REVIEW OF FOSSIL RODENTS FROM THE NEogene SIWALIK BEDS OF INDIA AND PAKISTAN

by CRAIG C. BLACK

ABSTRACT. Sixteen species of rodents belonging to nine genera and five families are now known from the Neogene Siwalik Series of India and Pakistan. Detailed descriptions, illustrations and discussion are given for all species of rhizomyids, ctenodactyloids and tachyomyids; brief mention is made of the hystricids and murids. The most abundant material is that of rhizomyids for which two distinct lineages are recognized: Rhizomyoides to Rhipidomys and Kaasiaomys-Protomys to Tachyomyoides. The Asian and African rhizomyids and ctenodactyloids are compared, and Pseudocricetus indicus is recognized as the only tachymyid known outside Africa.

Fossil vertebrates from the 'Siwalik Hills' and the Salt Range of India and Pakistan have been known for more than a 150 years. The first serious student of vertebrate fossils found in the middle and later Tertiary sediments along the southern edge of the Himalaya Mountains was Dr. Hugh Faulkner who, together with Lt. P. T. Cautley, began publishing on Indian fossil vertebrates in the 1830s. Their series entitled Fauna Antiqua Siwalensis was the first monographic treatment of this material. Their studies were added to and expanded upon by Richard Lydekker in the latter part of the 19th century. Since Lydekker's time, many students have published on Siwalik fossil vertebrates. Notable among these later students are Drs. Guy E. Pilgrim, W. D. Matthew, and E. H. Colbert. More recently there has been renewed interest in the collection and study of vertebrate fossils from this area as is evidenced by the work of K. N. Prasad of the Indian Geological Survey and the recent expeditions to northern India of the Peabody Museum of Yale University under the direction of E. L. Simons.

Throughout the history of the study of vertebrates from the Siwalik Hills, there has been a noticeable absence of papers dealing with the smaller vertebrates, lizards, snakes, birds, insectivores, and rodents. In most collections from the Siwaliks, small vertebrate specimens are extremely rare. In 1933, Colbert was able to record only ten specimens of fossil rodents as having been recovered from all of the Siwalik beds. There were other specimens of fossil rodents present at that time in the collections of both the Indian Geological Survey and the British Museum of Natural History but these were unknown to Colbert. The presence of such additional material was indicated by Hinton's (1933) short note in the Annals and Magazine of Natural History in which he briefly diagnosed several new species of fossil rodents. In 1937, A. E. Wood published a description of additional fossil rodent material collected by the Yale University Expedition in Northern India in 1932. In recent years a great deal of new material of small vertebrates has been added to the fauna of the Siwalik series by both Prasad and Simons (personal communication). These collections include a number of rodents and primates which are as yet undescribed.

The purpose of the present paper is twofold. Of greatest importance, perhaps, is the description and presentation of figures of the material upon which Hinton (1933) based his brief diagnosis of new genera and species of Indian Tertiary rodents. Some
confusion has resulted in the subsequent literature on Asian fossil rodent material due to
the brevity of Hinton's original descriptions and the absence of illustrations of type
specimens in that note. These various areas of confusion are discussed and clarified
below. The second function of this report is to form a basis on which the description
of the new collections can be built. The newer materials have been collected with
a much better understanding of the need for exact stratigraphic information accompa-
nying each individual specimen. Unfortunately, this is not true of the older materials
and exact locality and stratigraphic position are in many cases either poorly or totally
unknown. All fossil rodents described from the Siwalik series are at least briefly con-
sidered here; however, the later Pleistocene occurrences of rodents in Asia are not dealt
with. The fossil murids and hystricids of the Siwaliks have not been examined person-
ally by me. Therefore, only brief citations are given for specimens belonging to these two
families of rodents.

For many years the whereabouts of the collection which formed the basis for Hinton's
(1933) brief note was unknown. After Dr. Hinton's death, much of the material upon
which he had been working was sent to the British Museum of Natural History. A
search of these collections by the author in 1964 and again in 1965, failed to disclose
the Siwalik rodent specimens. However, in 1965 through the kindness of Professor
R. J. G. Savage at the University of Bristol, I learned that this portion of the Hinton
collection was in his care in the Geology Department at the University of Bristol. While
in India in 1964, and before the whereabouts of the India Geological Survey collection
of rodents from the Siwaliks was known, I was very kindly given permission to study
this material if it could be found. In this regard I want to thank, particularly, the Director
of the Geological Survey of India, Dr. R. C. Roy, the Chief Palaeontologist, Mr.
M. B. A. Sastry, and Mr. K. N. Prasad, vertebrate palaeontologist with the Indian
Geological Survey, for allowing me to complete Hinton's preliminary work. In 1968,
I was able to visit R. J. G. Savage at Bristol and at that time he very kindly turned over
to me all of the Indian Geological Survey specimens mentioned in Hinton's original
paper. Dr. Savage also put at my disposal all of Dr. Hinton's original notes on this
collection, together with a series of illustrations prepared by Mr. Terzi for the mono-
graph which Hinton had envisaged on the Indian Siwalik rodents. The illustrations in
this paper are Mr. Terzi's. I offer my sincerest thanks to the members of the Indian
Geological Survey mentioned above and to Dr. R. J. G. Savage for making this paper
a possibility.

Abbreviations used:  A.M.N.H.—American Museum of Natural History
G.S.I.—Geological Survey of India
Y.P.M.—Yale Peabody Museum
a-p—antero-posterior
mm—millimetres
tr—transverse

Suborder SCIUROMORPHA Brandt 1855
Family CTENODACTYLAE Zittel 1893

Schaub (1958, p. 780) was the first to separate the Tataromyidae as a family of rodents
distinct from the living ctenodactylids. In so doing, he recognized Bohlin (1946) as the
original describer of the family. Lavocat (1961, p. 52) also used the family Tataromyidae, attributing first usage to Bohlin (1946). He included within this family the genera Tataromys, Karakoromys, Africanomys, Sayimys, and Metasayimys. The Tataromyidae together with the Family Ctenodactyloidae he grouped together in the Superfamily Ctenodactylidae. Bohlin (1946), however, never used the name Tataromyidae as a formal, familial designation. He (1946, p. 75) placed the genus Tataromys in the family Ctenodactyloidae and later (p. 132) he said, 'In conclusion, I may say that I can see no serious objection to the hypothesis that Tataromys and Sayimys are closely related forms.' Later (p. 133) Bohlin says, 'The similarity between Sayimys and Ctenodactylus is so great that it seems superfluous to separate the fossils from the living Ctenodactylidae, which may be survivors of the Sayimys line.' Unfortunately, Bohlin then went on (1946, p. 133–134) and used the term 'Tataromyidae' (his quotation marks) when talking about a subfamilial grouping of ctenodactylids. However, nowhere in his 1946 work did Bohlin use the term Tataromyidae as a family unit—distinct from the living ctenodactylids.

Wood (1955, 1965) has recognized the Family Ctenodactyloidae as including both the living genera and those extinct forms placed by Schaub and Lavocat in the 'Tataromyidae.' This procedure is followed here.

