



## EARLY BRANCHING AMONG BASAL MURINE RODENTS WITH THE DESCRIPTION OF A NEW GENUS

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**Abstract:** The Siwalik record includes the oldest stem representatives of the Murinae, and notably the genus *Progonomys*, the oldest known murine genus that dispersed broadly across the Old World. In this study we erect a new Siwalik murine genus to clarify the content of the genus *Progonomys*. This new genus elucidates an early stem, a hitherto unrecognized branch of the subfamily Murinae. While it did not disperse as *Progonomys* did, so far as known, it attests to southern Asia's real and potential significance to early murine diversity and as one source of the Indo-Malayan dispersal of murine rodents.

**Key words:** Siwalik, Murinae, *Progonomys*, *Karnimata*, Miocene

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### Introduction

True mice (Murinae ILLIGER, 1811) comprise the most diverse subfamily of mammals. Their living diversity is distributed across Asia, Europe, Africa, Australia, Pacific islands, and globally as commensals with humans. The earliest intercontinental dispersal of true mice (Murinae) from southern Asia to Europe, the Levant, and Africa has been called a major phenomenon in the evolutionary history of rodents (López-Antoñanzas et al. 2019). The recognition of this Late Miocene biogeographic pattern relies to a large extent on the fossil record of rodent fossils in the Siwalik Group, Potwar Plateau, northern Pakistan. The Siwalik record of fossil murine rodents is fundamental to understanding these topics because it comprises an extended yet closely spaced and well dated series of paleontological localities from a physiographically circumscribed area called the Potwar Plateau, ranging in age from 18 to 6 Ma (Flynn et al. 2020, 2025). Rich information on the Siwalik fauna extends into India (Patnaik et al. 2022, Sehgal et al. 2023). Through that series of fossils, murine origins have been traced through dental morphology from basal members to crown clades (Jacobs 1977, 1978, Jacobs and Downs 1994, Kimura et al. 2013b, 2015, 2016, 2021, Flynn et al.

2020). The evolutionary data derived from fossils, combined with resolved molecular phylogenetics encompasses living murine species diversity today (Lecompte et al. 2008, Rowe et al. 2008, Kimura et al. 2015, Stepan and Schenk 2017, Aghová et al. 2018, López-Antoñanzas et al. 2024). This provides a framework for unravelling biogeography (Jacobs and Flynn 2005, Aghová et al. 2018, Rowe et al. 2019) and allows for isotopic and morphological approaches to changing ecology through time (Kimura et al. 2013a, b) and detects the cladogenesis of the Murini ILLIGER, 1811 (represented by *Progonomys* SCHAUB, 1938 and its descendants) and the Arvicanthini LECOMPTE, APLIN, DENYS, CATZEFLIS, CHADES et CHEVRET, 2008 clade (represented by *Karnimata* JACOBS, 1978 and its descendants) with an initial timing of morphological splitting at ~11.2 Ma (Kimura et al. 2015, 2021). The early stock occurring in the narrow time span between 11.6 and 11.2 Ma show high morphological variation on the first molar, one endmember similar to *Progonomys hussaini* CHEEMA, RAZA, FLYNN, RAJPAR et TOMIDA, 2000 and the other extreme endmember similar to *Karnimata fejfari* KIMURA, FLYNN et JACOBS, 2017, both of which occur in younger rocks between 10.5 and 10.1 Ma (Kimura et al. 2017), which makes taxonomic assignments difficult. Flynn et al. (2020) presented a practical solution

by calling the early stock indeterminate *Progonomys/Karnimata* grade (interchangeably early stock of *P. cf. hussaini* and *K. cf. fejfari*). Through continued work, we confirmed that the occurrence of a basal species named *Progonomys morganae* KIMURA, FLYNN et JACOBS, 2017, which coexisted with *P. hussaini* and *K. fejfari*, even predates the *Progonomys-Karnimata* split (Kimura et al. 2021). Following best practices of phylogenetic systematics and phylogenetic species concept (de Queiroz 2007a, b), we take this opportunity to recognize dental features that distinguish early murines and name a new genus for the previously published early Siwalik variant originally called *Progonomys morganae*.

Characters that distinguish genera and species of Siwalik murines are quite subtle, but the close temporal spacing of fossil localities can show a gradation of characters in an evolutionary continuum, which leads to cases of taxonomic uncertainty. Kimura et al. (2021) addressed that issue explicitly, which inevitably led to the clarification that is the purpose of this paper. Kimura et al. (2017) had named a new species as *Progonomys morganae*, which appeared to be the best option at the time although we noted that *P. morganae* deviated somewhat from the pattern of other Siwalik *Progonomys*. Flynn et al. (2020) noted that the anterolingual margin of the M1 is unusual in lacking a strong inflection. That observation was reinforced by Kimura et al. (2021: fig. 3B) who presented data indicating that the anterostyle (t1) angle in *P. morganae* is lower than in other Siwalik *Progonomys* species, resulting in a more symmetrical anterior lobe of M1. In this study we provide more anterostyle data and modify

our previous assignment of *P. morganae* from the Siwaliks by erecting a new genus, which more appropriately reflects early branching in murines.

## Materials and methods

This study is a reevaluation of YGSP specimens described by Kimura et al. (2017) and Flynn et al. (2020) with additional specimens reported in Kimura et al. (2021) from “Y” localities of the Potwar Plateau, Punjab, Pakistan. YGSP denotes the Yale Geological Survey of Pakistan collection. We also recognize that specimens referred to the basal species have been reported in India (Bhandari et al. 2021, Patnaik et al. 2022).

