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, ctenodactylids and thryonomyids; 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 *Rhizomys* and *Kanisamys-Protachyoryctes* to *Tachyoryctes*. The Asian and African rhizomyids and ctenodactylids are compared, and *Paraulacodus incidus* is recognized as the only thryonomyid 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 Faukner who, together with Lt. P. T. Cautley, began publishing on Indian fossil vertebrates in the 1830s. Their series entitled *Fauna Antiqua Sivalensis* 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. Pilgram, 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 materal was indicated by Hinton's (1933) short note in the *Annals and Magazine of Natural History* in which he very 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 two-fold. 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

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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 ilustrations 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 accompanying 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 considered 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 personally 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 monograph 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 CTENODACTYLIDAE 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*, *Africanonmys*, *Sayimys*, and *Metasayimys*. The Tataromyidae together with the Family Ctenodactylidae he grouped together in the Superfamily Ctenodactyloidae. Bohlin (1946), however, never used the name Tataromyidae as a formal, familial designation. He (1946, p. 75) placed the genus *Tataromys* in the family Ctenodactylidae 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 Ctenodactylidae 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 Miocene (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_3.

Horizon and locality. 'Nagry 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*.

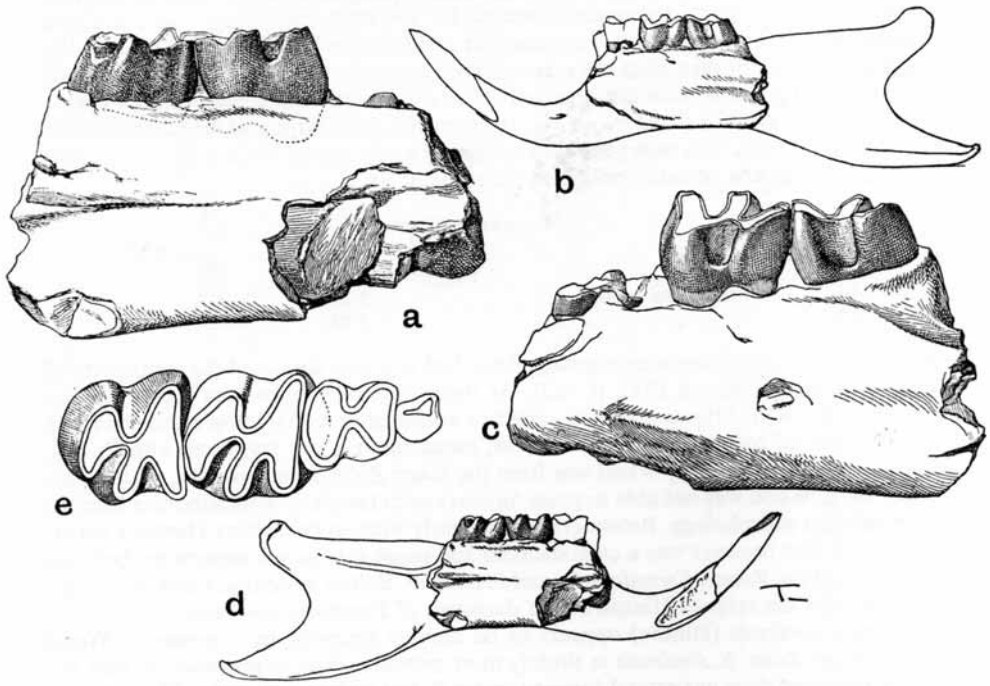
Sayimys sivalensis (Hinton)

Text-fig. 1

1933 *Pectinator sivalensis* Hinton, p. 622.

Holotype. G.S.I. D284 (register number K16/326), left mandibular fragment with M_2–M_3.

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



TEXT-FIG. 1. *Sayimys sivalensis*, G.S.I. D284, Holotype. a. Internal view of mandible, ×8. b. External view of mandible reconstructed, ×3. c. External view of mandible, ×8. d. Internal view of mandible reconstructed, ×3. e. Occlusal view M_2–M_3 (P_4–M_1 hypothetical), ×8.

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 M_2, absent on M_3.

Description. There is only a small portion of the mandible preserved with the diastema, alveolus for P_4 and the ascending ramus missing. The mandible under M_2 and M_3 is quite shallow. Internally, there is a deep groove under M_3 which extends below the posterior root of M_2; 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_2 and M_3 are moderately worn. The anterior borders of both teeth are straight, lacking the central projection seen on the anterior faces of M_1–M_3 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_3. 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

M_2	a–p	occlusal	2·25	maximum		2·60
M_3		,,	1·95	,,		2·30
M_2		transverse maximum		2·25	2·30	
M_3		,, ,,		2·30	2·10	

Discussion. This specimen was originally described as a new species of the ctenodactylid 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_4–M_3. 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 ctenodactylid 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_4 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 do 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 ctenodactylid 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 $P^{4/4}$ and 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 ctenodactylids, *Africanomys* and *Metasayimys*, as well as a new species of *Sayimys*, all from the late Miocene of Morocco. *Africanomys* is clearly distinct from the Asian ctenodactylids 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. *Metasayimys* and *Sayimys jebeli* (Lavocat 1961) are based upon a total of three isolated teeth and are insufficiently known to be compared with other ctenodactylids. From Lavocat's descriptions and illustrations, it appears possible that only a single genus of ctenodactylid 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 ctenodactylids (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 ctenodactylid *Tataromys* and it could easily have been so in the African ctenodactylids 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 ctenodactylids were pointed out. These include (1) reduced P_4; (2) enlarged hypoconulid; (3) increase in size from P_4 to M_3; 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 ctenodactylids 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 ctenodactylids 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 P^4–M^2; mure complete on P^4–M^2; metaloph not completely fused into posteroloph on M^2; central valley wide on P^4–M^2, open buccally; ectolophid complete on M_2; anteroconid on M_2.

Included species. Type only.

