NEW RHIZOMYINE RODENT SPECIMENS FROM THE LATE PLIOCENE (UPPER SIWALIKS) OF INDIA: PHYLOGENETIC IMPLICATIONS

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ABSTRACT The ancestors of bamboo rats of south and south-east Asia and those of the root rats of Africa were quite common in the Middle and Late Miocene Siwalik deposits of India and Pakistan. However, their diversity dropped significantly in the Pliocene and Pleistocene. A derived late Pliocene form of the extinct rhizomyine genus *Rhizomyides* was recognized and named *Rhizomyoides saketiensis* based on two dentary fragments. This late rhizomyine has good provenance but appears to be a junior synonym of the species *Rhizomyides lydekkeri* from an unrecorded locality. We here report a partial skull (~ 2.6 Ma) and a palate (~ 3 Ma), plus a few molars of this species confirming the distinct nature of this species. Our phylogenetic analysis places *Rhizomyides lydekkeri* close to the Middle Siwalik *Rhizomyides sivalensis* and Afghan *Rhizomyides platytomeus* and *Rhizomyides carbonnelli,* implying late Neogene migration between Afghanistan and Indo-Pakistan. Micro-CT scanning allowed a better understanding of internal features, particularly assessing molar wear stages, without cutting the specimens. The skull features such as low skull profile, extremely elongated and gently curved snout, very long incisive foramina but strong incisors lead us to propose that *Rhizomyides lydekkeri* was most probably moderately fossorial.

KEYWORDS Upper Siwaliks, India, Rodents, Rhizomyinae, Phylogeny

INTRODUCTION

Professor Louis Jacobs' monograph on "Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan" published in 1978 has remained a benchmark contribution. This paper was one of the key motivations for one of us (RP) to undertake a Ph.D on the Siwalik muroid rodents. Professor Jacobs went on to publish many more interesting papers on these rodents (Jacobs et al., 1989;1990; Flynn and Jacobs, 1999) and remains active in this research (Kimura et al., 2013; 2017; 2021; Flynn et. al., 2020). As a tribute to his excellent contribution and keeping the legacy alive, an attempt has been made here to describe some new rhizomyine specimens from late Pliocene deposits exposed near Chandigarh, India. The paper also discusses phylogeny and paleobiogeography in the light of emerging hypotheses.

Today, the Bamboo Rat subfamily is confined to south, south-east Asia (tribe: Rhizomyini) and east Africa (tribe: Tachyoryctini) (Gogolevskaya et al., 2010), where they live a fully subterranean way of life. Living Asian bamboo rats include three species of *Rhizomys* and one species of *Cannomys*, while the African mole rats *Tachyoryctes*, comprise at least two extant species. Both the Asian *Rhizomys* (+ *Miorhizomys*) and the African *Tachyoryctes* have a long fossil record since they emerged in the Late Miocene, whereas there is no record of *Cannomys* fossils. Rhizomyines were widespread since the Late Oligocene. Over 30 fossil species belonging to 11 genera (*Prokanisamys, Kanisamys, Rhizomyides, Protachyoryctes, Tachyoryctes, Eicooryctes, Miorhizomys, Anepsirhizomys, Rhizomys* (*Brachyrhizomys*)*, Pronakalimys* and *Nakalimys*) have been recorded from China, Thailand, India, Pakistan, Afghanistan and Africa (Black, 1972; Flynn, 1982, 1983; Vasishat, 1985; López-Antoñanzas et al., 2013, 2015).

Our rhizomyine specimens come from two rich Late Pliocene localities namely, Khetpurali and Kanthro (2.5 km
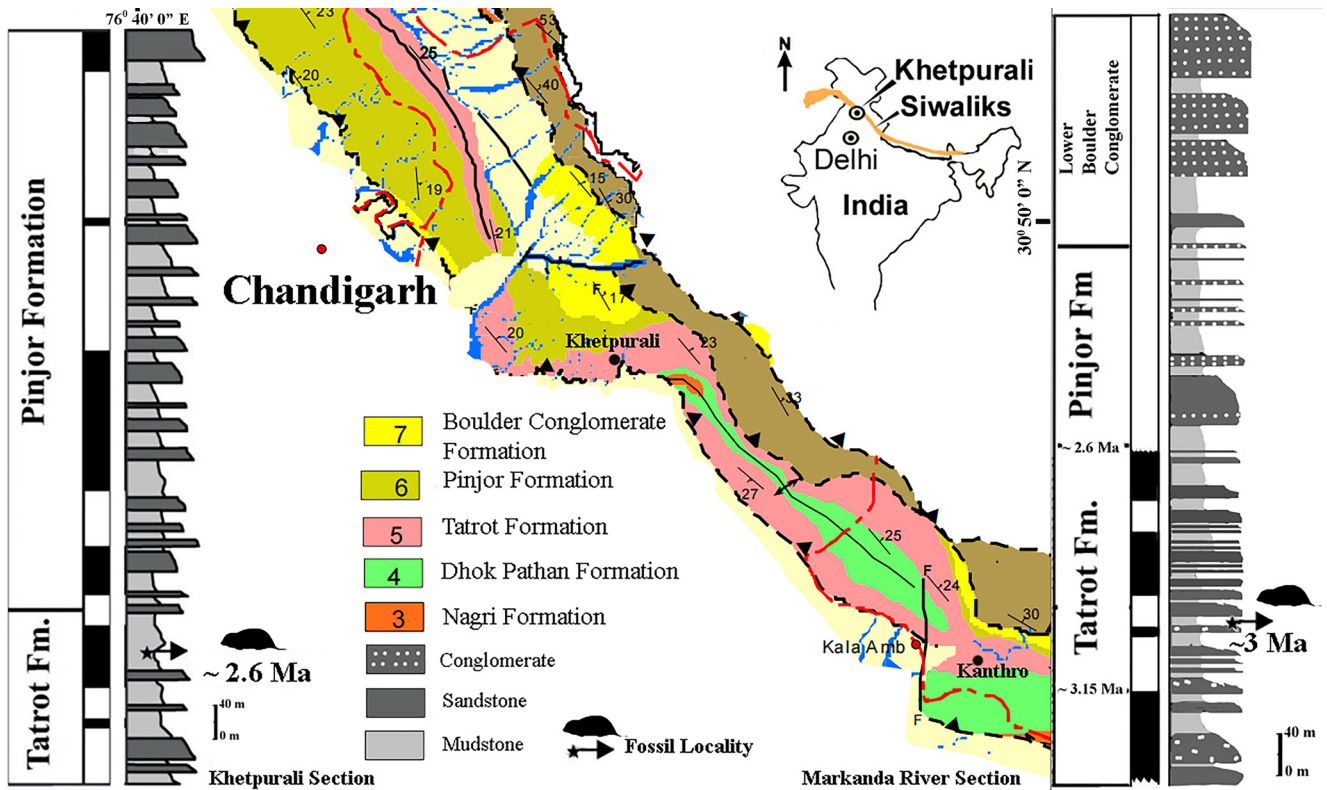
FIGURE 1. Geological map of the area (after Eliyas et al., 2017) showing the two fossil sites, palaeomagnetically dated section near Khetpurali (Tandon et al.,1984) and near Markanda River (Azzaroli and Napoleone, 1982).

north of Saketi) (Fig. 1). Both these sections have been tied to nearby paleomagnetic sections in stream-cut exposures (Tandon et al., 1984; Azzaroli and Napoleone, 1982). The Khetpurali locality has been estimated to be ~2.6 Ma and Kanthro locality would be ~3 Ma old.

MATERIAL AND METHODS

Materials

All the specimens described here come from field collections. The Khetpurali PU KPR-1 skull and the isolated teeth though from the same site were not found in association. The Kanthro (Saketi) PU KR-1 palate and the isolated teeth described earlier are also not associated. The isolated m3 and M3 were earlier assigned as *Rhizomyides* sp. and Cf. *Brachyrhizomys* by Patnaik (2001). One lower incisor described earlier from Kanthro (Patnaik, 2003) has also been included in this study. The two partial mandibles from Saketi on which the species *Rhizomyioides saketiensis* was erected by Gupta et al. (1978) are from a nearby locality and included in this study.

