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ONE MORE SIWALIK SURPRISE: THE OLDEST RECORD OF *MUS* (MAMMALIA, RODENTIA) FROM THE LATE MIOCENE OF NORTHERN PAKISTAN

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ABSTRACT Louis L. Jacobs developed the outlines of murine evolution through original fieldwork in the Siwalik Hills of the Potwar Plateau in northern Pakistan. His discovery of middle Miocene age *Antemus*, an early stem murine, unveiled the roots of the modern mouse radiation of the later Miocene. He developed a hypothesis on the early late Miocene divergence of extant murine lineages, and included fossil *Progonomys* in the modern *Mus* lineage. A younger Miocene Siwalik locality produced a species close to the living house mouse. Louis named it *Mus auctor* and, as an early record of ~6.5 Ma on the present time scale, it seemed to define the emergence of modern mice. Since then, we have explored more thoroughly the Siwalik sequence and studied its series of rodent assemblages, including newer collections that antedate *Mus auctor*. We were surprised to discover a very small species of *Mus* older than *Mus auctor* and falling into the interval of 7.2 to 8.0 Ma. Morphometric analysis established it as a member of the modern genus and, although preceding *Mus auctor*, the new species proved more derived in some characters. Jacobs' hypotheses that *Progonomys* is in the *Mus* lineage and that *Mus auctor* is readily transformed from *Progonomys* appear to be validated. However, before *Mus auctor* was in place, a derived species of *Mus*, formally named here, was present on the Potwar Plateau. The center of evolution of the genus *Mus* was likely in southeastern Asia, and from time to time the Potwar Plateau sampled the periphery of that evolution. It is Jacobs' vision that led to this discovery, and we take this opportunity to explore in his honor the phylogenetic context of this new species.

KEYWORDS Murines, *Mus*, Pakistan, Siwaliks, Miocene

INTRODUCTION

An outline of rodent evolution in South Asia was developed by Louis L. Jacobs through his groundbreaking work in the 1970s. He was part of a collaboration of scientists from several institutions that has studied the well-exposed Siwalik sequence of the Potwar Plateau over the last half century. With direction from then-major advisor Prof. Everett H. Lindsay of the University of Arizona, Louis explored the thick Neogene sequence of the Potwar Plateau in Pakistan. At first attracted by the riches of the Plio-Pleistocene, Louis soon saw that the real challenge lay in the systematic screening of superposed deposits to document the history of Siwalik small mammals, especially rodents. He opened his fossil-hunting campaign by screening productive horizons of the Chinji Formation (middle Miocene), the Dhok Pathan Formation (two late Miocene levels), and the Plio-Pleistocene of the Upper Siwaliks.

Louis discovered that small mammals were richly preserved in Siwalik rocks of various ages. Given the long succession of thousands of meters of sediment and application of magnetostratigraphic dating by Lindsay and coauthors (e.g., Opdyke et al. 1979), the ages of most sites could be estimated to an accuracy of ~100,000 years (ages recalculated by Barry et al. 2013). Louis unveiled a rich assemblage of diverse small mammals in the middle Miocene Chinji Formation. Among the rodents of age calculated at 13.6 Ma (Ma = mega-annum, million years), were primitive muroids (Jacobs 1977) that proved to be basal mice. Given their antiquity preceding modern rats and mice, these represented a stem murine that Louis named *Antemus chinjiensis*. Jacobs (1978) put forward the hypothesis that the roots of the modern mouse and rat tribes (exemplified today by *Mus* and *Rattus*) could be found in late Miocene

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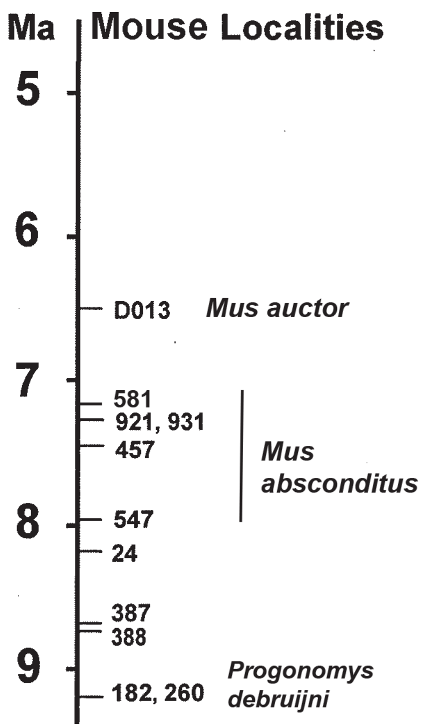