Genus Sayimys Wood 1937

Type species. Sayimys perplexus Wood, 1937, p. 73.

Diagnosis. 'Jaw shallow with very heavy masseteric crests and gently sloping coronoid; angle not continuous with lower end of masseteric fossa, but begins to diverge from corpus beneath M$_2$; P$_4$ quadrate with V-shaped loph and postero-external cingulum; molars with anterior V-shaped crests and posterior crest connected to middle of posterior arm.' (Wood 1937, p. 73.)

Included species. S. perplexus, S. sivalensis, and S. obliquidens.

Range. Chinji and Nagri Zones of the Siwalik Series, and Miocone (Taben-buluk) of China. Does not include Sayimys and Metasayimys of Lavocat (1961) for which see below.

Sayimys perplexus Wood

1937 Sayimys perplexus Wood, p. 73

Holotype Y.P.M. 13800, partial left mandible with P$_4$–M$_4$.

Horizon and locality. 'Nagri Zone, Survey of India Map no. 53NE/4, B-6, East of Hari Talyangar' (Wood, op. cit.).

Diagnosis. Larger than Sayimys sivalensis; anterior loph on M$_1$ and M$_2$ bent at midpoint rather than running straight across tooth; metaconid and entoconid more widely separated on M$_2$–M$_3$ than in S. sivalensis.

Description. A thorough description has been given by Wood (1937). The relationships of the two Siwalik species of Sayimys are discussed below under S. sivalensis.
Sayimys sivalensis (Hinton)

1933 Pectinator sivalensis Hinton, p. 622.

Holotype. G.S.I. D284 (register number K16/326), left mandibular fragment with M1–M3.

Horizon and locality. Lower Siwaliks, Chinji Zone, Late Miocene; Chinji Beds, near Chinji, Attock District, Salt Range, Pakistan.


Diagnosis. Smaller than Sayimys perplexus; anterior loph straight, perpendicular to axis of tooth row; hypolophids shorter transversely than in S. perplexus or S. obliquidens; valley between metaconids and entoconids shallow; only faint posterior shelf, or cingulum, on M3, absent on M2.

Description. There is only a small portion of the mandible preserved with the diastema, alveolus for P1, and the ascending ramus missing. The mandible under M2 and M3 is quite shallow. Internally, there is a deep groove under M2 which extends below the posterior root of M2; here it merges into the internal face of the mandible. The
masseteric crest is very prominent and forms a heavy shelf under $M_1$ and the anterior half of $M_2$. The incisor ends below $M_2$ at the point where the internal mandibular furrow ends.

Judging from the roots, $M_1$ is smaller than $M_2$ and $M_3$. $M_2$ is evidently the largest tooth in the series as it is slightly larger than $M_3$. Both $M_4$ and $M_5$ are moderately worn. The anterior borders of both teeth are straight, lacking the central projection seen on the anterior faces of $M_4$–$M_5$ in Sayimys perplexus and S. obliquidens. The entoconid is set close to the metaconid with a rather narrow valley separating these cusps. This results in a more nearly transverse direction for the crest connecting entoconid and protoconid. The valley between the entoconid and hypoconulid passes further into the interior of the tooth than does the metaconid-entoconid valley. On the postero-buccal slope of the hypoconid there is a slightly swollen ridge representing the posterior cingulum but there is no such structure on $M_5$. The hypoconulid is large and the posterolophid broad on both teeth. The valley between entoconid and posterolophid is closed by a low connection from the posterolophid into the slope of the entoconid.

### Measurements in mm

<table>
<thead>
<tr>
<th>Tooth</th>
<th>a-p</th>
<th>Ocular</th>
<th>Transverse</th>
<th>Maximum</th>
<th>Maximum</th>
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<tr>
<td>$M_1$</td>
<td>2-25</td>
<td>1-95</td>
<td>2-30</td>
<td>2-50</td>
<td>2-60</td>
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<tr>
<td>$M_2$</td>
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**Discussion.** This specimen was originally described as a new species of the ctenodactyloid genus Pectinator (Hinton 1933, p. 622). As there were no illustrations accompanying this note, Wood (1937) was unable to compare his material with Hinton’s and described a new genus of rodent, Sayimys perplexus, based upon a jaw fragment with $P_1$–$M_2$. The specimen described by Wood was from the Nagri Zone of the Siwaliks. At the time of his work, Wood was not able to place Sayimys as to family or even suborder because of its peculiar morphology. Bohlin (1946), evidently without consulting Hinton’s paper, recognized that Sayimys was a ctenodactyloid and made extensive comparisons between Sayimys and the Recent Ctenodactylus and Pectinator. Bohlin, of course, knew of Wood’s work but did not refer to Hinton’s brief diagnosis of Pectinator sivalensis.

**Sayimys sivalensis** (Hinton) appears to be directly ancestral to S. perplexus Wood of the Nagri Zone. S. sivalensis is slightly more primitive than S. perplexus in that the masseteric crest does not extend forward under $P_1$ but rather ends under $M_1$, nor does it form as wide a shelf as it does in S. perplexus. The molars of S. sivalensis are lower crowned, have straighter anterior margins, more transversely directed protoconid-entoconid connections, and shallower metaconid-entoconid valleys than those of S. perplexus. In all of these characters, S. sivalensis is more primitive than S. perplexus but it is clearly ancestral to the later species.

There is now general recognition of the ctenodactyloid affinities of Sayimys. That the Siwalik material belongs in Wood’s genus rather than in the living African genus, Pectinator, also appears certain. Sayimys differs from the modern form in having larger and more complex P4 & 4 in possessing molars which are lower crowned and which exhibit a more complex occlusal pattern. Sayimys lower molars are in turn less complex and higher crowned than those of the late Oligocene Karakoromys, Tataromys, and Leptotatoromys. A fourth late Oligocene genus, Yindirtemys (Bohlin 1946), is known
from only a single tooth and cannot be adequately compared with other members of the family. Lavocat (1961) has described two genera of eutradactylids, *Africanomys* and *Metasaymyris*, as well as a new species of *Sayimys*, all from the late Miocene of Morocco. *Africanomys* is clearly distinct from the Asian eutradactylids in the isolated condition of the metacone of the upper molars and the small trigonid basin of the lower molars. No isolated premolars are known for this genus. *Africanomys* and *Sayimys* evidently represent two independent lines of development from a *Tataromys* -like stock. *Metasaymyris* and *Sayimys jebei* (Lavocat 1961) are based upon a total of three isolated teeth and are insensibly known to be compared with other eutradactylids. From Lavocat’s descriptions and illustrations, it appears possible that only a single genus of eutradactylid is actually present in the Beni Mellal fauna and this is *Africanomys*. A third genus, *Dubiomys*, was described by Lavocat from the same fauna and is based upon two teeth. Lavocat (1961, p. 66-67) discussed the similarity of these two teeth to milk premolars of eutradactylids (tataromyids in his sense) as figured by Bohlin (1946, fig. 19). However, Lavocat preferred to consider *Dubiomys* as *Rodentia incertae sedis* because of the distinct anterior tubercule on the occlusal surface. Bohlin (1946) has shown that this tubercule is extremely variable in the eutradactylid *Tataromys* and it could easily have been so in the African eutradactylids as well. I believe *Dubiomys* is probably based on nothing more than two deciduous lower premolars of *Africanomys*.