Range. ?Upper Chinji Zone, Siwalik Series, Pakistan.

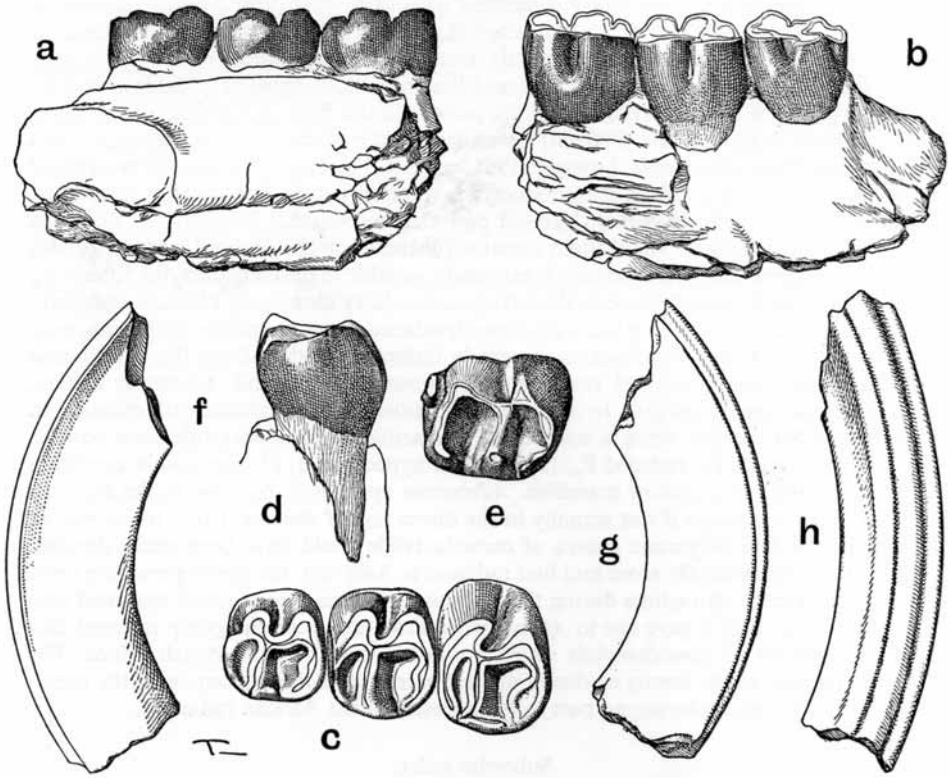
Paraulacodus indicus Hinton

Text-fig. 2

1933 *Paraulacodus indicus* Hinton, p. 621

Holotype. G.S.I. D283, partial right maxillary with P^4–M^2.

Hypodigm. G.S.I. D281, left upper incisor, D282 fragment of right mandible with M_2 and the type.



TEXT-FIG. 2. *Paraulacodus indicus*, all approx. ×6. a. External view, P^4–M^1, G.S.I. D283, holotype. b. Internal view, same. c. Occlusal view, same. d. Posterior view, RM_2, 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 [$K^{16/305}$] 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^4–M^2, are essentially identical in structure differing primarily in an increase in size from P^4 to M^2. Also, on M^2 there is preserved a short remnant of the metaloph with a very shallow pit between it and the posteroloph. On P^4 and M^1 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^2 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 end 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

	a–p	tr
I^1	3·20	2·10
P^4	2·55	2.95
M^1	2·55	3.45
M^2	2·95	4·00
M_3	3·60	3·50–3·20

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 *Paraulacodus* to *Thryonomys* 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 lophed upper and lower cheek teeth, the construction of the mure and ectolophid) little can be said about the relationship of *Paraulacodus* to *Thryonomys*. 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 *Thryonomys* seems probable.

Lavocat (1961) and Wood (1968) would derive the Thryonomyidae from the African Phiomyidae. 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 Thryonomyidae from some mid-Tertiary phiomyid, then *Paralaucodus* 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. Sivancanthion complicatus Colbert 1933, p. 3.

Diagnosis. 'An hystricomorph 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).

Sivancanthion complicatus Colbert

1933 *Sivancanthion complicatus* Colbert, p. 3.

Holotype. A.M.N.H. 19626, a partial left mandible with P_4–M_2 and a partial right mandible with P_4–M_2.

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

Diagnosis. As for genus.

Description. This material has been adequately described by Colbert.

Discussion. Colbert considered *Sivancanthion 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 P_4 (incomplete) and M_1–M_2.

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 Hasnot, Punjab.

Diagnosis. P_4 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.

Specimens: B.M. 15923, immature skull and jaws; A.M.N.H. 19909, LM_1.

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 M_1 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 by far the most common of Siwalik rodent fossils. While some genera, i.e. *Kanisamys* and *Protachyorctes*, are clearly distinct from the modern *Rhizomys*, *Cannomys*, 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*.

