Journal of Paleontology, page 1 of 18

Published by Cambridge University Press
on behalf of The Paleontological Society
0022-3360/22/1937-2337
doi: 10.1017/jpa.2022.41

JOURNAL OF PALEONTOLOGY A PUBLICATION OF THE Paleontological SOCIETY

A new genus of treeshrew and other micromammals from the middle Miocene hominoid locality of Ramnagar, Udhampur District, Jammu and Kashmir, India

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Abstract.—The fossil record of treeshrews, hedgehogs, and other micromammals from the Lower Siwaliks of India is sparse. Here, we report on a new genus and species of fossil treeshrew, specimens of the hedgehog *Galerix*, and other micromammals from the middle Miocene (Lower Siwalik) deposits surrounding Ramnagar (Udhampur District, Jammu and Kashmir), at a fossil locality known as Dehari. The treeshrew from Dehari (*Sivatupaia ramnagarensis* n. gen. n. sp.) currently represents the oldest record of fossil tupaiids in the Siwaliks, extending their time range by ca. 2.5–4.0 Myr in the region. Dietary analyses suggest that the new tupaiid was likely adapted for a less mechanically challenging or more frugivorous diet compared to other extant and fossil tupaiids. The occurrence of *Galerix* has only been recently documented from the Indian Siwaliks and the Dehari specimens help establish the likely presence of a relatively large Siwalik *Galerix* species in the Ramnagar region. In addition to the new treeshrew and hedgehogs, new specimens of the rodents *Kanisamys indicus*, *Sayimys sivalensis*, and Murinae indet. from Dehari help confirm that age estimates for the Ramnagar region are equivalent to the Chinji Formation in Pakistan, most likely corresponding to the middle to upper part of the Chinji Formation.

UUID: http://zoobank.org/56fb160c-2df8-4cd3-be91-af4dc02d0979

Introduction

The Lower Siwalik Subgroup is well exposed in areas surrounding the town of Ramnagar, India, ∼38 km northeast of Jammu city (Udhampur District, Jammu and Kashmir), and contains exposures of Middle Miocene deposits where a large number of fossil-bearing localities have been worked over the past century. In particular, the region is well known for fossil primates, such as *Sivapithecus indicus* Pilgrim, 1910; *Sivaladapis palaeindicus* (Pilgrim, 1932); *Ramadapis sahnii* Gilbert et al., 2017; and *Kapi ramnagarensis* Gilbert et al., 2020; as well as associated large mammals (Brown et al., 1924; Lewis, 1934; Colbert, 1935; Dutta et al., 1976; Vasishat et al., 1978; Thomas and Verma, 1979; Basu, 2004; Gilbert et al., 2014, 2017, 2019, 2020). In recent years, many fossil rodents, including *Kanisamys* cf. *K. potwarensis* Flynn, 1982a; *Kanisamys indicus* Wood, 1937; *Antemus chinjiensis* Jacobs, 1977; *Sayimys sivalensis* (Hinton, 1933); *Megacricetodon daamsi* Lindsay, 1988; *Megacricetodon sivalensis* Lindsay, 1988; *Myocricetodon sivalensis* Lindsay, 1988; *Myomimus* sp.; *Tamias urialis* (Munthe,

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1980); *Punjabemys downsi* Lindsay, 1988; and *Punjabemys mikros* Lindsay, 1988, have also been reported from Ramnagar (Parmar and Prasad, 2006; Sehgal and Patnaik, 2012; Sehgal, 2013; Parmar et al., 2015, 2016, 2017).

Despite growing evidence of a diverse micromammal fauna, to date there are no reports of any treeshrews from Ramnagar, and they are relatively rare in the Indian Siwaliks in general. Previously, Dutta (1975) reported a rib cage, possibly attributable to *Tupaia*, from the Indian Upper Siwaliks, but this specimen has never been formally described or figured (Sargis, 2001). Chopra and Vasishat (1979) recovered a partial cranium of a tupaiid from the Middle Siwaliks of Haritalyangar (Himachal Pradesh State, India), placing it in a new taxon, *Palaeotupaia sivalicus* Chopra and Vasishat, 1979, which firmly established tupaiids in the Indian Siwaliks by ca. 10–8.5 Ma (Pillans et al., 2005). However, most authors since then have followed Luckett and Jacobs (1980) in considering *Palaeotupaia* as virtually identical to extant *Tupaia*, synonymizing the former into the latter genus. The hedgehog *Galerix* is also relatively rare in the Indian Siwaliks, although species such as *Galerix rutlandae* Munthe and West, 1980, and *G. wesselsae* Zijlstra and Flynn, 2015, have been reported from the Lower Siwaliks of the Punjab as well as Sindh Province, Pakistan (Munthe and West, 1980; Zijlstra and Flynn, 2015).

The present study reports newly recovered fossil teeth from the Dehari locality in the Ramnagar region that can be attributed to a new treeshrew genus and species (named below) and a relatively large, indeterminate species of *Galerix*. Additionally, we describe new dental specimens of previously documented rodents, including *Kanisamys indicus* and *Sayimys sivalensis*, as well as specimens of Murinae indet. preserving a mix of *Antemus* and *Progonomys* features. The murines, in particular, are biochronologically informative, and provide an updated age estimate for the Dehari deposits, specifically, and the Ramnagar region, more broadly.

Geological setting

Much of the Ramnagar region has long been considered to be roughly equivalent to the Chinji Formation on the Potwar Plateau, Pakistan (Brown et al., 1924; Pilgrim, 1927; Colbert, 1935; Gregory et al., 1938; Vasishat et al., 1978; Gaur and Chopra, 1983; Nanda and Sehgal, 1993; Basu, 2004). Recent rodent biochronological studies based on limited material suggest the area correlates to the middle or lower half of the Chinji Formation, with an age estimate of ca. 13.8–12.5 Ma (Parmar and Prasad, 2006; Sehgal and Patnaik, 2012; Patnaik, 2013; Gilbert et al., 2014, 2020; Parmar et al., 2015, 2017, 2018; Singh et al., 2018; but see below). Fossil specimens presented here are from the Dehari locality (N32°46′59.4″N, 75°16′39.5″E), ∼0.5 km northeast of Dehari village and ∼5 km southwest of the town of Ramnagar (Fig. 1).This location is part of the same small area of exposures where previously described specimens from Dehari were mapped (Parmar and Prasad, 2006; Parmar et al., 2015, 2017; Singh et al., 2018) and are from the same general stratigraphic position. Lithologically, the sites are dominantly characterized by red to reddish-brown mudstones alternating with thick, fine-grained, gray sandstones. Additionally, thin intraformational clay conglomerate beds containing shells and bivalves are preserved within the paleosols. The present micromammals were recovered from these clay conglomerates by bulk sampling and by a maceration process as described below.

Materials and methods

The micromammal teeth were recovered by macerating ∼200 kg of sediments from Dehari in the Biostratigraphy Lab at the Wadia Institute of Himalayan Geology (WIHG), Dehradun (India), originally collected by R.K. Sehgal (Fig. 1) during the 2017 and 2019 field seasons. The sediments were broken into fragments and then soaked in plastic tubs with buffered acetic acid and water. The loose material was wet sieved through 20, 40, and 60 mesh sieves (ISTM). Material collected in the sieves was dried in the sun and microvertebrates were sorted using a fine brush under a binocular microscope housed at WIHG. The specimens described in this paper are housed in the WIHG, and bear the acronym WIMF/A (Wadia Institute Micro Fossil Series A).

In order to facilitate the study of these small micromammal teeth, three-dimensional (3D) imaging was obtained using high-resolution micro-CT (μCT), housed in the Molecular Imaging Center of the Keck School of Medicine of the University of Southern California (Los Angeles, CA, USA). Each fossil tooth was scanned individually within a plastic sample holder (i.e., centrifuge tube), with the specimen held securely in place using foam and soft cotton to prevent movement artefacts during the scan. Scans were obtained with a GE Phoenix Nanotom M system (GE Inspection Technologies, Lewistown, PA, USA) with the following parameters: voltage = 120; current = 70; filter = 2.5 mm Al + Al 0.5 mm; averaging = 2; magnification = 27.778–33.335; isometric voxel dimensions = 0.00299–0.00359 mm. 3D surface renderings of each specimen were created in Amira 3D v.2021.1 software (Thermo Fisher Scientific, Inc., Waltham, MA, USA) from image stacks of 16-bit unsigned DICOM images after undergoing a median (2 pixel) filter. These 3D surfaces, as shown in Figures 2, 7, and 8, are available to download from MorphoSource (www.morphosource.org) as part of the project "Siwalik Fossils from Ramnagar (Jammu and Kashmir), India."

Following the methods of Selig et al. (2019a, b, 2020), 3D geometric morphometric (3DGM) analyses were conducted using data from the new treeshrew specimen (WIMF/A 4699) in relation to a large sample of extant and fossil treeshrew m2s, where available. The same 18 landmarks taken by Selig et al. (2020) were collected on WIMF/A 4699 in the Avizo v.8.1.1 software (Thermo Fisher Scientific, Inc., Waltham, MA) using the landmark editor function, then the landmark data for this specimen were added to the accessible sample (N = 46) from the Selig et al. (2020) dataset (i.e., two specimens, *Ptilocercus lowii* Gray, 1848 [YPM MAM 10179] and *Dendrogale murina* Schlegel and Müller, 1843, UAM: Mamm 103000 had to be excluded; see Supporting Information [SI] Table 1 and SI Dataset 1 for list of included specimens). A Generalized Procrustes Analysis (GPA) was performed to scale, rotate, and translate the landmark data, followed by a Principal Components Analysis (PCA) in the software package Morphologika2 (O'Higgins and Jones, 2006) using wireframes to visualize

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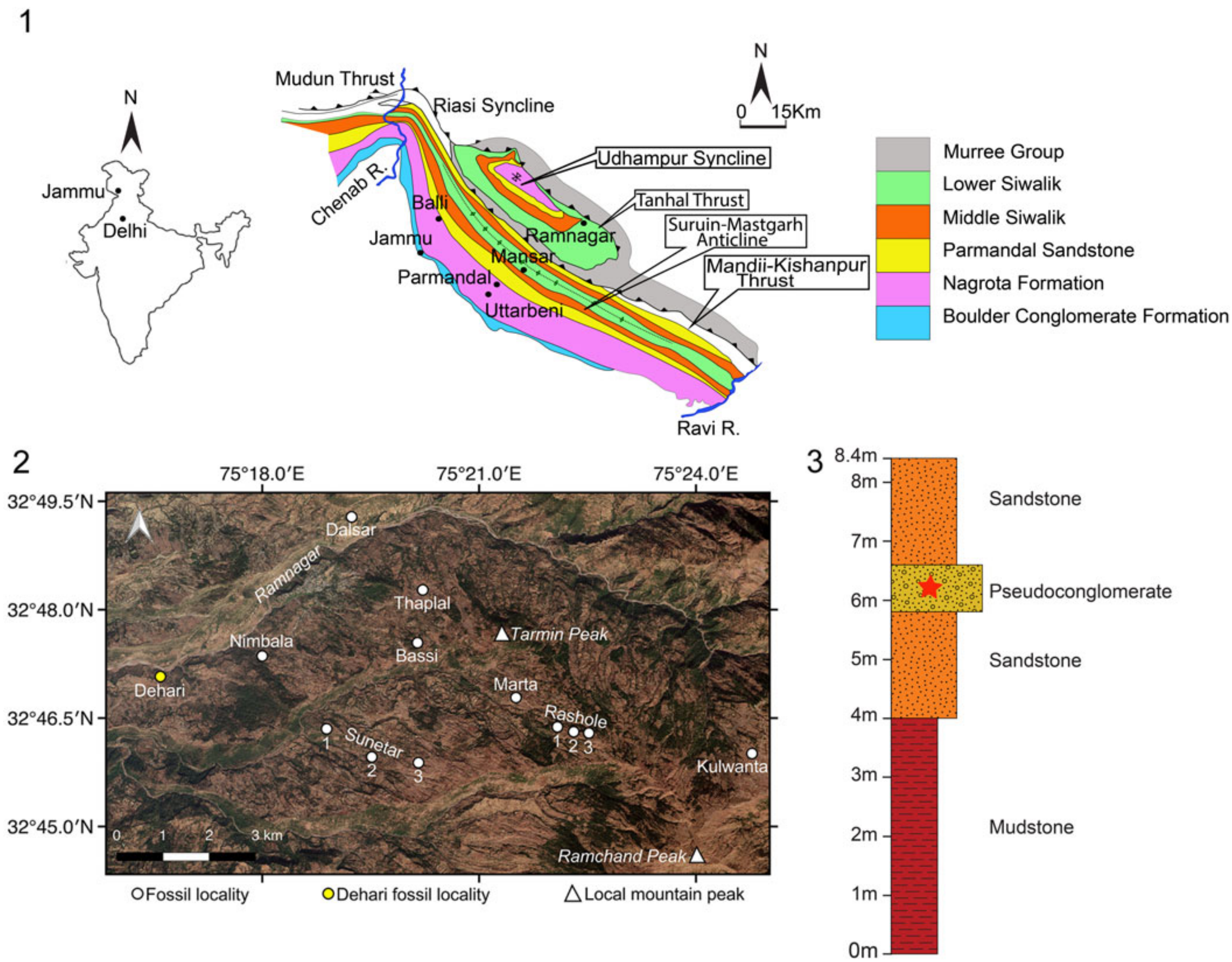

Figure 1. (**1**) General geological map of the Siwaliks Jammu sub-Himalaya (modified after Gupta and Verma, 1988; Basu, 2004). (**2**) Enlarged map of the Siwalik Group surrounding Ramnagar showing the Dehari locality discussed in the text (yellow circle) and other fossil localities. (**3**) Simplified stratigraphic section of the study locality (Dehari).