FIGURE 1. Temporal occurrence (stratigraphic order) of key small mammal sites of the Potwar Plateau that sample the *Mus* lineage. Locality Y182 at 9.2 Ma lacks *Mus* but records its predecessor *Progonomys debruijni*. *Progonomys* continues higher in the section into younger localities. Tiny *Mus absconditus* occurs at sites from 8.0 to 7.2 Ma. Younger D013 (6.5 Ma) has the different species *Mus auctor;* by then *Progonomys* is absent.

assemblages of the Dhok Pathan Formation on the Potwar Plateau. A productive horizon at 9.2 Ma (Y182) contained the distinct murine genera *Progonomys* and *Karnimata* that demonstrated diversification by that time, postdating *Antemus* (Jacobs and Pilbeam 1980). The hypothesis of Jacobs, placing the late Miocene murine *Progonomys* in the ancestry of living *Mus*, was buttressed by morphological features that seemed corroborated in a younger late Miocene Siwalik assemblage at 6.5 Ma. This assemblage contained the early mouse *Mus auctor* - by then *Progonomys* was gone.

It appeared that between 9.2 and 6.5 Ma *Progonomys* had disappeared and *Mus,* specifically *Mus auctor,* took its place. Our current work shows that the picture is not so simple. With Jacobs, Lindsay, and the late Will Downs, we continued to sample multiple horizons for small mammals, and developed over 100 productive Siwalik horizons yielding rodents. In the 1990s we concentrated on the late Miocene stratigraphy of the Hasnot area (for location see Barry et al. 2002, Winkler et al. 2011). Fossil murine rodents recovered there and from mid-Miocene deposits, formed the core of dissertation research including morphometric analysis by one of us (YK). Our samples include fossils from several horizons between 9.2 and 6.5 Ma (Fig. 1). These serve to test the simplistic hypothesis of gradual evolution and replacement of *Progonomys* by *Mus*, and the assumption that the transition was near 6.5 Ma. We find a more complex picture, with an unexpected record of the genus *Mus* preceding *Mus auctor.*

ABBREVIATIONS

D: designation for D013, a locality in the Dartmouth-Peshawar system that occurs high in the Dhok Pathan Formation on the Potwar Plateau, age estimated at 6.5 Ma. It is the type locality for *Mus auctor.*

M, **m**: prefix for molars followed by tooth position. M1, M2, M3 are upper molars; lower case signifies lower molars.

Y: prefix for localities in the Yale-Harvard locality system, e.g., Y024 through Y931.

YGSP: acronym for specimens in the Yale-Geological Survey of Pakistan catalogue of Siwalik fossils.

NOMENCLATURAL ACTS

This published work and the nomenclatural acts it contains have been registered in ZooBank. The ZooBank LSID number for this publication is urn:lsid:zoobank.org:act:48FF0897-D2EF-416F-8EBC-7495E9B550B0.

SYSTEMATICS

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

Genus *Mus* Linnaeus, 1758

***Mus absconditus* sp. nov.**

Holotype — YGSP 52920, first upper molar, left M1, (Fig. 2A.

Etymology — From Latin *absconditus* for "hidden". This species of *Mus* was hidden in the fossil record until a large array of fossil horizons was screened for small mammals.

Type Locality and Age — Y921, about 7.3 Ma based on current magnetostratigraphic interpolation (see for example

FIGURE 2. Upper molars of *Mus absconditus* sp. nov. from the Potwar Plateau Dhok Pathan Formation of northern Pakistan. Scale bar equals 1 mm, anterior is upward. **A**, left M1 (YGSP 52920, holotype); **B**, left M1 (YGSP 54354); **C**, right M2 (YGSP 54520, reversed); **D**, right M2 (YGSP 54523, reversed); **E**, left M3 (YGSP 54424); **F**, left M3 (YGSP 34477). SEM images were obtained with a Zeiss Gemini 360 SEM equipped with a variable pressure secondary electron (VPSE) detector at 50 Pa chamber pressure with 20 kV accelerating voltage in the VP mode.

