



Arvicolini (Rodentia) from the Irvingtonian of north-central Kansas, USA

Richard J. Zakrzewski and Gabe S. Bever

ABSTRACT

The Fiene local fauna, located in north-central Kansas, is one of the few Pleistocene microfaunas in the state located outside the Meade Basin. The fauna includes a variety of vertebrate taxa, including a small but diverse assemblage of arvicoline rodents. Seven morphotypes of the first lower molar are recognizable among the specimens assignable to Arvicolini. These include a form with five closed triangles assigned to *Microtus* sp., three morphotypes with four closed triangles assigned to *M. paroperarius*, and three morphotypes with three closed triangles assigned to *M. llanensis*, *M. meadensis*, and *Allophaiomys* sp. The co-occurrence of these forms supports an Irvingtonian age for the site, and constitutes a relatively rare taxonomic assemblage for the Great Plains. The Fiene thus may prove important for testing future questions of provinciality in arvicoline biochronology and faunal dynamics.

Recent phylogenetic hypotheses, based largely on molecular sequence data, have complicated the interpretation of isolated fossil teeth by proposing the extant species of North American *Microtus* are monophyletic and that taxa characterized by three closed triangles on the m1 evolved independently from five-triangled forms. The ability of fossil assemblages, such as Fiene, to meaningfully inform broad questions of arvicoline evolution requires that paleontologists improve their ability to place isolated teeth into this expanded phylogenetic context. Rather than depressing paleontological study, this requirement hopefully will be embraced as an opportunity to expand research on the arvicoline dentition.

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INTRODUCTION

One of the major, if not the major, contribution of the late Charles A. Repenning to paleontology was to increase our understanding of the evolutionary relationships, biostratigraphy, and paleobiogeography of arvicoline rodents. Although he published on all arvicoline groups, perhaps his greatest interest was in those species historically considered to be part of or closely related to *Microtus* (i.e., Arvicolini; Galewski et al., 2006). Therefore, it seems appropriate in a volume honoring Charles Repenning that we report and discuss specimens assignable to Arvicolini from a new site in north-central Kansas, the Fiene local fauna (l.f.).

The Fiene l.f., located in Smith County (Co.), is one of a small number of Pleistocene localities in Kansas outside the Meade Basin (Figure 1.1). The fossils from this locality include more than 40 identifiable taxa of actinopterygians, amphibians, reptiles (including birds), mammals, and both aquatic and terrestrial molluscs (Bever et al., 1999). The geologic setting of Fiene consists of relatively thin deposits of reddish clayey sands and silts containing caliche nodules deposited over Cretaceous limestone. The nature of the sediments, interpreted within the context of their associated fauna, suggests both lacustrine and fluvial influences, and we hypothesize that the locality was deposited within an oxbow lake. No external age control currently exists for the site, and the recognized stratigraphic division to which the Fiene sediments belong (if any exists) is unclear. The Pleistocene localities geographically closest to Fiene are Courtland Canal and Hall Ash Pit—approximately 60 km to the east (Eshelman and Hager, 1984). The lithologically similar sediments of these localities (to those of Fiene) were suggested by Eshelman and Hager (1984) to be equivalent in part to the Loveland Formation (Frye and Leonard, 1952). The section containing the Hall Ash Pit contains a bedded ash that was fission-track dated to a mean age of 0.706 ± 0.017 Ma (Eshelman and Hager, 1984). A better understanding of the lithologic and stratigraphic relationships between the Pleistocene localities of north-central Kansas and with the classic sequences of the Meade Basin is needed.

Based on the occlusal pattern of the first lower molar (m1), seven different Arvicolini morphotypes can be distinguished. These include one form with five closed triangles assigned to *Microtus* sp.; three morphotypes with four closed triangles, all assigned to *M. paroperarius* as Variants A, B, C; and three morphotypes with three closed triangles assigned to *M. llanensis*, *M. meadensis*, and

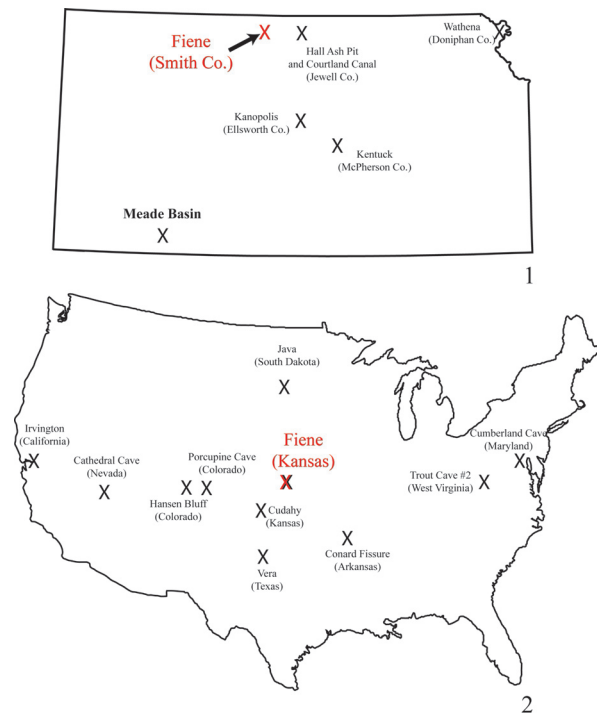


FIGURE 1. Maps showing the geographic position of the Fiene local fauna relative to other U.S. microvertebrate localities mentioned in the text that are in Kansas but outside the Meade Basin (1) and outside of Kansas (2). Co. = county.

Allophaiomys sp. The only other sites (Figure 1.2) where at least four of these species occur together are Cathedral Cave, White Pine Co., Nevada (Bell, 1995; Jass, 2006, 2007), Porcupine Cave, Park Co., Colorado, in the Pit (level 4) and CM Velvet Room (level 3) sites (Bell et al., 2004a), and Cudahy, Meade Co., Kansas (Paulson, 1961; Bell and Repenning, 1999). Four of the taxa also may occur at Hansen Bluff, Alamosa Co., Colorado (Bell et al., 2004a), but the *Allophaiomys* record from Hansen Bluff (Rogers et al., 1992, figure 9A) is based on an isolated lower third molar (m3), which is a non-diagnostic element at the generic level (Bell and Barnosky, 2000). *Microtus llanensis* does not occur in the Colorado and Nevada sites, and *Allophaiomys* sp. is not found at Cudahy.

Other sites in Kansas, outside the Meade Basin, from which at least one of the taxa found at Fiene include Hall Ash Pit (*Microtus* sp., *M. paroperarius*) and Courtland Canal (*Allophaiomys* sp.) in Jewell Co., Kanopolis (*M. llanensis*) in Ellsworth Co., Kentuck (*Allophaiomys* sp.) in McPherson Co., and Wathena (*Allophaiomys* sp.) in Doniphan Co. (Figure 1.1). Other non-Kansas sites mentioned in this study (Figure 1.2) include Irvington (California), Java (South Dakota), Vera (Texas),

Conard Fissure (Arkansas), Trout Cave #2 (West Virginia), and Cumberland Cave (Maryland).

MATERIALS AND METHODS

The original and early finds from Fiene were collected in situ by Robert L. Levin. Subsequently, we collected and gently washed approximately 400 pounds of matrix through a fine screen (0.7 mm mesh). The recovered arvicolines consisted primarily of isolated teeth. Four m1s are in mandibles. The specimens are housed at Fort Hays State University in the Sternberg Museum of Natural History, Section of Vertebrate Paleontology (FHSM VP), Hays, Kansas.