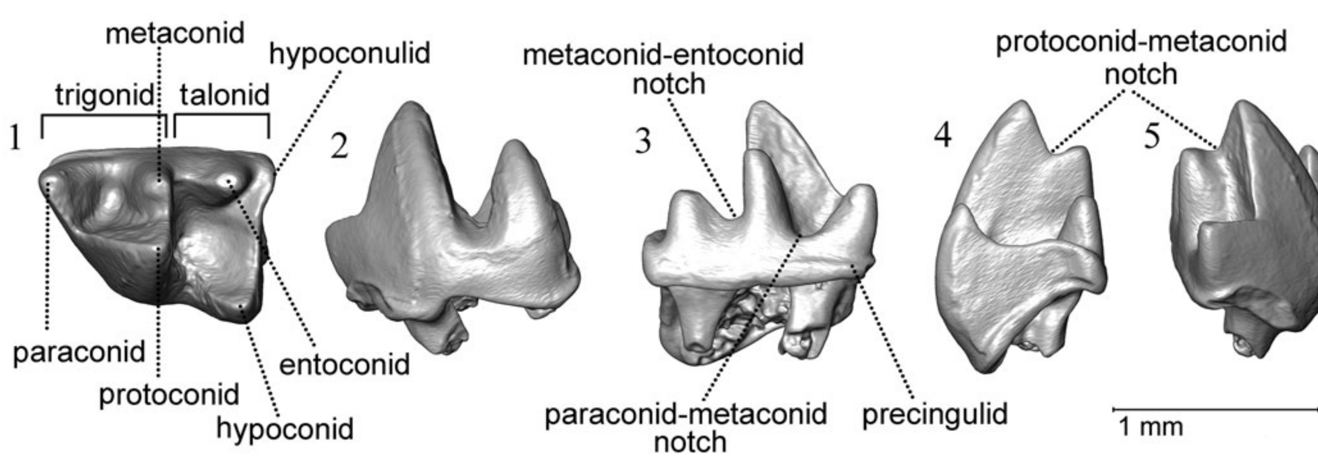

Figure 2. *Sivatupaia ramnagarensis* n. gen. n. sp., WIMF/A 4699 (holotype). 3D surface renderings of tooth in: (**1**) occlusal; (**2**) buccal; (**3**) lingual; (**4**) posterior; (**5**) anterior views.

https://doi.org/10.1017/jpa.2022.41 Published online by Cambridge University Press

Table 1. Comparative dental measurements (mm) of extant and fossil treeshrews. Max Width = maximum width; Max Length = maximum length. Comparative measurements from Chopra and Vasishat (1979), Chopra et al. (1979), Jacobs (1980), Qiu (1986), Mein and Ginsburg (1997), Ni and Qiu (2012), and the current study. *Tupaia glis* (Diard, 1820); *Tupaia minor* Günther, 1876; *Tupaia montana* Thomas, 1892; and *Tupaia miocenica* Mein and Ginsburg, 1997,

Taxon	Specimen No.	Locality	Element	Length (mm)	Trigonid Width (mm)	Talonid Width (mm)	Max Width/ Max Length	Talonid Width/ Trigonid Width	Age
Prodendrogale yunnanica	IVPP V 8282.2	Lufeng, Yunnan, China	M1	2.50	—	—	—	—	Late Miocene
Prodendrogale yunnanica	IVPP V 8281	Lufeng, Yunnan, China	M2	2.25	2.60	—	—	—	Late Miocene
Prodendrogale yunnanica	IVPP V 8282.10	Lufeng, Yunnan, China	M3	1.50	2.60	—	—	—	Late Miocene
Prodendrogale yunnanica	IVPP V 8282.12	Lufeng, Yunnan, China	m1	2.45	1.40	1.60	0.65	1.14	Late Miocene
Prodendrogale yunnanica	IVPP V 8282.13	Lufeng, Yunnan, China	m2	2.40	1.40	1.35	0.58	0.96	Late Miocene
Prodendrogale engesseri	IVPP V 18216.3	Yuanmou, Yunnan, China	M1	2.15	2.53	—	—	—	Late Miocene
Prodendrogale engesseri	IVPP V 18216.4	Yuanmou, Yunnan, China	M2	2.00	2.38	—	—	—	Late Miocene
Prodendrogale engesseri	IVPP V 18216.7	Yuanmou, Yunnan, China	M3	1.65	2.25	—	—	—	Late Miocene
Prodendrogale engesseri	IVPP V 18216.12	Yuanmou, Yunnan, China	m2	2.22	1.42	1.42	0.64	1.00	Late Miocene
Prodendrogale engesseri	IVPP V 18216.13	Yuanmou, Yunnan, China	m3	1.80	1.05	—	—		Late Miocene
Tupaia glis	Sbu:no number	Unknown (Morphosource)	m2	3.25	2.02	2.14	0.66	1.06	Recent
Tupaia glis	Sbu:no number	Unknown (Morphosource)	m2	3.17	2.01	2.25	0.71	1.12	Recent
Tupaia glis	Sbu:no number	Unknown (Morphosource)	m2	3.17	2.01	2.26	0.71	1.12	Recent
Tupaia sp. (cf. *T. glis*)	ummz:58982	Unknown (Morphosource)	m2	3.47	2.16	2.09	0.62	0.97	Recent
Tupaia sp. (cf. *T. glis*)	ummz:58979	Unknown (Morphosource)	m2	3.23	2.18	2.11	0.67	0.97	Recent
Tupaia sp. (cf. *T. glis*)	ummz:58980	Unknown (Morphosource)	m2	3.38	2.25	2.24	0.67	1.00	Recent
Tupaia sp. (cf. *T. glis*)	ummz:58981	Unknown (Morphosource)	m2	3.35	2.23	2.12	0.67	0.95	Recent
Tupaia sp. (cf. *T. glis*)	ummz:58984	Unknown (Morphosource)	m2	3.30	2.22	2.29	0.69	1.03	Recent
Tupaia sp. (cf. *T. glis*)	ummz:58978	Unknown (Morphosource)	m2	3.42	2.38	2.38	0.70	1.00	Recent
Tupaia minor	ummz:117120	Unknown (Morphosource)	m2	2.28	1.35	1.35	0.59	1.00	Recent
Tupaia minor	ummz:117121	Unknown (Morphosource)	m2	2.51	1.47	1.40	0.59	0.95	Recent
Tupaia montana	ummz:113339	Unknown (Morphosource)	m2	3.44	2.04	2.06	0.60	1.01	Recent
Tupaia montana	ummz:123395	Unknown (Morphosource)	m2	3.54	2.22	2.20	0.63	0.99	Recent
Tupaia storchi	IVPP V 18218	Yuanmou, Yunnan, China	m3	2.51	1.60	1.25	0.64	0.78	Late Miocene
Tupaia miocenica	T Li 175	Li Mae Long, Thailand	M2	3.57	4.79	—	—	—	?Miocene
Tupaia sp.	YGSP 8090	Pakistan	?m1/m2	—	—	—	—	—	Late Miocene
Tupaiinae indet.	PUA 15	Haritalyangar, India	M1–M3	—	—	—	—	—	Late Miocene
Tupaiinae indet.	PUA 16	Haritalyangar, India	m2	—	—	—	—	—	Late Miocene
Palaeotupaia sivalicus	PUA I-3	Haritalyangar, India	P3–M2	—	—	—	—	—	Late Miocene
***Sivatupaia ramnagarensis* n. gen. n. sp.**	**WIMF/A 4699**	**Dehari 2, Ramnagar, India**	**m1 or m2**	**1.17**	**0.76**	**0.87**	**0.74**	**1.14**	**Middle Miocene**

differences in shape along the resulting PC axes. For visualization, the Procrustes coordinates were also submitted to a PCA in the software package PAST v.4.03 (Hammer et al., 2001) along with a UPGMA cluster analysis based on the generic-level averages of the first five PC scores among the included taxa to assess phenetic affinities.

In order to make inferences of dietary adaptations about the fossil treeshrew, Dirichlet normal energy (DNE), 3D orientation patch count rotated (3D-OPCR), and relief index (RFI) were measured in WIMF/A 4699 relative to a large sample of other extant and fossil treeshrews previously measured by Selig et al. (2020) (see SI Table 1). These methods are among a suite of dental topographic metrics that quantify functional aspects of the occlusal surface of teeth that can be tied directly to dietary adaptations (Ungar and M'Kirera, 2003; Evans et al., 2007; Boyer, 2008; Bunn et al., 2011, Winchester, 2016). For example, DNE quantifies occlusal curvature, so teeth with sharper crests and cusps have higher DNE values. High DNE values relate to more mechanically challenging diets, such as insects, whereas lower values relate to the processing of soft foods, such as fruit (Bunn et al., 2011; Winchester, 2016). 3D-OPCR is a measure of surface complexity, so teeth with more crests, cusps, and ridges have higher values. High 3D-OPCR values also relate to insectivory, whereas low values relate to the consumption of softer foods, such as fruits (Evans et al., 2007; Winchester, 2016). Finally, RFI is a measure of relative crown height—teeth with relatively taller cusps or relatively taller teeth overall have higher RFI values. High RFI values relate to the consumption of insects, whereas low values relate to the consumption of softer foods (Ungar and M'Kirera, 2003; Boyer, 2008).

Prior to analyzing WIMF/A 4699 for topographic analyses, the 3D surface was simplified to 10,000 faces and smoothed to 100 iterations with a lambda at 0.6 following the protocol of Selig et al. (2019b, 2020). All three topographic metrics were measured using MorphoTester v.1.1.1 software (Winchester, 2016) using the default settings for DNE and the patch count set at 5 for 3D-OPCR. A second PCA was performed on the covariance matrix including the species means of these three topographic metrics, thus allowing visualization of overall variation in dental topography across species in our sample. All 3DGM and dental topographic data were collected by a single observer (KRS). See Selig et al. (2020) for additional methodological details.

The dental terminologies used here follow Jacobs (1978) for murids; Ziegler (1990) for erinaceids; Jacobs (1978), Flynn (1982a), and López-Antoñanzas et al. (2013) for rhizomyines; Baskin (1996) and López-Antoñanzas and Knoll (2011) for ctenodactylines; and Jacobs (1980) for tupaiids.

Repositories and institutional abbreviations.—American Museum of Natural History, New York, NY (AMNH); Geological Survey of India (GSI); Howard University-Geological Survey of Pakistan (H-GSP); Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China (IVPP); Thailand Li Mae Long (T Li); Panjab University Anthropology (PUA); University of Alaska Museum of the North, Fairbanks, AK (UAM); Wadia Institute Micro Fossil Series A (WIMF/A); University of Michigan Museum of Zoology (UMMZ); Pakistan Museum of Natural History (PMNH); Vertebrate Palaeontology Laboratory/Jammu University/Lower Siwalik Mammals (VPL/JU/LSM); Vertebrate Palaeontology Laboratory/Rajeev Patnaik-Haritalyangar Micromammal (VPL/RP-HM); Yale Peabody Museum of Natural History, Yale University, New Haven, CT (YPM); Yale-Geological Survey of Pakistan (YGSP).

Systematic paleontology

Scandentia Wagner, 1855
Tupaiidae Gray, 1825
Genus *Sivatupaia* new genus

Type species.—*Sivatupaia ramnagarensis* n. gen. n. sp., only known species, from the site of Dehari near Ramnagar, Udhampur district, Jammu and Kashmir, India.

Diagnosis.—As for type species (see below).

Etymology.—The genus name *Sivatupaia* is derived from a combination of *Siva*, from being found in the Siwaliks (=Sivaliks), and *Tupaia* for treeshrew.

Remarks.—As for type species (see below).

Sivatupaia ramnagarensis new species
Figure 2

Holotype and only known specimen.—WIMF/A 4699 (Wadia Institute Micro Fossil Series A); moderately worn, left lower m1 or m2 (Fig. 2).

Diagnosis.—*Sivatupaia ramnagarensis* n. gen. n. sp. differs from known extant tupaiid genera *Anathana* and *Dendrogale* in lower molar features, having a well-developed metaconid and entoconid, as well as a relatively vertical hypoconulid. It differs from *Prodendrogale* by having a smaller hypoconulid and a narrower notch separating the entoconid and hypoconulid. It is also much smaller than *Prodendrogale yunnanica* Qiu, 1986 (see measurements in Table 1). *Sivatupaia ramnagarensis* n. gen. n. sp. demonstrates some similarities to the lower molars of *Tupaia* due to its more distinct entoconid, hypoconulid, and vertical hypoconulid. However, it is distinct from all other treeshrew specimens in shape, displaying a combination of a relatively narrow crown, a mesially shifted paraconid, a tall and more lingually shifted protoconid resulting in a narrow trigonid, and a tall trigonid compared to the talonid (See Figs. 3.1, 4.1, and supplementary material SI Dataset 1). *Sivatupaia ramnagarensis* n. gen. n. sp. generally exhibits lower topographic values compared to other extant and fossil treeshrew genera as well (Fig. 5; see also SI Table S1).

Occurrence.—Dehari locality; ∼0.5 km northeast of Dehari village and ∼5 km southwest of the town of Ramnagar, Udhapur District, Jammu and Kashmir, India (Fig. 1); Middle Miocene of Lower Siwaliks.

Description.—WIMF/A 4699 is a moderately worn, left lower m1 or m2 (Fig. 2). As is typical of primitive placentals, it has three cusps in the trigonid (paraconid, protoconid, and

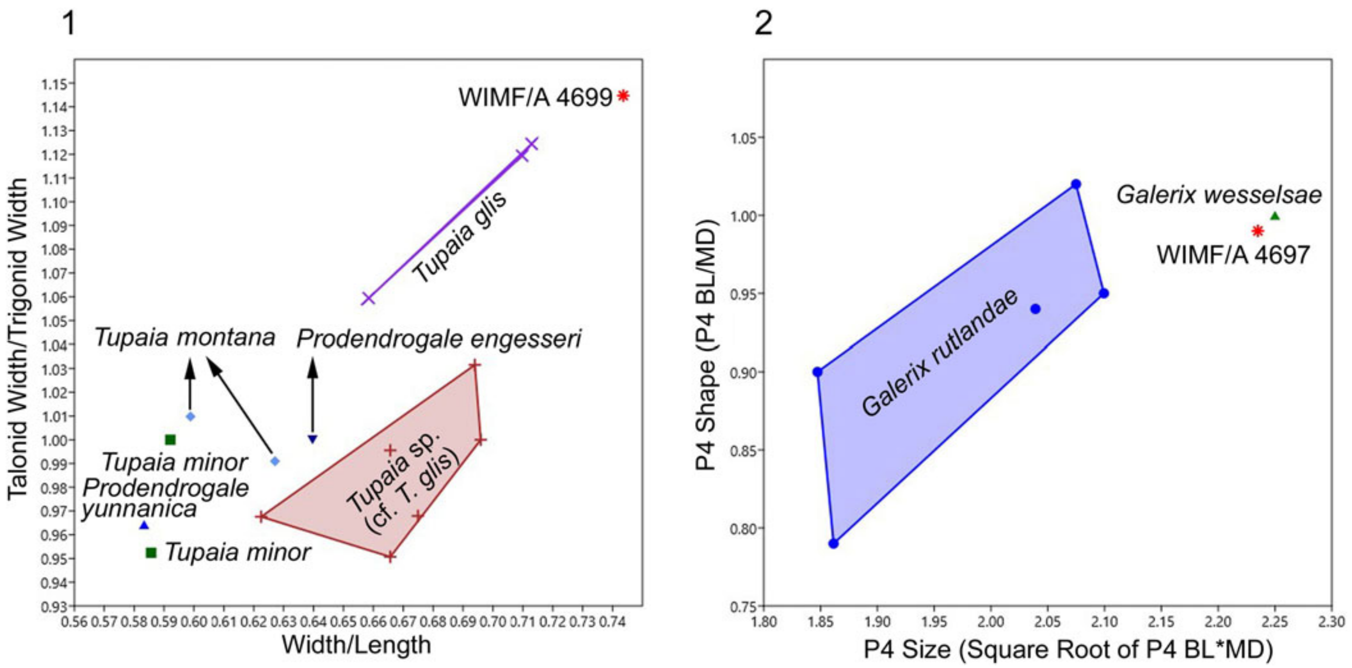

Figure 3. (**1**) Scatterplot of tupaiid m2 specimens illustrating the ratio of tooth width/length vs. talonid width/trigonid width. (**2**) Scatterplot of *Galerix* P4 shape (BL/MD) vs. size (square root of BL*MD).

metaconid) and three in the talonid (hypoconid, entoconid, and hypoconulid). The trigonid basin is narrow and open lingually, with a strong and lingually positioned paraconid that is shorter than the metaconid and protoconid. The metaconid is smaller than the protoconid, but the protoconid is shifted toward the midline of the crown so that it is positioned close to metaconid. The talonid basin is large and closed, and it is ~10–15% wider than the trigonid at its maximum distal breadth (Table 1). The hypoconid is the largest cusp on the talonid, positioned at the distobuccal corner of the crown. The hypoconulid is small and shifted lingually, being located directly posterior to the relatively large entoconid at the distolingual corner of the tooth. The cristid obliqua is relatively mesiodistally oriented, extending from the hypoconid to meet the trigonid at the base of the protoconid, slightly buccal to this cusp. The notch separating the paraconid and metaconid is similar in depth to, or slightly deeper than, the notch separating the metaconid and entoconid. A moderately developed precingulid is present on the mesial end of the tooth and extends around to the lingual part of the trigonid, but no buccal cingulid is present. The specimen preserves the remnants of two roots.

