SYSTEMATIC REVISION OF CTENODACTYLIDAE (MAMMALIA, RODENTIA) FROM THE MIOCENE OF PAKISTAN

by

Jon A. BASKIN *

CONTENTS

* Department of Geosciences, Texas A&M University-Kingsville, Kingsville, TX, 78363, U.S.A.

Key-words: Rodents, Siwalik, Miocene, Ctenodactylidae, *Prosayimys*, *Sayimys*.

Mots-clés: Rongeurs, Siwalik, Miocène, Ctenodactylidae, *Prosayimys*, *Sayimys*.

Palaeovertebrata, Montpellier, 25 (1): 1–49, 8 fig., 1 pl.
(Reçu le 21 Octobre 1994, accepté le 16 Mars 1995, publié le 18 Mars 1996)

ABSTRACT

Extensive sampling of the Siwalik deposits of the Potwar Plateau of northern Pakistan and from the Zinda Pir dome of central Pakistan has produced a fossil record of Miocene ctenodactylids that can be correlated with the paleomagnetic time scale. The early Miocene *Prosayimys flynni* (n. gen., n. sp.) is recognized as the first ctenodactylid in the Indian subcontinent. *Prosayimys* is ancestral to *Sayimys*. From the late early Miocene to the early late Miocene, there is an anagenetic succession of three species of *Sayimys*: *S.* cf. *S. intermedius*, *S. sivalensis*, and *S. chinjiensis* (n. sp.). *Sayimys chinjiensis* gave rise to the late late Miocene *S. perplexus*. A second lineage is represented by *Sayimys minor*, *S.* sp. A, and *S.* sp. B.

RESUME

Un matérial abondant de Cténodactylidés fossiles provient des gisements des Siwaliks du Plateau du Potwar au Nord du Pakistan et du Zinda Pir Dome au Pakistan central. Ces séries sédimentaires ont livré une histoire évolutive détaillée des Cténodactylidés miocènes d'Asie qui peut être corrélée avec l'échelle magnétostratigraphique. *Prosayimys flynni* (n. gen., n. sp.), du Miocène inférieur, est le plus ancien vrai Cténodactylidé du sous-continent indien. *Prosayimys* a donné naissance au genre *Sayimys*. Depuis la fin du Miocène inférieur jusqu'au début du Miocène supérieur, se sont succédées, au sein d'une lignée évolutive anagénétique, trois espèces de *Sayimys*: *S.* cf. *S. intermedius*, *S. sivalensis*, et *S. chinjiensis* (n. sp.). *Sayimys chinjiensis* a donné naissance à *S. perplexus* à la fin du Miocène supérieur. Une deuxième lignée est représentée par *Sayimys minor*, *S.* sp. A, et *S.* sp. B.

INTRODUCTION

Although all four living genera of the rodent family Ctenodactylidae are found only in Africa, it is now well established that this family had its origins in Asia (Black, 1972; Wood, 1977; Wang, 1994). Miocene deposits of southern Asia have produced an excellent record of fossil ctenodactylids. The genus *Sayimys* was first described by Wood (1937) from a lower jaw that he designated the holotype of *S. perplexus*. The specimen had been collected from the late Miocene Nagri beds of the Siwalik sequence near Haritalyangar, in northern India. As reflected in the etymology of the species name, Wood (1937) was unsure of the affinities of his genus. Four years earlier, Hinton (1933) had described *Pectinator sivalensis* from a partial lower jaw from the Siwalik Chinji beds of the Salt Range of Pakistan. *Pectinator* is an extant ctenodactylid rodent which occurs in Ethiopia and Somalia. Hinton's discovery of a fossil ctenodactylid was neglected for almost 40 years, because the description was brief and there were no illustrations of the specimen (Jaeger, 1971, p. 122). Schaub (1958, p. 782) had briefly suggested the Chinji jaw might be better assigned to *Sayimys*. However, this was not formally accepted until the specimen was relocated and described in detail by Black (1972), along with illustrations that Hinton had planned to use in a monograph on Siwalik rodents. Black (1972) identified Hinton's species as *Sayimys sivalensis*.

Figure 1.— Map of Pakistan showing principal fossil localities discussed in this paper.

Bohlin (1946) is widely acknowledged for being the first to recognize a definitive fossil record for the Ctenodactylidae. He (1946) described a new species of *Sayimys*, *S. obliquidens*, from the early Miocene Hsishui Fauna of Taben Buluk (Qiu Z., 1990) of Gansu, China, and unequivocally established that *Sayimys* and four additional genera from the Oligocene of Mongolia and China are ctenodactylids. Important collections of Miocene ctenodactylids have since been made in Morocco (Lavocat, 1961; Jaeger, 1971, 1977), Sardinia (de Bruijn & Rümke, 1974), and Saudi Arabia (Sen & Thomas, 1979; Thomas and others, 1982). Beginning in the 1970's intensive screen washing of Neogene sediments in southern Asia, in India and especially Pakistan, has greatly increased the knowledge of rodent evolution in this region (see review in Jacobs and others, 1989). Large collections of *Sayimys* have been obtained from the Siwalik sequence in northern Pakistan and the Manchar Formation in southern Pakistan. Munthe (1980) fully described and illustrated for the first time upper and lower dentitions of *S. sivalensis* from the Siwaliks of northern Pakistan. De Bruijn and others (1981) described a new species, *S. minor*, from the Murree Formation in the Banda Daud Shah area of northern Pakistan. De Bruijn and others (1989) described evolutionary trends in *Sayimys* from five successive levels in the Manchar Formation, spanning an interval from approximately 19 to 13 Ma. They recognized a transition from *S. intermedius* (previously known only from Saudi Arabia) to *S. sivalensis*. These African, European, and Asian fossils have allowed researchers to study variation of Miocene ctenodactylids in time and space (Wood, 1977).

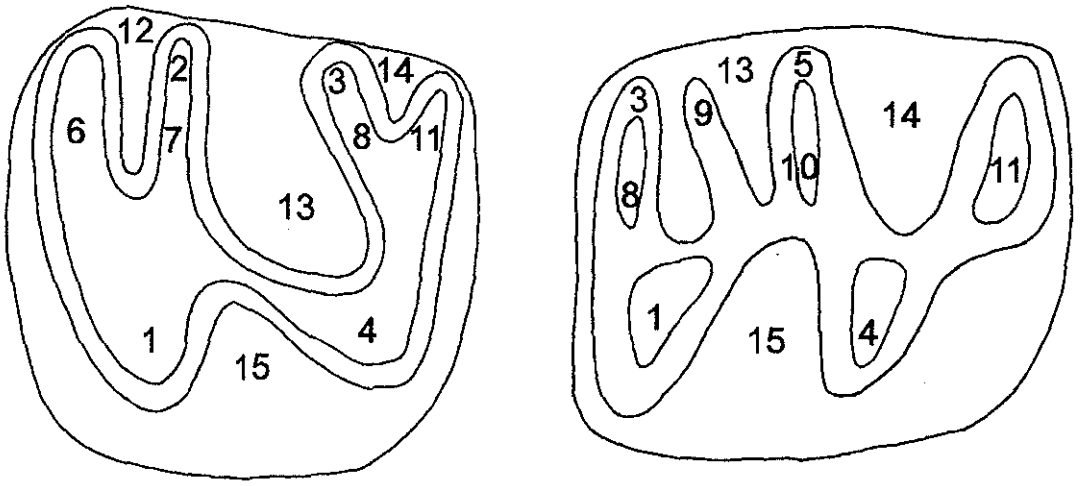


Figure 2.— Ctenodactylid dental terminology. 1 - Protocone (–id); 2 - Paracone; 3 - Metacone (–id); 4 - Hypocone (–id); 5 - Entoconid; 6 - Anteroloph; 7 - Protoloph; 8 - Metaloph (–id); 9 - Metalophulid II; 10 - Hypolophid; 11 - Posteroloph (–id); 12 - Paraflexus; 13 - Mesoflexus (–id); 14 - Metaflexus (–id); 15 - Hypoflexus (–id).

The present study is able to give a much more detailed look at the evolution of ctenodactylids in Pakistan over an 11 million year interval, from 20 to 9 Ma, thanks to cooperative research undertaken with the Geological Survey of Pakistan and the Pakistan Museum of Natural History by North American paleontologists working with D. Pilbeam and E. H. Lindsay. Localities in Pakistan discussed in this paper are shown in Figure 1.

GEOLOGY AND AGE

The Siwalik Group of Pakistan and India is a thick (ca. 3 km) sequence of fluvial sediments that have been shed off the rising Himalaya Mountains. Fossils from the Siwaliks have been studied for over 160 years (for a brief overview of Siwalik stratigraphy and faunas see Lindsay and others, 1980). The majority of specimens described in the present paper are from the middle and late Miocene of the Potwar Plateau near Chinji village. In the Potwar Plateau of northern Pakistan, the Siwaliks can be subdivided into lower, middle, and upper units (Flynn and others, 1990a). The lower and middle Siwaliks were deposited in the middle and late Miocene. From bottom to top, the lower Siwaliks consist of the Murree or Kamlial Formations and Chinji Formation; the middle Siwaliks, the Nagri and Dhok Pathan Formations. The successive units are usually lithologically indistinguishable (all are highly variable) and time transgressive (Flynn and others, 1990a). The use of formation names for faunal assemblages has therefore caused some difficulties, particularly for older collections that were made without precise biostratigraphic information. The paleomagnetic stratigraphy and lithostratigraphy of the lower Siwaliks of the Potwar Plateau were

described by Johnson and others (1985). Barry and others (1985) made the initial correlations of the Potwar fossil localities to the paleomagnetic section. Jacobs and others (1989) presented a relatively complete correlation of Potwar Plateau localities with the paleomagnetic section. The biostratigraphy of this region was summarized by Flynn and others (1990a). As noted previously (Jacobs and others, 1989), *Sayimys* appears in the Potwar Plateau close to the base of the Siwalik section, at 18.3 Ma, and last appears at 9 Ma. There is a possible younger occurrence at about 7 Ma.

Important new collections of ctenodactylids from the early to middle Miocene (20-17 Ma) are from the Dera Ghazi Khan area of central Pakistan (Friedman and others, 1992; Downing and others, 1993). Fossils were collected from the upper Chitarwata and lower Vihowa formations on the southeastern flank of the Zinda Pir Dome. The lower Vihowa formation correlates with the lower Murree or Kamlial Formations of the Potwar Plateau (Friedman and others, 1992) and with the lower Manchar Formation. The upper Chitarwata Formation represents a somewhat earlier time interval and documents the first occurrence of ctenodactylids in south Asia.

Terms used for the description of ctenodactylid dental morphology in occlusal view are illustrated in Figure 2. The term stria (–id) is used for the continuation of the flexus (–id) on the lateral of the tooth as used by Stirton (1935). The term long (length) or short when applied to a flexus (–id) refers to the transverse dimension; wide (width) or narrow to the anterior-posterior dimension.

SYSTEMATIC PALEONTOLOGY

Family CTENODACTYLIDAE ZITTEL, 1893

Genus *PROSAYIMYS* gen. nov.

Type species: *Prosayimys flynni* sp. nov.

Included species: the type species only.

Diagnosis: Lower crowned than *Sayimys*, *Akzharomys*, *Africanomys*, and *Metasayimys*. Unlike these genera, the lower molars and lower deciduous premolar of *Prosayimys* have a persistent metalophulid II, which arises from the juncture of the hypolophid with the posterior arm of the protoconid and extends obliquely, usually to the internal margin near the metaconid. *Prosayimys* is higher crowned and more lophate than *Tataromys*, *Yindirtemys*, and *Karakoromys* and also differs from these three genera in having the hypoflexus of upper molars oblique anteriorly. On the upper molars of *Prosayimys*, the internal side is only moderately higher crowned than the external side and the paraflexus is longer than the metaflexus. On the lower molars, the mesostriid and metastriid are of approximately equal depth. The height of the metaconid, entoconid, and posterolophid above the termination of the mesostriid or the metastriid is equal to or less than the height of enamel below the termination.

Comparisons

Prosayimys differs from the Asian Oligocene and Early Miocene genera *Tataromys*, *Yindirtemys*, and *Karakoromys* in its greater height of crown, more pronounced lophodonty, absence of an anterior cingulum on the lower molars, and in having the hypoflexus of upper molars oblique anteriorly vs. oblique posteriorly (*Tataromys* and *Yindirtemys*) or transverse (*Karakoromys*). In the lower molars of *Tataromys*, *Kakaromys*, and *Yindirtemys*, the termination of the hypoflexid is usually anterior to the hypolophid and there is a pronounced indentation between the hypoconid and posterolophid which may demarcate a hypoconulid. On the P^4 of *Prosayimys*, the anteroloph does not connect with the paracone, a derived characteristic of Miocene ctenodactylids. As in *Tataromys*, the other Oligocene ctenodactylids, and the early Miocene Sardinian *Sardomys* and *Pireddamys*, the lower molars and DP_4's of *Prosayimys* have a metalophulid II that persists through late wear. *Prosayimys* is much lower crowned and much less lophodont than *Sardomys* and *Pireddamys*. *Prosayimys*, along with the Oligocene Asian ctenodactylids and *Sardomys*, has upper molars with a long paraflexus. In *Sardomys* and *Pireddamys*, the flexi and flexids show a much greater tendency to form enamel lakes and the lower molars lack a posteroexternal cingulum.

Prosayimys is smaller than *Sayimys* or *Akzharomys* and its dentition is lower crowned and less lophate. It displays the unilateral hypsodonty of the upper molars that distinguishes *Sayimys* from *Tataromys* (Bohlin, 1946, p. 122), but only to a moderate degree. In *S. obliquidens* and *A. mallos*, a metalophulid II apparently is occasionally present. In *S. obliquidens*, the mesoflexid I is short and narrow. *Akzharomys mallos*, *S. obliquidens*, and *S.* cf. *S. intermedius* have a relatively long paraflexus on the upper molars, as in *Prosayimys*.

The cheek teeth of *Africanomys* and *Metasayimys* are higher crowned and more lophate than in *Prosayimys*. The two African genera differ further from *Prosayimys* in having the upper and lower premolars very reduced; the upper molars with the paraflexus very short to absent and the metaflexus short; and the lower molars with the mesoflexid shorter than the metaflexid and with the metalophulid II, if present, that fuses at a very early wear stage with the metaconid. In *Metasayimys*, crown cementum is present in the molars.

Etymology: *Pro-* a prefix meaning before, for the presumed ancestral relationship of this taxon to *Sayimys*.

Prosayimys flynni sp. nov.

(Figure 3; Plate 1 A-E; Table 1)

Holotype: 295, left M_3.

Hypodigm: ZP no. 311, 313, 317, left DP^4; 314, 315, right DP^4; 275, left P^4; 274, 276, 277, right P^4; 283, 286, 287, left M; 282, 284, right M; 279, 288, 289 left M^1; 280, 291, 292 right M^1; 290, right M^2; 281, 285, 307, left M^3; 293, right M^3; 312, left DP_4; 316, right DP_4; 294, left P_4; 299, 303, left $M_?$; 300, 301, right $M_?$; 296-298, 305, 306, 309,

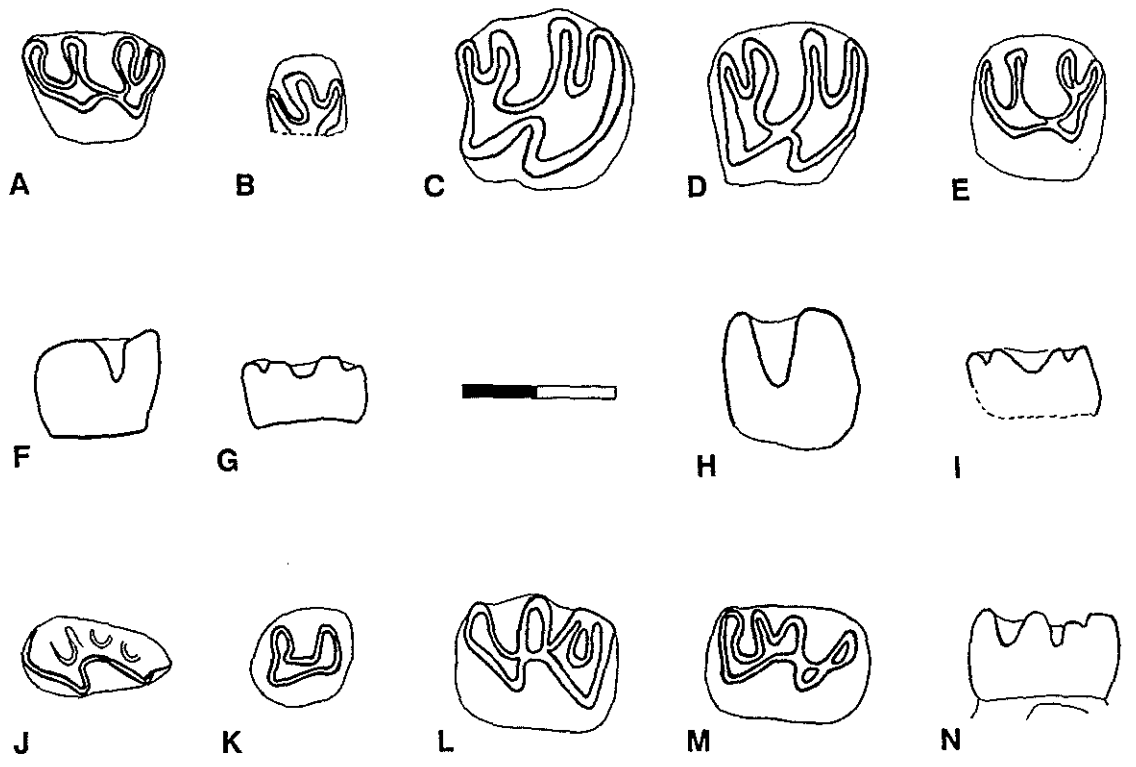


Figure 3.— *Prosayimys flynni* new genus and new species. **A-E, J-M**: occlusal view. **F, H, N**: internal view. **G, I**: external view.
A. left DP^4 Z113/311; **B.** left P^4 Z113/275; **C.** right M^1 Z113/292; **D.** right M^2 Z113/290; **E.** left M^1 Z113/289; **F.** left M^1 Z113/289; **G.** left M^1 Z113/289; **H.** right M^3 Z113/293; **I.** right M^3 Z113/293; **J.** right DP_4 Z113/316; **K.** left P_4 Z113/294; **L.** right M_{1-2} Z113/304; **M.** left M_3 Z113/295; **N.** left M_3 Z113/295.
Scale represents 2 mm.

left M_{1-2}; 304, 308, 310, right M_{1-2}; 295, left M_3; 302 right M_3.