Tooth measurements (Tabs 1, 2) and characteristic dental traits of M1 of *P. morganae* were compared with basal murines from the Potwar Plateau and primitive species of *Progonomys* from other regions examined by López-Antoñanzas et al. (2019), who categorized *Progonomys morganae* (herein named a new genus) as primitive *Progonomys* along with basal Siwalik species (*P. hussaini* and *P. debruijini* JACOBS, 1978) and five other species or regional forms (*P. manolo* LÓPEZ-ANTOÑANZAS, RENAUD, PELÁEZ-CAMPOMANES, AZAR, KACHACHA et KNOLL, 2019, *P. ibrahimi* (SEN, 2003), *P. shalaensis* QIU et LI, 2016, *P. sinensis* QIU, ZHENG et ZHANG, 2004, *P. hispanicus* MICHAX, 1971 from Pezinok, Slovakia, older *P. hispanicus* from La Roma, Spain) based on M1 outline shape of murine rodents determined through Fourier analysis.

**Table 1. Taxon codes and localities for selected species.**

Species	Taxon code	Selected localities	Reference
<i>Antemus chinjiensis</i>	ANTchinjiensis	Y491, Y641, Y640, Y59, Y430, Y651, Y750, Y718, Y690, Y825, Y714; Potwar Plateau, northern Pakistan	Kimura et al. (2021)
<i>Karnimata cf. fejfari</i>	KT cf. fejfari	Y791, Y797 (11.2 Ma); Potwar Plateau, northern Pakistan	Kimura et al. (2021)
<i>Karnimata fejfari</i>	KTfeifari	Y259, Y450, Y311; Potwar Plateau, northern Pakistan	Kimura et al. (2021)
<i>Karnimata darwini</i>	KTdarwini	Y224 (9.4 Ma), Y182 (9.2 Ma), Y367 (9.0 Ma); Potwar Plateau, northern Pakistan	Kimura et al. (2021)
“Pre- <i>Progonomys</i> ”	“Pre- <i>Progonomys</i> ”	Y504 (11.6 Ma), Y83 (11.5 Ma), Y76 (11.4 Ma), Y809 (11.3 Ma); Potwar Plateau, northern Pakistan	Kimura et al. (2021)
<i>Progonomys cf. hussaini</i>	PR cf. hussaini	Y791, Y797 (11.2 Ma); Potwar Plateau, northern Pakistan	Kimura et al. (2021)
<i>Progonomys hussaini</i>	PRhussaini	Y259, Y450, Y311; Potwar Plateau, northern Pakistan	Kimura et al. (2021)
<i>Progonomys debruijini</i>	PRdebruijini	Y182 (9.2 Ma); Potwar Plateau, northern Pakistan	Kimura et al. (2021)
<i>Maneramus morganae</i>	Mmorg-Potwar	Y76 (11.4 Ma), Y791 (11.2 Ma), Y450 (10.2 Ma); Potwar Plateau, northern Pakistan	Kimura et al. (2017, 2021); this study
<i>Maneramus morganae</i>	Mmorg-Tapar-BH	Tapar, Kutch, India	Bhandari et al. (2021)
<i>Maneramus morganae</i>	Mmorg-Pasuda-BH	Pasuda, Kutch, India	Bhandari et al. (2021)
“ <i>Maneramus morganae</i> ”	“Mmorg”-Tapar-PT	Tapar, Kutch, India	Patnaik et al. (2022)
<i>Progonomys prasadi</i>	PRprasadi	Tapar, Kutch, India	Patnaik et al. (2022)
<i>Progonomys manolo</i>	PRmanolo	Zahleh, Bekaa Valley, central Lebanon	López-Antoñanzas et al. (2019)
<i>Progonomys ibrahimi</i>	PRibrahimi	Locality 84 of Sinap Tepe, Kazan, Ankara, Turkey	Sen (2003)
<i>Progonomys hispanicus</i>	PRhis-Pez	Pezinok, Slovakia	Joniak (2016)
<i>Progonomys hispanicus</i>	PRhis-LaRoma	La Roma 4B & 4C, Teruel, Spain	Renaud and van Dam (2002)
<i>Progonomys cathalai</i>	PRcatha-Herault	Montredon, Hérault, France	Renaud and van Dam (2002)
<i>Progonomys shalaensis</i>	PRshalaensis	Shala, Nei Mongol, China	Qiu and Li (2016)
<i>Progonomys sinensis</i>	PRsinensis	Localities 19, 38, Shaanxi, China	Qiu et al. (2004)

**Table 2. Measurements (mm) for molars of *Maneramus morganae* from Siwalik localities compared with other early murine samples.**