Methods

Micro-CT scanning of the partial skull PU KPR-1 and palate PU KR-1 was undertaken at the IIT, Mumbai X-Ray microscope facility using Zeiss, Xradia Versa 520. The fossils were also studied under Leica S8APO microscope. For photography and measurements Racold stereozoom microscope was used. Several images were taken using JEOL 6490 SEM housed at the Department of Geology, Panjab University. The dental terminology for *Rhizomyides* follows López-Antoñanzas et al. (2013) (Fig. 2).

Phylogenetic Analysis

The phylogenetic analysis of the morphological data was conducted using PAUP version 4.0a169 Swofford (2002) phylogenetic software package, employing the bootstrap method with heuristic search. The taxa were identified based on synapomorphic characters observed in specimens, published descriptions, and photographs. All the characters were given equal weight, and their order was not considered. Missing characters were denoted as "?" and gaps as "-". The text files were converted into NEXUS file formats using
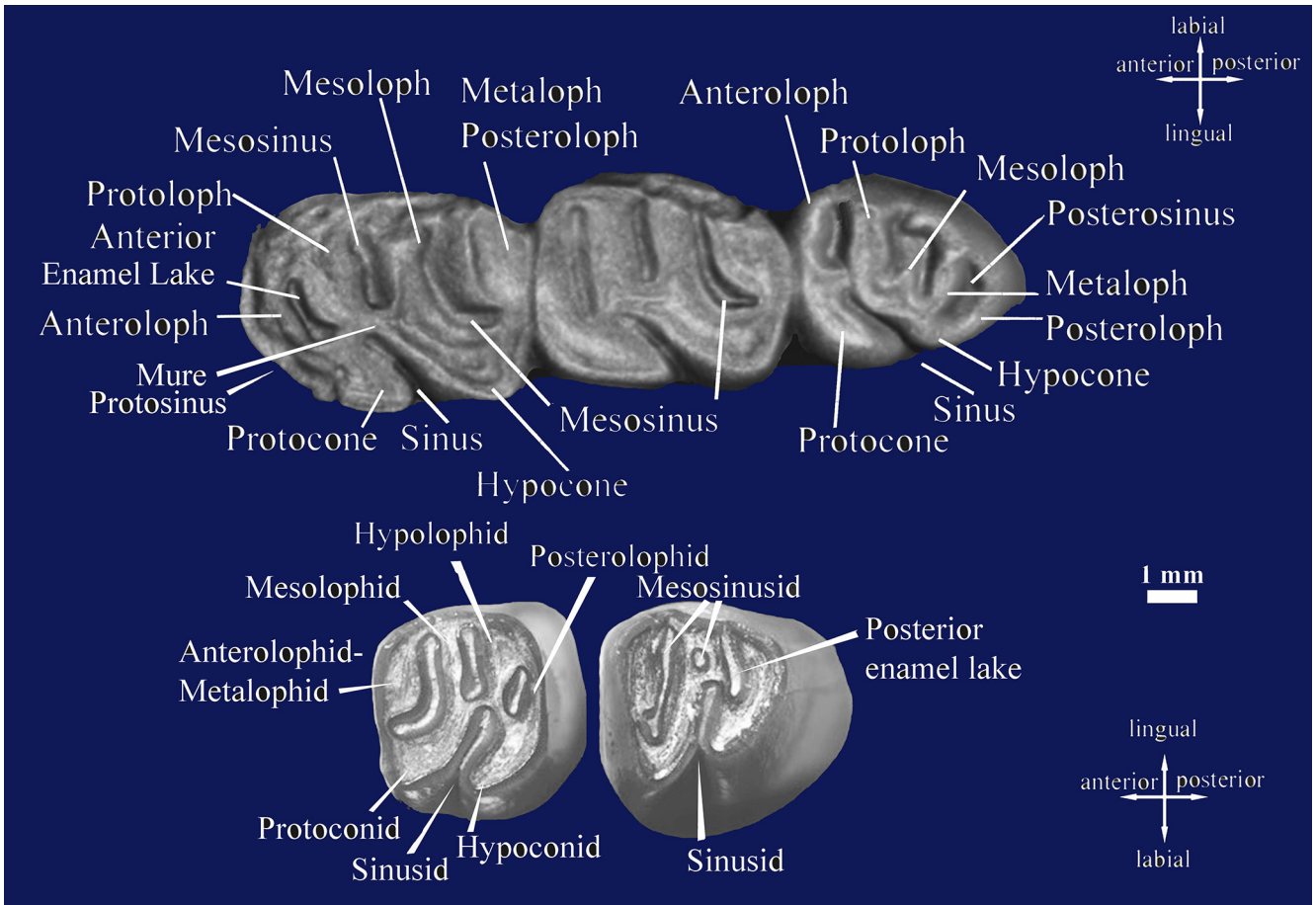
FIGURE 2. Dental terminology for *Rhizomyides* follows López-Antoñanzas et al. (2013). The upper molars are from the palate PU KPR-1, the left m2 is PU KPR-2 and left m3 is PU KPR-4.

Mesquite, version 3.5.1 (Madison and Madison, 2018). For this study, the parsimony optimality criterion was selected, and 50000 bootstrap replicates were performed, retaining 10 trees per replicate through the branch-swapping algorithm of the tree bisection-reconnection (TBR) method. A total of 5000 most parsimonious trees (Maxtrees) were retained. Branch support values for each tree were determined using the random addition sequence of taxa over 10000 replicates (Felsenstein, 1985). The 50% majority rule consensus tree was constructed based on the 5000 most parsimonious trees obtained in this study.

Abbreviations — PU KPR, Khetpurali rhizomyine and PU KR Kanthro rhizomyine, SM-Saketi Mammals; YGSP, Yale Geological Survey of Pakistan, DP, Darmouth Peshawar; NHMUK, Natural History Museum London, AMNH, American Museum of Natural History, GSI-Geological Survey of India; AFG-Afghanistan; BAM, Bamian, PEC, Pul-e Charkhi.

M1-First Upper Molar, M2-Second Upper Molar, M3-Third Upper Molar, m1 First Lower Molar, m2- Second Lower Molar, m3-Third Lower Molar.

SYSTEMATIC PALAEONTOLOGY

Family SPALACIDAE Gray, 1821
Subfamily RHIZOMYINAE Winge, 1887
Genus *RHIZOMYIDES* Bohlin, 1946
RHIZOMYIDES LYDEKKERI (Hinton, 1933)
Synonymy: 1972 *Rhizomyoides sivalensis* Black (in part), p. 249
1978 *Rhizomyoides saketiensis* Gupta et al., p. 112
(Fig. 3 A-J) (Table 1, 2)