Locality: Z113, Dalana section, Chitarwata Formation, Zinda Pir Dome, Pakistan.

Age: 21 Ma; Early Miocene.

Diagnosis: as for genus.

Etymology: patronym for Dr. Lawrence J. Flynn in recognition of his contributions to the knowledge of the Neogene rodent fauna of southern Asia.

Description

The permanent cheek teeth are higher crowned than the deciduous teeth, both in the absolute height of the cusps and in the height of enamel at the base of the striae and striids. The upper molars are otherwise more similar to the DP^4 than in *Sayimys*.

- DP^4

Subtrapezoidal occlusal outline, shorter lingually. The protocone and subequal

Prosayimys flynni n. gen & n. sp.

		N	Range	Mean	SD
DP^4	length	3	1.55 – 1.70	1.633	
	anterior width	2	1.42 – 1.52	1.475	
	posterior width	3	1.35 – 1.50	1.425	
P^4	length	4	1.08 – 1.22	1.119	
M^{1-2}	length	7	1.62 – 2.12	1.854	0.201
	anterior width	5	1.70 – 2.20	1.890	0.207
	posterior width	5	1.60 – 2.10	1.810	0.225
M^3	length	4	1.88 – 2.08	1.944	
	anterior width	2	1.82 – 2.05	1.930	
	posterior width	3	1.70 – 1.98	1.820	
DP_4	length	1	1.88		
	posterior width	1	1.10		
P_4	length	1	1.15		
	width	1	1.18		
M_{1-2}	length	7	1.88 – 2.12	2.004	0.106
	anterior width	7	1.30 – 1.72	1.568	0.137
	posterior width	9	1.40 – 1.78	1.661	0.123
M_3	length	2	1.95 – 2.02	1.988	
	anterior width	2	1.30 – 1.48	1.388	
	posterior width	2	1.32 – 1.52	1.425	

Table 1.— Statistical summary of measurements (in mm) of teeth of *Prosayimys flynni* new genus and species from Pakistan.

hypocone are joined by a horizontal mure. The hypoflexus is relatively short and narrow, but the hypostria is deep. The paraflexus is longer, wider, and deeper (i.e. it will persist to a greater wear stage) than the metaflexus. The anteroloph joins the protocone at the anterior margin of the protocone. The paracone joins the protocone medially. The metaloph connects the metacone with the hypocone in the least worn specimen, with the posteroloph in the others. In the least worn specimen (311), the anteroloph terminates at a distinct parastyle. There are three roots.

• P^4

All the specimens are broken, preserving either the internal or external moities. They appear similar to illustrations of *S. intermedius* from locality 81.14a from the lower Manchar formation (de Bruijn and others, 1989, plate II). They differ in having the protoloph more oblique, connecting the paracone with the posterior arm of the protocone.

• M^{1-3}

Subquadrate occlusal outline. The M^1's are presumably smaller than the M^2's. The paraflexus and metaflexus persist until very late wear. The paraflexus is deeper and longer than the metaflexus. The anteroloph is connected to the anterior arm of the protocone. The protoloph connects to the medial or posterior margin of the protocone. The hypoflexus is deeper, but shorter, than the mesoflexus and flexes anteriorly. The mesoflexus extends slightly more than halfway across the tooth and flexes posteriorly at its internal termination. The protocone is slightly larger than the hypocone. In unworn specimens the metaloph is connected to the hypocone, but with little wear it connects to the posteroloph. The two broken teeth tentatively identified as M^3's have a relatively smaller, more posteriorly directed hypocone with a greater indentation along the posterior margin.

• DP_4

The two specimens are worn and broken. The occlusal outline is elongate oval and narrow anteriorly. The anteroconid is close to the protoconid, but the more complete specimen (ZP 316) is too worn to determine if the anteroconid were connected or isolated. A metalophulid II is apparently present. The labial parts of the protoconid and hypoconid are directed anteriorly.

• P_4

One moderately damaged and slightly worn specimen (ZP 294) is known. There is a single large root. The tooth shows loss of enamel. The three major cusps of the ctenodactylid P_4 are the protoconid, metaconid and entoconid (Dawson and others, 1984). This tooth most closely resembles the illustration of P_4 of *S. obliquidens* or perhaps *Tataromys* (Bohlin, 1946, figs. 30c, 19-32). The occlusal outline is subquadrate. The crests form a "U"-shaped rather than a "Y"-shaped pattern. The transversely elongate metaconid connects to the anteroposteriorly elongate protoconid along the anterior margin. There is a slight constriction where the two cusps join and a shallow groove down the anterior face. The posterior arm of the protoconid extends almost directly posteriad where it connects to a small cuspid (the hypoconid of Bohlin), the posterior crest extends along the posterior margin to the entoconid on the internal margin.

• M_{1-2}

The occlusal outline is subrectangular. The presumed M_1 is smaller than the M_2. The height of the entoconid is less than the height of enamel below the base of the entoconid. The mesoflexid and metaflexid are approximately equal in length and extend to the midline of the tooth. Metalophulid II is present and extends from the juncture of the posterior arm of the protoconid with the hypolophid towards the metaconid and is separate from it in little worn specimens. With wear metalophulid II connects with the metaconid forming an enamel lake. The transversely directed hypolophid is opposite the hypoflexid; the hypolophid connects with the posterior arm of the protoconid at an angle. The posteroexternal cingulum is moderately developed. A hypoconulid is present on the posterolophid of little worn specimens.

• M_3

The specimens tentatively identified as M_3 are similar to M_{1-2}, but have a poorly developed posteroexternal cingulum and the posterolophid is directed more posteriorly.

Comparisons with species of *Sayimys*

Prosayimys flynni is smaller than species of *Sayimys*, but the size range overlaps considerably with *S. minor* and *S.* cf. *S. intermedius*. It is much smaller than *S. obiquidens*, *S. sivalensis*, *S. perplexus*, and *S. badaunensis*. A long paraflexus on the upper molars is a primitive characteristic that also occurs in *S. obiquidens* (Bohlin, 1946, fig. 30) and specimens referred to *S. intermedius* from the lower Manchar Formation (de Bruijn and others, 1989, plates I and II) and the Al-Sarrar Local Fauna of Saudi Arabia (Thomas and others, 1982), as well as in Oligocene ctenodactylids and *Sardomys*. *Sayimys obliquidens* is the only species of *Sayimys* with metalophulid II, but it occurs infrequently and apparently is more closely appressed to the metalophid (Bohlin, 1946, fig. 30c).

Sayimys minor is also small and has the lophs on the lower molars less well developed than in other species of *Sayimys* (de Bruijn and others, 1981). *Sayimys minor* is more lophate than *P. flynni* and lacks metalophulid II. The upper molar of *S. minor* from the type locality is heavily worn, which may account for the lack of a paraflexus and metaflexus, although it has a slight indentation on the posterointernal margin.

The M_1–M_2 of *Sayimys intermedius* from the middle Miocene Hofuf Formation of Saudi Arabia (Sen & Thomas, 1979) have the hypolophid oriented transversely and the metastriid nearly as deep as the mesostriid. Specimens from the Manchar Formation of Pakistan referred to *S. intermedius* (de Bruijn and others, 1989) typically have the hypolophid oriented transversely on M_{1-2}, obliquely on M_3. In the lower molars referred to *S.* cf. *S. intermedius* in the present paper, the hypolophid is oriented as in the Manchar specimens and the metastriid penetrates the lingual side much less than the mesostriid (as is apparently the case in the illustrations of the Manchar specimens). In *P. flynni*, the hypolophid is oriented transversely on all lower molars and the metastriid nearly as deep as the mesostriid.

Genus *SAYIMYS* WOOD, 1937

Type species: *Sayimys perplexus* WOOD, 1937, p. 73.

Included species: The type species and *S. sivalensis* (HINTON, 1933, p. 622); *S. obliquidens* BOHLIN, 1946, p. 118; *S. intermedius* (SEN & THOMAS, 1979, p. 35); *S. minor* DE BRUIJN, HUSSAIN & LEINDERS, 1981, p. 94; *S. badaunensis* VASISHAT, 1985, p. 113; and *S. chinjiensis* n. sp.

Distribution: late Early Miocene, Vihowa Formation; Middle Miocene, lower Manchar Formation; and Middle and Late Miocene, Siwalik beds of Pakistan; Late Miocene and Early Pliocene, Siwalik beds of India; Middle Miocene, Hofuf and Dam Formations of Saudi Arabia; and late Early Miocene of Gansu, China.

Emended diagnosis: Ctenodactylid rodents with mesodont, lophate, and rooted cheek teeth, that lack crown cementum. The DP^3 is present. P^4/P_4 are relatively large compared to the molars. Upper cheek teeth are unilaterally high-crowned (internal side higher crowned than external side). On P^4, the anteroloph does not connect with the paracone. The upper molars are relatively quadrate (not anteroposteriorly elongate rectangles), and have the hypocone subequal in size to the protocone, an anteriorly directed hypoflexus, and a paraflexus (primitively) and metaflexus. The lower cheek teeth have a posteroexternal cingulum frequently present and the anterior cingulum absent. Metalophululid II is usually absent on the lower molars. On M_1 and M_2, the mesoflexid is typically equal in length to or longer than the metaflexid. Mandible with a well-developed masseteric crest that runs horizontally to at least the level of the anterior root of M_1. The mental foramen is relatively high on the mandible and is situated anterior to the P_4.

Comparisons

Metasayimys can be distinguished from *Sayimys* by the smaller size of the premolars relative to the molars, more convex upper molars, shallower and shorter mesoflexid on lower molars, and the occasional presence of cement on the crown (Jaeger, 1971; de Bruijn and others, 1989). *Sardomys* also has cement on M_2 and M_3. In the lower molars of *S. obliquidens*, *Africanomys*, and *Metasayimys*, the mesoflexid is shorter than the metaflexid. Both *Africanomys* and *Metasayimys* have a short metalophulid II that in very early wear fuses with the metaconid, producing the short, transverse mesoflexid, according to Jaeger (1971). A short mesoflexid also occurs on M_2 and M_3 of some of the *Sayimys* described in the present paper and on the type specimen of *S. sivalensis*. De Bruijn and others (1989, p. 195) state that south Asian *Sayimys* have a longitudinal depression on the lower incisors, but do not describe or illustrate it. Flynn (pers. comm.) describes a specimen as having a rounded, crenulated, undepressed lower incisor. De Bruijn & Rümke (1974) state that *Sardomys* and *Pireddamys* have grooved incisors, in contrast to *Sayimys*. In *S. obliquidens*, the incisors are keeled (Bohlin, 1946). The lower incisor referred to *S. intermedius* is reported to be similar to that of *S. obliquidens* and unlike that of *Metasayimys* (Sen & Thomas, 1979, p. 36). *Metasayimys* has grooved upper incisors and smooth lower incisors. *Africanomys* differs from *Sayimys* in having more reduced premolars, upper molars with metacone connected to the posteroloph, and in the structure of the DP_4. The incisors are not known.

The DP_4 of *Sayimys* resembles that of *Metasayimys* and *Sardomys* in possessing an anteroconid, a derived characteristic. The primitive *Tataromys* has an anteriorly placed protoconid, the metaconid situated posterior to the protoconid, a metalophulid II connected to the metaconid, the entoconid connected posteriorly to the hypoconid, and no anteroconid. The DP_4 of *Africanomys* is similar to that of *Tataromys*, but differs in having the metaconid opposite or anterior to the protoconid and not connected to it, in having a better developed connection between the metaconid and metalophulid II, and in having the entoconid connecting anteriorly with the hypoconid. In *Sayimys*, the DP_4 has an anteroconid and has the metaconid connected anteriorly with protoconid, not connected to metalophulid II as in *Africanomys*. In *Metasayimys* the anteroconid of DP_4 is usually isolated as in *S. intermedius*, although it may be connected to the

metaconid by a low crest (Jaeger, 1971). The metaconid in *M. curvidens* sometimes has a posteroexternally extending arm which usually does not join the posterior arm of the protoconid (Jaeger, 1971, p. 127). A metalophulid II is present in *S. minor*. The DP_4 of *Sardomys* usually has an isolated anteroconid and a metalophulid II.

Akzharomys is larger and has higher crowned upper molars than *Sayimys*. Metalophulid II is present on little worn teeth. As noted by Shevyreva (1994), *Akzharomys mallos* may have been derived from *S. obliquidens*, but the latter species is tentatively retained in *Sayimys* pending further study.

Sayimys minor DE BRUIJN, HUSSAIN & LEINDERS, 1981

Sayimys minor de Bruijn, Hussain, and Leinders, 1981, p. 94.

Type locality and **age**: Murree Formation, Banda Daud Shah, Pakistan, early Miocene, greater than 18 Ma.

Emended diagnosis: The smallest species of *Sayimys*. P^4 lacks an anteroloph except in an unerupted specimen. Upper molars with anteroloph usually absent. The P_4 lacks a posterolophid. The DP_4 has a metalophulid II. Lower molars lack metalophulid II. The M_3 has a wide mesoflexid that is much shorter than the metaflexid. The masseteric crest extends slightly anterior of the anterior root of M_1.

Discussion and **comparisons**

Some of the above diagnostic characters are taken from specimens from localities Y 721 and 747 (ca. 18.3 Ma), which are tentatively referred to this species. The topotypic sample of *S. minor* consists only of four teeth, at least one of which may belong to another taxon. The holotype (an M_{1-2}) is only very slightly smaller than specimens from Pakistan referred to *S.* cf. *S. intermedius*, but has more slender lophs, has deeper penetration of the mesostriid and metastriid on the lingual face, and is somewhat lower crowned. The topotypic upper molar of *S. minor* (de Bruijn and others 1981, plate 3, fig. 4) is a worn tooth which lacks a paraflexus and has only a slight indentation for a metaflexus, similar in morphology to heavily worn specimens from localities Y 721 and 747, but much larger, within the size range of *S.* cf. *S. intermedius*, to which species it may be better referred. The topotypic M_3 is also similar in size to *S.* cf. *S. intermedius*, but has a wide and short mesoflexid. *Sayimys sivalensis* also has a short mesoflexid on M_3, but is much larger and has a much shallower metastriid on both M_2 and M_3. A major distinction between *S. minor* and *S. intermedius* is the morphology of the DP_4. The topotypic DP_4 of *S. minor* (De Bruijn and others, 1981, plate 3) is broken anteriorly (so that the morphology of the anteroconid is unknown), cuspate, low crowned, and has metalophulid II that probably connected to the metaconid (de Bruijn and others, 1981), unlike the lophate and higher crowned DP_4 of *S. intermedius*. The less worn DP_4 from Y747 has a very short metalophulid II and appears more lophate, although probably not higher crowned, than the type of *S. minor*. The DP^4 from locality Y 721 is also cuspate, as is that of *Sayimys* sp. A from locality Y 592.

Sayimys cf. *S. minor* DE BRUIJN, HUSSAIN & LEINDERS, 1981

(Figure 4 A-J; Plate 1 F, G; Table 2)

Referred localities and **ages**: Kamlial Formation, Potwar Plateau, Pakistan, early middle Miocene. Y 721, 18.3 Ma; Y 747, approximately 18.3 Ma.

Referred material: GSP 45374, left DP^4; 33113, right DP^4; 36353, 45369, 45371, 45379, left M^{1-2}; 33116, 45370, 45372, 45373, right M^{1-2}; 45380, right M^3; 45377, 45381, left P_4; 45378, right P_4; 33114, 45367, 45376, left M_{1-2}; 33115, 45375, right M_{1-2}; 33112, left M_3; 45368, right M_3; from Y721. GSP 48144, right maxillary fragment with DP^4; 21997, 48122, left P^4; 48123-48126, right P^4; 48143, right maxillary fragment with P^4–M^2; 48112, 48146, left M^{1-2}; 48114, 48147-48153, 48155, 48156, right M^{1-2}; 48157, left M^3; 22000, left DP_4; 48113, right DP_4; 21998, 48118, 48121, left P_4; 48119, 48120, right P_4; 48136, left mandible fragment with M_1, M_2, and alveolus for P_4; 21999, 48115, 48116, 48129, 48134, 48135, left M_{1-2}; 48127, 48128, 48131, 48132, 48137, 48139, 48140, right M_{1-2}; 33077, 48141, 48142, left M_3; 33078, 48117, 48133, 48138, right M_3; from Y 747.

Description

GSP 48144 has an alveolus for a small, single rooted DP^3.

• DP^4

The principal cusps of the specimens from Y 721 are not submerged into the lophs. The specimen from Y 747 is approximately 20% larger and more lophate, although more worn. The anteroloph is continuous with the anterior arm of the protocone. The protoloph connects medially to anteriorly with the protocone. The metacone is a transversely elongate cusp, that connects with the middle of the posteroloph only after moderate wear. The hypocone is smaller than and situated slightly internal to the protocone. The hypoflexus is short, wide, and shallow.

• P^4

The tooth is single rooted, but with a groove on the anterior side. The protocone is slightly larger than the paracone. The posteroloph is short and connects lingually with the protoloph. The anteroloph is absent, except in one unerupted specimen (48126), but will disappear with little wear. It is absent in a second unerupted specimen (48143). The protoloph is nearly transverse.