Barry et al. 2013).

Referred Specimens — From Y457, 7.4 Ma, M1 YGSP 34473; M2 34468, 34492; M3, 34469, 34477; m1 34495, 52913, 52914; m3 34493. From Y547, 8.0 Ma, dentary with m1-m3 33322; m1 33307. From Y581, 7.2 Ma M1 52938; m1 52935. From Y921, M2 54290; m1 54292, 54293; m3 54291. From Y931, 7.3 Ma, M1 52972-52980, 54351-54355; M2 54519-54525; M3 54424, 54425; m1 54350, 54413-54422, m2 54526-54533; m3 54423. See Figs. 2, 3 and Tables 1, 2.

Diagnosis — Small species of *Mus*, of fossil species in southern Asia only *Mus narmadaensis* Kotlia et al., 2011 is as small; oldest record of the genus, 7.2 to 8.0 Ma. First molars narrow; M1 anterostyle pinched and posterior in position (posterior to double anterocone), variably reduced metacone, usually no vestige of a posterior cingulum; M2 with pinched anterostyle; m1 lacks tma or it is very weak, anterior four cusps of m1 form an ‘x’ pattern that is central or buccal to the midline in position, lingual anteroconid only slightly larger than labial anteroconid, labial cingulum weak; m2 with exceptionally small labial anteroconid and moderate labial cingulum with variable c1 and c3; m3 is relatively large (more reduced in size in other species of *Mus*; see Tables 2-4, Fig. 4).

Description — This small *Mus* is represented by one partial dentary with molars and by isolated teeth. Some of the teeth are broken but measurements of length or width can be tabulated (Table 1). Upper and lower first molars are narrow, width to length ratio being 0.595 for M1 and 0.610 for m1. Roots are generally broken but enamel is usually well-preserved.

The upper first molar has the apomorphic murine eight cusps. The double anterocone is large and the well-developed, oblique anterostyle is pinched so that its long dimension is anterobuccal-posterolingual. Shifted posteriorly, it lies lingual to the large protocone. The large enterostyle is linked to the posterolingual corner of the protocone. The hypocone is nearly as large as the protocone and both are larger than the paracone. The metacone is smaller and appressed to the hypocone, indistinct in some specimens. Unworn M1 may show an indistinct remnant of the posterior cingulum. The long slope of the anterocone is smooth but one tooth has a slight precingulum.

M2 is broader anteriorly than posteriorly. The straight anterior cingulum joins a large pinched anterostyle and a small buccal cusp, the “labial anterocone”. The most prominent cusp, the protocone, is between a large paracone and the posteriorly turned enterostyle, which may reach the base of the hypocone but is not confluent with it. The hypocone is large and confluent with the smaller metacone. There is a small posterior cingulum.

The small M3 is dominated by one chevron, composed of a large protocone flanked by its enterostyle and paracone. It is triangular and tapers posteriorly more strongly than that of *Mus auctor*. At the anterolingual corner of the tooth is a