Measurements were taken on the lower first molar (m1) and the upper third molar (M3) to the nearest 0.01 mm using a Gaertner measuring microscope. Variables measured on m1 (Figure 2.3) were the same as taken by Pfaff (1990) with the addition of the width of the anterior cap (A–A') from Repenning (1992). Terminology used when discussing the teeth is defined in Figure 3 and where first used in the text. Ratios for the variables measured on m1 were determined using the method proposed by Van der Meulen (1978). Variables measured on the M3 (Figure 2.4) were defined by Repenning (1992). Descriptive statistics were determined for each variable measured on m1 and M3. The mean values of the variables for each morphotype were compared using a Student's *t* test with $P < 0.05$. Statistical analyses were performed using Microsoft Excel®. Juvenile specimens and those etched or damaged so that none of the variables could be measured were not included in the analyses. Measurements of teeth from other sites were taken from the literature.

SYSTEMATIC ACCOUNTS

Microtus von Schrank, 1798

Material. 11 Lm1s, FHSM VP-13771, 15637, 15644, 15647, 15648, 15654, 15710, 15711, 15734, 15749, 16382; 10 Rm1s, FHSM VP-15635, 15643, 15645, 15652, 15662–15664, 15668–15670.

Description. Twenty-one m1s of *Microtus* are characterized by five closed triangles and are assigned to *Microtus* sp. The teeth are ever growing and exhibit strong development of cementum in buccal re-entrant angles one through three and lingual re-entrant angles one through four. Presence and development of cementum varies from absent to strong in buccal re-entrant angle four and lingual

re-entrant angle five. The teeth exhibit positive enamel differentiation (Martin, 1987).

A slight majority ($n = 12$, 57.1%) has an anterior cap with shallow re-entrants in buccal angle four and lingual angle five. This shallowness provides for a wider A–A' (observed range = 0.33–0.63 mm) and the appearance of slightly less developed triangles six and seven (Figure 3.1). The remainder ($n = 9$, 42.9%) have deeper re-entrants that allow for a narrower A–A' (observed range = 0.20–0.30 mm) and the appearance of better-developed triangles six and seven (Figure 3.2). The buccal re-entrant angle four and lingual re-entrant angle five of *Microtus* sp. are deeper than those of Variants A and C of *M. paroperarius* and *M. llanensis*. The opening between triangles five and six (AC) is narrower than in *M. paroperarius* and *M. llanensis*, and the opening between triangles four and five (C) is narrower than in *M. llanensis* and *M. meadensis*. The length of the anteroconid complex (A), total length (L), and length across triangles four and five (W) in *Microtus* sp. is greater than in *M. llanensis* (Table 1).

Two of the teeth assigned to *Microtus* sp. have a relatively square-shaped sixth triangle that includes a slight indentation at the approximate midpoint of its buccal edge (Figure 3.3). This indentation, often called a prism fold (Zakrzewski, 1967, figure 1A), occurs infrequently in extant species of *Microtus* (Zakrzewski, 1985). It occurs more commonly in some species of extinct, presumably more basal, arvicolines (e.g., *Ogmondontomys*, *Cosmymys*). When present in these forms, it is found on triangle four.

The five closed triangle morphotype was considered a variant of *Microtus paroperarius* by Paulson (1961) in his study of the Cudahy arvicolines; however, we follow the taxonomic conclusions of Bell and Repenning (1999) who assigned this morphotype to an unidentifiable species of *Microtus*. The m1s from Fiene are the same size as those from Cudahy but smaller than those from Irvington (Table 2).

Comments. An m1 characterized by five closed triangles may represent the plesiomorphic condition for the most recent common ancestor of all North American *Microtus* (Bell and Bever, 2006), and apparently this morphotype was widespread across North America during the middle Pleistocene. However, with the exception of Fiene where m1s with five closed triangles constitute 43.8% of a combined sample of four- and five- triangle forms ($n = 48$) and Cathedral Cave (Jass, 2007), the five-triangle morphotype constitutes a very low percent-

