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# 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*)

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**Abstract:** The early late Miocene is an interval of increased diversification for murine rodents. Whereas the genus *Progonomys* became widespread throughout Eurasia by 10 Ma, it appears from the known paleontological record that southern Asia is the arena of evolution and diversification at the base of the Murinae. The Siwalik fossil record of the Potwar Plateau in northern Pakistan preserves fossil evidence relevant to unraveling this history. Murine rodents are recorded there throughout the middle Miocene, and diversification began in Siwalik assemblages before 11 Ma. The well-established *Progonomys* and *Karnimata* lineages were already present between 11 and 10 Ma, and these represent extant murine crown groups. Here we document diversity in Siwalik murines dating to 10.5 to 10.1 Ma, and clarify their recognition by naming a new species of *Karnimata* and referring specimens of *Progonomys* from this interval to *P. hussaini*. In addition, we define at least two other uncommon murine species that coexist with them. One of these is an early record of *Parapodemus*, a fossil genus of Tribe Apodemurini, which constitutes a calibration point for the *Apodemus/Tokudaia* split. Together, these fossil taxa provide further evidence bearing on the major split among murines leading to the clades Murini and Arvicanthini.

**Key words:** Murinae, *Mus*, *Apodemus*, *Progonomys*, *Karnimata*, Siwaliks, Pakistan, Miocene

## Introduction

The fossil record of murine rodents from the Siwalik Group of the Potwar Plateau, Pakistan, is significant for several important reasons. First, it provides a relatively dense temporal record comprising stratigraphically superposed samples of fossils ranging in age from approximately 14 to 6.5 Ma with a younger horizon at 1.8 Ma (Keller et al. 1977) also recorded. This record allowed the development of a specific time-calibrated hypothesis of the origin and early cladogenic events within murine rodents (Jacobs and Flynn 2005, Kimura et al. 2016), the most diverse group of living mammals. The documentation of the fossil record of murines enhanced correlation within the Siwaliks of the Indo-Pakistan Subcontinent (Patnaik 2013), and with Europe and Asia, specifically China (Flynn et al. 2013, Flynn and Wessels 2013), based on immigration events and biogeographic first occurrence data, and contributes to

understanding paleoenvironments and the tempo and mode of faunal change (Flynn and Jacobs 1982, Barry et al. 1991, 2013, Kimura et al. 2013a, b). This understanding of murine evolution from the fossil record is directly relevant to the calibration of molecular clocks (Jacobs and Pilbeam 1980, Jacobs and Flynn 2005, Kimura et al. 2015). While the Siwalik fossil record of murines overwhelmingly comprises isolated teeth collected by screening (Badgley et al. 2004), which early on hindered phylogenetic analysis, more recently the fossil record has been combined with dietary interpretation by means of isotopes, quantitative tooth morphology, and extensive comparisons with living species to develop a more comprehensive evolutionary history of the group in South Asia. These studies converge on refined fossil calibration for the group, especially age constraints on phylogenetic nodal positions, and show timing of acquisition of different biological properties in diverging

lineages (Kimura et al. 2013a, b, 2015, 2016). In most of our studies, we have simplified our arguments by focusing on the most abundant species of one lineage and its counterpart in its sister. As a consequence of detailed studies, we note that uncommon morphological variations represent separate species.

Here we examine the murine record from three localities (Y 259, Y 311, Y 450) from the upper part of the Nagri Formation. These localities have consistent taxonomic composition and document the interval between 10.1 and 10.5 Ma, as demonstrated through magnetic polarity stratigraphy, a time early in the cladogenesis of the Murini (represented by *Progonomys*) and Arvicanthini-Otomyini-Millardini clades (represented by *Karnimata*; Kimura et al. 2015). We are honored to offer this contribution to Professor Rudolf Musil and Professor Oldřich Fejfar in celebration of their long and distinguished careers. Professor Fejfar in particular has followed our work in the Siwaliks since our collective beginning over forty years ago. In fact, one of the first papers on murines from this project was published in Časopis pro mineralogii a geologii (Praha) (Jacobs 1979), which was recommended for print by Professor Fejfar.

## Material

The basis for our systematic treatment of early murines is isolated molars retrieved from fossiliferous sediment by wet screening. Small mammal localities in the Nagri Formation of the Siwaliks are relatively few compared to underlying and overlying formations because fluvial sandstone is the dominant lithology of the Nagri Formation. We focus on the three small mammal sites known from the upper part of that formation in the Potwar area of northern Pakistan, localities Y 311, 450, and 259. Locality Y 311 is likely the same as the well-known (Moonen et al. 1978) Sethi-Nagri collecting area sampled in a number of collections. This is the youngest of the sites, and it occurs high in Chron C5n.2n at the 950 m level in the Chinji-Nagri section of Johnson et al. (1982: 27). Y 259 is oldest, between units E and F in the Kaulial Kas section of Barry et al. (1982: fig. 2), and midway through C5n.2n. Locality Y 450 occurs stratigraphically between Y 259 and Y 311. Ages are interpolated by stratigraphic thickness within the long Chron C5n.2n. All three sites are calibrated securely on the Ogg (2012) geomagnetic time scale as 10.1 Ma, 10.2 Ma, and 10.5 Ma. Field teams
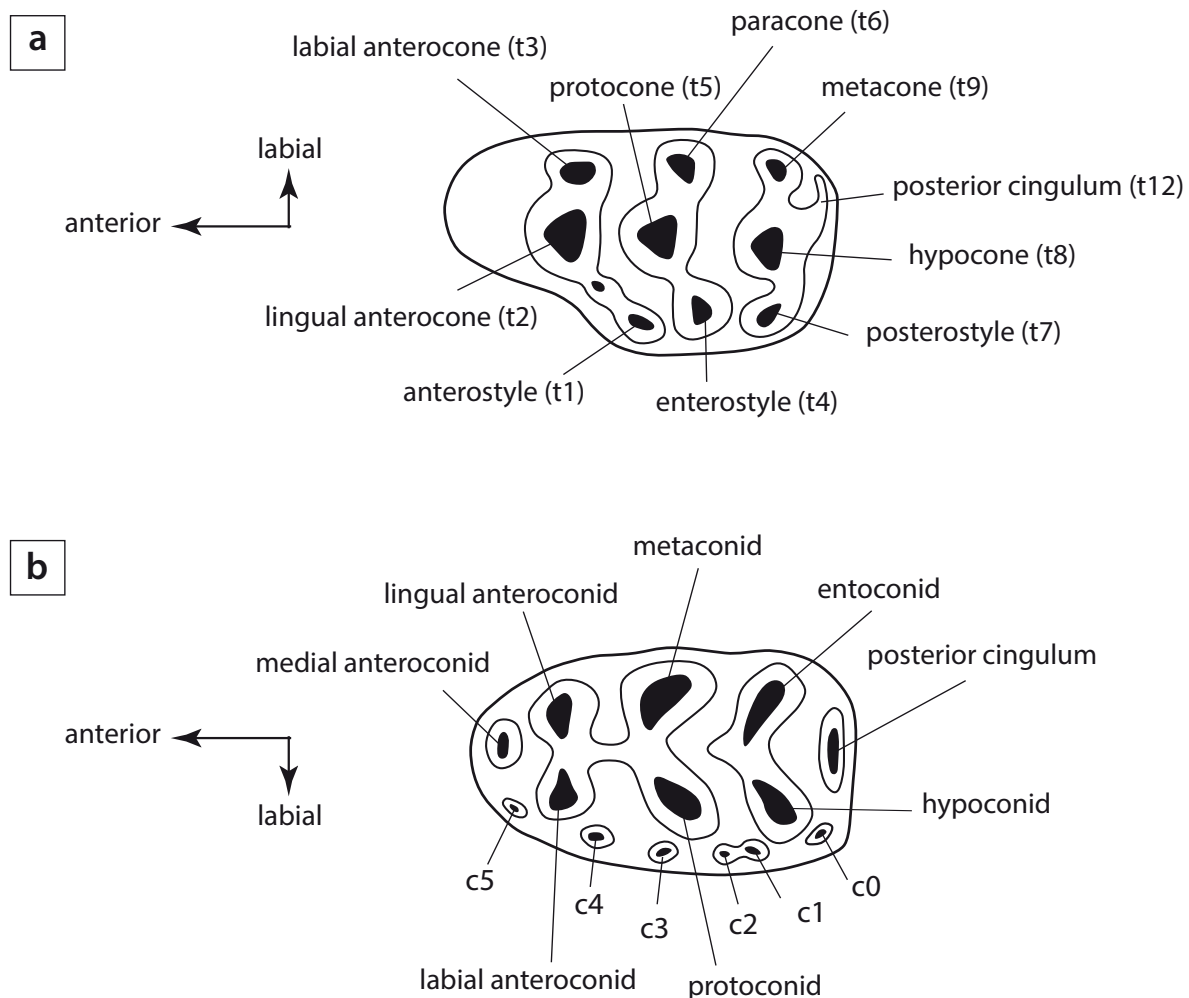


**Text-fig. 1. Line drawings of idealized murine left first molars, M1 above (a) and m1 below (b). Standard Cope-Osborn terminology is used for the cusps, with equivalent t1 to t12 terminology and specialized cingulum cusp names for m1.**

processed bulk samples of fossiliferous sediment from each locality in tandem screen-bottom boxes by washing in water. Diluted acetic acid was required to eliminate matrix cement for locality Y 259, after which the sediment was thoroughly rinsed and rescreened. The concentrate was treated by utilizing a heavy liquid (sodium polytungstate) to separate fossils from the matrix, and the residue was sorted by microscope.

The murine rodent fossils are isolated cheek teeth, representing three upper molar (M1–M3) and three lower molar (m1–m3) loci. Sample size is large for localities Y 311 and 259 (174 and 329 identified murine teeth, respectively), smaller for the intervening locality Y 450 (40 teeth identified). We used morphological details of the crowns and root structure to recognize species. The dominant species are *Progonomys hussaini* Cheema et al., 2000, and *Karnimata* sp. nov. A few specimens represent other species (see below) and a proportion of the fossils are fragmentary or currently not recognized to be identifiable.

Descriptions utilize standard Cope-Osborn cusp terminology (Text-fig. 1). The figure is modified from Kimura et al. (2013b), and shows also the widely used t1 to t12 terminology. Teeth were measured using a Keyence VHX-1000 digital microscope, with major axis (length) parallel to the tooth row, and width perpendicular to that axis; maximum dimensions were recorded. The Leo 1450

scanning electron microscope was used to view and image isolated murine molars at a magnification of 90×. All images were made in the variable pressure mode, using pre-purified nitrogen at a pressure of 15–25 Pa, working distance of 15 mm. The backscattered electron detector was set at 20 Kv, 55 pA beam; specimens in Text-figs 2 and 6: 25 Kv and 320 pA beam.