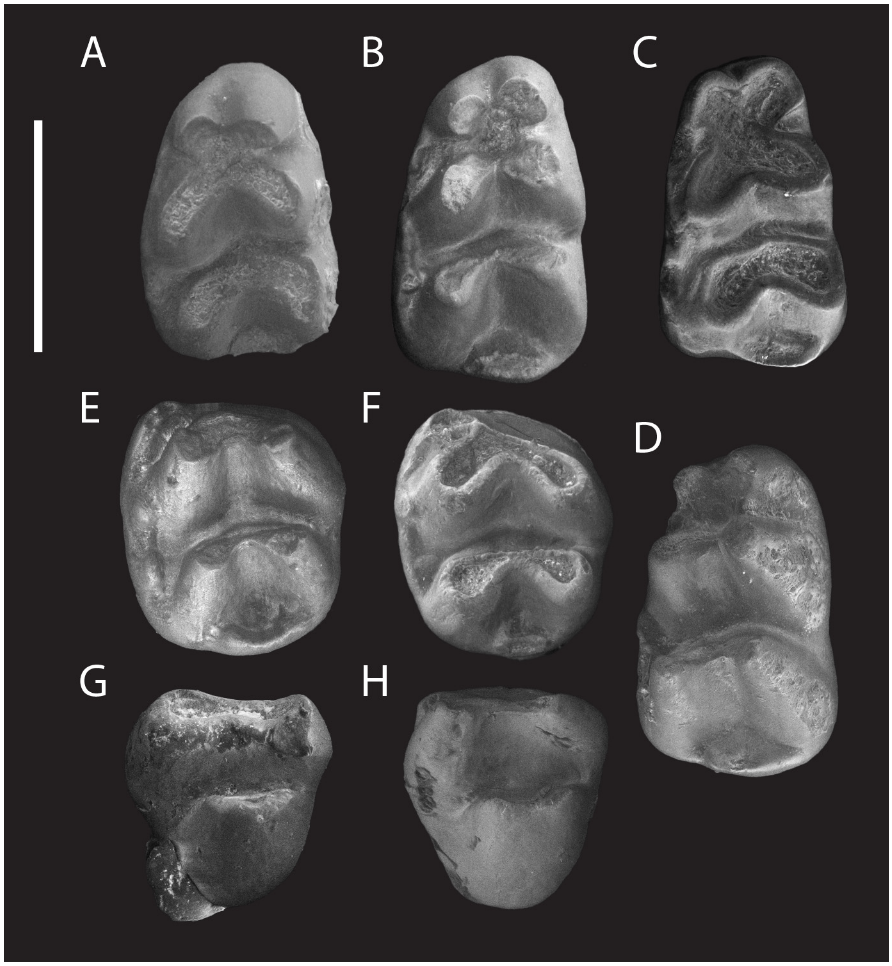

FIGURE 3. Lower molars of *Mus absconditus* sp. nov. Scale bar equals 1 mm, anterior is upward. **A**, right m1 (YGSP 52914, reversed); **B**, right m1 (YGSP 54421, reversed); **C**, left m1 (YGSP 54420); **D**, right m1 (YGSP 33307, reversed); **E**, left m2 (YGSP 52921); **F**, left m2 (YGSP 54531); **G**, left m3 (YGSP 52921); **H**, left m3 (YGSP 54423). Laser ablated craters on the lingual side of YGSP 52914 and 33307 are sites to obtain the stable carbon isotope values of Kimura et al. (2013a).

prominent anterostyle, opposed by a remnant "labial anterocone" at the opposite end of the anterior cingulum. The hypocone, not as large relatively as in *Mus auctor*, is fused with an indistinct metacone.

The narrow m1 (Fig. 3) has six major cusps. The anterior end of the tooth is dominated by four appressed cusps, the double anteroconid close to the protoconid and metaconid. The lingual anteroconid is slightly larger than the labial anteroconid unlike Upper Siwaliks *Mus flynni* Patnaik, 2001 or *M. jacobsi* Kotlia,1992, which have lingual anteroconid twice the size of the labial one. Wear lends an asymmetrical X-pattern with respect to the midline of the tooth, whereas in one specimen (YGSP 33307, Fig. 3D) the junction of the four cusps lies lingual to it. A deep transverse valley isolates the large hypoconid and entoconid. The strong posterior cingulum proceeds from the hypoconid, but develops an independent oval facet with wear (e.g., YGSP 54421). At the anterior end of the tooth there is no small medial anteroconid (tma). The labial cingulum is weak but usually bears a small c1 cusp, occasionally a minute c3.

Two transverse pairs of cusps dominate m2. The largest cusp, the protoconid, joins the metaconid near the midline of the tooth. A deep transverse valley separates them from the large hypoconid and the entoconid. Diagnostic for the species, a distinct labial anteroconid is present, and the posterior cingulum is a pinched oval as in m1. The labial cingulum is weak, but bears a small c3 and variably a c1.

The small, triangular m3 has a straight anterior connection

TABLE 1. Molar measurements of *Mus absconditus* sp. nov.