Locality	Specimen ID	Tooth position	Length	Width	References
450	YGSP 33180	left M1	1.62	0.92	Kimura et al. (2017)
450	YGSP 33202	left M1	–	1.08	Kimura et al. (2017)
450	YGSP 54091	left M1	1.63	0.97	Kimura et al. (2017)
311	YGSP 54160	left m1	–	–	Kimura et al. (2017)
311	YGSP 54180	right m2	–	0.93	Kimura et al. (2017)
311	YGSP 34563	left M2	1.30	1.02	Kimura et al. (2017)
311	YGSP 34523	right m1	1.50	0.85	Kimura et al. (2017)
311	YGSP 36167	right m1	1.53	1.00	Kimura et al. (2017)
311	YGSP 36168	right m1	1.58	0.98	Kimura et al. (2017)
259	YGSP 34159	left m1	1.50	0.94	Kimura et al. (2017)
259	YGSP 34238	right M2	1.27	1.03	Kimura et al. (2017)
259	YGSP 34033	left M3	0.72	0.75	Kimura et al. (2017)
797	YGSP 36837	right M2	1.33	1.02	Kimura et al. (2017)
791	YGSP 34963	left M1	1.77	1.01	Flynn et al. (2020)
809	YGSP 54059	left m1	1.45	0.88	Flynn et al. (2020)
809	YGSP 54049	right m1	1.35	0.85	Flynn et al. (2020)
504	YGSP 33670	right m1	1.48	0.92	Flynn et al. (2020)
76	YGSP 33558	right m2	1.05	0.91	Flynn et al. (2020)
504	YGSP 33649	left M2	1.13	0.95	Flynn et al. (2020)
504	YGSP 33672	left M2	1.15	1.05	Flynn et al. (2020)
76	YGSP 33593	left M1	1.55	0.91	This study
504	YGSP 33637	left M1	–	–	This study
504	YGSP 33638	right M1	–	–	This study

Four dental traits examined in this study include the van Dam index (Kimura et al. 2013a), the anterostyle angle, the protocone-enterostyle angle, and the metaloph angle. These morphometric traits differentiate major clades (stemming from the *Mus/Arvicanthis* split) and show trends in murine evolution (Kimura et al. 2013a, b, 2021). The dataset of Kimura et al. (2013a, b) was updated in Kimura et al. (2021) for taxonomy and additional trait data. For Siwalik murines from the Potwar Plateau, dental measurements were based on 2D images using a Keyence VHX-1000 digital microscope. For other taxa, the four traits were measured in ImageJ based on SEM images available in the original literature (Renaud and van Dam 2002, Sen 2003, Qiu et al. 2004, Joniak 2016, Qiu and Li 2016, López-Antoñanzas et al. 2019, Bhandari et al. 2021, Patnaik et al. 2022). Length and width data for some species were taken from tables and scatter plots (see above references); those of *P. ibrahimi*, *Progonomys hispanicus*, and *Progonomys cathalai* SCHAUB, 1938 were kindly provided by Dr. Raquel López-Antoñanzas and Dr. Sabrina Renaud. Since our earlier report, two studies have presented materials of *P. morganae* from India. These were from different localities in central Kutch, India (Bhandari et al. 2021, Patnaik et al. 2022) and examined separately in comparison with Pakistani *P. morganae*. The default setting of the ggplot2 package in R (Wickham 2016) is followed for boxplots. The full dataset is available upon request. The taxon codes of Table 1 are used in Text-figs 3–5.

## Systematic palaeontology

**Order Rodentia BOWDICH, 1821**  
**Suborder Supramyomorpha D'ELIÁ, FABRE et LESSA, 2019**  
**Family Muridae ILLIGER, 1811**  
**Subfamily Murinae ILLIGER, 1811**

**Genus *Maneramus* KIMURA, JACOBS, FLYNN et PATNAIK**  
**gen. nov.**

<http://zoobank.org:act:75A9F650-73C8-4E4D-841A-2F4A2246EFAB>

Type species. *Progonomys morganae* KIMURA, FLYNN et JACOBS, 2017.

Etymology. From the Latin, *mane* (early), plus *ramus* (branch).

Diagnosis. As for the type species.

***Maneramus morganae* (KIMURA, FLYNN et JACOBS, 2017)**  
**comb. nov.**

2017 *Progonomys morganae* sp. nov.; Kimura et al., p. 200, text-fig. 3a.

Holotype. YGSP 33180, isolated left M1.

Type locality. Locality Y450 (10.2 Ma), Hasnot area, Potwar Plateau, Pakistan, early Late Miocene Nagri Formation.