Etymology.—Species name *ramnagarensis* is in reference to the Ramnagar area (Jammu region, India), where the type specimen was found.

Remarks.—WIMF/A 4699 was identified as a tupaiid treeshrew after multiple comparisons with other micromammal taxa. Shrews and most microchiropteran bats generally have a buccal cingulum as well as a paraconid and metaconid that are more deeply separated than the present specimen. The adapisoricids display a hypoconulid on the lower molars that is oriented in a median or slightly lingual position (Krishtalka, 1976a), whereas the hypoconulid of WIMF/A 4699 is more strongly displaced lingually directly behind the entoconid. Early Tertiary erinaceids are characterized by having greatly reduced hypoconulids (Krishtalka, 1976a). The hypoconulid in the present specimen is not greatly reduced.

Within treeshrews, WIMF/A 4699 differs from ptilocercids by the absence of a buccal cingulum and a trigonid that is much higher than the talonid (Li and Ni, 2016). WIMF/A 4699 is most similar to tupaiids on account of the lingual position of the hypoconulid (close to and directly behind the entoconid), the absence of a buccal cingulum, and the lack of a deep notch between the paraconid and metaconid (Jacobs, 1980). Because WIMF/A 4699 displays a well-developed metaconid and entoconid, as well as a relatively vertical hypoconulid, it differs from the genera *Anathana* (Lyon, 1913) and *Dendrogale* (Jacobs, 1980). WIMF/A 4699 compares well with *Prodendrogale yunnanica* Qiu, 1986, from the late Miocene of Lufeng, Yunnan, China, but differs by having a smaller hypoconulid and a narrower notch separating the entoconid and hypoconulid. In addition, the present molar (length = 1.17 mm, trigonid width = 0.76 mm, talonid width = 0.87 mm; see Table 1) is only half the size of the *Prodendrogale yunnanica* m1 (Table 1; original length = 2.45 mm, trigonid width = 1.40 mm, talonid width = 1.60 mm; see Ni and Qiu, 2012, table 1). It is similar to the lower molars that tentatively were attributed to *Tupaia* from Late Miocene deposits of Pakistan (Jacobs, 1980) and Haritalyangar, Middle Siwaliks, India (Chopra et al., 1979) due to its more distinct entoconid, hypoconulid, and vertical hypoconulid. The wider talonid relative to the trigonid in WIMF/A 4699 (Fig. 3.1) is more typical of a tupaiid m1, but m2s sometimes can have a wider talonid to trigonid breadth ratio among tupaiids (see Butler, 1980; Table 1). In addition, among living

Tupaia, a precingulum is never found on m1, but often can be found on m2 or m3 (Steele, 1973). Thus, the specimen is either an m1 or an m2, although the mesially restricted cingulum perhaps makes m2 more likely.

Given the similarity in shape and morphological features seen in isolated m1s and m2s among tupaiids (as evinced by the difficulty in distinguishing them), WIMF/A 4699 was included in a large 3D dataset of extant and fossil treeshrew m2s for morphometric overall shape and dental topographic analyses. A PCA of Procrustes-fitted landmarks demonstrates that WIMF/A 4699 is morphologically distinct from other treeshrew specimens, plotting outside of the extant and fossil treeshrew convex hulls (tupaiid and ptilocercid) at the positive end of PC 1 (Fig. 4.1). PC 1 is related to relative crown breadth, the position of the paraconid, the relative height of the protoconid/trigonid, and the position of the protoconid/relative breadth of the trigonid, with taxa possessing narrower crowns, more mesially shifted paraconids, taller protoconids/trigonids compared to the talonid, and more lingually shifted protoconids resulting in narrower trigonids at the positive end of PC 1. PC 2 seems most closely associated with features such as crown height, paraconid position, protoconid position/trigonid breadth, and hypoconulid/postcristid position, with lower crowns, mesially shifted paraconids, buccally shifted protoconids/wider trigonids, and mesially shifted hypoconulid/postcristids found at the positive end of PC 2. WIMF/A 4699 has an intermediate value on PC 2 and plots within the tupaiid range but outside of the ptilocercid range (Fig. 4.1). Finally, a UPGMA cluster analysis of the first 5 PCs representing ~66.7% of the variation strongly suggests that WIMF/A 4699 is phenetically distinct from all known extant and fossil treeshrews in terms of its overall shape (Fig. 4.4). Thus, in combination with its very small size relative to all known fossil and extant treeshrews, WIMF/A 4699 represents a new genus and species, *Sivatupaia ramnagarensis*, which we place within Tupaiidae for now given its lack of a buccal cingulum (distinguishing it from ptilocercids) combined with other general aspects of shape that are more similar to tupaiids (e.g., relatively tall trigonids, see PC2 and PC3 in Fig. 4.2).

Dietary analyses also demonstrate the distinctiveness of WIMF/A 4699 relative to other scandentians. Dental topographic analyses (DTA) suggest that WIMF/A 4699 generally displays lower topographic values compared to the comparative extant and fossil sample (Fig. 5; see also SI Table 1). Furthermore, a PCA based on the DTA again places WIMF/A 4699 outside of the known range of variation among extant and fossil treeshrews on PC 1, confirming its unique morphology and

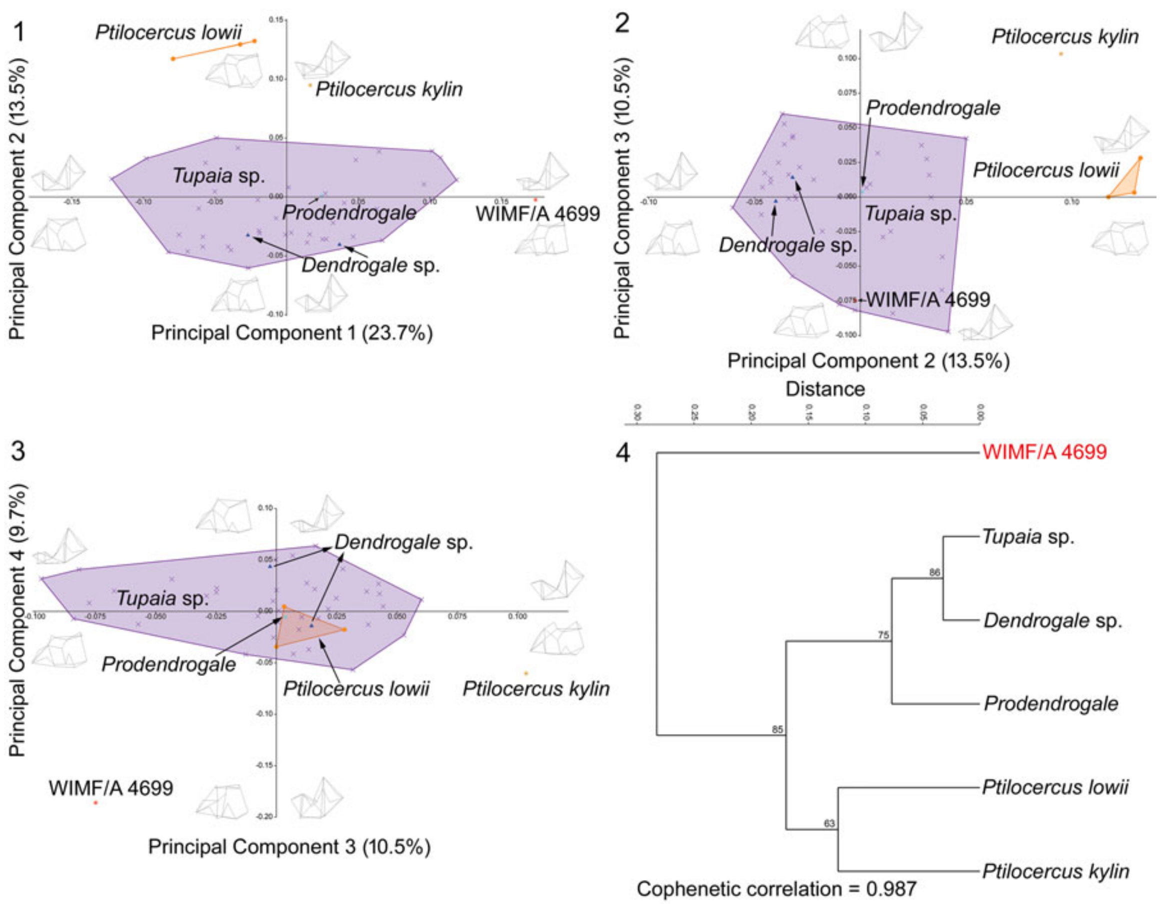

Figure 4. Results of PCA and UPGMA cluster analyses resulting from a 3DGM analysis of m2 shape in extant and fossil treeshrews. Wireframe outlines in occlusal and buccal views representing the extreme shape loadings at the ends of each PC axis are provided for visual comparison. (**1**) PC 1 vs. PC 2; (**2**) PC 2 vs. PC 3; (**3**) PC 3 vs. PC 4; (**4**) dendrogram resulting from UPGMA cluster analysis of genus/species averages for the first 5 PCs. The cophenetic correlation (cc) is high, indicating that the dendrogram is an accurate representation of the pairwise distances among taxa. Note that WIMF/A 4699 is phenetically distant from both extant and fossil tupaiids and ptilocercids. Numbers below branches represent bootstrap support values based on 10,000 replicates.

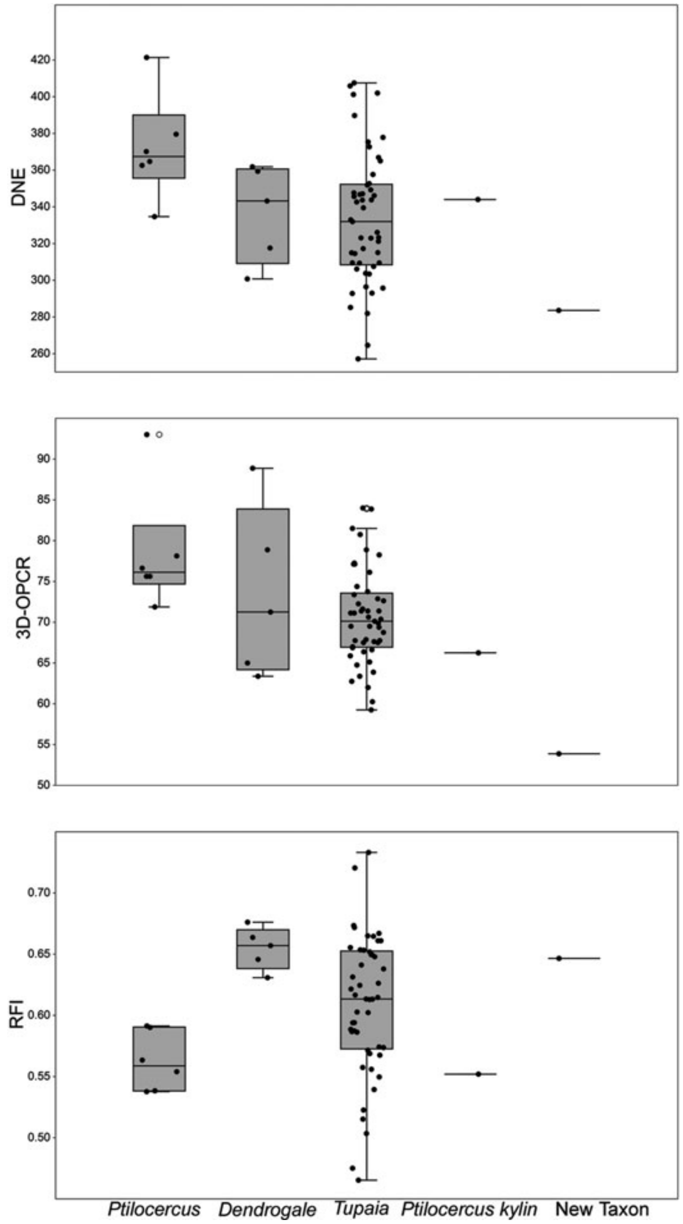

Figure 5. Box plots of DNE, 3D-OPCR, and RFI for species of *Ptilocercus*, *Dendrogale*, and *Tupaia*, along with *Ptilocercus kylin* and the new taxon (*Sivatupaia ramnagarensis* n. gen. n. sp.).

likely dietary adaptations (Fig. 6). Thus, it appears that this newly discovered treeshrew was better adapted to a more frugivorous or less mechanically challenging diet with considerably less shearing than seen in many other scandentian taxa. Whether this is a primitive retention or represents a derived adaptation is currently unknown and will depend on future clarification of the scandentian fossil record and Euarchontan relationships, more broadly.

Eulipotyphla Waddell, Okada, and Hasegawa, 1999
Erinaceidae Fischer, 1814
Genus *Galerix* Pomel, 1848

Type species.—*Galerix exilis* (de Blainville, 1840).

Galerix sp.
Figure 7

Occurrence.—Dehari locality at Ramnagar (Udhampur District, Jammu and Kashmir, India), and K2 Kulwanta locality at Ramnagar (Parmar et al., 2022).

Description.—The outline of WIMF/A 4697's crown is trapezoidal, as is distinctive of *Galerix* P4s. The crown is relatively broad labiolingually and short mesiodistally (max breadth/max length ratio = 0.99). There is a low rounded ridge that curves mesially at the paracone margin, forming a small parastyle. The paracone is the largest cusp. A crest moves downwards posteriorly from the paracone, then turns sharply in a buccal direction (almost 90°), ascending upwards towards the metacone in the distobuccal corner of the crown, forming a sharply demarcated distobuccal notch and flange in occlusal outline. On the lingual side of the crown, the protocone and hypocone are relatively low cusps, and the protocone is slightly larger than the hypocone. The protocone is slightly mesial relative to the paracone, and it is slightly worn on its occlusal surface. The hypocone is distinct and situated just distal to the protocone, directly across from the distinctive buccal notch and mesial to the metacone, such that the protocone and hypocone are spaced much more closely together than the paracone and metacone. A small crest is present between the protocone and hypocone. A posterior cingulum runs along the distal margin of the tooth, from the metacone to the hypocone, with a slight extension at the distolingual corner of the tooth. Three roots appear to have been present, of which the lingual one has the largest diameter.