Locality	Specimen ID	Length	Width	Tooth position
Y457	34473	1.5	0.95	M1/
Y457	34468	1.25	1.05	M2/
Y457	34492	1.1	0.95	M2/
Y457	34469	0.6	0.8	M3/
Y457	34477	0.75	0.9	M3/
Y457	34495	NA	0.95	/m1
Y457	52913	1.4	0.95	/m1
Y457	52914	1.45	0.8	/m1
Y457	34493	NA	NA	/m3
Y547	33307	1.45	0.95	/m1
Y547	33322	1.5	0.95	/m1
Y547	33322	1.1	0.95	/m2
Y547	33322	0.85	0.75	/m3
Y581	52938	NA	1.05	M1/
Y581	52935	1.45	0.75	/m1
Y921	52920	1.44	0.79	M1/
Y921	54290	1	1.15	M2/
Y921	54292	1.4	0.9	/m1
Y921	54293	NA	0.8	/m1
Y921	54291	0.8	0.8	/m3
Y931	52972	1.61	0.92	M1/
Y931	52973	1.57	0.86	M1/
Y931	52974	1.54	0.96	M1/
Y931	52975	1.55	0.9	M1/
Y931	52976	1.57	0.88	M1/
Y931	52977	1.59	0.92	M1/
Y931	52978	1.61	0.91	M1/
Y931	52979	1.6	0.9	M1/
Y931	52980	1.67	0.89	M1/
Y931	54351	1.55	0.95	M1/
Y931	54352	NA	1.05	M1/
Y931	54353	NA	NA	M1/
Y931	54354	1.6	1.05	M1/
Y931	54355	NA	0.95	M1/
Y931	54519	1	0.85	M2/
Y931	54520	1.05	0.85	M2/
Y931	54521	1.1	0.85	M2/
Y931	54522	0.95	0.9	M2/
Y931	54523	1.05	0.85	M2/

TABLE 1. Continued

Locality	Specimen ID	Length	Width	Tooth position
Y931	54524	1.1	1.05	M2/
Y931	54525	1	0.9	M2/
Y931	54424	0.75	0.75	M3/
Y931	54425	0.85	0.8	M3/
Y931	54350	1.55	0.8	/m1
Y931	54413	NA	0.95	/m1
Y931	54414	NA	1	/m1
Y931	54415	1.35	0.85	/m1
Y931	54416	NA	NA	/m1
Y931	54417	1.3	0.75	/m1
Y931	54418	NA	NA	/m1
Y931	54419	NA	0.8	/m1
Y931	54420	1.25	0.8	/m1
Y931	54421	1.3	0.85	/m1
Y931	54422	NA	0.8	/m1
Y931	54526	0.9	0.85	/m2
Y931	54527	0.95	0.85	/m2
Y931	54528	0.95	0.85	/m2
Y931	54529	NA	NA	/m2
Y931	54530	0.9	0.85	/m2
Y931	54531	0.95	0.85	/m2
Y931	54532	1.05	1	/m2
Y931	54533	1.05	0.9	/m2
Y931	54423	0.85	0.8	/m3

between protoconid and metaconid. A reduced labial anteroconid is variable, usually present. The large, central hypoconid incorporates a remnant of the entoconid. There is no hint of a buccal cingulum.

Comparisons — Yuri Kimura studied the Potwar succession of murine rodents as part of her dissertation under Prof. Louis Jacobs. Her multifaceted work included morphometric analysis of dental morphology and firmly established by comparison with living mice that the mouse sample studied here represents a species of *Mus* (Kimura et al. 2013a, b). Kimura et al. (2015, 2016, 2021) further demonstrated that the older early late Miocene differentiation of the murine genera *Progonomys* and *Karnimata* witnessed in the Siwalik fossil record pertained respectively to the roots of the living *Mus* and *Arvicanthis* tribes. This was bolstered by consistent

TABLE 2. Dental measurements (in mm) and statistics for *Mus absconditus* sp. nov., see Table 1

Tooth position	Length					Width				
	n	min	mean	max	sd	n	min	mean	max	sd
M1	13	1.44	1.57	1.67	0.06	16	0.79	0.93	1.05	0.07
M2	10	0.95	1.06	1.25	0.08	10	0.85	0.94	1.15	0.11
M3	4	0.60	0.74	0.85	0.10	4	0.75	0.81	0.90	0.06
m1	11	1.25	1.40	1.55	0.09	17	0.75	0.86	1.00	0.08
m2	8	0.9	0.98	1.10	0.08	8	0.85	0.89	1.00	0.06
m3	3	0.8	0.83	0.85	0.03	3	0.75	0.78	0.80	0.03