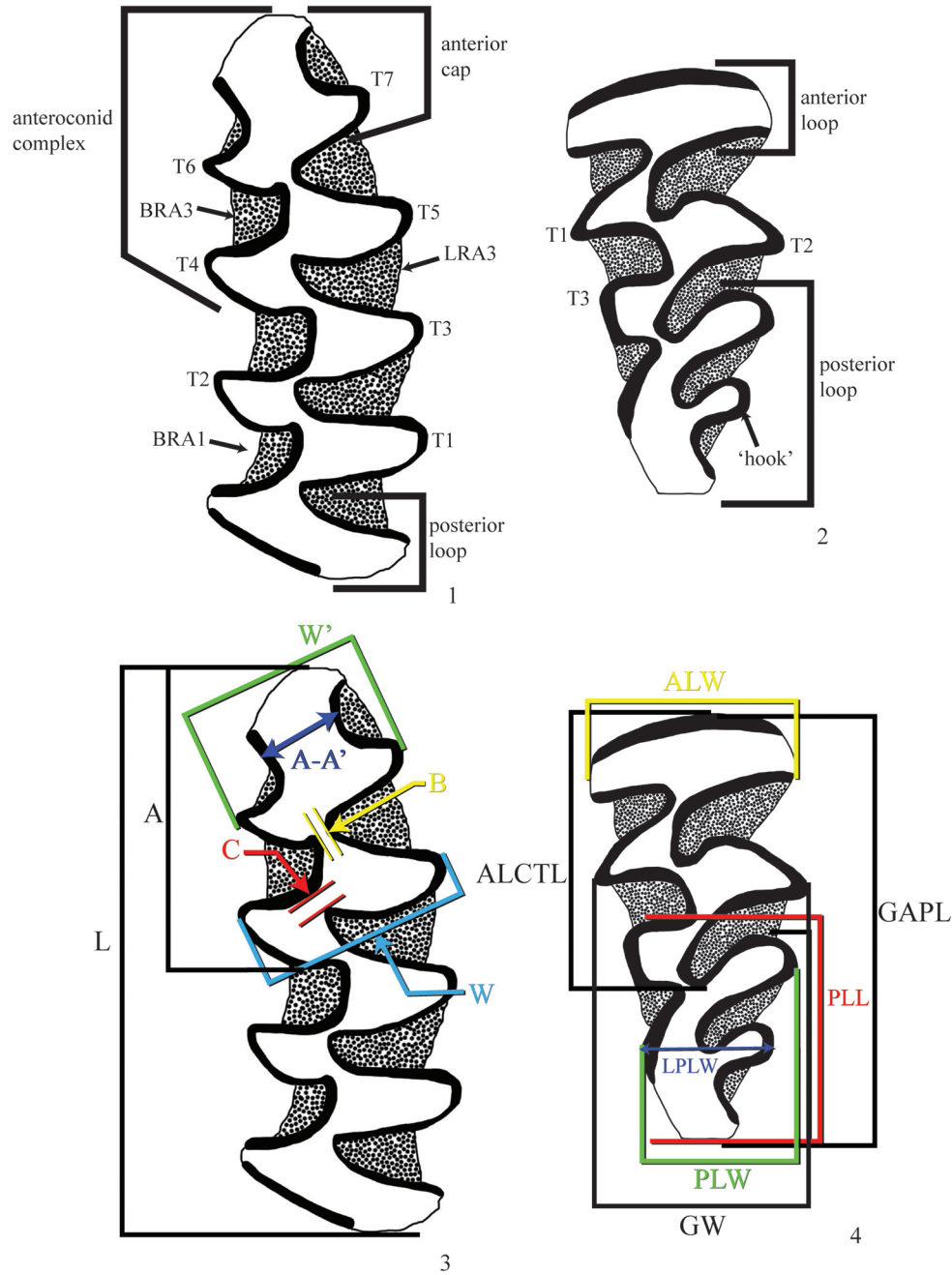


FIGURE 2. Occlusal view of lower first molars (m1; 1, 3) and upper third molars (M3; 2, 4) illustrating selected anatomical terms (1, 2) and measurements (3, 4) used in this study. Abbreviations: **A**, length of the anteroconid complex of m1; **A-A'**, width of the anterior cap of m1; **ALCTL**, length of anterior loop and central triangles of M3; **ALW**, width of anterior loop of M3; **B**, width of opening between triangles 5 and 6 on m1; **BRA**, buccal re-entrant angle; **C**, width of opening between triangles 4 and 5 on m1; **GAPL**, greatest anteroposterior length of M3; **GW**, greatest width of M3; **L**, greatest length of m1; **LPLW**, width of last segment of posterior loop of M3; **LRA**, lingual re-entrant angle; **OW** (not shown), greatest width of m1 measured perpendicular to the long axis of the occlusal surface; **PLL**, length of posterior loop of M3; **PLW**, width of posterior loop of M3; **T**, triangle; **W**, greatest straightline distance between the apices of triangles 4 and 5 on m1; **W'**, greatest straightline distance between the apices of triangles 6 and 7 on m1. Measurements of m1 and their associated abbreviations are from Pfaff (1990) with the exception of A-A', which was redrawn from Repenning (1992).

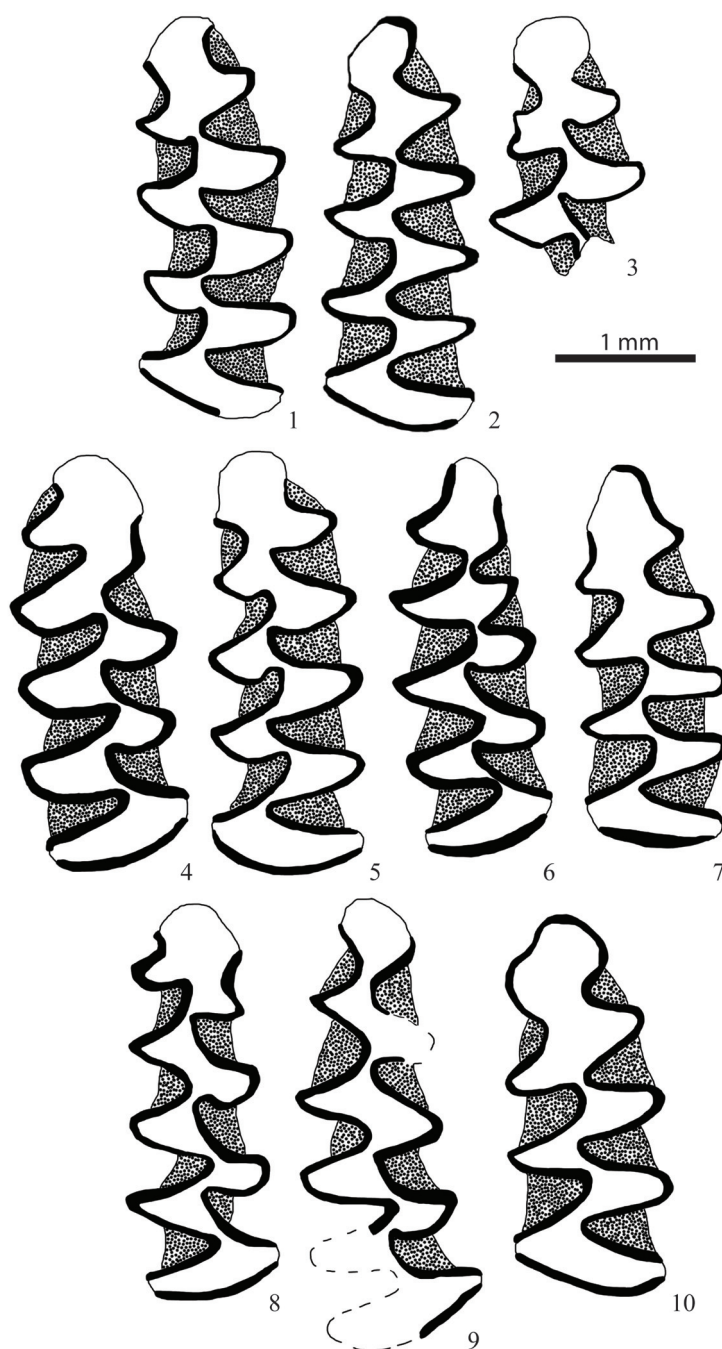


FIGURE 3. Occlusal view of lower first molars (m1) representing the different morphotypes observed in the Fiene Arvicolini sample. Left m1s (VP-15648, -15644, -15711) exhibiting morphotypes A-C respectively of *Microtus* sp. (1, 2, 3). Right m1 (VP-15636), left m1 (VP-15674), and right m1 (VP-15634) exhibiting morphotypes A-C respectively of *Microtus paroperarius* (4-6). Left m1 (VP-13797) of *Microtus ilanensis* (7). Right m1s (VP-15692 and -15750) of *Microtus meadensis* (8 and 9). Note the presence of 'secondary wings' on VP-15750. Left m1 (VP-15712) of *Allophaiomys* (10).

age of the total sample relative to the four-triangle morphotype at other sites. For example, the five-triangle morphotype constituted 2.5% of the *M. paroperarius* sample at Cumberland Cave (n =

152) and 8–9% of the *M. paroperarius* sample from Sunbrite Ash Pit (n = 59). The five-triangle morphotype represented 17% of the combined five- and four-triangle sample of Trout Cave #2 (n = 18;

TABLE 1. Measurements of m1s from Fiene. Abbreviations: **A**, length of anteroconid complex; **B**, width of opening between triangles 5 and 6; **A-A'**, width of anterior cap; **C**, width of opening between triangles 4 and 5; **L**, total length; **OW**, greatest width; **W**, distance across triangles 4 and 5; **W'**, distance across triangles 5 and 6.