**Abbreviations**

JAL (Jalalpur locality), PMNH (Pakistan Museum of Natural History), Y (prefix for localities of the Yale-Geological Survey of Pakistan field expeditions), and YGSP, acronym for Yale-Geological Survey of Pakistan specimens.
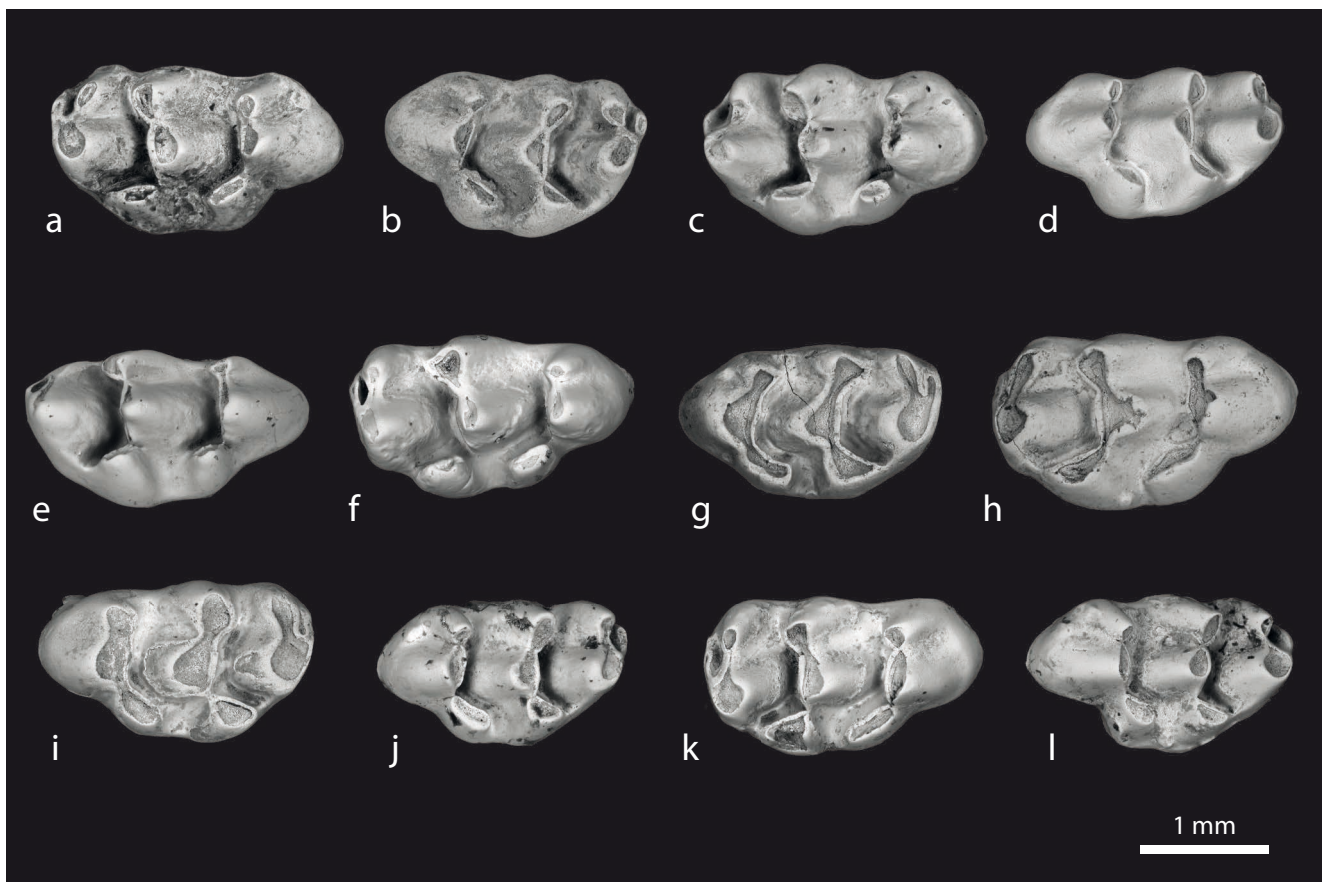
## Systematic palaeontology

### Family Muridae Illiger, 1811

### Genus *Progonomys* Schaub, 1938

### *Progonomys hussaini* Cheema et al., 2000

Holotype. PMNH 5062, left M1.

Type locality. JAL-101, Jalalpur area, District Chakwal, early late Miocene Nagri Formation, no nearby dated section.



**Text-fig. 2. First upper molar variation in *Progonomys husssaini* from three localities in the upper part of the Nagri Formation, Potwar Plateau, Pakistan. The 12 molars are oriented with buccal side upward, each at the same 1 mm scale, making size variation apparent. a) YGSP 33187 from locality Y 450; b) 34556, c) 54131, d) 54143, e) 54151, f) 54152, all from Y 311; g) 33937, h) 33947, i) 33957, j) 33959, k) 33963, l) 33976 all from Y 259. Figures a, c, e, f, h, k are all right M1; the others are left M1.**

Referred material. 68 molars from Y 311, 12 from Y 450, 160 from Y 259.

Description and additional notes. This species is already described (Cheema et al. 2000), but we illustrate 12 molars (Text-fig. 2) to show observed variation in M1. These molars display apparent variation due to wear, and true minor differences in cusp position and proportions. M1 are generally narrow, although a few, such as Text-fig. 2b are relatively broader. In all, the anterostyle touches, but is generally posterior to the double anterocone. The labial anterocone is distinctly smaller than its lingual pair, and the anterior part of the molar is quite asymmetrical, with a deep inflection of the first chevron at the anterostyle. The precingulum is weakly developed in some teeth, and bears no cuspule. The enterostyle is posterior in position, weakly connected to the protocone (isolated in Text-fig. 2f). There is no stephanodonty (paracone-metacone, t6-t9, connection undeveloped). The posterior cingulum is usually prominent. These molars are larger than the younger Siwalik *Progonomys debruijni* Jacobs, 1978 (~9 Ma), and with less inclined cusps. Molars of Text-fig. 2 exhibit variable cusp inclination, a feature difficult to assess in late wear, and the chevrons are positioned closely (limited antero-posterior distance between them).

Discussion. This species is adequately described and illustrated by Cheema et al. (2000), with the caveat that their sample includes several specimens that we would now identify as *Karnimata* (differentiation of the taxa developed below). Cheema et al. (2000: 73) suspected that a second species might be present in the hypodigm, but the total sample size was too small to defend this position at the time. For example, PMNH 5063 and 5085 figured by Cheema et al. (2000: fig. 5b, e) would be classified now as *Karnimata* (see below). Other tooth positions show variation that we can now defend as evidence of two species: gracile m2 (PMNH 5096) and m3 (PMNH 5115) represent *Progonomys hussaini* and contrast with their more robust counterparts. Cheema et al. (2000) used biochronological arguments to date JAL-101 to about 11 to 10 Ma. Identity of the species in sites of 10.5 to 10.1 Ma in Potwar paleomagnetic sections confirms this age.

In some past publications beginning with Jacobs and Flynn (2005) and continuing in Kimura et al. (2013a, b, 2015, 2016), we applied the name *Progonomys hussaini* to older samples from low in the Nagri Formation and top of the Chinji Formation (approximately 11.5 to 11 Ma). We now realize that murids of that age are distinctly more primitive and should be excluded from *P. hussaini*.

*Progonomys sinensis* Qiu et al., 2004 from Lantian, Shanxi Province, China, is a larger species of about the same age (Kaakinen 2005) as Y 311. It shows a similar conservative stage of evolution as *P. hussaini*. All early *Progonomys* across Eurasia show similar molar structures despite some variation in size, and relative sizes of cusps (see Mein et al. 1993). Reasonable conclusions on dental morphology and metrics led Wessels (2009) to consider *P. hussaini* and *P. sinensis* as junior synonyms of the somewhat younger *P. cathalai* Schaub, 1938, type locality of which is Montredon in southern France. Yet, given the straight-line distance from the Potwar to the Mediterranean of >3000

km, and the much farther distance from China to Spain, species identity on such a scale seems unlikely. We argue that population variation can be used to defend recognition of separate species. We do think that the similarity of distant populations reflects close relationship; minor local differentiation followed after dispersal from the Indian subcontinent between 11 and 10 Ma, with westward spread to the Mediterranean area and then northeastward dispersion to Shanxi, as hypothesized by Flynn and Wessels (2013). It is likely that the populations over this vast area were distinct, if difficult to define morphologically.

Current age estimates for *Progonomys* place its dispersal to Europe (Mein et al. 1993) in late mammal zone MN 9, around 10 Ma. Our geohistorical view of Siwalik murine evolution sees *P. hussaini* as the Potwar successor of a somewhat older successful disperser that was the progenitor of *P. cathalai* and *P. sinensis*. Samples of Siwalik *Progonomys* older than 10.5 Ma (Jacobs and Flynn 2005) remain to be studied in a future publication.

### *Progonomys morganae* sp. nov.

Holotype. YGSP 33180, left M1, Text-fig. 3a.

Etymology. Named in honor of Dr. Michèle E. Morgan in recognition of her extensive contributions to research on the Siwalik mammalian faunas of Pakistan, in particular meticulous field work and ongoing data analysis, and perpetual optimism in interpreting the fossil record.

Type locality. Y 450, Hasnot area, early late Miocene Nagri Formation, 10.2 Ma.

Referred material. From Y 450, YGSP 54091, left M1 and 33202, broken left M1. From Y 311, six molars: left M2, YGSP 34563, left m1 54160, three right m1 34523, 36167, 36168, worn right m2 54180. From Y 259, three molars, left m1 YGSP 34159, right M2 34238, left M3 34033. Also from older locality Y 797, 11.2 Ma: YGSP 36837, right M2.

Measurements. See Table 1.

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*. *Progonomys morganae* sp. nov. has an elongated M1 (high L/W ratio) and a narrow m1 with small, closely appressed anteroconid cusps.

Description. The few teeth that can be attributed to this species share small size. M1 and M2 show the low degree of cusp inclination comparable to *Progonomys hussaini*. The anterior lobe of M1 is dominated by the large, lingual anterocone of the first chevron, located near the midline of the tooth. The small labial anterocone is lateral to it; the anterostyle is posterior in position, connected to the posterolingual corner of the large lingual anterocone. The holotype M1 has only a shallow, marginal anterolingual indentation, no deep inflection at the anterostyle, unlike *Progonomys hussaini*. YGSP 54091 (Text-fig. 3b) does have an anterolingual inflection. In both, the chevrons are well-separated, anteroposteriorly. The anterostyle is

| YGSP Number | Locality | Element | Length | Width |
|---|---|---|---|---|
| 33180 holotype | Y 450 | Left M1 | 1.62 | 0.92 |
| 33202 | Y 450 | Left M1 | – | 1.08 |
| 54091 | Y 450 | Left M1 | 1.63 | 0.97 |
| 54160 | Y 311 | m1 frag. | – | – |
| 54180 | Y 311 | Right m2 | – | 0.93 |
| 34563 | Y 311 | Left M2 | 1.30 | 1.02 |
| 34523 | Y 311 | Right M1 | 1.50 | 0.85 |
| 36167 | Y 311 | Right m1 | 1.53 | 1.00 |
| 36168 | Y 311 | Right m1 | 1.58 | 0.98 |
| 34159 | Y 259 | Left m1 | 1.50 | 0.94 |
| 34238 | Y 259 | Right M2 | 1.27 | 1.03 |
| 34033 | Y 259 | Left M3 | 0.72 | 0.75 |
| 36837 | Y 797 | Right M2 | 1.33 | 1.02 |
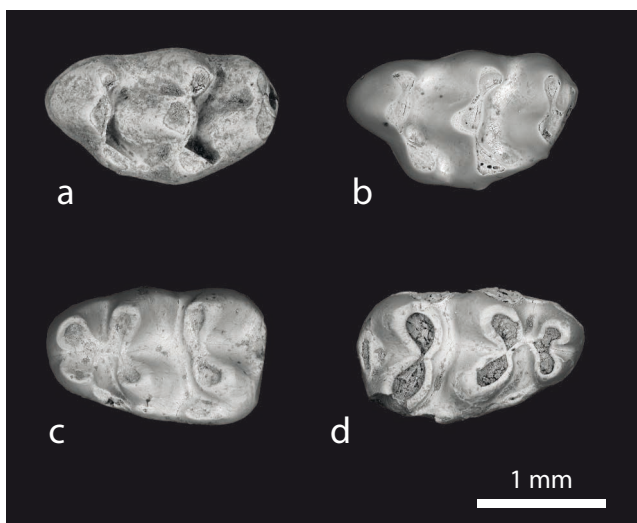


**Text-fig. 3.** *Progonomys morganae* **molars from the upper part of the Nagri Formation. a) YGSP 33180, holotype, from Y 450 and b) 54091 from Y 450; both left M1 with buccal side upward. c) 34159 from Y259; and d) 36168 from Y 311, left and right m1, respectively, with lingual side upward. Scale for all is 1 mm.**

laterally compressed. M1 lacks a precingulum. The second chevron is nearly symmetrical, the enterostyle being somewhat posterior in position; it weakly joins the large hypocone. There is no stephanodonty and the posterior cingulum is thin. M1 is slender, elongated relative to width (L/W ratio of holotype = 1.76; for YGSP 54091 = 1.68); this is apparent in greater distances between chevrons relative to *P. hussaini*.

M2 has a near-symmetrical major chevron, and the enterostyle turns posteriorly toward the hypocone. The anterostyle is small but shows wear from an early stage; the minute labial anterocone shows no wear. The posterior cingulum is present. M3 is quite small (Tab. 1) and has a minute anterostyle; there is only a bead of enamel at the position of the labial anterocone.