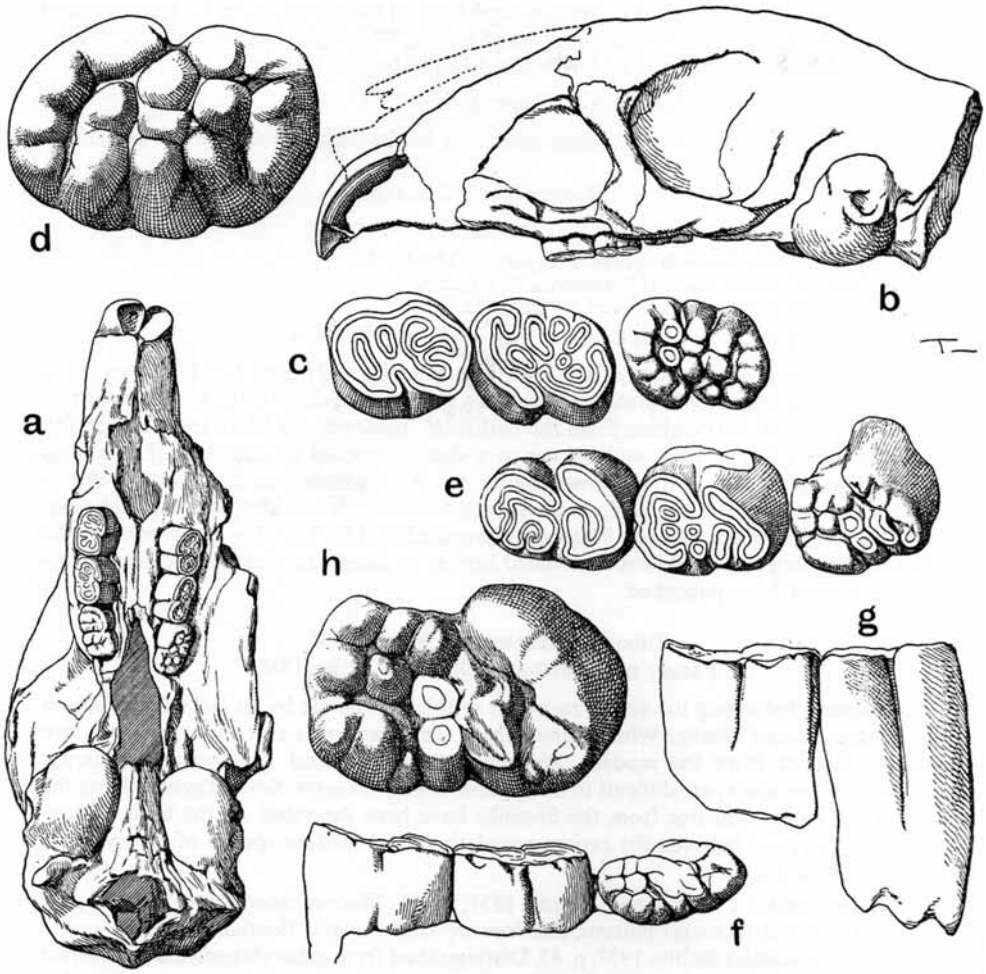
These genera are:

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

Tachyoryctoides Bohlin 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. M_1–M_3 have a square occlusal outline and the occlusal pattern of M_1 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 brachyodont cheek teeth (Schaub 1958, p. 718), otherwise with pattern as in modern *Rhizomys* (Bohlin 1946, p. 68).

Rhizomyoides Bohlin 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.



TEXT-FIG. 3. *Hystrix* cf. *H. leucurus*, B.M. 15923. a. Ventral and b, lateral views of skull. c. d, and e. Occlusal views LM^1–M^3, LM^3, RM^1–M^3, f. Lateral view LM_1–M_2, occlusal view M_3. g. Occlusal view, M_3.

I have not had an opportunity to see any of the material assigned to *Tachyoryctoides*, *Pararhizomys* 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_1 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. pruinosus*; 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, Chinji Zone, where *Kanisamys indicus* and *Rhizomyoides punjabiensis* 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 emend 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 *Protachyoryctes*. *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.

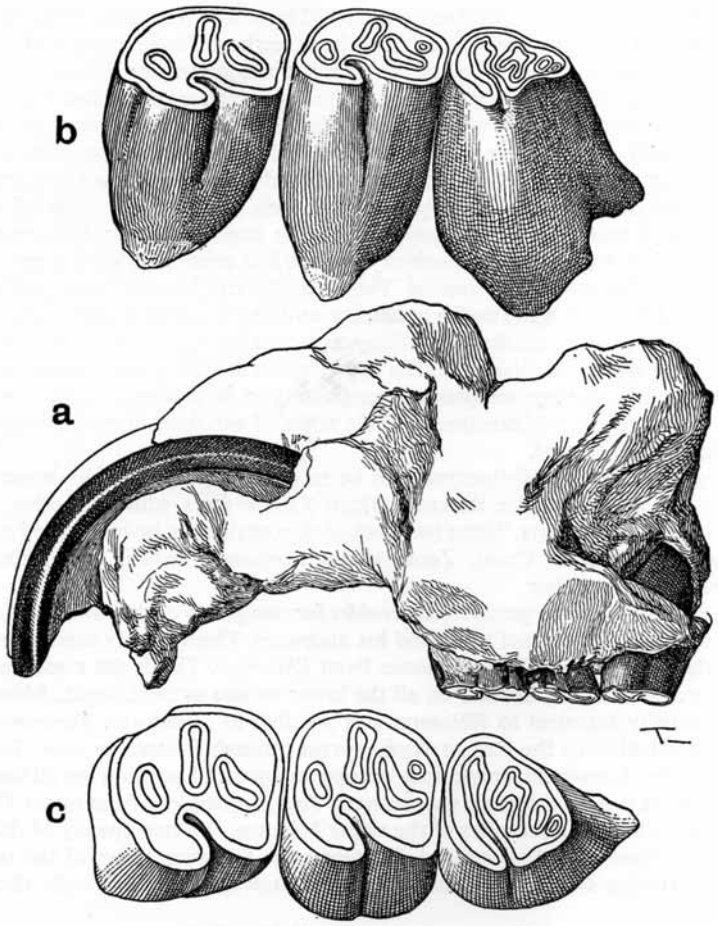
Included species. Rhizomyoides sivalensis, R. punjabiensis, R. nagrii, R. pilgrimi, R. pinjoricus.

Range. Chinji, Nagri and Pinjor Zones of the Siwalik series, Miocene to Pleistocene.

Rhizomyoides sivalensis (Lydekker)

Text-figs. 4–5

1884 *Rhizomys sivalensis* Lydekker, p. 106.
1933 *Rhizomys lydekkeri* Hinton, p. 621.
1946 *Rhizomyoides sivalensis* (Lydekker) Bohlin, p. 68.