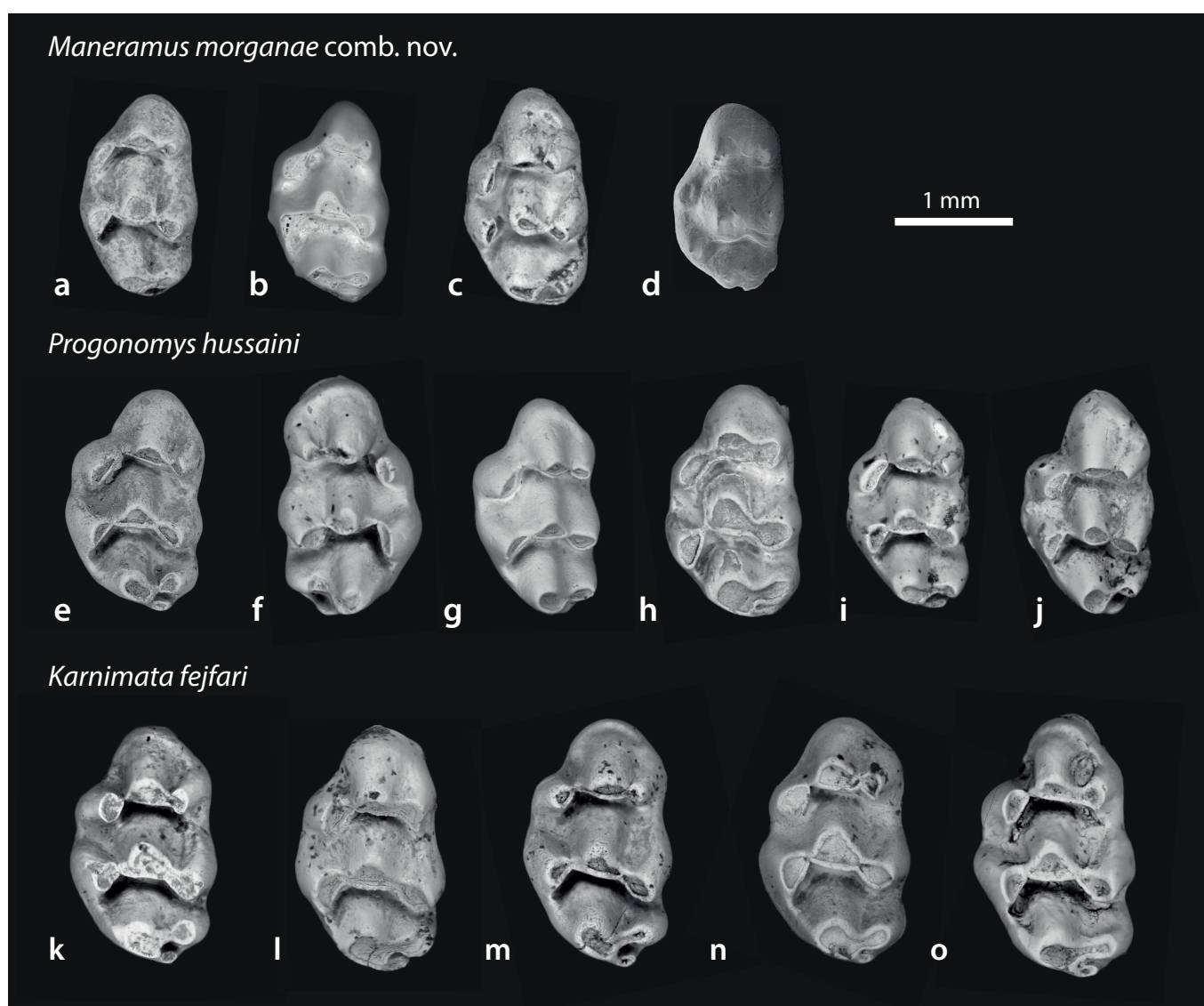
Referred material. As listed by Kimura et al. (2017), from Potwar Plateau localities Y450, YGSP 54091, left M1 and 33202, broken left M1. From Y311 (10.1 Ma), six molars: left M2, YGSP 34563, left m1 54160, three right m1 34523, 36167, 36168, worn right m2 54180. From Y259 (10.5 Ma), three molars, left m1 YGSP 34159, right M2 34238, left M3 34033; from low in the Nagri Formation, Y797 (11.2 Ma), YGSP 36837, right M2. Additional specimens were recognized and reported by Kimura et al. (2021) who referred a left M1 from Y791, YGSP 34963. Here we ascribe more material (Tab. 2), adding specimens from upper levels of the Chinji Formation, localities Y504, Y809, and Y76, which extend the time range for the species back to 11.6 Ma (see Text-figs. 1, 2). See Table 2 for measurements.

Age range. 11.6–10.1 Ma.

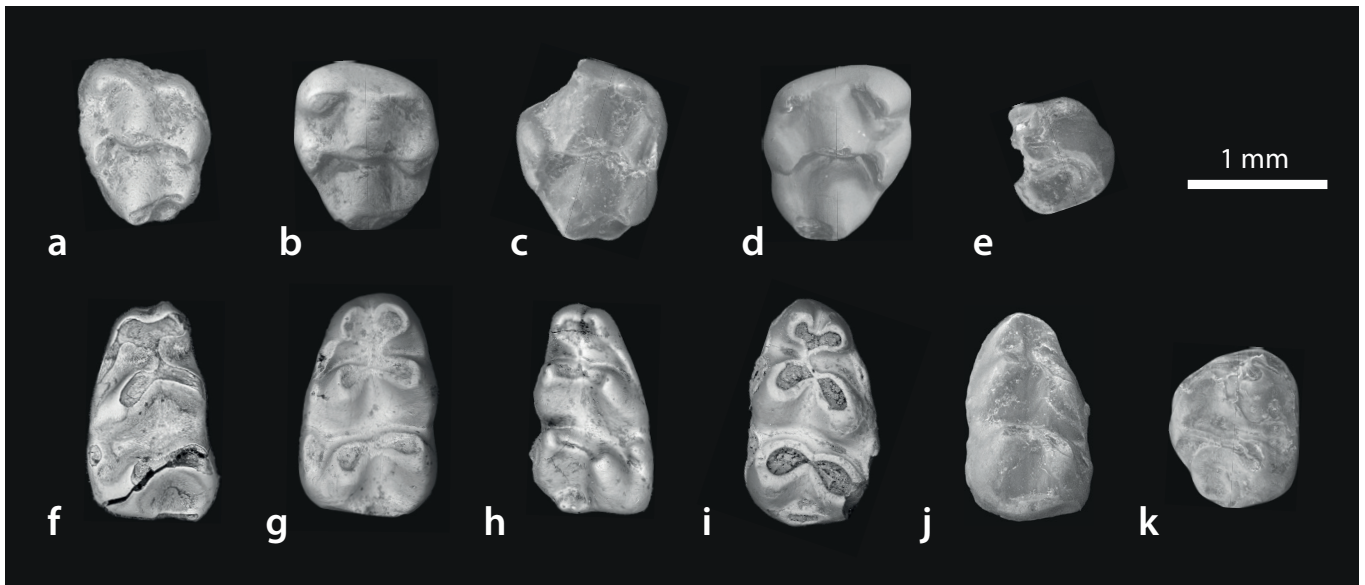
Original diagnosis. Small size, similar to that of *Progonomys shalaensis* QIU et LI, 2016 and *P. minus* SEN,

2003; molars are narrower than either, particularly than *P. minus*. Dimensions of *P. morganae* lie at the small periphery of the size range for *P. cathalai* SCHAUB, 1938, and its M1 length is about 15% less than that of *P. hussaini* CHEEMA et al., 2000. Elongated M1 (high L/W ratio; see Text-figs 3, 4); narrow m1 with small, closely appressed anteroconid cusps.