The slender m1 shows the murid double anteroconid as twinned cusps at the midline of the tooth, closely appressed,

and much smaller than the protoconid and metaconid (Text-fig. 3c, d). There is no room for a medial anteroconid and the labial cingulum is weak, bearing a c1, variable in size, and minute c3 or c4. The m2 is represented only by one well-worn specimen.

D i s c u s s i o n . This uncommon small *Progonomys* is a contemporary of abundant *P. hussaini* and early *Karnimata*. Its size does not overlap that of *P. hussaini*. It is somewhat smaller than the mean size of *P. debruijni*, and has less strongly inclined cusps and less anteriorly expanded base of the anterocones than the latter. Individuals in some populations of *P. cathalai* (Wessels 2009) are near the size observed for the small Siwalik *Progonomys morganae*. *Progonomys morganae* is conservative in most features, except for the slender molars and strongly appressed anteroconids of m1; *P. morganae* has a thinner posterior cingulum than other species of the genus.

Very close in molar length to *P. shalaensis* and *P. minus*, *Progonomys morganae* differs in having a narrower M1, that is, a higher L/W ratio. The L/W ratio of *P. shalaensis* is 1.65 (Qiu and Li 2016), and that of *P. minus* is 1.5 (Sen 2003).

### Genus *Karnimata* Jacobs, 1978

### *Karnimata fejfari* sp. nov.

H o l o t y p e . YGSP 34546, left M1, Text-fig. 4c.

E t y m o l o g y . For Oldřich Fejfar, vertebrate paleontologist well known for his seminal works on Neogene mammal research, especially small mammals.

T y p e   l o c a l i t y . Y 311, upper part of the Nagri Formation, Siwalik Group, Chinji and Sethi-Nagri area of the Potwar Plateau, northern Pakistan, age 10.1 Ma.

M a t e r i a l . 98 isolated molars from locality Y 311 (enumerated in Appendix). Additional material from other localities: 23 molars from Y 450, 161 molars from Y 259 (Text-figs 4, 5).

M e a s u r e m e n t s . See Appendix.

D i a g n o s i s . *Karnimata* slightly smaller than *K. darwini*, with anterostyle somewhat less anterior in position. M1 (L/W ratio = 1.65) more slender than *K. darwini* (L/W ratio = 1.56).

D e s c r i p t i o n . Molar cusp inclination is less than that of *Progonomys hussaini*, so that upper molar chevrons appear to lie relatively forward, even in early wear. M1 has eight major cusps, three in each of the first two chevrons. Its length/width ratio is 1.65. In the first chevron, the lingual anterocone is largest, labial anterocone smaller but prominent. The anterostyle (t1), generally rounded to somewhat laterally compressed, is linked to the posterolingual corner of the lingual anterocone, and is anterolingual to the protocone. The labial anterocone is more anterior in position than t1, and is rounded or occasionally shows a short posterior spur. In the second chevron, the protocone is the largest cusp, followed closely by the enterostyle (t4) and paracone. The enterostyle has a prominent posterior spur joining the hypocone low on its base. The paracone is completely isolated from the metacone (no hint of stephanodonty), although late in wear a short posterior spur may become evident. A short posterior
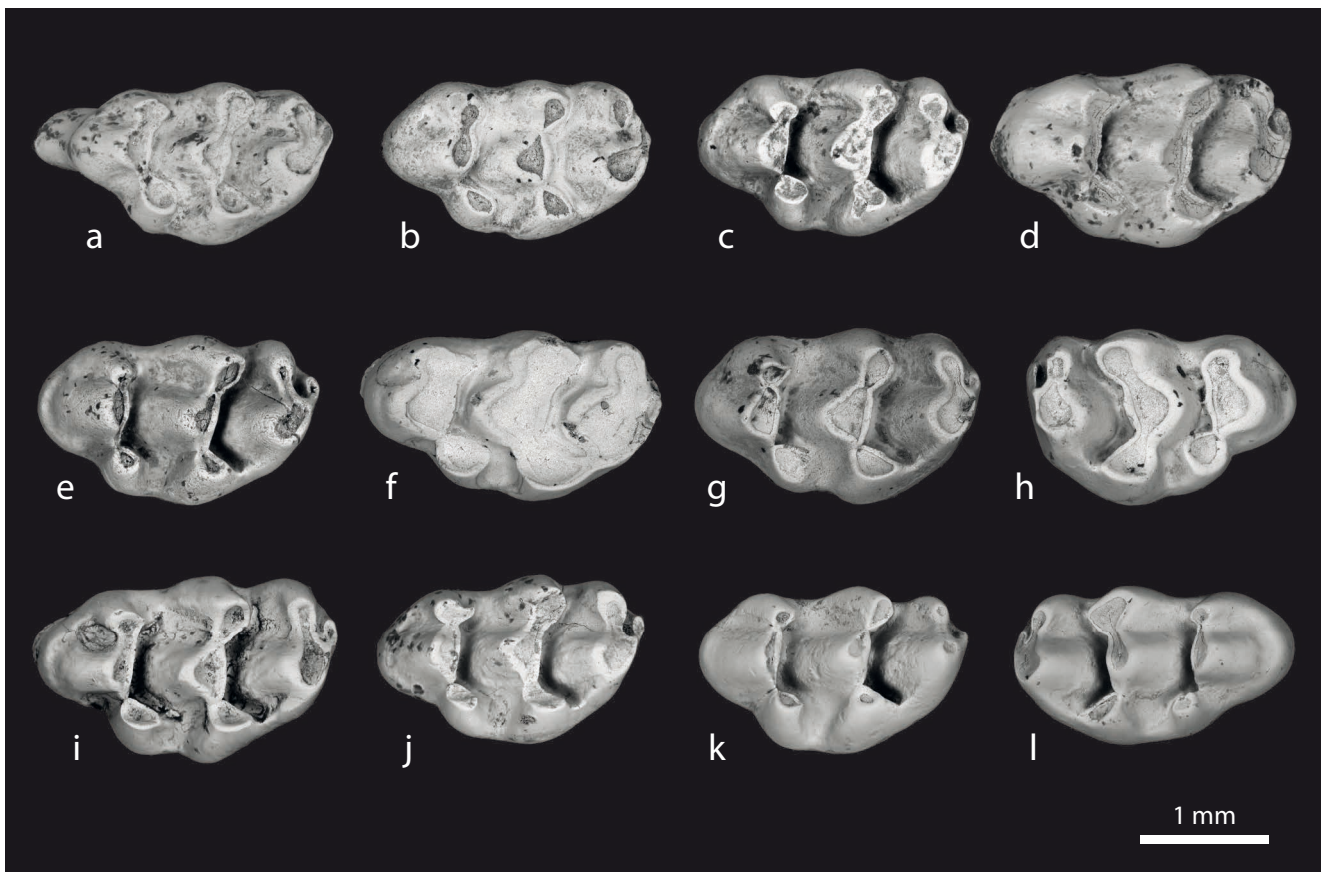
**Text-fig. 4. First upper molars of *Karnimata fejfari* sp. nov. from type locality Y 311, all figured with buccal side upward. a) YGSP 34551, b) 34544, c) 34546 holotype, d) 34548, e) 34540, f) 34547, g) 34554, h) 36162, i) 54126, j) 54127, k) 54147, l) 54153. All at same 1 mm scale, all left M1 except for right h and l.**

cingulum is well developed and the precingulum, although variable, is normally present. M1 has an anteroposteriorly expanded lingual root, a large anterior root, and a posterior root. While roots are broken on many specimens, most but not all of the well-preserved teeth show an additional central rootlet.

M2 resembles M1 in that it is robust with round cusps, not greatly inclined. The major chevron (paracone-protocone-enterostyle) dominates the tooth, but the anterostyle is a prominent cusp located anterolingually. The small labial anterocone is always present and usually shows wear. The enterostyle has a posterior spur in contact with the base of the hypocone. The metacone is small and separated from the paracone until late wear. The short posterior cingulum is usually clear. M2 has three roots.

We found no convincing bimodal distinction among the M3 from the type locality Y 311 to assign them with confidence to *K. fejfari* versus *Progonomys*. The available specimens show some variation in size and possibly the larger ones represent mostly *K. fejfari*; the smaller ones *Progonomys hussaini*. Also, the larger M3 generally have widths greater than lengths. All M3 have large anterostyles, but the labial anterocone differs in prominence among specimens; in some it is quite small. We propose without conviction that the larger specimens with strong labial anterocones represent *K. fejfari*. Three are listed in the appendix. One slightly smaller M3 from Y 450 (Appendix) has a strong labial anterocone and may also represent *K. fejfari*.

Lower molars are robust. The protoconid-metaconid and hypoconid-entoconid pairs of cusps are angled somewhat and span m1 broadly. The twinned anteroconid cusps are smaller, and there is generally a narrow shelf anterior to them, on which a minute medial anteroconid occurs in a few specimens. Wear on the posterior cingulum produces an oval loop of enamel. The labial cingulum is generally well developed, and usually bears accessory cusp c1, variably c3. Two roots anchor the tooth, and some specimens show a central rootlet. Posterior lower molars carry on the theme of m1 robustness. Their opposite cusp pairs are broad. The outline of m2 departs from rectangularity because its extended labial anteroconid supplies greater length than on the lingual side of the tooth. The hypoconid-entoconid cusp pair is nearly as broad as the protoconid-metaconid pair. The posterior cingulum is distinct. The labial cingulum is well-developed, bears c1, and usually has a cusp in position of c3. There are two roots. The m3 (see Cheema et al. 2000: fig. 6c) is distinguished by breadth of its anterior cusp pair to match the adjacent m2. The m3 is a small tooth with single, teardrop posterior cusp located somewhat lingual to the tooth midline. There is a small labial anteroconid, high enough to develop a wear facet. The labial cingulum is absent, except for an infrequent swelling of enamel representing c1. There is no posterior cingulum and two roots are present.

D i s c u s s i o n . In Siwalik murid assemblages of around 9 Ma (Dhok Pathan Formation, which overlies the
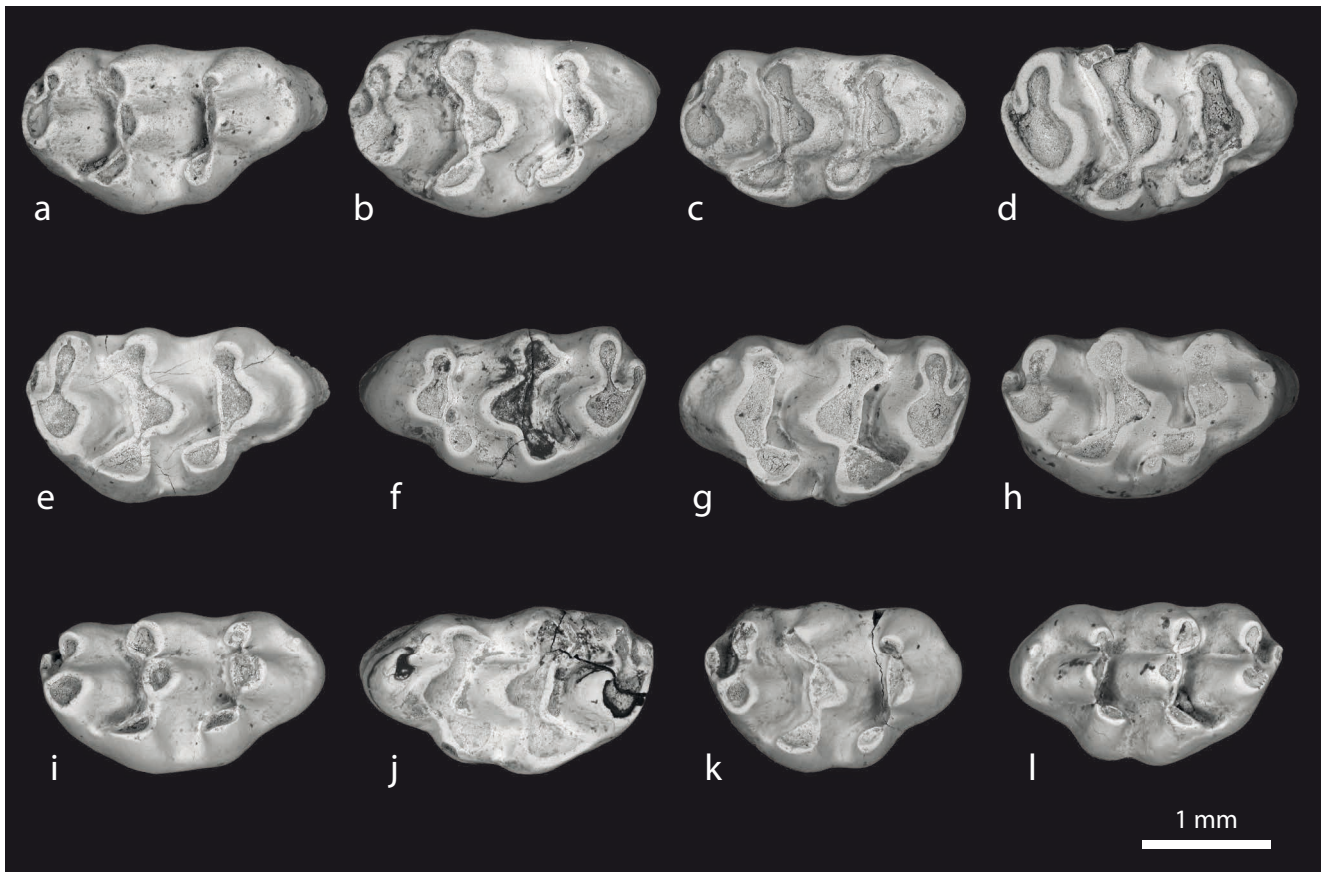
**Text-fig. 5.** First upper molars of *Karnimata fejfari* sp. nov. from localities Y 450 (a–d) and Y 259 (e–l). a) YGSP 33181, b) 33182, c) 33185, d) 33186, e) 33945, f) 33940, g) 33948, h) 33958, i) 33960, j) 33946, k) 33967, l) 33973. Figured at same scale, buccal upward, all right M1 except for left f, g, j, l.

