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A new Early Pleistocene North American prairie vole from the Java local fauna of South Dakota, USA

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ABSTRACT

Previously known as *Allophaiomys* cf *pliocaenicus*, a new species of *Pedomys* is described from the early Pleistocene Java local fauna of South Dakota. Biostratigraphic correlations place the fauna between 2.0 and 1.29 Ma. *Pedomys javaensis* n. sp. is characterised by a first lower molar (m1) with three closed triangles (T) and a simple anteroconid (ACD) with a rare development of buccal re-entrant angle 5 defining an incipient T7. Connections between T5 and the ACD and T4–5 are broad, and the enamel is, on average, slightly positively differentiated. The M3 is simple, with distinct T5 and a relatively deep, posteriorly directed third lingual re-entrant angle. Twenty-two per cent of the Java m1s share morphological characters with *Pedomys*, prairie voles, suggesting that *Pedomys* originated from an early Pleistocene North American *Allophaiomys*-like ancestor. In the calculated ratios of m1 measurements, the new species lies morphologically between the Old World *Allophaiomys deucalion* and *A. pliocaenicus*.

Introduction

The genus *Allophaiomys* Kormos (1933) includes species of early Pleistocene voles considered to represent an evolutionary grade ancestral to all later, small, hypselodont (hypsodont, evergrowing cheek teeth) voles that today comprise the dominant small mammal herbivores in the Holarctic pastoral ecosystems. Widely known in the Old World, they were first reported from North America by Martin (1975) from localities in Kansas and South Dakota. Since then, *Allophaiomys* has been reported from Kansas (Eshelman and Hager 1984), Maryland (Van der Meulen 1978), Pennsylvania (Guilday et al. 1984; Repenning 1992), Colorado (Rogers et al. 1992), West Virginia (Repenning and Grady 1988; Repenning 1992), Nebraska (Koenigswald and Martin 1984; Martin and Schultz 1985), Nevada (Bell 1995; Bell and Barnosky 2000), New Mexico (Repenning 1992; Rogers et al., 2002), Utah (Gillette et al. 1999), Texas (Winkler and Gose 2003), South Carolina (Albright et al. 2009) and the Yukon Territory of Canada (Barendregt et al. 1991; Repenning 1992). Repenning (1992) and Bell et al. (2004) provided summaries of the known North American geographic and temporal distribution and previous taxonomic assignments of many of these records. Currently, North American *Allophaiomys* is referred to as either *Allophaiomys pliocaenicus* or *Microtus pliocaenicus* (Martin 1989; Repenning 1992; Martin et al. 2003; Bell et al. 2004) because investigators have been unable to distinguish North American fossil samples from Old World *A. pliocaenicus* Kormos (1933). Most of the original *A. pliocaenicus* material from Betfia 2, Hungary described by Kormos, including the 99 first lower molars examined by Van der Meulen (1973), is missing and presumed destroyed during World War II and thereafter. However, an unexpected discovery of *Allophaiomys* material from Betfia 2 in the Hungarian Geological Museum by Prof. Laszlo Kordos provided the basis for a detailed report by Hir (1998), allowing further comparison with North American *Allophaiomys*. Although characters of other molars are occasionally considered, the determination

of fossil arvicoline taxonomy concentrates on characters and measurements of the first lower molar (m1). All *Allophaiomys* samples display a range of m1 morphotypes, from very simple three-triangle (T) forms to somewhat more complex m1s, and it is through those complexities that incipient evolutionary trajectories can be inferred (Rekovets and Nadachowski 1995; Maul et al. 2007). For convenience, we lump all extinct and extant North American *Microtus*-like voles with at least four closed triangles on m1 and positive enamel differentiation into the genus *Microtus*, and assume that an *Allophaiomys*-level population ancestral to *Microtus* would display a tendency to close at least T4 and possibly T5 as well (the 'rattecepoid' m1 morphology of Rabeder 1981; Rekovets and Nadachowski 1995). In North America we would likewise assume that a tendency towards T4–5 confluent (wide dentine connection between T4 and T5; the 'open' condition) would represent a trajectory towards species that display this morphology, including extinct and extant *Pedomys* and *Pitymys* species, a few unusual extant species in Mexico and Central America, and the extinct *Microtus meadensis* Hibbard (1944). The recent study by Liu et al. (2022) of *Neodon* in the Tibetan-Himalayan region, in which species with both open and closed T4–5 on m1 were recognised, suggests we need to be cautious about these assumptions; indeed, both *Microtus oaxacensis* from Mexico and *M. guatemalensis* from Guatemala display both open and closed T4–5 on m1 in the same species (Martin 1987). Additionally, *Microtus umbrosus* from Mexico exhibits a simple m1, with only three triangles plus T4–5 widely confluent with the anteroconid as in *Allophaiomys*.

In this study, we compare a sample of arvicoline molars from the early Pleistocene Java local fauna of South Dakota allocated to *Allophaiomys* (Martin 1975, 1989; Repenning 1992) with North American species with T4–5 open on m1 and Old World *Allophaiomys* in an attempt to determine the phylogenetic position of the Java population. We begin with a review of the North American species with T4–5 open on m1. After eliminating some

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species, we compare *Pedomys* and *Pitymys* m1s to identify morphological features unique to each that would allow recognition of developmental tendencies towards *Pedomys* or *Pitymys* in variable *Allophaiomys*-like ancestral m1 samples. This is followed by an examination of the Java m1 sample, allocated to three m1 morphotypes. In the systematic section of the paper, we describe a new species of *Pedomys*, concluding that section with a comparison of the Java species with *Allophaiomys pliocaenicus* Kormos (1933) and *A. deucalion* Kretzoi (1969).

Materials and methods

Occlusal dental terminology and m1 measurements for arvicoline molars are provided in Figure 1, modified from Van der Meulen (1973). The anteroconid complex (ACC) includes the length of m1 anterior to the anterior border of T3, or the approximate anterior border of the ancestral cricetid metaconid.

The dental terminology most often used to describe arvicoline molars is derived predominantly from Van der Meulen (1973, 1978). Van der Meulen used the term 're-entrant angles' to describe the spaces between triangles. However, these spaces are created by the folding of enamel, and it is difficult to convey the details of re-entrant angle shape without terminology for the folded enamel edges defining the spaces. Consequently, we often use the term 're-entrant fold' to describe enamel shape or tendency. The internal limit of a re-entrant fold is termed its apex, which may orient in different directions.

L = left, R = right except for measurements, where L = greatest occlusal length, W = width across T4–5 measured from internal enamel borders. Widths for m2-m3 are the greatest measurements from external enamel borders. Lower molars identified with lower case letters, and upper molars with upper case (e.g. Lm2 = left second lower molar). Provergent = re-entrant folds angled anteriorly; postvergent = re-entrant folds angled posteriorly; horizontal = re-entrant folds angled approximately perpendicular to long axis of tooth.

Closure of occlusal structures refers to the extent of dentine connection (confluency) between them, as in 'the posterior loop of m1 is closed from T1 (not confluent)' or 'T1 and T2 are open (confluent)'. If enamel borders of adjacent occlusal structures (such as triangles, or a triangle and the ACD) are in contact or separated by only a slight dentine channel, they are considered to be closed. If they are connected by a moderately developed or wide dentine channel, they are considered confluent.

Enamel of arvicoline molars may express either negative or positive differentiation or be undifferentiated. In negative differentiation, as is typical for *Mimomys*, the posterior edges of triangles of lower molars are thicker than anterior edges and the opposite in upper molars. In positive differentiation, the posterior edges are thinner than the anterior edges, with the opposite on the uppers. In undifferentiated enamel, the anterior and posterior edges are roughly equal. Tesakov's (1998a) BTQ index was used to calculate differentiation, according to the following formula:

$$BTQ = ((SDQ1 + SDQ2 + SDQ3)/3) * 100$$

where SDQ_n = thickness of enamel of posterior edge/thickness of enamel of anterior edge for triangles 1–3, measured at the midpoint of each edge. SDQ is an abbreviated German expression for enamel band differentiation. BTQ abbreviates Tesakov's (1998a) basic triangle quotient, implying that the SDQ measurements are restricted to T1–3. BTQ > 100 = negative differentiation, BTQ 100 = undifferentiated, and BTQ < 100 = positive differentiation. In reality, no BTQ values are exactly equal to 100, so the mean and range of enamel differentiation in a given sample is best understood as a central tendency with varying proportions of specimens expressing the three conditions.

Analysis of variance (ANOVA) tests were done on means of m1, A/L, B/W and C/W ratios for *Pedomys javaensis* n. sp., *A. deucalion* and *A. pliocaenicus* with Pearson Statcrunch. Tests were performed one-way, two-tailed, without the assumption of homoscedasticity, followed by Tukey's HSD post-hoc test, with 0.05 level of significance. Comparative measurement and ratio data for Old and New World *Allophaiomys* and related genera are provided in Table 1.

Institutional abbreviations: SDSM = South Dakota School of Mines and Technology, Museum of Geology; UCMVZ = University of California, Berkeley, Museum of Zoology; MHP = Museum of the High Plains, Goodland, KS.
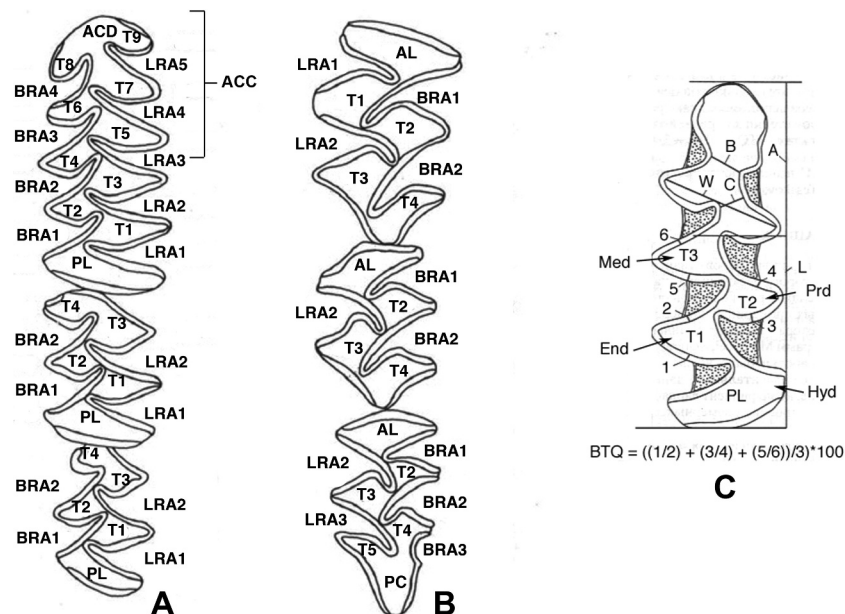
Figure 1. Arvicoline dental terminology and measurement variables. A) = *Ondatra zibethicus*, left lower molars, B) = *Ondatra zibethicus*, left upper molars, C) = *Allophaiomys* sp., Lm1. ACD = anteroconid, ACC = anteroconid complex, AL = anterior loop, Med = metaconid, Prd = protoconid, End = entoconid.   BRA = buccal re-entrant angle, LRA = lingual re-entrant angle, PL = posterior loop, PC = posterior cap, T = triangle. (A [length of ACC], L [length m1], B, C, W) = measurements used to construct ratios. Isolated numbers in C correspond to measurements of enamel thickness on anterior and posterior edges of triangles.