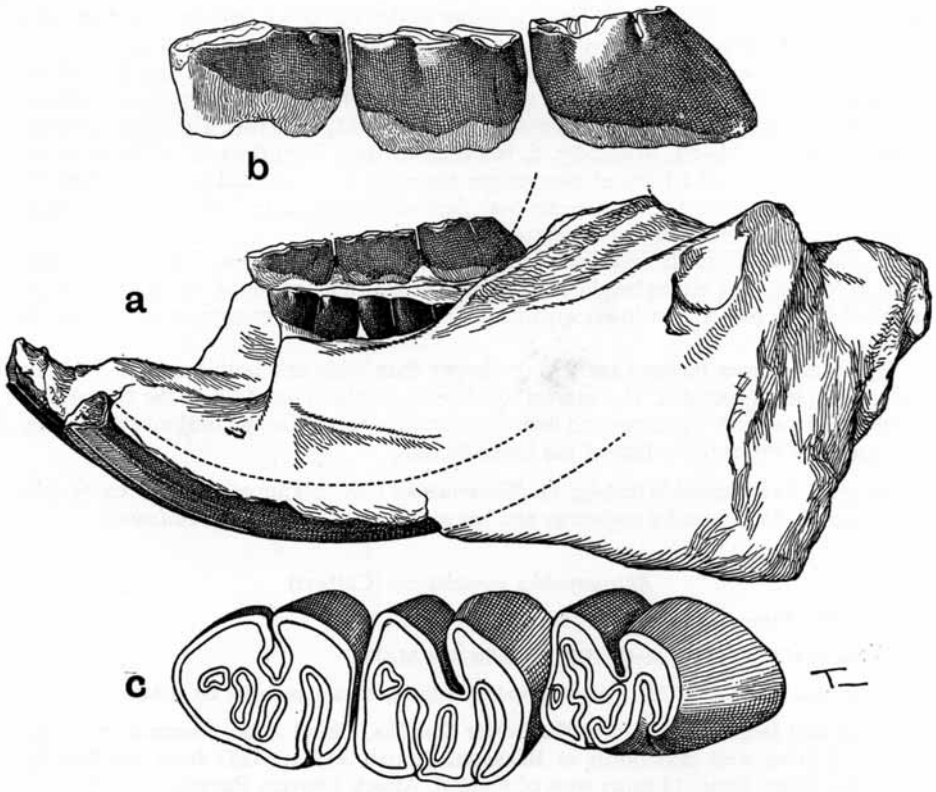


TEXT-FIG. 4. *Rhizomyoides sivalensis*, G.S.I. D277. a. Lateral view of skull fragment, ×3. b and c. Lateral and occlusal views, LM^1–M^3, ×7.

Holotype. G.S.I. D97, partial left mandible with M_2–M_3 (figured by Lydekker, 1884, fig. 1, p. 106).

Referred specimens. G.S.I. D275 (formerly D97a) partial right mandible with M_2–M_3 and D276 (formerly D97b) partial right mandible with M_1–M_3, D277, partial skull and jaws with R and L M 1/1–M3/3, BM 15925, type of *R. lydekkeri*, partial right mandible with M_1–M_3, 15926 partial right mandible with M_2, 15927, partial left mandible with M_1–M_2 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 Asnot, Punjab, Middle Siwaliks. The BM specimens are described (Lydekker 1885, p. 233–334) as being from the Pliocene



TEXT-FIG. 5. *Rhizomyoides sivalensis*, G.S.I. D277. a. Lateral view mandible, ×3. b and c. Medial and occlusal views M_1–M_3, ×7.

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 M_2 only during early wear stages; anterior lingual re-entrant of M_3 with anterior and posterior arms.

Description. The mandible is rather shallow under M_1–M_3 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 Asnot. 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 M_1–M_3 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 M_2 having three lingual re-entrants while M_1 and M_3 have two. The small anterior fossettid seen in M_1–M_3 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 M_3 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_1–M_3. The crown height of the molars is shown in text-fig. 4. M^1 is longer than either M^2–M^3 but is also lower crowned. The single lingual re-entrant of M^1–M^3 is rather short.

Upper and lower incisors are slightly deeper than wide and both have the anterior face of the teeth rounded. The enamel overlaps on to about one-fifth of the lateral and medial faces of both the upper and lower incisors. There is a distinct median ridge along the centre of the anterior face of the lower incisor.

Discussion. As indicated in text-fig. 11, *Rhizomyoides sivalensis* appears to be a reasonable ancestor for *Rhizomyoides pinjoricus* and hence, ultimately, of Recent *Rhizomys*.

Rhizomyoides punjabiensis (Colbert)

1933 *Rhizomys punjabiensis* Colbert, p. 1.

Holotype. A.M.N.H. 19762, partial right mandible with M_2–M_3.

Referred specimen. G.S.I. D287, a partial mandible with M_2–M_3 and posterior bit of M_1.

Horizon and locality. Type from the Lower Siwaliks, Chinji Zone, Miocene, near the base, 23 miles west and north of Bilaspun, Punjab. G.S.I. D287 from the Middle Siwaliks, Nagri Zone, $1\frac{1}{4}$ miles west of Kaulial, Attock District, Punjab.

Emended diagnosis. Smallest species of *Rhizomyoides*; mandible light; lower incisor nearly equilaterally triangular in cross section; cheek teeth brachyodont; three lingual re-entrants on M_2, two on M_3.