Dawson (1964) has described an extremely interesting rodent from the late Eocene of Mongolia. She recognized two species, *Advenimus burkei* and *Advenimus bohlini*, and assigned three other jaws to *Advenimus* sp. *Advenimus* was placed with question in the family Sciuravidae while a number of similarities to eutradactylids were pointed out. These include (1) reduced P4; (2) enlarged hypoconulid; (3) increase in size from P4 to M3; and (4) a shallow mandible. *Advenimus* appears to be close to the ancestry of the Ctenodactylidae if not actually in the direct line of descent. From an animal of this type the late Oligocene genera of eutradactylids could have been easily derived. Ctenodactylids evidently arose and first radiated in Asia with the group persisting there until the Pliocene. Sometime during the Miocene a *Tataromys*-like stock migrated into North Africa where it gave rise to *Africanomys*. From this base, the group radiated into the four genera of eutradactylids which are now found living in North Africa. The Asiatic portion of the family evidently did not persist after the Pliocene with the terminal genus, *Sayimys*, playing no part in the ancestry of the African radiation.

**Suborder indet.**

**Family thryonomyidae Pocock 1922**

**Genus paraulacodus Hinton**

*Type species.* *Paraulacodus indicus* Hinton 1933, p. 621.

**Diagnosis.** Upper incisor with two grooves; cheek teeth increase in size from P4-M2; mure complete on P4-M2; metaloph not completely fused into posteroloph on M2; central valley wide on P4-M2, open buccally; ectolophid complete on M2; anteroconid on M2.

**Included species.** Type only.

**Range.** ?Upper Chinji Zone, Siwalik Series, Pakistan.
1933 *Paraulacodus indicus* Hinton, p. 621

*Holotype.* G.S.I. D283, partial right maxillary with P4-M1.

*Hypodigm.* G.S.I. D281, left upper incisor, D282 fragment of right mandible with M2 and the type.

**Text-Fig. 2.** *Paraulacodus indicus*, all approx. x 6. a. External view, P4-M1, G.S.I. D283, holotype. b. Internal view, same. c. Occlusal view, same. d. Posterior view, M2, G.S.I. D282. e. Occlusal view, same. f, g, h. Lateral, medial, and anterior views of upper incisor, G.S.I. D281.

*Horizon and locality.* The type D283 is listed on a sheet sent by the Indian Geological Survey to Dr. Hinton as being unregistered and locality unknown, horizon Upper Chinji?. D282 is also unregistered but the locality is given as near Chinji, Salt Range and horizon as upper Chinji. The incisor, lamentably, is the only specimen catalogued with a register number [K.10110] and the locality is given as 'below Kookar Dhok, Attock District, Salt Range area, Upper Chinji Zone'. There is no basis for assuming that these specimens were associated in any way when collected although they were all
in one vial when I received the collection. Likewise, there is no certainty that these specimens are contemporaneous or from the same approximate horizon.

**Diagnosis.** Same as for genus.

**Description.** The upper cheek teeth, P\(^1\)–M\(^3\), are essentially identical in structure differing primarily in an increase in size from P\(^1\) to M\(^3\). Also, on M\(^3\) there is preserved a short remnant of the metaloph with a very shallow pit between it and the posteroloph. On P\(^1\) and M\(^3\) the metaloph and posteroloph are completely fused. The teeth have three lophs with the anteroloph and protoloph separated by a narrow valley while the protoloph and posteroloph are separated by a wide central valley which opens buccally. The mure is complete on P\(^4\)–M\(^3\) with the narrow lingual valley curving anteriorly behind the protocone as it passes into the tooth.

The lower molar also displays three lophs with the valleys separating the lophs of nearly equal size. The protolophid and hypolophid both run at right angles to the long axis of the tooth. The posterolophid curves from the hypoconid through a distinct hypoconulid around to the base of the entoconid. The posterolophid lies slightly below the level of the protolophid and hypolophid. There is a very faint line of separation between the hypoconid and buccal end of the hypolophid; nevertheless, the buccal valley is completely closed off from the posterior valley. The posterior arm of the protoconid forms most of the ectolophid passing directly posteriorly to fuse with the buccal arm of the hypolophid.

The upper incisor displays two grooves which set off a wide median ridge on the anterior face of the tooth. These grooves are set in equally from the lateral and medial margins of the tooth. Enamel overlaps only slightly onto the side of the incisor. In cross section the tooth is narrowly triangular with the posterior border rounded.

**Measurements in mm**

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<th>a-p</th>
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<td>P(^4)</td>
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<tr>
<td>M(^4)</td>
<td>3.60</td>
<td>3.50–3.20</td>
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**Discussion.** This is the first and only record of the Thryonomyidae, or cane rats, in Asia. The group today is restricted to Africa south of the Sahara and there is only a single living genus with six species. Walker (1964, p. 1069) gives a geologic range of Miocene to Recent in Africa and Pliocene of Europe and Asia for the Thryonomyidae but to my knowledge there is no African record earlier than the Pleistocene and there is no European record. Those genera listed in Simpson (1945) as *Thryonomyidae incertae sedis* are now considered to be members of the Family Rhizomyidae (Wood 1955, 1968).

The identification of a thryonomyid in Asia on the basis of only a few teeth is of course open to question. However, many other Asian-African ties seen in the Siwalik fauna suggest that the presence of cane rats in Asia during the later Tertiary is certainly a possibility to be considered. These faunal similarities coupled with the rather remarkable morphological approach of *Paraalocodidae* to *Thryonomyus* strongly suggest, to my
mind at least, that cane rats were part of the early Pliocene Asiatic fauna south of the Himalayas.

Other than the details of morphological proximity (i.e. the grooved incisors, the three lopped upper and lower cheek teeth, the construction of the mure and ectolophid) little can be said about the relationship of Paralacodon to Thyromys. The Siwalik form is certainly much more generalized in structure with the wide posterior valley of the upper cheek teeth and the wide valleys of the lower molar than is the Recent genus. Nevertheless, there is great overall resemblance between the two genera and Hinton’s (1933) original description of this material as being related to the Recent Thyromys seems probable.

Lavocat (1961) and Wood (1968) would derive the Thyromyidae from the African Phiomiyidae. This certainly seems the most probable ancestry for the group on the basis of available evidence. There is nothing known in the Tertiary fauna of Europe or Asia which could serve as an ancestor for the Family. If one assumes an African origin for the Thyromyidae from some mid-Tertiary phiomyd, then Paralacodon probably moved from Africa to Asia at the time that ctenodactylids were moving in the other direction.

**Suborder HYSTRICOMORPHA Brandt 1855**
**Family HYSTRICIDAE Burnett 1830**
**Genus SIVANCANTHION Colbert 1933**

*Type species.* *Sivanchion complicatus* Colbert 1933, p. 3.