Type Locality — Saketi and Kanthro, Himachal Pradesh
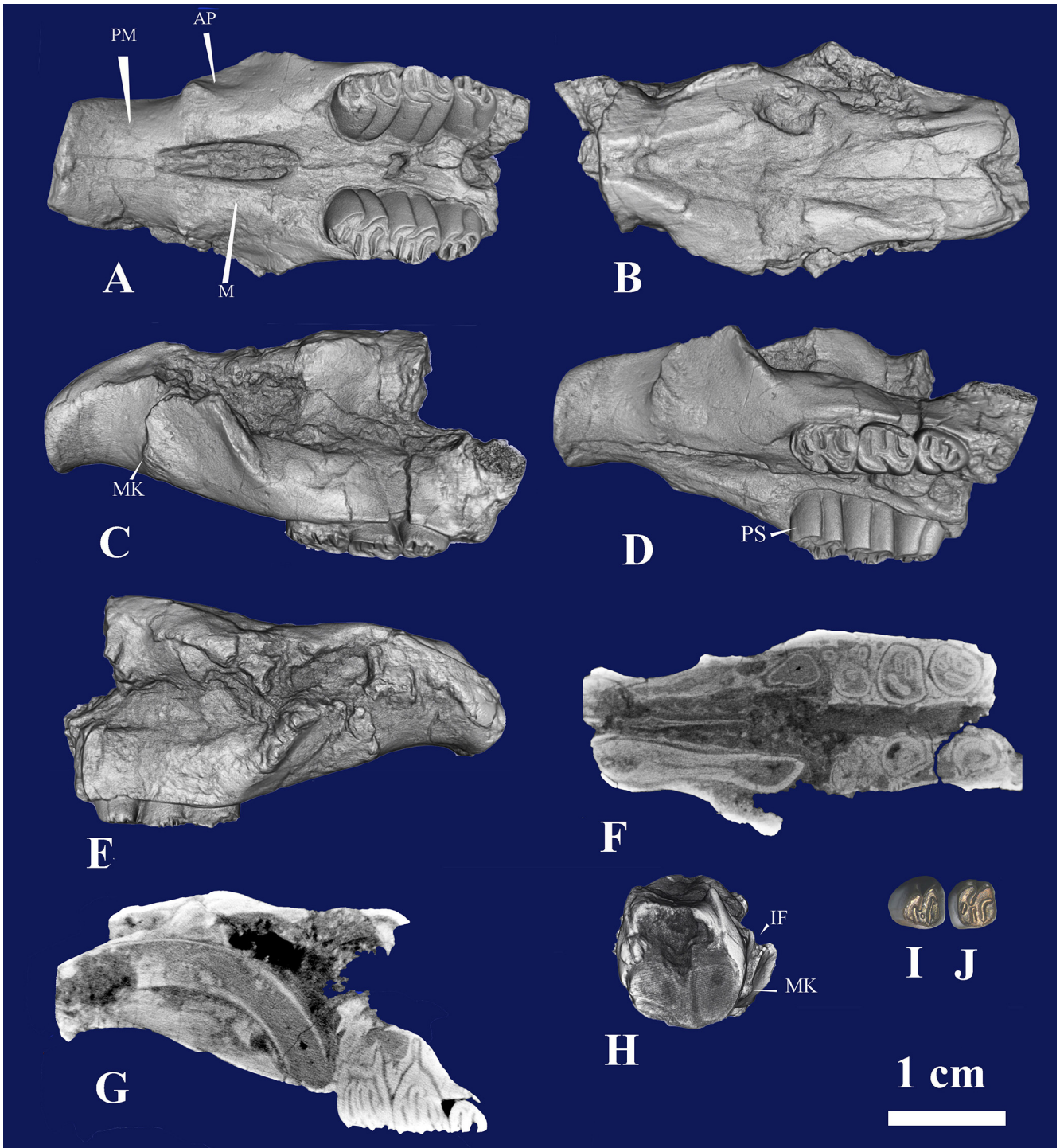
FIGURE 3. Upper and lower molars of *Rhizomyides lydekkeri* from Khetpurali. A-H: PU KPR-1, A, ventral view; B, dorsal view; C, lateral view (left side); D, skull tilted to show the occlusal surface of the left upper molars; E, lateral view (right side); F, micro-CT image at a depth parallel to the ventral surface; G, micro-CT image through left incisor and row of molars. H, frontal view showing nasal bones above broken incisors. I, isolated left m3 (PU KPR-2) and left m2 (PU KPR-3). PM-Pre-maxilla; AP-Anterior plate of the zygoma; IF-Infraorbital foramen; M-Maxilla; MK-Masseteric Knob; PS-Protosinus.

(India).

Referred Material — PU KPR-1 a partial skull with well-preserved palate; PU KPR-2, left m2; PU KPR-3, left m2; PU KPR-4 left m3. PU KR-1, palate with all the teeth preserved; GSI-19549 partial mandible with m2m3 and i1; GSI-19549 partial mandible with m3 and i1; VPL/RP-SM-79, isolated m3 and VPL/RP-SM-80, isolated M3 assigned earlier as *Rhizomyides* sp., cf. *Brachyrhizomys* sp., respectively (Patnaik, 2001); VPL/RP-SM-791, i1 isolated lower incisor considered *Rhizomyides* sp. (Patnaik, 2003).The type specimen of *R. lydekkeri* Hinton, 1933, NHMUK PV OR 15925.

Emended diagnosis — Skull and upper dentition of this large species of *Rhizomyides* were not known before. A robust skull having very long snout, long incisive foramina, an infraorbital foramen with a keyhole pattern, very large, hypsodont and lophodont molars showing a strong gradient of wear. Lingual sinus deep antero-labially oriented, mesoloph long and complete on M1M2M3; M1 three rooted with metaloph-posteroloph fused, posterior lake (posterosinus) retained on M3. Mandibles with strong masseteric crest anteriorly extended and inflated under m2; very large hypsodont lower m1, m2 and m3 with a mure lingual to a deep sinusid; large posterior enamel lake on m3, triangular lower incisors with a single, fine ridge.

Description — The partial skull of *Rhizomyides lydekkeri* has a low profile (about 18 mm from M2 occlusal surface to skull roof). The snout is slender (12 mm high and 10 mm wide at the incisive foramen) includes a very long diastema (22.5 mm) about twice the length of the tooth row (12.5 mm, Fig. 3D). Both the dorsal and ventral surfaces of the snout curve gently. The premaxillae and nasals reach posteriorly to join the frontals in an extremely jagged suture. The maxilla forms the narrow anterior root of the zygoma and the ascending zygomatic plate, which in turn encloses a myomorphous keyhole infraorbital foramen. A masseteric knob is also present at the anterior margin of the zygomatic plate. A slit-like infraorbital canal within the foramen shows a keyhole pattern (Fig. 3H). The maxilla-premaxilla suture lies right at the infraorbital foramen and zygomatic plate, and extends ventrally to intersect the anterior end of the incisive foramina. Incisive foramina are very long (12 mm) and broad (up to 3.5 mm), situated 2 mm anterior to M1 and 12 mm posterior to the robust I1. Nutritive foramina are located anteromedial to the internal root of M1. The I1 is strongly

TABLE 1. Measurements of upper and lower teeth of *Rhizomyides lydekkeri,* including holotype (estimate due to breakage) and those of other known fossil species from the region.

Tooth No.	Locus	Specimen No.	Length in mm	Width in mm
		Rhizomyides lydekkeri		
1	M1	PU KPR-1	4.8	3.5
2	M2	PU KPR-1	4.2	3.5
3	M3	PU KPR-1	3.5	3.4
4	m2	PU KPR-2	3.4	3.5
5	m2	PU KPR-3	3.5	3.5
6	m3	PU KPR-4	3.5	3.8
7	M1	PU KR-1	4.5	5.3
8	M2	PU KR-1	4.5	5.0
9	M3	PU KR-1	4.8	4.5
10	m2	GSI-19549	5.2	6
11	m3	GSI-19549	5	5
12	i1	GSI-19549	4.5	4.1
13	m3	GSI-19550	5	5
14	i1	GSI-19550	4.5	4.1
15	m3	SM-79	4.2	4.7
16	M3	SM-80	4.0	3.8
17	i1	SM-791	4.2	4.0
18	m1	NHMUK PV OR 15925	~5.5	4.2
19	m2	NHMUK PV OR 15925	5.0	5.5
20	m3	NHMUK PV OR 15925	6.0	~5.0
21	i1	NHMUK PV OR 15925	7.8	4.3
		R.sivalensis		
22	m2	GSI D97	5.46	5.06
23	m3	GSI D97	6.13	4.50
24	m2	GSI D276	5.25	4.31
25	m3	GSI D279	5.44	4.31
26	m2	YGSP 15319	4.00	4.94
27	m3	YGSP 15319	5.38	4.63
28	m3	DP 394	5.00	4.00
		R.punjabensis		
29	m2	AMNH 19762	2.75	2.75
30	m3	AMNH 19762	3.06	2.54
		R. carbonnelli		
31	m2	PEC 101	3.52	4.13
32	m3	PEC 101	3.96	4.01
		R. mirzadi		
33	M2	BAM 3	3.40	3.16
34	m1	BAM 1	3.93	2.59
35	m2	BAM 2	3.99	3.51
		R. platytomeaus		
36	m1	AFG 059	5.62	4.48
37	m2	AFG 059	5.25	5.38
38	m3	AFG 059	6.65	4.84
39	i1	AFG 059	4.42	3.78

TABLE 2. Measurements for the partial skull PU KPR-1 (*Rhizomyides lydekkeri*) compared with *Miorhizomys nagrii*, *Miorhizomys choristos* and *Kanisamys sivalensis* (data from Flynn, 1982; Flynn et al., 1990).