Taxon	N	X	SE	sd	Range	parameter
<i>Microtus</i> sp.	15	2.87	0.07	0.27	2.38-3.32	L
<i>M. paroperarius A</i>	12	2.84	0.03	0.12	2.57-3.01	
<i>M. paroperarius B</i>	5	2.91	0.06	0.13	2.79-3.10	
<i>M. paroperarius C</i>	4	2.8	0.04	0.07	2.70-2.88	
<i>M. paroperarius</i>	21	2.85	0.03	0.12	2.57-3.10	
<i>M. llanensis</i>	32	2.63	0.04	0.2	2.25-3.07	
<i>M. meadensis</i>	5	2.88	0.09	0.22	2.70-3.23	
<i>Allophaiomys</i>	1	2.71				
<i>Microtus</i> sp.	18	1.47	0.04	0.18	1.17-1.80	a
<i>M. paroperarius A</i>	12	1.37	0.03	0.11	1.21-1.58	
<i>M. paroperarius B</i>	6	1.44	0.03	0.07	1.35-1.57	
<i>M. paroperarius C</i>	5	1.38	0.04	0.09	1.28-1.47	
<i>M. paroperarius</i>	23	1.39	0.02	0.1	1.21-1.58	
<i>M. llanensis</i>	34	1.26	0.03	0.15	0.89-1.59	
<i>M. meadensis</i>	7	1.55	0.07	0.19	1.34-1.79	
<i>Allophaiomys</i>	1	1.28				
<i>Microtus</i> sp.	18	0.38	0.03	0.12	0.20-0.63	A-A'
<i>M. paroperarius A</i>	12	0.51	0.02	0.07	0.41-0.64	
<i>M. paroperarius B</i>	6	0.45	0.03	0.08	0.35-0.56	
<i>M. paroperarius C</i>	5	0.48	0.04	0.08	0.43-0.63	
<i>M. paroperarius</i>	23	0.48	0.02	0.08	0.35-0.64	
<i>M. llanensis</i>	24	0.57	0.01	0.07	0.43-0.72	
<i>M. meadensis</i>	6	0.38	0.05	0.12	0.20-0.51	
<i>Allophaiomys</i>	1					
<i>Microtus</i> sp.	13	0.02	0.005	0.02	0-0.05	b
<i>M. paroperarius A</i>	13	0.17	0.008	0.03	0.14-0.22	
<i>M. paroperarius B</i>	6	0.11	0.004	0.01	0.09-0.12	
<i>M. paroperarius C</i>	5	0.21	0.005	0.01	0.19-0.22	
<i>M. paroperarius</i>	24	0.16	0.008	0.04	0.09-0.22	
<i>M. llanensis</i>	25	0.16	0.006	0.04	0.09-0.25	
<i>M. meadensis</i>	7	0.03	0.005	0.01	0.01-0.05	
<i>Allophaiomys</i>	1	0.26				

Pfaff, 1990). The samples at Cudahy and Hansen Bluff historically referred to *M. paroperarius* contained five closed triangles with frequencies of 7.3% and 8.1%, respectively (Bell and Repenning, 1999). Although unreported by Eshelman and Hager (1984), the sample of m1s allocated to *M. paroperarius* from Hall Ash Pit ($n = 13$) contains a single five triangle, right m1 (7.7%).

These low percentages could be interpreted as supporting the conclusions of Paulson (1961) that the five-triangle morphotype is a variant of *M. paroperarius*. However, without a broadened understanding of variability in the development system producing these morphotypes and the phy-

logenetic pattern of that variability (sensu Wagner and Altenberg, 1996; see Bever 2009), the relative abundance of a variant morphology provides little empirical support for a taxonomic conclusion. We do not assign our five-triangle sample to a species following the recommendation of Bell and his coauthors, who in a series of recent papers (Bell and Repenning, 1999; Bell and Barnosky, 2000; Bell et al., 2004a; Bell and Bever, 2006) presented cogent arguments, based on variation observed in extant populations, to refrain from assigning isolated teeth to the species level when the morphological data alone do not support such a refined identification. Historically, size, gestalt assessments of morpho-

TABLE 1 (continued).

Taxon	N	X	SE	sd	Range	parameter
<i>Microtus</i> sp.	17	0.03	0.006	0.03	0-0.10	c
<i>M. paroperarius A</i>	13	0.02	0.005	0.02	0-0.08	
<i>M. paroperarius B</i>	6	0.02	0.007	0.02	0-0.04	
<i>M. paroperarius C</i>	5	0.02	0.005	0.01	0.01-0.03	
<i>M. paroperarius</i>	24	0.02	0.003	0.02	0-0.08	
<i>M. llanensis</i>	35	0.18	0.006	0.03	0.13-0.26	
<i>M. meadensis</i>	7	0.14	0.005	0.01	0.13-0.17	
<i>Allophaiomys</i>	1	0.23				
<i>Microtus</i> sp.	18	0.85	0.03	0.12	0.53-0.98	W'
<i>M. paroperarius A</i>	11	0.88	0.02	0.07	0.78-1.00	
<i>M. paroperarius B</i>	6	0.88	0.03	0.07	0.80-1.00	
<i>M. paroperarius C</i>	5	0.85	0.04	0.08	0.73-0.93	
<i>M. paroperarius</i>	22	0.87	0.01	0.07	0.73-1.00	
<i>M. llanensis</i>	34	0.81	0.02	0.11	0.55-1.07	
<i>M. meadensis</i>	7	0.82	0.03	0.09	0.71-0.96	
<i>Allophaiomys</i>	1					
<i>Microtus</i> sp.	17	0.94	0.03	0.12	0.64-1.14	W
<i>M. paroperarius A</i>	12	1	0.02	0.08	0.89-1.17	
<i>M. paroperarius B</i>	6	1.01	0.01	0.03	0.98-1.06	
<i>M. paroperarius C</i>	5	1.01	0.02	0.05	0.98-1.09	
<i>M. paroperarius</i>	23	1.01	0.01	0.06	0.89-1.17	
<i>M. llanensis</i>	34	0.86	0.02	0.1	0.70-1.03	
<i>M. meadensis</i>	7	0.9	0.02	0.05	0.83-0.99	
<i>Allophaiomys</i>	1	0.95				
<i>Microtus</i> sp.	18	1.05	0.03	0.11	0.79-1.19	OW
<i>M. paroperarius A</i>	13	1.09	0.02	0.07	0.96-1.19	
<i>M. paroperarius B</i>	6	1.12	0.01	0.03	1.08-1.16	
<i>M. paroperarius C</i>	5	1.12	0.03	0.06	1.08-1.22	
<i>M. paroperarius</i>	24	1.11	0.01	0.06	0.96-1.22	
<i>M. llanensis</i>	34	1.04	0.02	0.1	0.85-1.24	
<i>M. meadensis</i>	7	1.09	0.01	0.03	1.05-1.14	
<i>Allophaiomys</i>	1	1.15				

logical uniqueness, and both stratigraphic and geographic distributions played an important role in refining taxonomic assignments to the species level (Bell and Bever, 2006; see Bever, 2005 for a more general discussion of this methodology and its potential consequences). Discriminant function analyses of morphometric data (Smartt, 1977; Wallace, 2006) and observations of enamel microstructure (Schmelzmuster; Wallace, 1999) have demonstrated initial success in distinguishing extant species of *Microtus*. The results of these studies, with regards to their general application to taxonomic problems, however, suffers from sampling issues, and many additional species need to be studied to demonstrate the taxonomic distribu-

tion and phylogenetic polarity of these morphological data and thus the range of their usefulness.

***Microtus paroperarius* Hibbard, 1944**

Material. Variant A, 6 Lm1s, FHSM VP-13796, 15061, 15639, 15641, 15735, 15748; 9 Rm1s, FHSM VP-13795, 15636, 15640, 15649, 15651, 15653, 15655, 15657, 15659. Variant B, left dentary with m1–m2, FHSM VP-15674; 2 Lm1s, FHSM VP-13821, 15638; 3 Rm1s, FHSM VP-15642, 15656, 15767. Variant C, 4 Lm1s, FHSM VP-15660, 15658, 15671–15672; 2 Rm1s, FHSM VP-15634, 15648.