WIMF/A 4698 is similar in outline and morphology to WIMF/A 4697, but slightly larger and significantly more worn, with damage to both the mesial and distal borders of the crown.

Materials.—WIMF/A 4697 left P4, WIMF/A 4698 right P4.

Remarks.—The present P4 specimens can be referred to the genus *Galerix* on the basis of a large paracone, being broad labiolingually and short mesiodistally, the presence of a small parastyle curving around the paracone margin, a well-developed distal cingulum, and a clear notch on the buccal margin between the metacone and paracone resulting in a distinctive buccal flange at the distobuccal margin of the tooth (Zijlstra and Flynn, 2015). In Pakistan, two species of *Galerix*, *G. rutlandae* and *G. wesselsae*, are distinguished mainly on the basis of size, with smaller specimens belonging to *G. rutlandae* and larger ones referred to *G. wesselsae* (Zijlstra and Flynn, 2015). The present specimens are larger than all measured *G. rutlandae* P4s and are more similar to *G. wesselsae* in size, and the shape of the occlusal crown (width/length ratio) is very similar to the shape of the only complete *G. wesselsae* P4 known (see Table 2; Fig. 3.2). Some caution is needed given that only two P4s are currently known from Dehari and the previously documented sample sizes of *G. rutlandae* and *G. wesselsae* P4s are small, making

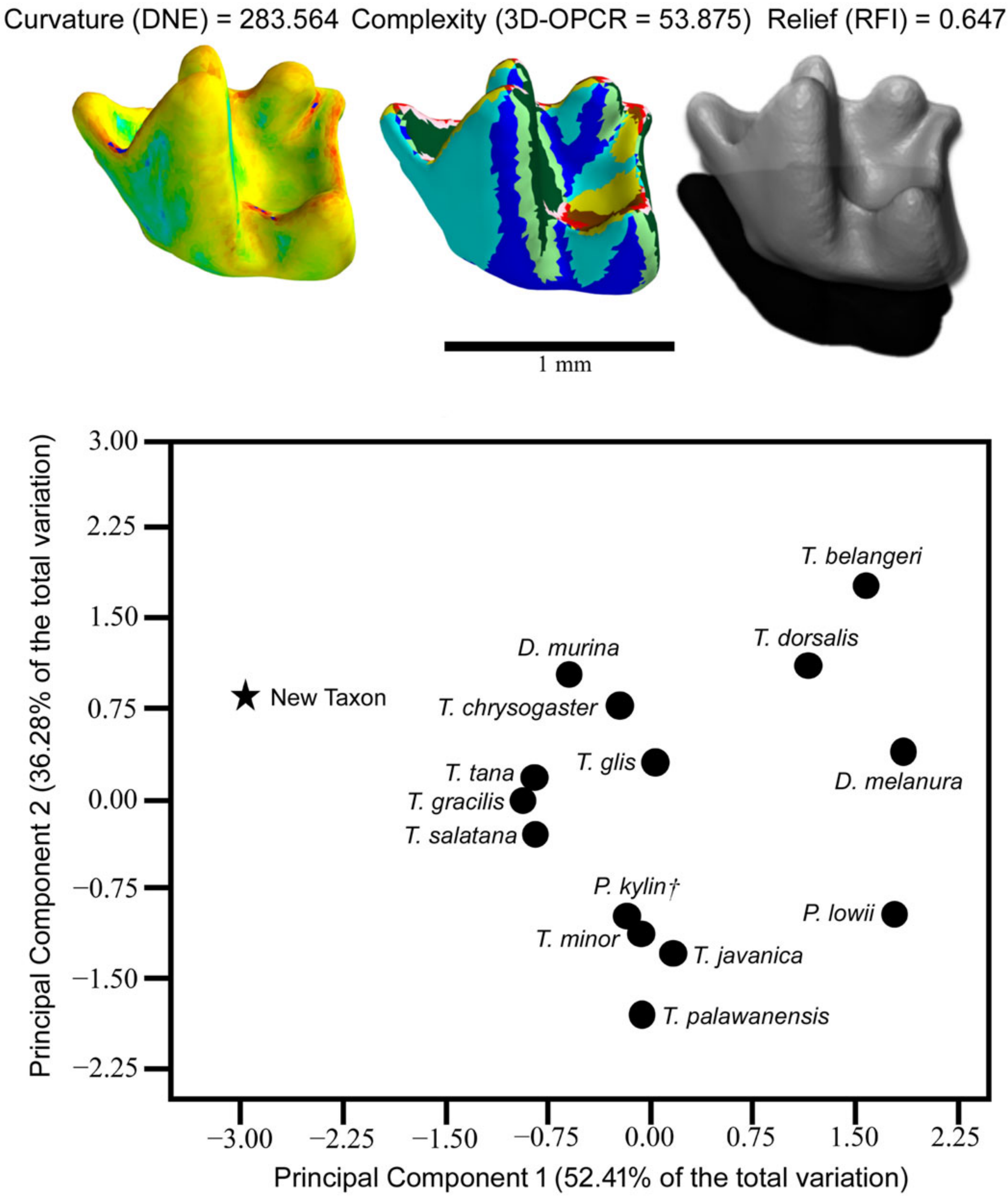

Figure 6. Top: Reconstructed meshes showing the topographic maps of DNE, 3D-OPCR, and RFI for WIMF/A 4699. Bottom: Scatterplot depicting PC 1 and PC 2 of species means for all three topographic variables. The scatterplot indicates how curvature (DNE), complexity (3D-OPCR), and relief (RFI) load along the axes. Taxa inferred to be more insectivorous sit on the right side of the plot whereas taxa inferred to be more frugivorous sit on the left side.

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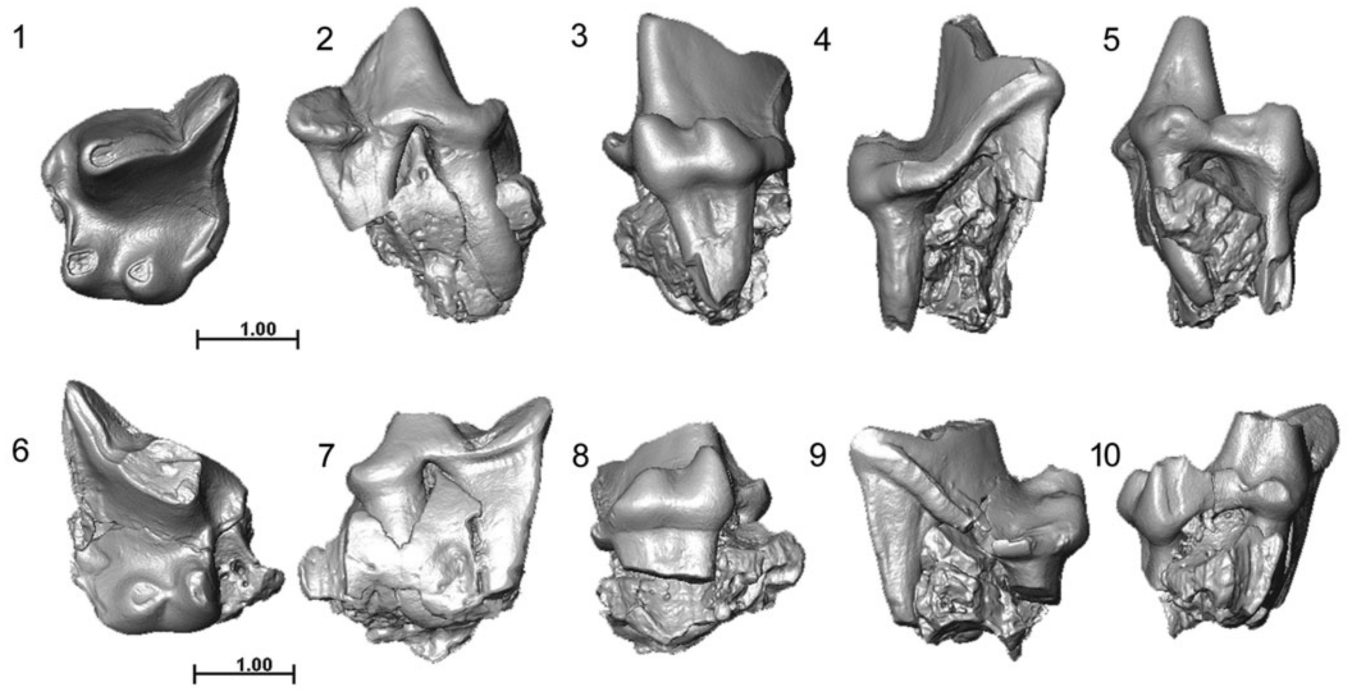

Figure 7. 3D surface renderings of *Galerix* sp. P4s. (**1–5**) WIMF/A 4697, left P4 in: (**1**) occlusal; (**2**) buccal; (**3**) lingual; (**4**) posterior; and (**5**) anterior views; (**6–10**) WIMF/A 4698, right P4 in: (**6**) occlusal; (**7**) buccal; (**8**) lingual; (**9**) posterior; (**10**) anterior views. Scales = 1 mm.

the full range of variation in both taxa unclear for this tooth position. Furthermore, Parmar et al. (2022) recently described an M2 from their K2 Kulwanta locality at Ramnagar and assigned it to *G. rutlandae*, raising the possibility that the two Dehari P4s may represent large P4s of that taxon. In fact, the M2 from Kulwanta is also relatively large (see measurements in Parmar et al., 2022)—larger in overall area than the sample of *G. rutlandae* specimens measured by Zjilstra and Flynn (2015)—and within the range of *G. wesselsae* in terms of overall size (SI Table S2; SI Fig. S1). Despite the larger overall size of the specimen, Parmar et al. (2022) attributed the Kulwanta M2 to *G. rutlandae* based on occlusal features, including a strong connection between the protocone and hypocone as well as a connection between the protocone and metaconule.

Table 2. Comparative dental measurements (mm) of *Galerix rutlandae* and *Galerix wesselsae* P4s from Pakistan and India. Max Width = maximum width; Max Length = maximum length; Area = Max Width × Max Length. Comparative measurements from Zijlstra and Flynn (2015) and the current study.

Taxon	Specimen	Locality	Element	Length (mm)	Width (mm)	Max Width/ Max Length (Shape)	Square root of Area (Size)	Age (Ma)
Galerix rutlandae	CH BS 401	CH BS	P4	1.90	—	—	—	Unknown
Galerix rutlandae	PMNH400x-1	Dhok Tahlian	P4	2.07	—	—	—	Unknown
Galerix rutlandae	H-GSP 82.24-35	Seh 82.24	P4	1.88	—	—	—	ca. 16.3–13.5
Galerix rutlandae	YGSP 24465	Y059	P4	2.10	1.98	0.94	2.04	13.6
Galerix rutlandae	YGSP 34852	Y641	P4	2.10	1.65	0.79	1.86	13.7
Galerix rutlandae	YGSP 39492	Y668	P4	1.78	—	—	—	13.4
Galerix rutlandae	YGSP 34858	Y698	P4	1.95	1.75	0.90	1.85	13
Galerix rutlandae	YGSP 34882	Y714	P4	2.05	2.10	1.02	2.07	12.8
Galerix rutlandae	YGSP 34905	Y718	P4	n/a	1.80	—	—	13.2
Galerix rutlandae	YGSP 34883a	Y726	P4	2.15	2.05	0.95	2.10	13
Galerix sp.	H-GSP 82.24-38	Seh 82.24	P4	n/a	2.15	—	—	ca. 16.3–13.5
Galerix sp.	H-GSP 82.24-42	Seh 82.24	P4	2.15	—	—	—	ca. 16.3–13.5
Galerix wesselsae	H-GSP 81.14-4713	Seh 81.14	P4	n/a	2.17	—	—	? <17 Ma
Galerix wesselsae	H-GSP 81.14a-4291	Seh 81.14a	P4	2.20	—	—	—	? <17 Ma
Galerix wesselsae	H-GSP 82.24-39	Seh 82.24	P4	2.25	2.25	1.00	2.25	ca. 16.3–13.5
Galerix wesselsae	H-GSP 82.24-40	Seh 82.24	P4	n/a	2.32	—	—	ca. 16.3–13.5
Galerix wesselsae	H-GSP 84.24-4242	Seh 84.24	P4	2.30	—	—	—	? <17 Ma
Galerix wesselsae	YGSP 49012	Y642	P4	2.02	—	—	—	15.2
Galerix wesselsae	YGSP 24530	Y709	P4	1.75	2.05	1.17	1.89	14.3
Galerix wesselsae	YGSP 36191	Y802	P4	2.61	—	—	—	16.8
Galerix wesselsae	YGSP 36192	Y802	P4	2.30	—	—	—	16.8
Galerix wesselsae	YGSP 36193	Y802	P4	2.20	—	—	—	16.8
***Galerix* sp.**	**WIMF/A 4698**	**Ramnagar (Dehari 2)**	**P4**	**n/a**	**2.20**	**—**	**—**	**ca. 12.4–11.6**
***Galerix* sp.**	**WIMF/A 4697**	**Ramnagar (Dehari 2)**	**P4**	**2.25**	**2.22**	**0.99**	**2.23**	**ca. 12.4–11.6**

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Taken together, it seems that the Dehari *Galerix* specimens and the Kulwanta specimen are all larger than typical *G. rutlandae* (more similar in size to *G. wesselsae*), and yet the more diagnostic M2 displays features argued to be more consistent with *G. rutlandae*. The consistency in size across all three Ramnagar teeth suggests to us that it is most parsimonious to assume all of the Ramnagar *Galerix* specimens belong to a single species, but the unique mix of M2 features and relatively large size does not fit perfectly with *G. rutlandae* or *G. wesselsae* as defined from the Potwar Plateau. Therefore, we have determined that it is most prudent to formally assign all of these specimens to *Galerix* sp. indet., pending additional data.

Rodentia Bowdich, 1821
Spalacidae Gray, 1821
Rhizomyinae Winge, 1887
Genus *Kanisamys* Wood, 1937

Type species.—*Kanisamys indicus* Wood, 1937.

Kanisamys indicus Wood, 1937
Figure 8.1

Holotype.—YPM 13810, partial right dentary with m1–m3, comes from the Chinji Zone, south of Chinji Village, Pakistan (Wood, 1937, pl. 68, fig. 7).

Occurrence.—Dehari locality at Ramnagar (Udhampur District, Jammu and Kashmir, India).