*Diagnosis.* ’An hystricormorph of medium size, considerably smaller than the modern species of *Hystrix* and *Acanthion*. Dental formula 1-0-1-3. Angle of mandibular ramus very strong, as in other Hystricidae. Hystricomorph pattern of the molar enamel complicated by secondary foldings.’ (Colbert, 1933).

**Sivanchion complicatus** Colbert 1933

*Holotype.* A.M.N.H. 19626, a partial left mandible with P3-M3 and a partial right mandible with P4-M3.

*Horizon and locality.* Chinji Zone, level of Chinji Rest House, 4 miles northeast of Chinji Rest House, Salt, Range northern Punjab.

*Description.* As for genus.

*Discussion.* Colbert considered *Sivanchion complicatus* to be a specialized offshoot from the main evolutionary sequence leading to *Acanthion*.

**Genus HYSTRIX Linnaeus 1758**

*Hystrix sivalensis* Lydekker

1878

*Hystrix sivalensis* Lydekker, p. 98

*Holotype.* G.S.I. D96, a partial right mandible P4 (incomplete) and M3-M4.
Horizon and locality. Siwaliks, Punjab. Lydekker (1884) could give no more precise data for the type specimen which was found by Mr. Theobald. Matthew (1929, p. 559) states that the type is from the Middle Siwaliks of Hasanot, Punjab.

Diagnosis. P₄ large; cheek teeth low crowned.

Description. This specimen has been described by Lydekker (1884), Matthew (1929) and Colbert (1935).

**Hystrix** cf. **H. leucurus**

Text fig. 3

1884 *Hystrix sivalensis* Lydekker (in part), p. 110, fig. 5.
1929 *Hystrix cf. leucurus* Matthew, p. 559, fig. 55.
1935 *Hystrix sivalensis* Colbert, p. 72, fig. 32.


Discussion. These specimens are from the Upper Siwaliks and have much higher crowned cheek teeth than those of **H. sivalensis**. Matthew (1929) was evidently the first to recognize that this material was distinct from the earlier **H. sivalensis**. As Matthew states (1929, p. 560), this material may well belong to a distinct species ancestral to **H. leucurus**. Colbert assigned the AMNH lower molar to **H. sivalensis** but this tooth is much higher crowned than is M₃ in **H. sivalensis** and compares favourably with the BM skull and jaws in this character. The illustration prepared by Mr. Terzi for Dr. Hinton of the British Museum skull and jaws is included here as an adequate illustration of this dentition has never been published.

**Suborder MYOMORPHA** Brandt 1855

**Family RHIZOMYIDAE** Miller and Gidley 1918

Specimens belonging to various members of this Family are far the most common of Siwalik rodent fossils. While some genera, e.g. **Kanisamys** and **Protaechyoretes**, are clearly distinct from the modern **Rhizomys**, **Cannamys**, and **Tachyoryctes**, a larger number of specimens are difficult to distinguish from **Rhizomys**. Several genera from the Chinese Tertiary and one from the Siwaliks have been described on the basis of supposed distinctions between the extinct populations and modern species of **Rhizomys**.

These genera are:

**Pararhizomys** Chardin and Young 1931, p. 11. Distinguished from **Rhizomys** by small size, simple molar pattern, and low crowned molars; Pontian of China.

**Tachyoryctoides** Bohlín 1937, p. 43. Distinguished from other rhizomyids by anterior cingulum which is free at its lingual and buccal ends, there being short valleys between the anterior cingulum and metaconid and protoconid. M₃ have a square occlusal outline and the occlusal pattern of M₃ is quite different from that of the other genera; late Oligocene of China.

**Brachyrhizomys** Chardin 1942 (original reference not seen). Distinguished from other rhizomyids by brachydont cheek teeth (Schaub 1938, p. 718), otherwise with pattern as in modern **Rhizomys** (Bohlín 1946, p. 68).

**Rhizomysoides** Bohlín 1946, p. 68. Distinguished from **Rhizomys** by the presence of three main lingual re-entrants in all lower molars; Miocene–early Pleistocene of India and Pakistan.
I have not had an opportunity to see any of the material assigned to *Tachyoryctoides*, *Parahizomys* or *Brachyrhizomys*. For this reason and as these genera are based on material from China which was evidently a distinct and separate faunal province from India, at least during the Pontian (Kurten 1952, p. 31), I have not considered the validity of these taxa in discussion of the various Siwalik rhizomyid species.

The three modern rhizomyid genera inhabit Africa (*Tachyoryctes*) and southeastern Asia (*Rhizomys* and *Cannomys*). *Cannomys* is monotypic while three species of *Rhizomys*
(Walker 1964, p. 867) and fourteen (Allen 1939) or two (Bigalke 1968, p. 276) of Tachyoryctes are presently recognized. The cheek teeth of Tachyoryctes and Cannomys are higher crowned than are those of Rhizomys. The incisors are heavier in Rhizomys than in either Cannomys or Tachyoryctes and the upper incisors of Rhizomys are opisthodont (project nearly vertically) while those of Cannomys and Tachyoryctes are proodont (project forward). In Rhizomys the proximal end of the massive upper incisor lies just above the divergent roots of M\(_2\) and has suppressed any development of a hypsodont first upper molar. Suppression of hypsodonty in an upper molar must of necessity be coupled with suppression of hypsodonty in the opposing lower. Consequently, in Rhizomys but not in Cannomys or Tachyoryctes, the first upper and lower cheek teeth are lower crowned than are the two behind. This character can be seen in many of the fossil specimens and has been quite useful in helping to determine relationships of the extinct forms. Finally there is a considerable difference in the shape of the lower incisor between the three living species of Rhizomys. The lower incisor is nearly equilaterally triangular in R. sinensis; it is greatly compressed transversely in R. pruinatus; and it is massive and nearly triangular in R. sumatrensis. This range of variation of incisor shape is also seen in the Siwalik species.

Two distinct groups of rhizomyids can be recognized in the Siwalik material. One appears to be related to the Recent African Tachyoryctes while the other includes Rhizomyoides and Rhizomys. These two lines of rhizomyids can be recognized as distinct back into the Miocene, Chini Zone, where Kanisamys indicus and Rhizomyoides punjabensis occur together.

I have retained Bohlin's genus Rhizomyoides for one group of the Siwalik rhizomyids. In order to do so, I have had to amend his diagnosis. There is only one feature which consistently distinguishes all fossil species from Rhizomys. This is the presence of three lingual re-entrants on M\(_2\) but not on all the lower molars as he thought. Rhizomyoides was undoubtedly ancestral to Rhizomys and possibly to Cannomys. Kanisamys stands in a similar position to the Recent Tachyoryctes through Protochoryctes. Tachyoryctoides, the oldest known rhizomyid may occupy an ancestral position for all later rhizomyids but there is a considerable gap between Tachyoryctoides of the upper Oligocene and Rhizomyoides and Kanisamys of the upper Miocene. No new species of rhizomyids are added to those already described. However, the full description of the specimens available to Hinton does add significantly to our knowledge of the Siwalik rhizomyids.

Genus rhizomyoides Bohlin 1946

*Type species.* Rhizomys sivalensis (Lydekker) 1884.