Table 1. Length of m1, m1 ratios, and enamel differentiation for select samples of *Allophaiomys* and *Pedomys*.

Species	Locality	L N	L mean	L OR	L s	A/L N	A/L mean	A/L OR	A/L s	B/W N	B/W mean	B/W OR	B/W s	C/W N	C/W mean	C/W OR	C/W s	SDQ1/BTQ N	SDQ1/BTQ mean	SDQ1/BTQ OR	SDQ1/BTQ s	Source
Europe																						
Allophaiomys deucalion	Neuleiningen 2, 3	3	2.76	2.64–2.89	0.13	3	41.5	40.1–42.4	-	-	-	-	-	-	-	-	-	3	136.4*	(128.3–141.3)	7	Lippi et al. (1998)
	Zuurland 50–56 m	4	2.74	2.56–2.88	-	4	40	38–42	-	3	32	28.1–35.8	-	-	-	-	-	3	123.8*	(110–141)	-	Van Kolfschoten (1998)
	Zuurland 42–44 m	13	2.83	2.61–3.88	-	13	41.8	37–44	-	14	31	27.1–37.3	-	-	-	-	-	14	115.4*	(101–141)	-	Van Kolfschoten (1998)
	Villány 5 (type locality)	16	2.75	2.46–3.06	-	16	39.9	35–43	-	14	36.8	30–50	-	14	24.6	15–34	-	-	-	-	-	Van der Meulen (1974)
	Villány 5 (holotype)	-	3.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	104.4*	-	-	Hir (1998)
	Kolinany 3																	15	118.7*	100.5–138.5	12.3	Lippi et al. (1998)
	Tizdar	20	2.66	2.50–2.87	0.11	20	40.2	34.6–46.0	2.8	25	30.7	22.4–41.1	5.3	26	19.4	13.3–26.0	3.3	27	116.7	87–166.5	18.8	Tesakov (1998a)
	Kryzhanovka 4	20	2.69	2.40–2.90	0.13	20	42	35.4–49.1	3	29	29.3	17.9–37.3	4.7	29	18.2	9.0–25.4	4.4	24	110.3	88.5–142.7	14.7	Tesakov (1998a)
	Kamyk	87	2.74	2.28–3.28	0.19	85	39.9	32.8–43.7	2									41	99.2*	81.5–121.4	10.5	Garapich and Nadachowski (1996)
	Zabia Cave	44	2.7	2.44–3.02	0.14	44	41.5	35.8–45.7	1.8									26	102*	83.3–123.3	12.8	Garapich and Nadachowski (1996)
A. tchumakovi	Rudnyi Altai	8	2.63	2.25–2.90	-	8	43.9	42–48	-													Zazhigin (1998)
A. pliocaenicus	Betfia 9/B	1219	2.51	1.92–3.03	0.18	1219	42.6	33.5–49.4	2.5	1206	22.8	1.40–44.8	6.9	1207	19.6	1.70–34.5	5.2	200	107.2*	68.6–150.6	23.9	Hir (1998)
	Betfia 9/C	389	2.67	2.1–3.13	0.19	389	41.8	35.1–47.5	2.3	396	26.2	8.90–104.9	7.7	394	20	4.40–120.6	6.7	200	111.5*	85.1–147.6	10	Hir and Venczel (1998)
	Betfia 2 (type locality)	96	2.65	2.3–3.02	0.16	96	43.7	40–48	0.8	89	25.3	8.0–35	–	89	22	15–30	-	-	-	-	-	Van der Meulen (1973)
	Betfia 2 (type locality)	146	2.62	2.23–3.23	0.18	146	42.7	38.18–49.73	2	144	24.1	7.27–38.18	6.2	144	19.8	10.30–30.91	4.1	146	100.3*	65.7–132.1	12.5	Hir (1998)
	Betfia 2 (holotype)	-	2.62	-	-													-	87.5*	-	-	Hir (1998)
	Betfia 2 (holotype)	-	2.65	-	-													-	105.3*	-	-	Hir (1998)
	Venta Micena	21	2.78	2.46–3.19	-	21	42	38–48	-	21	25	14–36	-	21	18	11–28	-	-	-	-	-	Agusti et al. (1986)
	Venta Micena	8	2.59	2.26–2.91	0.17	7	45	42.2–48.8	2	9	23.92	17.4–33	7.22	8	21.4	16.1–27.3	4.5	6	96.7	83.1–105.4	4.9	this study
A. ruffoi	Pirro Nord (PN34)	31	2.84	2.52–3.17	0.12	31	41.93	39.58–46.41	1.59	31	31.06	18.44–42.85	5.51	31	19.3	11–27.45	4.3	29	106.1*	88.9–116.2	6.4	Lippi et al. (1998); Massini et al. (1998)
	Cava Sud (type locality)	63	2.81	2.54–3.08	0.12	63	42.8	38.03–46.60	1.49	63	26.35	16.83–41.66	4.78	63	19.7	6.42–30.77	4.7	62	109*	87.8–133.0	9.1	Lippi et al. (1998); Massini et al. (1998)
	Pirro 13	43	2.72	2.47–3.07	0.14	43	45.82	41.11–50	2.26	49	25.26	16.43–37.10	4.83	49	18.9	9.68–27.28	4.2	-	-	-	-	Lopez-Garcia et al. (2015)
A. lavocati	TELRU (type locality)	301	2.64	2.27–3.02	0.12	301	48.74	43.55–54.54	1.43	351	21.92	4.92–37.29	7.3	351	25.8	13.3–36.21	3.6	10	54.6	40.1–70.8	10.2	Laplana and Cuenca-Bescos (2000); this study
	Vallparadis	1	2.57	-	-	1	46.69		-	2	17.63	13.42–21.84	-	2	24.2	23.17–25.29	-	-	-	-	-	Minwer-Barakat et al. (2011)
	El Chapparal	26	2.77	2.53–3.11	0.13	26	49.56	43.86–52.77	2.28	26	17.69	8.74–26.37	4.17	26	22.2	12.62–54.56	6.5	-	-	-	-	Lopez-Garcia et al. (2015)

(Continued)

Table 1. (Continued).

Species	Locality	L				A/L				B/W				C/W				SDQ1/BTQ				Source
		N	mean	OR	s	N	mean	OR	s	N	mean	OR	s	N	mean	OR	s	N	mean	OR	s	
Allophaiomys sp.	Kentuck	11	2.85	2.55–3.10	0.17	11	42.7	39–47	1.9	11	32.1	22–40	5.5	11	25.6	19–33	4.4	-	-	-	-	Van der Meulen (1978)
	Wathena	11	2.76	2.60–2.92	0.11	11	43.6	42–45	1.1	11	31.3	20–41	5.9	11	23.1	17–31	4.5	-	-	-	-	Van der Meulen (1978)
	Borchers (SH, AA, RF)	2	2.98	2.89–3.06	0.12	2	45.8	44–48		3	31.1	29–33		3	22.5	19–26		4	92.4	90–94		Martin et al. (1998); Martin et al. (2003)
Pedomys javaensis	Java	76	2.73	2.33–3.14	0.19	76	42.8	36.8–47.2	2.1	91	33.2	12.9–75.0	8.4	93	24.4	13–36	5.59	90	91.9	50–158.3	18.5	Martin (1989); Martin et al. (1998)
P. guildayi	Cumberland Cave	94	2.58	2.27–3.07	0.18	94	45.7	42–50	1.7	94	26	13–36	3.97	94	20.4	9–31	4.1					Van der Meulen (1978)
P. australis	Haile 16A	27	3.11	2.73–3.52	0.2	27	44.7	41–49	3.1	27	19.5	10–27	4.91	27	18.7	11–34	4.1					Martin (1995)
P. parmaleei	Yarbrough Cave	16	2.38	2.19–2.56	0.13	16	48	46–52	1.6	16	15.5	11–27	4.28	16	17.3	11–27	4.5					Martin (2011)
	Cheek Bend Cave	16	2.27	1.99–2.41	0.11	16	48.7	46–51	1.4	16	17.2	8–27	5.13	16	17.1	12–25	4.2					Martin (2011)
P. ochrogaster/ llanensis	Conard Fissure	47	2.72	2.32–3.26	0.18	47	48.3	45–51	1.6	47	18.8	7–32	5.94	47	21.6	12–31	3.9					Van der Meulen (1978)
	New Trout Cave No. 2	44	3.18	2.51–3.59	0.04	44	47.2	40–52	0.4	44	19.8	10–31	0.9	44	21	13–29	0.6					Pfaff (1990)
P. ochrogaster (Recent)	Tennessee	10	2.64	2.25–3.06	0.29	10	48.2	47–52	1.5	10	21.7	10–30	6.14	10	21.2	16–27	4.2					Martin (1991)
	Minnesota	14	2.37	2.09–2.58	0.15	14	50.3	47–54	1.8	14	19.9	7–35	8.48	14	21.3	14–27	4.5					Martin (1991)
	Great Plains	38	3.01	2.68–3.36	0.15																	Martin (1991)
	New Mexico	36	3.23	2.92–3.55	0.15																	Martin (1991)
	South Dakota																	6	37.3	27–55	9.2	This study; RAM personal collection

*SDQ; "(see text)"
No asterisk = BTQ

Results

Discrimination of *Pedomys* and *Pitymys* and the phylogenetic relationship of the Java arvicoline

As noted in the Introduction, there are several extinct and extant North American hypselodont arvicoline species with m1s that overlap the m1 morphology of the Java population, including the following: Extinct: *Pedomys guildayi* Van der Meulen (1978); *Pedomys australis* Martin (1995); *Pedomys parmaleei* Martin et al. (2011); *Pitymys cumberlandensis* Van der Meulen (1978); *Microtus meadensis* Hibbard (1944). Extant: *Pedomys ochrogaster* Wagner, 1842 (in Schreber 1777); *Pitymys pinetorum* Le Conte (1830); *Pitymys quasiater* Coues (1874); *Microtus umbrosus* Merriam (1898); *Microtus oaxacensis* Goodwin (1966); *Microtus guatemalensis* Merriam (1898).