• M^{1-2}

As indicated by GSP 48143 (Plate 1 F), the M^1 is significantly smaller than M^2. Specimen GSP 36353, which is represented by the labial half of the tooth, has a paraflexus that is longer and deeper than the metaflexus. In seven other specimens from Y 721 and 11 from Y 747 preserving this region, there is no paraflexus. In those specimens with little wear, the anteroloph and/or protoloph tapers as it extends labially, indicating that in at least some specimens, absence of a paraflexus is real, not an artifact of wear. The mesoflexus is deep and extends approximately 65% across the width of the tooth to the mure in the least worn specimens; it extends to the halfway point in the

Sayimys cf. *S. minor* from YGSP 721

		N	Range	Mean	SD
DP^4	length	2	1.35 – 1.42	1.388	
	anterior width	1	1.38		
	posterior width	1	1.25		
M^{1-2}	length	7	1.32 – 1.62	1.521	0.101
	anterior width	5	1.32 – 1.60	1.485	0.105
	posterior width	5	1.30 – 1.55	1.455	0.104
M^3	posterior width	1	1.82		
P_4	length	3	0.95 – 1.05	0.992	
	width	3	0.95 – 1.07	1.000	
M_{1-2}	length	1	1.65		
	anterior width	1	1.45		
	posterior width	1	1.45		
M_3	length	1	2.15		
	anterior width	1	2.00		
	posterior width	2	1.30 – 1.65	1.475	

Sayimys cf. *S. minor* from YGSP 747

		N	Range	Mean	SD
DP^4	length	1	1.60		
	anterior width	1	1.50		
	posterior width	1	1.35		
P^4	length	6	0.87 – 1.20	1.021	0.114
	width	6	1.37 – 1.77	1.554	0.140
M^{1-2}	length	9	1.57 – 1.85	1.686	0.108
	anterior width	7	1.60 – 2.25	1.939	0.263
	posterior width	6	1.57 – 2.13	1.729	0.219
M^3	length	1	1.75		
	anterior width	1	2.00		
	posterior width	1	1.65		
DP_4	length	2	2.03 – 2.05	2.038	
	anterior width	2	0.95 – 1.00	0.975	
	posterior width	2	1.15 – 1.20	1.175	
P_4	length	5	0.95 – 1.25	1.070	0.114
	width	5	1.15 – 1.37	1.290	0.088
M_{1-2}	length	13	1.57 – 2.37	2.029	0.219
	anterior width	12	1.50 – 2.07	1.810	0.192
	posterior width	16	1.43 – 2.15	1.723	0.184
M_3	length	5	2.05 – 2.27	2.140	0.089
	anterior width	5	1.77 – 2.00	1.865	0.088
	posterior width	6	1.55 – 1.83	1.654	0.097

Table 2.— Statistical summary of measurements (in mm) of teeth of *Sayimys* cf. *S. minor* from Pakistan.

others. In lightly worn specimens, the metaloph and posteroloph form a "Y"-shaped occlusal pattern. With moderate wear, the metaflexus is lost.

• M^3

The specimen from Y 747 has a well developed paraflexus and no metaflexus, although it appears that a short posteroloph was present at an earlier wear stage. In the posterior tooth fragment from Y 721, the hypocone is relatively small and is directed obliquely posteriad. The posteroloph is much shorter and less wide than the metaloph.

The masseteric crest extends in front of the anterior root of M_1.

• DP_4

Both specimens are worn, one heavily. The anteroconid region is short and the anteroconid is conical and isolated. The metalophid is concave anterior. A short metalophulid II is present on the least worn specimen (GSP 48113). The hypolophid is transverse.

• P_4

The occlusal outline is subquadrate to rectangular. There is a "y"-shaped dental pattern formed by ridges connecting the protoconid with the metaconid and entoconid. The posterior arm of the protoconid extends linearly to the metaconid in two specimens and to the middle of the posterior margin in four. The hypolophid is directed transversely along the posterior margin. There is no posterolophid. The posteroexternal cingulum is weak to well developed and has a prominent stylid in most specimens.

• M_{1-2}

As indicated by GSP 48136 (Plate 1 G), the M_1 is significantly smaller than M_2. The anterior margin is flat to concave. The metaflexid is slightly longer than or approximately equal in length to the mesoflexid in specimens that are probably M_1's. The mesoflexid is shorter than the metaflexid in specimens that are probably M_2's. The mesostriid is usually much deeper than the metastriid. There is no metalophulid II. In the specimens that are probably M_1's, the hypolophid is opposite the hypoflexid, more or less transverse, and not aligned with the posterior arm of the protoconid and the hypoconulid is present on the posterior cingulum. In the specimens that are probably M_2's, the hypolophid is usually more oblique and may be partially aligned with the posterior arm of the protoconid. The posterolabial cingulum is weakly developed. One specimen (GSP 48134) has a stylid connected to the end of the posterolophid that restricts the opening to the metaflexid.

• M_3

The anterior margin is concave. The posterior margin is rounded. In the specimens from Y 747, the metaflexid is longer, shallower, and narrower than the mesoflexid. The hypolophid is oblique and aligned with the posterior arm of the protoconid.

In the specimens from Y 721, the metalophid is oblique. The hypolophid is nearly transverse, but is confluent with the posterior arm of the protoconid. The terminations of

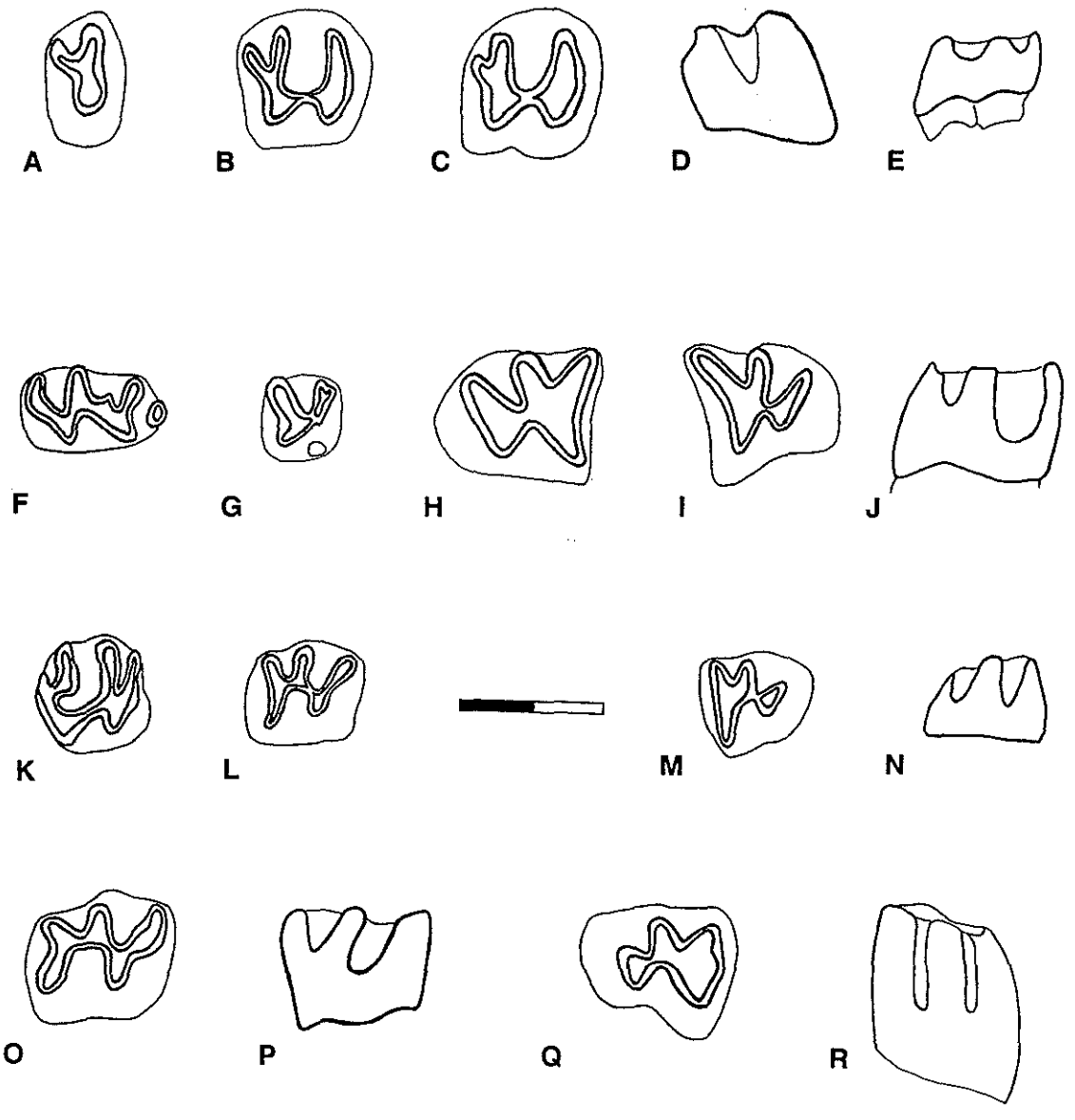


Figure 4.— **A-J** *Sayimys* cf. *S. minor*. **A-C, F-I**: occlusal view. **D, J**: internal view. **E**: external view.
A. right P^4 Y747/48125; **B**. right M^{1-2} Y721/33116; **C**. right M^{1-2} Y747/48152; **D**. right M^{1-2} Y747/48152; **E**. right M^{1-2} Y747/48152; **F**. left DP_4 Y747/48113; **G**. left P_4 Y721/45377; **H**. right M_3 Y747/33078; **I**. left M_3 Y721/33112; **J**. left M_3 Y721/33112.

K-N *Sayimys* sp. A. **K-M**: occlusal view. **N**: internal view.
K. right M^{1-2} Y592/45355; **L**. left M_{1-2} Y591/45351; **M**. left M_3 Y592/45360; **N**. left M_3 Y592/45360.

O-R *Sayimys* sp. B. **O, Q**: occlusal view. **P, R**: internal view.
O. right M_{1-2} Y797/33090; **P**. right M_{1-2} Y797/33090; **Q**. right M_3 Y797/36160; **R**. right M_3 Y797/36160.

Scale represents 2 mm.

the hypoflexid and metaflexid are opposite each other. The metaflexid is longer than the mesoflexid. The metastriid is shallower than the mesostriid. The hypoconid is small.

Discussion and **comparisons**

The specimens from Y 721 and/or Y 747 may represent a new species, but *S. minor* must be fully characterized with additional material from the Murree Formation at Banda Daud Shah to determine the differences between the two samples. The upper cheek teeth are considerably smaller than those of other species of *Sayimys*. The P^4 is derived relative to other *Sayimys* in the absence of an anteroloph. Although the anteroloph and posteroloph of P^4 become less prominent in *S. sivalensis* and *S. chinjiensis* (perhaps associated with increasing crown height), *S.* cf. *S. minor* is probably too specialized to be ancestral to these species. *Sayimys* cf. *S. minor* is likewise precociously specialized in usually lacking an anteroloph on M^{1-2}.

The DP_4 is larger than the topotypic DP_4 of *S. minor* and appears to have been more lophate, although probably not higher crowned. The metalophulid II does not extend to the metaconid as in the Murree specimen. On three of the P_4's, there is a weak posterior offshoot at the juncture of the posterior arm of the protoconid and the hypolophid. This appears to be similar to that described for *S. obliquidens*. The transversely directed hypolophid on P_4 is similar to that of *S.* cf. *S. intermedius*, but there is no posterolophid.

The holotype of *S. minor* is similar in size and morphology to the only M_{1-2} from Y 721 on which length and width measurements can be made. Specimens from Y 747 that are probably M_1's are also similar in size and morphology to the holotype of *S. minor* (de Bruijn and others, 1981), although most are somewhat larger. Little worn specimens are similar to the holotype of *S. minor* in being less lophate than in other species of *Sayimys*.

The M_3's from Y 747 are the same size as the complete, little worn M_3 from Y 721 (specimen GSP 33112), but have a more oblique hypolophid and appear to be slightly higher crowned. They are similar in size and morphology to the topotypic M_3 of *S. minor* (de Bruijn and others, 1981), but are somewhat higher crowned and do not have quite as broad a lingual opening to the metastriid. The M_3 of *S.* cf. *S. intermedius* from Pakistan (de Bruijn and others, 1989) is similar in size, but differs in usually having the metaflexid slightly shorter than the mesoflexid and greater height of enamel below the mesostriid. The M_3 from Y 721 is similar in size to the Murree *S. minor*, but the hypolophid is much more transverse.

Sayimys sp. A

(Figure 4 K-N; Table 3)

Localities and **ages**: Kamlial Formation, Potwar Plateau, Pakistan, middle Miocene. Y 592, 16.3 Ma; Y 591, 16.2 Ma.

Referred material: GSP 45356, left DP^4; 45355, 45362, right M^{1-2}; 45359, left M_{1-2}; 45360, left M_3; 45358, right M_3; from Y 592. GSP 45351, left M_{1-2}; 45353, right M_{1-2}; from Y 591.

Sayimys sp. A

		N	Range	Mean	SD
DP^4	length	1	1.30		
	anterior width	1	1.20		
	posterior width	1	1.05		
M^{1-2}	length	2	1.55 – 1.55	1.550	
	anterior width	2	1.45 – 1.65	1.550	
	posterior width	1	1.40		
M_{1-2}	length	2	1.42 – 1.50	1.463	
	anterior width	2	1.25 – 1.28	1.263	
	posterior width	3	1.20 – 1.30	1.250	
M_3	length	1	1.85		
	anterior width	1	1.40		
	posterior width	1	1.25		

Table 3.— Statistical summary of measurements (in mm) of teeth of *Sayimys* sp. A from Pakistan.

Description

• DP^4

Trapezoidal occlusal outline. This unworn tooth is low crowned. The protocone and hypocone are distinct cusps, not submerged in their lophs. The paracone and metacone are incorporated into their lophs, but are taller.

• M^{1-2}

Subquadrate occlusal outline. In the little worn tooth the paraflexus is longer and deeper than the metaflexus. The anteroloph is a spur that is shorter and narrower than the protoloph.

• M_{1-2}

The specimen from Y 592 is very worn. The mesoflexid is very short. The metaflexid is an island. There is a slight posteroexternal shelf. The teeth from Y 591 are relatively cuspate. The protoconid and metaconid are connected by a concave anterior lophid. The hypolophid is slightly oblique to transverse and is narrowly connected to the posterior arm of the protoconid and the anterior arm of the hypoconid at nearly 90 degree angles. The hypoflexid is long, wide, and deep and has flattened internal termination opposite the hypolophid. The metaflexid is as deep as and longer than the mesoflexid, but will close to form an enamel island first, because of the shallower metastriid. The posteroexternal cingulum is poorly developed.

• M_3

In the unworn specimen (GSP 45360), the metaconid and entoconid are tall and slender and the hypoconid is situated on the midline of the tooth. The internal

termination of the posterolophid is much lower than the hypolophid. The mesoflexid and metaflexid are equally deep, but the mesoflexid is shorter and narrower. The mesostriid is relatively narrow. The hypolophid is initially short and nearly transverse, but becomes more oblique and longer with wear.

Comment

The small teeth from localities Y 591 and Y 592 are similar to those of *S.* cf. *S. minor* in their small size and having cuspate deciduous premolars, a short mesoflexid on M_3, and a transverse hypolophid on M_2. They differ in having a small anteroloph on the upper molar, a deeper metastriid, a low internal termination of the posterolophid on M_3, and in having taller cusps.

The larger specimens from localities Y 591 and Y 592 are referred to *S.* cf. *S. intermedius*. It is possible that the small specimens from these two localities could also belong to this species. There is a large difference in size between first and second molars in several species of *Sayimys*. However, the specimens assigned to *S.* sp. A are smaller than and differ in morphology from *S.* cf. *S. intermedius*.

Sayimys intermedius (SEN & THOMAS, 1979)

Metasayimys intermedius Sen & Thomas, 1979, p. 35.
Sayimys intermedius de Bruijn, Boon, and Hussain, 1989, p. 195.

Type locality and **age**: Hofuf Formation, Saudi Arabia, middle Miocene, approximately from 14 Ma.

Discussion

The material from the type locality consists of a mandible with DP_4, M_1–M_2, plus an isolated incisor (Sen & Thomas, 1979). The length of the M_2 is 2.09, not 2.9. De Bruijn and others (1989) assigned specimens from the lower Manchar Formation of Pakistan to this species. Additional material from the type locality in Saudi Arabia is needed to confirm this assignment. Specimens from Pakistan differ from the holotype in having the anteroconid on the DP_4 larger, usually more ovate, and more separated from the mure that connects the protoconid and metaconid, and in having M_{1-2} with the metastriid shallower than the mesostriid.

Sayimys cf. *S. intermedius* (SEN & THOMAS, 1979)

(Figure 5; Table 4)

Referred localities and **ages**: Dalana section, Vihowa Formation, Zinda Pir Dome, Pakistan, early middle Miocene: Z 122; Z 120. Kamlial Formation, Potwar Plateau, Pakistan, early middle Miocene: Y 802, 17 Ma; Y 592, 16.3 Ma; Y 591, 16.2 Ma.

Referred material: GSP 45123, left DP^3; 45125, 45520 left DP^4; 332, left P^4; 333, left M; 45518, left M^3; 45124, right M^3; 45519, 334, left M_3; from Z 122. GSP 21859, right DP^4; 45364, left M^{1-2}; 21860, 21861, right M^1; 21862, right DP_4; 21863, left M_{1-2};

45365, 45366, left M_3; from Y 802. GSP 328, left DP^4; 45119, left P^4; 329, left M; 45116, 45118, 323, 326, right M^{1-2}; 45117, 327, right M^3; 318, 319, left DP_4; 36157, right DP_4; 45120, 45122, left M_{1-2}; 45121, 320 right M_{1-2}; 325 left M_3; 322, right M_3; from Z 120. GSP 45357, left DP^4; 45354, 45361 right M^{1-2}; from Y 592. GSP 45352, right M_{1-2}; from Y 591.