*Emended diagnosis.* Three main lingual re-entrants in M\(_2\).


*Range.* Chini, Nagri and Pinjar Zones of the Siwalik series, Miocene to Pleistocene.

**Rhizomyoides sivalensis** (Lydekker)

1884 *Rhizomys sivalensis* Lydekker, p. 106.
1933 *Rhizomys lydekkeri* Hinton, p. 621.
1946 *Rhizomyoides sivalensis* (Lydekker) Bohlin, p. 68.
b and c. Lateral and occlusal views, LMe-M5, × 7.

*Holotype.* G.S.I. D97, partial left mandible with M2-M3 (figured by Lydekker, 1884, fig. 1, p, 106).

*Referred specimens.* G.S.I. D275 (formerly D97a) partial right mandible with M1-M2 and D276 (formerly D97b) partial right mandible with M3-M4, D277, partial skull and jaws with R and L M1/M3, BM 15925, type of *R. lydekkeri*, partial right mandible with M2-M3, 15926 partial right mandible with M3, 15927, partial left mandible with M1-M2 and 15927a, two isolated molars.

*Horizon and locality.* Probably Middle Siwaliks for the type. The G.S.I. registry number for the type and all other specimens except D277 is H.T. 17 with locality given as Haritalyangar, Simla Hills. D277 is listed as from Assnot, Punjab, Middle Siwaliks. The BM specimens are described (Lydekker 1885, p. 233–334) as being from the Pliocene.
of the Siwalik Hills. In sum all the specimens may be from the Nagri Zone, Middle Siwaliks.

*Emended diagnosis.* Medium sized; mandible rather shallow and thin; incisors only slightly deeper than wide; molars hypsodont; anterior and central lingual re-entrants confluent internally on M₂ only during early wear stages; anterior lingual re-entrant of M₃ with anterior and posterior arms.

*Description.* The mandible is rather shallow under M₁–M₃ in D277 but is deeper in the in the specimens from Haritalyangar. The masseteric ridge is also more swollen on the mandibles from Haritalyangar than on those from Atnot. There are also slight dental differences between the specimens from the two localities. These include somewhat larger overall size and greater reduction in the lingual re-entrants on M₁–M₃ in the Haritalyangar material. All of these characters suggest that the type and other
specimens from Haritalyangar, listed together under the G.S.I. registry number H.T. 17, are slightly younger than the associated partial skull and jaws from Asnot.

Other than the slight size difference and reduction in the length of the lingual re-entrants, the molars of all specimens are quite similar. They are moderately hypsodont with M₄ having three lingual re-entrants while M₃ and M₂ have two. The small anterior fossettid seen in M₋₋₋₋₋₋ in text-fig. 5, has been isolated from the end of the anterior lingual re-entrant. At advanced wear stages there are three isolated internal fossettids on M₄ but the anterior two of these are both derived from the anterior lingual re-entrant, not from two separate lingual re-entrants.

The upper cheek teeth have their primary buccal fossettids, mirroring the condition seen in M₋₋₋₋₋₋. The crown height of the molars is shown in text-fig. 4. M₁ is longer than either M₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋₋_-
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those represented in the material before me . . . . In fact the referred specimen D287 is somewhat smaller (Table 1) than the type. *Rhizomyoides punjabiensis* is a small, generalized rhizomyid and could have been ancestral to the later Siwalik species which differ from it primarily in size and degree of hypsodonty. *R. punjabiensis* is easily distinguished from *Kaulisamy indica*, the only other contemporary rhizomyid, by the absence of distinct transverse ridges and intervening valleys, larger size, and lower crowned M₃-M₄. These two lines of rhizomyid development may have shared a common ancestor sometime during the middle Miocene.

**Text-fig. 6.** *Rhizomyoides nagrii*, G.S.I. D273, holotype. a and b. Lateral and medial views of the mandible. ×2. Occlusal view, M₃-M₄. × 5.

*Rhizomyoides nagrii* (Hinton)

Text-fig. 6

1933 *Rhizomyys nagrii* Hinton, p. 621.

**Holotype.** G.S.I. D273, a partial left mandible with M₃-M₄ slightly broken.

**Referred specimens.** G.S.I. D285, partial left mandible with part of M₃ and M₄; Y.P.M. 13805, partial right and left mandible with M₃-M₄.

**Horizon and locality.** Type from Middle Siwaliks, Nagri Zone, near Haritalyangar, Simla Hills, India; referred specimens also from the Middle Siwaliks, Nagri Zone, with D285 from about six furlongs SSW of Kaulial, Attock District, Punjab and the Y.P.M. specimens from ½ mile N of Danger, Survey of India Map No. 53 A/NE, B-6 (Wood 1937, p. 64).

**Emended diagnosis.** Larger than *Rhizomyoides punjabiensis* but smaller than all other species of *Rhizomyoides* (Table 1); mandible heavy and deep in relation to molar size; incisor considerably deeper than broad; cheek teeth mesodont; three lingual re-entrants on M₃, two on M₄.

**Description.** Wood (1937, p. 65–66) described two rhizomyid jaws which in the absence of an adequate description of the type specimen by Hinton, he could only provisionally
BLACK: SIWALIK RODENTS

refer to *R. nagrit*. The type jaw and dentition (D273) agree in most respects with the description and figures given by Wood. The only noticeable difference is one of size, with the type specimen and a second referred mandible (D285), both being about 16% smaller than the two mandibles in the Yale Collection.

The mandible is quite deep in relation to cheek tooth length. In *R. nagrit* the ratio depth of mandible to alveolar length of M₁–M₃ is greater than 1 (1:14) while in *R. punjabiensis* it is less than 1 (0:75); this ratio is higher in *R. nagrit* than in any other species of *Rhizomyoides* or *Rhizomys*. This suggests that initial selection was for increased size of the mandible, possibly to accommodate early increase in incisor depth and overall size. Once a certain optimum size of the mandible had been achieved then selection acted to increase the area of occlusal surface of M₁–M₃ bringing the depth of mandible—alveolar length of M₁–M₃ relationship back closer to or slightly under one (Table 1).

The cheek teeth are badly worn in all specimens except D285 in which only M₃ is preserved. In the worn condition (Wood 1937, figs. 1–2) there are three lingual re-entrants on M₂ and two on M₃. When unworn the main valley between the protolophid and mesolophid on M₃ is set off from a small, shallow pit at the inner margin of the tooth. With wear a small fossettid would develop briefly in this region.

The lower incisor is deeper than in *R. punjabiensis*. Its anterior face is slightly rounded with the enamel extending well around on to the lateral face but just lapping over on to the medial surface.

Discussion. *Rhizomyoides nagrit* can be derived quite easily from *R. punjabiensis* through greater increase in jaw size over tooth length. In occlusal pattern the two species are very similar with *R. nagrit* having somewhat higher crowned teeth and hence more persistent fossettids. I do not believe that *R. nagrit* was ancestral to any of the latter species of *Rhizomyoides*.

*Rhizomyoides pilgrimi* (Hinton)

Text-fig. 7

1933 *Rhizomys pilgrimi* Hinton, p. 621.