The dentitions of these species have been illustrated in several accounts (Hibbard, 1944; Van der Meulen 1978; Pfaff 1990; Martin 1987, 1995, 1998; Martin et al. 2011; Bell and Barnosky 2000). *Microtus umbrosus* and *M. guatemalensis* display negative enamel differentiation. In *M. guatemalensis*, the m1 may express a simple form like *Allophaiomys*, with T4–5 widely confluent with the ACD, or a complex form with T4–5 closed and incipient T6–7. The M3 of *M. umbrosus* is simple, but the triangles are often bulbous, with deep reentrant folds. The enamel is undifferentiated in *M. oaxacensis*, but this species displays an m1 and M3 morphology that rivals other North American *Microtus*, such as *M. pennsylvanicus*, in complexity. The M3, for example, may have six closed triangles, and T4–5 may be closed on m1. If the evolution of enamel differentiation in hypselodont arvicolines progresses from negative-undifferentiated-positive, and if molars with more triangles are derived relative to those with a simpler morphology, then *M. umbrosus*, *M. guatemalensis* and *M. oaxacensis* represent lineages independent of those representing *Pedomys* and *Pitymys*. The latter have retained the simple M3 morphology of *Allophaiomys* and express only undifferentiated (Java population, *Pitymys cumberlandensis*) or positively differentiated (all other *Pedomys* and *Pitymys* species) enamel and T4–5 on m1 remain open.

Other than the unusual extant species noted above and *Pedomys* and *Pitymys* species, in North America, the remaining species with T4–5 confluent on m1 is the extinct *Microtus mead-ensis*. Originally described as *Pitymys meadensis* (Hibbard 1944), this species was later referred to the Old World genus *Terricola* by Repenning (1992). Bell and Barnosky (2000) discussed the taxonomic status of this species, and we agree with the section of their assessment considering this species as a middle Pleistocene *Microtus* of unknown ancestry, although *M. meadensis* cannot be securely placed in *Microtus*. *M. meadensis* is a classic component of fossil localities from directly under the Lava Creek B ash (0.64 Ma) such as Cudahy, Kansas (Paulson 1961), and has also been reported from levels in Porcupine Cave, Wyoming, that may be somewhat older (Bell and Barnosky 2000). First lower molars of *M. meadensis* are easily separable from those of *Pedomys* and *Pitymys* by their complex form, with T6–7 usually well defined on the ACD by deep penetration of BRA4 and LRA5, and thin triangle enamel edges. BRA3 and LRA4 are always opposite. We will not consider *M. meadensis* or the Mexican and Guatemalan arvicolines further here, although it is conceivable that some if not all of these species, together with *Pitymys* and *Pedomys*, could represent a taxonomically distinct clade if future fossil remains reveal a common North American *Allophaiomys* ancestor.

Van der Meulen (1978), Martin (1991) and Pfaff (1990) presented a series of characters and measurements that serve to discriminate the m1 of extant *Pedomys* from that of *Pitymys*. These are summarised and illustrated in Figure 2:

(1) Shape of BRA3 and other buccal re-entrants – BRA3 of *Pitymys*, even when shallow, tends to be provergent. BRA3 of *Pedomys* is often wide and shallow. In *Pitymys*, the buccal reentrants in general tend to be narrow and provergent, resulting, especially in *P. cumberlandensis*, in a 'Christmas tree' appearance. In *Pedomys*, the buccal re-entrants tend to be wider and shallower, without the distinct anterior turn of the enamel fold apex.

(2) Size and shape of ACD – The ACD tends to be smaller and simpler in *Pedomys*, often with minimal development of T6-7 relative to *Pitymys*, in which T6 is often well defined by a deeper BRA3-4.

(3) Anterior border of T4 – The anterior border of T4 is often relatively horizontal to the long axis of m1 in *Pedomys*, whereas in *Pitymys*, the anterior enamel border of T4 slopes posteriorly.

(4) Enamel thickness – Extant *Pedomys ochrogaster*, *Pitymys pinetorum* and *P. quasiater* display positive enamel differentiation, with posterior enamel borders of triangles thinner than the anterior borders. However, both macroscopic observation and microscopic measurements show that, on average, the enamel on both edges is thicker in *Pitymys* than in *Pedomys* (Martin 1991). Because all hypselodont voles with positive enamel differentiation evolved from ancestors with negative and then undifferentiated enamel as the tangential layer became reduced on the posterior triangle edges of lower molars (Koeniswald 1980; Martin et al. 1998), ancestral species in North America can be expected to demonstrate undifferentiated and perhaps a combination of undifferentiated and negatively differentiated enamel. This condition is well expressed in the thick, undifferentiated enamel of *Pitymys cumberlandensis* (Van der Meulen 1978; Pfaff 1990) and the less thick and, on average, slightly positively differentiated enamel of the Java population.

(5) Development of a distinct anterolophid – Because of the wide BRA3 and LRA4 in *Pedomys* there is often an elongated dentine channel connecting T4-5 with the ACD. In northern and western populations of *Pitymys pinetorum*, the dentine channel connecting T4-5 and the ACD tends to be short and closed or nearly closed. These populations also have the largest, most distinctive ACD shape. This combination is never seen in *Pedomys*. In late Pleistocene and modern *P. pinetorum* from Florida and Georgia, T4-5 may be highly confluent with the ACD, as in *Pedomys*, and a few m1s may display a pattern reminiscent of both *Allophaiomys* and *Pedomys* (Figure 2). However, in those cases, LRA5 is still slightly developed, differing from *Allophaiomys*. Furthermore, the posterior enamel border of both T4- and T5 in southeastern *Pitymys pinetorum* is thinned to a greater extent than in *Pedomys*, producing a unique triangular shape in which the posterior borders of T4-5 appear straight rather than concave. These specimens are usually rare in any sample, and the remainder of the sample always displays a more typical *Pitymys* m1 morphology.

Note that a rare *Allophaiomys* m1 morphotype has been reported in extant *Pedomys ochrogaster* (Harris 1988; Figure 2).

We allocated 79 complete Java m1s to three morphotypes, 1) *Allophaiomys*-like, 2) *Pedomys* or *Pitymys*-like and 3) *Microtus*-like, defined as follows: 1) dentine connection between T5-ACD wide, no development of T6 or T7; 2) T6 and/or T7 at least incipiently developed, BRA3 shallow and not distinctly provergent. A slight concavity in the antero-lingual area of the ACD is interpreted as an incipient LRA5; 3) LRA3 relatively deep, BRA3 shallow and wide, no development of T6 or T7 (Figure 3). Morphotype 3) mimics the 4-triangle m1 form of species such as *Microtus paroperarius* Hibbard (1944). It is conceivable that some, if not all, of the m1s in this category (9/11%) represent variants of the new species described here; we are not including them in the new species pending further study. Specimens
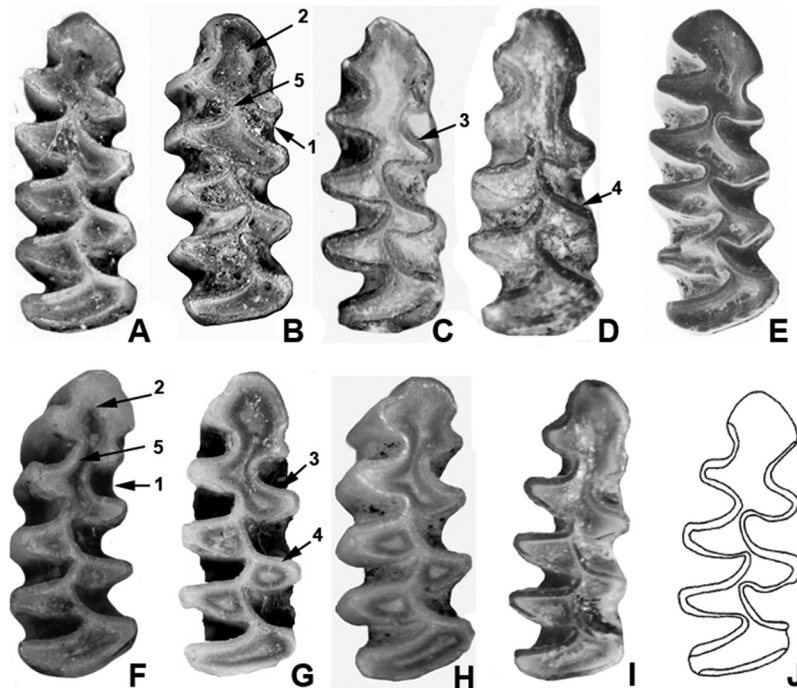
Figure 2. Discrimination of *Pedomys* and *Pitymys* first lower molars. A = *Pitymys pinetorum* (Recent, KY; personal collection R. Martin [PCRM]), B = *P. pinetorum* (sub-Recent, Cutoff Cave, KY; PCRM), C = *P. pinetorum* (late Pleistocene, Reddick 1A, FL; PCRM), D = *P. pinetorum* (late Pleistocene, Reddick 1A–1, FL; PCRM), E = *P. quasiater* (Recent, UCMVZ 96859; from Repenning 1983), F = *Pedomys ochrogaster* (Recent, barn owl pellets, SD; PCRM). G = *P. ochrogaster* (Recent, barn owl pellets, SD; PCRM), H = *P. ochrogaster* (Recent, barn owl pellets, SD; PCRM), I = *P. ochrogaster* (Recent, Meade Co., KS; PCRM), J = *P. ochrogaster* Recent, MHP 5637, Nebraska; from Harris (1988, figure 2). 1 = shape of BRA 3, 2 = relative size of ACD, 3 = slope of anterior enamel border of T4, 4 = thickness of enamel, 5 = presence or absence of distinct anterolophid. For comparison of characters, see text.

considered juvenile (thin enamel, and/or trapezoidal form from labial view) were excluded.

Absence of *Pitymys* features in the Java sample indicates that the evolutionary/developmental trajectory of the Java population was not towards *Pitymys*. Instead, four Java m1s in category 2) display *Pedomys* synapomorphies, especially clear in Figure 3 of SDSM 160298, where the anterior border of T4 is nearly horizontal posterior to a wide, C-shaped BRA3. A slight indentation represents an incipient LRA5. *Pitymys* m1s never display this combined morphotype. These observations allow recognition of the Java population as a new species of *Pedomys*.