Description

- DP^3

Suboval occlusal outline, with a central valley.

- DP^4

The paraflexus is deeper, wider, and longer than the metaflexus. The mesoflexus is much longer than the paraflexus. The metaloph connects with the middle of the posteroloph. The hypoflexus is broad and shallow.

- P^4

The tooth has two fused roots. On the specimen from Z 122, the anteroloph is short and the posteroloph is absent, in spite of little wear. The protocone has an almost circular occlusal pattern, caused by constriction of the enamel at the middle of the anterior and posterior margins. The specimen from Z 120 has the protocone larger than the paracone. The anteroloph and posteroloph join the anterior and posterior arms of the protocone, respectively. The anterior flexus is slightly longer than the posterior flexus. The protoloph is transverse.

- M^{1-2}

The paraflexus and metaflexus are usually short, extending, at most, 20% across the width of the tooth. In GSP 45354, the paraflexus is longer, extending more than 40% across the occlusal surface. In most specimens, the metaflexus persists longer than the paraflexus. The internal part of the mesoflexus is as deep as the hypoflexus, but the mesostria closes to form an enamel island when the tooth is very worn. The tooth is wider anteriorly than posteriorly. In GSP 45364 the hypocone is distinctly smaller than the protocone, but there is a small interdental facet on the posterior margin, indicating that this tooth is not M^3.

- M^3

The paraflexus is very long; in the little worn GSP 45124, it extends to the protocone. The anteroloph connects with the anterior arm of the protocone. The metaflexus initially extends about one quarter the width of the tooth from the external margin to where it contacts the posteroloph.

- DP_4

Specimen GSP 21862 has a median, isolated, conical anteroconid. The anteroconid region is short. In this little worn specimen, the cusps are distinct and connected by lophids. The protoconid and metaconid are connected by a transverse

Sayimys cf. *S. intermedius*

		N	Range	Mean	SD
DP^4	length	4	1.35 – 1.80	1.613	
	anterior width	4	1.22 – 1.62	1.419	
	posterior width	4	1.20 – 1.62	1.438	
P^4	length	1	1.00 – 1.20	1.100	
	width	2	1.68 – 1.85	1.763	
M^{1-2}	length	6	1.78 – 2.22	1.971	0.168
	anterior width	4	2.10 – 2.20	2.150	
	posterior width	5	1.82 – 2.08	1.940	0.104
M^3	length	2	1.80 – 2.12	1.963	
	anterior width	2	1.95 – 2.12	2.038	
	posterior width	4	1.60 – 1.75	1.675	
DP_4	length	4	1.88 – 2.38	2.031	
	anterior width	3	1.05 – 1.30	1.158	
	posterior width	5	1.15 – 1.45	1.325	0.120
M_{1-2}	length	3	1.78 – 2.12	1.950	
	anterior width	3	1.50 – 1.75	1.608	
	posterior width	4	1.45 – 1.75	1.619	
M_3	length	4	1.85 – 2.30	2.088	
	anterior width	4	1.80 – 2.02	1.881	
	posterior width	6	1.48 – 1.72	1.563	0.107

Table 4.— Statistical summary of measurements (in mm) of teeth of *Sayimys* cf. *S. intermedius* from Pakistan.

lophid. A median hypoconulid is present on the posterolophid. The protoconid and entoconid are connected obliquely by a curved (concave anterointernally) loph. There is a weakly-developed posteroexternal cingular shelf.

In specimens from Z 120, the hypolophid is more or less transverse and offset slightly from the posterior arm of the protoconid. Specimen GSP 318, the least worn, has cusps not fully submerged in the lophs. In GSP 36157, the anteroconid is transversely elongate, convex anteriorly, slightly wider externally, and separated by a valley from the metaconid and protoconid. The metalophid is concave anterior. The mesoflexid is longer than the metaflexid and is directed more anteriorly.

• M_{1-2}

The occlusal outline is subrectangular. The mesoflexid is deeper than and equal in length to or slightly longer than the metaflexid. In the two least worn specimens, the mesoflexid curves strongly anteriad constricting the metalophid, leaving the metaconid a distinct cusp. The hypolophid is transverse to slightly oblique and is not directly aligned with the posterior arm of the protoconid, except in the heavily worn specimens. The posterolabial ledge is weakly developed.

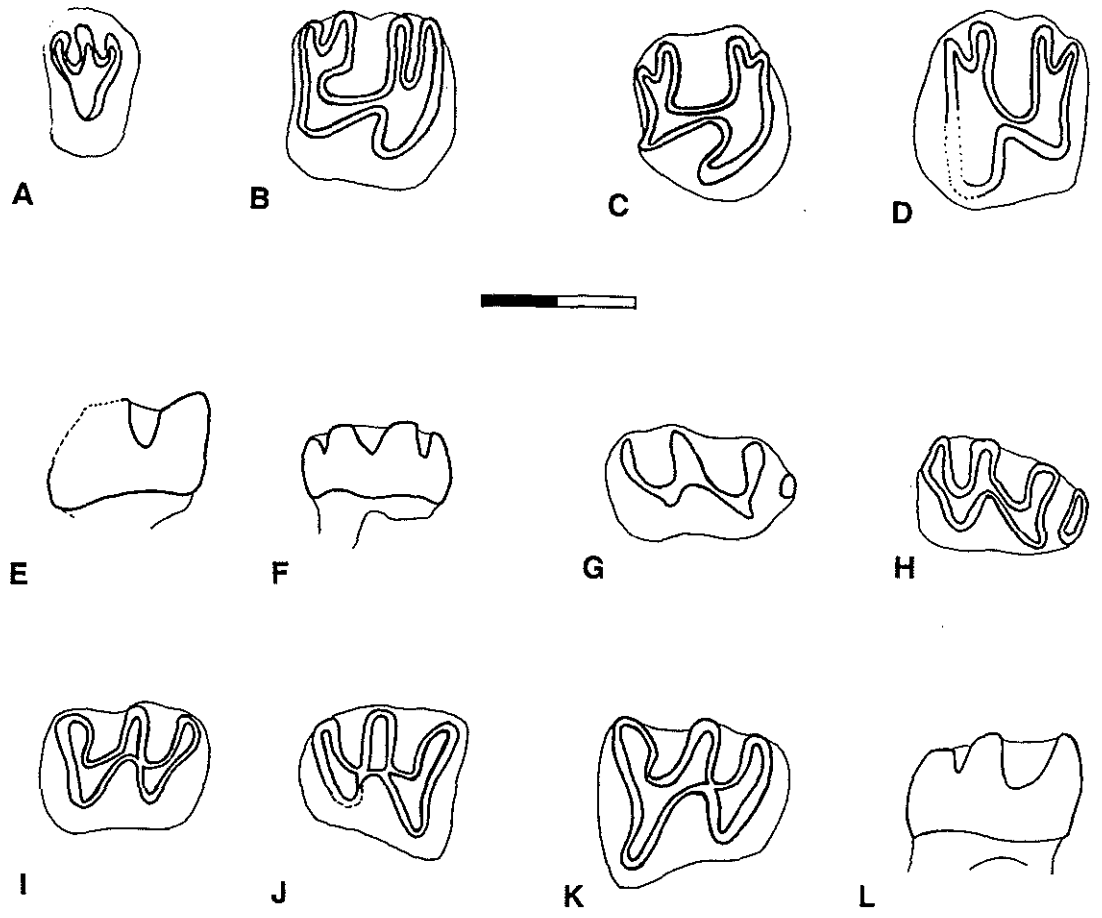


Figure 5.— *Sayimys* cf. *S. intermedius*. **A-D, G-K**: occlusal view. **E, L**: internal view. **F**: external view.
A. left P^4 Z120/45119; **B**. right M^{1-2} Y592/45354; **C**. right M^3 Z120/327; **D**. left M^{1-2} Y802/45364; **E**. left M^{1-2} Y802/45364; **F**. left M^{1-2} Y802/45364; **G**. right DP_4 Y802/21862; **H**. right DP_4 Z120/36157; **I**. left M_{1-2} Z120/45122; **J**. right M_3 Z120/322; **K**. left M_3 Z122/334; **L**. left M_3 Z122/334.
Scale represents 2 mm.

• M_3

The posterior margin is rounded. The anterior margin is slightly concave, with the metaconid anterior to the protoconid. The hypoconid is smaller than the protoconid. The mesoflexid is deeper and wider than the metaflexid and has a much broader and deeper mesostriid. In specimens from localities Z 122 and Z 120, the mesoflexid and metaflexid are equal in length, extending almost halfway across the tooth; from locality Y 802, the mesoflexid is longer than the metaflexid.

On specimen GSP 334 from locality Z 122, the hypolophid is oblique, but offset somewhat from the posterior arm of the protoconid. The metaflexid and hypoflexid flex anteriorly and posteriorly respectively and terminate opposite each other, causing a narrow bridge between the anterior arm of the hypoconid and the hypolophid. One

specimen (GSP 45519) which is missing the protoconid and metaconid has a prominent, low ectostylid in the hypoflexid.

The hypolophid is slightly oblique on specimen GSP 45366 from locality Y 802. In GSP 45365 it is oblique and aligned with posterior arm of the protoconid. In specimens from locality Z 120, the hypolophid is opposite the hypoflexid and is transverse to very slightly oblique.

Comparisons

The tooth identified as DP^3 is significantly larger than the *Sayimys sivalensis* DP^3 described by Munthe (1980). The P^4 differs from that of the Manchar *S.* cf. *S. intermedius* or *P. flynni* in lacking a posterointernal reentrant fold. The anteroloph and posteroloph on 45119 are longer than in P^4's referred to *S. sivalensis* by Munthe (1980, fig. 6). A conspicuous paraflexus and metaflexus characteristic of *S.* cf. *S. intermedius* (as well as *P. flynni* and *S. obliquidens*) occur on upper molars from localities Z 122 (?ca. 17.5 Ma) to Y 592 (16.3 Ma). On M^1 and M^2, the paraflexus and metaflexus are prominent, but for the most part are shorter than in the specimens illustrated for the Manchar *S.* cf. *S. intermedius* or in *P. flynni*, but this may be a function of wear.

The DP_4's from locality Z 120 are similar in size and shape to those of *S.* cf. *S. intermedius* from the lower Manchar Formation (de Bruijn and others 1989, plates I and II). The DP_4 from locality Y 802 is similar in shape, but much smaller than, the large *Sayimys* sp. from the Manchar Formation (de Bruijn and others 1989, plate I, fig. II). In DP_4's from younger localities (beginning with Y642, 15.1 Ma), the anteroconid is connected medially to the protoconid and metaconid, and the tooth is more strongly lophate.

On the M_{1-2}, the hypolophid is more transverse than in *S. obliquidens* or *S. sivalensis*. In *S.* cf. *S. intermedius* from the Manchar Formation there is variation in the obliqueness of the hypolophid, particularly M_3. The broken M_{1-2} from Y 591 is tentatively referred to this species because of its size.

Sayimys sp.

Locality: Y 731, Kamlial Formation, Potwar Plateau, Pakistan.

Age: 16.7 Ma; middle Miocene.

Referred material: GSP 45363, right DP^4.

Comment

This tooth is relatively large, larger than specimens referred to *S.* cf. *S. intermedius* from Pakistan. It is similar in size to larger specimens of *S. sivalensis*. It may belong to the same taxon as the large specimens from locality 81.14 in the Manchar Formation (de Bruijn and others, 1989), which is approximately the same age.

Sayimys sivalensis (HINTON, 1933)

(Figure 6; Table 5)

Pectinator sivalensis Hinton, 1933, p. 622.
Sayimys sivalensis Black, 1972, p. 241.
Sayimys sivalensis de Bruijn, Boon, and Hussain, 1989, p. 201.

Emended diagnosis: A large, moderately high-crowned species. Upper molars frequently with very short paraflexii and with metaflexii that persist through moderate wear. Anteroloph and posteroloph shorter than protoloph and metaloph, respectively. The DP_4 has the anteroconid connected to the metalophid. The hypolophid on M_2 is oblique. The M_2 and M_3 have a shallow metastriid. The masseteric crest extends to below the anterior root of M_1.

Type locality: Chinji beds, near Chinji village, Pakistan.

Age: middle Miocene.

Discussion and comparisons

The holotype of *S. sivalensis* is a lower jaw with M_2–M_3 from the Chinji beds near Chinji, Pakistan. The Chinji Formation ranges in age from about 14.3 to 10.8 Ma in this region (Johnson and others, 1985) and it is not known from where in the Chinji section this specimen was collected. The present study indicates that specimens referred to *S. sivalensis* from the upper part of the lower Manchar Formation by de Bruijn and others (1989) and specimens from the upper Kamlial and lower Chinji of the Potwar Plateau (which are equivalent in age and morphology to these Manchar specimens) are a different species from specimens referred to *S. sivalensis* from the upper part of the Chinji (Munthe, 1980). Unfortunately, the two species are best distinguished only by the morphology of the upper molars, which almost always lack a paraflexus in the upper Chinji species. *Sayimys sivalensis* has upper molars that are larger, higher crowned, and with shorter paraflexi and metaflexi than in *S.* cf. *S. intermedius*.

The type specimen of *S. sivalensis* is unusual in that it has the masseteric crest extending to the level of the M_1 (Black, 1972, fig. 1c). In *S. obliquidens*, *S. chinjiensis* n. sp., and the type specimen (from Saudi Arabia) of *S. intermedius*, it extends to below the P_4. In the specimen referred to *S. minor* (GSP 48136), it extends just anteriad of the M_1. However in *Metasayimys*, *Pireddamys*, the Oligocene ctenodactylids, it extends to below the M_1, which is presumed to be the primitive state. Therefore, for this character, the type of *S. sivalensis* is more primitive than the type of *S. chinjiensis* n. sp., which comes from the upper Chinji. Additionally, *S. sivalensis* appears to be lower crowned than specimens from the upper Chinji. An unusual feature of the holotype of *S. sivalensis* is that the mesoflexid is very short on M_2 and M_3. However, this may be an artifact of the relatively unworn state of the specimen. With wear, it appears that the mesoflexid will lengthen to equal the metaflexid. Several of the lower molars from locality Y 733 have relatively short mesoflexids. It is assumed, *ceteris paribus*, that *S. sivalensis* is from the lower Chinji beds.

Referred localities and ages: Kamlial Formation, Potwar Plateau, Pakistan, middle Miocene: Y 642 and Y 682, 15.1 Ma. Chinji Formation, Potwar Plateau, Pakistan;

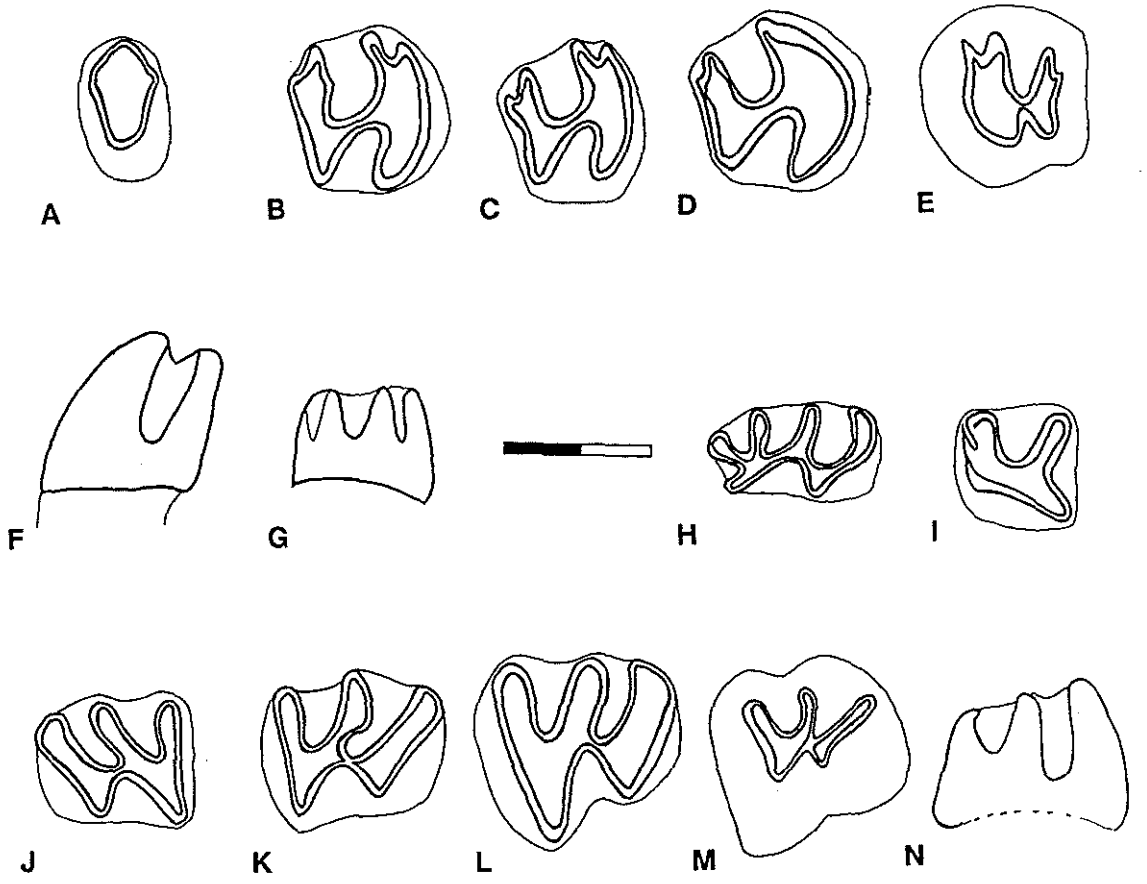


Figure 6.— *Sayimys sivalensis*. **A-E, H-M**: occlusal view. **F, N**: internal view. **G**, external view.
A. right P^4 Y709/33085; **B**. right M^{1-2} Y709/45313; **C**. right M^3 Y709/45315; **D**. right M^3 Y682/21865; **E**. left M^{1-2} Y733/45257; **F**. left M^{1-2} Y733/45257; **G**. left M^{1-2} Y733/45257; **H**. left DP_4 Y709/33094; **I**. right P_4 Y733/45299; **J**. right M_{1-2} Y733/45288; **K**. left M_{1-2} Y682/21868; **L**. left M_3 Y733/45292; **M**. left M_3 Y430/45220; **N**. left M_3 Y430/45220.