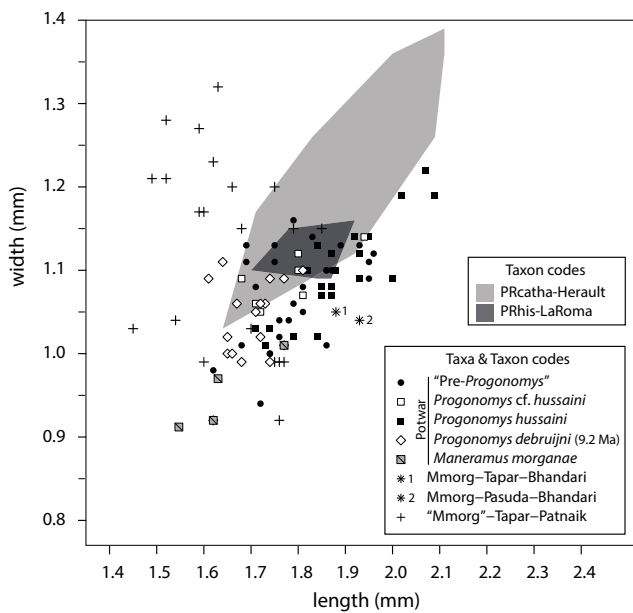
Revised diagnosis. In addition to the original diagnosis, a combination of the following characters is unique in *Maneramus*. M1 outline more symmetrical along the longitudinal axis than in derived *Progonomys*; low value (~1.7) for grazing indication (the van Dam index in Kimura et al. 2013a), as in Asian *Progonomys* (*P. shalaensis*, *P. sinensis*); small angle of M1 anterostyle with a median of 30°, similar to *P. hispanicus*; large angle between a transverse axis and a line connecting protocone and enterostyle in M1 with a median of ~70°, greater than younger *P. debruijni* and species from other regions, especially *Progonomys sinensis* (Text-fig. 5).



Text-fig. 1. Upper first molars of *Maneramus morganae* comb. nov. (a–d) from the Potwar Plateau, Pakistan, compared to M1 of *Progonomys hussaini* (e–j) and *Karnimata fejfari* (k–o) from the same region. a: YGSP 33180, holotype, left M1 from locality Y450 (10.2 Ma), b: YGSP 54091, left M1 from Y450, c: YGSP 34963, left M1 from Y791 (11.2 Ma), d: YGSP 33593, left M1 from Y76 (11.4 Ma), e: YGSP 34556 from locality Y311 (10.1 Ma), f: YGSP 54131 from Y311, g: YGSP 54143 from Y311, h: YGSP 33957 from locality Y259 (10.5 Ma), i: YGSP 33959 from Y259, j: YGSP 33976 from Y259, k: YGSP 34546, holotype from type locality Y311 (10.1 Ma), l: YGSP 34548 from Y311, m: YGSP 34540, n: YGSP 34554 from Y311, o: YGSP 54126 from Y311. Images of *Progonomys hussaini* and *Karnimata fejfari* were compiled from Kimura et al. (2017).



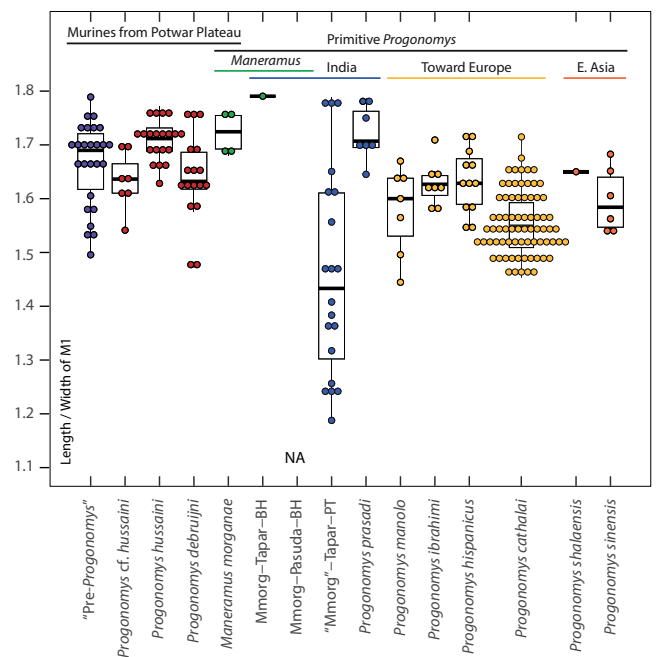
Text-fig. 2. Molars of *Maneramus morganae* comb. nov. from the Potwar Plateau, Pakistan. a: YGSP 33672, left M2 from Y504 (11.6 Ma), b: YGSP 33649, left M2 from Y504 (11.6 Ma), c: YGSP 34563, left M2 from Y311 (10.1 Ma), d: YGSP 36837, left M2 from Y311 (10.1 Ma), e: YGSP 34033, left M3 from Y259 (10.5 Ma), f: YGSP 54059, left m1 from Y 809 (11.4 Ma), g: YGSP 34159, left m1 from Y259 (10.5 Ma), h: YGSP 33670, right m1 from Y504 (11.6 Ma), i: YGSP 36168, right m1 from Y 311 (10.1 Ma), j: YGSP 34523, right m1 from Y311 (10.1 Ma), k: YGSP 33558, right m2 from Y76 (11.4 Ma). Scales corrected from Flynn et al. (2020).