Nagri Formation), two common species are clearly evident. *Karnimata darwini*, somewhat larger than *K. fejfari*, is the most abundant, followed by *Progonomys debruijni*, which is considerably smaller than *P. hussaini*. Nagri localities Y 311, Y 450, and Y 259 have the same two lineages, but the species are less derived, and they are close in size at those sites (Text-fig. 6). Although size range overlaps with *P. hussaini*, *K. fejfari* is moderately larger with relatively broader, more heavily built molars. The morphological and size distinctions between the two lineages, so clear at 9 Ma, are subtle at 10 Ma.

Samples of isolated teeth from later Nagri localities currently available to us allow us to distinguish *Karnimata* from *Progonomys* for most teeth at most loci. There is some overlap in morphology such that some teeth may be misidentified. In fact, several specimens were assigned incorrectly to taxa in Kimura et al. (2013a, b, 2016). Following are the traits that we used to distinguish the species.

For M1, we utilized the defining characteristic of anterostyle position. This is not always absolutely distinctive for populations of 10.5 to 10 Ma. By 9.2 Ma, anterostyle position is a fixed diagnostic (= qualitative) character delimiting the separate species in their diverging lineages, but not so at 10 Ma (Kimura et al. 2016). *Progonomys* has a more posterior anterostyle which tends to be laterally compressed, unlike the anterior, conical anterostyle of *Karnimata*. *Progonomys hussaini* has slightly more inclined cusps than *Karnimata fejfari*. This is not always clearly

the case, especially in worn teeth, but is an additional aid in identification. As noted above, the double anterocone of *Progonomys* is more asymmetrically placed than is the M1 of *Karnimata*, with larger lingual anterocone and more asymmetrical anterior margin.

Most M2 of *Karnimata fejfari* are recognizable by moderate cusp inclination less than that of *Progonomys*, which is most evident for the protocone, the major anterocentral cusp. Its apex is not strongly inclined, such that the anterior surface of the cusp is steep (Text-fig. 7). M2 is also relatively broader than in *Progonomys*, with a heavier lingual anterocone (t3).

Lower molars of *Karnimata fejfari* are more heavily built than those of *Progonomys hussaini*. The first molar has a strong labial cingulum, usually with prominent accessory cusps, and the double anteroconids are more divergent and independent. Lower m2 resembles m1 in its strong labial cingulum and tooth breadth. The breadth comparable to that of m1 is apparent posteriorly as well as anteriorly with the second loph equal almost to the first loph. The broad posterior end of m2 is reflected in m3, whose anterior loph is broader than that of *P. hussaini* (Text-fig. 8c). The m3 of *P. hussaini* is smaller overall, and with a lower labial anteroconid. The contrast in m3 is seen in Cheema et al. (2000), in which their figures 6b and 6c represent *P. hussaini* and *K. fejfari*, respectively.

Among the third molars of Text-fig. 8 we illustrate several M3, which generally present difficulties for identification.
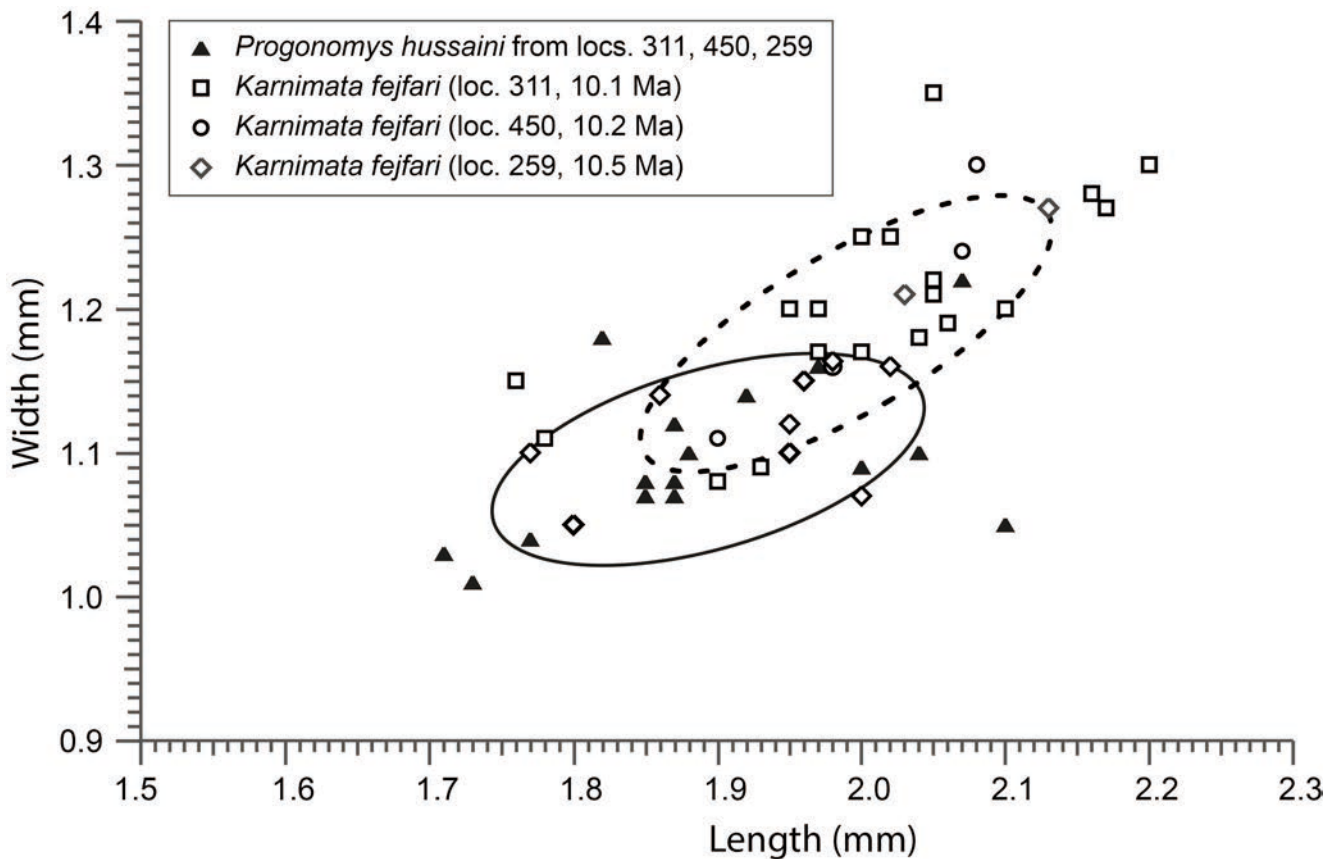
**Text-fig. 6.** Scatter diagram of length and width of M1 specimens in *Progonomys hussaini* and *Karnimata fejfari* from localities Y 259, 450, 311. The solid line ellipse is a 55% concentration ellipse for *P. hussaini*, and the dashed ellipse is a 55% concentration ellipse for *Karnimata fejfari*, all specimens combined.
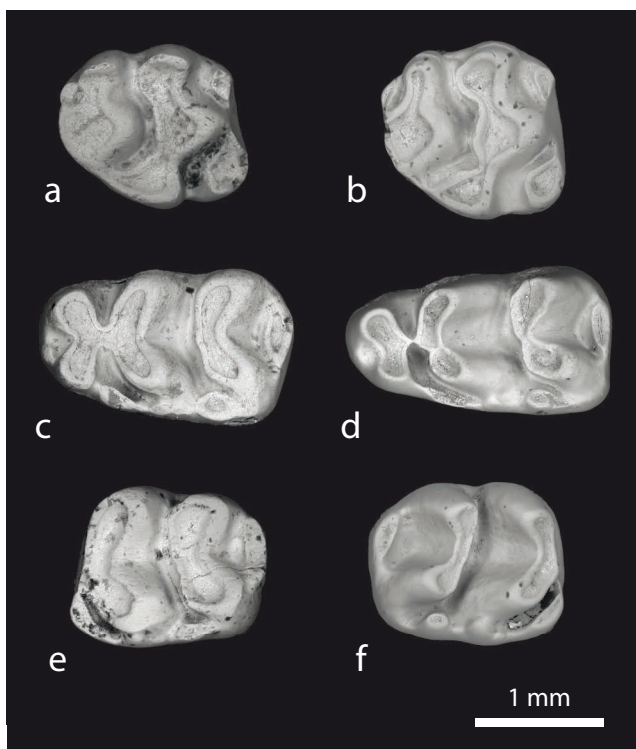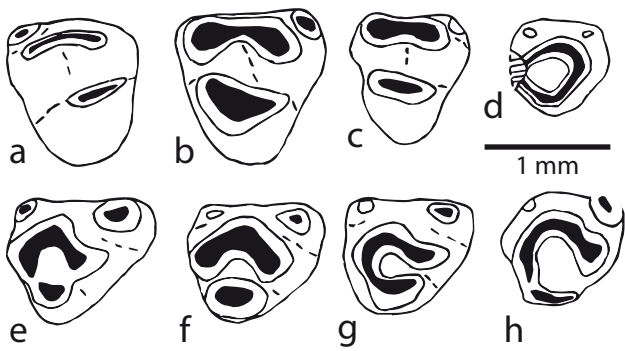


**Text-fig. 7.** Molars referred to *Karnimata fejfari* sp. nov. from type locality Y 311. Right M2, a) YGSP 34588 and b) 54187, buccal upward. Lower teeth c) YGSP 34528 and d) 36166 both left m1, and e) 36170 and f) 54176, left and right m2; c–f figured lingual side upward. All teeth same scale.

Whereas the m3 locus shows two morphological states and sizes that are useful for species assignment, the morphological variation in M3 is more graded. Text-fig. 8e and 8f shows larger M3 specimens with stronger anterostyle and labial anterocone, which we propose may represent *K. fejfari*. These teeth, and the somewhat smaller referred specimen from Y 450 (Text-fig. 8g) are wider than long. All three contrast with YGSP 34574 from Y 311 (Text-fig. 8h), which we attribute to *P. hussaini*. The much smaller M3 of *Progonomys morganae* (Text-fig. 8d) has low anterostyle and labial anterocone.

Our current interpretation sees *Karnimata* as a long-lived lineage with roots in a diversification of *Progonomys*-like murids, perhaps beginning around 11 Ma. *Karnimata* represents the earliest clear indication of a major split in murid evolution, lying at the base of the *Mus*/*Arvicanthis* split (Kimura et al. 2015). Early *Karnimata* as old as ~11 Ma is not easily distinguished from early *Progonomys*. Closer to 10 Ma, *Karnimata fejfari* encompasses a recognizable, early step in arvicanthine evolution. *Karnimata* survived to the end of the Miocene in the Indian subcontinent, and to the early Pliocene of Afghanistan (Brandy 1979). *Karnimata* has been thought to occur in the late Miocene of Shanxi and Inner Mongolia, China, but Qiu and Li (2016) distinguish this material as new genus *Karnimatoides*.