Scale represents 2 mm.

middle Miocene: Y 709, 14.3 Ma; Y 501 and Y 680, 14.1 Ma; Y 733 and Y 589, 14.0 Ma; Y 491, 13.8 Ma; Y 665, 13.7 Ma; Y 59, 13.6 Ma; Y 651, 13.5 Ma; Y 430, 13.3 Ma; Y 718, 13.0 Ma.

Referred material: GSP 45346, 45347, left M^{1-2}; 45348, left DP_4; from Y 642. GSP 45350, left M^{1-2}; 21864, 21866, right M^{1-2}; 45349, left M^3; 21865, right M^3; 21867, right DP_4; 21868, right M_{1-2}; 21869 left M_3; from Y 682. GSP 45338, left DP^4; 45319, 45320, 45339, right DP^4; 33085, right P^4; 45312, 45323-45325, 45335, 45337, left M^{1-2}; 33084, 33097, 45313, 45314, 45316, 45317, 45336, right M^{1-2}; 45318, left M^3; 45315, right M^3; 33093, 33094, left DP_4;, 33096, 45322, 45333, left P_4; 45345, right P_4; 33079, left M_1; 33108, right M_1; 33095, 33107, 45340, left M_2; 33081, 33082, 45327, 45328, 45341, 45342, right M_2; 45331, 45344, left M_3; 33080, 45321, 45332,

right M_3; 45326,45329,45330, 45343, M_2 or M_3; from Y 709. GSP 45308, right DP^4; from Y 501. GSP 45309, 45310, left M^1 or M^2; from Y 680. GSP 45275, left DP^4; 45274, 45276, 45277, right DP^4; 45270, 45271 left P^4; 45272, right P^4; 21871, 45252-45259, 45261, 45264-45266, left M^{1-3}; 21870, 28172, 45260, 45262, 45263, 45267-45269, right M^{1-3}; 45291, 45302-45306, left DP_4; 45307, right DP_4; 45296, 45297, left P_4; 45298-45301, right P_4; 45278-45282, left M_{1-2}; 45284-45286, 45288-45290, right M_{1-2}; 33098, 45292, 45293, left M_3; 45283, 45287, 45294, 45295, right M_3; from Y 733. GSP 45250, right DP^4; 45251 left M_{1-2}; from Y 589. GSP 45234, 45236, left DP^4; 45232, 45235, right DP^4; left P^4; 45225-45227, left M^{1-2}; 45228, 45229, 45233, right M^{1-2}; 45230, left M^3; 45231, 45246, 45247, left DP_4; 45248, right DP_4; 45245, left P_4; 45237, 45238, 45242, left M_{1-2}; 45239, 45240, 45243, right M_{1-2}; 45241, 45243, left M_3; from Y 491. GSP 45224, left M^{1-2}; from Y 665. GSP 36264, right ?DP^4; 27415, left M_{1-2}; from Y 59. GSP 27422, left M^{1-2}; 27423, 36429, right M^{1-2}; from Y 651. GSP 45219, right DP^4; 45218, right M^{1-2}; 45222, right M_{1-2}; 45220, left M_3; 45223, right M_3; from Y 430. GSP 45214, left M^{1-2}; 45212, right M^{1-2}; 45213, left ?DP_4; 45215, left M_3; from Y 718.

Description

• DP^4

Subtrapezoidal occlusal outline, shorter internally. The protocone and subequal hypocone are joined by a horizontal mure. The hypoflexus is relatively short and the hypostria is deep. The paraflexus is wider, deeper, and longer than the metaflexus. The protocone joins the anteroloph at the anterior margin of the protocone. The metaloph connects with the middle of the posteroloph. In specimen GSP 45236 from Y 491 the hypoflexus is short and the hypostria shallow; the metaflexus is equal in length to and narrower than the paraflexus.

• P^4

Similar to but larger and higher crowned than in more primitive species. The occlusal pattern is nearly ovoid; the anteroloph and posteroloph are very weakly developed to nearly absent. In one specimen (GSP 45172), the external root is deeply furrowed at its tip.

• M^{1-2}

The specimens from the Kamlial Formation are badly broken and/or worn. None have an anteroloph, although the anteroexternal margin may have a shallow indentation. The metaflexus, when present, is short and will persist only through moderate wear. The mesoflexus is very deep at its internal termination.

In specimens from the Chinji Formation, the anteroloph and posteroloph are usually shorter than the protoloph and metaloph, respectively. The paraflexus and metaflexus are short and shallow and usually present except in extreme wear. An anteroloph is absent in only one specimen (GSP 45336) of the 18 from localities Y 709 and Y 733 that preserve this region and in which the metaflexus has not been worn away. This nearly unworn specimen is also unusual in having a closed, slit-like metaflexus. The other specimens from these localities that lack a paraflexus are heavily

Sayimys sivalensis

		N	Range	Mean	SD
DP^4	length	13	1.60 – 2.10	1.815	0.160
	anterior width	14	1.35 – 1.80	1.559	0.125
	posterior width	14	1.30 – 1.75	1.438	0.118
P^4	length	4	1.10 – 1.20	1.156	
	width	4	1.85 – 2.00	1.913	
M^{1-2}	length	35	1.60 – 2.25	1.896	0.154
	anterior width	31	1.65 – 2.65	2.003	0.225
	posterior width	32	1.50 – 2.45	1.856	0.223
M^3	length	8	1.72 – 2.52	2.197	0.240
	anterior width	8	2.08 – 2.58	2.406	0.157
	posterior width	9	1.55 – 2.38	2.017	0.230
DP_4	length	9	2.00 – 2.42	2.194	0.119
	anterior width	11	1.10 – 1.35	1.195	0.093
	posterior width	14	1.10 – 1.52	1.296	0.102
P_4	length	11	1.05 – 1.55	1.318	0.139
	anterior width	11	1.25 – 1.50	1.332	0.085
M_{1-2}	length	21	1.78 – 2.50	2.154	0.220
	anterior width	27	1.38 – 2.50	1.856	0.279
	posterior width	22	1.42 – 2.18	1.790	0.198
M_3	length	12	2.15 – 2.75	2.396	0.165
	anterior width	12	1.82 – 2.48	2.202	0.186
	posterior width	10	1.35 – 2.08	1.905	0.219

Table 5.— Statistical summary of measurements (in mm) of teeth of *Sayimys sivalensis* from Pakistan.

worn and also lack a metaflexus. The paraflexus is present on only two specimens from Y 491 and is very shallow and disappears after light to moderate wear. On GSP 45224 from Y 665, the anteroloph is very short and the enamel is pitted. The left molar from Y 718 has a very short anteroloph and the posteroloph is a short spur. The metaflexus is deeper, wider, and longer than the paraflexus, except for GSP 45257 in which both persist to near the base of the enamel. In some specimens, the terminations of the mesoflexus and hypoflexus extend slightly beyond the midline of the tooth. At their terminations, the mesoflexus and hypoflexus are about equal in depth, although the mesoflexus will close to form an enamel island first.

• M^3

The hypocone is smaller than the protocone. On little worn GSP 45349, the anteroloph is a short spur, the metaflexus short and shallow; on the worn GSP 21865,

both are absent, although the anterior and posterior lophs are constricted at their external terminations. The Chinji specimens are similar to M^{1-2}, but with hypocone smaller than protocone.

• DP_4

The occlusal outline is ovate. The cusps are lophate. Specimen GSP 45348 is moderately worn and has a large anteroconid, slightly lingual to midline of tooth, connected medially to metalophid and the anterior arm of protoconid. The mesoflexid and shallower metaflexid are about equal in length. The hypolophid is directed obliquely forward and is continuous with the posterior arm of the protoconid, but not directly aligned with it. The posteroexternal shelf is poorly developed. The posterolophid is rounded posteriorly. A median hypoconulid was probably present in the unworn state.

Specimen GSP 21867 is well worn. The medial anterolophid connecting the anteroconid with the metalophid is long and narrow. The mesoflexid is deeper and wider than the metaflexid.

In the Chinji specimens, the anteroconid is large. The protoconid is anterior to metaconid. The metalophid is transverse. The posterolabial shelf is moderately developed. The posterior cingulum is convex posteriorly. The reentrant between the anteroconid and protoconid opens more or less anteriorly. The posterior arm of protoconid extends obliquely to the somewhat more transverse hypolophid. The mesoflexid and metaflexid are about equal in length. The hypolophid is opposite the hypoflexid.

In specimens from Y 709, the anteroconid is slightly internal to the midline and is connected obliquely to anterior arm of protoconid. In specimens from Y 733, the anteroconid is subcentrally placed. In one little worn specimen (GSP 45306), the tip of the anteroconid is isolated, but with slight wear, it connects with the thin, transversely directed anterior mure. In the only complete specimen (GSP 45246) from Y 491, the anteroconid is conical and will connect with the anterior arm of the protoconid only after heavy wear.

• P_4

Single rooted and very lophate. The occlusal outline is usually quadrate, although a few specimens are wider than long. A ridge extends from the entoconid to the protoconid and from the metaconid to this ridge, just posterior to the protoconid, forming a "y"-shaped occlusal pattern. The anterior flexid is less deep than the internal flexid. The posterolophid is absent in specimens from Y 709. In three little worn specimens from Y 733, there is a vestige to a trace of the posterolophid; in one it is absent. The posteroexternal cingulum is weakly developed to absent. The specimen from Y 491 is much smaller than those from localities Y 709 and Y 733, is noticeably wider than long and has a very shallow anterior flexid.

• M_1 or M_2

These teeth could be tentatively separated only in specimens from the Chinji

Formation. The occlusal outline is subrectangular. In specimens from the Kamlial formation, the hypolophid is oblique and aligned with the posterior arm of the protoconid. The anterior arm of the hypoconid is constricted at its connection with the posterior arm of the protoconid. The metaflexid is longer than the mesoflexid, but the metastriid is much shorter than the mesostriid. The hypoflexid is broad. The posteroexternal shelf is very weak.

• M_1

The M_1 is presumed to be smaller and have a greater length to width ratio than M_2. The mesoflexid is wider and deeper than the metaflexid, but the two are subequal in length. The anterior margin is concave. The hypolophid is nearly transverse (as in the type of *S. perplexus*) to oblique (more so in Y 733 and younger localities) and is usually offset from the posterior arm of the protoconid. The posteroexternal cingulum is very weak.

• M_2

Larger than the M_1. The protoconid and opposite metaconid are connected by a relatively straight lophid. The hypolophid is more oblique and aligned with the posterior arm of the protoconid, although the alignment is a curved arc, not a straight line. The mesoflexid is deeper, wider, and usually equal in length to the metaflexid in the specimens from the older Chinji localities. The metaflexid is shallower and usually slightly longer than the mesoflexid in the younger localities. The metastriid is very shallow. The posterobuccal shelf is moderately well developed to weak. In specimens from Y 59, there is a strong posteroexternal cingulum.

• M_3

The hypolophid is oblique and directly aligned and continuous with the posterior arm of the protoconid. The tooth from Y 682 is broken posteroexternally. The mesoflexid is shorter than the metaflexid. The metastriid is very shallow.

On the Chinji specimens, the posterior margin is rounded, and the posteroexternal cingulum is poorly developed to absent. The hypoconid is much smaller than the protoconid. The mesoflexid is wider and deeper than the metaflexid. The mesoflexid is initially much shorter than the metaflexid, but with wear the two become approximately equal in length. The metaconid-protoconid-entoconid make a "V", with the metaconid anterior to the protoconid. The posterior root lies beneath the entoconid and the termination of the posterolophid. The mesoflexid is deeper and usually slightly shorter than the metaflexid in specimens from Y 491. Specimen GSP 45220 from Y 430 is nearly unworn and has the mesoflexid shorter and broader than the metaflexid. The metastriid is deeper than in the type of *S. sivalensis*.

Comments

Several of the teeth from the Kamlial Formation localities are relatively large, but are within the range of variation for *S.* cf. *S. intermedius* or *S. sivalensis* reported by de Bruijn and others (1989).

Most of the specimens from Y 709 have pits in the enamel; many are heavily pitted. Andrews (1990) has described how digestion by a predator can pit and remove the enamel.

Sayimys cf. *S. sivalensis*

Referred localities and **ages**: Y 726 and Y 698, Chinji Formation, Potwar Plateau, Pakistan; 12.7 Ma; middle Miocene.

Referred material: GSP 42510, left P^4; 45204, left maxillary fragment with M^1–M^2; 45206, 42509, left M^{1-2}; 42507, left M^3; 42505, 42508 left M_{1-2}; from Y 726. GSP 45203, right M_{1-2}; from Y 698.

Description

• P^4

Two rooted. The anteroloph is very short. The posteroloph is more prominent. The external portion of the transverse crest is offset posteriorly. The protocone is circular.

• M^{1-2}

The specimens are moderately to heavily worn. There is no paraflexus. A short metaflexus is present on the least worn specimen. The M^1 is much smaller than the M^2.

• M^3

The specimen is little worn, but heavily pitted. The anteroloph is vestigial, the metaflexus is long, and the metastria is deep.

• M_{1-2}

The mesoflexid is much shorter than the metaflexid on the little worn, but broken 45205. The mesoflexid and metaflexid are subequal in length in the worn and abraded specimen from Y 698.

Sayimys chinjiensis new species

(Figure 7; Plate 1 H; Table 6)

Sayimys sivalensis Munthe, 1980, p. 17.

Holotype: 45186, left mandible fragment with P_4–M_1.

Hypodigm: 45184, left P^4; 45185, right P^4; 45183, left M^{1-2}; 45186, left mandible fragment with P_4–M_1; 45188, right P_4; 45187, left M_3.

Locality: Y 634, Chinji Formation, Potwar Plateau, Pakistan.

Age: 11.9 Ma; middle Miocene.

Diagnosis: Moderately high crowned cheek teeth with relatively thick enamel base. The paraflexus is absent on the upper molars. A short metaflexus is present on M^1 and M^2

and is usually absent on M^3. On M_3 the metastriid extends relatively deeply on the internal face. *Sayimys chinjiensis* is more derived than *S. sivalensis* in greater height of crown, the extension of the masseteric crest to below the P_4, and in having upper molars almost always lacking a paraflexus. *Sayimys chinjiensis* differs from *S. perplexus* in having the posteroexternal cingulum less well developed on P_4 and M_2, the trigonid and talonid subequal in width on M_1 and M_2, and a less well developed masseteric crest.

Etymology: *Chinji*, in reference to Chinji village, the general area where this species was collected. Plus *-ensis* (Latin) locative suffix.

Description

- P^4

Two roots. The anteroloph and posteroloph are weakly developed. On the lightly worn specimen (45185), the transverse crest is offset, the external portion is slightly anterior to the internal portion.

The masseteric crest is robust and extends to below the posterior half of the P_4. The mental foramen is anterior to the P_4, close to the dorsal margin of the lateral surface.

- P_4

The occlusal pattern is "y"-shaped. The posteroexternal cingulum is weakly developed.

- M_1

The hypolophid is oblique. The mesoflexid and metaflexid are approximately equal in length.

- M_3

The metaflexid is longer than the mesoflexid.

Comments and comparisons

Munthe (1980) synonymized *S. perplexus* (WOOD, 1937) with *S. sivalensis*, based on his large sample from the uppermost Chinji Formation. His sample is reassigned to the new species *S. chinjiensis*, along with other specimens from the upper Chinji and Nagri. Specimens from the upper Kamlial and lower Chinji in the Potwar Plateau and equivalents in the Manchar Formation are assigned to *S. sivalensis*. The *Sayimys* from the Chinji Formation at Banda Daud Shah (Wessels and others, 1982) is tentatively referred to *S. chinjiensis* because of the absence of a paraflexus on the two upper molars. The type of *S. perplexus* from Haritalyangar (Wood, 1937) has P_4–M_2 with prominent posteroexternal cingula, P_4 with a stylid at the base of the mesoflexid, and a wide trigonid and narrow talonid on M_1 and M_2. Specimens of *S. perplexus* from Haritalyangar identified by Vasishat (1985) also have relatively narrow talonids on the lower molars. A referred specimen from the same locality (Prasad, 1970) has M_1 and M_2 dimensions similar to those of *S. chinjiensis*. However, based on available material of *S. perplexus*, *S. chinjiensis* is not synonymous with *S. perplexus*.