TABLE 3. Length and width ratios of upper molars in *Mus* species. Data from Kotlia (2008), Kotlia et al. (2011), and references therein; original measurements in this study for *M. absconditus*. Note: *M. jacobsi* and *M. narmadaensis* do not appear in Fig. 4b since third molars are lacking

Genus	Species	Age	M3/M1		M3/M2	
			Length ratio	Width ratio	Length ratio	Width ratio
Mus	*absconditus*	7.5 Ma	0.47	0.87	0.70	0.86
Mus	*auctor*	6.5 Ma	0.37	0.80	0.60	0.84
Mus	*flynni*	2.5 Ma	0.41	0.76	0.74	0.85
Mus	*jacobsi*	2.4 Ma	NA	NA	NA	NA
Mus	*dhailai*	50 ka	0.33	0.55	0.51	0.65
Mus	*narmadaensis*	Upper Pleistocene	NA	NA	NA	NA
Mus	*dulamensis*	30 ka	0.38	0.53	0.65	0.62
Mus	*dunni*	Extant	0.34	0.56	0.65	0.65
Mus	*booduga*	Extant	0.32	0.62	0.62	0.68

TABLE 4. Length and width ratios of lower molars in *Mus* species. See Table 3 for notes

Genus	Species	Age	m3/m1		m3/m2	
			Length ratio	Width ratio	Length ratio	Width ratio
Mus	*absconditus*	7.5 Ma	0.56	0.91	0.80	0.88
Mus	*auctor*	6.5 Ma	0.49	0.78	0.65	0.73
Mus	*flynni*	2.5 Ma	0.39	0.62	0.71	0.71
Mus	*jacobsi*	2.4 Ma	0.34	0.54	0.48	0.57
Mus	*dhailai*	50 ka	0.41	0.67	0.59	0.64
Mus	*narmadaensis*	Upper Pleistocene	0.51	0.86	NA	NA
Mus	*dulamensis*	30 ka	0.41	0.68	0.58	0.64
Mus	*dunni*	Extant	0.43	0.67	0.69	0.69
Mus	*booduga*	Extant	0.39	0.78	0.60	0.67

molecular studies (e.g., Aghová et al. 2018) that found Tribe Rattini as sister to (outside) these murine groups after the earliest split of Tribe Phloeomyini. The early divergence of the Rattini is not recorded in dental morphological traits in the Siwalik record (Flynn et al. 2020).

Among murini *Progonomys* is primitive in most characters. Jacobs (1978) noted that the genus shows low crowned molars with low connections between cusps and undeveloped