Systematic Palaeontology
Class Mammalia Linnaeus (1766)
Order Rodentia Bowditch (1821)
Family Cricetidae Fischer de Waldheim (1817)
Subfamily Arvcolinae Gray (1821)
Genus *Pedomys* Baird (1857)
Pedomys javaensis, sp. nov.
(Figures 3–6)
= *Allophaiomys* cf *A. pliocaenicus* Martin (1975)
= *Microtus* (*Phaiomys*) *pliocaenicus* Martin (1989)

Type specimen
SDSM 160298, Rm1 (Figure 3)

Measurements of type m1 (greatest length, width in mm)
3.04, 0.96.

Referred specimens
Specimens reported as *Microtus* (*Phaiomys*) *pliocaenicus* from Java, South Dakota (Martin 1989) including the following m1s all previously published by Martin (1989) as SDSM 12965: SDSM 160255–160268,

160270–160276, 160279–160283, 160285–160286, 160288–160292, 160295–160306, 160308–160309, 160311–160317, 160319–160322, 160325–160327, 160659–160662, 160666–160668, 160671–160672.

Type locality and horizon
Java, Walworth Co., South Dakota. Early Pleistocene.

Differential diagnosis of species
Pedomys javaensis differs from *Allophaiomys deucalion* in a greater tendency towards positive enamel differentiation. The observed range in *A. deucalion* does not include specimens below a BTQ or SDQ value of 80, whereas *P. javaensis* from the Java assemblage includes about 25% specimens with BTQ below 80 (Martin et al. 1998). The ACD of m1 is shorter (lower A/L ratio), and the dentine channel between T4 and T5 is narrower (lower C/W ratio) in *A. deucalion* than in *P. javaensis*. The M3 in *P. javaensis* is more complex than in *A. deucalion*, with T4–5 incipiently developed and deep, postvergent LRA3 in 90% of specimens. In *A. deucalion* T5 is often small and LRA3 is shallow (Van der Meulen 1974; Tjutkova and Kaipova 1996; Tesakov 1998a, b; Schelinsky et al. 2015). Only 8% of the M3s in the Java sample display this morphotype.

P. javaensis differs from *A. pliocaenicus* and *A. ruffoi* in expressing, on average, wider connections between T4–5 and the ACD and between T4 and T5 (greater B/W ratio; Table 1, 2; Figure 4).

Allophaiomys lavocati Laplana and Cuenca-Bescós, 2000 from Trinchera Elefante, Lower Red Unit in Spain, is a relatively advanced species, with more positively differentiated enamel and a narrower connection between the ACD and T4–5 than in *P. javaensis* (Laplana and Cuenca-Bescós 2000).

Although measurements were not provided, according to Zazhigin (1998), the enamel of all *A. tchumakovi* Zazhigin (1998) molars are negatively differentiated and the M3s illustrated by Zazhigin (1998) are all very simple, as in *A. deucalion*. However,
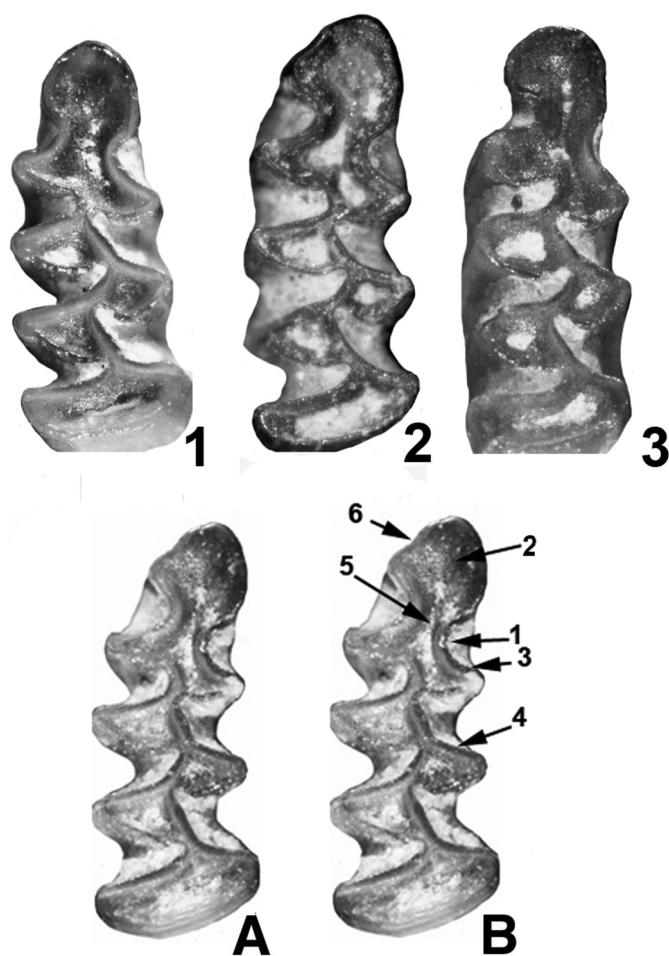
Figure 3. Java arvicoline m1 morphotypes and holotype m1: 1 = category 1 (SDSM 160285, rev), 2 = category 2 (SDSM 160255, rev), 3 = category 3 (SDSM 160294, rev). Rev = reversed. A = SDSM 160298 = holotype rm1 of *Pedomys javaensis*, n. sp., occlusal view. B = holotype m1 labeled as follows: 1 = shallow, wide BRA3, 2 = small ACD, 3 = anterior border T4 horizontal, 4 = relatively thin enamel, 5 = distinct anterolophid connecting T4–5 and the ACD, 6 = incipient LRA5.

the *Allophaiomys tchumakovi* dentition needs a more complete description to make a meaningful comparison.

In North America, *Pedomys* m1s can be distinguished from all extinct and extant *Pitymys* species m1s by the following generally plesiomorphic characters: 1) wider connection between the ACD and T4-T5, 2) wider connection between T4 and T5, 3) less of a tendency to express T6–7 and associated anterior re-entrant angles, 4) lack of a tendency for deep, provergent re-entrants and 5) thinner enamel on both triangle edges.

As shown in Table 1 and Figures 2, 3, *P. javaensis* differs from other *Pedomys* species in the same three features noted above for *Pitymys*, plus displaying less frequent BRA4 and LRA5. Although enamel differentiation has not been measured in other extinct *Pedomys*, most published illustrations and descriptions note that *P. guildayi*, *P. australis* and *P. parmaleei* display positive differentiation (Pfaff 1990; Martin 1995; Martin et al. 2011). The most common m1 morphotype in *P. javaensis* is a primitive *Allophaiomys*-like form with a range of enamel differentiation from negative through positive.

Description

Mandible: The mandible of *P. javaensis* is small but robust, with the distinguishing characters of arvicolines as described by Repenning (1968, pp. 49–50) (Figure 5). The ascending ramus begins

approximately opposite T4 of m1. The dorsal masseteric crest (dmc) and dorsal edge of the ascending ramus are well separated, as is typical for arvicolines. The dmc and ventral masseteric crest (vmc) fuse at the level of the anteroconid of m1, and a small anterior masseteric crest (amc) extends to the anterior level of m1, ending posterior to and slightly dorsal to the mental foramen. The mental foramen is located laterally on the diastema, approximately in line with the fusion point of the dmc and vmc.

m1: The m1 of *P. javaensis* is composed of a posterior loop, three closed triangles and a primarily simple but variable ACD (Figure 3). Most m1s (category 1; 53 specimens/67%) correspond to Van der Meulen's form 1a (1978, fig. 2), with minimal or no development of T6–7. When at least one of these triangles is incipient, and if a slight indentation in the ACD indicates an incipient BRA4 or LRA5, the latter do not contain cement. Nevertheless, there is a gradient of complexity running from a dominant *Allophaiomys*-like morphology through a form with *Pedomys* features (category 2; 17 specimens/22%). Of the latter, four specimens (5%) collectively expressed the *Pedomys* synapomorphies identified above (Figure 3).

m2: The m2 is composed of a posterior loop and four triangles. T3–4 may be widely confluent or nearly closed, but the enamel apex of BRA4 never fuses with the anterior wall of T4.

m3: Triangles 1 and 2 are widely confluent and T4 is vestigial. The dentine channel between the posterior loop and T1 and between T2-T3 is narrow (Martin 1989; fig. 8E-G).

M1, M2: These teeth were described by Martin (1989). They are conservative, unremarkable and will not be described again here. The M2 does not possess a rudimentary T5 ('*pennsylvanicus* fold'; Bell and Repenning 1999).

M3: The M3 has an anterior loop, two complete triangles and a posterior loop with incipient T3–4. The most common morphotype (90%) is a complex form with modestly developed T4–5 and a deep, postvergent LRA3. LRA4 is present but does not contain cement (Martin 1989; fig. 8A-D).

Remarks: As noted in the Introduction, *Allophaiomys* has been reported from several sites across North America. The m1 samples from these sites are small, and therefore it is difficult at this time to determine their taxonomic status. Those described from the Borchers Badlands of Kansas, the earliest documented record of *Allophaiomys* in North America, express a simple, or category 1) morphology, and Martin et al. (2003) suggested they may represent a species distinct from the Java population. Martin and Schultz (1985, fig. 12) illustrated two m1s from beneath the Coleridge ash in the Sappa Formation of Nebraska that they referred to as '*Allophaiomys* sp. A' and '*Allophaiomys* sp. B'. The former is representative of the simplest morphotype in category 1) while species B could be allocated to *Pedomys*. Consequently, for now we refrain from including them and other North American *Allophaiomys* records in *Pedomys javaensis*. Until further studies are made of these samples, we recommend allocating them to *Allophaiomys* sp.

Pfaff (1990) followed Martin's (1987) recognition of *Pedomys* rather than *Allophaiomys* when at least 25% of the m1s in a sampled population expressed cementum in BRA4 and/or LRA5. In this study, the features above are considered more salient, with cementum in both BRA4 and LRA5 used to recognise the earliest *P. ochrogaster*.