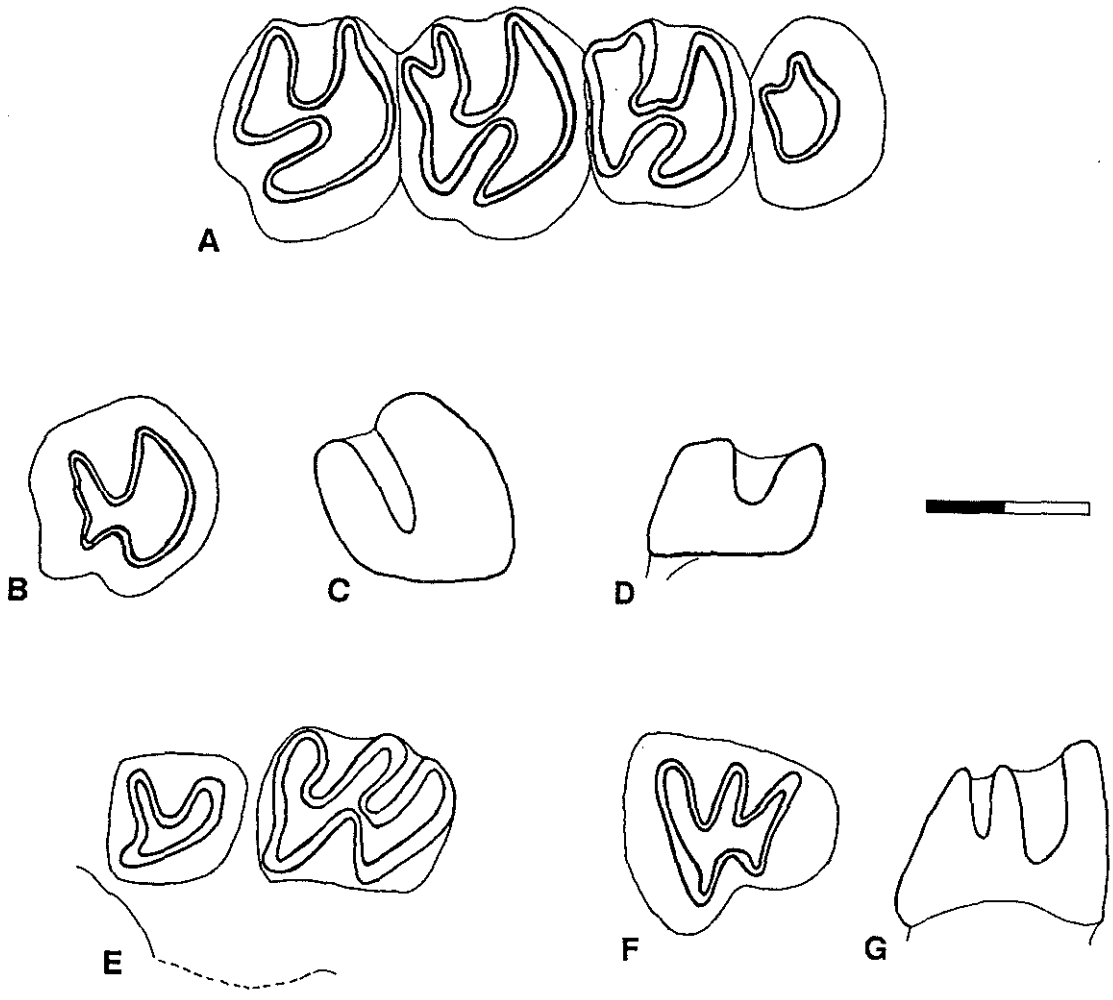


Figure 7.— *Sayimys chinjiensis* new species. **A, B, E, F**: occlusal view. **C, G**: internal view. **D**: external view. **A**. right P^4–M^3 Y311/48411; **B**. right M^3 Y504/45162; **C**. right M^3 Y504/45162; **D**. right M^3 Y504/45162; **E**. left P_4–M_1 Y434/45186, dashed line indicates broken edge; **F**. left M_3 Y504/45177; **G**. left M_3 Y504/45177.
Scale represents 2 mm.

Referred localities and **ages**: Chinji Formation, Potwar Plateau, Pakistan, middle Miocene: Y 496, 12.1 Ma; Y 504, 11.1 Ma; Y 76, 10.8 Ma; Y 797, 10.6 Ma; Y 636, 10.5 Ma. Nagri Formation, Potwar Plateau, Pakistan, late Miocene: Y 259, 9.75 Ma; Y 450, 9.25 Ma; Y 311, 9.1 Ma.

Referred material: GSP 45193, left DP^4; 45200, right DP^4; 45190, 45192, left M^{1-2}; 45191, 45199, right M^{1-2}; 45197, 45201, left DP_4; 45198, right DP_4; 45517, right P_4; 36388, right M_{1-2}; 45196, left M_3; 45195, right M_3; from Y 496. GSP 45170, left DP^4; 45171, right DP^4; 45160, left M^{1-2}; 45161, 45163-45168, right M^{1-2}; 45162, right M^3; 45179-45181, left DP_4; 45182, right DP_4; 45173-45176, right M_{1-2}; 45172, 45177, left

M_3; 45178, right M_3; from Y 504; GSP 45155, 45157, left M^{1-2}; 45156, left M^3; 45158, 45159, right M_3; from Y 76. GSP 36150, right DP^4; 36148, 36152, left M^1; 33092, right M^1; 36145, 36154, left M^2; 36146, right M^2; 36155, left M^3; 33091, 36149, 36560, left M_{1-2}; 36151, 36566, right M_{1-2}; 36147, right M_3; from Y 797. GSP 45154, left M^1; 45153, left M_2; from Y 636; GSP 45150, right M^{1-2}; 45151, right M^3; 45152, right M_2; from Y 259. GSP 45140, 45141, right M^{1-2}; 45412, left M^3; 45148, left DP_4; 45144, right M_{1-2}; 45145-45147, right M_3; from Y 450. GSP 45135, left DP^4; 48411, right palate fragment with P^4, M^1–M^3; 45136, 45137, left P^4; 45127, 45138, left M^{1-2}; 21875, left DP_4; 45134, right DP_4; 45139, 45131, right M_1; 45129, 45130, 45132, right M_2; 45133, left M_3; 45128, right M_3; from Y 311.

Description

• DP^4

The paraflexus is wider, longer, and deeper than the metaflexus. The mesoflexus is somewhat longer than the prominent hypoflexus. In specimens from the Chinji Fm., the protocone is connected to the hypocone by a horizontal to slightly oblique mure. The specimen from Y 311 has anterior half much wider than the posterior half; the protocone connected to the smaller hypocone by a very oblique mure; and the posteroloph very short.

• P^4

The Nagri Fm. specimen is three rooted, with two lingual roots. The anteroloph is vestigial to absent and the posteroloph is very weakly developed.

• M^{1-2}

The protocone and hypocone are subequal in size. As indicated by the palates from Y311 (Fig. 7A) and the Daud Khel Local Fauna (Munthe, 1980, fig. 7), the M^1 is noticeably smaller than the M^2. The metacone is apparently more widely separated from the posteroloph on M^1.

In specimens from the Chinji Fm., the paraflexus may be weakly developed. In the only unbroken, not heavily worn specimen from Y 496, the anterior loph has a very strong anteroexternal constriction. One moderately worn specimen from Y 76 has a trace of a paraflexus. In specimens from Y 797, the paraflexus is absent, although the anterior loph (fused anteroloph and protoloph) is constricted along its anteroexternal margin; in the larger teeth, identified as M^2, the anterior loph curves posteriorly at its external termination. A short metaflexus is present in the specimen from Y 496. The metaflexus is absent in one little worn specimen and one moderately worn specimen from Y 504. The metaflexus is very short and disappears with heavy wear, as in the tooth from Y 76.

In specimens from the Nagri Fm., there is no paraflexus, but the anterior loph is slightly pinched anterior of the paracone. In specimens from Y 311, the posteroloph is very short, weakly developed, and directed posteroexternally. The hypostria is a narrow deep slit. The mesostria is narrow, shallow, and forms a "V". Because of unilateral hypsodonty, the internal side is much longer than the external side, as is typical of all

Sayimys chinjiensis n. sp.

		N	Range	Mean	SD
DP^4	length	6	1.62 – 2.10	1.850	0.181
	anterior width	6	1.40 – 1.80	1.579	0.155
	posterior width	6	1.38 – 1.62	1.488	0.110
P^4	length	4	1.20 – 1.58	1.325	
	width	3	1.88 – 1.98	1.933	
M^{1-2}	length	20	1.68 – 2.52	2.025	0.216
	anterior width	22	1.65 – 2.55	2.127	0.257
	posterior width	23	1.58 – 2.38	1.984	0.237
M^3	length	4	2.30 – 2.45	2.367	
	anterior width	3	2.55 – 2.80	2.658	
	posterior width	3	2.18 – 2.40	2.275	
DP_4	length	7	2.12 – 2.52	2.325	0.161
	anterior width	8	1.15 – 1.45	1.294	0.116
	posterior width	9	1.22 – 1.60	1.414	0.135
P_4	length	3	1.32 – 1.62	1.467	
	width	2	1.25 – 1.58	1.413	
M_{1-2}	length	13	1.90 – 2.75	2.225	0.252
	anterior width	12	1.65 – 2.70	2.002	0.319
	posterior width	15	1.55 – 2.50	1.937	0.242
M_3	length	8	2.35 – 2.55	2.447	0.073
	anterior width	6	2.35 – 2.60	2.438	0.089
	posterior width	9	1.65 – 2.25	1.942	0.188

Table 6.— Statistical summary of measurements (in mm) of teeth of *Sayimys chinjiensis* new species from Pakistan.

Sayimys. The mesostria begins at about the same height above the base of the enamel as does the hypostria.

• M^3

In the moderately worn specimen from Y797 and the little worn specimen from Y 76, the paraflexus and metaflexus are absent. In the Nagri specimens, the paraflexus and metaflexus may be represented by slight indentations.

• DP_4

The posterior arm of the protoconid and oblique hypolophid are not directly aligned except when moderately to heavily worn. The anteroconid connects centrally with the protoconid and metaconid. The protoconid-metaconid connection is usually nearly transverse, although the protoconid is slightly anterior to the metaconid. The two

smaller specimens from Y 504 have a better defined anterior, rather than medial, connection between the protoconid and metaconid. In the little worn specimens from this locality, the tip of the anteroconid is isolated from the anterior mure, which does connect with the base of the anteroconid.

• M_{1-2}

The oblique hypolophid is aligned with the posterior arm of the protoconid. In specimens from Y 797, the mesoflexid is equal in length to and wider and deeper than the metaflexid, and the posteroexternal cingulum is moderately well developed. In the Nagri specimens, the metaflexid is longer and narrower than the mesoflexid and closes to form an enamel island much earlier. The posteroexternal cingulum is poorly to moderately developed.

• M_3

The mesoflexid and metaflexid are approximately equal in length. In specimens from the Nagri Fm., the posteroexternal cingulum is absent in one specimen, present in another. The posterior arm of the protoconid and oblique hypolophid are confluent. The metastriid is nearly as deep as the mesostriid.

Comment

Some of the smaller teeth from Y 504 may possibly be better assigned to the higher crowned *Sayimys* sp. B. The lower molars from Y 76 are broken, but appear to have moderate height of crown. One little worn M_3 has a deep opening to the metaflexid. The DP^4 from Y 311 resembles specimens GSP 45170 from Y 504 and GSP 45193 from Y 496. These three are smaller and more square than the other DP^4's assigned to *S. chinjiensis*. The P^4 from the Nagri is three rooted versus two rooted for the specimen from the Chinji.

Sayimys sp. B

(Figure 4 O-R; Table 7)

Locality: Y 797, Chinji Formation, Potwar Plateau, Pakistan.

Age: 10.6 Ma, middle Miocene.

Referred material: GSP 36159, left DP^4, 36158, right DP^4; 36153, right M^{1-2}; 36560, left M_{1-2}; 33090, left M_{1-2}; 36160, right M_3.

Description

These teeth are relatively high crowned, both in terms of the total height of the enamel and the height of the enamel below the floor of the flexids.

• DP^4

The protocone is anteroposteriorly elongate. The hypoflexus is very short and very shallow. The paraflexus and metaflexus are both short and narrow.

Sayimys sp. B

		N	Range	Mean	SD
DP^4	length	2	1.72 – 1.78	1.750	
	anterior width	2	1.45 – 1.45	1.450	
	posterior width	2	1.40 – 1.40	1.400	
M^{1-2}	length	1	1.85		
M_{1-2}	length	3	1.85 – 2.20	1.992	
	anterior width	2	1.52 – 1.92	1.725	
	posterior width	3	1.65 – 1.90	1.750	
M_3	length	2	2.00 – 2.00	2.000	
	anterior width	2	1.80 – 1.90	1.850	
	posterior width	2	1.55 – 1.82	1.688	

Table 7.— Statistical summary of measurements (in mm) of teeth of *Sayimys* sp. B from Pakistan.

• M^{1-2}

There is one worn, external half of an upper molar that has greater height of crown below the mesoflexus than is typical for other *Sayimys*.

• M_{1-2}

In the lightly worn tooth, the metalophid is relatively short and directed obliquely anterior from the mure, but will become more transverse with wear. The mesoflexid is short and shallow. The occlusal length of the mesoflexid does not lengthen appreciably with wear, therefore the metalophid will remain considerably shorter than the hypolophid. The hypolophid is transverse, will become slightly oblique with wear, but will not line up with the posterior arm of the protoconid. The entoconid is not vertical, but leans anteriorly. The metaflexid is much shallower and longer than the mesoflexid. The posterolophid is long and directed obliquely posteriorly. The hypoflexid is long and deep and has a broad internal termination. There is no posteroexternal cingulum.

• M_3

The tooth is nearly unworn. There is a slight ridge in the middle of the anterior margin, but this will be lost after little wear. The hypolophid is oblique. The hypoconid is small and situated close to the midline of the tooth. The posterolophid is very short. The mesoflexid and metaflexid are both short. The metastriid is nearly as long as the mesostriid. Both of these and the hypostriid are narrow. There is no posteroexternal cingulum. Height of tooth at the metaconid = 2.40; height of enamel below the mesostriid = 0.88.

Comment

These teeth are little worn, which affects the occlusal pattern. However their relatively small size, height of crown, and shortness of the internal lophids of the molars are unlike specimens assigned to *S. chinjiensis*. The internal length of the opening to the metaflexid on M_3 is much longer and narrower than in other species. The deciduous premolars are smaller, more elongate, have more poorly developed protocones, and much shallower hypoflexii than specimens assigned to *S. chinjiensis*. Some of the smaller upper molars from this locality assigned to *S. chinjiensis* could possibly belong to this species, but none appear exceptionally high crowned, although this may be caused by wear and breakage. The lower molars resemble those of *Africanomys minor* (Jaeger, 1977), but in external view the M_3 has a deeper metastriid.

Locality: Y 496, Chinji Formation, Potwar Plateau, Pakistan.

Age: 12.1 Ma; middle Miocene.

Referred material: GSP 45194, left M_3.

Description

This specimen differs from the other two specimens identified as M_3's from this locality in its smaller size and short, broad metalophid and short, broad, transverse hypolophid. The mesostriid and metastriid begin at approximately the same height above the base of the enamel and are relatively narrow. The specimen is identified as M_3 because of the short mesoflexid and the backward sloping posterior root.

Sayimys cf. *S.* sp. B

Locality: Y 714, Chinji Formation, Potwar Plateau, Pakistan.

Age: 12.5 Ma; middle Miocene.

Referred material: GSP 49738, ?left P^4; 45202, left M_{1-2}.

Description

• P^4

Single rooted and relatively high crowned. There is no posteroloph. Median constrictions of the enamel separate the external and internal occlusal surfaces. The protoloph is very oblique, with the paracone situated at the posteroexternal side of the tooth.

The lower molar is badly worn, pitted, and abraded

Comment

P^4 of *Sayimys* usually has at least two roots; this P^4 is single rooted and more square, with a "y"-shape occlusal pattern. The tooth is somewhat similar to one illustrated by Munthe (1980, fig. 6C, which is probably a left not right tooth), but differs

in lacking a posteroloph and having the metaflexus on the posterior side, opposite the anterior flexus, constricting the enamel pattern medially. The small size and apparently transverse hypolophid of the lower molar suggest that it pertains to this small undescribed species of *Sayimys*.

?*Sayimys perplexus*

Locality: Y 457, Dhok Pathan Formation, Potwar Plateau, Pakistan.

Age: 7.3 Ma; late Miocene.

Referred material: GSP 45126, left DP^4.

Description

- DP^4

Only the internal half is preserved. The paraflexus is relatively large.

Comment

This specimen may be misidentified or have the wrong locality information.

BIOCHRONOLOGY OF *PROSAYIMYS* AND *SAYIMYS*

Figure 8 presents the stratigraphic ranges of *Prosayimys* and the species of *Sayimys*. *Prosayimys flynni* occurs at locality Z 113 at the base of the upper Chitarwata Formation of the Zinda Pir Dome. In the Marri Bugti area of Baluchistan, approximately 200 km to the southwest, the Chitarwata Formation has produced a fauna with a rodent assemblage very different from that of the Siwaliks. Ctenodactyloids are present in the Bugti Fauna, but they are represented by an endemic radiation of archaic chappatimyids and the Baluchimyinae (Flynn and others, 1986). The lower Chitarwata Formation in the Zinda Pir area has produced a rodent fauna (Downing and others, 1993; Flynn & Cheema, 1994) similar to that from the Bugti area. Evidently, *Prosayimys* in the upper Chitarawata Formation represents the first appearance of ctenodactylids on the Indian subcontinent, having immigrated from China or central Asia. Locality Z 113 also marks the first appearance of primitive cricetid rodents in the Zinda Pir area (Downing and others, 1993).

Prosayimys retains many features seen in the Oligocene and early Miocene ctenodactylids *Tataromys* and *Karakoromys*. It represents a more primitive stage of ctenodactylid evolution than that seen in the Siwaliks or lower Manchar Formation and likely occurs earlier. The only species of *Sayimys* with metalophulid II is *S. obliquidens*, which has this structure much less well developed, and which could be derived from a form similar to *P. flynni*. In fact *P. flynni* could be ancestral to all later occurring ctenodactylids.