Holotype. G.S.I. D278, partial right mandible with M₂–M₃.

Referred specimens. G.S.I. H.T. 6, partial left mandible with M₁; M₂–M₃; G.S.I. D286, partial right mandible with M₁–M₃.

Horizon and locality. Type from Middle Siwaliks, Nagri Zone. Haritalyangar, Simla Hills, India. Field number of the referred specimens is K21/619 but no horizon or locality is recorded. D286 bears field number K23/329, and is listed as being from the Upper Siwaliks, near Malukal, Attrock District.

Emended diagnosis. Largest species of *Rhizomyoides*; M₃ as long as wide; anterior and central lingual re-entrants of M₃ confluent internally; molars moderately hypsodont; lower incisor much deeper than broad; mandible quite deep but not thick in relation to overall size.

Description. All three specimens exhibit almost exactly the same dental pattern with the (?) younger specimen, D286, being slightly smaller than the two jaws from the Nagri Zone. The mandible is quite deep. The masueteric crest terminates below the
posterior end of \( M_1 \). This crest is heavy under \( M_2 \) but merges into the lower portion of the ascending ramus posteriorly. The coronoid portion of the ramus rises very steeply from the alveolar level of the jaw between \( M_2 \) and \( M_3 \).

\( M_1 \), as preserved, is considerably narrower than \( M_2-M_3 \) and is lower crowned. \( M_2 \) and \( M_3 \) are both longer than they are wide. The three lingual and single buccal re-entrants of \( M_2 \) are of equal length with the anterior and central lingual valleys confluent internally at the earliest wear stages. On \( M_3 \) the buccal re-entrant and the posterior lingual re-entrant are joined to form a single transverse valley during the early wear stages. The anterior lingual re-entrant of \( M_4 \) sends a very short and shallow spur posteriorly towards the centre of the occlusal surface. After moderate wear, two lingual and one buccal re-entrants are seen on \( M_4 \).

The lower incisor is large and much deeper than wide. The anterior face of the incisor is flat and the lateral face is slightly convex. Enamel is restricted to very limited overlap on the lateral and medial surfaces.

**Discussion.** *Rhizomyoides pilgrimi* is one of the most specialized species of the genus, combining large size with a dental pattern which is little changed from that of *Rhizo-**
**myoides nagrii**. If the age given for D286 is correct and the specimen is indeed from the Upper Siwaliks, there was essentially no change in this species from Pliocene to early Pleistocene time. In this case, *R. pilgrimi* could not have been ancestral to *R. pinjoricus* nor to *Rhizomys* for in both reduction of lingual re-entrants on *M*₂ has taken place.

**Rhizomyoides pinjoricus** (Hinton)

Text-fig. 8

1933 *Rhizomys pinjoricus* Hinton, p. 621.

*Holotype*. G.S.I. D278, partial right mandible with *M*₁–*M*₃.

*Referred specimen*. G.S.I. D280, partial right and left mandible with *M*₂–*M*₃.

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**TEXT-FIG. 8. Rhizomyoides pinjoricus, G.S.I. D278, holotype. a and b. Lateral and medial views of the mandible, ×2. c. Occlusal view *M*₂–*M*₃, ×5.**

**Horizon and locality.** All specimens from Upper Siwaliks, lower Pinjor Zone, early Pleistocene, Simla area, India.

**Emended diagnosis.** Between *Rhizomyoides nagrii* and *R. sivalensis* in size (Table 1); *M*₂ wider than long; central and posterior re-entrants of *M*₃ quite short; anterior lingual re-entrant and buccal re-entrant most prominent on *M*₃, only one present on *M*₂; lower incisor essentially equilaterally triangular; mandible quite thick but not deep in relation to overall size.

**Description.** The mandible of *Rhizomyoides pinjoricus* is the most massive of all species of the genus. It is quite thick through the region of the massteric crest, as thick as the mandible of *R. pilgrimi*, but it is much shallower under *M*₃ than is the jaw of *R. pilgrimi*. The mandibles of *R. pinjoricus* thus appear heavy and stout when compared with those of other species of the genus. There is no distinct massteric crest on either of the jaws referred to this species.

*M*₂ is appreciably wider than long and *M*₃ is nearly square in occlusal outline. Both
teeth give the impression of antero-posterior compression when compared with other species of the genus. Probably as a result of this trend towards wider molars, there has been selection for reduction in the number of re-entrants and emphasis on elongation of those remaining. On $M_2$, there is a long anterior fossettid, isolated from a lingual re-entrant, and a long buccal re-entrant which, in D280, has nearly fused with a very small lingual, medial fossettid, the remnant of a small central, medial re-entrant. There is a second, small lake, postero-internal to the buccal valley, which was isolated from the postero-lingual re-entrant. Thus, the original three lingual re-entrants which are so well developed in other, earlier species of Rhizomyoides, have been reduced to one major anterior re-entrant and the two short, shallow central and posterior valleys. On $M_3$, there are only two long transverse re-entrants remaining, one arising from the buccal side of the tooth and one from the lingual side.

The lower incisor is as wide as deep. The anterior face is flat with the enamel overlapping the lateral and medial faces equally. In cross-section the incisor has the shape of an equilateral triangle.

Discussion. Rhizomyoides pinjoricus is closer in dental morphology to species of the Recent Rhizomyidae than is any other species of Rhizomyoides. R. pinjoricus is not as advanced as Rhizomyidae in that a vestigial third lingual re-entrant is present on $M_2$. This re-entrant has been greatly reduced in size, however, over the condition found in earlier species of Rhizomyoides. In this regard, R. pinjoricus, if not directly ancestral to Rhizomyidae, certainly reflects a stage through which the ancestors of Rhizomyidae must have passed. As indicated in text-fig. 11, R. pinjoricus probably evolved from R. sivalensis.

Genus Kaniasamy Wood 1937

Type species. Kaniasamy indicus Wood 1937, p. 66.

Emended diagnosis: Molars low crowned to mesodont; lower molars essentially four-lophed; posterior arm of protoconid forms central loph; anterior cingulum of $M_1$ large, bulbous; $M_3$ large.

Included species. K. indicus and K. sivalensis.

Range. Chinji and Nagri Zones of the Siwalik Series.

Kaniasamy indicus Wood

Text-fig. 9

1933 Theridamys sp. Hinton.
1937 Kaniasamy indicus Wood.

Holotype. Y.P.M. 13810 right mandible with $M_2$-$M_4$.

Referred specimen. G.S.I. D271, fragment of left mandible with $M_2$-$M_3$.

Horizon and locality. The type from 'Chinji Zone, Survey of India Map No. 43 D/6, B–1, South of Chinji' (Wood 1937, p. 68). The referred specimen from Lower Siwaliks, Chinji Zone, Field No. K16/326 near Chinji, Attock District, Salt Range, Pakistan.