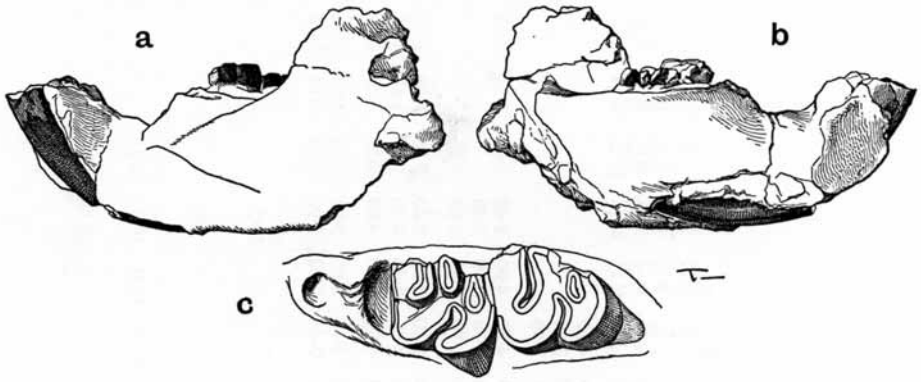
Description. This is an extremely small species (Table 1) and is by far the most generalized of *Rhizomyoides* species. The cheek teeth are low crowned and the mandible is slender and shallow. The incisor of *Rhizomyoides punjabiensis* is nearly equilaterally triangular in cross section. It shows a flattened medial face and slightly convex lateral one (Colbert 1933, p. 2). The occlusal surfaces of the cheek teeth are tilted so that the lateral margins of M_1–M_3 are higher than the medial margins; they face inward and upward. This orientation of the lower cheek teeth is characteristic of all known species of rhizomyids, fossil and Recent. The lingual and buccal re-entrants of M_2–M_3 are shallow and the anterior and middle lingual re-entrants of M_2 tend to fuse with wear leaving two lingual re-entrants in M_2 as there are in M_3.

Discussion. Hinton (1933, p. 621) evidently did not recognize that D287 was a specimen of Colbert's species, as he stated 'This [*R. punjabiensis*] is a smaller species than any of

TABLE 1. Measurements in mm of species of *Rhizomyoides*

	PINJOR			NAGRI											CHINJI	
	R. pinjoricus GSI D280	*R. pinjoricus* Type, GSI D279	*R. pilgrimi* GSI D286	*R. pilgrimi* K21/619, GSI	*R. pilgrimi* Type, GSI D278	*R. sivalensis* GSI D277	*R. sivalensis* GSI D277	*R. sivalensis* GSI D276	*R. sivalensis* GSI D275	*R. sivalensis* Type, GSI D97	*R. nagrii* GSI D285	*R. nagrii* YPM 13085	*R. nagrii* YPM 13805	*R. nagrii* Type, GSI D273	*R. punjabiensis* GSI D287	*Rhizomyoides punjabiensis* Type, AMNH 19762
M_1 a–p							4·50	4·60								
tr						3·10	3·20	3·00								
tr						3·85	3·85	3·50								
M_2 a–p	3·75	3·75	4·50	4·60	4·65	4·15	4·20	4·40	4·00	4·40	3·00	3·55	3·50	3·00	2·30	2·70
tr	4·80	4·75		4·35	4·35	4·00	3·90	3·70	3·90	4·50					2·35	2·40
tr	4·80	4·75		4·65	4·60	4·35	4·20	3·90	3·90	4·60	3·10				2·55	
M_3 a–p	4·20	4·15	5·60	5·70	5·25	5·00	5·00	5·20	4·80	5·40	3·70	3·80	3·80	3·70	3·10	3·10
tr	4·40	4·15		4·35	4·45	3·85	3·90	4·35	3·60	4·20	2·80	3·60	3·55		2·25	
tr	4·10	4·15		4·20	4·30	3·70	3·70	4·00	3·50	4·00	2·50	2·60	2·60		2·00	2·60
I_1 a–p	4·60		5·40	6·40	6·40	3·50	3·45	3·75	4·00	3·80	3·50	4·60	4·60	3·70	1·80	
tr	4·50		3·50	4·50	4·50	2·80	2·80	3·45	2·80	2·90	2·50	3·10	3·10	2·50	1·50	
depth mand. below M_2	14·4		17·9	17·7						12·5				11·4	5·9	
width mand. below M_2		10·1		10·2	9·7					8·0				6·7	3·5	
alveolar length M_1–M_3		14·8	15·5	16·6		14·2	14·6	15·9	15·0	16·0	10·2			10·0	7·8	
ratio $\frac{\text{alveo. len.}}{\text{depth mand.}}$	0·97		1·07							0·80				1·14	0·75	

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 *Kanisamys indicus*, the only other contemporary rhizomyid, by the absence of distinct transverse ridges and intervening valleys, larger size, and lower crowned M_2–M_3. 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, M_2–M_3, ×5.

Rhizomyoides nagrii (Hinton)

Text-fig. 6

1933 *Rhizomys nagrii* Hinton, p. 621.
1937 *Rhizomys* cf. *R. nagrii* Wood, p. 64.

Holotype. G.S.I. D273, a partial left mandible with M_2–M_3 slightly broken.

Referred specimens. G.S.I. D285, partial left mandible with part of M_2 and M_3; Y.P.M. 13805, partial right and left mandible with M_2–M_3.

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 $\frac{1}{4}$ 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 M_2, two on M_3.

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

refer to *R. nagrii*. 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. nagrii* the ratio depth of mandible to alveolar length of M_1–M_3 is greater than 1 (1·14) while in *R. punjabiensis* it is less than 1 (0·75); this ratio is higher in *R. nagrii* 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 M_1–M_3 bringing the depth of mandible—alveolar length of M_1–M_3 relationship back closer to or slightly under one (Table 1).

The cheek teeth are badly worn in all specimens except D285 in which only M_3 is preserved. In the worn condition (Wood 1937, figs. 1–2) there are three lingual re-entrants on M_2 and two on M_3. When unworn the main valley between the protolophid and mesolophid on M_3 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 nagrii* 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. nagrii* having somewhat higher crowned teeth and hence more persistent fossettids. I do not believe that *R. nagrii* 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 M_2–M_3.