Mein et al. (1993) considered the possibility that the holotype of Siwalik *Karnimata darwini* might represent the European species, *Progonomys woelferi* Bachmeyer et

**Text-fig. 8.** Line drawings of third molars from the upper part of the Nagri Formation; 8a–b and 8e–g are referred to *Karnimata fejfari*, 8c and 8h are referred to *Progonomys hussaini*, and 8d represents *Progonomys morganae*. a) left m3 YGSP 34573, b) right m3 YGSP 34568, c) right m3 YGSP 34574, d) left M3 YGSP 34033 from Y 259, e) right M3 YGSP 34595, f) right M3 YGSP 34596, g) right M3 YGSP 33197 from Y 450, h) right M3 YGSP 34597. All teeth drawn to same scale, anterior is upward; black shading represents dentine exposed by wear; hatching on 8d represents breakage.



**Text-fig. 9.** First upper molars of *Parapodemus badgleyae* sp. nov. (a–d) and Muridae, gen. et sp. indet. (e). a) YGSP 33936, holotype, locality Y 259, b) 33939 from Y 259, c) 34542 from Y 311, d) 34543 from Y 311, e) 34559 from Y 311. All molars but c are left molars, all figured with buccal side upward and at the same scale.

WILSON, 1979, possibly rendering the genus name a junior synonym. However, Storch and Ni (2002) ruled this out, noting the anterior position of the anterostyle, which unlike *Progonomys* is characteristic of *Karnimata*. Kimura et al. (2013b, 2015) further showed that *K. darwini* is encased in a lineage separate from *Progonomys*, and that *Karnimata* is the most basal genus known of the tribes Arvicanthini-Otomyini-Millardini clade.

### Genus *Parapodemus* SCHAUB, 1938

### *Parapodemus badgleyae* sp. nov.

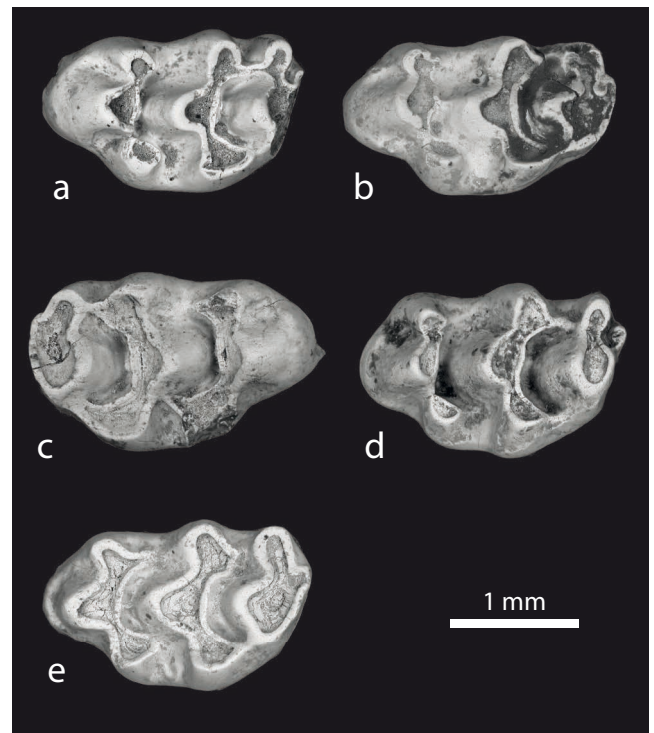H o l o t y p e . YGSP 33936, left M1, Text-fig. 9a (length × width = 1.79 × 1.14 mm).

E t y m o l o g y . For Dr. Catherine Badgley, vertebrate paleobiologist and paleoecologist, pioneer in Siwalik research, well known for her syntheses of disparate paleobiological data in interpreting the fossil record.

T y p e   l o c a l i t y . Y 259, upper part of the Nagri Formation, Siwalik Group, Potwar Plateau, northern Pakistan, age 10.5 Ma.

R e f e r r e d   m a t e r i a l . One additional left M1 from locality Y 259 (YGSP 33939, 1.84 × 1.09 mm), two M2 from Y 259 (YGSP 34206 [1.25 × 1.17] and 34233 [1.2 × 1.13]), and two M1 from Y 311, YGSP 34542 (right, 2.05 × 1.19 mm) and 34543 (left, 1.95 × 1.19 mm) (Text-fig. 9).

D i a g n o s i s . Smaller than *Parapodemus hariensis*, molar lengths about 10% less, and relatively more slender, widths about 15% less; size falls at the lower end of the range for *P. gaudryi*. Stephanodonty moderately developed; thin paracone-metacone (t6-t9) connection; a low crest leads from the enterostyle to the hypocone (weak t4-t8 connection in late wear).

D e s c r i p t i o n . Four M1 are illustrated in Text-fig. 7a–d. The first chevron is not as asymmetrical as in

*Progonomys*. The labial anterocone is smaller than the lingual anterocone, which has a weak connection to the anterostyle until moderate wear. The anterostyle is conical to oval and is not as posterior in position as in *Progonomys*. The enterostyle is large and includes a posteriorly projecting spur with connection low on the hypocone. More prominent is the buccal connection between paracone and metacone (t6-t9), evident even in early wear. Hence, stephanodonty is moderate. The posterior cingulum is strong and there is a shelf-like precingulum. Three roots are present, a large oval lingual root that is anteroposteriorly elongated, a large anterior root, and a posterior root; no rootlet is evident.

The robust M2 is slightly longer than wide, with large anterostyle extending the tooth outline anterolingually. The labial anterocone is small, but distinct and shows wear from an early stage. The posterior spur from the enterostyle abuts the hypocone. The most prominent feature of M2 is that the paracone and metacone are closely positioned and connected early in wear. Roots are broken.

D i s c u s s i o n . For the validity of *Parapodemus*, we follow de Bruijn et al. (1999) and Sen (2003), and recognize four species from Europe: *P. gaudryi* (DAMES, 1833), *P. lugdunensis* SCHAUB, 1938, *P. barbarae* VAN DE WEERD, 1976, *P. meini* MARTÍN SUÁREZ et FREUDENTHAL, 1993 as well as Siwalik forms (below). Martín Suárez and Mein (1998) had a different viewpoint and transferred most species previously considered under *Parapodemus* to the genus *Apodemus* KAUP, 1829; they retained the type species *P. gaudryi* in *Parapodemus*. *Parapodemus* is similar

in morphology to *Apodemus* but lacks t7 as the major difference in M1 (de Bruijn et al. 1999). None of the Siwalik *Parapodemus* specimens have a swollen structure in the crest connecting the enterostyle to the hypocone. De Bruijn (1976) elucidated the morphological variation of the type species, *P. gaudryi*, including size, and its advanced stephanodonty. This species as well as *P. barbarae* and *P. meini* are not only larger and more stephanodont than *P. badgleyae*, but are considerably younger. The remaining species, *Parapodemus lugdunensis*, was until now the earliest record of the genus and has been considered to be the most basal (Van de Weerd 1976, Martín Suárez and Mein 1998). Based on comparison with SEM images in Martín Suárez and Freudenthal (1993), stephanodonty of the species is slightly more advanced than that of the Siwalik *Parapodemus badgleyae* in that the inclination of the metacone (t9) toward the paracone (t6) is greater. The Siwalik species is older and appears to be more plesiomorphic than any known species of *Parapodemus*.

Jacobs (1978) noted the presence of *Parapodemus* in the Dhok Pathan Formation at locality Y 182A, 9.2 Ma, contemporary with *Karnimata darwini* and *Progonomys debruijni*. It was described but not named, its large size distinctive. Working in the Haritalyangar region of India, Vasishat (1985) found a similar large murid and named it *Parapodemus hariensis*. Despite unclear illustrations, his jaw fragments from east of Haritalyangar village include lower molars comparable in size to specimens from site Y 182A (Jacobs 1978). We accept provisionally the species name as applicable to the Y 182A Potwar sample. Our new *Parapodemus* fossils from the older Nagri Formation in the Potwar region are smaller. We recognize their distinction from the younger material as *Parapodemus badgleyae* sp. nov.

Mein et al. (1993) considered *Parapodemus* from locality Y 182A to express morphological variation within *Karnimata darwini*, a view followed by other scholars. The discovery of *Parapodemus* specimens from older localities is important because these specimens show that moderate stephanodonty (weak t6-t9 and t4-t8 connections without t7) was already present by 10.5 Ma. At these localities (Y 259, Y 311), the morphological difference regarding stephanodonty is distinct between *Parapodemys badgleyae* and coexisting *Karnimata fejfari*. The M1 specimens that are assigned to *P. badgleyae* should not be considered morphological variants of *K. fejfari*.

Freudenthal and Martín Suárez (1999) discuss further the validity of *P. gaudryi* and point out the separate and ancient radiation of the *Apodemus* group. They argue that the origin of *Apodemus*, and we would add *Parapodemus*, should be sought among earlier murines, such as the early late Miocene "*Progonomys*" of the Siwaliks. We note here that in our interpretation, the *Parapodemus* lineage extends in the Siwaliks from 10.5 Ma to 9 Ma or younger.

### Muridae gen. et sp. indet.

M a t e r i a l . Only known specimen is YGSP 34559, left M1 from locality Y 311, upper part of the Nagri Formation, 10.1 Ma, dimensions 2.05 × 1.23 mm, L/W ratio = 1.67 (Text-fig. 9e).

D e s c r i p t i o n . Twinned first and second chevrons, with strongly individualized labial as well as lingual anterocone, the lingual anterocone central and somewhat larger than the other two cusps. The enterostyle is about the same size as the paracone. The posterior cingulum is short, and the precingulum shelf is developed. In moderate wear the paracone is not connected to the metacone, although the enterostyle shows a weak connection forming with the hypocone. Although broken, three roots are indicated, including a single, large lingual root, no rootlet in evidence.

D i s c u s s i o n . This M1 presents features that do not match any other Siwalik murine. Its large size is comparable to that of *Parapodemus badgleyae*, but YGSP 34559 shows no paracone-metacone connection, which should be in evidence at this stage of wear. Although the distinctive cusp pattern without stephanodonty distinguishes YGSP 34559 from other known Siwalik species, the specimen conceivably represents a variant of *Parapodemus badgleyae*.

## Discussion

### Fossil calibration for the *Apodemus/Tokudaia* split

*Parapodemus* was apparently not abundant in the Siwaliks, but several murine genera with various degrees of stephanodonty are diverse and common in Europe. They include the ancestor-descendant lineage of *Parapodemus-Apodemus*, for which continuous morphological change of M1 and m1 has been shown (summarized in Michaux et al. 1997, Freudenthal and Martín Suárez 1999; also Renaud et al. 2005). The long record of *Apodemus* in the late Neogene of Western Europe has been utilized for fossil calibration of rodent molecular phylogeny. Most commonly, the earliest stratigraphic occurrence of *Apodemus jeanteti* MICHAUX, 1967 and *Apodemus dominans* KRETZOI, 1959 at 7 Ma (Michaux et al. 1997) is applied to the split between extant *A. mystacinus* (DANFORD et ALSTON, 1877) and *A. sylvaticus* (LINNAEUS, 1758) (e.g., Michaux et al. 2002, Chevret et al. 2005, Veyrunes et al. 2005, Lecompte et al. 2008, Pagès et al. 2012, Schenk et al. 2013). This application is based on Michaux (1971), who proposed anagenetic relationships between extinct species and corresponding extant descendant species. More recently, the earliest occurrence of *Parapodemus*, supposed to date to 11 Ma (Martín Suárez and Mein 1998), was applied to the split between the Apodemurini-Malacomyini clade and the Praomyini-Murini clade (e.g., Rowe et al. 2011, Fabre et al. 2013, Missoup et al. 2016). This record of *Parapodemus lugdunensis* from Buzhor 1, Moldova, is based on a single M1 (Mein et al. 1993, Martín Suárez and Mein 1998). Buzhor 1 is now considered late Vallesian in age (~10 Ma), based on revised magnetostratigraphic correlation, given a new radioisotopic date (Vasiliev et al. 2011), and on biochronologic evidence discussed in Sinitsa and Delinchi (2016). Taking this into consideration, Aghova et al. (2016) applied the oldest reliable age (9.6 Ma) of well represented *Parapodemus lugdunensis* to the *Apodemus/Tokudaia* split. Although the Buzhor 1 specimen may actually belong to *Parapodemus*, we propose that *P. badgleyae* is more appropriate for the basal split of the Apodemurini because it has a greater reliable age estimate. Contemporaneous with younger (~10 Ma) *P. badgleyae*, *Sinapodemus* SEN, 2003 was defined for

fossils from the Sinap Formation, Turkey. *Sinapodemus* closely resembles *Parapodemus* but lacks the connection between the paracone and metacone. Because of the lack of the connection, Wessels (2009) synonymized *Sinapodemus ibrahimi* Sen, 2003 with *Progonomys cathalai* although Sen (2003) recognized other specimens as *P. cathalai* from the same locality that produced *Sinapodemus*.