Description.—WIMF/A 4689 is longer than wide with moderate lophodonty and a well-preserved, though worn, protocone, hypocone, paracone, and metacone. The lingual cusps (protocone and hypocone) are taller than the buccal cusps (paracone and metacone), and the remains of three roots can be observed on the inferior surface of the crown. The protocone is slightly smaller than the hypocone and directed posterolingually. The specimen displays an anteroloph, protoloph, mesoloph, metaloph, and posteroloph, but no anterolingual flexus is present. The protoloph is posterobuccally oriented from the protocone-mure junction, and the mesoloph is relatively long. A small mesostyle is present buccal to the mesoloph. The metaloph and posteroloph join at the buccal margin of the crown, forming a small posterosinus. The lingual re-entrant is short and curves anteriorly. The anterosinus separates the anteroloph from the protoloph, and the mesosinus separates the protoloph from the mesoloph in addition to separating the mesoloph from the metaloph. No ectoloph is present.

Material.—WIMF/A 4689, left M2.

Remarks.—WIMF/A 4689 is more similar to *K. indicus* than to other species of *Kanisamys*, including *K. potwarensis*, *K. sivalensis* Wood, 1937, and *K. nagrii* Prasad, 1968, because of its smaller size (length = 1.95 mm, width = 1.86 mm; see Table 3), shape (width/length; see Fig. 9.1), and low crown height (0.56 mm). Besides the crown height, *K. indicus* has a crown that is longer than wide, a short lingual re-entrant, a strong mesoloph, and a distinct metaloph from posteroloph, whereas *K. potwarensis* is characterized as having a width greater than the length, a slender mesoloph, and a fused metaloph with posteroloph (Flynn, 1982b). M2s of *K. nagrii* and *K. sivalensis* are highly lophodont, unlike WIMF/A 4689. Earlier, Parmar et al. (2018) reported *K. indicus* from Dehari, and those specimens share similar characters with the present specimen. Therefore, WIMF/A 4689 is assigned here to *K. indicus* on account of occlusal crown features, overall shape, and height.

Ctenodactylidae Zittel, 1893
Ctenodactylinae Hinton, 1933
Genus *Sayimys* Wood, 1937

Type species.—*Sayimys perplexus* Wood, 1937.

Sayimys sivalensis (Hinton, 1933)
Figure 8.2

Holotype.—GSI D284, left partial dentary with m2–m3 from the Middle Miocene Chinji Formation, Pakistan (Hinton, 1933).

Occurrence.—Dehari locality at Ramnagar (Udhampur District, Jammu and Kashmir, India).

Description.—WIMF/A 4695 is a left M2 (or possibly M3) that is broken distally. An anteroloph is absent. The anterior cusps (protocone and paracone) are larger than the posterior cusps (hypocone and metacone). The paraflexus is absent. The mesoflexus and hypoflexus are about equal in depth and terminate opposite to each other. The metaflexus is present, but short and shallow. The posteroloph is shorter than the metaloph. The specimen exhibits three roots.

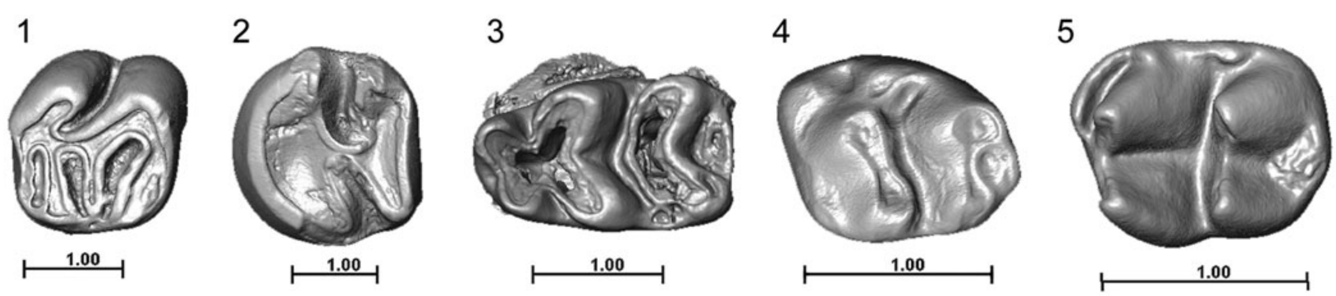

Figure 8. 3D surface renderings in occlusal view of (**1**) WIMF/A 4689 *Kanisamys indicus* M2; (**2**) WIMF/A 4695 *Sayimys sivalensis* M2 or M3; (**3**) WIMF/A 4693 Murinae indet. m1; (**4**) WIMF/A 4692 Murinae indet. m2; (**5**) WIMF/A 4696 Murinae indet. M2. Scales = 1 mm.

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Table 3. Comparative dental measurements (mm) of WIMF/A 4689 and previously described *Kanisamys* specimens. Max Width = maximum width; Max Length = maximum length; Area = Max Width × Max Length. Comparative measurements from Black (1972), Flynn (1981, 1982a), Wessels and de Bruijn (2001), Parmar et al. (2018), and this study.

Taxon	Specimen No.	Locality	Elements	Length (mm)	Width (mm)	Max Width/ Max Length (Shape)	Square root of Area (Size)
K. indicus	H-GSP 8227	Manchar Fm., Pakistan	M2	2.12	1.98	0.93	2.05
K. indicus	H-GSP 8425	Manchar Fm., Pakistan	M2	1.94	2.08	1.07	2.01
K. indicus	H-GSP 8114	Manchar Fm., Pakistan	M2	2.00	1.96	0.98	1.98
K. indicus	H-GSP 8214	Manchar Fm., Pakistan	M2	1.92	1.98	1.03	1.95
K. indicus	H-GSP 8224	Manchar Fm., Pakistan	M2	1.84	1.93	1.04	1.88
K. indicus	Y GSP 8097	Chinji Fm. Pakistan	M2	2.38	2.25	0.95	2.31
K. indicus	YPM 13810	Chinji Fm. Pakistan	M2	2.25	2.13	0.95	2.19
K. indicus	GSI D271	?Chinji Fm., Pakistan	M2	2.31	2.06	0.89	2.18
K. indicus	Y GSP 8372	Chinji Fm. Pakistan	M2	2.44	2.13	0.87	2.28
K. indicus	Y GSP 8105	Chinji Fm. Pakistan	M2	2.63	2.19	0.83	2.40
K. indicus	VPL/JU/LSM/9	Ramnagar, India	M2	2.15	2.06	0.96	2.10
K. indicus	**WIMF/A4689**	**Ramnagar (Dehari 2), India**	**M2**	**1.95**	**1.86**	**0.95**	**1.90**
K. potwarensis	Y GSP 8117	Chinji Fm. Pakistan	M2	2.56	2.56	1.00	2.56
K. potwarensis	Y GSP 8374	Chinji Fm. Pakistan	M2	2.44	2.69	1.10	2.56
K. potwarensis	Y GSP 8088	Chinji Fm. Pakistan	M2	2.50	2.81	1.12	2.65
K. sivalensis	Y GSP	(Y182) Nagri Fm. Pakistan	M2	2.51	2.47	0.98	2.49
K. sivalensis	Y GSP	(Y388) Nagri Fm. Pakistan	M2	2.53	2.61	1.03	2.57
K. sivalensis	Y GSP	(Y24) Nagri Fm. Pakistan	M2	2.62	2.44	0.93	2.53
K. nagrii	Y GSP 8309	Nagri Fm. Pakistan	M2	2.50	2.0+	—	—
K. nagrii	AMNH30000	Haritalyangar Fm. India	M2	2.40	1.90	0.79	2.14
K. nagrii	Y GSP 8124	Nagri Fm. Pakistan	M2	2.30	2.30	1.00	2.30

Materials.—WIMF/A 4695, left partial M2.

Remarks.—Five ctenodactylid species belonging to two genera, *Prosayimys* and *Sayimys*, are currently recognized in the Indian subcontinent during the Neogene (López-Antoñanzas and Sen, 2003; López-Antoñanzas and Knoll, 2011). *Prosayimys flynni* Baskin, 1996, is found in the Early Miocene Chitarwata Formation of Zinda Pir Dome, Pakistan, and at least four species of *Sayimys* are recognized at many Neogene sites across India and Pakistan (López-Antoñanzas and Sen, 2003; López-Antoñanzas and Knoll, 2011). The M3 of *S. sivalensis* is slightly larger than the M2–M3 of *S. baskini* López-Antoñanzas and Sen, 2003, and *S. intermedius* Sen and Thomas, 1979 (López-Antoñanzas and Sen, 2003). In addition to its occlusal features, WIMF/A 4695 can be referred to *S. sivalensis* on the basis of its overall size and shape (length = 2.25 mm, anterior width = 2.41 mm, posterior width = 2.02 mm), which fall clearly within the range of *S. sivalensis* M2s and M3s (Table 4; Fig. 9.2).

Muridae Illiger, 1811
Murinae Illiger, 1811

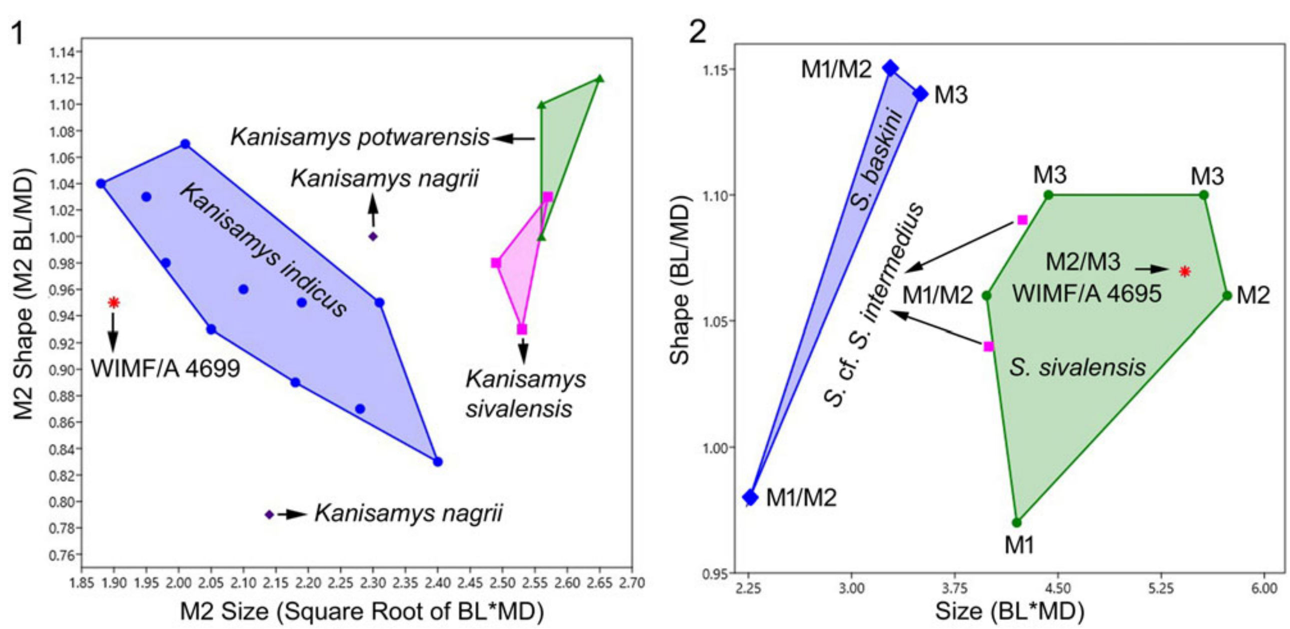

Figure 9. (**1**) Scatterplot of M2 shape (BL/MD) vs. size (square root of BL*MD) of Siwalik *Kanisamys* specimens. (**2**) Scatterplot of M2-M3 crown shape (BL/MD) vs. size (BL*MD) of Siwalik *Sayimys* specimens.

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Table 4. Comparative dental measurements (mm) of WIMF/A 4695 and other *Sayimys* specimens. Max = maximum; Ant = anterior; Post = Posterior. Comparative measurements from Munthe (1980), Baskin (1996), López-Antoñanzas and Sen (2003), and the current study.

Taxon	Locality	Elements (Sample size)	Mean Length (Range) in mm	Mean Width (Range) in mm	Mean Max Width/ Max Length	Mean Ant. Width/ Mean Post. Width	Formation
Sayimys sivalensis (including *S. chinjiensis*)	Potwar Plateau, Pakistan	M1/M2 (L = 55; W = 53, 55)	1.94 (1.60–2.52)	Ant: 2.05 (1.65–2.65) Post: 1.91 (1.50–2.45)	1.06	1.07	Kamlial, Chinji, and Nagri
Sayimys sivalensis (including *S. chinjiensis*)	Potwar Plateau, Pakistan	M3 (L = 12; W = 11, 12)	2.25 (1.72–2.52)	Ant: 2.47 (2.08–2.80) Post: 2.08 (1.55–2.40)	1.10	1.19	Kamlial, Chinji, and Nagri
Sayimys sivalensis	Daud Khel, Potwar Plateau, Pakistan	M1 (L = 29, W = 29, 29)	2.08 (1.84–2.24)	Ant: 2.02 (1.68–2.36) Post: 1.92 (1.68–2.20)	0.97	1.05	Chinji
Sayimys sivalensis	Daud Khel, Potwar Plateau, Pakistan	M2 (L = 31, W = 31, 31)	2.33 (1.96–2.60)	Ant: 2.46 (2.12–2.80) Post: 2.20 (1.92–2.56)	1.06	1.12	Chinji
Sayimys sivalensis	Daud Khel, Potwar Plateau, Pakistan	M3 (L = 21; W = 21, 21)	2.28 (1.96–2.64)	Ant: 2.50 (2.28–2.72) Post: 1.77 (1.56–1.96)	1.10	1.41	Chinji
***Sayimys sivalensis* WIMF/A 4695**	**Ramnagar (Dehari 2), India**	**M2**	**2.25**	**Ant: 2.41 Post: 2.02**	**1.07**	**1.19**	**Mansar (Chinji-age)**
Sayimys cf. *S. intermedius*	Zinda Pir Dome and Potwar Plateau, Pakistan	M1/M2 (L = 6; W = 4, 5)	1.97 (1.78–2.22)	Ant: 2.15 (2.10–2.20) Post: 1.94 (1.82–2.08)	1.09	1.11	Vihowa and Kamlial
Sayimys cf. *S. intermedius*	Zinda Pir Dome and Potwar Plateau, Pakistan	M3 (L = 2; W = 2, 4)	1.96 (1.80–2.12)	Ant: 2.04 (1.95–2.12) Post: 1.68 (1.60–1.75)	1.04	1.22	Vihowa and Kamlial
Sayimys baskini (= *Sayimys* cf. *S. minor)*	YGSP721, Potwar Plateau, Pakistan	M1/M2 (L = 7; W = 5, 5)	1.52 (1.32–1.62)	Ant: 1.49 (1.32–1.60) Post: 1.46 (1.30–1.55)	0.98	1.02	Kamlial
Sayimys baskini (= *Sayimys* cf. *S. minor)*	YGSP721, Potwar Plateau, Pakistan	M3 (L = X; W = X, 1)	—	Post: 1.62	—	—	Kamlial
Sayimys baskini (= *Sayimys* cf. *S. minor)*	YGSP747, Potwar Plateau, Pakistan	M1/M2 (L = 9; W = 7, 6)	1.69 (1.57–1.85)	Ant: 1.94 (1.60–2.25) Post: 1.73 (1.57–2.13)	1.15	1.12	Kamlial
Sayimys baskini (= *Sayimys* cf. *S. minor)*	YGSP747, Potwar Plateau, Pakistan	M3 (L = 1; W = 1, 1)	1.75	Ant: 2.00 Post: 1.85	1.14	1.08	Kamlial

Murinae indet.
Figure 8.3–8.5

Occurrence.—Dehari locality at Ramnagar (Udhampur District, Jammu and Kashmir, India).

