloph. The M^1 (Fig. 9A) has a strong anteroloph, usually with a distinct anterocone, while M^2 (Fig. 9B) and M^3 (Fig. 9C) have a narrow anteroloph which is distinct from the protoloph only near the buccal margin of the tooth. The posteroloph is separated from the metacone by a shallow flexus, becoming a fossette with slight wear, in M^1 and M^2. The posteroloph is better developed in M^3, where it and the metaloph enclose a large and deep fossette.

The morphology of M^1 is not so variable as that of M^2 or M^3. Only the development of the M^1 mesoloph is notably variable; it is absent in one specimen (H-GSP 2250) and very short in most others. The mesoloph is never longer than in H-GSP 2238 (Fig. 9A). Two M^1s have a slight swelling at the buccal margin of the posterobuccal flexus which could be interpreted as a weak mesostyle. The mesoloph is better developed in M^2, where it is never entirely absent and almost reaches the buccal margin of the tooth in several specimens. Two M^2s also have strong mesostyles; in one case (H-GSP 2257) this is contained within the buccal flexus rather than being positioned on the buccal margin. Size and length/width ratio is quite variable in M^2. Although the roughly triangular M^3 usually shows a simple pattern of three or four fossettes when worn (see Jacobs, 1978, Fig. 7B), there are five or even six fossettes in several lightly worn Daud Khel specimens. Folds in the lingual surface

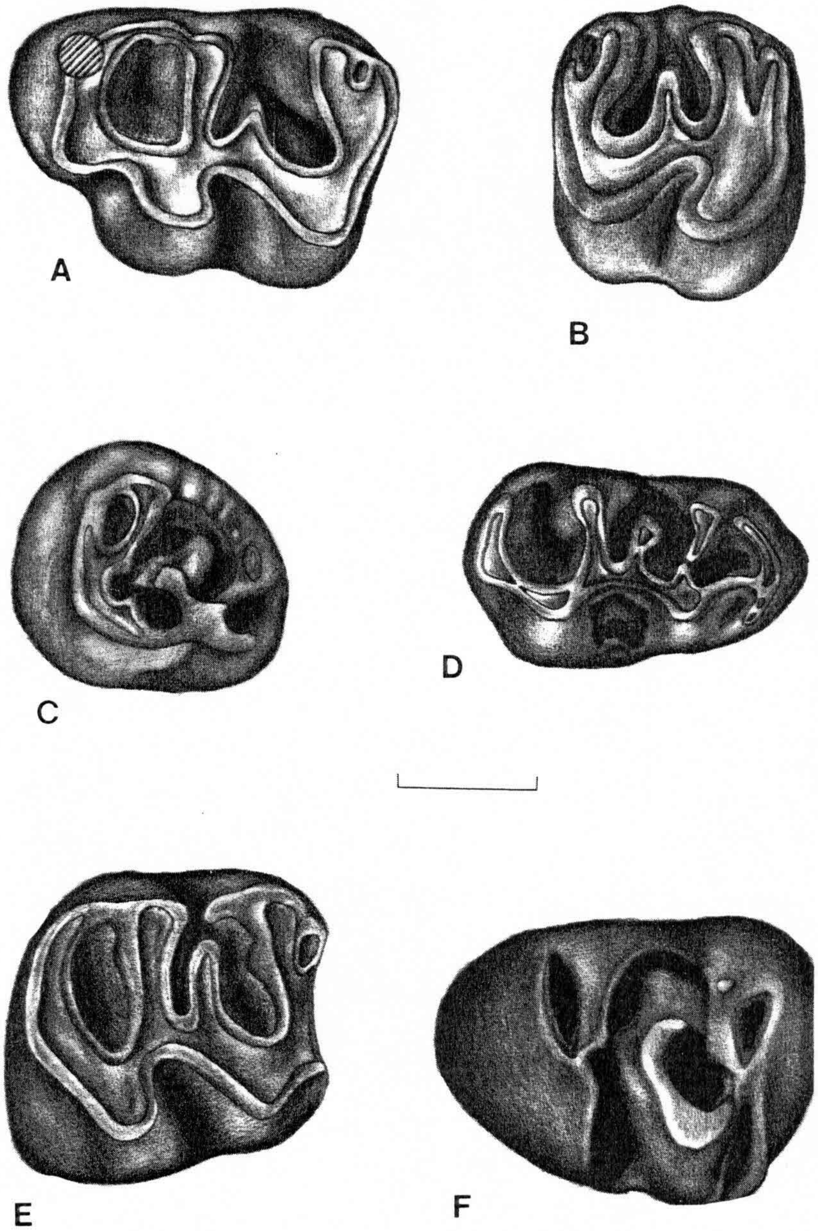

Fig. 9. Teeth of *Kanisamys indicus.* A—Left M^1, H-GSP 2238. B—Right M^2, H-GSP 2255. C—Left M^3, H-GSP 2262. D—Right M_1, H-GSP 2276. E—Right M_2, H-GSP 2286. F—Right M_3, H-GSP 2307. Scale bar equals 1.0 millimeter.

suggest a tendency for the Daud Khel M^3s to develop the lingual flexus, but only H-GSP 2266 has a flexus which keeps the lingual fossette open to the lingual surface at a late wear stage.