Recently, Horáček et al. (2013) studied the great morphological variation of *Micromys* Dehne, 1841, which is a basal genus in the Rattini, and therefore closer to *Rattus* Fischer [de Waldheim], 1803. Yet *Micromys* possesses the t6-t9 connection and a large t7 like *Apodemus*, leading Horáček et al. (2013) to give an alternative taxonomic interpretation for *Parapodemus*. According to their working hypothesis, *Parapodemus* is paraphyletic, mixing the early stock of the *Apodemus* lineage with the *Micromys* lineage. Therefore *Parapodemus badgleyae* could be a basal species in the Apodemurini or in the Rattini. In our current interpretation, because the major morphological divergence for Siwalik murines corresponds to the *Mus/Arvicanthis* split, which is more internal than the *Mus/Rattus* split, the occurrence of *P. badgleyae* younger than the proposed *Mus/Arvicanthis* split, is reasonably consistent with assigning *P. badgleyae* to the *Apodemus* lineage until other evidence is provided. Here we treat the appearance of *Parapodemus badgleyi* as a calibration point for Tribe Apodemurini.

**Most recent common ancestor of the Apodemurini**

Referred Specimen – Holotype (M1 specimen, YGSP 33936) of *Parapodemus badgleyae*.

Paleontological Event – The first stratigraphic occurrence of the genus *Parapodemus*.

Stratigraphic Occurrence (Age) – Locality Y 259 (median age estimate, 10.5 Ma); Nagri Formation, Siwalik Group; Potwar Plateau, northern Pakistan.

Age Determination – Magnetic polarity stratigraphy correlated to the Geomagnetic Polarity Time Scale of Ogg (2012).

Minimum Age – 9.2 Ma; median age of Y 182A, which yields a species of *Parapodemus* that is provisionally considered *P. hariensis*.
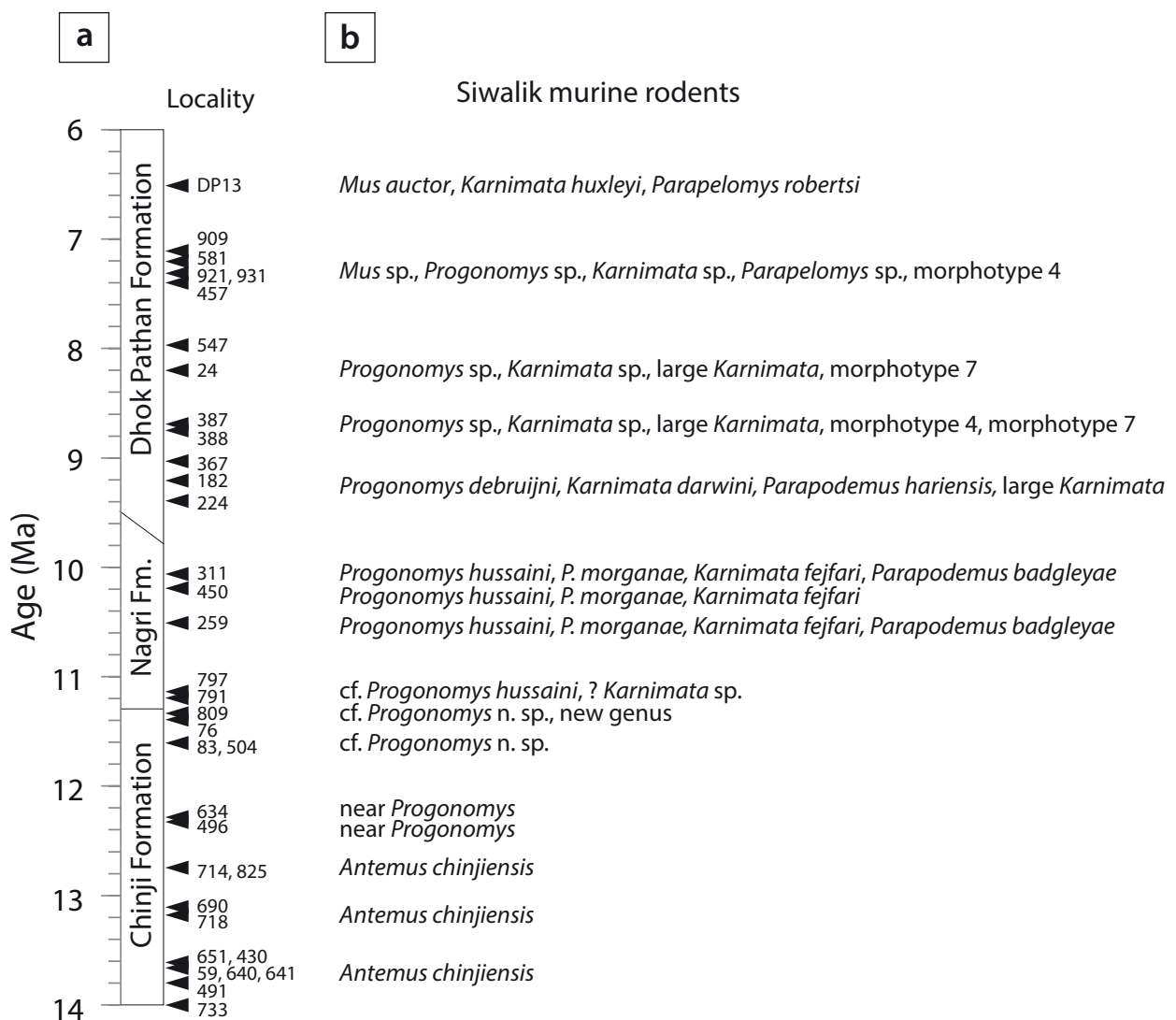


**Text-fig. 10. List of Siwalik murine rodents. a) Stratigraphic occurrence of fossil localities of the Potwar Plateau, Pakistan. b) Murine species recovered from the Siwaliks, updated from Kimura et al. (2015). All localities but DP 13 have Y as prefix.**

Maximum Age – 16 Ma; the earliest stratigraphic occurrence (Y 592) of stem murine *Potwarmus primitivus* LINDSAY, 1988.

Reference – This study.

## Conclusion

The diversification of murine rodents in the Indian subcontinent began in the early late Miocene, well before 10.5 Ma. Stratigraphic occurrences of Siwalik murine rodents are updated in Text-fig. 10. The dominant lineages in the ~9 Ma Dhok Pathan Formation are rooted in the older Nagri Formation. Jacobs and Downs (1994, using a different time scale) recognized that the Dhok Pathan *Progonomys* and *Karnimata* were represented by different species in the older Nagri Formation. The older forms were less derived, with overlapping ranges of variation. Kimura et al. (2015) showed that these lineages, based in the extinct genera *Progonomys* and *Karnimata*, represent the *Mus* LINNAEUS, 1758 and *Arvicanthis* LESSON, 1842 clades of crown murines, respectively. The splitting event may have initiated about 11.2 Ma (Kimura et al. 2016).

Larger samples over the years allowed naming of Nagri *Progonomys hussaini* CHEEMA et al., 2000. Herein, we name the earlier *Karnimata* species after fossil rodent expert Oldřich Fejfar. *Karnimata fejfari* coexisted with *Progonomys hussaini* over an interval of at least 10.5 to 10.1 Ma. Together, they appear to have dominated the muroid faunas of the time, *Karnimata* being more common than *Progonomys*.

These were not the only murine lineages present during the early late Miocene. At least three contemporary genera were already present outside southern Asia. They are *Progonomys* and *Parapodemus* in Europe (Martín Suárez and Mein 1998) and *Progonomys* and *Sinapodemus* in Anatolia (Sen 2003). Both *Parapodemus* and *Sinapodemus* are related to the long-lived lineage of extant *Apodemus*. Thus murid diversification antedated 11 Ma. Also present in the samples surveyed here dating to 10.5 to 10.1 Ma are the small and uncommon *Progonomys morganae*, characterized by narrow first molars, and the stephanodont *Parapodemus badgleyae*.

*Parapodemus badgleyae* provides a calibration point for the molecular tree, since it represents the last common ancestor of the Apodemurini. In our interpretation the genus is related to *Apodemus*, sister lineage to the *Mus*-Praomyini clade. Presence of *Parapodemus* at 10.5 Ma is further evidence that the *Mus*/*Arvicanthis* split is older, and calls for rapid splitting events that today are perceived as evolution at the tribe-level. As our studies of murine evolution in the Siwalik theater of evolution continue, we shall focus on assemblages immediately preceding those studied here, those in excess of 11 Ma.

## Acknowledgements

## References

Aghova, T., Gauthier, D., Granjon, L., Kimura, Y., Bryja, J. (2016): Integrative phylogeography of rodents from Sudanian savanna. – In: Tkadlec, E. (ed.), Programme and Abstract Book, 15th Rodens et Spatium: International Conference on Rodent Biology, July 25th–29th, Olomouc, the Czech Republic, p. 17.

Badgley, C., Flynn, L. J., Taylor, L. H., Jacobs, L. L. (2004): A consideration of the paleontological contributions of Will Downs with a general correlation of Chinese fossil localities. – Vertebrata PalAsiatica, 42: 340–344.

Barry, J. C., Lindsay, E. H., Jacobs, L. L. (1982): A biostratigraphic zonation of the middle and upper Siwaliks of the Potwar Plateau of northern Pakistan. – Palaeogeography, Palaeoclimatology, Palaeoecology, 37: 95–130.
https://doi.org/10.1016/0031-0182(82)90059-1

Barry, J. C., Morgan, M. E., Winkler, A. J., Flynn, L. J., Lindsay, E. H., Jacobs, L. L. (1991): Faunal interchange and Miocene terrestrial vertebrates of southern Asia. – Paleobiology, 17(3): 231–145.
https://doi.org/10.1017/S0094837300010587

Barry, J. C., Behrensmeyer, A. K., Badgley, C. E., Flynn, L. J., Peltonen, H., Cheema, I. U., Pilbeam, D., Lindsay, E. H., Raza, S. M., Rajpar, A. R., Morgan, M. E. (2013): The Neogene Siwaliks of the Potwar Plateau, Pakistan. – In: Wang, X., Flynn, L. J., Fortelius, M. (eds), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 373–399.
https://doi.org/10.7312/columbia/9780231150125.003.0015

Brandy, L. D. (1979): Rongeurs nouveaux du Néogène d'Afghanistan. – Comptes Rendus de l'Académie des Sciences, Paris, Sér. D, 289: 81–83.

Bruijn, H. de (1976): Vallesian and Turolian rodents from Biotia, Attica and Rhodes (Greece). II. – Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B, 79: 372–384, 5 plates.

Bruijn, H. de, Sarac, G., Van den Hoek Ostende, L. W., Roussiakis, S. (1999): The status of the genus name *Parapodemus* SCHAUB, 1938; new data bearing on an old controversy. – In: Reumer, J. W. F., De Vos, J. (eds), Elephants have snorkels! Papers in honour of Paul Y. Sondaar. DEINSEA, 7: 95–112.

Cheema, I. U., Raza, S. M., Flynn, L. J., Rajpar, A. R., Tomida, Y. (2000): Miocene small mammals from Jalalpur, Pakistan, and their Biochronologic Implications. – Bulletin of the National Science Museum, Ser. C, 26(1-2): 57–77.