Description.—WIMF/A 4696 (M2) has a somewhat trapezoidal occlusal outline. On the anterior margin, an anterostyle (t1) and labial anterocone (t3) are present, t1 being larger than t3. The enterostyle (t4) is triangular, longitudinally elongated, isolated from and positioned posteriorly to the protocone (t5). The paracone (t6) is fairly large and strongly connected to t5. Both these cusps (t5 and t6) lie at the same height. The hypocone (t8) is large and is connected to the smaller metacone (t9), almost lying at the same height. The groove between the anterostyle (t1) and enterostyle (t4) is shallow and similar in depth to the groove between the enterostyle (t4) and hypocone (t8). None of the cusps shows longitudinal (i.e., mesiodistal) connections. The posterior cingulum is ridge-like, connected to t8, and separated from t9 by a small and narrow groove. The tooth has three roots.

The WIMF/A 4693 (m1) prelobe comprises a posteriorly placed labial anteroconid that is slightly smaller than the more anteriorly placed lingual anteroconid. The anteroconids and the cusps of the second lobe (metaconid-protoconid) have a rather asymmetrical, centrally positioned “X” shaped longitudinal connection; the metaconid and protoconid are also weakly connected to each other. A medial anteroconid is absent. The cusps of the third lobe, the hypoconid, and entoconid are transversely connected. There is no central mure present, and thus a continuous central sinusoid is present in front of the third lobe. The labial cingulum is well developed and a prominent C1 is present. The posterior cingulum is elongated and augen- (lentil-) shaped.

WIMF/A 4692 (m2) exhibits a rectangular occlusal outline. A labial anteroconid is present, and the second (metaconid-protoconid) and third (entoconid-hypoconid) chevrons are slightly oblique. The cusps are gently inclined mesiodistally. A weak labial cingulum is present with an isolated cuspid C1. The posterior cingulum is elongate and lens-/lentil-shaped.

Materials.—WIMF/A 4696 right M2, WIMF/A 4693 left m1, WIMF/A 4692 right m2.

Remarks.—The present M2 is similar to that of *Antemus chinjiensis* reported from the Lower Siwalik of Potwar, Pakistan (Jacobs, 1978) and Ramnagar, India (Sehgal and Patnaik, 2012) in terms of overall size and having an enterostyle (t4) that is isolated from the protocone (t5). However, WIMF/A 4696 (length = 1.30 mm, width = 1.00 mm; see SI Table S3) is slightly elongated and narrower in shape (see Fig. 10.1) compared to those of *Antemus chinjiensis* (original range of length = 1.00–1.28 mm and original range of width = 1.02–1.20 mm) described by Jacobs et al. (1989) and Sehgal and Patnaik (2012). The present m1 (length = 1.99 mm, width = 1.17 mm; see SI Table S3) is also distinct from those of *Antemus chinjiensis* in having a strong asymmetrical “X” shaped longitudinal connection between the first two lobes and being larger in overall size. In size and shape (see Fig. 10.2), it is a good match for the ca. 12.4 Ma sample from site Y496 (Potwar, Pakistan) that was originally described as “near *Progonomys*” (Jacobs and Flynn, 2005; Kimura et al., 2013), but more recently referred to “post-*Antemus*” by Kimura et al. (2021). The second lower molar (length = 1.25 mm, width = 1.00 mm; see SI Table S3) falls within the size of *Antemus chinjiensis* (see Fig. 10.3), but differs in having gently inclined cusps as well as having a weaker cingulum.

Discussion

Historically, treeshrews have been intensively studied to understand their evolutionary significance and phylogenetic position relative to other members of Euarchontoglires, in particular primates and dermopterans (McKenna, 1963, 1966; Jacobs, 1980; Sargis, 2001, 2002a, b, 2004). Currently, treeshrews are regarded as close relatives of dermopterans and primates within the Superorder Euarchonta (e.g., see Murphy et al., 2001; Helgen, 2005; Janečka et al., 2007; O’Leary et al., 2013; Sargis et al., 2013; Zhang et al., 2019). However, their evolutionary

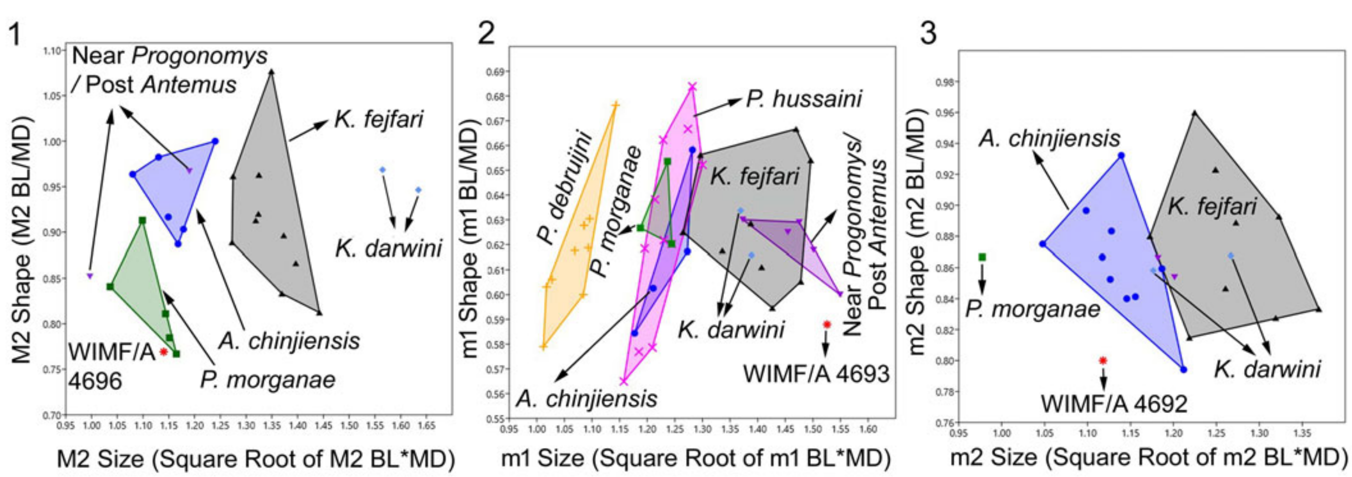

Figure 10. Scatterplot of molar shape (BL/MD) vs. size (square root of BL*MD) in Siwalik murid specimens (see SI Table 3) including *Antemus chinjiensis* Jacobs, 1977; *Karnimata fejfari* Kimura et al., 2017; *Karnimata darwini* Jacobs, 1978; *Progonomys morganae* Kimura et al., 2017; *Progonomys debruijni* Jacobs, 1978; and *Progonomys hussaini* Cheema et al., 2000. (**1**) M2; (**2**) m1; (**3**) m2.

https://doi.org/10.1017/jpa.2022.41 Published online by Cambridge University Press

history and phylogenetic position relative to other extant and fossil euarchontans are still debated in part due to the lack of a detailed fossil record (Sargis, 2004). Scandentia, the mammalian order including treeshrews, is classified into two families: Tupaiidae and Ptilocercidae (Helgen, 2005). Previously, fossil taxa such as *Entomolestes granger*, *E. nitrens*, and *Tupaiodon morrisi* were considered to be tupaiids originating at the beginning of the Cenozoic (Matthew, 1909; Gregory, 1913; Matthew and Granger, 1924). However, many of these species were later demonstrated to belong to different families such as Erinaceidae, Adapisoricidae, and Nyctitheriidae (Simpson, 1931; Krishtalka, 1976b; Krishtalka and West, 1977). *Anagale gobiensis* Simpson, 1931, from the Oligocene Ulan Gochu Formation of Mongolia and the Paleocene genus *Adapisoriculus* were once considered to be close relatives of the Tupaiidae (Simpson, 1931; Van Valen, 1965), but their affinities to living treeshrews were later disputed (Chopra and Vasishat, 1979; Jacobs, 1980). As such, there is currently no fossil record of Paleogene treeshrews except for *Ptilocercus kylin* Li and Ni, 2016, from the early Oligocene (ca. 34 Ma) of China, representing the oldest definitive fossil ptilocercid (Li and Ni, 2016).

Undoubted Miocene tupaiid fossils have been discovered in Pakistan (Jacobs, 1980), India (Dutta, 1975; Chopra and Vasishat, 1979), Thailand (Mein and Ginsburg, 1997), and China (Qiu, 1986; Ni and Qiu, 2002, 2012). Jacobs (1980) reported a large treeshrew rostrum from ca. 10 Ma Miocene deposits in Pakistan, but he did not identify this specimen to the genus level. In India, Dutta (1975) reported a possible *Tupaia* rib cage from the Tatrot beds of the Upper Siwaliks. Chopra and Vasishat (1979) reported a new species of tupaiid, *Palaeotupaia sivalicus*, from the Middle Siwaliks of Haritalyangar, which is now widely regarded as representing the extant genus *Tupaia*. Based on an M2 specimen, Mein and Ginsburg (1997) named *Tupaia miocenica* from Thailand, and Qiu (1986) described a new genus and species, *Prodendrogale yunnanica,* based on isolated teeth and a jaw fragment from Lufeng, China. Finally, Ni and Qiu (2012) reported two new species, *Tupaia storchi* Ni and Qiu, 2012, and *Prodendrogale engesseri* Ni and Qiu, 2012, from isolated teeth at the late Miocene Yuanmou *Lufengpithecus* locality in Yunnan Province, China.

Sivatupaia ramnagarensis n. gen. n. sp., dating to the middle Miocene, is significant in extending the temporal and morphological range of tupaiid evolution. Specifically, the occurrence of WIMF/A 4699 at Dehari (Ramnagar), likely correlating to the upper half of the Chinji Formation, extends the time range of fossil tupaiids downward in the Siwalik fossil record. Furthermore, *S. ramnagarensis* n. gen. n. sp. is distinct in its morphology and dietary adaptations compared to other living and fossil treeshrews. It further expands the known dental ecospace of treeshrews and suggests that tupaiids may have been more ecologically diverse in the past (Selig et al., 2020). Its small size and distinctive shape make it difficult to place definitively within the extant treeshrew families, and the lower molar topographic values surface suggests a more frugivorous and/or less challenging diet compared to other known treeshrew taxa.

Galericines (hedgehogs) are poorly known from Southeast and East Asia, with small samples from Pakistan (Zijlstra and Flynn, 2015), China (Li et al., 1983; Storch and Qiu, 1991), and Thailand (Mein and Ginsburg, 1997; Cailleux et al., 2020). In Pakistan, *Galerix* is represented by two taxa, *G. rutlandae* Munthe and West, 1980, and the older and larger *G. wesselsae* Zijlstra and Flynn, 2015. *Galerix wesselsae* first appears around 19 Ma, and was apparently replaced by *G. rutlandae* during the Middle Miocene, ca. 14.3–14.1 Ma (Zijlstra and Flynn, 2015). *Galerix rutlandae* then persists in Pakistan until ca. 11.6 Ma (Zjilstra and Flynn, 2015). In Thailand, the tribe Galericini is represented by two genera, *Galerix* (*G. rutlandae*) and *Lantanotherium* (*L. anthrace* Cailleux et al., 2020, and *Lantanotherium* sp.) from the Middle Miocene (13.4–13.2 Ma) of the Mae Moh Basin (Cailleux et al., 2020).

In the Indian Siwaliks, a galericine M2 was recently described from the K2 locality at Kulwanta, Ramangar, as *G. rutlandae* based on a number of subtle dental features shared with *G. rutlandae* specimens on the Potwar Plateau (Parmar et al., 2022). However, the Kulwanta M2 is larger in terms of measured area (mesiodistal length × buccolingual breadth) than known *G. rutlandae* M2s from Pakistan, and instead is more similar to *G. wesselsae* in size (SI Table S2; SI Fig. S1). The *Galerix* P4 specimens from Dehari are also larger than the few *G. rutlandae* P4s that have been described from Pakistan, and on this basis the P4s from Dehari and the M2 from Kulwanta are interpreted most parsimoniously as the same species. Because the more diagnostic M2 from Kulwanta appears more similar to *G. rutlandae* in known dental features, and yet all of the Ramnagar specimens appear larger and more similar to *G. wesselsae* in size, it is difficult to confidently assign the Ramnagar *Galerix* specimens to any known species at this time. Instead, we prefer to recognize them as *Galerix* sp. indet. until additional specimens are found to confirm the presence of *G. rutlandae* or further suggest that a distinct, larger hedgehog species is present at Ramnagar. In any case, the newly described specimens from Kulwanta and Dehari represent the first erinaceid fossils from the entire Siwalik deposits of India.

Previous to the current micromammal collection, Parmar et al. (2015, 2018) recorded *Megacricetodon daamsi*, *Kanisamys indicus*, *Sayimys sivalensis*, *Myomimus* sp., and *Tamias urialis* from Dehari. In combination with *Kanisamys* cf. *K. potwarensis* (Parmar and Prasad, 2006), they estimated a ca. 13.6–13.2 Ma age range for Dehari, projected from Potwar biostratigraphy (Parmar et al., 2018). In our present collection from Dehari, the murine specimens possess an interesting mix of features seen in both *Antemus* and later "pre-*Progonomys*" or *Progonomys* (see Kimura et al., 2021). The m1 specimen WIMF/A 4693, in particular, is most similar in size and shape to the population most recently referred to as "post-*Antemus*" from a ca. 12.4 Ma site on the Potwar Plateau, Pakistan (Fig. 10.2; Kimura et al., 2021). Although the m2 (WIMF/A 4692) is more similar to *Antemus chinjiensis* in size and shape (Fig. 10.3), both lower molars described here are also more robust and express weaker cingulae, similar to *Progonomys* in these features. The upper M2 WIMF/A 4696 displays features present in *Antemus* (e.g., an isolated enterostyle), but also features reminiscent of later pre-*Progonomys* and *Progonomys*, such as its overall longer and narrower shape (Fig. 10.1). It is currently unclear whether these specimens document a single variable species that is transitional between *Antemus* and *Progonomys*, perhaps similar to the "post-*Antemus*" population on the Potwar Plateau, or whether there are two lineages present at Dehari: *Antemus*/"post-*Antemus*" and pre-*Progonomys*/*Progonomys*.

https://doi.org/10.1017/jpa.2022.41 Published online by Cambridge University Press

In either case, this mix of murine dental features begins to appear around 12.4 Ma at site Y496 on the Potwar Plateau and would be most consistent with an age range at Dehari between ca. 12.7–11.6 Ma (i.e., between the last appearance date of *Antemus* samples and the first appearance date of the more derived pre-*Progonomys* samples). An age for Dehari at the older end of this range also would be consistent with previous reports of *Megacricetodon daamsi* (LAD ca. 12.5 Ma on the Potwar Plateau; Flynn et al., 1995) from the locality (Parmar et al., 2015). The only reported rodent taxon known from Dehari that would appear at odds with an age of ca. 12.7–11.6 Ma would be *K.* cf. *K. potwarensis* (Parmar and Prasad, 2006), which has a LAD of ca. 13.2 Ma on the Potwar Plateau (Flynn et al., 1995). However, we note that the original assignment to this species was only tentative, and the measurements of the m2 and m3 in this small *Kanisamys* specimen are closer in size to *K. indicus*, particularly the sample described from the Manchar Formation in Sindh Province (Wessels and de Bruijn, 2001). Most recently, Bhandari et al. (2021) suggested that this specimen is in fact *K. indicus*, which has a LAD of ca. 11.4 Ma. Thus, it appears as if the reported rodents from Dehari are all consistent with an age range between ca. 12.7–11.6 Ma. In any case, if confirmed with future specimens, the presence of “post-*Antemus*”-like murines in combination with other biochronological and geochronological data may help to narrow down the possible age range of Dehari even further, and the Ramnagar region more broadly.