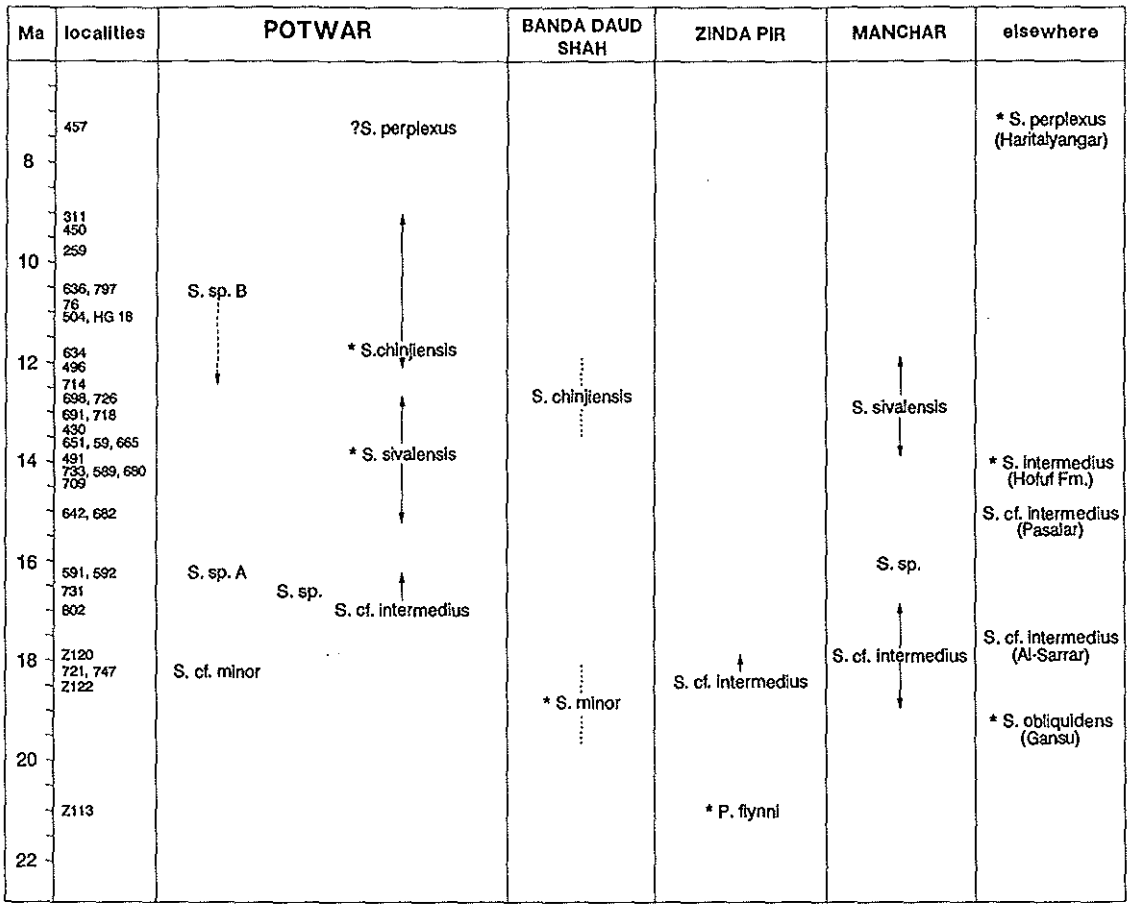


Figure 8.— Biochronology of *Prosayimys* and *Sayimys*. Asterisk indicates type locality. Dotted lines represent uncertain ages of Banda Daud Shah localities. Dashed line indicates presumed range.

Sayimys obliquidens (Bohlin, 1946) from the early Miocene of China (Qiu Z., 1990) is one of the oldest previously described species of this genus. According to Bohlin, this species has relatively large premolars (unlike *Metasayimys*), upper molars with a prominent paraflexus and metaflexus, lower molars with a metalophulid II in one little worn specimen (M_2), relatively oblique lophids and a posterointernal cingulum. Jaeger (1971) referred *S. obliquidens* to the late Miocene African genus *Metasayimys*. However, Wood (1977) has detailed why the original assignment to *Sayimys* is correct. Wood (1977) derived *S. perplexus* from *S. obliquidens*. Munthe (1980) believed that *S. obliquidens* was morphologically distinct enough from Siwalik *Sayimys* to warrant the future establishment of a separate genus for this taxon. De Bruijn and others (1989) provisionally referred *S. obliquidens* to *Sayimys*. The distinctive characters of this species, such as long paraflexi and metaflexi on the upper molars and presence of metalophulid II on lower molars are primitive characters seen in Oligocene genera (Wood, 1979) and *Prosayimys*. Munthe (1980) proposed that *S. obliquidens* was

ancestral to later *Sayimys*. Shevyreva (1994) suggested that *S. obliquidens* was a member of a Central Asian lineage that gave rise to the genus *Akzharomys*.

De Bruijn and others (1981) described the small species *S. minor* from the Murree Formation in northern Pakistan at Banda Daud Shah and considered it the oldest and most primitive species of *Sayimys* from southern Asia. Unfortunately, at the type locality, this species is known only from four isolated teeth. Flynn and others (1986) noted that the Murree rodent fauna occurs above the presumed regional unconformity, which has been dated at 18.3 Ma near Chinji. Bernor and others (1988) considered this Murree locality to be older than the lower Manchar Formation at Gaj (which has produced *S.* cf. *S. intermedius*), which is about 18-19 Ma, and younger than the Bugti Fauna (Flynn and others, 1986). In the present paper, *S.* cf. *S. minor* is reported from the lower Kamlial Formation of the Potwar Plateau. A *Sayimys* similar to *S. minor* also occurs in the early Aragonian Horlak fauna, Anatolia, Turkey, in the Lower Manchar Formation of southern Pakistan, and from the early Miocene Sihong Fauna, Xiacaowan Formation of China (Sümengen and others, 1990).

Sayimys intermedius was first described from the Miocene Al Jadidah Fauna, Hofuf Formation in Saudi Arabia (Sen & Thomas, 1979). This species was originally allocated to *Metasayimys*. Munthe (1980) suggested that this species might be referable to *Sayimys*, because it is more similar morphologically to *S. sivalensis* than to *M. curvidens*. De Bruijn and others (1989) unequivocally placed *S. intermedius* in *Sayimys*. The type specimen of *S. intermedius* (SEN & THOMAS, 1979) is a lower jaw with DP_4, M_1–M_2. The only other material reported from the type locality is an isolated lower incisor. The DP_4 has an isolated anteroconid; M_1 and M_2 have mesoflexid as long as the metaflexid, as is typical of *Sayimys*. Thomas (1983) interpreted that the age of the Al Jadidah Fauna was at the MN6/MN7 boundary (about 14 Ma).

Additional Saudi Arabian material from the Al-Sarrar Local Fauna has been referred questionably to this species (Thomas and others, 1982). The material is briefly described but not illustrated, nor are dental measurements given. The Al-Sarrar fauna is tentatively placed in MN4a, about 17-18 Ma (Thomas and others, 1982; Savage, 1990). *Sayimys* cf. *S. intermedius* has also been reported from middle Miocene of Turkey at Pasalar (Flynn & Jacobs, 1990). This specimen has a very broad and deep mesostriid. A ctenodactylid referred to *Metasayimys*, but represented only by isolated incisors, occurs in the Miocene Hatzeva Formation, Negev, Israel (Goldsmith and others, 1982). These specimens were compared to *S. intermedius*, which then was considered a species of *Metasayimys*. This locality was assigned to MN3a about 20-22 Ma (Tchernov and others, 1987), which would make it perhaps the earliest record of *Sayimys*. However, Tassy (1990) considers the Negev Fauna better assigned to the MN4-MN5 zones, 16-18 Ma, about the same age as the Al-Sarrar fauna.

Sayimys cf. *S. intermedius* is recognized from the lower part of the Lower Manchar Formation from Gaj in southern Pakistan (de Bruijn and others, 1989) and (in the present paper) from the lower Vihowa Formation of the Zinda Pir Dome and the Kamlial Formation of the Potwar Plateau. Bernor and others (1988) assigned an age of 17-19 Ma for the lower part of the Lower Manchar. The lower Vihowa formation correlates with the lower Murree or Kamlial Formations of the Potwar Plateau. Friedman and others (1992) interpreted the age of the lower Vihowa Formation to be

16-18 Ma. Lindsay (1994) assigned an age of 18-22 Ma for the lower Vihowa. Differences between the Saudi Arabian and Pakistani material are discussed above. Persistence of a rodent species such as *S. intermedius* over 5 million years and 3500 km would be highly unusual. More and better descriptions of the Saudi Arabian, Pakistani, and Pasalar material are needed before accepting this hypothesis of wide geographic and temporal distribution of *S. intermedius*.

In the Potwar section, DP_4's with an isolated anteroconid (*S.* cf. *S. intermedius*) are known from 17 Ma; those with anteroconid connected to the metalophid (*S. sivalensis*) appear first about 15 Ma, which is older than the type locality of *S. intermedius*. The type locality for *S. sivalensis* is lower Siwaliks, Chinji beds, near Chinji, Attock District, Salt Range, Pakistan (Hinton, 1933; Black, 1972). The type specimen could have come from nearly anywhere in the Chinji section in this area, which spans 14.3 to 10.8 Ma (Johnson and others, 1985). Black (1972) concluded that *S. sivalensis* was ancestral to the later occurring *S. perplexus*, and distinguished the former by its smaller size, shorter and weaker masseteric crest, and lower crowned teeth with straighter anterolophids, less oblique hypolophids, and shallower metastriids. The present paper interprets that *S. sivalensis* is most similar to specimens from the lower Chinji. In the Potwar Plateau, paleomagnetically constrained records of *S. sivalensis* occur from 15.1 Ma, in the upper Kamlial Formation, to approximately 13 Ma, in the lower Chinji Formation.

Munthe (1980) analyzed over 200 specimens of mainly isolated cheek teeth of *Sayimys* from the Daud Khel Local Fauna of the western Potwar Plateau. The fossils are from the uppermost red mudstone unit of the Chinji Formation (Munthe, 1980). Jacobs and others (1989) placed this locality at about 11 Ma. Munthe (1980) concluded that the *Sayimys* from this locality represented a single species which displayed variability in size and morphology. As a result of this he synonymized the genotypic *S. perplexus* with *S. sivalensis*, because specimens similar in size and morphology to the two nominate species could be found in his quarry sample (with the exception of the greater metalophid width on M_2 on the type of *S. perplexus*). He cautioned that since the Daud Khel locality was temporally intermediate between the type localities for *S. sivalensis* and *S. perplexus*, his specimens could represent a chronoclinal population between distinct smaller Chinji and larger Nagri species. In the present paper, the Daud Khel specimens are assigned to the new species, *S. chinjiensis*. In the Potwar section, *Sayimys chinjiensis* first appears at 12 Ma and persists until 9 Ma, from the upper Chinji to the Nagri. Specimens referred to *S. sivalensis* from the Chinji Formation at Banda Daud Shah (Wessels and others, 1982) may represent the earliest occurrence of *S. chinjiensis*, since there is no mention of presence of an anteroloph. More specimens are needed to confirm this identification. The age of H-GSP 107 is 12-14 Ma (Bernor and others, 1988; Jacobs and others, 1990).

Wood (1937) noted that the type specimen of *S. perplexus*, the type species of the genus, was from the Nagri Zone near Haritalyangar, India. Flynn and others (1990b) stated that the Nagri Formation in this region is younger than in the Potwar Plateau of Pakistan, and that the most fossiliferous horizons in the Haritalyangar region are equivalent in age to the Dhok Pathan Formation (approximately 7.6-6.9 Ma) in the Potwar section. The holotype of *S. perplexus* is from the same locality and horizon, east

of Haritalyangar, as the holotype of *Kanisamys sivalensis* (Wood, 1937). At Haritalyangar, fossils also occur lower in the section. The type of *K. nagrii* Prasad, likely from about 9.5-9.0 Ma (Flynn, 1982), corresponds approximately to the last unequivocal appearance of *Sayimys* in the Potwar Plateau (Jacobs and others, 1989, 1990). However, Flynn and others (1990b) noted that hominoid and sivaladapid primates have younger records at Haritalyangar than they do in the Potwar sequence. *Sayimys* also had a younger record in India. Vasishat (1978, 1985) described partial upper and lower dentitions of *S. perplexus* from about 500 m. east of Haritalyangar. Prasad (1968) described a partial mandible of *S. perplexus* from about 600 m. east of Haritalyangar, which would place it high in the section, perhaps even younger than 7 Ma (Johnson and others, 1983, figs. 4-6).

Vasishat (1985) described a new species, *S. badaunensis*, from the Tatrot Formation in the Haritalyangar area, which indicates the possible survival of this genus into the Pliocene. *Sayimys* has also been recognized from the Pliocene of North Africa (Munthe, 1987). However, the two isolated teeth and mandibular fragment from Libya are probably better referred to *Africanomys*, as indicated by the short mesostriids and position of the mandibular crest.

The presumed DP^4 from Y 457, dated at 7.3 Ma, may indicate the presence of *S. perplexus* from the Dhok Pathan in the Potwar section. The virtual absence of ctenodactylids in the Potwar Plateau after 9 Ma is probably not a sampling artifact. Although there are numerous productive micromammal producing localities in the Potwar Plateau in the interval from 8.9 to 6.6 Ma (Jacobs and others, 1990), Y 457 is the only site that has produced a possible ctenodactylid. Barry and others (1990) note that the interval from 9.5 to 7.0 Ma is the time of lowest diversity in the Potwar Plateau, perhaps caused by decreased precipitation and increased seasonality, which may have led to the extirpation of *Sayimys* in this region.

Previous studies have recognized a single anagenetic lineage of *Sayimys* in southern Asia. De Bruijn and others (1989) suggested that the poorly known *S. minor* and *S. perplexus* are the beginning and end members, respectively, of the *Sayimys* [cf. *S.*] *intermedius-sivalensis*[*-chinjiensis*] lineage. They (1989) described assemblages of isolated cheek teeth from five successive levels of the Lower Manchar Formation in southern Pakistan. Bernor and others (1988) correlated these localities with the paleomagnetically dated section in the Potwar Plateau. The section spans an approximately 6 million year interval. De Bruijn and others (1989) recognized *S.* cf. *S. intermedius* from the lower part of the section (two levels spanning approximately 19-17 Ma), a form transitional between *S.* cf. *S. intermedius* and *S. sivalensis* (from about 17-16 Ma), and *S. sivalensis* from two upper levels (approximately 14-12 Ma). Evolutionary trends that they recognized include increase in size of upper and lower third molars, development of an anterolophid connecting the anteroconid with the protoconid and metaconid on DP_4, increased obliqueness of the lophs of the lower molars, and increase in crown height. Upper molars from the youngest locality have very reduced to absent anterolophs.

The present paper agrees with de Bruijn and others (1989) in recognizing an anagenetic *S.* cf. *S. intermedius-S. sivalensis-S. chinjiensis* lineage in Pakistan. More material of *S. perplexus* is needed, but it seems likely, as concluded by previous

investigators, that it is the end member of this lineage. Unfortunately at this time, the small sample size and gaps between sampling localities do not permit interpretation of the tempo and mode of evolutionary change within this lineage. The age and identification of *Sayimys* from the Chinji Formation at Banda Daud Shah are the only source of data that could indicate a possible cladogenetic event in this lineage. However, at present there is no unequivocal evidence of temporal overlap between *S. sivalensis* and *S. chinjiensis*.

However, more than one lineage of *Sayimys* is present in Pakistan during the middle and late Miocene. This has already been suggested by the presence of a larger species (represented only by two teeth) in the Lower Manchar section at the same locality (H-GSP 81.14) as the *S.* cf. *S. intermedius-sivalensis* transitional form (de Bruijn and others, 1989). Its phylogenetic relationships are not discussed, although they stated that further comparisons with *S. obliquidens* were warranted, which suggests they may have considered it an immigrant from central Asia. This seems unlikely, given the greater age and relatively primitive morphology of *S. obliquidens*. This Manchar species is more primitive than *S. sivalensis* (the DP_4 has an isolated anteroconid) and is most likely derived from Pakistani *S.* cf. *S. intermedius*, assuming that the size difference is great enough to recognize it as a separate species. This large species may also be present slightly earlier in the Potwar section at Y 731, although the large DP^4 could again be just an extreme variant of *S.* cf. *S. intermedius*. This presumed taxon is indicated by *S.* sp. on Fig. 8.

If the specimens from Y 721 are correctly assigned to *S. minor*, then this species is too specialized to be ancestral to the Pakistani *S.* cf. *S. intermedius*. In any event, the taxon from Y 721 represents a separate lineage. The small size, upper molars with reduced to absent anteroloph, lower molars with short mesoflexids indicate a relationship with *S.* sp. A, which in turn may be ancestral to *S.* sp. B.

The phylogenetic position of *S. obliquidens* relative to the south Asian *Sayimys* requires further study. In several features it is structurally intermediate between *P. flynni* and *S.* cf. *S. intermedius*. It must also be kept in mind that *S.* cf. *S. intermedius* from Pakistan has not been demonstrated conclusively to be identical with the species identified from Saudi Arabia.

RELATIONSHIPS OF *PROSAYIMYS* AND *SAYIMYS* TO OTHER CTENODACTYLID GENERA

Bohlin (1946) and Black (1972) suggested a close relationship between *Sayimys* and the Oligocene to early Miocene *Tataromys*. Wood (1977) indicated that *Sayimys* and *Africanomys* are derived from a form similar to the middle Oligocene *Terrarboreus* or *Woodomys*. Dawson and others (1984) suggested that until more material is known, it was best to consider the latter two genera Ctenodactyloidea *incertae sedis*. Wang (1984) included *Terrarboreus* in the ctenodactyloid family Yuomyidae, but now (Wang, 1994) considers *Terrarboreus* and *Woodomys* junior synonyms of *Karakoromys*. Flynn and others (1986) considered *Tataromys* and

Karakoromys the primitive sister taxa of the middle Miocene and younger ctenodactlids. In their cladogram (1986, fig. 4) these two genera are united by an autapomorphy: anterior cingulum present on lower molars. *Karakoromys* has upper molars with an incomplete metaloph, P_4 with hypoconid, and lower molars with short metalophulid II. It appears for the most part too primitive to be the immediate ancestor of *Prosayimys* or *Sayimys*. Bohlin (1946) considered *Karakoromys* ancestral to *Tataromys*. Wang (1991) noted that *Leptotataromys* is a junior synonym of *Tataromys* and fully characterized *Yindirtemys*, noting its close relationship with *Tataromys*. As in *Sayimys*, *Yindirtemys* has unilaterally hypsodont upper molars and lacks an anterior cingulum on the lower molars (Wang, 1991). It differs from *Sayimys* in having more cuspate and more complex teeth, with structures such as an anterocone on the upper molars. *Prosayimys* is derived from a form similar to *Yindirtemys* or *Tataromys*. *Sayimys* is almost certainly derived from *Prosayimys*.