Statistical comparison of the Java Pedomys *with* Allophaiomys deucalion *and* A. pliocaenicus

Statistics (grand mean, standard deviation, standard error) of m1 ratios are given in Appendix 1. Results of Tukey's HSD in Table 2 indicate the following: 1) there is no significant difference in length of
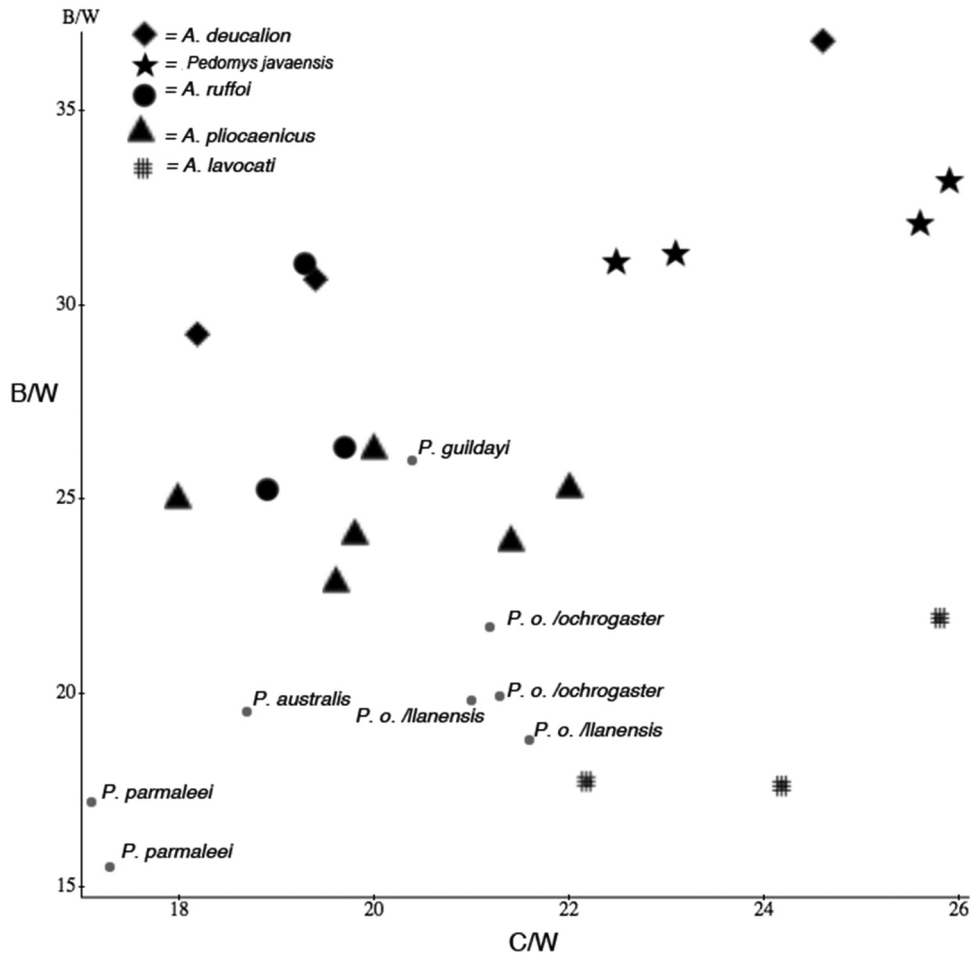
Figure 4. B/W × C/W plot for *Allophaiomys* and *Pedomys* species. Points represent sample means from Table 1. The *Allophaiomys deucalion* sample within the range of *P. javaensis* is from the type locality, Villány 5.
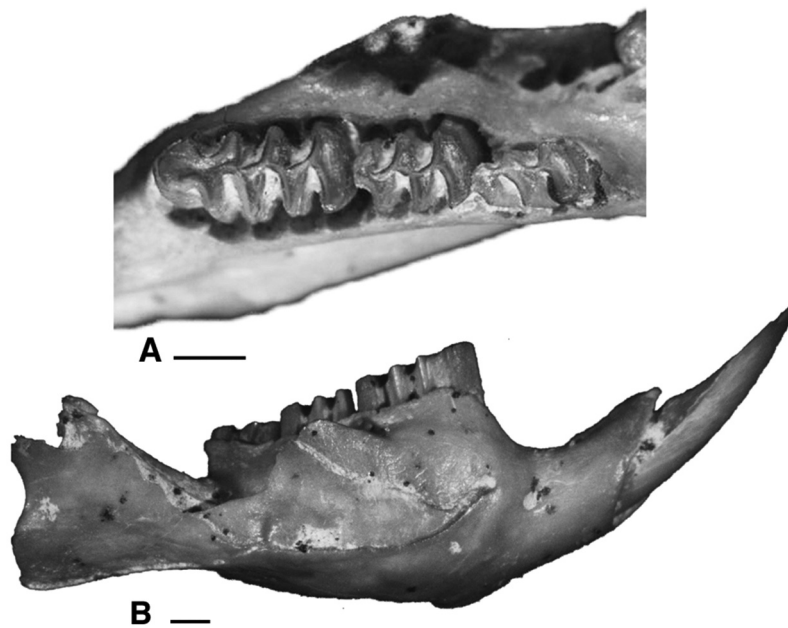

Figure 5. *Pedomys javaensis* n. sp., SDSM 12993, paratype right mandible with m1-m3. A = occlusal view, B = labial view. Scale bars = 1 mm.

Table 2. Tukey's HSD probabilities for Lm1, A/L, B/W, C/W and enamel differentiation based on tests of sample means (Table 1). java = *A. javaensis*, deuc = *A. deucalion*, plio = *A. pliocaenicus*.

L m1	p	A/L	p	B/W	p	C/W	p	Diff	p
java x deuc	0.09	java x deuc	0.007*	java x deuc	1	java x deuc	0.11	java x deuc	0.001*
java x plio	0.83	java x plio	0.59	java x plio	0.0002*	java x plio	0.03*	java x plio	0.16
deuc x plio	0.06	deuc x plio	0.02*	deuc x plio	<0.0001*	deuc x plio	0.91	deuc x plio	0.005*

* = statistically significant at p < 0.05

m1 among the Java *Pedomys*, *Allophaiomys pliocaenicus* or *A. deucalion*, 2) the anteroconid complex is significantly longer (A/L ratio) in the Java *Pedomys* and *A. pliocaenicus* than in *A. deucalion*, 3) the enamel channel connecting T5 and the anteroconid (B/W ratio) is significantly wider in the Java *Pedomys* and *A. deucalion* than in *A. pliocaenicus* (Figure 4), 4) the enamel channel connecting T4 with T5 (C/W ratio) is significantly wider in the Java *Pedomys* than in *A. pliocaenicus* and *A. deucalion* (Figure 4), and 5) the enamel is more negatively differentiated in *A. deucalion* than in either the Java *Pedomys* or *A. pliocaenicus*. These statistics were run on sample means (Table 1), and there is some overlap for all variables at ±2*s*. It is for this reason that relatively large samples must be utilised and a series of measurements and ratios compared. Nevertheless, these data demonstrate that *Pedomys javaensis* is the most primitive known species of the genus, with an m1 morphology intermediate between *A. deucalion* and *A. pliocaenicus*.

Discussion

Dental variability

The m1 morphology of *Pedomys javaensis* ranges from simple forms characteristic of Old World *Allophaiomys deucalion* and *A. pliocaenicus* through more complex morphotypes representative of extinct and extant *Pedomys*. Variation is extensive, but a similar range of morphology is also observed in extinct *Pedomys australis* and *P. ochrogaster* /*llanensis* and extant *P. ochrogaster* (Harris 1988; Pfaff 1990; Martin 1991, 1995), with an obvious shift from simpler to more complex morphotypes towards modern time. Because of the presence of *Pedomys* characters in a few m1s and the absence of *Pitymys* features in the Java sample, we can conclude that the Java population is more closely related to *Pedomys* than to *Pitymys*. However, the absence of *Pedomys* characters in category 1 m1s, the dominant Java m1 morphotype, provides a theoretical possibility that two species are represented, a common *Allophaiomys* and a rare *Pedomys*. As noted above, based on two m1s, Martin and Schultz (1985) concluded there were two species of *Allophaiomys* present in the Sappa assemblage. However, a complete continuum of features is represented when both categories 1 and 2 of the Java m1s are combined. Neither quantitative nor qualitative bimodality is indicated. As noted above, this interpretation is bolstered by the appearance of category 1 m1s in extant *P. ochrogaster*

The problem of deciphering the number of species in large, variable samples, is a universal problem in palaeontology and has been especially prevalent with the speciose arvicolines, where their fossil history is well documented and large samples are often available. Rabeder (1981), Rekovets and Nadachowski (1995) and Maul et al. (2007) developed models of m1 evolution from the earliest *Allophaiomys* through extant descendants, showing how population morphology shifted through time in different lineages. Various studies have also documented the intraspecific mosaic evolution in fossil arvicoline species (Barnosky 1993; Marcolini and Martin 2008; Martin et al. 2011). It seems clear that, at least for arvicoline m1 occlusal morphology, there is usually extensive intraspecific population variation that evolves in somewhat constrained and comprehensible trajectories through time. Thus, despite the presence of both primitive and somewhat advanced m1 morphotypes in the Java sample, available evidence on the history of dental morphology in *Allophaiomys* and its presumed descendants, plus observed variation in fossil and extant populations, suggests that the Java sample of m1s with T4–5 confluent represents a single species intermediate between *Allophaiomys* and *Pedomys* in which *Pedomys* m1 morphotypes first appear.

General evolutionary and dispersal patterns

The genus *Allophaiomys*, and *A. pliocaenicus* in particular, has often been mentioned as a potential ancestor for many of the extant Holarctic small arhizodont voles (Chaline 1972; Rabeder 1981; Martin 1989; Repenning 1992; Rekovets and Nadachowski 1995; Martin and Tesakov 1998). However, with more detailed information on the distribution and evolution of enamel histological banding patterns (the schmelzmuster of Koenigswald 1980) and occlusal morphology in arvicolines, it has become apparent that the small arhizodont voles are likely polyphyletic, descended from several ancestors with negative and undifferentiated molar enamel between about 2.2–1.5 Ma. Examples include the extinct genera *Allophaiomys*, *Victoriamys*, *Tibericola* and *Orcemys* and the extant *Microtus* complex, including numerous extant arvicolinin clades often considered distinct genera (e.g. *Stenocranius*, *Iberomys*, *Chionomys*, *Neodon*, *Terricola*, *Pedomys*, *Pitymys*) (Nadachowski 1991; Cuenca-Bescós et al. 1995; Ünay et al. 2001; Martin 2012a; Martin et al. 2017). The conversion from rhizodonty to arhizodonty apparently occurred entirely in the Old World, as potential *Mimomys* ancestors (e.g. *Mimomys tornensis*) are absent from North America but plentiful in the Old World (Garapich and Nadachowski 1996; Kościów and Nadachowski 2002). Most extant hypselodont vole species developed positive enamel differentiation, and the evolution from negative-undifferentiated-positive differentiation can be seen within *Allophaiomys*, with the earliest species expressing mostly negative or undifferentiated molars (*A. deucalion*, *A. tchumakovi*, *A. pliocaenicus* [early]) and later populations of *A. pliocaenicus*, *A. lavocati* and *P. javaensis* with a higher proportion of positively differentiated molars. As noted above, the presence of macroscopic negative differentiation in extant *Microtus umbrosus* Merriam (1898) and *M. guatemalensis* Merriam (1898) is a conundrum that needs explanation.