Conclusions

A number of micromammal specimens recently have been discovered at Ramnagar, and the current sample contains hedgehogs, biochronologically informative rodent specimens, and the earliest known treeshrew from the Indian Siwaliks. The treeshrew, which is represented by an isolated m1 or m2, represents a new genus and species, *Sivatupaia ramnagarensis* n. gen. n. sp. We place *S. ramnagarensis* n. gen. n. sp. within Tupaiidae, and note its morphological distinctiveness suggesting a less mechanically challenging, and perhaps more frugivorous, diet compared to other extant and fossil tupaiids. Hedgehog specimens described here appear to represent the genus *Galerix*, but clear identification to the species level is not possible at this time. Finally, murine rodent specimens showing a combination of *Antemus*-like and *Progonomys*-like features are most similar to murine specimens known from ca. 12.7–11.6 Ma localities on the Potwar Plateau, which may suggest a similar age for Dehari and have implications for the age of Ramnagar more broadly, roughly equivalent to the middle to upper section of the Chinji Formation.

Acknowledgments

RKS, NPS, and APS thank the Director, Wadia Institute of Himalayan Geology, Dehradun for the research facilities (contribution no. WIHG/201). This research was supported by the Leakey Foundation, the PSC-CUNY faculty award program, Hunter College, and the U.S. National Science Foundation (BCS Award nos. 1945736, 1945743, 1945618). We thank T. Skorka at the University of Southern California’s Molecular Imaging Center (MIC) for assisting with μCT scanning; the MIC receives funding from the U.S. National Institutes of Health (NIH S10 RR027665 01). KRS is supported by the Kalbfleisch Fellowship, Richard Gilder Graduate School, AMNH. We thank E. Sargis, E. Seiffert, L. Flynn, and L. Jacobs for helpful advice, directions to important papers, and assistance with specimen identification. L. Flynn and L. Jacobs also provided valuable and constructive comments on an earlier version of this paper. V. Parmar kindly provided information on the geographic location of previously worked Dehari sites.

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8kprr4xqk.

The list of specimens included in the analyses and results of the topographic analysis for Dirichlet normal energy (DNE), three-dimensional orientation patch count rotated (3D-OPCR), and relief index (RFI) are available in Supplemental Data (SI Table S1 and SI Dataset 1). Comparative measurements of *Galerix rutlandae* and *G. wesselsae* M2 specimens along with a plot illustrating the large size of the M2 from Kulwanta are found in SI Table S2 and SI Figure S1. Comparative measurements of murine specimens, including the specimens described here, are provided in SI Table S3.

References

Baskin, J.A., 1996, Systematic revision of Ctenodactylidae (Mammalia, Rodentia) from the Miocene of Pakistan: Palaeovertebrata, v. 25, p. 1–49.

Basu, P.K., 2004, Siwalik mammals of the Jammu Sub-Himalaya, India: an appraisal of their diversity and habitats: Quaternary International, v. 117, p. 105–118.

Bhandari, A., Bajpai, S., Flynn, L.J., Tiwari, B.N., and Mandal, N., 2021, First Miocene rodents from Kutch, western India: Historical Biology, v. 33, p. 3471–3479.

Black, C.C., 1972, Review of fossil rodents from the Neogene Siwalik beds of India and Pakistan: Palaeontology, v. 15, p. 238–266.

Bowdich, T.E., 1821, An Analysis of the Natural Classifications of Mammalia for the Use of Students and Travellers: Paris, J. Smith, 115 p.

Boyer, D.M., 2008, Relief index of second mandibular molars is a correlate of diet among prosimian primates and other euarchontan mammals: Journal of Human Evolution, v. 55, p. 1118–1137.

Brown, B., Gregory, W.K., and Hellman, M., 1924, On three incomplete anthropoid jaws from the Siwaliks, India: American Museum Novitates, v. 130, p. 1–8.

Bunn, J.M., Boyer, D.M., Lipman, Y., St Clair, E.M., Jernvall, J., and Daubechies, I., 2011, Comparing Dirichlet normal surface energy of tooth crowns, a new technique of molar shape quantification for dietary inference, with previous methods in isolation and in combination: American Journal of Physical Anthropology, v. 145, p. 247–261.

Butler, P.M., 1980, The tupaiid dentition, *in* Luckett, W.P., ed., Comparative Biology and Evolutionary Relationships of Tree Shrews: New York, Plenum Press, p. 171–204.

Cailleux, F., Chaimanee, Y., Jaeger, J.-J., and Chavasseau, O., 2020, New Erinaceidae (Eulipotyphla, Mammalia) from the Middle Miocene of Mae Moh, Northern Thailand: Journal of Vertebrate Paleontology, v. 40, e1783277. https://doi.org/10.1080/02724634.2020.1783277.

Cheema, I.U., Raza, S.M., Flynn, L.J., Rajpar, A.R., and Tomida, Y., 2000, Miocene small mammals from Jalalpur, Pakistan, and their Biochronologic Implications: Bulletin of the National Science Museum, ser. C, v. 26, p. 57–77.

Chopra, S.R.K., and Vasishat, R.N., 1979, Śivalik fossil tree shrew from Haritalyangar, India: Nature, v. 281, p. 214–215.

Chopra, S.R.K., Kaul, S., and Vasishat, R.N., 1979, Miocene tree shrews from the Indian Śivaliks: Nature, v. 281, p. 213–214.

Colbert, E.H., 1935, Siwalik mammals in the American Museum of Natural History: Transactions of the American Philosophical Society, v. 26, p. 1–401 de Blainville, H.M.D., 1840, Ostéographie des Mammifères Insectivores (*Talpa*, *Sorex* et *Erinaceus*, L.): ostéographie ou description iconographique comparée du sqelette et du système dentaire des mammifères récent et fossiles pour server de base à la zoologie et à la géologie: Paris, E. Thunot et C[e], v. 6, p. 1–115.

Diard, 1820, Report of a meeting of the Asiatic Society for March 10th, 1820: Asiatic Journal and Monthly Register for British India and its Dependencies, v. 10, p. 477–478.

Dutta, A.K., 1975, Micromammals from Siwaliks: Indian Minerals, v. 29, p. 76–77.

Dutta, A.K., Basu, P.K., and Sastry, M.S.A., 1976, On the new finds of hominids and additional finds of pongids from the Siwaliks of Ramnagar area, Udhampur District, J & K State: Indian Journal of Earth Sciences, v. 3, p. 234–235.

Evans, A., Wilson, G., Fortelius, M., and Jernvall, J., 2007, High-level similarity of dentitions in carnivorans and rodents: Nature, v. 445, p. 78–81.

Fischer, G., 1814, Zoognosia, Tabulis Synopticis Illustrata. Third Edition: Moscow, Typis Nicolai S. Vsevolozsky, 465 p.

Flynn, L.J., 1981, Biostratigraphy and Systematics of Siwalik Rhizomyidae (Rodentia) [Ph.D. Dissertation]: Tucson, Arizona, University of Arizona.

Flynn, L.J., 1982a, Systematic revision of Siwalik Rhizomyidae (Rodentia): Geobios, v. 15, p. 327–389.

Flynn, L.J., 1982b, A revision of fossil rhizomyid rodent from northern India and their correlation to a rhizomyid biochronology of Pakistan: Geobios, v. 15, p. 583–588.

Flynn, L.J., Morgan, M.E., Pilbeam, D., Jacobs, L.L., and Lindsay, E,H., 1995, Neogene Siwalik mammalian lineages: species longevities, rates of change, and modes of speciation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 115, p. 249–264.

Gaur, R., and Chopra, S.R.K., 1983, Palaeoecology of the Middle Miocene Siwalik sediments of a part of Jammu and Kashmir State (India): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 43, p. 313–327.

Gilbert, C.C., Patel, B.A., Friedman, A.C., Pugh, K.D., Fleagle, J.G., and Patnaik, R., 2014, New Lower Siwalik localities near Ramnagar, India: implication for the earliest Asian Great Apes and other mammalian lineages: Journal of the Palaeontological Society of India, v. 5, p. 353–365.

Gilbert, C.C., Patel, B.A., Singh, N.P., Campisano, C.J., Fleagle, J.G., Rust, K.L., and Patnaik, R., 2017, New sivaladapid primate from Lower Siwalik deposits surrounding Ramnagar (Jammu and Kashmir State), India: Journal of Human Evolution, v. 102, p. 21–41.

Gilbert, C.C., Sehgal, R.K., Pugh, K.D., Campisano, C.J., May, E., Patel, B.A., Singh, N.P., and, Patnaik, R., 2019, A new *Sivapithecus* specimen from Ramnagar (Jammu and Kashmir), India and a taxonomic revision of Ramnagar hominoids: Journal of Human Evolution, v. 135, 102665. https://doi.org/10.1016/j.jhevol.2019.102665.

Gilbert, C.C., Ortiz, A., Pugh, K.D., Campisano, C.J., Patel, B.A., Singh, N.P., Fleagle, J.G., and Patnaik, R., 2020, New Middle Miocene ape (Primates: Hylobatidae) from Ramnagar, India fills major gaps in the hominoid fossil record: Proceedings of the Royal Society B, Biological Sciences, v. 287, 20201655. https://doi.org/10.1098/rspb.2020.1655.

Gray, J.E., 1821, On the natural arrangement of vertebrose animals: London Medical Repository, v. 15, p. 296–310.

Gray, J.E., 1825, Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to each tribe: Annals of Philosophy, n.s., ser. 2, v. 10, p. 337–344.

Gray, J.E., 1848, Description of a new genus of insectivorous Mammalia, or Talpidae, from Borneo: Proceedings of the Zoological Society of London, 1848, p. 23–24.

Gregory, W.K., 1913, Relationship of the Tupaiidae and Eocene lemurs, especially *Notharctus*: Bulletin of the Geological Society of America, v. 24, p. 241–252.

Gregory, W.K., Hellman, M., and Lewis, G.E., 1938, Fossil anthropoids of the Yale-Cambridge India expedition of 1935: Carnegie Institution of Washington Publication, v. 495, p. 1–27.

Günther, A., 1876, Remarks on some Indian and, more especially, Bornean mammals: Proceedings of the Zoological Society of London, 1876, p. 424–428.

Gupta, S.S., and Verma, B.C., 1988, Stratigraphy and vertebrate fauna of the Siwalik Group, Mansar-Uttarbani section, Jammu district, J & K: Journal of the Palaeontological Society of India, v. 33, p. 117–124.

Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001, PAST: paleontological statistics software package for education and data analysis: Palaeontologia Electronica, v. 4. http://palaeo-electronica.org/2001_1/past/issue1_01.htm..

Helgen, K.M., 2005, Order Scandentia, *in* Wilson, D.E., and Reeder, D.M., eds., Mammal Species of the World, Third Edition: Baltimore, The Johns Hopkins University Press, p. 104–109.

Hinton, M.A.C., 1933, Diagnoses of new genera and species of rodents from Indian Tertiary deposits: Annals and Magazine of Natural History, v. 72, p. 620–622.

Illiger, C.D., 1811, Prodromus Systematis Mammalium et Avium Additis Terminis Zoographicis Uttriusque Classis: Berlin, Salfeld, 301 p.

Jacobs, L.L., 1977, A new genus of murid rodent from the Miocene of Pakistan and comments on the origin of the Muridae: PaleoBios v. 25, p. 1–12

Jacobs, L.L., 1978. Fossil rodents (Rhizomyidae and Muridae) from Neogene Siwalik deposits, Pakistan: Museum of Northern Arizona Bulletin, v. 52, p. 1–103.

Jacobs, L.L., 1980, Siwalik fossil tree shrews, *in* Luckett, W.P., ed., Comparative Biology and Evolutionary Relationships of Tree Shrews: New York, Plenum Press, p. 205–216.

Jacobs, L.L., and Flynn, L.J., 2005, Of mice…again: the Siwalik rodent record, murine distribution, and molecular clocks, *in* Lieberman, D.E., Smith, R.J., and Kelley, J., eds., Interpreting the Past: Essays on Human, Primate, and Mammal Evolution in Honor of David Pilbeam: American School of Prehistoric Research Monograph Series 5, (Boston, MA: Brill Academic Publishers, Inc.), p. 63–80.

Jacobs, L.L., Flynn, L.J., and Downs, W.R., 1989, Neogene rodents of Southern Asia, *in* Black, C.C., and Dawson, M.R., eds., Papers on Fossil Rodents in Honour of Albert Elmer Wood: Natural History Museum of Los Angeles County, Science Series, v. 33, p. 157–177.

Janečka, J.E., Miller, W., Pringle, T.H., Wiens, F., Zitzmann, A., Helgen, K.M., Springer, M.S., and Murphy, W.J., 2007, Molecular and genomic data identify the closest living relative of Primates: Science, v. 318, p. 792–794.

Kimura, Y., Jacobs, L.L., and Flynn, L.J., 2013, Lineage-specific responses of tooth shape in murine rodents (Murinae, Rodentia) to Late Miocene dietary change in the Siwaliks of Pakistan: PLoS ONE, v. 8, e76070. https://doi.org/10.1371/journal.pone.0076070.

Kimura, Y., Flynn, L.J., and Jacobs, L.L., 2017, Early Late Miocene murine rodents from the upper part of the Nagri Formation, Siwalik Group, Pakistan, with a new fossil calibration point for the tribe Apodemurini (*Apodemus/Tokudaia*): Fossil Imprint, v. 73, p. 197–212.

Kimura, Y., Flynn, L.J., and Jacobs, L.L., 2021, Tempo and mode: evidence on a protracted split from a dense fossil record: Frontiers in Ecology and Evolution, v. 9, 642814. https://doi.org/10.3389/fevo.2021.642814.

Krishtalka, L., 1976a, Early Tertiary Adapisoricidae and Erinaceidae (Mammalia: Insectivora) of North America: Bulletin of Carnegie Museum of Natural History, v. 1, p. 1–40.