The Daud Khel M_1 (Fig. 9D) and M_2 (Fig. 9E) have strong metalophid, hypolophid and posterolophid, with M_1 also having a well-developed anterolophid. This morphology is reversed in M_3 (Fig. 9F), where the posterolophid is very strong and arcuate, while the anterolophid is small. The mesolophid is well-developed in the lower molars; it is very short in only two M_1s and reaches the lingual margin after only slight wear in 10 of 21 M_3s.

In addition to variability in size (Table 5) and the development of the mesolophid, the Daud Khel lower molars vary primarily in the degree of development of the anterior cingulum on M_2 and M_3. This cingulum is prominent, and possess a buccal as well as a lingual component, in many specimens (Figs. 9E, F), but it is absent on others. Three M_1s, including H-GSP 2276 (Fig. 9D), also possess a small stylid at the buccal margin of the posterobuccal flexus.

Discussion: Considering the range of variation in the two large samples of *Kanisamys* described to date (Jacobs, 1978, and this paper), it is difficult clearly to separate *K. indicus* from *K. sivalensis*. All of the morphological characters cited as diagnostic of the two species (Wood, 1937; Black, 1972) seem to be found in each of the large samples. The cuspidate or lophate character of the molars, the development of the mesolophid, the presence of the buccal anterior cingulum on M_2-M_3, and other features which might be used to identify individual specimens are too variable in large samples to be considered diagnostic at the species level.

Crown-height and size remain as possible diagnostic characters. Crown-height has not been quantified and it appears to be sufficiently variable in the Daud Khel sample to make it useless in differentiating these taxa. I refer the Daud Khel sample to *Kanisamys indicus* on the basis of size. The tooth dimensions are rather variable, but they generally fall below the figures for *K. sivalensis* (Black, 1972a, p. 259; Jacobs, 1978, Table 2). Most observed ranges from the Daud Khel sample overlap those from locality 182A (Jacobs, 1978) to some extent, but the dimensions of the Daud Khel sample are smaller. Since the difference appears to be significant, I recognize *K. indicus* and *K. sivalensis* as distinct species at present.

The two previously described specimens of *K. indicus* fall within the observed range of the Daud Khel rhizomyid sample in all dimensions. So does the specimen described by Prasad (1970) as *Kanisamys nagrii*, except that its M_3 is shorter than any Daud Khel specimens. This specimen may be assignable to *K. indicus; K. nagrii* is certainly inadequately diagnosed. The M^2 described by Jacobs (1978, p. 22) as Rhizomyidae indeterminate is morphologically identical to several specimens in the Daud Khel collection. Although it is slightly larger than the observed range of Daud Khel M^2 (Table 5), I consider it to represent *K. indicus.*

I agree with Jacobs (1978) that *Kanisamys bamiani* (Lang and Lavocat, 1968) is probably not distinct from *Kanisamys sivalensis* (or *K. indicus*) in occlusal morphology. However, if the magnification given by Lang and Lavocat for their figure of the *K. bamiani* holotype M_1 is correct, this tooth is much too large to fall within the range of described *K. sivalensis.*

No new information regarding rhizomyid phylogeny is provided by the Daud Khel *Kanisamys* material. Black's (1972a) hypothesis that *Kanisamys* led to *Protachyoryctes* and Recent African *Tachyoryctes* remains a reasonable interpretation of the available evidence.

Table 5. Measurements of *Kanisamys indicus* cheek teeth from Daud Khel.

	Length					Width				
	N	OR	X	s	V	N	OR	X	s	V
M^1	17	2.56-2.88	2.72	.09	3.3	17	1.80-2.32	2.11	.15	7.1
M^2	7	1.96-2.44	2.15	.19	8.8	7	2.12-2.52	2.31	.16	6.9
M^3	13	1.76-2.24	1.97	.14	7.1	13	1.64-2.16	1.86	.15	8.1
M_1	10	2.12-2.56	2.34	.13	5.6	10	1.60-1.76	1.68	.05	3.0
M_2	21	1.96-2.48	2.22	.16	7.2	21	1.88-2.56	2.13	.14	6.6
M_3	21	1.96-2.64	2.37	.20	8.4	21	1.64-2.04	1.86	.12	6.4

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