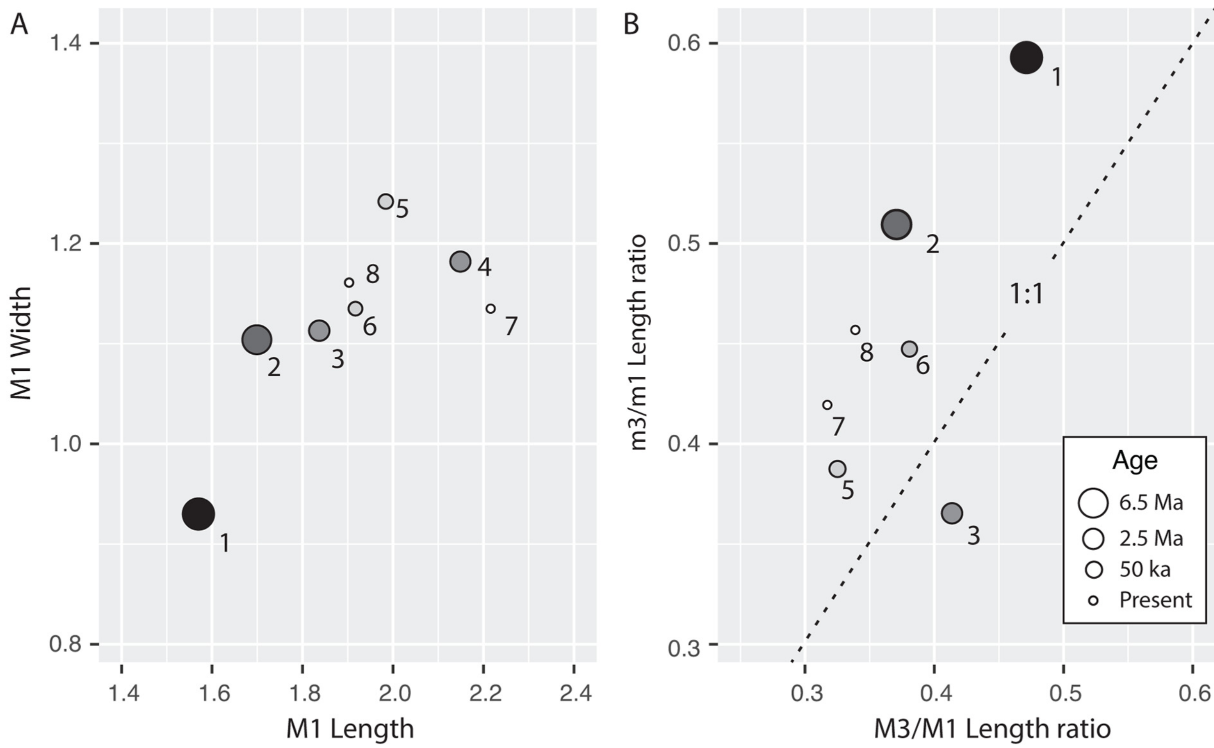

FIGURE 4. Scatter plots of tooth measurements in eight species of *Mus*, corresponding to Tables 2-4. **A**, M1 length vs. M1 width. **B**, M3/M1 length ratio vs. m3/m1 length ratio. **1**, *Mus absconditus* sp. nov.; **2**, *Mus auctor*; **3**, *Mus flynni*; **4**, *Mus jacobsi*; **5**, *Mus dhailai*; **6**, *Mus dulamensis*; **7**, *Mus dunni*; **8**, *Mus booduga*. Larger symbols represent older species. Dashed line on the right is 1:1 ratio.

stephanodonty. As a murin feature inherited by *Mus* the genus indicates a pinched anterostyle and enterostyle of M1, which is posterior in position. *Mus* is distinguished first by its small size. In contrast to *Progonomys*, the genus shows stronger transverse connections between cusps, a sloping anterocone on M1, reduced or absent posterior cingulum on M1, asymmetrical "X" on m1, and third molars proportionally reduced in size (Fig. 4). *Mus auctor* is little transformed from *Progonomys* in such features.

Mus absconditus of 8.0 to 7.2 Ma differs from younger *Mus auctor* in several key features. It is smaller, and its molars are relatively slenderer (width to length ratio = 0.65 in *Mus auctor*). Most *M. absconditus* M1 lack a precingulum, but at 6.5 Ma nearly half of the *Mus auctor* M1 has this structure, and its M1 metacone is usually distinct. The protrusion and degree of tapering of the anterior edge of the lingual anterocone on M1 compared to that of the labial anterocone is greater (derived) in *M. auctor* than in *M. absconditus* and even more significant in Pliocene-Pleistocene *M. jacobsi* and *M. flynni.* The "X" pattern of m1 is more anteriorly positioned in *M. absconditus* than *M. auctor*. The labial cingulum of m1 and m2 is less prominent in *M. absconditus*. *M. auctor* shares with extant *Mus* an anteriorly displaced lingual anteroconid on m1. In summary, whereas *M. auctor* is primitive for *Mus* in many but not all dental features, the size and morphology of *M. absconditus* molars is mostly advanced with respect to other *Mus.*

Mus auctor is the only other *Mus* known from the Miocene of southern Asia. Sen (1983), however, named the larger *Mus elegans* from the earliest Pliocene of Afghanistan. Its metacone on M1 is reduced and there is usually a precingulum. The labial cingulum on m1 and m2 is weak, less prominent than in *Mus auctor* (see Table 5).