Description. The present specimen is slightly more worn than the type of Kaniasamy indicus (Wood 1937). However, in size and crown pattern the two specimens are in
near perfect agreement. The last two lower molars in both specimens show an occlusal pattern of four crests. These are somewhat better developed in the referred specimen, particularly on the M₄, due to its more advanced stage of wear. There is no indication of the short lingual and buccal portions of the anterior cingulum on the referred specimen although these can be distinguished on the type. In the more worn specimen, the posterior protoconid arm has fused with the internal slope of the elevated lingual wall of both M₃ and M₄. The posterior protoconid arm and the hypolophid are clearly separated by a narrow fossettid on M₃–M₄ and the hypolophid and posterior crest are also separated by slightly larger and deeper fossettids on both teeth.

Measurements are given below for both the type and the referred specimen. Wood (1937, p. 73) gives measurements for the type which were taken on the occlusal surface of the teeth. On M₄ particularly this measurement is somewhat misleading as the occlusal surface measures 1.95 mm, yet the maximum length of M₄ below the occlusal surface is 2.30 mm. All measurements given here are for the maximum dimensions.

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Kanisamys sivalensis Wood

1937  *Kanisamys sivalensis* Wood, p. 70.

Holotype. Y.P.M. 13801, partial left mandible with M₃–M₄.

Horizon and locality. 'Nagri Zone Survey of India No. 53 A/NE, B-6, east of Hari Talyangar' (Wood 1937, p. 70).

Emended diagnosis. Larger than *Kanisamys indicus*; teeth moderately high crowned (mesadont); molar pattern lophate; buccal arm of anterior cingulum absent on M₄–M₅.

Description. This species has been fully described by Wood (1937). Discussion of the relationships of *K. sivalensis* and *K. indicus* are given after the description of *Protoachyoryctes* below.

Genus PROTACHYORYCITES Hinton 1933


Diagnosis. Molars high crowned; larger than *Kanisamys* approaching size of *Tachyoryctes*; crown pattern reduced to essentially three lophs; M₃ longer than M₄ with 3 distinct lingual re-entrants; posterior columns of M₄–M₅ and anterior column of M₆
not completely isolated during early wear stages as in *Tachyoryctes*; re-entrants on M₃-M₄ pass directly into centre of the teeth, not angled anteroposteriorly.

*Included species.* Type only.

*Range.* Earliest Pleistocene of Pakistan.

*Protachyoryctes tatroti* Hinton

Text-fig. 10

1933 *Protachyoryctes tatroti* Hinton, p. 620.

*Holotype.* G.S.I. D272, partial right mandible with m₁-m₃.

*Hypodigm.* Type only.

*Horizon and locality.* Tatrot State, earliest Pleistocene, Tatrot, Salt Range, Pakistan.

*Diagnosis.* As for the genus.

*Description.* The main body of the mandible and part of the ascending ramus are preserved with the diastema anterior to M₁ broken and lost. The masseteric fossa is very poorly defined along its ventral border but appears to begin below the posterior half of M₂. The masseteric crest runs posteriorly and slightly ventrally. Below the posterior half of M₁ and most of M₂ the crest is quite strong but fades into the posterior part of the mandible behind M₂. Anterior to M₂, the incisor lies medial to the cheek teeth. As the incisor passes posteriorly, it curves laterally and terminates in a bulbous process.
on the ascending ramus above the alveolar level of the cheek teeth. The mandible is rather shallow but thick beneath M₃.

The lower molars are larger and somewhat higher crowned than those of *Kanisamys sivalensis*. However, when the relative sizes of the two species are considered, the teeth of *Protaechyonycetes tatroli* are only slightly higher crowned than those of the earlier *Kanisamys sivalensis*. *Protaechyonycetes tatroli* appears to be of nearly the same size as *Tachyonycoides* (Bohlin 1937, p. 44) but differs greatly from the Chinese form in details of M₁–M₃ occlusal pattern, and particularly in the size of M₂ in relation to the size of

M₂, M₃ is composed of three lophs which slant across the tooth from the outside to the inside anteroposteriorly. The two buccal re-entrants are both rather shallow and do not extend down to the base of the crown. The two lingual re-entrants pass further across the occlusal surface of the tooth but are also rather shallow and would soon be obliterated on the lingual face of the tooth. Wear has proceeded far enough on M₄ to completely destroy the small fossettid seen on the M₄ of *Kanisamys sivalensis*. The posterior protococonid arm (pseudo-mesolophid of Wood) has also fused into the entoconid-hypoconid loph so that there is a single rather wide lingual lophid on M₄. In occlusal outline the first lower molar is much narrower and more elongate than are M₂ and M₃.

The second lower molar is almost square in its occlusal outline. There are three lophs present on the occlusal surface separated on the lingual half of the tooth by two narrow but shallow valleys. The buccal re-entrant is also quite narrow but extends down the entire buccal face of the tooth. On M₃ there is still a faint indication of the posterior protococonid arm as well as the hypoconid-entoconid crest. With slightly further wear these two crests would fuse into the single, central loph of M₃.

The third lower molar is considerably longer than M₁ or M₂; however, at the present state of wear, the occlusal surface does not give the appearance of such length. Whereas the three transverse lophs of M₁–M₃ are separated lingually, on M₄, the anterior and
central lophs are fused along the lingual margin. There is a long curving valley which
separates the anterior and medial lophs on M₄. In addition, there are two small fossettids,
one in the middle of the anterior loph just internal to the metacristid and the second,
quite small, on the median loph just internal to the entoconid. As on M₃, the buccal
re-entrant is open almost to the base of the crown.

The lower incisor is smaller than one might expect considering the size of the cheek
teeth. It is narrowly triangular in cross-section with a rounded anterior edge. The enamel
extends on to about one-fifth of the medial surface of the tooth. The lateral surface of
the incisor is more gently rounded and the enamel extends about one-third of the way
on to this surface. The enamel is very thin throughout and along the anterior surface
bears a very low, narrow ridge along the mid-line of the tooth.

Affinities. The specimens described by Wood (1937) as Kanisamys indicus and Kanisamys
sivalensis together with the specimen which Hinton referred to as Protachyoryctes
tatroti form what appears to be a direct phylectic sequence. Kanisamys indicus is known
from the Chinji and is hence the oldest species in this sequence. It is also the smallest
and has the lowest crowned cheek teeth. The anterior cingulum of M₁ and M₂ is still
quite prominent on Kanisamys indicus as is the posterior protoconid arm or pseudomesolophid.
Even at the most advanced wear stages, the posterior protoconid arm
would not be completely fused with the entoconid-hypoconid crest as it is in later
members of this lineage. Kanisamys sivalensis of the Nagri Zone is considerably higher
crowned than Kanisamys indicus but the crosslophs on M₁–M₄ are still prominent.
There is still a basin, or small fossettid, between the metaconid and anterior cingulum
on M₁–M₄. The buccal arm of the anterior cingulum is no longer evident on M₃–M₄,
as it is in the earlier species. The posterior protoconid arm is still distinct and separated
by a deep valley from the entoconid-hypoconid crest. The posterior cingulum forms a
wall, slightly separated from the entoconid lingually on M₄ but fused with the ento-
conid on M₃. This is quite similar to the conditions seen in Kanisamys indicus. The last
known member of this sequence, Protachyoryctes tatroti, has molars which are higher
crowned than those of Kanisamys sivalensis. At this stage the posterior protoconid arm
and anterior cingulum of M₁–M₄ are almost completely fused, forming, with the posterior
cingulum, three main transverse crests. Thus, from a basically four-loped condition in
the earliest member, Kanisamys indicus, the sequence ends in a three-loped condition
in Protachyoryctes tatroti. Tachyoryctoides (Bohlin, 1937) does not appear to be closely
related to either Kanisamys or Protachyoryctes. Bohlin (1946, p. 69) suggests that
Tachyoryctoides may be close to the ancestry of Tachyoryctes. The occlusal pattern of
Tachyoryctoides obtruschevii (Bohlin 1937, fig. 103) and the short M₁ of that species
do not resemble the conditions found in modern Tachyoryctes.