The Blancan-Irvingtonian boundary in North America is defined by the *Allophaiomys* immigration event at about 2.0 Ma, with a boundary stratotype in the Meade Basin of southwestern Kansas (Martin 2008). *Allophaiomys* is first recorded in North America from the Short Haul locality, located 1 m above the Borchers site and the Huckleberry Ridge ash, the latter dated at 2.07 Ma (Singer 2014). Although ancestral taxa for *Allophaiomys* are restricted to the Old World, the Short Haul record is the earliest confirmed global date for *Allophaiomys*. Currently, the earliest Old World reports of *Allophaiomys* are from a series of early Pleistocene sites on the Taman Peninsula of Russia (Tesakov 1998a, 1998b; Schelinsky et al. 2015),
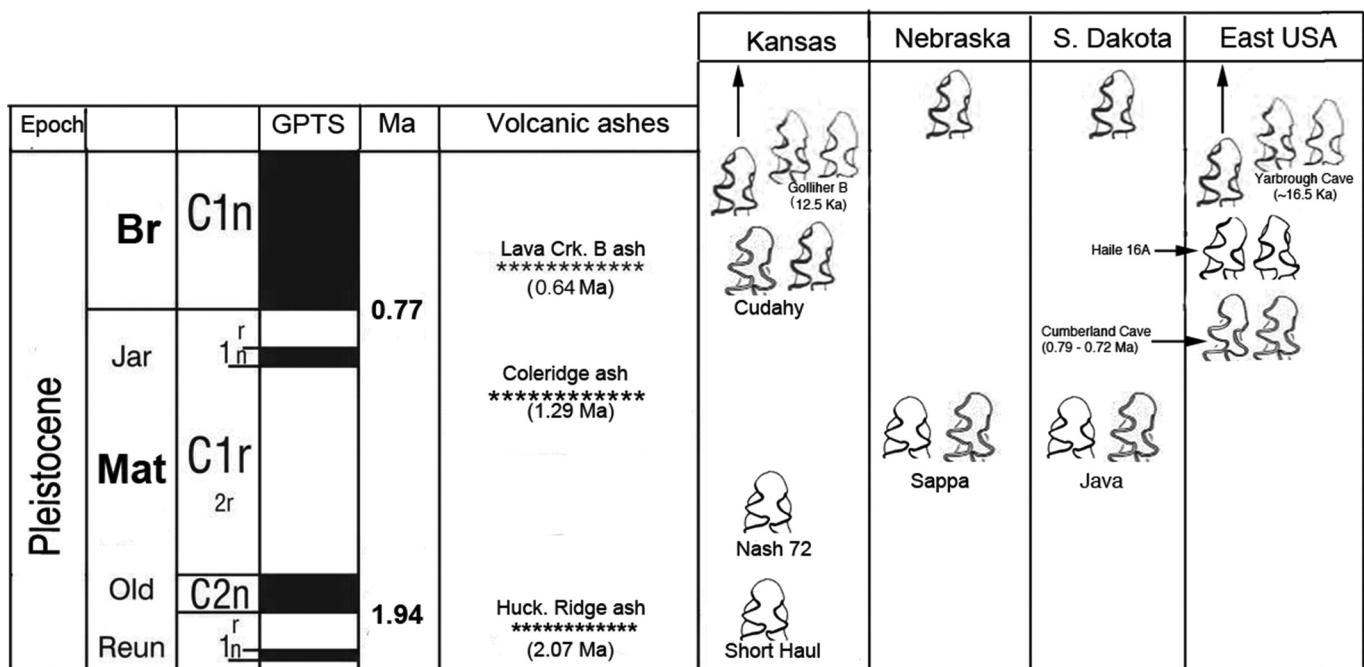
Figure 6. Replacement chronology for select North American *Allophaiomys* and *Pedomys* m1 morphotypes. GPTS = geomagnetic polarity timescale, Br = Brunhes, Ma = millions of years ago, Mat = Matuyama, Jar = Jaramillo, Old = Olduvai, Reun = Reunion, n = normal, r = reversed, Crk. = Creek, Huck. = Huckleberry. Golliher record from Martin et al. (2011); Haile 16A record from Martin (1995); Yarbrough Cave record from Martin (1991).

considered as part of the Psekups faunal sequence, dated between 2.1 and 1.8 Ma. The small sample of m1s from the Borchers Badlands precludes allocation to either *Pedomys* or *Pitymys*, as they fall into our morphotype category 1).

Numerous records of *Allophaiomys* across Eurasia and North America testify that this genus spread rapidly through the Holarctic, in North America following the Rocky Mountains south to Colorado (Rogers et al. 1992) and the Appalachian chain into Maryland (Van der Meulen 1978; Repenning and Grady 1988). Records from the Great Plains of South Dakota (Martin 1989), Kansas (Eshelman and Hibbard 1981; Martin et al. 2003) and Texas (Winkler and Gose 2003) are considered to be from glacial intervals. The type locality for *Pedomys javaensis*, Java, is an isolated paleostream channel, and cannot be securely dated. We consider a few of the taxa initially reported by Martin (1989), such as *Pliophenacomys*, *Hibbardomys*, *Guildayomys* and *Pliolemmus*, to be reworked Blancan intrusives, and the remaining species indicate an early Pleistocene deposition date between 2.0 and 1.29 Ma (Figure 6). The last appearance of *Allophaiomys* may be about 0.85 Ma in Porcupine Cave, Wyoming (Bell and Barnosky 2000), although that date cannot be confirmed. Younger records have been reported (e.g. Cathedral Cave NV [Jass and Bell 2011]; Little Dell Dam, UT [Withnell et al. 2022]), but with conflicting dates and rodent assemblages that, at least currently, appear unlikely (e.g. *Allophaiomys* and modern *Ondatra zibethicus* at <150 Ka). The latest confirmed date for *Allophaiomys* is from the Sappa assemblage of Kansas (Martin and Schultz 1985), lying beneath the Coleridge ash, correlative with the Mesa Falls tuff, dated by Lanphere et al. (2002) at 1.29 Ma (coincidentally roughly the same age originally suggested for the Little Dell Dam, Utah, *Allophaiomys* record by Gillette et al. 1999).

Phylogenetic patterns among North American *Allophaiomys, Pedomys* and *Pitymys*

The available comparative dental data suggest that North American *Pedomys javaensis* was ancestral to a clade of four species: the extant *P. ochrogaster* and extinct *P. guildayi* Van der Meulen (1978), *P. australis* Martin (1995) and *P. parmaleei* Martin et al. (2011). Van der Meulen (1978) noted the morphological similarity of *P. guildayi* (treated as *Microtus* [*Pedomys*] *guildayi*) from Cumberland Cave, Maryland, to *Allophaiomys* and the Old World *Phaiomys*, and without providing morphological criteria concluded they should be treated as separate taxa because they likely evolved independently. Pfaff (1990) transferred *Pedomys* out of *Microtus*, recognising the species *P. guildayi* and *P. llanensis*, and we follow that classification, with the caveat that *P. llanensis* is likely an early form of *P. ochrogaster*, which we treat as the chronomorph *P. ochrogaster /llanensis* (Martin 1995; Martin et al. 2011) because some m1s illustrated by Pfaff (1990) from Trout Cave No. 2, West Virginia, have cementum in both BRA4 and LRA5, as is common in extant *P. ochrogaster*. A closer examination of variation in m1s of the Cumberland Cave *Pedomys guildayi* demonstrates that some m1s in this population share *Pedomys* synapomorphies. As noted above, evolution towards extant *Pedomys* can be recognised, in part, by the shape of BRA3 on m1 (Figure 2). This m1 morphotype is represented by illustrations A, B, C and E of *P. guildayi* in fig. 7 of Van der Meulen (1978). The m1 of Van der Meulen's fig. 7G is more advanced, with a rudimentary T4–5 and overall morphology seen commonly in *P. o. /llanensis* (Pfaff 1990). These observations allow *P. guildayi* to be confidently referred to *Pedomys* on morphological grounds, and also demonstrate the high probability that *Pedomys guildayi*, and thus more dentally derived *Pedomys* species, evolved from a North American ancestor like *P. javaensis*.

Figure 6 presents a replacement chronology for select North American *Allophaiomys* and *Pedomys* m1 morphotypes. Although the *Allophaiomys* m1 morphotypes from the Borchers Badlands sites are all simple, in our category 1), the number of specimens is too small to be certain more complex morphotypes were absent. The rodent community from Java is similar to that from Sappa (Martin and Schultz 1985) and we consider both to be older than the Coleridge ash at 1.29 Ma but younger than the Borchers Badlands localities (Short Haul, Nash 72). The Cumberland Cave *Pedomys guildayi* at about 0.76 Ma is dentally advanced from the Java population (Van der Meulen 1978; Withnell et al. 2022). *Pedomys* fossil samples with entirely modern morphology (BRA4 and LRA5 present and one or both filled with cement) appear in numerous Rancholabrean sites above the Lava Creek B ash, but none beyond radiocarbon age are dated precisely, so we do not know exactly when the modern *P. ochrogaster* m1 became genetically fixed. A diminutive and somewhat dentally primitive prairie vole, *P. parmaleei*, has been recovered from late Wisconsinan localities in Kansas and several eastern Appalachian states (Martin et al. 2011), and may have been distributed in taiga or tundra habitats along the Laurentide ice front. Because m1 samples of *P. parmaleei* include a significant percentage of relatively simple m1 morphotypes as compared to contemporaneous late Pleistocene *P. ochrogaster* populations, we can speculate that *P. parmaleei* originated independently of either *P. o. /llanensis* or *P. guildayi*.

Origin of *Pitymys* remains problematic primarily because the currently oldest extinct *Pitymys, P. cumberlandensis* Van der Meulen (1978), from Cumberland Cave, is such a distinct species, with thick, undifferentiated enamel and open and confluent triangles on all molars. Van der Meulen (1978) considered *P. cumberlandensis* ancestral to extant *P. pinetorum* (which he regarded as an unrecognised clade of distinct species including *P. nemoralis, P. pinetorum* and *P. parvulus*) but did not identify a potential North American ancestor, concluding that North American *Pitymys* descended from a 'genus of unknown origin with distinct dental characteristics of unknown origin' (Van der Meulen 1978, p. 129). Based on a set of unique dental features, Martin (2012b) concluded *P. cumberlandensis* was not likely ancestral to *P. pinetorum*.