Mus occurs in younger deposits of India. Both the Pliocene *Mus jacobsi* Kotlia, 1992 and *Mus flynni* Patnaik, 2001 are larger than the Potwar *Mus*. Their M1 anterostyle is less compressed and less deflected posteriorly, and the anterocone with precingulum is elongated. Two Pleistocene species in India (Kotlia 1995, 2008) are also large. *Mus dhailai* Kotlia, 1995 has simplified third molars and a less compressed anterostyle. *Mus dulamensis* Kotlia, 2008 has a strong M1 precingulum with accessory prestyles. Small *Mus narmadaensis*

TABLE 5. Key features of some South Asian Neogene species of *Mus*

Mus absconditus	Small size	Narrow molars	Weak M1 precingulum	Variable M1 posterior cingulum	Anterior X pattern on m1	Weak m1-2 labial cingulum
Mus auctor	Medium size	Wide molars	Usual precingulum	Posterior cingulum absent	X pattern not shifted anteriorly	Cingulum developed
Mus jacobsi	Large	Wide	Usual precingulum	Cingulum absent	Anterior X pattern	Weak labial cingulum
Mus flynni	Large	Wide	Strong	Absent	Not shifted	Weak
Mus dhailai	Large	Wide	Weak	Damaged	Not shifted	Weak
M. dulamensis	Large	Narrow	Strong	Absent	Anterior	Weak
M. elegans	Medium size	Narrow molars	Usual precingulum	Cingulum absent	Anterior m1 X pattern	Moderate cingulum

Kotlia et al. 2011 has compressed anteroconids on m1, and a strongly reduced posterior cingulum.

The latest Miocene and early Pliocene of Yushe Basin, Shanxi Province, northern China, does not record *Mus*, but has the closely related *Huaxiamys*. Those species are somewhat larger than Siwalik *Mus*, and are distinctive in stephanodonty. The compressed anterostyle on M1 of *Huaxiamys* is an oblique blade continuing through the lingual anterocone (Wu and Flynn 1992).

DISSCUSSION AND CONCLUSIONS

The Dhok Pathan Formation of the Potwar Plateau, Pakistan, records the rich history of Siwalik late Miocene mammalian assemblages. Low in the formation at locality Y182, Louis Jacobs (1978) found and named the murine rodents *Progonomys debruijni* and *Karnimata darwini*. In younger deposits he described the early mouse *Mus auctor*. Louis proposed that his *Progonomys* was close to *Mus* and evidenced that Tribe Murini had differentiated by the early late Miocene. More recently, Kimura et al. (2015, 2021) corroborated this, specifying that *Progonomys* and *Karnimata* represent the distinct murine tribes Murini and Arvicanthini, respectively. She could estimate the age limits on the *Progonomys-Mus* transition as well: Locality Y182 is about 9.2 Ma and D013 yielding *Mus auctor* dates to 6.5 Ma. *Mus* had appeared during the late Miocene in the fossil record of the Potwar Plateau.

Jacobs and Flynn (2005) saw some complexity in the origin of the genus and Kimura et al. (2016, 2021) recognized a small species of *Mus* preceding *Mus auctor*. It was clearly an unnamed member of the genus but more derived in some features than *Mus auctor*. Here we name this early *Mus* and distinguish its morphological features. It is small and derived in some characters such as reduced metacone, infrequent and low precingulum on M1, a weak labial cingulum on lower molars, lack of tma on m1. Meanwhile, *M. absconditus* possesses a basal trait in that its lingual anterocone is less protruded and less tapering than any other *Mus* species.

While *Mus auctor* may look like a diminutive *Progonomys debruijni*, *Mus absconditus* shows that the origin of the genus is complex. Evidently *Mus absconditus* evolved elsewhere in South Asia and its lineage immigrated to the Potwar Plateau. *Mus auctor* may also be an immigrant, arriving after *Mus absconditus*. It remains to be determined exactly the pattern of decline of *Progonomys* and rise of early *Mus*. Probably the evolution of modern Murini (*Mus* and close relatives) centered in southeastern Asia and the peripheral Potwar sampled the edges of that radiation.

As to the time of origin of extant Murini, the pattern and timing of the appearance of *Mus* provides a minimum age constraint. The fossil *Mus* recorded at locality Y547 is the oldest record of the genus and argues that its group was present by at least 8.0 Ma (Kimura et al. 2015, 2021). Future discoveries of *Mus* fossils will reveal the pattern of dispersal of the genus and provide a better temporal framework for molecular phylogeny.

Today we benefit from the labors of many and inherit a wealth of well-dated small mammal samples that were not previously available. It is the efforts of Louis Jacobs and others that have built the Potwar record for us to read.

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