Text-fig. 3. Length vs. width of the upper first molar (M1) of *Maneramus morganae* comb. nov. and selected murines from the Siwaliks of Pakistan and India. European *Progonomys cathalalai* and *P. hispanicus* are shaded polygons. Taxon codes are as in Table 1.

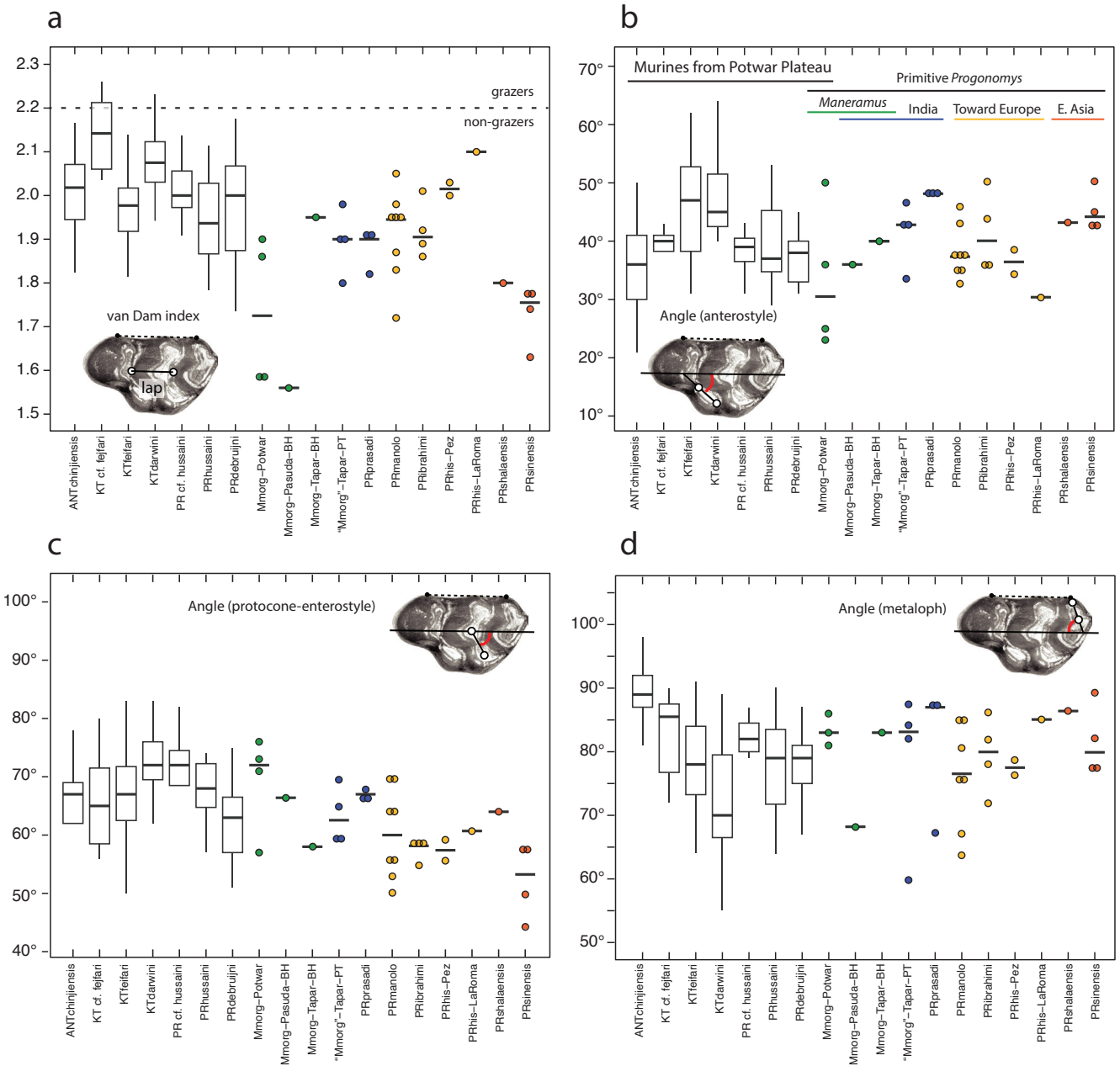
## Discussion

Our morphometric data present high morphological variation in the small sample size of *Maneramus*, indicating M1 shape of *Maneramus* is not fixed as diagnosable yet. However, this new genus consistently possesses an elongated, symmetric M1, which clearly differentiates it from *Progonomys hussaini* and *Karnimata fejfari* (Text-fig. 1) whose



Text-fig. 4. Length-over-width ratio of M1 for *Maneramus morganae* comb. nov. and selected murines from the Siwaliks of Pakistan and India, with primitive *Progonomys* from other regions. Primitive *Progonomys* includes all species categorized under that group in López-Antoñanzas et al. (2019). Taxon codes are as in Table 1.