Referred specimens. G.S.I. H.T. 6, partial left mandible with ½ M_1; M_2–M_3; G.S.I. D286, partial right mandible with M_2–M_3.

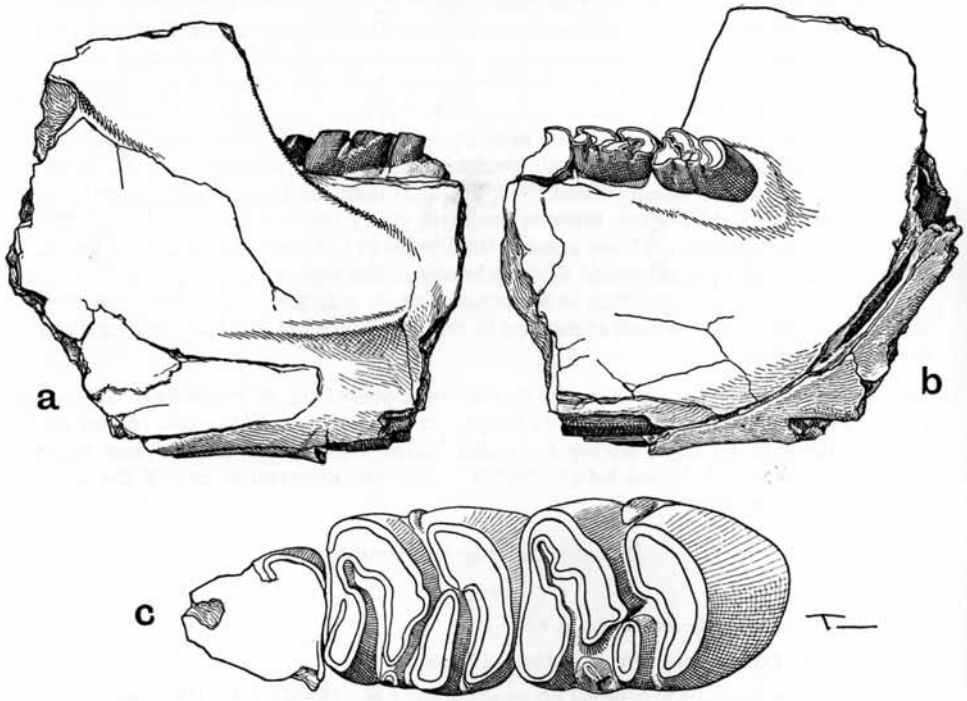
Horizon and locality. Type from Middle Siwaliks, Nagri Zone. Haritalyangar, Simla Hills, India, Field number of the referred specimens is K21/619 but no horizon or locality is recorded. D286 bears field number K23/329, and is listed as being from the Upper Siwaliks, near Malukal, Attock District.

Emended diagnosis. Largest species of *Rhizomyoides*; M_2 as long as wide; anterior and central lingual re-entrants of M_2 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 masseteric 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



TEXT-FIG. 7. *Rhizomyoides pilgrimi*, G.S.I. D278, holotype. a and b. Lateral and medial views of the mandible, ×2½. c. Occlusal view M_2–M_3, ×7.

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_3 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_3.

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.

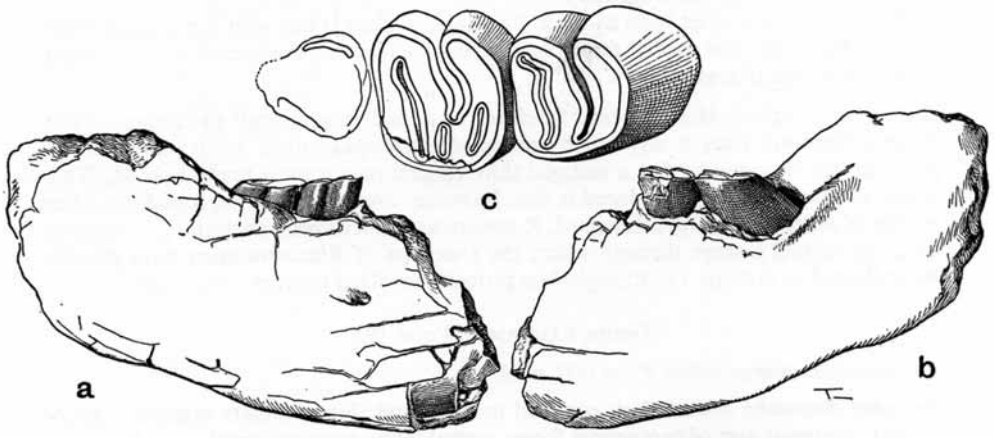
Rhizomyoides pinjoricus (Hinton)

Text-fig. 8

1933 *Rhizomys pinjoricus* Hinton, p. 621.

Holotype. G.S.I. D278, partial right mandible with M_2–M_3.

Referred specimens. G.S.I. D280, partial right and left mandible with M_2–M_3.



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, Simila 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_2 quite short; anterior lingual re-entrant and buccal re-entrant most prominent on M_2, only one present on M_3; 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 masseteric crest, as thick as the mandible of *R. pilgrimi*, but it is much shallower under M_2 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 masseteric 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 *Rhizomys* than is any other species of *Rhizomyoides*. *R. pinjoricus* is not as advanced as *Rhizomys* 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 *Rhizomys* certainly reflects a stage through which the ancestors of *Rhizomys* must have passed. As indicated in text-fig. 11, *R. pinjoricus* probably evolved from *R. sivalensis*.

Genus KANISAMYS Wood 1937

Type species. *Kanisamys 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.

Kanisamys indicus Wood

Text-fig. 9

1933 *Theridomys* sp. Hinton.
1937 *Kanisamys indicus* Wood.

Holotype. Y.P.M. 13810 right mandible with M_1–M_3.