Description. The m1s (n = 27) of *M. paroperarius* are characterized by four closed triangles. The

TABLE 2. Descriptive statistics for length of the five-triangled m1s from selected Irvingtonian sites. Data for Cudahy from Bell and Repenning (1999); for Irvington from Bell and Bever (2006).

Locality	N	X	s.d.	Range
Fiene	15	2.87	0.27	2.38-3.32
Cudahy	58	2.8	0.2	2.4-3.4
Irvingtonian	12	3.45	0.21	3.1-3.7

teeth are ever growing and exhibit strong development of cementum in buccal re-entrant angles one through three and lingual re-entrant angles one through four. Presence and development of cement varies from absent to strong in buccal re-entrant angle four and lingual re-entrant angle five. The teeth exhibit positive enamel differentiation.

Three morphotypes are recognized within the Fiene sample. The majority ($n = 15$, 55.6%; Variant A for discussion) has the pattern that characterizes the species wherein triangle five opens broadly ($b > 0.13$ mm) into the anterior cap on which a shallow buccal re-entrant angle four and lingual re-entrant angle five are present (Figure 3.4). The other morphotypes are divided evenly ($n = 6$ each; 22.2%) between specimens that show intermediate closure (Figure 3.5) of triangle five ($b < 0.13$ mm, Variant B for discussion) and those in which triangles five and six are equivalent (Variant C for discussion). Our Variant B is equivalent to the two morphotypes of Bell and Repenning (1999) showing intermediate closure; i.e., 1 enamel band width of opening (B1) and < 2 and > 1 enamel band width opening (B2). In three of the six specimens exhibiting Variant C, the confluent triangles five and six are closed off from the anterior cap (Figure 3.6). Bell and Repenning (1999) reported that 60 of the m1s from Cudahy have confluent triangles one and two. This morphotype was not found in the Fiene sample.

In statistical analyses, Variants A, B, and C were treated as independent samples and as a combined sample. Results obtained from the independent samples may not be meaningful because of small sample size, which tended to skew the measurements to one end of the range of variation observed in the non-*paroperarius* morphotypes. This skewness, on occasion, not only led to results suggesting significant differences between the individual *paroperarius* variants and the non-*paroperarius* samples but also between the combined sample of *paroperarius* and the latter samples. Keeping the previous in mind, a summary of the significant differences follows.

When the three variants are compared to each other, Variant B, as expected based on the way it was defined, is narrower between triangles five and six (B) than in Variants A and C, and Variant A is narrower between triangles five and six (B) than in Variant C (Table 1). The latter result is due to the confluence of triangles five and six in Variant C. Significant differences with *Microtus* sp. are listed in that section.

The combined and Variant A samples of *M. paroperarius* have a deeper buccal re-entrant angle four and lingual re-entrant angle five than *M. llanensis*. The constriction between triangles five and six (B) is wider in all *M. paroperarius* samples than in *M. meadensis*; wider in Variant C and narrower in Variant B than in *M. llanensis*. The constriction between triangles four and five (C) in all samples of *M. paroperarius* is narrower than in either *M. llanensis* or *M. meadensis*. This feature results from the former taxon having four closed triangles and the latter two taxa having triangles four and five confluent. The length across triangles six and seven (W') of the combined and Variant A samples and the length across triangles four and five (W), length of anteroconid complex (A), and total length (L) in all samples of *M. paroperarius* is greater than in *M. llanensis*. Except for Variant C, the m1 of *M. paroperarius* is wider (OW) than that of *M. llanensis* and is longer across triangles four and five (W) than *M. meadensis*. Variant A has a shorter anteroconid complex (A) than *M. meadensis* (Table 1).

The lengths of the *Microtus paroperarius* m1s (L) from Fiene fall within the range of those from Cudahy and encompass the range of those from Hall Ash Pit (Table 3). A similar relationship for length and ratio data exists between the m1s from Fiene and those from other selected Irvingtonian sites (Table 4). No significant differences were found in the lengths of Variant B m1s from Cudahy, whereas the m1 of Variant A in Cudahy was significantly shorter than that of *Microtus* sp. (Bell and Repenning, 1999). A mean length of 2.64 mm ($n = 22$) was reported for m1s of *M. paroperarius* from the Pit locality at Porcupine Cave (Bell and Barnosky, 2000). This mean value is smaller than that from any of the other sites considered herein and near the lower end of many of the observed ranges (Tables 3 and 4).

Comments. In their discussion of *Microtus paroperarius*, Bell et al. (2004a) suggested the relationships of this taxon to *M. operarius* (a junior synonym of *M. oeconomus*) be carefully reconsidered. They pointed out that the close morphologi-

TABLE 3. Descriptive statistics for length of the m1 of *Microtus paroperarius* from selected Irvingtonian sites. Data for Cudahy from Bell and Repenning (1999); for Hall Ash Pit from Eshelman and Hager (1984).

Local Fauna	N	X	s.d.	Range
Fiene (all)	20	2.85	0.12	2.57-3.10
Fiene (var. A)	11	2.84	0.12	2.57-3.10
Cudahy (var. A)	801	2.7	0.15	2.20-3.20
Fiene (var. B)	5	2.91	0.13	2.79-3.10
Cudahy (var. B1)	24	2.8	0.15	2.40-3.00
Cudahy (var. B2)	30	2.8	0.21	2.30-3.30
Fiene (var. C)	4	2.8	0.07	2.70-2.88
Cudahy (var. D)	60	2.7	0.13	2.40-3.10
Hall Ash Pit	9	2.8		2.63-2.97

TABLE 4. Descriptive statistics for total length (L) and selected ratios from the m1s of *Microtus paroperarius* from selected Irvingtonian faunas. Abbreviations: **A**, length of anteroconid complex; **B**, width of opening between triangles 5 and 6; **C**, width of opening between triangles 4 and 5; **W**, distance between triangles 4 and 5. Data for Sunbrite, Conard Fissure, and Cumberland Cave from Van der Meulen (1978); for Trout Cave #2 from Pfaff (1990); for Hall Ash Pit from Eshelman and Hager (1984)..

Local Fauna	N	X	SE	sd	Range	parameter
Fiene	14	2.81	0.04	0.14	2.50-3.01	L
Hall Ash Pit	9	2.8			2.63-2.97	
Sunbrite	46	2.79	0.02	0.14	2.41-3.10	
Conard Fissure	5	2.73	0.08	0.17	2.61-3.01	
Trout Cave #2	17	2.89	0.06	0.25	2.51-3.39	
Cumberland Cave	60	2.74	0.03	0.19	2.39-3.21	
Fiene	14	48.25	0.66	2.45	43.7-52.5	A/L
Sunbrite	46	48.2	0.28	1.92	43-52	
Conard Fissure	5	48	0.71	1.58	46-50	
Trout Cave #2	17	49.2	0.5	2	45.5-52.2	
Cumberland Cave	60	48.5	0.23	1.76	45-54	
Fiene	13	16.49	0.93	3.36	11.2-21.4	B/W
Sunbrite	51	17.5	1.02	7.29	<5-35	
Conard Fissure	3	17.3	1.45	2.52	15-20	
Trout Cave #2	17	16.1	1.4	5.7	5.9-25.2	
Cumberland Cave	66	19.2	0.83	6.73	<5-36	
Fiene	14	2.02	0.51	1.91	0-7.5	C/W
Sunbrite	54	<5			<5	
Conard Fissure	3	<5			<5	
Trout Cave #2	17	2.5	0.5	2	0-5.8	
Cumberland Cave	74	<5			<5-13	

cal similarity between the two taxa was implied by Hibbard (1944) in his choice of names, by Paulson (1961) in his study of the Cudahy material, and by Van der Meulen's suggestion (1978) that the two taxa could not be separated on the basis of dentition. In addition, all the examined specimens of *M. oeconomus operarius* in the Frank Pitelka Alaska collection at the Museum of Vertebrate Zoology, University of California, Berkeley, have the Variant

A morphology of *M. paroperarius* (Bell, personal commun., 2010).