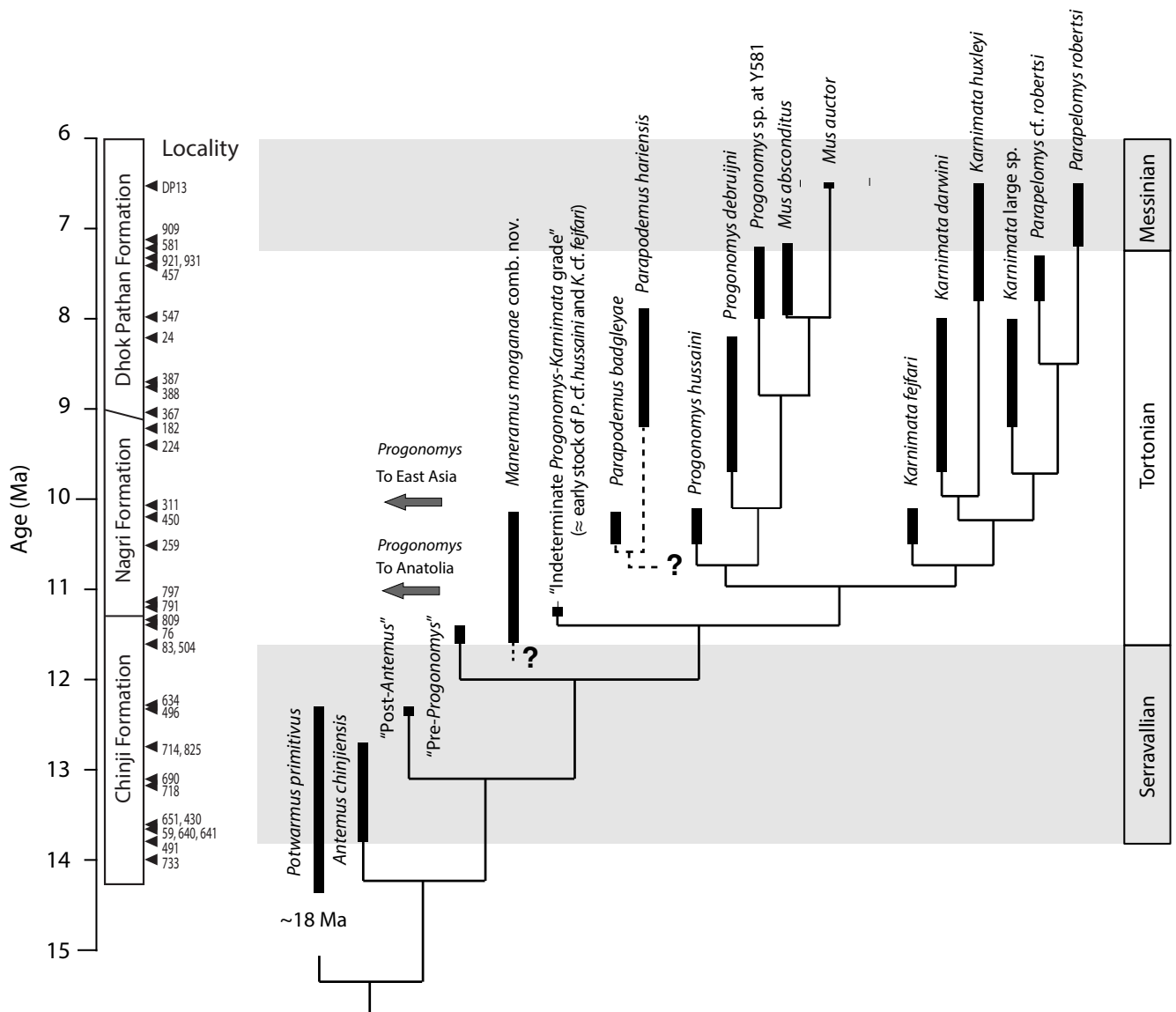
stratigraphic ranges overlap with *Maneramus*. Another rationale for validity of *Maneramus* is the later well-defined cladogenetic event recognized as splitting of between *Progonomys* and *Karnimata* in the Potwar murines (Text-fig. 6) as summarized in Kimura et al. (2021) and the introduction of this study. An initial split of *Progonomys* and *Karnimata* (Murini/Arvicanthini split) took place at around 11.2 Ma, but certainly by 10.5 Ma, whereas the



**Text-fig. 5.** Boxplots and dotplots for four dental traits on M1 of *Maneramus morganae* comb. nov., selected Siwalik murines, and primitive *Progonomys* from other regions. **a:** van Dam index, lap (= distance between the lingual anterocone and protocone) over width, **b:** angle (anterostyle), acute angle between the anterostyle and the longitudinal axis of the tooth, **c:** angle (protocone-enterostyle), acute angle formed by a line connecting the centers of protocone and enterostyle with the longitudinal axis of the tooth, **d:** angle (metaloph), acute angle between the major axis of the metacone (= a metaloph) and the longitudinal axis of the tooth. A van Dam index of 2.2 (dashed line) is reasonably considered as a threshold for a grazing diet based on the results of Kimura et al. (2013a) and van Dam (1997). In tooth images, points are connected by a dotted line as a reference for a longitudinal axis of the tooth, which passes through the apex of the arcuate-shaped protocone (Kimura et al. 2013a). Median lines are in the box of the first and third quartiles (Q1 and Q3) with whiskers to  $Q3 + 1.5 \times$  the interquartile range (IQR) and to  $Q1 - 1.5 \times$  IQR. In dot plots, black bars indicate the median of each dataset. Taxon codes are as in Table 1.