S.no	Cranial elements	Rhizomyides lydekkeri	Miorhizomys nagrii	Miorhizomys choristos	Kanisamys sivalensis
1.	Diastema length	22.5	17.3	18	15
2.	Snout height	12	9.5	13.7	9
3.	Snout width	10	10.8	13	10
4.	Incisive foramen length	12	5.9	7	6
4.	Incisive foramen width	3.5	-	3.6	2.5
4.	Incisive foramen-first molar distance	2.5	-	5	2.5
5.	Molar row length (upper)	12.5	9.0	12	7.4
6.	Palate width (outer margin at second molar)	17	13.4	14.6	-
7.	Distance between second molars (inner margin)	4.5	5.5	4.2	-
8.	Skull height (at and including second molar)	18	18.3	24.5	15
9.	Incisor cross section	4.0, 3.5	-	4.6,3.0	-

recurved and contained within the maxilla anterior to the molar row, but its capsule abuts the anterior side of the M1 root (Fig. 3F & G). The palatine foramina lie opposite the posterior end of M2. Posterior emargination of the palate extends anterior to the midline of M3. The robust incisors, low skull profile, very elongated and gently curved snout, and long incisive foramina may indicate that *Rhizomyides lydekkeri* was moderately fossorial.

The M1 (Fig. 2 and 3) occlusal outline is nearly rectangular in early wear but becomes squarish to round after moderate wear (Fig. 4). This tooth is three rooted with the anterolingual root the most developed (Fig. 3F). M1, somewhat larger than the M2 and M3, comprises four prominent transverse lophs (anteroloph, protoloph, mesoloph and metaloph-posteroloph). The anteroloph connects lingually to the protoloph through the protocone and labially to the protoloph, isolating an anterior enamel lake. The mesoloph, which is a long antero-labial continuation of the hypocone, joins labially the metaloph–posteroloph, isolating a posterior enamel lake (posterior mesosinus), which is larger than the anterior one. The M1 has a distinct deep lingual sinus directed strongly antero-labially towards the anterior lake. A faint protosinus is present at the antero-lingual border of the tooth (Fig. 3D). The M1 has a short mure.

The M2 (Figs. 2, 3) occlusal outline is nearly rectangular in early wear but appears squarish after moderate wear (Fig. 3) and somewhat rounded near the base as seen through the micro-CT image (Fig. 3F). M2 comprises four prominent transverse lophs (anteroloph, protoloph, mesoloph and metaloph-posteroloph). The anteroloph connects lingually to the protoloph through the protocone and labially to the protoloph, isolating an anterior enamel lake. The mesoloph is a long antero-labial continuation of the hypocone, joining labially with the metaloph-posteroloph to isolate a posterior enamel lake (posterior mesosinus), which is larger than the anterior one. The lingual sinus is deep and directed steeply anteriorly towards the anterior lake. The M2 has a short mure and is four rooted.

The occlusal outline of the M3 (Figs. 3, 4) is oval with its posterior part being narrower than the anterior. The outline becomes round at the base of the molar (Fig. 3F). It has five lophs, the posteroloph is the shortest. The lingual sinus is deep. In very late wear the protocone and hypocone are joined to enclose a large lingual lake (Fig. 4E). This is evident from the micro-CT scan image taken at the base of the molar (Fig. 3F). The anteroloph is a long and narrow continuation of the protocone. The protoloph and mesoloph extend from the middle of the tooth to the labial margin. In very early wear the mesoloph is divided with a buccal cusp (Fig. 3). The metaloph joins with the hypocone and with the lingual end of the posteroloph, forming a posterosinus. The M3 has a short mure and is three rooted.

The m1 of NHMUK PV OR 15925 is slightly damaged on the lingual side and anteriorly. The occlusal outline of the m1 is oval, with the anterior part being much narrower than posteriorly. The anteroconid is fused with the anterolophid

which in turn is attached to the metalophid lingually leaving a large anterosinusid. A protosinusid is present labially and the labial sinus is deep. Mesolophid is long and complete and joins the metalophid to enclose an anterior mesosinusid. It also joins lingually to the hypolophid enclosing the posterior mesosinusid. Posterolophid and hypolophid enlcose a large posterosinusid. The specimen shows a posterior metaconid-protoconid connection. The tooth has a midline mure.

The occlusal outline of m2 is squared (Fig. 3J). It has four major lophids: anterolophid-metalophid, mesolophid, hypolophid and long posterolophid (Figs. 2 and 3). The mesolophid extends labially from the protoconid. Hypoconid extends to posterolophid which in turn joins hypolophid lingually to form the posterior enamel lake. Lingual joining of anterolophid-metalophid and mesolophid leads to the formation of an anterior mesosinusid lake. A posterior mesosinusid lake is formed by the lingual joining of mesolophid and hypolophid. The sinusid is deep, but a central mure is present, very narrow in early wear. m2 is four rooted.

The m3 is hypsodont (occlusal measurement excludes the posteriorly flaring base) and has a triangular occlusal outline (Figs. 3 and 4). The main lophids are the anterolophid-metalophid, mesolophid shortened in early wear, hypolophid and posterolophid. The protoconid is V-shaped and its posterior arm (an abbreviated mesolophid in early wear) is broad and oblique. The hypolophid is directed lingually from the narrow mure that lies lingual to the deep sinusid. In later wear the mesolophid joins the hypolophid lingually to form a small lake (mesosinusid). Posterolophid and hypolophid join lingually to form a large posterior enamel lake. Root structure is not preserved.

Comparisons — The type species of *Rhizomyides* is *Rhizomyides sivalensis* (Lydekker, 1884). Bohlin (1946) had perceived that the fossil is distinct from any living species. *R. sivalensis* is a relatively common rhizomyine in the late Miocene of the Indian subcontinent. It is significantly larger than early Late Miocene *R. punjabiensis.* Gupta et al. (1978) realized that a yet larger form of the genus occurs in the Late Neogene of the subcontinent and distinguished Late Pliocene fossils as *R. saketiensis* (holotype GSI 19549). Their intuition was accurate, but Hinton (1933) had realized the same and named *R lydekkeri* based on two jaws (holotype, NHMUK PV OR 15925). Unfortunately, the locality was not recorded and Black (1972) preferred to synonymize them with *R. sivalen*sis. Renewed collecting with accurate locality

information yields the new material described here and permits us to emend the diagnosis of this large rhizomyine.

The holotype of *Rhizomyides lydekkeri* is represented by a mandible with broken molars and incisor. The type of *R. saketiensis* (GSI 19549) was represented by two jaw fragments, one preserving m2-3, the other with broken m2. Table 1 includes estimated length and width of m1-3 in the holotype NHMUK PV OR 15925. The description above of the molars embraces both NHMUK PV OR 15925 and GSI 19549. These two specimens add to the impression that this late *Rhizomyides* has relatively broad molars. They also demonstrate a stout lower incisor (4.4 mm wide in NHMUK PV OR 15925) with enamel that is very gently rounded and bears a fine ridge. The dentary bone is not particularly deep.