Repenning and Grady (1988) identified both *Allophaiomys* cf *pliocaenicus* and *Pitymys hibbardi* Holman (1959) from the early Pleistocene Cheetah Room of Hamilton Cave West Virginia. Repenning (1992) later observed that the Cheetah Room *Pitymys hibbardi* m1s graded from simple three-triangle *Allophaiomys*-like forms through *Pitymys pinetorum* morphotypes, and he identified both together (Repenning 1992, p. 39) colloquially as '*Allophaiomys* cf. *A. pliocaenicus – Pitymys hibbardi*'. Repenning also noted that one of us (RAM) was comparing *P. hibbardi* with *P. pinetorum*, and if a synonymy of the two was accomplished, the Cheetah Room population would require a new name. *Pitymys hibbardi* was indeed synonymised with *P. pinetorum* (Martin 1995). However, a new name cannot be provided for the Cheetah Room vole material until an evaluation is made of the Hamilton Cave small, arhizodont arvicolines to determine the number of species represented. At this point, it is informative that a fossil sample with *Pitymys* m1 morphotypes also includes *Allophaiomys*-like specimens. Coming full circle, it may be, as suggested by Repenning (1992), that both *Pedomys* and *Pitymys* originated from North American *Allophaiomys*.

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References

Albright LB III, Sanders AE, Weems RE, Cicimurri DJ, Knight JL. 2009. Cenozoic vertebrate biostratigraphy of South Carolina, U. S. A., and additions to the fauna. Bull Florida Mus Nat Hist. 57(2):77–236.

Baird SF. 1857. Mammals: general report upon the zoology of the several Pacific railroad routes.Vol. 8 part 1. Senate executive document No. 78 Washington, D.C

Barendregt RW, Thomas FF, Irving E, Baker J, Stalker A, MacsChurcher CA. 1991. Stratigraphy and paleomagnetism of the Jaw Face section, Wellsch Valley site, Saskatchewan. Can J Earth Sci. 28(9):1353–1364. doi: 10.1139/e91-119.

Barnosky AD. 1993. Mosaic evolution at the population level in *Microtus pennsylvanicus*. In: Martin R, and Barnosky A, editors. Morphological change in quaternary mammals of North America. New York: Cambridge U Press; pp. 25–59. doi: 10.1017/CBO9780511565052.003.

Bell CJ. 1995. A middle Pleistocene (Irvingtonian) microtine rodent fauna from White Pine County, Nevada, and its implications for microtine rodent biochronology. J Vert Paleo. 15:18A.

Bell CJ, Barnosky AD. 2000. The microtine rodents from the pit locality in Porcupine Cave, Park County, Colorado. Ann Carnegie Mus. 69(2):93–134. doi: 10.5962/p.330537.

Bell CJ, Repenning CA. 1999. Observations on dental variation in *Microtus* from the Cudahy Ash Pit fauna, Meade County, Kansas, and implications for Irvingtonian microtine rodent biochronology. J Vert Paleo. 19(4):757–766.

Bell CJ, Repenning CA, Barnosky AD. 2004. Arvicoline rodents from Porcupine Cave: identification, spatial distribution, taxonomic assemblages, and biochronologic significance. In: Barnosky A, editor. Biodiversity response to climate change in the Middle Pleistocene. Berkeley: U California Press; pp. 207–263. doi: 10.1525/california/9780520240827.003.0019.

Bowditch TE. 1821. An analysis of the natural classifications of Mammalia for the use of students and travelers. Paris: Smith.

Chaline J. 1972. Les rongeurs du Pléistocène moyen et supérieur de France. Paris: Cahiers Paléontologie (CNRS).

Coues E. 1874. Synopsis of the Muridae of North America. Proc Philadelphia Acad Nat Sci. 26:173–196.

Cuenca-Bescós G, Canudo JI, Laplana C. 1995. Los arvicólidos (Rodentia, Mammalia) de los niveles inferiores de Gran Dolina (Pleistoceno inferior, Atapuerca, Burgos, España). Spanish J Palaeontol. 10(2):202–218. doi: 10.7203/sjp.24137.

Eshelman R, Hager M. 1984. Two Irvingtonian (medial Pleistocene) vertebrate faunas from north-central Kansas. In: Genoways H, and MR D, editors. Contributions in Quaternary vertebrate paleontology: a volume in memorial to John E. Guilday. Special Pub no. 8. Pittsburgh: Carnegie Mus Nat Hist; pp. 384–404.

Eshelman RE, Hibbard CW. 1981. Nash local fauna (Pleistocene: Aftonian) of Meade County, Kansas. Contribs Mus Paleontol, U Michigan. 25 (16):317–326.

Fischer de Waldheim G. 1817. Adversaria zoological fasciculus primus. Mémoires de la Société Impériale des Naturalistes de Moscou. 5:357–428.

Garapich A, Nadachowski A. 1996. A contribution to the origin of *Allophaiomys* (Arvicolidae, Rodentia) in central Europe: the relationship between *Mimomys* and *Allophaiomys* from Kamyk (Poland). Acta Zool Cracov. 39 (1):179–184.

Gillette DD, McDonald HG, Hayden MC. 1999. Preliminary report on the Little Dell Dam fauna, Salt Lake Utah (middle Pleistocene, Irvingtonian land mammal age. In: Gillette D, editor. Vertebrate paleontology in Utah. Misc pub 99-1. Salt Lake City: Utah Dept Nat Resources; pp. 495–500.

Goodwin GG. 1966. A new species of vole (genus *Microtus*) from Oaxaca, Mexico. Amer Mus Novs No. 2243:1–4.

Gray JE. 1821. On the natural arrangement of vertebrate animals. London Medical Repository. 15:296–310.

Guilday JE, Cotter JFP, Cundall D, Evenson EB, Gatewood JB, Morgan AV, Morgan A, McCrady AD, Peteet DM, Stuckenrath R, et al. 1984. Paleoecology of an Early Pleistocene (Irvingtonian) cenote: preliminary report on the Hanover Quarry No. 1 Fissure, Adams County, Pennsylvania. In: Mahaney W, editor. Correlation of Quaternary chronologies. Norwich, UK: Geo Books; pp. 119–132.

Harris AH. 1988. Late Pleistocene and Holocene Microtus (Pitymys) (Rodentia: Cricetidae) in New Mexico. J Vert Paleo. 8(3):307–313. doi: 10.1080/02724634.1988.10011713.

Hibbard CW. 1944. Stratigraphy and vertebrate paleontology of pleistocene deposits of southwestern Kansas. Bull Geol Soc America. 55:707–754.

Hir J. 1998. The Allophaiomys type-material in the Hungarian collections. Paludicola. 2(1):28–36.

Holman JA. 1959. Birds and mammals from the Pleistocene of Williston, Florida. Bull Florida St Mus. 5(1):1–24. doi: 10.2307/1440060.

Jass CN, Bell CJ. 2011. Arvicoline rodent fauna from the Room 2 excavation in Cathedral Cave, White Pine County, Nevada, and its biochronologic significance. J Vert Paleo. 31(3):684–691. doi: 10.1080/02724634.2011.563764.

Koenigswald W von. 1980. Schmelzstruktur und morphologie in den molaren der Arvicolidae (Rodentia). Abhandlungen der Senckenberischen Naturforschenden Gesellschaft. 539:1–129.

Koenigswald W von, Martin LD. 1984. Revision of the fossil and Recent lemmi-nae (Rodentia, Mammalia). In: Mengel R, editor. Vol. 9, Papers in vertebrate paleontology honoring Robert Warren Wilson. Pittsburgh: Carnegie Mus Nat History. Special pub; pp. 122–137.

Kormos T. 1933. Neue Wuhlmäuse aus dem Oberpliozän von Puspökfurdö. Neue Jahr Minerol Geol Paleontol. 69:323–346.

Kościów R, Nadachowski A. 2002. Type populations of some Mimomys species (Arvicolidae, Rodentia) at the Pliocene/Pleistocene boundary in central Europe. Folia Zool. 51:93–104.

Kretzoi M. 1969. Skizze einer Arvicoliden Phylogenie-Stand 1969. Vert Hung Mus Hist-Nat Hungary. 11:155–193.

Lanphere MA, Champion DE, Izett GA, Obradovich JD. 2002. Revised ages for tuffs of the Yellowstone Plateau volfanic field: assignment of the Huckleberry Ridge Tuff to a new geomagnetic polarity event. Bull Geol Soc America. 114 (5):559–568.

Laplana C, Cuenca-Bescós G. 2000. Una nueva especie de Microtus (Allophaiomys) (Arvicolidae, Rodentia, Mammalia) en el Pleistoceno Inferior de la Sierra de Atapuerca (Burgos, España). Rev Esp Paleontol. 15 (1):77–87. doi: 10.7203/sjp.15.1.22088.

Le Conte J. 1830. Annals of the lyceaum of natural history. New York. 3:133.

Linnaeus C. 1766. Systema naturae per regna tria naturae, secundum classes, Ordines, genera, species, cum characteribus and Differentiis. 12th Reformata: Vol. I Laurentii Salvii. 10.5962/bhl.title.68927

Lippi P, Masini F, Maul L, Abbazzi L. 1998. Evolutionary changes of enamel differentiation in Pleistocene Mediterranean and Middle European populations of Microtus (Rodentia, Arvicolidae). Paludicola. 2(1):50–61.

Liu S, Zhou C, Meng G, Wan T, Tang M, Yang C, Murphy RW, Fan Z, Liu Y, Zeng T, et al. 2022. Evolution and diversification of mountain voles. Rodentia: Cricetidae. Nature Comms Biol. doi: 10.1038/s42003-022-04371-z.htt//doi.org/10.1038/s42003-.

López-García M, Luzi E, Berto C, Peretto C, Arzarello M. 2015. Chronological context of the first hominin occurrence in southern Europe: the Allophaiomys ruffoi (Arvicolinae, Rodentia, Mammalia) from Pirro 13 (Piro Nord, Apulia, southwestern Italy). Quat Sci Rev. 107:260–266.

Marcolini F, Martin RA. 2008. Mosaic evolution in first lower molars of Pliocene Ogmodontomys (Rodentia: Arvicolidae) from the Meade basin of southwestern Kansas. Neues Jarbuch für Geologie und Paläeontologie Abh. 249 (3):313–332. doi: 10.1127/0077-7749/2008/0249-0313.