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 *Kanisamys 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 M_3, 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 M_2 and M_3. The posterior protoconid arm and the hypolophid are clearly separated by a narrow fossettid on M_2–M_3 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 M_3 particularly this measurement is somewhat misleading as the occlusal surface measures 1·95 mm, yet the maximum length of M_3 below the occlusal surface is 2·30 mm. All measurements given here are for the maximum dimensions.

		TYPE YPM YPM 13810 *Kanisamys indicus*	D271 *K. indicus*	TYPE YPM 13801 *K. sivalensis*	TYPE D272 *Protachyoryctes tatroti*
M_1	a–p	2·30	—	2·90	3·20
	tr	1·50	—	1·85	2·10
	tr	1·80	—	2·10	2·40
M_2	a–p	2·00	1·95	2·40	2·95
	tr	2·00	1·85	2·40	2·90
	tr	2·00	1·85	2·35	3·10
M_3	a–p	2·30	2·40	3·00	3·70
	tr	1·85	1·80	2·40	2·80
	tr	1·65	1·65	2·10	2·65

Kanisamys sivalensis Wood

1937 *Kanisamys silvalensis* Wood, p. 70.

Holotype. Y.P.M. 13801, partial left mandible with M_1–M_3.

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

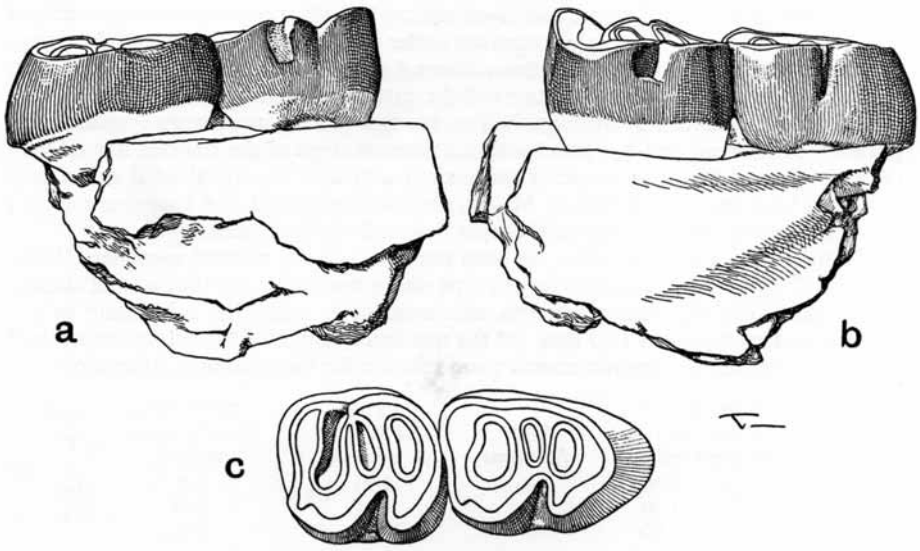
Emended diagnosis. Larger than *Kanisamys indicus*; teeth moderately high crowned (mesodont); molar pattern lophate; buccal arm of anterior cingulum absent on M_2–M_3.

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 *Protachyoryctes* below.

Genus PROTACHYORYCTES Hinton 1933

Type species. Protachyoryctes tatroti, Hinton 1933, p. 620.

Diagnosis. Molars high crowned; larger than *Kanisamys* approaching size of *Tachyoryctes*; crown pattern reduced to essentially three lophs; M_1 longer than M_2 with 3 distinct lingual re-entrants; posterior columns of M_2–M_3 and anterior column of M_3



TEXT-FIG. 9. *Kanisamys indicus*, G.S.I. D271. a and b. Medial and lateral views of M_2–M_3, approx. ×14. c. Occlusal view M_2–M_3, approx. ×14.

not completely isolated during early wear stages as in *Tachyoryctes*; re-entrants on M_2–M_3 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 m_1–m_3.

Hypodigm. Type only.

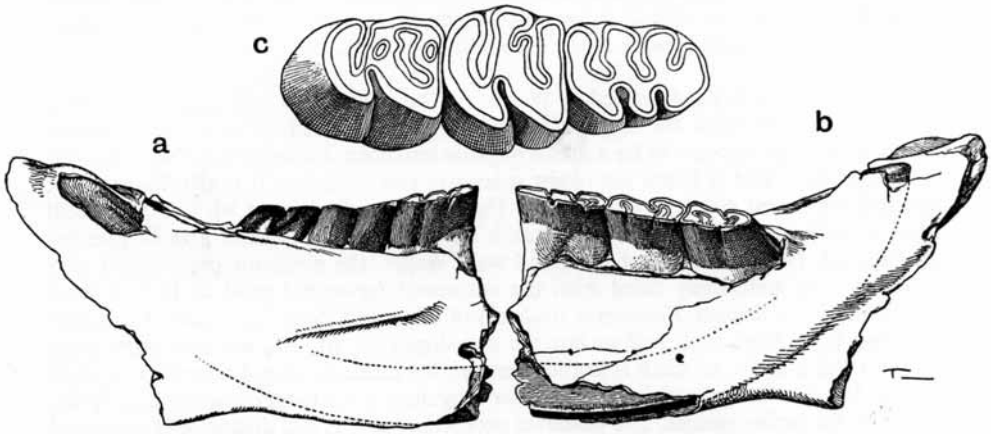
Horizon and locality. Tatrot State, earliest Pleistocene, Tatrot, Salt Range, Pakistan.

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 M_1 broken and lost. The masseteric fossa is very poorly defined along its ventral border but appears to begin below the posterior half of M_1. The masseteric crest runs posteriorly and slightly ventrally. Below the posterior half of M_1 and most of M_2 the crest is quite strong but fades into the posterior part of the mandible behind M_2. Anterior to M_1, 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 M_1–M_3.