The partial skull would be the largest among the Siwalik *Rhizomyides*, with the longest diastema and incisive foramina (Table 2). The partial skull of *Rhizomyides lydekkeri* may be compared with the skull of the early tachyoryctine *Kanisamys sivalensis* (Flynn, 1982) in having a low profile, a slender snout and a slit-like infraorbital canal within the foramen forming a keyhole constriction and a very longer incisive foramina compared to the modern burrowers *Rhizomys* and *Cannomys* with a stout skull, indicating less subterranean habits. In contrast the skulls of the bamboo rats *Miorhizomys nagrii* and *Miorhizomys choristos* (Flynn, 1982; Flynn et al., 1990) have solid incisors, short snouts and incisive foramina, all pointing towards a fossorial lifestyle (Table 2).

Rhizomyides lydekkeri molars are significantly larger than any known species of *Rhizomyides*. The upper and lower dentition of *Rhizomyides lydekkeri* differs from the Late Miocene (6.5-5.5 Ma) Siwalik species of *Rhizomyides sivalensis* being larger in size with a smaller posterior enamel lake on M3. The much smaller early Late Miocene (11.2-10.1 Ma) taxon *Rhizomyides punjabiensis* differs from the present species in having a shallow dentary, masseteric crest with a short anterior extension, and weak inflation; a short mesolophid on m2 and m3, a mesostyle on M1 and no posterior enamel lake on M3. The intermediate-size *Rhizomyoides carbonnelli* from the Late Miocene-Early Pliocene of Pul-e Charkhi, Kabul, Afghanistan (Brandy, 1979a, b, 1981) has short mesolophids on m2m3; an anterosinusid on m3; metaloph and posteroloph separate on M2, and no mesoloph on M3. *Rhizomyides platytomeus* from the Pliocene Sarobi Basin, Afghanistan (Flynn et al., 1983) rivals *R. lydekkeri* in size, but can be separated in having a constricted mure on m2 and a short
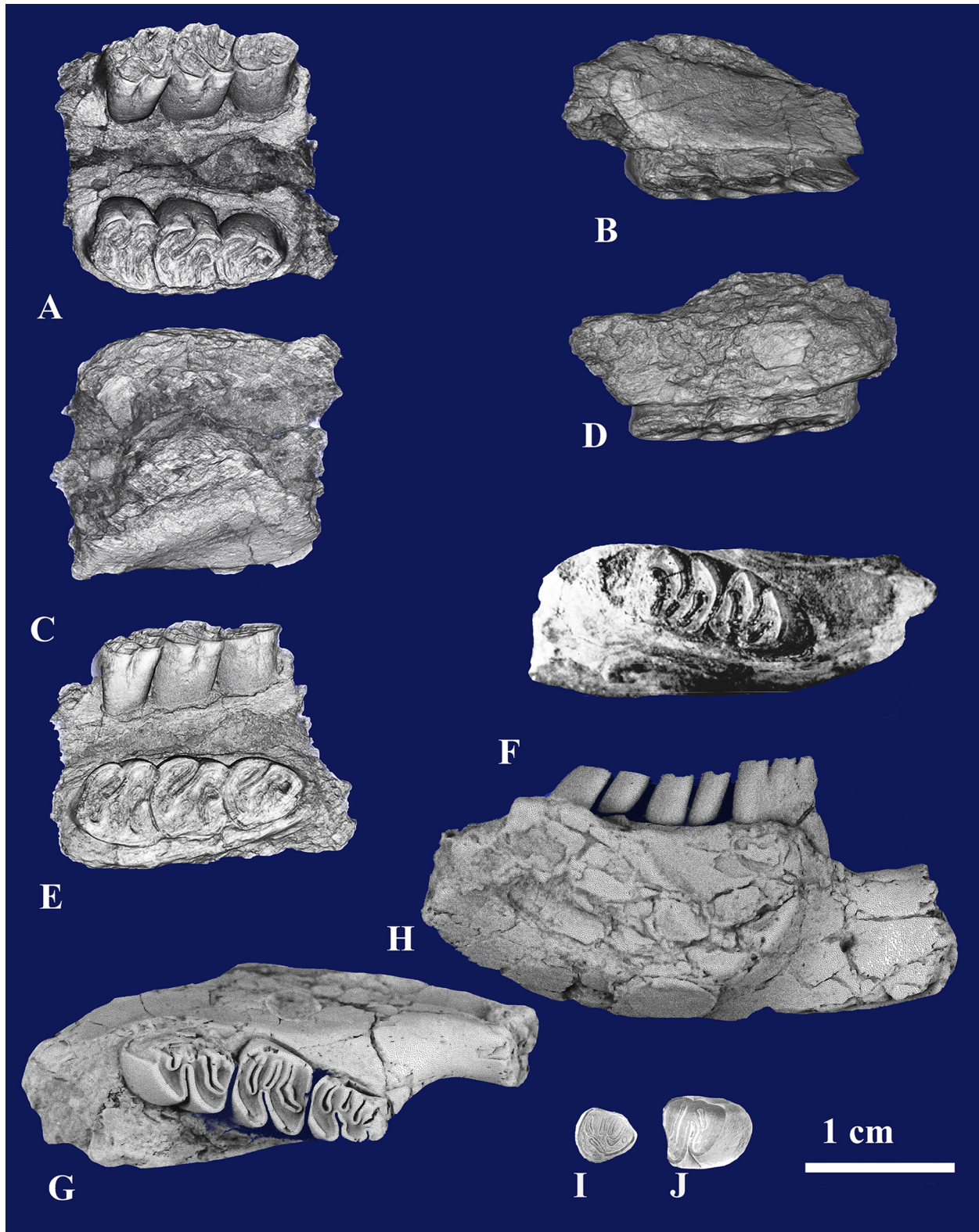
FIGURE 4. *Rhizomyides lydekkeri* from Kanthro and Saketi villages, Himachal Pradesh. A-E, PU KR-1, palate with all the teeth preserved; F, GSI-19549 partial mandible with m2m3 and i1, assigned as *R. saketiensis* (Gupta et al., 1978); G and H, occlusal and labial views of the mandible, the type specimen of *R. lydekkeri* NHMUK PV OR 15925; I, VPL/RP-SM-79, isolated M3 and J, VPL/RP-SM-80 isolated m3 formerly assigned respectively as *Rhizomyides* sp. and cf. *Brachyrhizomys* by Patnaik (2001).

mesolophid on m3. *Rhizomyides mirzadi* (Lang and Lavocat, 1968) a poorly-represented form from the Late Miocene of Afghanistan can be distinguished from *Rhizomyides lydekkeri* by its smaller size, short mesolophids on m2-3, and in having a masseteric crest with a short anterior extension but no inflation.

Rhizomyides lydekkeri differs from Middle Miocene *Kanisamys indicus* (16.8-11.4 Ma, Flynn et al., 2020) in having upper and lower molars with long and complete mesolophs/ mesolophids. Molars of *Kanisamys indicus*, *K. potwarensis,* and Late Miocene *K. sivalensis* are smaller, lower crowned and less lophodont than those of *Rhizomyides lydekkeri.* Among larger tachyoryctins from the Siwaliks (but smaller than *R. lydekkeri*) *Protachyoryctes tatroti* (Hinton, 1933) from the Latest Miocene (6.9-6.5 Ma) Dhok Pathan Formation (Flynn, 1982) has shallow sinusids. Compared to *Rhizomyides lydekkeri,* m2 of *Protachyoryctes tatroti* and Late Miocene *Eicooryctes kaulialensis* (Flynn, 1982) are more hypsodont. Lower molars of Plio-Pleistocene *Anepsirhizomys pinjoricus* are very hypsodont, have their lingual and labial sinusids open, and the mesolophids are short lying close to the hypolophids. The species of African *Tachyoryctes* have hypsodont teeth, lack a mesolophid on the m2 and m3 and protosinus on the M1.

The extinct bamboo rats (Rhizomyini) differ at the tribe level in many features. The molars of *Miorhizomys nagrii, Miorhizomys harii* and *Miorhizomys choristos* are smaller, with short mesolophs/mesolophids, no protosinus on M1, and lack ornamentation on i1 (Flynn, 1982, Patnaik, 2020). Species of the modern rhizomyines *Rhizomys* and *Cannomys* clearly differ dentally from the present species in having a mesolophid on m2 a long continuation of the protoconid, no mure on lower molars, no ornamentation on lower incisors.