Chevret, P., Veyrunes, F., Britton-Davidian, J. (2005): Molecular phylogeny of the genus *Mus* (Rodentia: Murinae) based on mitochondrial and nuclear data. – Biological Journal of the Linnean Society, 84: 417–427. https://doi.org/10.1111/j.1095-8312.2005.00444.x

Fabre, P., Pagès, M., Musser, G. G., Fitriana, Y. S., Fjeldså, J., Jennings, A., Jønsson, K. A., Kennedy, J., Michaux, J., Semiadi, G., Supriatna, N., Helgen, K. M. (2013): A new genus of rodent from Wallacea (Rodentia: Muridae: Murinae: Rattini), and its implication for biogeography and Indo-Pacific Rattini systematics. – Zoological Journal of the Linnean Society, 169: 408–447. https://doi.org/10.1111/zoj.12061

Flynn, L. J., Jacobs, L. L. (1982): Effects of changing environments on Siwalik rodent faunas of northern Pakistan. – Palaeogeography, Palaeoclimatology, Palaeoecology, 38: 129–138. https://doi.org/10.1016/0031-0182(82)90067-0

Flynn, L. J., Lindsay, E. H., Pilbeam, D., Raza, S. M., Morgan, M. E., Barry, J. C., Badgley, C. E., Behrensmeyer, A. K., Cheema, I. U., Rajpar, A. R., Opdyke, N. D. (2013): The Siwaliks and Neogene evolutionary biology in South Asia. – In: Wang, X., Flynn, L. J., Fortelius, M. (eds), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 353–372. https://doi.org/10.7312/columbia/9780231150125.003.0014

Flynn, L. J., Wessels, W. (2013): Paleobiogeography and South Asian small mammals: Neogene latitudinal faunal variation. – In: Wang, X., Flynn, L. J., Fortelius, M. (eds), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 445–460. https://doi.org/10.7312/columbia/9780231150125.003.0018

Freudenthal, M., Martín Suárez, E. (1999): Family Muridae. – In: Rössner, G. E., Heissig, K. (eds), The Miocene Land Mammals of Europe. Verlag Dr. Friedrich Pfeil, München, pp. 401–409.

Horáček, I., Knitlová, M., Wagner, J., Kordos, L., Nadachowski, A. (2013): Late Cenozoic History of the Genus *Micromys* (Mammalia, Rodentia) in Central Europe. – PLoS ONE, 8(5): e62498 (19 pp.). https://doi.org/10.1371/journal.pone.0062498

Jacobs, L. L. (1978): Fossil Rodents (Rhizomyidae and Muridae) from Neogene Siwalik Deposits, Pakistan. – Museum of Northern Arizona Press Bulletin, 52: 1–103.

Jacobs, L. L. (1979): Tooth cusp homology of murid rodents based on Miocene fossils from Pakistan. – Časopis pro mineralogii a geologii, 24(3): 301–304.

Jacobs, L. L., Downs, W. R. (1994): The Evolution of Murine Rodents in Asia. – In: Tomida, Y., Li, C., Setoguhi, T. (eds), Rodent and Lagomorph Families of Asian Origins and Diversification. National Science Museum Monograph, Tokyo, 8: 149–156.

Jacobs, L. L., Flynn, L. J. (2005): Of Mice … Again: The Siwalik Rodent Record, Murine Distribution, and Molecular Clocks. – In: Lieberman, D. E., Smith, R. J., Kelley, J. (eds), Interpreting the Past: Essays on Human, Primate, and Mammal Evolution. Brill Academic Publishers, Inc., Boston, pp. 63–80.

Jacobs, L. L., Pilbeam, D. (1980): Of mice and men – fossil-based divergence dates and molecular clocks. – Journal of Human Evolution, 9: 551–555. https://doi.org/10.1016/0047-2484(80)90062-7

Johnson, N. M., Opdyke, N. D., Johnson, G. D., Lindsay, E. H., Tahirkheli, R. A. K. (1982): Magnetic polarity stratigraphy and ages of Siwalik group rocks of the Potwar Plateau, Pakistan. – Palaeogeography, Palaeoclimatology and Palaeoecology, 37: 17–42. https://doi.org/10.1016/0031-0182(82)90056-6

Kaakinen, A. (2005): A long terrestrial sequence in Lantian – a window into the late Neogene palaeoenvironments of northern China. – Publications of the Department of Geology, University of Helsinki, D4, 49 pp.

Keller, H. M., Tahirkheli, R. A. K., Mirza, M. A., Johnson, G. D., Johnson, N. M., Opdyke, N. D. (1977): Magnetic polarity stratigraphy of the Upper Siwalik deposits, Pabbi Hills, Pakistan. – Earth and Planetary Science Letters, 36: 187–201. https://doi.org/10.1016/0012-821X(77)90198-4

Kimura, Y., Flynn, L. J., Jacobs, L. L. (2016): A paleontological case study for species delimitation in diverging fossil lineages. – Historical Biology, 28(1-2): 189–198. https://doi.org/10.1080/08912963.2015.1022175

Kimura, Y., Hawkins, M. T. R., McDonough, M. M., Jacobs, L. L., Flynn, L. J. (2015): Corrected placement of *Mus-Rattus* fossil calibration forces precision in the molecular tree of rodents. – Scientific Reports, 5(14444): 1–9. https://doi.org/10.1038/srep14444

Kimura, Y., Jacobs, L. L., Cerling, T. E., Uno, K. T., Ferguson, K. M., Flynn, L. J., Patnaik, R. (2013a): Fossil mice and rats show isotopic evidence of niche partitioning and change in dental ecomorphology related to dietary shift in Late Miocene of Pakistan. – PLoS ONE, 8(8): e69308 (10 pp.). https://doi.org/10.1371/journal.pone.0069308

Kimura, Y., Jacobs, L. L., Flynn, L .J. (2013b): Lineage-specific responses of tooth shape in murine rodents (Murinae, Rodentia) to Late Miocene dietary change in the Siwaliks of Pakistan. – PLoS ONE, 8(10): e76070 (12 pp.). https://doi.org/10.1371/journal.pone.0076070

Lecompte, E., Aplin, K., Denys, C., Catzeflis, F., Chades, M., Chevret, P. (2008): Phylogeny and biogeography of African Murinae based on mitochondorial and nuclear gene sequences, with a new tribal classification of the subfamily. – BMC Evolutionary Biology, 8: 199 (21 pp.). https://doi.org/10.1186/1471-2148-8-199

Martín Suárez, E., Freudenthal, M. (1993): Muridae (Rodentia) from the Lower Turolian of Crevillente (Alicante, Spain). – Scripta Geologica, 103: 65–118.

Martín Suárez, E., Mein, P. (1998): Revision of the genera *Parapodemus*, *Apodemus*, *Rhagamys*, and *Rhagapodemus* (Rodentia, Mammalia). – Géobios, 31: 87–97. https://doi.org/10.1016/S0016-6995(98)80099-5

Mein, P., Martín Suárez, E., Agustí, J. (1993): *Progonomys* Schaub, 1938 and *Huerzelerimys* gen. nov. (Rodentia); their evolution in Western Europe. – Scripta Geologica, 103: 41–64.

Michaux, J. (1971): Muridae (Rodentia) Néogènes d'Europe sud-occidentale. Évolution et rapports avec les formes actuelles. – Paléobiologie Continentale, 2: 1–67.

Michaux, J., Aguilar, J.-P., Montuire, S., Wolff, A., Legendre, S. (1997): Les Murinae (Rodentia, Mammalia) Néogènes du sud de la France: Évolution et Paléoenvironements. – Géobios, 20: 379–385.
https://doi.org/10.1016/S0016-6995(97)80042-3

Michaux, J. R., Chevret, P., Fillippucci, M.-G., Macholand, M. (2002): Phylogeny of the genus *Apodemus* with a special emphasis on the subgenus *Sylvaemus* using the nuclear IRBP gene and two mitochondrial markers: cytochrome b and 12SrRNA. – Molecular Phylogenetics and Evolution, 23: 123–136.
https://doi.org/10.1016/S1055-7903(02)00007-6

Missoup, A. D., Nicolas, V., Eiseb, S., Chung, E. K., Denys, C. (2016): Phylogenetic position of the endemic Mount Oku rat, *Lamottemys okuensis* (Rodentia: Muridae), based on molecular and morphological data. – Zoological Journal of the Linnean Society, 177: 209–226.
https://doi.org/10.1111/zoj.12361

Moonen, J. J. M., Sondaar, P. Y., Hussain, S. T. (1978): A comparison of larger fossil mammals in the stratotypes of the Chinji, Nagri and Dhok Pathan Formations (Punjab, Pakistan). – Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Ser. B, 81(4): 425–436.

Ogg, J. G. (2012): Geomagnetic polarity time scale. – In: Gradstein, F. M., Ogg, J. G., Schmitz, M. S., Ogg, G. M. (eds), The Geologic Time Scale 2012, Vol. 1. Elsevier, Amsterdam, pp. 85–113.
https://doi.org/10.1016/b978-0-444-59425-9.00005-6

Pagès, M., Chevret, P., Gros-Balthazard, M., Hughes, S., Alcover, J. A., Hutterer, R., Rando, J. C., Michaux, J., Hänni, C. (2012): Paleogenetic analyses reveal unsuspected phylogenetic affinities between mice and the extinct *Malpaisomys insularis*, an endemic rodent of the Canaries. – PLoS ONE, 7: e31123 (15 pp.).
https://doi.org/10.1371/journal.pone.0031123

Patnaik, R. (2013): Indian Neogene Siwalik mammalian biostratigraphy: An overview. – In: Wang, X., Flynn, L. J., Fortelius, M. (eds), Fossil Mammals of Asia: Neogene Biostratigraphy and Chronology. Columbia University Press, New York, pp. 423–443.
https://doi.org/10.7312/columbia/9780231150125.003.0017

Qiu, Z.-D., Li, Q. (2016): Neogene rodents from central Nei Mongol, China. – Palaeontologia Sinica, N. S., Ser. C, 30(whole series 198): i–xi, 1–684. (in Chinese with English summary)

Renaud, S., Michaux, J., Schmidt, D. N., Aguilar, J.-P., Mein, P., Auffray, J.-C. (2005): Morphological evolution, ecological diversification and climate change in rodents. – Proceedings of the Royal Society, London, B, 271: 609–617.
https://doi.org/10.1098/rspb.2004.2992

Rowe, K. C., Aplin, K. P., Baverstock, P. R., Moritz, C. (2011): Recent and rapid speciation with limited morphological disparity in the genus *Rattus*. – Systematic Biology, 60: 188–203.
https://doi.org/10.1093/sysbio/syq092

Sen, S. (2003): Muridae and Gerbillidae (Rodentia). – In: Fortelius, M., Kappelman, J., Sen, S., Bernor, R. L. (eds), Geology and Paleontology of the Miocene Sinap Formation, Turkey. Columbia University Press, New York City, pp. 125–140.

Schenk, J. J., Rowe, K. C., Steppan, S. J. (2013): Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. – Systematic Biology, 62: 837–64.
https://doi.org/10.1093/sysbio/syt050

Sinitsa, M. V., Delinschi, A. (2016): The earliest member of *Neocricetodon* (Rodentia: Cricetidae): a redescription of *N. moldavicus* from Eastern Europe, and its bearing on the evolution of the genus. – Journal of Paleontology, 90: 771–784.
https://doi.org/10.1017/jpa.2016.72

Storch, G., Ni, X.-J. (2002): New late Miocene murids from China (Mammalia, Rodentia). – Géobios, 35: 515–521.
https://doi.org/10.1016/S0016-6995(02)00043-8

Van de Weerd, A. (1976): Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. – Utrecht Micropaleontological Bulletins, Special Publication 2: 1–218

Vasiliev, I, Iosifidi, A. G., Khramov, A. N., Krijgsman, W. Kuiper, K., Langereis, C. G., Popov, V. V., Stoica, M., Tomsha, V. A., Yudin, S. V. (2011): Magnetostratigraphy and radio-isotope dating of upper Miocene–lower Pliocene sedimentary successions of the Black Sea Basin (Taman Peninsula, Russia). – Palaeogeography, Palaeoclimatology, Palaeoecology, 310: 163–175.
https://doi.org/10.1016/j.palaeo.2011.06.022

Vasishat, R. N. (1985): Antecedents of Early Man in Northwestern India: Paleontological and Paleoecological Evidences. – Inter-India Publications, New Delhi, 230 pp.