All three Siwalik species of this lineage show a very indistinct masseteric fossa but a
prominent boss below the posterior end of M₁ and most of M₄. In addition, all three
have an incisor which begins medial to M₁, passes under M₂ and lateral to M₃, rising
to a distinct, bulbous expansion on the lateral surface of the ascending ramus. The
mental foramen is preserved on the mandibles of Kanisamys sivalensis and Protachyoryctes
tatroti. In these two forms it lies well below the masseteric boss, almost directly under
the anterior root of M₄.

In all characters of the mandible these genera are quite close to the condition seen
in *Tachyoryctes* today. In the living Bamboo rats, there is no distinct masseteric fossa but a very heavy, enlarged boss which lies under the posterior end of the M₁ and M₂. In the modern species the incisor passes from the medial side of the jaw at its anterior end under the cheek teeth and terminates lateral to and above M₂ in a distinct bulbous expansion on the ascending ramus. The mandibles of the Siwalik forms show many more resemblances to the modern Cane rats of the genus *Tachyoryctes* than they do to

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**TEXT-FIG.** 11. Stratigraphic positions and suggested relationships of Siwalik rodents.

those of the modern Asian *Rhizomys*. In *Rhizomys* and *Rhizomyoides* there is a distinct masseteric fossa delimited along its inferior border from below M₁ all the way to the angle. There is no distinct masseteric boss in *Rhizomys* as there is in *Tachyoryctes* and in the Siwalik material. The course of the incisor is similar in *Rhizomys* and *Tachyoryctes*, although it begins slightly more lateral in *Rhizomys* than it does in *Tachyoryctes*. Finally, the jaws are much heavier and more massive in *Rhizomys* both relatively and absolutely than they are in *Tachyoryctes* and than they are in *Kanisamys* and *Protachyoryctes*.

The molar patterns of *Kanisamys* and *Protachyoryctes* are much closer to those of the modern *Tachyoryctes* than they are to *Rhizomys*. Some specimens of *Rhizomyoides* from the Siwaliks as well as Recent specimens of *Rhizomys* show that M₃ and M₄ are wider in relation to their length than they are in the *Tachyoryctes* group. The cross valleys on the molars of *Tachyoryctes*, *Protachyoryctes* and *Kanisamys* are much more persistent than are those of various contemporaneous species of *Rhizomyoides* and *Rhizomys*. In *Tachyoryctes*, the buccal valley has joined the posterior lingual valley to form a continuous cross connection isolating a posterior column on M₂ and M₄ during
early wear stages. On M₂, these two valleys are very nearly confluent but the enamel has not yet broken through so that the posterior loph is still narrowly joined to the central part of the tooth. On M₃, but not on M₁-M₂ of *Tachyoryctes*, the anterior internal column, or metacoid, of M₃ has been isolated with the anterior lingual valley swinging completely around the metacoid and opening on to the anterior face of the tooth. Thus, on M₃ there are three isolated lophs at least at some stages of wear. On M₃ there are two anterior lophs joined at the protoconid and an isolated posterior loph. On M₄ there are three lophs all of which are still confluent along the centre of the tooth.

In *Kanisamys* and *Protachyoryctes*, none of the lophs or columns have been isolated on M₂, M₃ or M₄. However, in *Protachyoryctes*, the buccal and posterior lingual valleys of M₃ are quite close and it is quite easy to visualize a succeeding stage in which they become fused and the posterior loph of M₃, isolated from the rest of the crown. This is also true for the posterior loph of M₃ and with the continued expansion of the anterior valley, both anteriorly and lingually around the metaconid, the metaconid would be isolated as a small antero-internal column. This isolation of distinct columns on the lower molars until occlusal wear is well advanced is characteristic of *Tachyoryctes* and somewhat different from the condition seen in *Rhizomys*. In the latter genus the outer margins of the transverse valleys are shallow and there is a tendency toward the formation of internal fossettids on the occlusal surface with the entire outer margin of the tooth ringed with enamel.

One final bit of evidence suggests the occurrence in the Siwaliks of both the African *Tachyoryctes*-like lineage and the Asian *Rhizomys* lineage. In the Chinji, Nagri and Tatrot Zones of the Siwaliks several species of *Rhizomyoides* (see above) occur together with *Protachyoryctes* and *Kanisamys*. These species are clearly much closer to the modern *Rhizomys* than to any other rhizomyid and they are quite different in morphology from the *Kanisamys indicus*—*Kanisamys sivalensis*—*Protachyoryctes tatroti* sequence. It seems relatively certain that African Bamboo rats of the family Rhizomyidae were present in India together with the more expected, Asian rhizomyids of the genus *Rhizomys*.

Family muridae Gray 1821
Genus rattus frisch 1875
Rattus colberti (Lewis)

1939 Mastomys colberti Lewis, p. 341.

Horototype. Y.P.M. 13798, partial skull with left M₁-M₃.

Horizon and locality. Nagri Zone ‘One half mile south of Tarzan village, northwestern Bilaspur Kehloor State, Punjab, India. Yale North India Expedition. Palaeontological Locality No. 41; Survey of India Map No. S 3A/NE, grid B-6’ Lewis (1939).

Diagnosis. An average sized species of *Mastomys* with relatively short palatine foramina, occurring in the lower Pliocene deposits of India’ (Lewis 1939).

Description. Lewis has given a complete description of this specimen.

Discussion. I have not seen the specimen. The illustrations provided by Lewis give the impression of a more advanced murid than one might expect to find in the Nagri Zone.
but the fossil history of the Muridae is very poorly known. Most recent authors consider *Mastomys* to be a synonym of *Rattus* and I have followed this classification here.

**Genus Nesokia Gray 1831**

*Nesokia* cf. *N. hardwicki* (Gray)

1884  *Mus (?)* sp. Lydekker, p. 126.
1885  *Nesokia* sp. (cf. *N. hardwicki*) Lydekker, p. 226.

**Specimen.** B.M. 16529 A, partial right mandible with M₃.

**Horizon and locality.** Upper Siwaliks, locality unknown.

**Discussion.** This specimen has never been adequately described nor compared with other murid material.

**REFERENCES**


COLBERT, H. B. 1933. Two new rodents from the Lower Siwaliks Beds of India. *Amer. Mus. Novit.*, 633, 1–6, 2 figs.


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