Phylogenetic analysis of Rhizomyine rodents

A phylogenetic analysis was carried out to determine the affinity of *Rhizomyides lydekkeri.* For phylogenetic analysis we constructed a morphological character matrix of thirty-nine ingroup rhizomyine taxa with the early spalacid *Debruijnia arpati* as outgroup (Table 3). The most parsimonious tree was constructed based on a total of 44 morphological characters, all characters were parsimony informative.

López-Antoanzas et al. (2013) published a comprehensive cladistic study for spalacids. We placed *Rhizomyides lydekkeri* in the phylogenetic tree of rhizomyines based on the features they identified for upper and lower molars and incisors.

1. Hypsodonty: Crown height on at least one side of the tooth greater than length or width of the tooth. This character has been scored as (0) absent; (1) moderate; (2) high.
2. Size: Length of the m2: (0) 1.5-2.5 mm; (1) 2.5-3.5 mm; (2) 3.5-4.5 mm; (3) 4.5-5.5 mm; (4) >5.5 mm.
3. Lophodonty: (0) weak; (1) moderate; (2) high.
4. Masseteric crest: (0) with long anterior extension; (1) with short anterior extension; (2) without anterior extension.
5. Lower masseteric crest: (0) inflated under m2; (1) not inflated.
6. Dentary depth: (0) shallow; (1) moderate; (2) deep.
7. Infraorbital foramen: (0) with ventral slit; (1) with abbreviated ventral slit; (2) without ventral slit.
8. Longitudinal ornamentation on the i: (0) double ridge; (1) single ridge; (2) absent.
9. Anteroconid on the m1: (0) discernible); (1) absent (fused with the anterolophid).
10. Mure on the m1: (0) present; (1) constricted; (2) absent.
11. Labial anterolophid on the m1: (0) present; (1) absent.
12. Mesolophid on the m1: (0) long and complete and separated from the hypolophid; (1) short and well separated from the hypolophid; (2) short and migrated towards the hypolophid; (3) absent; (4) a long continuation of the protoconid.
13. Posterior protoconid–metaconid connection on the m1: (0) present; (1) absent.
14. Anterosinusid on the m1: (0) present; (1) absent.
15. Mure on the m2: (0) present; (1) constricted; (2) absent.
16. Mesolophid on the m2: (0) long and complete and separated from the hypolophid; (1) short and well separated from the hypolophid; (2) short and near the hypolophid; (3) absent; (4) a long continuation of the protoconid.
17. Labial anterolophid on the m2: (0) present; (1) absent.
18. Hypolophid on the m2: (0) not isolated; (1) isolated.
19. Protosinusid on the m2: (0) present; (1) absent.
20. Anterosinusid on the m2: (0) present; (1) absent.
21. m3: (0) reduced (shorter than the m2); (1) enlarged (equal or larger than the m2).
22. Labial anterolophid on the m3: (0) present; (1) absent.

23. Mure on the m3: (0) present; (1) absent.

24. Mesolophid on the m3: (0) long and complete, separated from the hypolophid; (1) short, well separated from the hypolophid; (2) short, near the hypolophid; (3) absent; (4) a long continuation of the protoconid.

25. Posterosinusid on the m3: (0) large; (1) small; (2) absent (posterolophid fused with hypolophid).

26. Entoconid on the m3: (0) not distinguished; (1) distinguishable.

27. Protosinusid on the m3: (0) present; (1) absent.

28. Anterosinusid on the m3: (0) present; (1) absent.

29. Roots on the M1: (0) three; (1) four; (2) Hypselodont. (four roots on M1 is a modern rhizomyin trait.)

30. Protosinus on the M1: (0) present; (1) absent.

31. Mesoloph on the M1: (0) absent; (1) short; (2) long and complete; (3) long and complete but divided with a buccal cusp.

32. Mesostyle on the M1: (0) may be present; (1) absent.

33. Ectoloph on the M1: (0) present; (1) absent.

34. Anterocone on the M1: (0) distinct; (1) fused with the anteroloph.

35. Metaloph on the M1: (0) present and distinct from the posteroloph; (1) fused with the posteroloph.

36. Posterosinus on the M1: (0) present; (1) absent.

37. Mesoloph on the M2: (0) absent; (1) short; (2) long and complete; (3) long and complete but divided with a buccal cusp.

38. Longitudinal crest on the M2: (0) present; (1) absent.

39. Ectoloph on the M2: (0) present; (1) absent.

40. Metaloph on the M2: (0) present and distinct from the posteroloph; (1) early fused with the posteroloph; (2) absent.

41. Posterosinus on the M2: (0) present; (1) absent.

42. Anterosinus on the M3: (0) open; (1) enclosed by anteroloph and paracone; (2) absent.

43. Mesoloph on the M3: (0) absent; (1) short; (2) long and complete; (3) long and complete but divided with a buccal cusp.

44. Posterior lake on the M3: (0) large; (1) small; (2) absent.

RESULTS AND DISCUSSION

Phylogenetic analysis produced 50% majority rule consensus of 43 trees (Fig. 5); this was supported by modest bootstrap values. The phylogenetic analysis shows that our specimens share closest affinity with *Rhizomyides*. Initial attempts to identify the evolutionary relationships between extinct and extant Rhizomyinae based on synapomorphies of many genera were carried out by Flynn (1990) and López-Antoanzas et al. (2013). According to López-Antoanzas et al. (2013), the Asian *Prokanisamys* is the most basal genus of the ingroup, followed by the East African *Nakalimys*; our phylogenetic study supports their findings. *Prokanisamys* is also the oldest known genus of a monophyletic Rhizomyinae subfamily supported by characters; short anterior extension of masseteric crest; mesolophid on the m2 short and well separated from the hypolophid; mesolophid on the m3 long and complete, separated from the hypolophid. *Pronakalimys* and *Nakalimys* are an early African branch followed by *Kanisamys* and supported by lower masseteric crest inflated under m2; moderate dentary depth; mesolophid of m2 short and migrated towards the hypolophid; open anterosinus on the M3. *Kanisamys* comprises a sequential array of Asian species; *K. indicus* is supported by mesolophid on the m1 long and complete, separated from the hypolophid; retained posterior protoconid-metaconid connection on the m1.

Kanisamys potwarensis and more derived taxa are supported by presence of ectoloph on the M1; metaloph on the M1 fused with the posteroloph; absence of posterosinus on the M1 and metaloph on the M2 early fused with the posteroloph. *Kanisamys nagrii* has greater lophodonty, labial anterolophid lost on m2 and m3 with protosinusid absent on m2 and m3. *Kanisamys sivalensis* supported by hypsodont uppers; short mesoloph on the M1; metaloph on the M1 present and distinct from the posteroloph; presence of posterosinus on the M1. Two Miocene species previously considered as congeners with *Rhizomyides sivalensis* plot next to primitive *Miorhizomys*. These are *Rhizomyides mirzadi* and *R. punjabensis,* their node supported by m1 mesolophid short and well separated from the hypolophid; presence of labial anterolophid on the m3. *Miorhizomys micrus* and other derived taxa show a large posterosinusid on the m3; large posterior lake on the M3. *Rhizomys shajius* and *Miorhizomys harii* node is supported by constricted mure on the m1 and m2; *M. blacki and M. nagrii* node is supported by the absence of anterosinusid on the m1; mesolophid on the m2, long and complete and separated from the hypolophid.

Protachyoryctes tatroti and *Tachyoryctes makooka* node is supported by short mesolophid migrated toward the

TABLE 3. Character coding matrix used in the study (as per López-Antoanzas et al., 2013)) for the relationships between *Rhizomyides saketiensis* and other extinct and extant rhizomyine rodents.