earliest record of *M. morganae* is 11.6 Ma, predating the definitive split of dental morphology. Thus, fossils at 11.6–11.4 Ma cannot belong to the genus *Progonomys* and are accommodated by new genus *Maneramus* (Text-fig. 6). Major components of the Siwalik murines are undoubtedly represented by the *Progonomys/Karnimata* split and its common descendant lineages. However, minorities such as *Maneramus* are recognized in basal roots of the Murinae

with indeterminate grades such as “Pre-*Progonomys*” and unnamed “Genus C” (Flynn et al. 2020). *Maneramus* was certainly distributed in Pakistan and India during the time interval that true *Progonomys* dispersed westward and later to East Asia (López-Antoñanzas et al. 2019). Compared to the high dispersal ability in *Progonomys*, *Maneramus* seems to be a dead-end lineage restricted in South Asia. López-Antoñanzas et al. (2019), in their study of Levantine



**Text-fig. 6.** Time-calibrated tree for proposed phylogenetic relationships of major Siwalik murine rodents, utilizing the strap package in R (Bell and Lloyd 2015), with localities and range-through occurrences of the taxa in the Potwar Plateau, Pakistan. A phylogenetic relationship of *Maneramus* to other basal murines is currently indetermined. Modified from Kimura et al. (2021), where methodological details are found, supplementary with Kimura et al. (2017) and Flynn and Kimura (2023).

fossil murines, named a new species, *Progonomys manolo*, and provided a geometric morphometric comparison of all named species of *Progonomys*. They mention that *P. morganae* (now *M. morganae*) is slightly smaller *P. manolo* and differs “in having a short and cusp-like t12 on M1, in having a large cusp t1 on M2 and M3 and in having cingulum cuspids on m1 that are more numerous and developed than in the Pakistani species”. Thus, *M. morganae* supported as valid and different from all species of *Progonomys* warrants a separate generic epithet. The M1 elongation (high L/W ratio), a diagnostic trait for *Maneramus*, is observed as a variation for some basal Siwalik individuals but is not retained in any species outside South Asia (Text-fig. 4). We suggest that *Progonomys* populations that migrated toward Europe and East Asia did not possess this variation.

Data presented by Kimura et al. (2021) track specific dental characters of M1 in Siwalik murines through time,

most notably the cladogenic origin of the crown murine tribes Murini (plus Praomyini Lecompte, Aplin, Denys, Catzefflis, Chades et Chevret, 2008 and Apodemini Lecompte, Aplin, Denys, Catzefflis, Chades et Chevret, 2008) versus Arvicanthini (plus Otomyini Thomas, 1896 and Millardini Lecompte, Aplin, Denys, Catzefflis, Chades et Chevret, 2008). They show a low anterostyle (t1) angle for *M. morganae* through time alongside the distribution of measurements relating to the cladogenic event (Kimura et al. 2021: fig. 3B). A low anterostyle angle is certainly one of the diagnostic characters in *Maneramus*, whereas this character varies greatly in our limited samples (Text-fig. 5). Based on our morphometric measurements, we suggest that *P. morganae* reported by Bhandari et al. (2021) correctly represents *M. morganae* although one specimen from Tapar village shows a large van Dam index as an outlier of the genus; Tapar specimens identified by Patnaik et al. (2022)

may represent a different species or a possibly mix of species because size range is even greater than in *P. cathalai* (Text-fig. 3). This illustrates the difficulty of recognizing species based solely on dental morphology and emphasizes morphometric comparisons as made in this study.

*Maneramus morganae*, a new early branch to the Murinae, is yet uninformative relative to extant tribes still wanting a useful fossil record. The most significant tribes for which the fossil record has not yet provided precise divergence estimates are “Hapalomyini” (sensu Pagès et al. 2016; nomen nudum), Phloeomyini ALSTON, 1876, and the successful, by any measure, Rattini BRUNETT, 1830. These are all essentially modern Indo-Malayan species and are, according to molecular estimates, the earliest diverging clades of Murinae (Aghová et al. 2018). The origin of the oldest of these branches is estimated to be 16–14 Ma, which is not inconsistent with the Siwalik fossil record. However, the Siwalik fossil record is silent on this subject except in one significant way. There is suggestive evidence of biogeographic relationships between faunas, both modern and fossil between Pakistan and those farther to the east. For instance, Siwalik hedgehogs (Zijlstra and Flynn 2015), treeshrews (Jacobs 1980), and primates (Jacobs 1981, Barry et al. 1986, MacPhee and Jacobs 1986, Flynn and Morgan 2005, Zijlstra et al. 2013), as well as a number of large mammals, are indicative at several points in time in showing clear relationships to southeast Asia. Miocene fossils from Thailand have obvious Potwar affinities (Mein and Ginsburg 1997).

## Conclusions

The recognition of *Maneramus* as a distinct genus highlights an early, previously unrecognized lineage within the Murinae, emphasizing the complexity of murine evolution in South Asia. *Maneramus* consistently exhibits an elongated, symmetric M1, distinguishing it from *Progonomys* and *Karnimata*, despite overlapping stratigraphic ranges among the three. The temporal occurrence of *M. morganae* at 11.6–11.4 Ma precedes the definitive dental morphological divergence between *Progonomys* and *Karnimata*, supporting its taxonomic separation. While *Progonomys* successfully dispersed across Eurasia, *Maneramus* appears to represent a dead-end lineage restricted to South Asia. Its presence alongside early murine diversity in the Siwaliks underscores the region’s role as both a center of origin and a reservoir for murine evolutionary experimentation. Future discoveries, particularly of expanded morphometric datasets, may further clarify the evolutionary significance of *Maneramus* and its relationship to other basal murine lineages. Moreover, continued fossil sampling in the Siwaliks and adjacent regions may shed light on the earliest divergence events of key murine clades, particularly those with modern Indo-Malayan affinities.

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