A summary of the geographic and temporal distribution of *Microtus paroperarius* was provided by Bell et al. (2004a), who noted that recent finds of *M. paroperarius* west of the Rocky Mountains bring both the geographic and temporal range of the extinct species closer to that of the extant species. Although the Fiene specimens do not signifi-

TABLE 5. Descriptive statistics for the length of m1 of *Microtus Ilanensis* from selected Irvingtonian sites. Data for Kanopolis from Hibbard et al. (1978); for Cudahy from Paulson (1961); for Vera, Conard Fissure, and Trout Cave #2 from Pfaff (1990).

Local Fauna	N	X	SE	sd	Range
Fiene	32	2.63	0.04	0.2	2.25-3.07
Kanopolis	12	2.74	0.05	0.14	2.61-2.92
Cudahy	3	2.9			2.80-3.00
Vera	33	2.8			2.60-3.10
Conard Fissure	47	2.74	0.03	0.18	2.32-3.26
Trout Cave #2	44	3.18	0.04	0.28	2.51-3.59

cantly alter our current understanding of the geographic and temporal range of *M. paroperarius*, the Fiene record, with its multiple morphotypes, does reinforce the need to consider a wider range of variation when drawing conclusions regarding both the taxonomic identification and secondary biological properties of *M. paroperarius*.

***Microtus Ilanensis* Hibbard, 1944**

Material. 3 left dentaries with m1–m2, FHSM VP-13797, 15675, 15676; 19 Lm1s, FHSM VP-13774, 13798, 13822, 15677, 15680–15682, 15684, 15685, 15690, 15691, 15693, 15697, 15699–15702, 15706, 15707; 14 Rm1s, FHSM VP-13935, 15678, 15683, 15886–15689, 15695, 15696, 15698, 15703–15705, 15766.

Description. The m1s ($n = 36$) of *Microtus Ilanensis* are characterized by three closed triangles and a confluent triangle four and five (= primary wings of Repenning, 1992) that open into the anterior cap (Figure 3.7). The teeth are ever growing and exhibit strong development of cementum in buccal re-entrant angles one through three and lingual re-entrant angles one through four. Presence and development of cementum varies from absent to strong in buccal re-entrant angle four and lingual re-entrant angle five. The teeth exhibit positive enamel differentiation.

Based on the m1s, *Microtus Ilanensis* is the most abundant and least variable of the arvicoline morphotypes at Fiene. With few exceptions, it is also the shortest (L), narrowest (OW), has the shortest anteroconid complex (A), and widest openings between triangles (B, C; Table 1). These differences separate it from *M. meadensis*. Details of the differences with *M. paroperarius* and *Microtus* sp. are discussed under those sections.

The Fiene sample of *Microtus Ilanensis* has the lowest mean m1 length of any Irvingtonian locality for which mensural data are available (Table 5). The median m1 length for the Fiene sample is 2.63 mm, which is at or near the lower

end of the observed ranges of two of the three other samples for which 30 or more specimens were available. Whether this difference is the result of sampling or has some temporal or ecological significance is currently unclear.

Comments. An existing hypothesis suggests that *Microtus Ilanensis* is part of a phyletic line that begins with *Allophaiomys* sp. and ends in *M. ochrogaster* (Van der Meulen, 1978), and the morphology that characterizes *Allophaiomys* sp. may indeed be the ancestral condition for *M. Ilanensis*. There are sites in addition to Fiene, such as the Kentuck (Zakrzewski, 1985), where both morphotypes are present, and it is difficult to separate them from each other. However, the phylogenetic analysis of Conroy and Cook (2000) based on mtDNA sequence data supported a monophyletic North American *Microtus* in which the taxa characterized by three closed triangles were derived from five closed-triangle forms. These data complicate many historical hypotheses of dental evolution in arvicolines, including that of Van der Meulen (1978), and emphasize the need to integrate fossils into explicit phylogenetic hypotheses. Except for the occurrence at Trout Cave #2 (Pfaff, 1990), other records of *M. Ilanensis* are restricted to west of the Mississippi River, east of the Rockies, and south of the Nebraska/Kansas border.

***Microtus meadensis* (Hibbard, 1944)**

Material. 2 Lm1s, FHSM VP-15679, 15709; 5 Rm1s, FHSM VP-15692, 15694, 15708, 15733, 15750.

Description. The m1s ($n = 7$) of *Microtus meadensis* are characterized by three closed triangles and a confluent triangle four and five (primary wings of Repenning, 1992) that is closed off from, or opens very slightly into, the anterior cap (Figure 3.8). The latter character distinguishes *M. meadensis* from *M. Ilanensis*, wherein the confluent set of triangles exhibits a wide opening into the anterior cap. Other differences between *M. meadensis* and other

TABLE 6. Descriptive statistics for length of m1 of *Microtus meadensis* from Fiene and selected Meade Basin localities. Data for Sunbrite from Van der Meulen (1978); for Cudahy from Paulson (1961).

Locality	N	X	SD	Range
Fiene	6	2.83	0.22	2.70–3.23
Sunbrite	99	2.88	0.16	2.45–3.40
Cudahy	10	3		2.80–3.30

Fiene morphotypes are discussed in previous sections. Two of the seven m1s assigned to *M. meadensis* exhibit a second set of confluent triangles—triangles six and seven (secondary wings of Repenning 1992; Figure 3.9). The teeth are ever growing and exhibit strong development of cementum in buccal re-entrant angles one through three and lingual re-entrant angles one through four. Presence and development of cementum varies from absent to strong in buccal re-entrant angle four and lingual re-entrant five. The teeth exhibit positive enamel differentiation. The length of the m1s from Fiene fall within the range exhibited by the *M. meadensis* samples from the Cudahy and Sunbrite localities in the Meade Basin (Table 6).

Comments. A recent summary of the taxonomic status and geographic and temporal distribution of *Microtus meadensis* can be found in Bell et al. (2004a).

Allophaiomys Kormos, 1932

Material. Lm1, FHSM VP-15712.

Description. The remaining m1 consists of three closed triangles with a confluent triangle four and five that opens broadly into the anterior cap (Figure 3.10). No additional re-entrants are present on the anterior cap, which nominally is indicative of *Allophaiomys*, and we allocate this specimen to *Allophaiomys* sp. The length of the Fiene m1 falls within the range of *Allophaiomys* from the Kentuck, Wathena, and Java localities (Table 7). The samples from Kentuck and Java originally were assigned to *A. cf. A. pliocaenicus* (Martin, 1975). Although a close resemblance between these two samples and *A. pliocaenicus* was acknowledged by Van der Meulen (1978), he also recognized that the mean values for the ratio of the width of the opening between triangles five and six to the distance across triangles four and five (B/W) were intermediate between those of *A. pliocaenicus* and *A. deucalion* and therefore assigned the samples to *Allophaiomys* sp. The B/W value for FHSM VP-15712 from the Fiene falls within the range of the values for the Kentuck and Wathena (Table 7) sample. Based on the distribution of these values and the lack of discrete characters that support a more refined identification, we follow Van der Meulen in restricting our taxonomic assignment.