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 *Protachyoryctes tatroti* are only slightly higher crowned than those of the earlier *Kanisamys sivalensis*. *Protachyoryctes tatroti* appears to be of nearly the same size as *Tachyoryctoides* (Bohlin 1937, p. 44) but differs greatly from the Chinese form in details of M_1–M_3 occlusal pattern, and particularly in the size of M_1 in relation to the size of



TEXT-FIG. 10. *Protachyoryctes tatroti*, G.S.I. D272, holotype. a and b. Lateral and medial views of mandible, ×4. c. Occlusal view M_1–M_3, ×7.

M_3. M_1 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 M_1 to completely destroy the small fossettid seen on the M_1 of *Kanisamys sivalensis*. The posterior protoconid arm (pseudo-mesolophid of Wood) has also fused into the entoconid-hypoconid loph so that there is a single rather wide lingual lophid on M_1. In occlusal outline the first lower molar is much narrower and more elongate than are M_2 and M_3.

The second lower molar is almost square in an 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 M_2 there is still a faint indication of the posterior protocontid arm as well as the hypoconid-entoconid crest. With slightly further wear these two crests would fuse into the single, central loph of M_2.

The third lower molar is considerably longer than M_1 or M_2; however, at the present state of wear, the occlusal surface does not give the appearance of such length. Whereas the three transverse lophs of M_1–M_2 are separated lingually, on M_3, 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 M_3. In addition, there are two small fossettids, one in the middle of the anterior loph just internal to the metacontid and the second, quite small, on the median loph just internal to the entoconid. As on M_2, the buccal re-entrant is open almost to the base of the crown.

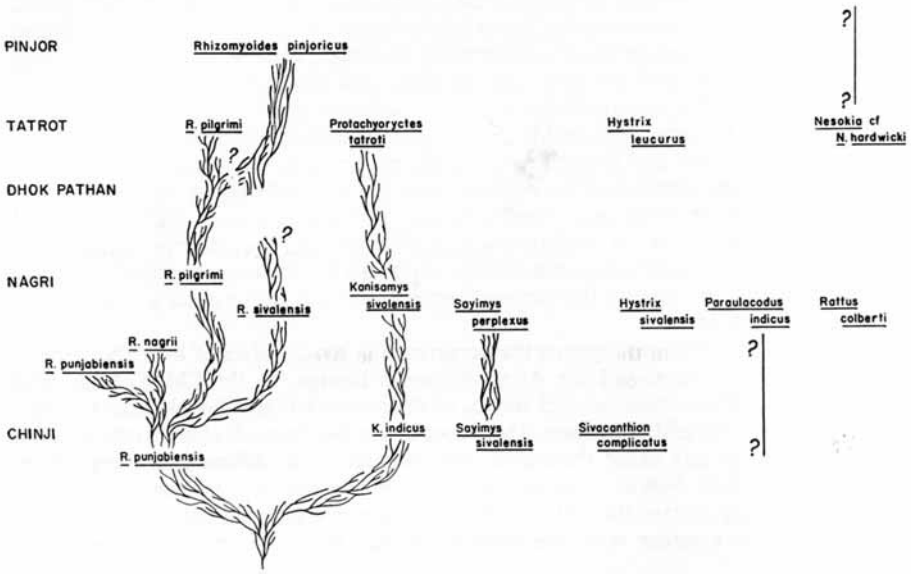
The lower incisor is smaller than one might expect considering the size of the cheek teeth. It is narrowly triangular in cross-section with a rounded anterior edge. The enamel extends on to about one-fifth of the medial surface of the tooth. The lateral surface of the incisor is more gently rounded and 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 phyletic 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 M_1 and M_2 is still quite prominent on *Kanisamys indicus* as is the posterior protoconid arm or pseudo-mesolophid. Even at the most advanced wear stages, the posterior protocontid 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 M_1–M_3 are still prominent. There is still a basin, or small fossettid, between the metacontid and anterior cingulum on M_1–M_3. The buccal arm of the anterior cingulum is no longer evident on M_2–M_3 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 M_1–M_3 but fused with the entoconid on M_3. 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 M_1–M_3 are almost completely fused, forming, with the posterior cingulum, three main transverse crests. Thus, from a basically four-lophed condition in the earliest member, *Kanisamys indicus*, the sequence ends in a three-lophed 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 *Tachyorytoides* may be close to the ancestry of *Tachyoryctes*. The occlusal pattern of *Tachyoryctoides obtrutschewi* (Bohlin 1937, fig. 103) and the short M_1 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 M_1 and most of M_2. In addition, all three have an incisor which begins medial to M_1, passes under M_2 and lateral to M_3, 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 M_1.

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 M_1 and M_2. 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 M_3 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



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 M_1 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 M_2 and M_3 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 M_2 and M_3 during

early wear stages. On M_1, 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 M_3 but not on M_1–M_2 of *Tachyoryctes*, the anterior internal column, or metaconid, of M_3 has been isolated with the anterior lingual valley swinging completely around the metaconid and opening on to the anterior face of the tooth. Thus, on M_3 there are three isolated lophs at least at some stages of wear. On M_2 there are two anterior lophs joined at the protocontid and an isolated posterior loph. On M_3, 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 M_1, M_2 or M_3. However, in *Protachyoryctes*, the buccal and posterior lingual valleys of M_2 are quite close and it is quite easy to visualize a succeeding stage in which they become fused and the posterior loph of M_2 isolated from the rest of the crown. This is also true for the posterior loph of M_3 and with the continued expansion of the anterior valley, both anteriorly and lingually around the metacontid, the metacontid 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.

Holotype. Y.P.M. 13798, partial skull with left M^1–M^3.

Horizon and locality. Nagri Zone 'One half mile south of Taraun village, northwestern Bilaspur Kehloor State, Punjab, India. Yale North India Expedition Palaeontological Locality No. 41; Survey of India Map No. 53 A/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 M_1.

Horizon and locality. Upper Siwaliks, locality unknown.

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

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CRAIG C. BLACK
Museum of Natural History
University of Kansas
Lawrence
Kansas

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