Flynn and others (1986) characterized the more advanced ctenodactylids as having the horizontal masseteric crest extending anteriorly to below the P_4 and losing metalophulid II. However, a metalophulid II is present in primitive *Sayimys* as well as *Sardomys* and *Pireddamys*. The latter two genera are from the Oschiri fauna of Sardinia, which is tentatively considered Orleanian (early Miocene) in age, 17-22 Ma.

The ctenodactylid genera *Metasayimys* and *Africanomys* were established by Lavocat (1961) for specimens from the middle Miocene Beni Mellal Fauna of Morocco. After obtaining abundant additional material, Jaeger (1971) reviewed the systematics of these two genera and synonymized the five ctenodactylid taxa named by Lavocat into one species in each of the above two genera. The type (and only currently recognized species) of the genus *Metasayimys* is *M. curvidens* (Wood, 1977). Thomas (1983) placed the Beni Mellal Fauna, the type locality of *M. curvidens* and *A. pulcher*, in MN7, about 13-14 Ma. The earliest occurrence of *Africanomys* is from Gebel Zelten, Libya. Savage (1990) correlated this fauna with MN3b, about 19-20 Ma; Moyà-Solà & Agustí (1990), with MN4, 17-18 Ma. Winkler (1994) suggested that the Gebel Zelten rodents are more likely earliest middle Miocene in age, probably about 15-16 Ma. *Africanomys* differs from *Metasayimys* and resembles *Tataromys* in having a primitive DP_4 that lacks an anteroconid. Wood (1977) derived *Metasayimys* from the coeval, but morphologically more primitive, *Africanomys*. The different structure of the DP_4's suggests that *Metasayimys* represents a separate immigration of ctenodactylids to Africa. Munthe (1980) proposed that *Sayimys sivalensis* was ancestral to *Metasayimys*. De Bruijn and others (1989) suggested that *Metasayimys* was derived from *S. minor*. Morphology of the dentition and mandible of *S. minor* described in this paper support this suggestion.

ACKNOWLEDGEMENTS

This study is the result of collaborative efforts by researchers and staff associated with the Geological Survey of Pakistan, Pakistan Museum of Natural History, Harvard University, and the University of Arizona. J. Barry, W. Downs, L.J. Flynn, L.L Jacobs, and E.H. Lindsay in particular were involved in the

collection of the ctenodactylid specimens. L.J. Flynn and E.H. Lindsay reviewed drafts of this manuscript. G. Longoria, C. Tipton, and R. Thomas assisted with the preparation of the figures.

LITERATURE CITED

ANDREWS, P. 1990. — Owls, caves, and fossils. University of Chicago Press, Chicago, 232 pp.

BARRY, J.C., FLYNN, L.J. & PILBEAM, D.R., 1990. — Faunal diversity and turnover in a Miocene sequence. Pp. 381-421. *In:* R.R. ROSS & W.D. ALLMON (Eds.), Causes of evolution: A paleontological perspective. University of Chicago Press, Chicago.

BARRY, J.C., JOHNSON, N.M., RAZA, S.M. & JACOBS, L.L., 1985. — Neogene mammalian faunal change in southern Asia: correlations with climatic, tectonic and eustatic events. *Geology*, 13: 637-640.

BERNOR, R.L., FLYNN, L.J., HARRISON, T., HUSSAIN, S.T. & KELLEY, J., 1988. — *Dionysopithecus* from southern Pakistan and the biochronology and biogeography of early Eurasian catarrhines. *Journal of Human Evolution*, 17: 339-358.

BLACK, C.C., 1972. — Review of fossil rodents from the Neogene Siwalik Beds of India and Pakistan. *Palaeontology*, 15: 238-266.

BOHLIN, B., 1946. — The fossil mammals from the Tertiary deposits of Taben-Baluk, western Kansu, Part II: Simplicidentata, Carnivora, Artiodactyla, Perissodactyla, and Primates. *Palaeontologia Sinica*, New Series C, 8b: 1-259.

BRUIJN, H. de, BOON, E. & HUSSAIN, S.T., 1989. — Evolutionary trends in *Sayimys* from the Lower Manchar Formation (Sind, Pakistan). *Koninklijke Nederlandse Akademie van Wetenschappen Proceedings*, Series B, 92: 191-214.

BRUIJN, H. de, HUSSAIN, S.T. & LEINDERS, J.J.M., 1981. — Fossil rodents from the Murree Formation near Banda Daud Shah, Kohat, Pakistan. *Koninklijke Nederlandse Akademie van Wetenschappen Proceedings*, Series B, 84: 71-99.

BRUIJN, H. de & RÜMKE, C.G., 1974. — On a peculiar mammalian association from the Miocene of Oschiri(Sardinia). *Koninklijke Nederlandse Akademie van Wetenschappen Proceedings*, Series B, 77: 46-79.

DAWSON, M.R., LI, Chuan-kuei & QI, Tao, 1984. — Eocene ctenodactyloid rodents (Mammalia) of eastern and central Asia. *In*: R.M. MENGEL (Ed.), Papers in vertebrate paleontology honoring R. W. Wilson. *Carnegie Museum of Natural History, Special Paper*, 9: 138-150.

DOWNING, K.F., LINDSAY, E.H., DOWNS, W.R. & SPEYER, S.E., 1993. — Lithostratigraphy and vertebrate biostratigraphy of the early Miocene Himalayan foreland, Zinda Pir Dome, Pakistan. *Sedimentary Geology*, 87: 25-37.

FLYNN, L.J., 1982. — Systematic revision of the Siwalik *Rhizomidae* (Rodentia). *Géobios*, Lyon, 15:327-389.

FLYNN, L.J. & CHEEMA, I.U., 1994. — Baluchimyine rodents from the Zinda Pir Dome, western Pakistan: systematic and biochronologic implications. *In*: T. SETOGUCHI, C. LI & Y. TOMIDA (Eds.), Rodent and Lagomorph Families of Asian Origins and Diversification. *National Science Museum, Tokyo, Monographs*, 8:115-129.

FLYNN, L.J. & JACOBS, L.L., 1990. — Preliminary analysis of Miocene small mammals from Pasalar, Turkey. *Journal of Human Evolution*, 19:423-436.

FLYNN, L.J., JACOBS, L.L. & CHEEMA, I.U., 1986. — Baluchimyinae, a new ctenodactyloid rodent

subfamily from the Miocene of Baluchistan. *American Museum Novitates*, 2841: 1-58.

FLYNN, L.J., JACOBS, L.L., BARRY, J.C., PILBEAM, D., BEHRENSMEYER, A.K. & KAPPELMAN, J.W., 1990a. — The Siwaliks of Pakistan: Time and faunas in a Miocene terrestrial setting. *Journal of Geology*, 98: 589-604.

FLYNN, L.J., SAHNI, A., JAEGER, J.-J., SINGH, B. & BHATIA, S.B., 1990b. — Additional rodents from the Siwalik beds of India. *Koninklijke Nederlandse Akademie van Wetenschappen Proceedings*, 93: 7-20.

FRIEDMAN, R., GEE, J., TAUXE, L., DOWNING, K. & LINDSAY, E.H., 1992. — The magnetostratigraphy of the Chitarwata and lower Vihowa formations of the Dera Ghazi Khan area, Pakistan. *Sedimentary Geology*, 81:253-268.

GOLDSMITH, N.F., TCHERNOV, E., GINSBURG, L., TASSY, P. & VAN COUVERING, J.A., 1982. — Ctenodactylid rodent in the Miocene Negev Fauna of Israel. *Nature*, 296: 645-647.

HINTON, M.A.C., 1933. — Diagnoses of new genera and species of rodents from Indian Tertiary deposits. *Annals and Magazine of Natural History*, 12: 620-622.

JACOBS, L.L., FLYNN, L.J. & DOWNS, W.R., 1989. — Neogene rodents of southern Asia. *In*: C.C. BLACK & M.R. DAWSON (Eds.), Papers on Fossil Rodents in Honor of Albert Elmer Wood. *Natural History Museum of Los Angeles County, Science Series*, 33: 157-177.

JACOBS, L.L., FLYNN, L.J., DOWNS, W.R. & BARRY, J.C., 1990. — *Quo vadis, Antemus*? The Siwalik muroid record. Pp. 573-586. *In*: E.H. LINDSAY, V. FAHLBUSCH & P. MEIN (Eds.), European Neogene Mammal Chronology. Plenum Press, New York and London.

JAEGER, J.-J., 1971. — Un cténodactylidé (Mammalia, Rodentia) nouveau, *Irhoudia bohlini* n. g., n. sp., du Pléistocène inférieur du Maroc. Rapports avec les formes actuelles et fossiles. *Notes du Service géologique, Maroc*, 31: 113-140.

JAEGER, J.-J. 1977. — Les rongeurs du Miocène moyen et supérieur du Maghreb. *Palaeovertebrata*, Montpellier, 8: 1-166.

JOHNSON, G.D., OPDYKE, N.D., TANDON, S.K. & NANDA, A.C., 1983. — The magnetic polarity stratigraphy at Haritalyangar (India) and a new appearance datum for *Ramapithecus* and *Sivapithecus* in Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 44: 223-249.

JOHNSON, N.M., STIX, J., TAUXE, L., CERVENY, P.F. & TAHIRKHELLI, R.A.K., 1985. — Paleomagnetic chronology, fluvial processes, and tectonic implications of the Siwalik deposits near Chinji Village, Pakistan. *Journal of Geology*, 93: 27-40.

LAVOCAT, R., 1961. — Le gisement de vértébres miocènes de Beni-Mellal (Maroc). Étude systématique de la faune de mammifères et conclusions générales. *Notes et Mémoires du Service géologique du Maroc*, 155: 29-145.

LINDSAY, E.H., 1994. — The fossil record of Asian Cricetidae with emphasis on Siwalik cricetids. *In*: T. SETOGUCHI, C. LI & Y. TOMIDA (Eds.), Rodent and Lagomorph Families of Asian Origins and Diversification. *National Science Museum, Tokyo, Monographs*, 8: 131-147.

LINDSAY, E.H., JOHNSON, N.M. & OPDYKE, N.P., 1980. — Correlation of Siwalik Faunas. Pp. 309-319. *In*: L.L. JACOBS, (Ed.), Aspects of Vertebrate History: Essays in Honor of Edwin Harris Colbert. Museum of Northern Arizona Press, Flagstaff.

MOYÀ-SOLÀ, S. & AGUSTÍ, J., 1990. — Bioevents and mammal successions in the Spanish Miocene. Pp. 357-373. *In*: E.H. LINDSAY, V. FAHLBUSCH & P. MEIN (Eds.), European Neogene Mammal Chronology. Plenum Press, New York and London.

MUNTHE, J., 1980. — Rodents of the Miocene Daud Khel Local Fauna, Mianwali District, Pakistan. Part 1. Sciuridae, Gliridae, Ctenodactylidae, and Rhyzomyidae. *Milwaukee Public Museum, Contributions in Biology and Geology*, 34: 1-36.

MUNTHE, J. — 1987. Small-mammal fossils from the Pliocene Sahabi Formation of Libya. Pp. 135-44. *In*: N.T. BOAZ, A. EL-ARNAUTI, A.W. GAZIRY, J. de HEINZELIN and D.D. BOAZ (Eds.), Neogene Paleontology and Geology of Sahabi. Alan R. Liss, Inc, New York.

PRASAD, K.N., 1970. — The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh, India. *Palaeontologica Indica*, N.S., 39: 1-55.

QIU, Zhanxiang, 1990. — The Chinese Neogene mammalian biochronology - Its correlation with the European Neogene. Pp. 527-556. *In*: E.H. LINDSAY, V. FAHLBUSCH & P. MEIN (Eds.), European Neogene Mammal Chronology. Plenum Press, New York and London.

SAVAGE, R.J.G., 1990. — The African dimension in early Miocene mammal faunas. Pp. 587-599. *In*: E.H. LINDSAY, V. FAHLBUSCH & P. MEIN (Eds.), European Neogene Mammal Chronology. Plenum Press, New York and London.

SCHAUB, S., 1958. — Simplicidentata. Pp. 659-818. *In*: J. PIVETEAU (Ed.), Traité de Paléontologie. Masson et Cie, Paris.

SEN, S. & THOMAS, H., 1979. — Découverte de rongeurs dans le Miocène moyen de la Formation Holuf (Province du Hasa, Arabie Saouidite). *Comptes Rendus sommaires de la Societé géologique de France*, 1979 (1): 34-37.

SHEVYREVA, N.S., 1994. — A new Miocene Ctenodactyloidea (Rodentia, Mammalia) from the Zaysan Basin (eastern Kazakhstan). *Paleontological Journal*, 28: 160-167.

STIRTON, R.A., 1935. — A review of the Tertiary beavers. *University of California Publications, Bulletin of the Department of Geological Sciences*, 23: 391-458.

SÜMENGEN, M., ÜNAY, E., SARAC, G., BRUIJN, H. de, TERLEMEZ, I. & GÜRBÜZ, M., 1990. — New Neogene rodent assemblages from Anatolia (Turkey). Pp. 61-72. *In*: E.H. LINDSAY, V. FAHLBUSCH & P. MEIN (Eds.), European Neogene Mammal Chronology. Plenum Press, New York and London.

TASSY, P., 1990. — The "Proboscidean Datum Event:" How many proboscideans and how many events. Pp. 237-252. *In*: E.H. LINDSAY, V. FAHLBUSCH & P. MEIN (Eds.), European Neogene Mammal Chronology. Plenum Press, New York and London.

TCHERNOV, E., GINSBURG, L., TASSY, P. & GOLDSMITH, N.F., 1987. — Miocene mammals of the Negev. *Journal of Vertebrate Paleontology*, 7: 284-310.

THOMAS, H., 1983. — Les Bovidae (Artiodactyla, Mammalia) du Miocène moyen de la Formation Hofuf (Province du Hasa, Arabie Saoudite). *Palaeovertebrata*, Montpellier, 13:157-206.

THOMAS, H., SEN, S., KHAN, M., BATTAIL, B. & LIGABUE, G., 1982. — The Lower Miocene fauna of Al-Sarrar (Eastern Province, Saudi Arabia). *ATLAL, Journal of Saudi Arabian Archaeology*, 5: 109-136.

VASISHAT, R.N., 1978. — First record of maxillary dentition of *Sayimys perplexus* (Ctenodactylidae) from the Indian Sivaliks. *Current Science*, 47: 859-860.

VASISHAT, R.N., 1985. — Antecedents of early man in northwestern India: paleontological and paleoecological evidences. Inter-India Publications, New Delhi, 230 pp.

WANG, B.-y., 1984. — *Dianomys* gen. nov. (Rodentia, Mammalia) from the lower Oligocene of Qujing, Yunnan, China. *Mainzer Geowissenschaftliche Mitteilungen*, 13: 37-48.

WANG, B.-y., 1991. — Discovery of *Yindirtemys* (Ctenodactylidae, Rodentia, Mammalia) from the late Oligocene of Nei Mongol, China. *Vertebrata PalAsiatica*, 29: 296-302. [In Chinese, with English summary].

WANG, B.-y., 1994. — The Ctenodactyloidea of Asia. *In*: T. SETOGUCHI, C. LI & Y. TOMIDA (Eds.), Rodent and Lagomorph Families of Asian Origins and Diversification. *National Science Museum, Tokyo, Monographs*, 8: 35-47.

WESSELS, W., BRUIJN, H. de, HUSSAIN, S.T. & LEINDERS, J.J.M., 1982. — Fossil rodents from the Chinji Formation, Banda Daud Shah, Kohat, Pakistan. *Koninklijke Nederlandse Akademie van Wetenschappen Proceedings*, Series B, 85: 337-364.

WINKLER, A.J., 1994. — The Middle/Upper Miocene dispersal of major rodent groups between southern Asia and Africa. *In*: T. SETOGUCHI, C. LI & Y. TOMIDA (Eds.), Rodent and Lagomorph Families of Asian Origins and Diversification. *National Science Museum, Tokyo, Monographs*, 8: 173-184.

WOOD, A.E., 1937. — Fossil rodents from the Siwalik beds of India. *American Journal of Science*, 36: 64-76.

WOOD, A.E., 1977. — The evolution of the rodent family Ctenodactylidae. *Journal of the Palaeontological Society of India*, Jurij Alexandrovich Orlov Memorial Number, 20: 120-137

ZITTEL, K.A. von, 1893. — Handbuch der Paläontologie. Abt 1. Paläozoologie. Bd. IX, Vertebrata (Mammalia). R. Oldenbourg, Munich, 799 pp.

LEGEND OF PLATE

PLATE 1

Prosayimys flynni (x 19)

A. right DP_4 Z113/316;

B. left DP^4 Z113/311;

C. right M^3 Z113/293;

D. right M_{1-2} Z113/304;

E. right M_{1-2} Z113/295;

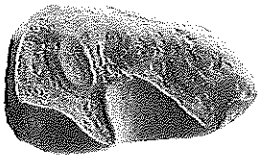
Sayimys minor (x 20)

G. right P^4–M^2 Y747/48143;

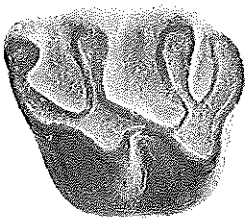
H. left M_1–M_2 Y747/48136;

Sayimys chinjiensis (x 20)

I. left P_4–M_1 Y434/45186.

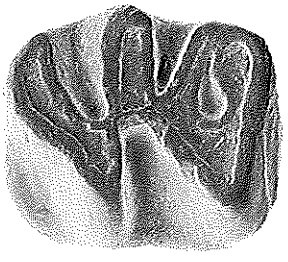


A

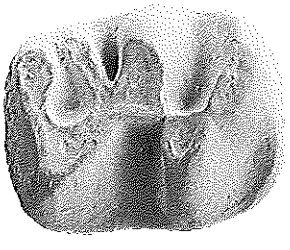


B

C



D



E

F

G

H