Table 7. Descriptive statistics for measurements and ratios from the m1 of *Allophaiomys* from selected Irvingtonian faunas. Abbreviations: **B**, width of opening between triangles 5 and 6; **L**, total length; **OW**, greatest width; **W**, distance across triangles 4 and 5. Data for Courtland Canal from Eshelman and Hager (1984); for Kentuck and Wathena from Van der Meulen (1978); for Aries, Short Haul, and Java from Martin et al. (2003).

Irvingtonian I.fs.						
Local Fauna	N	X	sd	Range	parameter	
Fiene	1	2.71			L	
Courtland Canal	6	2.99		2.85-3.24		
Kentuck	11	2.85	0.17	2.55-3.10		
Aries A	2	2.98	0.12	2.89-3.06		
Wathena	11	2.76	0.11	2.60-2.92		
Java	76	2.73	0.11	2.33-3.14		
Fiene	1	1.15			OW	
Courtland Canal	4	1.27	0.07	1.13-1.29		
Aries A	2	1.08	0.02	1.06-1.09		
Short Haul	1	1.16				
Java	91	0.91	0.08	0.63-1.17		
Fiene	1	27.4			B/W	
Kentuck	15	32.1	5.51	22-40		
Wathena	15	31.3	5.91	20-41		

Comments. The occurrence of a single specimen with a primitive morphotype in a sample of slightly less than 100 teeth presents us with at least two possible explanations. The first is to conclude that the specimen represents an individual of *Allophaiomys*. There are no specimens of *Microtus llanensis* in the Fiene sample that contain any hint of an *Allophaiomys* pattern as seen at some other localities. *Allophaiomys*, when present, is not found in great abundance at Kansas sites (Table 7). There is a minimum of four individuals with an *Allophaiomys* morphology at Courtland Canal (some 58 km northeast of Fiene)—a site that contains no *Microtus* morphotypes (personal observation). However, in the nearby Hall Ash Pit, we found a specimen with five closed triangles in the sample reported as *M. paroperarius* by Eshelman and Hager (1984)—but no *Allophaiomys*. *Allophaiomys* also is absent at Cudahy. There is a minimum of one individual of *Allophaiomys* in the Nash locality (Eshelman and Hibbard, 1981), four in Rick Forester, and two each in Aries A and Short Haul (Martin et al., 2003). It may be of importance that these Meade Basin records of *Allophaiomys* are all in the Borchers Badlands. If these *Allophaiomys*-like tooth records actually do represent the presence of *Allophaiomys* in the central Great Plains and are not a function of some taphonomic bias, they may reflect remnants of small populations either of early migrants moving into the area or stragglers that were leaving. As noted above, the relative scarcity of *Allophaiomys* records in Kansas is in contrast to the relative abundance of this taxon at sites in the Rocky Mountains, northern Great Plains, and Appalachians.

A second explanation is that FHSM VP-15712 belonged to an individual of *Microtus llanensis* that exhibited an *Allophaiomys* morphotype as an atavistic variant. Such a variant, however, has not been documented in any modern population of *Microtus*. The ability of a development system to produce this morphology as a population-level variant may have become extinct with *M. llanensis* or some other lineage, but this is difficult to support empirically. Another example of this type of intraspecific variation from the Fiene would be the two specimens mentioned under *Microtus* sp. that exhibit a prism fold. The difference in this case, as noted above, is that the presence of prism folds as a polymorphism in extant populations is documented.

Indeterminate Arvicolini

Upper Third Molars

Material. Morphotype A, 17 LM3s, FHSM VP-15770–15772, 15774, 15782, 15783, 15787–15789, 15791–15794, 15796, 15798, 15800, 15803; 21 RM3s, 15747, 15768, 15769, 15773, 15775–15781, 15784–15786, 15790, 15795, 15797, 15799, 15801, 15817, 15818; Morphotype B, 10 LM3s, FHSM VP-15805–15807, 15809–15815; 8RM3s, 15802, 15804, 15808, 15816, 15819–15822.

Description. Fifty-six isolated M3s were recovered from Fiene. Two morphotypes are present (referred to here as A and B for discussion). Morphotype A (n = 38) consists of an anterior loop, three triangles, and a complex posterior loop. The posterior loop consists of a triangle four that opens into a posterior dentine field that varies from an oval to one that contains a potential triangle six (called a hook by Repenning, 1992; Figure 2.2). A sequence of specimens showing the possible development of the hook is figured beginning with a oval posterior field (Figure 4.1), followed by anterior elongation of the posterior field (Figure 4.2), formation of a shallow lingual re-entrant angle four (Figure 4.3), and a deepening of lingual re-entrant angle four to isolate the hook (Figure 4.4). Twenty-one M3s of morphotype A lack evidence of a lingual re-entrant angle four. The remaining 17 teeth exhibit a slight to well-developed lingual re-entrant angle four. The posterior loop is longer in morphotype A (Table 8).

The relation of triangle three to the posterior loop is variable in morphotype A. Triangle three can be closed (n = 14) from the loop or it can have a narrow (n = 13), intermediate (n = 9), or wide (n = 3) opening into the loop. Likewise, triangle three can be anterior to (n = 24) or opposite (n = 15) triangle four. In the latter case, triangles three and four often have a common opening into the posterior loop. The anterior loop is always closed from triangle one. Sixteen specimens of morphotype A have triangle one closed off from triangle two, 16 exhibit some degree of openness, and in seven specimens of A, triangles one and two are confluent (Figure 4.1, 4.3; = rhomb of Bell and Repenning, 1999). Two specimens of morphotype A exhibit a slight opening between triangles two and three. One specimen of morphotype A exhibits a disrupted enamel pattern on the leading edge of triangle two.

Morphotype B (n = 18) consists of an anterior loop, two alternating triangles, a variable triangle three, and a simple posterior loop. Triangle three