Taxa/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Rhizomyides lydekkeri	2	1&3	2	0	0	2	2	1	1	1	1	0	0	0	0	0	1	0	1	1	1	1	0	0	0	0	1	1	0	0	2	1	1	1	1	1	2	1	1	1	1	1	2&3	1&0
Debruijnia arpati	0	0	1	?	?	?	?	?	?	0	0	0	0&1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	2	0	0	0	0	0	2	0
Rhizomys sumatrensis	2	4	2	2	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	0	1	1	1	4	2	1	1	1	1	1	3	1	1	1	1	1	3	1	1	1	1	2	3	2
Rhizomys sinensis	2	4	2	2	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	0	0	1	1	4	2	1	1	1	1	1	3	1	1	1	1	1	3	1	1	1	1	2	3	2
Rhizomys pruinosus	2	4	2	2	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	0	1	1	1	4	2	1	1	1	1	1	3	1	1	1	1	1	3	1	1	1	1	2	3	2
Rhizomys shansius	1	3	2	2	1	2	2	2	1	2	1	0	1	1	2	4	1	1	1	0	1	1	1	4	2	0	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	1	2	2
Rhizomys shajius	1	2	2	2	?	1	?	?	?	?	?	?	?	?	1	2	1	0	1	1	1	1	0	2	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cannomys badius	2	0&1	2	1	1	2	2	2	1	2	1	4	1	1	2	4	1	1	1	?	1	1	1	4	2	1	1	1	1	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2
Miorhizomys nagrii	1	1&2	2	1	1	1	1	2	1	0	1	0&1	1	1	0	0	1	0	1	1	0	1	0	0&2	1	0	1	1	0	1	2&3	0	1	1	1	1	2	0	1	1	1	1	1&2	1
Miorhizomys micrus	1	1	2	1	1	1	?	2	1	0	1	0	1	0	0	2	1	0	1	0	1	1	0	2	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miorhizomys blacki	1	2	2	2	1	1	1	2	?	?	?	?	?	?	0	0	1	0	1	1	1	1	0	2	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miorhizomys pilgrim	1	3	2	2	1	1	1	2	?	?	?	?	?	?	2	4	1	0	1	1	1	1	1	4	1&2	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miorhizomys harii	1	2	2	1	1	?	?	2	1	1	1	0	1	0	1	1	0	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miorhizomys tetracharax	1	2&3	2	2	1	1	1	2	1	1	1	0	1	0	1	0	1	0	1	0	1	1	1	4	2	1	0	0	1	?	?	?	?	?	?	?	2	1	1	?	0	1	1	1
Miorhizomys choristos	1	2&3	2	2	1	1	1	2	1	1	1	0&1	1	1	2	4	1	0	1	1	1	1	1	4	2	1	1	1	1	1	0	1	1	1	1	1	3	1	1	1	1	0	1	1
Protachyoryctes tatroti	1	2	2	0	0	1	?	1	1	0	1	2	1	0	1	2	1	0	1	0	1	1	0	2	0	0	1	0	0	0	2	1	1	0	1	1	2	0	1	1	1	?	?	?
Tachyoryctes makooka	1	1&2	2	?	?	?	1	?	1	1	1	2	1	0	1	2	1	0	1	0	1	1	0	2	0	0	1	0	0	0	2	1	1	1	1	1	2	0	1	1	1	1	2	2
Tachyoryctes pliocaenicus	1	0&1	2	0	0	1	1	1	1	2	1	2	1	0	2	2&3	1	0	1	0	1	1	1	3	1	0	1	0	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2
Tachyoryctes macrocephalus	2	2	2	0	0	1	1	1	1	2	1	3	1	0	2	3	1	0	1	1	1	1	1	3	2	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2
Tachyoryctes splendens	2	0&1	2	0	0	1	1	1	1	2	1	3	1	0	2	3	1	0	1	1	1	1	1	3	2	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2

TABLE 3. Continued.

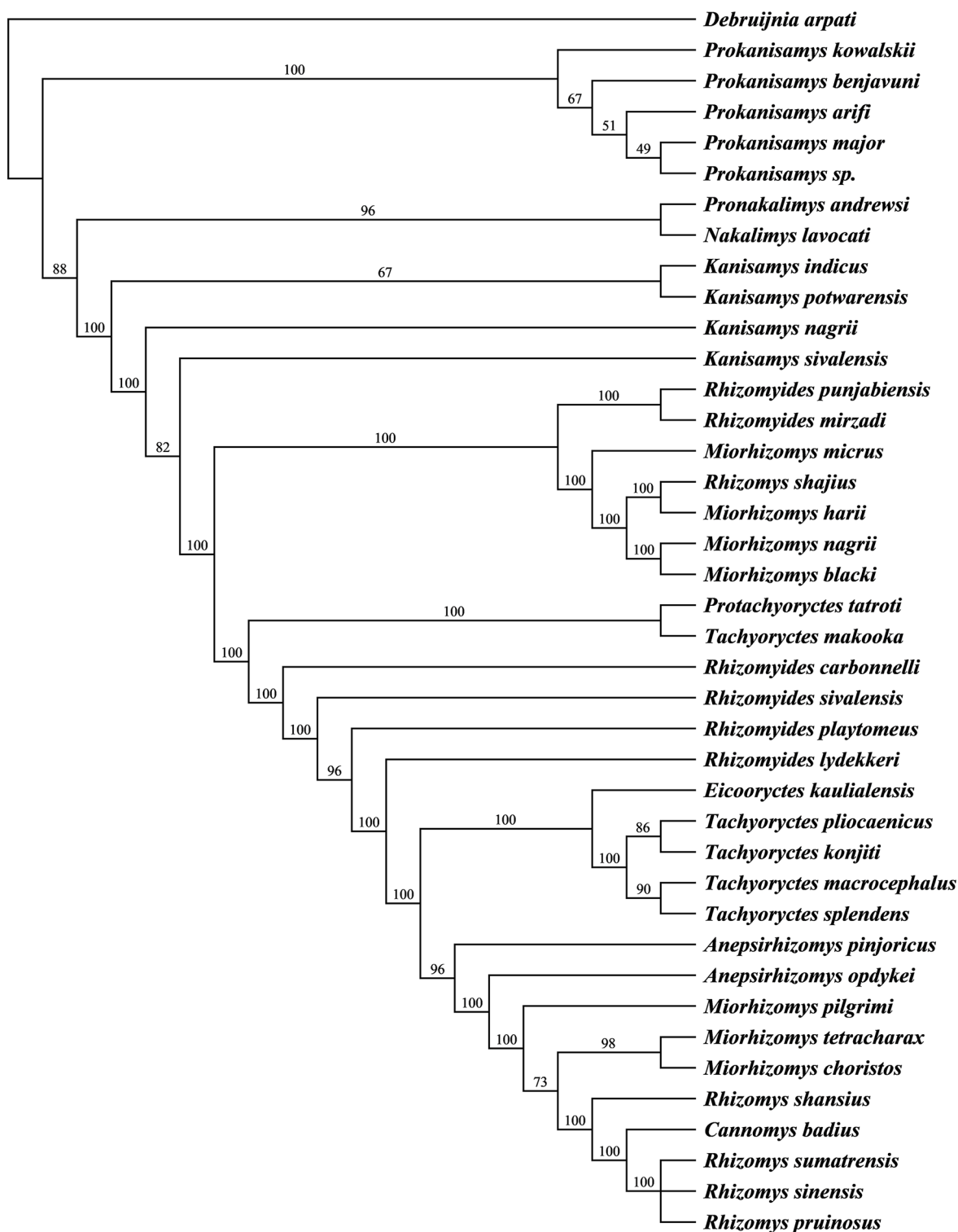| Taxa/Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Rhizomyides sivalensis	1	3	2	0	0	1	?	1	1	0	1	0	0	0	0	0	1	0	1	1	1	1	0	2	0	0	1	0	0	0	2	1	1	1	1	1	2	0	1	1	1	1	?	0
Rhizomyides punjabiensis	1	1	1	1	1	1	?	1	1	0	0	1	1	0	0	1&2	1	0	1	1	1	0	0	2	0	0	1	0	0	0&1	1&2	0	1	1	1	1	2	0	1	1	1	1	2	0
Rhizomyides carbonnelli	1	2	2	0	0	1	?	1	1	0	1	0	0	?	0	2	1	0	1	1	1	1	0	2	0	0	1	1	?	?	?	?	?	?	?	?	2	0	1	0	?	?	0	?
Rhizomyides playtomeus	1	3	2	0	0	1	?	1	1	0	1	0	0	?	1	0	?	0	1	1	1	?	?	2	0	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tachyoryctes konjiti	1	1	2	?	?	?	?	1	1	2	1	3	1	0	2	3	1	0	1	1	1	1	1	3	2	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	2	2	2
Kanisamys indicus	1	0	1	0	1	0	?	0	1	0	0&1	0	0&1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1&2	0	1	0	0	1	1	0
Kanisamys nagrii	1	0&1	2	0	1	0	1	1	1	0	0&1	0	0&2	1	0	0	2	1	0	1	0	1	0&1	0	2	0	0	1	0&1	0	0	1	0	1	0	0	2	0	1	0	0	1	1	0
Kanisamys sivalensis	1	1	2	0	1	0	1	1	1	0	0&1	0	0&2	1	0	0	2	1	0	1	0	1	1	0	2	0	0	1	0&1	0	0	1&2	0	1	0	1	2	0	1	0	0	1	1	0
Kanisamys potwarensis	1	0&1	1	0	1	0	?	1	1	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	2	0	1	1	0	1	1	0&1
Eicooryctes kaulialensis	2	1	2	1	0	1	?	1	1	1	1	2	0	1	1	2&3	1	0	1	1	1	1	0	3	0	0	1	1	2	1	2	1	1	1	1	1	2	1	1	1	1	?	?	?
Anepsirhizomys opdykei	2	4	2	2	1	1	?	?	1	1	1	0	0	?	2	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Anepsirhizomys pinjoricus	2	3	2	0	?	1	?	1	1	?	1	0	0	1	2	0	1	0	1	1	1	1	1	0	2	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pronakalimys andrewsi	0	0	1	0	0	1	?	?	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	0	0	0	1	0	1	0	0	0	0	1	1	2
Nakalimys lavocati	0	1&2	1	0	0	1	?	1	1	0	1	0	0	0	2	0	0	0	0	1	0	0	0&1	0	0	0	0	0	0	0	1	1	1	0	0	0	0&1	0	1	0	0	0	1	0
Prokanisamys kowalskii	0	0	0	?	?	?	?	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0	1	0
Prokanisamys arifi	0	0	0	?	?	?	?	0	0	0	0	0&1	0	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0&1	0	0	0	0	1	1	0
Prokanisamys benjavuni	1	0	1	?	?	?	?	?	0	0	0	1	0	0	0	1	0	0	0	0	0	0&1	0	1&3	0	0	0	0	0	1	0&1	1	0	0	0	0	1	0	0	0	0	0	0&1	0
Prokanisamys major	0	0	0	1	1	0	?	?	0	0	0	1	0	0	0	1	0	0	0	0	1	0&1	0	0&1	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	1	1	0
Prokanisamys sp.	0	0	0	?	?	?	?	?	?	?	?	?	?	?	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0&1	1	0	0	0	0	0	?	?	?	?	?	?	?
Rhizomyides mirzadi	1	1&2	2	1	1	?	?	?	1	0	1	1	0	0	0	2	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	1	1	?	?	?	?