Krishtalka, L., 1976b, North American Nyctitheriidae (Mammalia, Insectivora): Annals of Carnegie Museum, v. 46, p. 7–28.

Krishtalka, L., and West, R.M., 1977, Paleontology and geology of the Bridger Formation, southern Green River Basin, southwestern Wyoming, Part 2, the Bridgerian insectivore *Entomolestes granger*: Contributions in Biology and Geology, Milwaukee Public Museum, v. 14, p. 1–11.

Lewis, G.E., 1934, Preliminary notice of new man-like apes from India: American Journal of Science, v. 27, p. 161–181.

Li, C., Lin, Y., Gu, Y., Hou, L., Wu, W., and Qiu, Z., 1983, The Aragonian vertebrate fauna of Xiacaowan, Jiangsu. 1. A brief introduction to the fossil localities and preliminary report on the new material: Vertebrata PalAsiatica, v. 21, p. 313–327. [in Chinese]

Li, Q., and Ni, X., 2016, An early Oligocene fossil demonstrates treeshrews are slowly evolving "living fossils": Scientific Reports, v. 6, 18627. https://doi.org/10.1038/srep18627.

Lindsay, E.H., 1988, Cricetid rodents from Siwalik deposits near Chinji village. Part I: Megacricetodontinae, Myocricetodontinae and Dendromurinae: Palaeovertebrata, v. 8, p. 95–154.

López-Antoñanzas, R., and Knoll, F., 2011, A comprehensive phylogeny of the gundis (Ctenodactylinae, Ctenodactylidae): Journal of Systematic Palaeontology, v. 9, p. 379–398.

López-Antoñanzas, R., and Sen, S., 2003, Systematic revision of Mio-Pliocene Ctenodactylidae (Mammalia, Rodentia) from the Indian subcontinent: Eclogae Geologicae Helvetiae, v. 96, p. 521–529.

López-Antoñanzas, R., Flynn, L.J., and Knoll, F., 2013, A comprehensive phylogeny of extinct and extant Rhizomyinae (Rodentia): evidence for multiple intercontinental dispersals: Cladistics, v. 29, p. 247–273.

Luckett, W., and Jacobs, L., 1980, Proposed fossil tree shrew genus *Palaeotupaia*: Nature, v. 288, p. 104.

Lyon, M.W. 1913, Treeshrews: an account of the mammalian family Tupaiidae: Proceedings of the United States National Museum, v. 45, p. 1–188.

Matthew, W.D., 1909, The Carnivora and Insectivora of the Bridger Basin, Middle Eocene: Memoirs of the American Museum of Natural History, v. 9, p. 291–567.

Matthew, W.D., and Granger, W., 1924, New insectivores and ruminants from the Tertiary of Mongolia, with remarks on the correlation: American Museum Novitates, v. 105, p. 1–7.

McKenna, M.C., 1963, The early Tertiary primates and their ancestors: Proceedings of the XVI International Congress of Zoology, v. 4, p. 69–74.

McKenna, M.C., 1966, Paleontology and the origin of the primates: Folia Primatologica, v. 4, p. 1–25.

Mein, P., and Ginsburg, L., 1997, Les mammifères du gisement Miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement: Geodiversitas, v. 19, p. 783–844.

Munthe, J., 1980, Rodents of the Miocene Daud Khel local fauna, Mianwali district, Pakistan. Part 1. Sciuridae, Gliridae, Ctenodactylidae, and Rhizomyidae: Milwaukee Public Museum, Contributions in Biology and Geology, v. 34, p. 1–36.

Munthe, J., and West, R.M., 1980, Insectivora of the Miocene Daud Khel Local Fauna, Mianwali district, Pakistan: Contributions in Biology and Geology, Milwaukee Public Museum, v. 38, p. 1–17.

Murphy, W.J., Eizirik, E., Johnson, W.E., Zhang, Y.P., Ryder, O.A., and O'Brien, S.J., 2001, Molecular phylogenetics and the origins of placental mammals: Nature, v. 409, p. 614–618.

Nanda, A.C., and Sehgal, R.K., 1993, Siwalik mammalian faunas from Ramnagar (J. & K.) and Nurpur (H.P.) and lower limit of *Hipparion*: Journal of the Geological Society of India, v. 42, p. 115–134.

Ni, X., and Qiu, Z., 2002, The micromammalian fauna from the Leilao, Yuanmou hominoid locality: implications for biochronology and paleoecology: Journal of Human Evolution, v. 42, p. 535–546.

Ni, X., and Qiu, Z., 2012, Tupaiine tree shrews (Scandentia, Mammalia) from the Yuanmou *Lufengpithecus* locality of Yunnan, China: Swiss Journal of Palaeontology, v. 131, p. 51–60.

O'Higgins, P., and Jones, N., 2006, Tools for Statistical Shape Analysis. Hull York Medical School. http://sites.google.com/site/hymsfme/resources (accessed 29 September 2021).

O'Leary, M.A., Bloch, J.I., Flynn, J.J., Gaudin, T.J., Giallombardo, A., et al., 2013, The placental mammal ancestor and the post-K-Pg radiation of placentals: Science, v. 339, p. 662–667.

Parmar, V., and Prasad, G.V.R., 2006, Middle Miocene rhizomyid rodent (Mammalia) from the Lower Siwalik Subgroup of Ramnagar, Udhampur District, Jammu and Kashmir, India: Neues Jahrbuch für Geologie und Paläontologie Monatshefte, v. 2006, p. 371–384.

Parmar, V., Prasad, G.V.R., Kumar, J., Malik, M.A., and Norboo, R., 2015, Cricetid rodents from the Lower Siwalik Subgroup of Jammu, India: Biochronological significance: Palaeoworld, v. 24, p. 324–335.

Parmar, V., Magotra, R., Norboo, R., and Prasad, G.V.R., 2016, Rodent-based age appraisal of Ramnagar (J. & K.), India and its faunal correlation: Journal of the Palaeontological Society of India, v. 58, p. 87–92.

Parmar, V., Magotra, R., Norboo, R., and Prasad, G.V.R., 2017, Rodent-based age appraisal of the Lower Siwalik Subgroup of Kalaunta, Ramnagar, Jammu, India: Alcheringa, v. 41, p. 124–133.

Parmar, V., Prasad, G.V.R., and Norboo, R., 2018, Middle Miocene small mammals from the Siwalik Group of Northwestern India: Journal of Asian Earth Sciences, v. 162, p. 84–92.

Parmar, V., Norboo, R., and Magotra, R., 2022, First record of Erinaceidae and Talpidae from the Miocene Siwalik deposits of India. Historical Biology. https://doi.org/10.1080/08912963.2022.2034806.

Patnaik, R., 2013, Neogene Siwalik mammalian biostratigraphy: an overview, *in* Wang, X., Flynn, L.J., and Fortelius, M., eds., Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology: New York, Columbia University Press, p. 423–444.

Pilgrim, G.E., 1910, Notices of new mammalian genera and species from the Tertiaries of India: Records of the Geological Survey of India, v. 40, p. 63–71.

Pilgrim, G.E., 1927, A *Sivapithecus* palate and other primate fossils from India: Palaeontologia Indica, v. 14, p. 1–2.

Pilgrim, G.E., 1932, The fossil Carnivora of India: Memoirs of the Geological Survey of India, v. 18, p. 1–232.

Pillans, B., Williams, M., Cameron, D., Patnaik, R., Hogarth, J., Sahni, A., Sharma, J.C., Williams, F., and Bernor, R., 2005, Revised correlation of the Haritalyangar magnetostratigraphy, Indian Siwaliks: implications for the age of the Miocene hominids *Indopithecus* and *Sivapithecus*, with a note on a new hominid tooth: Journal of Human Evolution, v. 48, p. 507–515.

Pomel, A.N., 1848, Etudes sur les carnassiers insectivores (extrait), seconde partie: classification des insectivores: Archive des Sciences Physiques et Naturelles, Genève, v. 9, p. 244–251.

Prasad, K.N., 1968, The vertebrate fauna from the Siwalik beds of Haritalyangar, Himachal Pradesh, India: Memoirs of the Geological Survey of India, Palaeontologia Indica, n.s., v. 39, p. 1–56.

Qiu, Z.D., 1986, Fossil tupaiid from the hominoid locality of Lufeng, Yunnan: Vertebrata PalAsiatica, v. 24, p. 308–319.

Sargis, E.J., 2001, A preliminary qualitative analysis of the axial skeleton of tupaiids (Mammalia. Scandentia): functional morphology and phylogenetic implications: Journal of Zoology, London, v. 253, p. 473–483.

Sargis, E.J., 2002a, The postcranial morphology of *Ptilocercus lowii* (Scandentia, Tupaiidae): an analysis of primatomorphan and volitantian characters: Journal of Mammalian Evolution, v. 9, p. 137–160.

Sargis, E.J., 2002b, Functional morphology of the forelimb of tupaiids (Mammalia, Scandentia) and its phylogenetic implications: Journal of Morphology, v. 253, p. 10–42.

Sargis, E.J., 2004, New views on tree shrews: the role of tupaiids in primate supraordinal relationships: Evolutionary Anthropology, v. 13, p. 56–66.

Sargis, E.J., Woodman, N., Morningstar, N.C., Reese, A.T., and Olson, L.E., 2013, Morphological distinctiveness of Javan *Tupaia hypochrysa* (Scandentia, Tupaiidae): Journal of Mammalogy, v. 94, p. 938–947.

Schlegel, H., and Müller, S., 1843, Over de op de oostindische eilanden levende soorten van het eslacht Hylogalea: Verhandelingen over de Naturlijke Geschiedenis der Nederlandsche Overzeesche Bezittingen, v. 1843, p. 159–168.

Sehgal, R.K., 2013, Revised mammalian biostratigraphy of the Lower Siwalik sediments of Ramnagar (J. & K.), India and its faunal correlation: Journal of the Palaeontological Society of India, v. 58, p. 87–92.

Sehgal, R.K., and Patnaik, R., 2012, New muroid rodent and *Sivapithecus* dental remains from the Lower Siwalik deposits of Ramnagar (J&K, India): age implication: Quaternary International, v. 269, p. 69–73.

Selig, K.R., Sargis, E.J., Silcox, M.T., 2019a, Three-dimensional geometric morphometric analysis of treeshrew (Scandentia) lower molars: insight into dental variation and systematics: The Anatomical Record, v. 302, p. 1154–1168.

Selig, K.R., Sargis, E.J., and Silcox, M.T., 2019b, The frugivorous insectivores? Functional morphological analysis of molar topography for inferring diet in extant treeshrews (Scandentia): Journal of Mammalogy, v. 100, p. 1901–1917.

Selig, K.R., Sargis, E.J., Chester, S.G.B., and Silcox, M.T., 2020, Using three-dimensional geometric morphometric and dental topographic analyses to infer the systematics and paleoecology of fossil treeshrews (Mammalia, Scandentia): Journal of Vertebrate Paleontology, v. 94, p. 1202–1212.

Sen, S., and Thomas, H., 1979, Decouverte de rongeurs dans le Miocene moyen de la Formation Hofuf (Province du Hasa, Arabie saoudite): Compte Rendu Sommaire des Séances de la Société Géologique de France, v. 1, p. 34–37.

Simpson, G.G., 1931, A new insectivore from the Oligocene, Ulan Gochu horizon, of Mongolia: American Museum Novitates, v. 505, p. 1–22.

Singh, N.P., Gilbert, C.C., Patel, B.A., and Patnaik, R., 2018, The taphonomy and palaeoecology of the Middle Miocene hominoid locality of Ramnagar (Jammu and Kashmir, India): Journal of Asian Earth Sciences, v. 162, p. 69–83.

Steele, D.G., 1973, Dental variability in the tree shrews (Tupaiidae), *in* Zingeser, M.R., ed., Craniofacial Biology of Primates: 4th International Congress of Primatology, vol. 3, Basel, Karger, p. 154–179.

Storch, G., and Qiu, Z., 1991, Insectivores (Mammalia: Erinaceidae, Soricidae, Talpidae) from the Lufeng hominoid locality, Late Miocene of China: Geobios, v. 24, p. 601–621.

Thomas, H., and Verma, S.N., 1979, Découverte d'un primate adapiforme (Sivaladapinae sub fam. nov.) dans le Miocéne moyen des Siwaliks de la région de Ramnagar (Jammu et Cachemire, Inde): Comptes Rendus de l'Académie des Sciences de Paris, v. 289, p. 833–836.

Thomas, O., 1892, On some new Mammalia from the East-Indian Archipelago: The Annals and Magazine of Natural History, v. 6, p. 250–254.

Ungar, P.S., and M'Kirera, F., 2003, A solution to the worn tooth conundrum in primate functional anatomy: Proceedings of the National Academy of Sciences of the United States of America, v. 100, p. 3874–3877.

Van Valen, L., 1965, A Middle Palaeocene primate: Nature, v. 207, p. 435–436.

Vasishat, R.N., Gaur, R., and Chopra, S.R.K., 1978, Geology, fauna and palaeoenvironment of Lower Sivalik deposits around Ramnagar, India: Nature, v. 275, p. 736–737.

Waddell, P.J., Okada, N., and Hasegawa, M., 1999, Towards resolving the interordinal relationships of placental mammals: Systematic Biology, v. 48, p. 1–5.

Wagner, J.A., 1855, Die Säugethiere in Abbildungen nach der Natur: Leipzig, Weiger.

Wessels, W., and de Bruijn, H., 2001, Rhizomyidae from the lower Manchar Formation (Miocene, Pakistan): Annals of the Carnegie Museum, v. 70, p. 143–168.

Winchester, J.M., 2016, MorphoTester: an open source application for morphological topographic analysis: PLoS ONE, v. 11, e0147649. https://doi.org/10.1371/journal.pone.0147649.

Winge, H., 1887, Jordfundne og Nulevende Gnavere (Rodentia) fra Lagoa Santa, Minas Geraes, Brasilien: Med udsigt over Gnavernes Indbyrdes Slagtskab: Kjobenhavn, E Museo Lundii, v. 1, p. 1–178.

Wood, A.E., 1937, Fossil rodents from the Siwalik beds of India: American Journal of Science, v. 34, p. 64–76.

Zhang, L., Ameca, E.I., Cowlishaw, G., Pettorelli, N., Foden, W., and Mace, G.M., 2019, Global assessment of primate vulnerability to extreme climatic events: Nature Climate Change, v. 9, p. 554–561.

Ziegler, R., 1990, Didelphidae, Erinaceidae, Metacodontidae und Dimylidae (Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands: Stuttgarter Beiträge zur Naturkunde Serie B Geologie und Paläontologie, v. 158, p. 1–99.

Zijlstra, J., and Flynn, L.J., 2015, Hedgehogs (Erinaceidae, Lipotyphla) from the Miocene of Pakistan, with description of a new species of *Galerix*: Palaeobiodiversity and Palaeoenvironments, v. 95, p. 477–495.

Zittel, K., 1893, Traite de Paleontologie III, Paleozoologie Vertebrata (Pisces, Amphibia, Reptilia, Aves): Paris, Doin, 894 p.

Accepted: 28 April 2022