Martin RA. 1975. Allophaiomys Kormos from the Pleistocene of North America. In: Smith G, and Friedland N, editors. Studies on Cenozoic paleontology and stratigraphy, Claude W. Hibbard Memorial Vol. 3, U Michigan Mus Paleo, Papers on Paleontology. U Michigan; pp. 97–100.

Martin RA. 1987. Notes on the classification and evolution of some North American fossil Microtus (Mammalia: rodentia). J Vert Paleo. 7(3):270–283.

Martin RA. 1989. Arvicolid rodents of the early Pleistocene Java local fauna from north-central South Dakota. J Vert Paleo. 9(4):438–450. doi: 10.1080/02724634.1989.10011776.

Martin RA. 1991. Evolutionary relationships and biogeography of late Pleistocene prairie voles from the eastern United States. Illinois St Mus Scientific Papers. 23:251–260.

Martin RA. 1995. A new middle Pleistocene species of Microtus (Pedomys) from the southern United States, with comments on the taxonomy and early evolution of Pedomys and Pitymys in North America. J Vert Paleo. 15 (1):171–186. doi: 10.1080/02724634.1995.10011216.

Martin RA. 2008. Arvicolidae. In: Janis C, Gunnell G, and Jacobs L, editors. Evolution of Tertiary Mammals of North AmericaVol. II Cambridge, New York: pp. 480–497. 10.1017/CBO9780511541438.029

Martin RA. 2012a. Further notes on the Port Kennedy Cave arvicolid rodents. Paludicola. 9(1):13–20.

Martin RA. 2012b. Victoriamys, a new generic name for Chaline's vole from western Europe. Geobios. 45(5):445–450. doi: 10.1016/j.geobios.2012.01.001.

Martin RA, Bonk AC, Peláez-Campomanes P. 1998. Variation in enamel differentiation of Microtus molars from the Java local fauna, Walworth County, South Dakota. Paludicola. 2(1):74–77.

Martin RA, Hurt RT, Honey JG, Peláez-Campomanes P. 2003. Late Pliocene and early Pleistocene rodents from the northern Borchers Badlands (Meade County, Kansas), with comments on the Blancan–Irvingtonian boundary in the Meade basin. J Paleo. 77(5):985–1001. doi: 10.1666/0022-3360(2003) 077<0985:LPAEPR>2.0.CO;2.

Martin RA, Peláez-Campomanes P, Honey JG. 2011. Preliminary study of rodents from the Golliher B assemblage indicates an intense cold period near the end of the Pleistocene. Palaeo Elec. 14(3.35A):1–13.

Martin LD, Schultz CB. 1985. Small mammals of the Seneca and Sappa local faunas (post-Ogallala of Nebraska). In: Dort W, editor. Vol. 1, Institute for Tertiary Quaternary studies, TER-QUA symposium series. Lincoln: Nebraska Acad Sci; pp. 163–179.

Martin RA, Tesakov A. 1998. Time's arrow and the evolutionary position of Orthriomys and Herpetomys. Paludicola. 2(1):70–73.

Martin RA, Tesakov A. 1998. Introductory remarks. Does Allophaiomys exist? Paludicola. 2(1):1–7.

Martin RA, Tesakov A, Agustí J, Johnston K. 2017. Orcemys, a new genus of arvicolid rodent from the early Pleistocene of the Guadix-Baza basin, southern Spain. Comptes Rendus-Palevol. 17(4–5):310–319. doi: 10.1016/j.crpv.2017.06.006.

Maul LC, Heinrich W-D, Parfitt SA, Paunescu A-C. 2007. Comment on the correlation between magnetostratigraphy and the evolution of Microtus (Arvicolidae, Rodentia, Mammalia) during the early and middle Pleistocene. Cour Forsch Senck. 259:243–263.

Merriam CH. 1898. Description of two new subgenera and three new species of Microtus from Mexico and Guatemala. Proc Biol Soc Washington. 12:105–108.

Minwer-Barakat R, Madurell-Malapeira J, Alba DM, Aurell-Garrido J, de Esteban-Trivigno S, Moyà Solà S. 2011. Pleistocene rodents from the torrent de Vllparadís section (Terrassa, northeastern Spain) and biochronologial implications. J Vert Paleo. 31(4):849–865.

Nadachowski A. 1991. Systematics, geographic variation, and evolution of snow voles (Chionomys) based on dental characteristics. Acta Theriol (Warsz). 36:1–45. doi:10.4098/AT.arch.91-1.

Paulson GR. 1961. The mammals of the Cudahy fauna. Papers Michigan Acad Sci Arts Letters. 46:127–153.

Pfaff K. 1990. Irvingtonian Microtus and Pitymys (Mammalia, Rodentia, Cricetidae) from Trout Cave No. 2, West Virginia. Ann Carnegie Mus. 59 (2):105–134. doi: 10.5962/p.330562.

Rabeder G. 1981. Die arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich, Beiträge zur Paläontologie von Österreich. Institut für Paläontologie der Universität Wien. (8):1–343.

Rekovets L, Nadachowski A. 1995. Pleistocene voles (Arvicolidae) of the Ukraine. Paleontologia I Evolució. 28–29:145–245.

Repenning CA. 1968. Mandibular musculature and the origin of the subfamily arvicolinae (Rodentia). Acta Zool Cracov. 13(3):29–72.

Repenning CA. 1992. Allophaiomys and the age of the Olyor suite, Krestovka sections,Yakutia. Bull US Geol Surv No. 2037:1–98.

Repenning CA, Grady F. 1988. The microtine rodents of the Cheetah Room fauna, Hamilton Cave, West Virginia, and the spontaneous origin of Synaptomys. Bull US Geol Surv. (1853):1–32.

Rogers KL, Larson EE, Smith G, Katzman D, Smith GR, Cerling T, Wang Y, Baker G, Lohmann KC, Repenning CA, et al. 1992. Pliocene and Pleistocene geologic and climatic evolution in the San Luis Valley of south-central Colorado. Palaeogeogr Palaeoclimatol Palaeoecol. 94(1–4):55–86. doi:10.1016/0031-0182(92)90113-J.

Rogers KL, Repenning CA, Luiszer FG, Benson RD. 2002. Geologic history, stratigraphy, and paleontology of SAM Cave, north-central New Mexico. New Mexico Geology. 22(4):89–117. doi: 10.58799/NMG-v22n4.89.

Schelinsky VE, Gurova M, Tesakov AS, VV T, Frolov P, AN S. 2015. The early Pleistocene site of Kermek in western Ciscaucasia (southern Russia): stratigraphy, biotic record, and lithic industry (preliminary results). Quat Inter. 393:51–69. doi:10.1016/j.quaint.2015.10.032.

Schreber JCD. 1777. Die Säugthiere in Abbildungen nach der Natur mit Beschreibungen 1776-1778. Wolfgang Walther Erlangen. 3:377–440.

Singer BS. 2014. A Quaternary geomagnetic instability time scale. Quat Geochron. 21:29–52. doi:10.1016/j.quageo.2013.10.003.

Tesakov A. 1998a. Biostratigraphy of middle Pliocene-Eopleistocene of eastern Europe (based on small mammals). Trans Geol Inst Russian Acad Sci. 554:1–247.

Tesakov A. 1998b. Early stage of *Allophaiomys* evolution in eastern Europe. Paludicola. 2(1):98–105.

Tjutkova LA, Kaipova GO. 1996. Late Pliocene and Pleistocene micromammal faunas from southeastern Kazakhstan. Acta Zool Cracov. 39(1):549–557.

Ünay E, Emre A, Erkal T, Keçer M. 2001. The rodent fauna from the Adapazari pull-apart basin (NW Anatolia): its bearing on the age of the North Anatolian fault. Geodin Acta. 14(1):169–175. doi: 10.1080/09853111.2001.11432442.

Van der Meulen AJ. 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus*. Quaternaria. 17:1–144.

Van der Meulen AJ. 1974. On *Microtus (Allophaiomys) deucalion* (kretzoi, 1969) from the upper Villanyian (lower pleistocene) of Villány -5, Hungary. Proc K Ned Akad Wet, Series B. 77:259–266.

Van der Meulen AJ. 1978. *Microtus* and *Pitymys* (Arvicolidae) from Cumberland Cave, Maryland, with a comparison of some new and Old World species. Ann Carnegie Mus. 47:101–145. doi:10.5962/p.215820.

Van Kohflshoten T. 1998. The *Allophaiomys* record from Zuurland, the Netherlands. Paludicola. 2(1):110–115.

Winkler AJ, Gose W. 2003. Mammalian fauna and paleomagnetics of the middle Irvingtonian (early Pleistocene) Fyllan Cave and Kitchen Door localities, Travis County, Texas. In: Schubert B, Mead J, and Graham R, editors. Ice age cave faunas of North America. Bloomington: Indiana University Press; pp. 213–261.

Withnell CB, Bell CJ, Jass CN. 2022. Extraordinary accumulation of arvicoline rodents from Little Dell Dam (Pleistocene, Utah). Southwest Nat. 66 (2):91–101. doi: 10.1894/0038-4909-66.2.91.

Zazhigin V. 1998. Taxonomy and evolution of the genus *Allophaiomys* (Microtinae: Rodentia: Mammalia) in Siberia. Paludicola. 2(1):116–125.

Appendix 1

Table A1. Statistics for means of enamel differentiation and m1 dental ratios in *Pedomys javaensis*, *Allophaiomys deucalion* and *A. pliocaenicus*. N = number of means, O.R. = observed range, s = standard deviation, SE = standard error of grand mean, Diff = enamel differentiation.

	Diff					B/W					A/L					C/W				
	N	mean	O.R.	s	SE	N	mean	O.R.	s	SE	N	mean	O.R.	s	SE	N	mean	O.R.	s	SE
P. javaensis	2	92.2	91.9 - 92.4	0.35	0.25	4	31.9	31.3 - 33.2	0.95	0.48	4	43.7	42.7 - 45.8	1.44	0.72	4	24.3	22.5 - 25.9	1.73	0.86
A. deucalion	6	120.2	110.3 - 136.4	9.07	3.7	5	32	29.3 - 36.8	2.87	1.29	6	40.9	39.9 - 42	0.97	0.4	3	20.7	18.2 - 24.6	3.4	1.96
A. pliocaenicus	6	103.7	96.7 - 111.5	5.36	2.19	6	24.6	22.8 - 25.3	1.2	0.49	6	43	41.8 - 45	1.2	0.49	6	20.1	18 - 22	1.42	0.58