Majority-rule consensus tree

FIGURE 5. Cladogram illustrating the placement of *Rhizomyides lydekkeri* in relation to other fossil Rhizomyinae and their extant counterparts. 50% majority rule consensus of 49 trees shown above with bootstrap values assigned on branches. Branch swapping algorithm: tree bisection-reconnection (TBR) with reconnection limit = 8. Total number of rearrangements tried = 50000000, Score of best tree (s) found = 166. Number of trees retained = 49. Consistency index (CI) = 0.4398. Homoplasy index (HI) = 0.5602. Retention index (RI) = 0.8086. Rescaled consistency index (RC) = 0.3556.

hypolophid. The latter species represents an early expansion to East Africa. *Rhizomyides carbonnelli* and derived *R. sivalensis* and *R. platytomeus* are supported by lower masseteric crest inflated under m2; presence of posterior protoconid-metaconid connection on m1; length of m2 between 4.5 and 5.5 mm. *Rhizomyides lydekkeri* shows deeper dentary depth.

Eicooryctes kaulialensis is supported by length of m2 between 2.5 and 3.5 mm; and absence of mesolophid on m2. In this interpretation, it is at the base of a second expansion of tachyoryctines into East Africa: *Tachyoryctes macrocephalus* and derived *T. splendens, T. pliocaenicus* and *T. konjiti* are supported by absence of mure on m1; absence of posterior protoconid-metaconid connection on m1 and presence of anterosinusid on m1.

Anepsirhizomys is the first of the derived bamboo rats. *A. pinjoricus* and later derived taxa show a masseteric crest with reduced anterior extension. *A. opdykei* displays great hypsodonty and absence of posterior protoconid-metaconid connection on m1. *Miorhizomys pilgrimi* has mesolophid on m2 as a long continuation of the protoconid. *Miorhizomys tetracharax* and *M. choristos* lack mesoloph on the M1 but have short mesoloph on the M3 and small posterior lake on the M3. *Rhizomys shansius* shows entoconid as part of hypolophid on the m3; *Cannomys badius* and the extant *Rhizomys* species show incomplete mesoloph ending short of a buccal cusp on upper molars in early wear.

Flynn (1982, 1990) observed that, *Rhizomyides* and later *Kanisamys* shared many traits such as similar degree of hypsodonty, inclined masseteric crest, a strongly rounded I1, a large posterior enamel lake on M3. These observations led Flynn (1983) to suggest an earlier Miocene origin of *Rhizomyides* than reflected by its first occurrence in the fossil record and that it could have evolved from earlier *Kanisamys*. The fact that *Rhizomyides sivalensis* retained a strong mesolophid on the M2 (usually reduced in *K. sivalensis*) led Flynn (1982) to suggest that *R. sivalensis* may have evolved from *Kanisamys* outside Pakistan before the temporal range of *K. sivalensis* and later immigrated to the Potwar Plateau. The present partial skull displays several features similar to *Kanisamys* (Table 2). Our analysis is consistent with the hypothesis that *R. sivalensi*s immigrated to the Indian subcontinent and supports affinity of Siwalik *R. sivalensis* with the Afghan *R. carbonnelli* and *R. platytomeus*. Further, our hypothesis also allows later interchange of the

Rhizomyides lineage between Afghanistan and Indo-Pakistan.

Our results support the hypothesis by López-Antoanzas et al. (2013) and López Antoñanzas and Wesselman (2013) that the first dispersal of a tachyorhyctine (represented by Asian *Protachyoryctes tatroti*) to Africa (represented by *Tachyoryctes (Protachyoryctes) makooka*) likely happened in the Late Miocene, before the appearance of *Rhizomyides lydekkeri*. A second dispersal event to East Africa involving *Tachyoryctes pliocaenicus* could have taken place during the Pliocene (Fig. 5).

CONCLUSIONS

The distinct features of the newly discovered skull and palate support the definition of a large Plio-Pleistocene rhizomyine in northern India as perceived by Gupta et al. (1978) when they named *Rhizomyides saketiensis*. This form is a junior synonym of *R. lydekkeri,* which up to now had no locality context. We have included this species in a new phylogenetic analysis. Our phylogenetic analysis places *Rhizomyides lydekkeri* among the Late Miocene and Pliocene species of *Rhizomyides* of the Indian subcontinent and Afghanistan such as *R. sivalensis*, *R. carbonnelli*, and *R. platytomeus*. Further, the results are consistent with a dispersalist scenario between Afghanistan and Indo-Pakistan. The features of a low skull profile, extremely elongated and gently curved snout with very long incisive foramina, and strong incisors indicate that *Rhizomyides lydekkeri* was likely a moderately fossorial rodent.

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AUTHOR CONTRIBUTIONS

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