Veyrunes, F., Britton-Davidian, J., Robinson, T. J., Calvet, E., Denys, C., Chevret, P. (2005): Molecular phylogeny of the African pygmy mice, subgenus *Nannomys* (Rodentia, Murinae, *Mus*): implications for chromosomal evolution. – Molecular Phylogenetics and Evolution, 36:358–69.
https://doi.org/10.1016/j.ympev.2005.02.011

Wessels, W. (2009): Miocene rodent evolution and migration: Muroidea from Pakistan, Turkey, and northern Africa. – Geologica Ultraiectina, 307: 1–290.

**Appendix.** Molar dimensions (in mm) for *Karnimata fejfari* sp. nov. "*" indicates holotype; "~" signifies an approximate measurement for a damaged specimen; rt = right.

| Locality | YGSP # | molar | L | W |
|---|---|---|---|---|
| Y 311 | 34540 | left M1 | 2.04 | 1.18 |
| | 34541 | rt M1 | 2.06 | 1.19 |
| | 34544 | left M1 | 1.78 | 1.11 |
| | 34546* | left M1 | 2.00 | 1.17 |
| | 34547 | left M1 | 2.05 | 1.21 |
| | 34548 | left M1 | 2.02 | 1.25 |
| | 34550 | rt M1 | 2.17 | 1.27 |
| | 34551 | left M1 | 1.76 | 1.15 |
| | 34552 | left M1 | 2.10 | 1.20 |
| | 34554 | left M1 | 2.12 | 1.28 |
| | 34558 | rt M1 | 1.8+ | 1.20 |
| | 34560 | left M1 | 1.8+ | 1.30 |
| | 34561 | rt M1 | 1.8+ | 1.35 |
| | 34565 | left M1 | 2.20 | 1.30 |
| | 36162 | rt M1 | 2.05 | 1.22 |
| | 36164 | rt M1 | 1.95 | 1.20 |
| | 36165 | left M1 | – | 1.15 |
| | 54126 | left M1 | 2.16 | 1.28 |
| | 54127 | left M1 | 1.97 | 1.17 |
| | 54130 | rt M1 | 1.8+ | 1.30 |
| | 54146 | left M1 | 2.05 | – |
| | 54147 | left M1 | 1.90 | 1.08 |
| | 54148 | rt M1 | 1.97 | 1.20 |
| | 54149 | rt M1 | 2.00 | 1.25 |
| | 54150 | rt M1 | 2.05 | 1.35 |
| | 54153 | rt M1 | 1.93 | 1.09 |
| | 34588 | rt M2 | 1.38 | 1.27 |
| | 34591 | rt M2 | 1.30 | 1.40 |
| | 34602 | left M2 | 1.35 | 1.30 |
| | 34606 | left M2 | 1.35 | 1.30 |
| | 34607 | left M2 | 1.30 | 1.25 |
| | 54181 | rt M2 | 1.38 | 1.26 |
| | 54182 | rt M2 | 1.60 | 1.30 |
| | 54187 | rt M2 | 1.35 | 1.20 |
| | 54188 | rt M2 | 1.50 | 1.30 |
| | 54189 | rt M2 | 1.50 | 1.25 |
| | 54190 | left M2 | 1.35 | 1.25 |
| | 54192 | left M2 | 1.45 | 1.30 |
| | 54193 | left M2 | 1.30 | 1.35 |
| | 54194 | left M2 | 1.45 | 1.25 |
| | 54195 | left M2 | 1.50 | 1.30 |
| | 34594 | left M3 | 0.92 | 1.05 |
| | 34595 | rt M3 | 0.97 | 1.10 |
| | 34596 | rt M3 | 0.90 | 1.03 |
| | 33204 | left m1 | 1.70 | 1.05 |
| | 34515 | rt m1 | 1.75 | 1.10 |
| | 34516 | rt m1 | 1.85 | 1.10 |
| | 34521 | left m1 | 1.60 | 1.00 |
| | 34522 | rt m1 | 1.60 | 1.05 |
| | 34524 | rt m1 | 1.80 | 1.10 |
| | 34528 | left m1 | 1.85 | 1.21 |
| | 34529 | left m1 | 1.60 | 1.05 |
| | 34530 | rt m1 | 1.90 | 1.15 |
| | 34535 | left m1 | 1.80 | 1.20 |
| | 34536 | left m1 | 1.60 | 1.00 |
| | 34537 | left m1 | 1.75 | 1.10 |
| | 34575 | left m1 | 1.70 | 1.10 |
| | 34579 | left m1 | 1.80 | 1.05 |
| | 36166 | left m1 | 1.87 | 1.16 |
| | 36169 | rt m1 | – | ~1.10 |
| | 54132 | rt m1 | 1.85 | 1.10 |
| | 54134 | rt m1 | 1.80 | 1.10 |
| | 54136 | rt m1 | 1.85 | 1.05 |
| | 54137 | left m1 | 1.80 | 1.05 |
| | 54138 | left m1 | 1.80 | 1.10 |
| | 54161 | left m1 | 1.75 | 1.20 |
| | 54163 | left m1 | 1.65 | 1.05 |
| | 34608 | left m2 | 1.37 | 1.16 |
| | 34609 | left m2 | – | 1.15 |
| | 34611 | left m2 | 1.30 | 1.20 |
| | 34612 | left m2 | 1.30 | 1.20 |
| | 34614 | left m2 | 1.25 | 1.10 |
| | 34615 | rt m2 | 1.50 | 1.25 |
| | 34617 | left m2 | 1.35 | 1.20 |
| | 34619 | left m2 | 1.35 | 1.10 |
| | 34624 | rt m2 | 1.25 | 1.20 |
| | 34628 | rt m2 | 1.45 | 1.20 |
| | 34631 | rt m2 | 1.40 | 1.25 |
| | 34632 | rt m2 | 1.30 | 1.10 |
| | 34633 | rt m2 | 1.45 | 1.20 |
| | 34634 | rt m2 | 1.35 | 1.15 |
| | 36170 | left m2 | 1.35 | 1.22 |
| | 54170 | left m2 | 1.35 | 1.15 |
| | 54172 | left m2 | 1.40 | 1.05 |
| | 54174 | left m2 | 1.30 | 1.20 |
| | 54175 | rt m2 | 1.30 | 1.15 |
| | 54176 | rt m2 | 1.36 | 1.18 |
| | 54177 | rt m2 | 1.30 | 1.20 |
| | 54178 | rt m2 | 1.25 | 1.15 |
| | 34517 | rt m3 | 0.8+ | 1.05 |
| | 34568 | rt m3 | 1.15 | 1.05 |
| | 34569 | left m3 | 1.10 | 0.95 |
| | 34570 | rt m3 | 1.15 | 1.00 |
| | 34572 | rt m3 | 1.15 | 1.05 |
| | 34573 | left m3 | 1.10 | 0.95 |
| | 34576 | rt m3 | 1.10 | 1.00 |
| | 34578 | left m3 | 1.10 | 1.00 |
| | 36173 | rt m3 | 0.95 | 0.90 |
| | 54164 | left m3 | 1.10 | 0.95 |
| | 54165 | left m3 | 1.10 | 1.00 |
| | 54166 | left m3 | 1.00 | 0.85 |

| Locality | YGSP # | molar | L | W |
|---|---|---|---|---|
| Y 450 | 33181 | rt M1 | 1.98 | 1.16 |
| | 33182 | rt M1 | 2.08 | 1.30 |
| | 33185 | rt M1 | 1.90 | 1.11 |
| | 33186 | rt M1 | 2.07 | 1.24 |
| | 33192 | rt M1 | – | 1.25 |
| | 54094 | rt M1 | 2.20 | ~1.3 |
| | 33189 | rt M2 | 1.25 | 1.30 |
| | 33193 | rt M2 | 1.20 | 1.20 |
| | 33203 | rt M2 | 1.30 | 1.30 |
| | 54102 | left M2 | 1.35 | 1.25 |
| | 33197 | rt M3 | 0.85 | 0.95 |
| | 33206 | rt m1 | 1.80 | 1.10 |
| | 54090 | left m1 | 1.55 | 1.05 |
| | 54095 | rt m1 | 1.18 | 0.95 |
| | 54096 | left m1 | 1.70 | 1.05 |
| | 33195 | left m2 | 1.30 | 1.15 |
| | 33199 | rt m2 | 1.30 | 1.10 |
| | 54098 | rt m2 | 1.30 | 1.25 |
| | 54101 | left m2 | 1.25 | 1.15 |
| | 33196 | left m3 | 1.02 | 0.91 |
| | 33201 | rt m3 | 1.10 | 1.00 |
| | 54100 | rt m3 | 1.05 | 1.00 |

| Locality | YGSP # | molar | L | W |
|---|---|---|---|---|
| Y 259 | 33940 | left M1 | 2.00 | 1.07 |
| | 33945 | rt M1 | 2.03 | 1.21 |
| | 33946 | left M1 | 1.98 | 1.16 |
| | 33948 | left M1 | 2.13 | 1.27 |
| | 33958 | rt M1 | 2.02 | 1.16 |
| | 33960 | rt M1 | 1.95 | 1.12 |
| | 33964 | left M1 | 1.77 | 1.10 |
| | 33967 | rt M1 | 1.86 | 1.14 |
| | 33973 | left M1 | 1.96 | 1.15 |
| | 33981 | rt M1 | 1.6+ | 1.20 |
| | 33995 | rt M1 | 1.6+ | 1.20 |
| | 33999 | left M1 | 1.7+ | 1.20 |
| | 34004 | left M1 | 1.6+ | 1.25 |
| | 34009 | rt M1 | 1.95 | 1.10 |
| | 34010 | rt M1 | 1.80 | 1.05 |
| | 34171 | left M2 | 1.3+ | 1.25 |
| | 34172 | left M2 | – | 2.20 |
| | 34174 | rt M2 | 1.45 | 1.30 |

| 34175 | rt M2 | 1.35 | 1.25 |
|---|---|---|---|
| 34178 | rt M2 | 1.45 | 1.30 |
| 34182 | rt M2 | 1.25 | 1.15 |
| 34184 | left M2 | 1.30 | 1.20 |
| 34185 | rt M2 | 1.50 | 1.20 |
| 34186 | left M2 | 1.35 | 1.25 |
| 34236 | rt M2 | 1.35 | 1.25 |
| 33209 | rt m1 | 1.70 | 1.20 |
| 33211 | rt m1 | 1.75 | 1.10 |
| 33215 | left m1 | 1.70 | 1.05 |
| 33226 | rt m1 | 1.80 | 1.05 |
| 34103 | rt m1 | 1.80 | 1.20 |
| 34104 | rt m1 | 1.80 | 1.05 |
| 34105 | left m1 | 1.70 | 1.05 |
| 34108 | rt m1 | 1.65 | 1.10 |
| 34110 | rt m1 | 1.70 | 1.05 |
| 34111 | rt m1 | 1.80 | 1.15 |
| 34112 | left m1 | 1.80 | 1.10 |
| 34113 | left m1 | 1.75 | 1.05 |
| 34114 | left m1 | 1.75 | 1.05 |
| 34117 | rt m1 | 1.65 | 1.05 |
| 34119 | rt m1 | 1.80 | 1.10 |
| 34124 | left m1 | 1.65 | 1.00 |
| 34125 | rt m1 | 1.60 | 1.00 |
| 34127 | rt m1 | 1.70 | 1.05 |
| 34128 | rt m1 | 1.75 | 1.05 |
| 34132 | left m1 | 1.80 | 1.05 |
| 34134 | left m1 | 1.70 | 1.00 |
| 34147 | left m1 | 1.7+ | 1.05+ |
| 34157 | rt m1 | – | 1.05 |
| 34161 | left m1 | 1.60 | 1.05 |
| 34165 | rt m1 | 1.80 | 1.10 |
| 34170 | rt m1 | 1.70 | 1.05 |
| 33943 | left m2 | 1.3+ | 1.15 |
| 34069 | left m2 | 1.30 | 1.15 |
| 33942 | left m2 | 1.30 | 1.20 |
| 34084 | left m2 | 1.30 | 1.10 |
| 34085 | rt m2 | 1.25 | 1.05 |
| 34088 | left m2 | 1.25 | 1.05 |
| 34089 | rt m2 | 1.30 | 1.10 |
| 33900 | rt m3 | 1.05 | 1.00 |
| 33901 | left m3 | 1.05 | 1.05 |