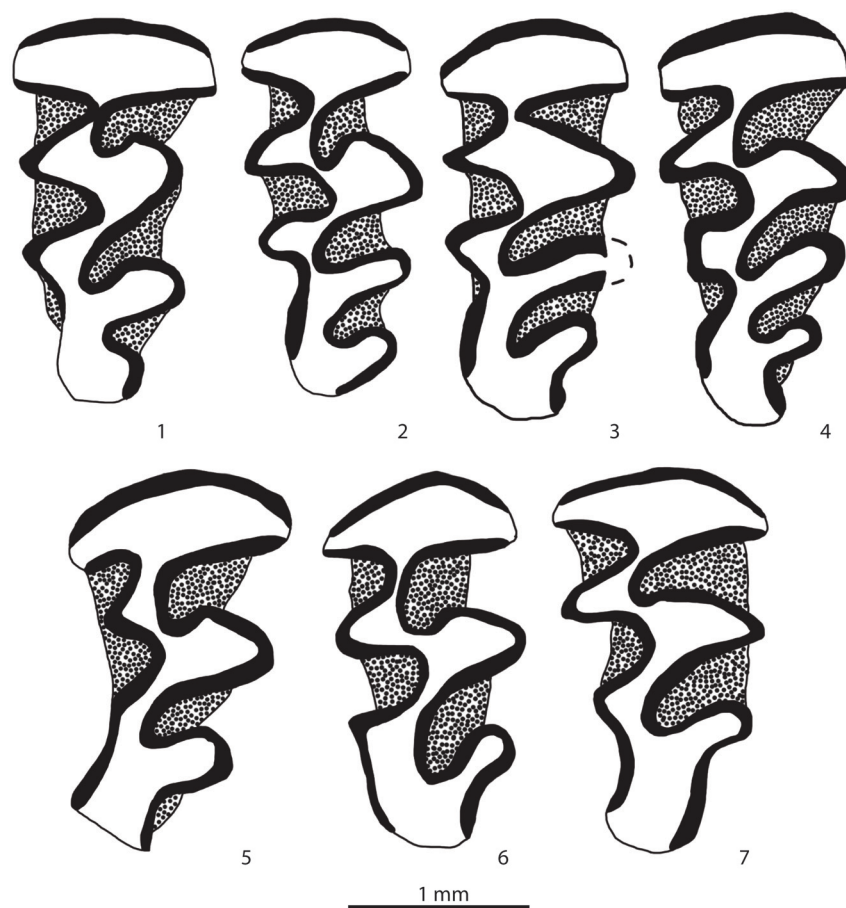


FIGURE 4. Occlusal view of upper third molars (M3) representing the different morphotypes observed in the Fiene Arvicolini sample. Right M3 (VP-15778) (1). Right M3 (VP-15790) (2). Right M3 (VP-15781) (3). Right M3 (VP-15784) (4). Right M3 (VP-15804) (5). Right M3 (VP-15820) (6). Right M3 (VP-1508) (7).

can be absent (Figure 4.5), poorly developed, and possibly considered part of the posterior loop (Figure 4.6), or better developed and opening into the posterior loop (Figure 4.7). A slight or moderately developed lingual re-entrant angle three often allows triangle four to form a hook (Figures 4.5–4.7). There is no evidence of triangles five and six. The posterior dentine field can be short (Figure 4.6) or elongate (Figure 4.7).

Three specimens in morphotype B, exhibit a slight opening between the anterior loop and triangle one, the remainder exhibit a closed condition. Ten specimens have triangle one closed off from triangle two, 10 specimens exhibit some degree of confluence, and nine specimens exhibit a slight opening between triangles two and three.

Both morphotypes exhibit positive enamel differentiation. Cementum is strongly developed in all re-entrants, except for the most posterior on each side, which often are not as deep as the others;

therefore, cementum can be absent to strongly developed.

Comments. Previously, most workers, when presented with the two morphotypes described above, would probably assign morphotype A to one of the taxa with four or five closed triangles on m1 and morphotype B among the taxa with three closed triangles on m1. Indirect support for this approach is suggested by the presence of four M3s with morphotype A in Hall Ash Pit in conjunction with *Microtus* sp. and *M. paroperarius*. However, Repenning (1992, figure 12A) described an associated skull and jaws of *Microtus paroperarius* from Hansen Bluff, wherein the M3 is more similar to morphotype B, the type associated with taxa possessing three closed triangles on m1. The third triangle opens into the posterior loop, triangle four forms a hook, and there is no evidence that a six triangle would develop. Therefore, because the Fiene M3s are all isolated and seven morphotypes of m1 are

Table 8. Descriptive statistics for measurements taken on the M3s from Fiene. Abbreviations: **GAPL**, greatest antero-posterior length; **ALCTL**, length of anterior loop and central triangles; **PLL**, length of posterior loop; **GW**, greatest width, **ALW**, width of anterior loop; **PLW**, width of posterior loop; **LPLW**, width of last segment of posterior loop.

Variable	N	X	Morph A		
			S.E.	s.d	O.R.
GAPL	34	1.91	0.02	0.12	1.66-2.19
ALCTL	34	0.92	0.01	0.05	0.77-1.02
PLL	35	0.99	0.02	0.09	0.84-1.20
GW	36	0.98	0.01	0.07	0.77-1.13
ALW	36	0.93	0.01	0.07	0.77-1.10
PLW	36	0.84	0.01	0.06	0.65-0.96
LPLW	35	0.59	0.01	0.07	0.44-0.73
			Morph B		
GAPL	18	1.85	0.03	0.14	1.64-2.11
ALCTL	18	1.01	0.02	0.08	0.89-1.20
PLL	18	0.84	0.03	0.11	0.66-1.01
GW	18	0.98	0.02	0.07	0.90-1.14
ALW	18	0.95	0.02	0.08	0.90-1.07
PLW	18	0.75	0.02	0.07	0.22-0.64
LPLW	18	0.45	0.02	0.07	0.38-0.65

present, assignment of the M3s to a more refined group species is not feasible at this time.

Upper Second Molars

Material. 43 LM2s, FHSM VP-13773, 13794, 13799, 13819, 15738, 16878–16915; 44 RM2s, FHSM VP-15739, 16916–16958.

Description. All ($n = 87$) of the M2s from Fiene consist of an anterior dentine field or loop that is closed off from the first triangle. Triangle one is closed off from triangle two, and triangle two is closed off from the posterior dentine field. In the majority of M2s ($n = 62$, 71.3%) the posterior dentine field is composed of a confluent potential triangle three and four (Figure 5.1). The posterior end of the field can be straight or round. It may be oriented posteriorly or at a slight angle. In the remaining M2s ($n = 25$; 28.7%), triangle three is better defined and ‘triangle four’ consists of an incipient ($n = 15$, Figure 5.2), intermediate ($n = 4$, Figure 5.3), well-developed ($n = 5$, Figure 5.4), or closed ($n = 1$, observed at base of tooth, Figure 5.5) posterior lingual dentine field. This field once was thought to diagnose *Microtus pennsylvanicus* in North America but is now known to occur at varying frequencies in other extant and fossil populations of *Microtus* (Zakrzewski, 1985; Bell and Repenning, 1999; Bell and Bever, 2006).

The relative size of the first and second triangles exhibits some variation in the Fiene sample. The two triangles appear to be of equal size in the majority of cases, but in 10 specimens (11.5%) tri-

angle one appears to be significantly smaller than triangle two. These specimens appear to be more robust than others in the sample. Four specimens (4.6%) display a disrupted enamel pattern on the leading edge of triangle two (Figure 5.6). Bell and Repenning (1999) stated that this type of abnormality is caused by a deformity of the enamel organ. They provide a limited summary of abnormal occurrences in their table 2.

The enamel of the occlusal surface exhibits positive differentiation. Cementum is present in the re-entrant angles except for buccal re-entrant angle three where cementum may be absent ($n = 32$, 36.8%), present in trace amounts ($n = 23$, 26.4%), or well developed ($n = 15$, 17.2%). The remaining M2s ($n = 17$, 19.5%) exhibit an intermediate stage of cementum development in buccal re-entrant angle three.

Comments. The M2s cannot be associated with any of the m1 morphotypes. Hopefully the discovery of associated materials or the application of new morphometric techniques (e.g., Polly and Head, 2004) will help to rectify this situation in the future.

The observed differences between the Fiene and Cudahy M2s may be due to the smaller sample size in the former (87 vs. 1,170). It does seem of some interest that the Fiene sample has a higher percentage than the Cudahy of M2s with a posterior dentine field (28.7% vs. 4.4%), including one specimen (1.1% vs 0%) with a closed field and more specimens (4.6% vs. 0.9%) with a disrupted

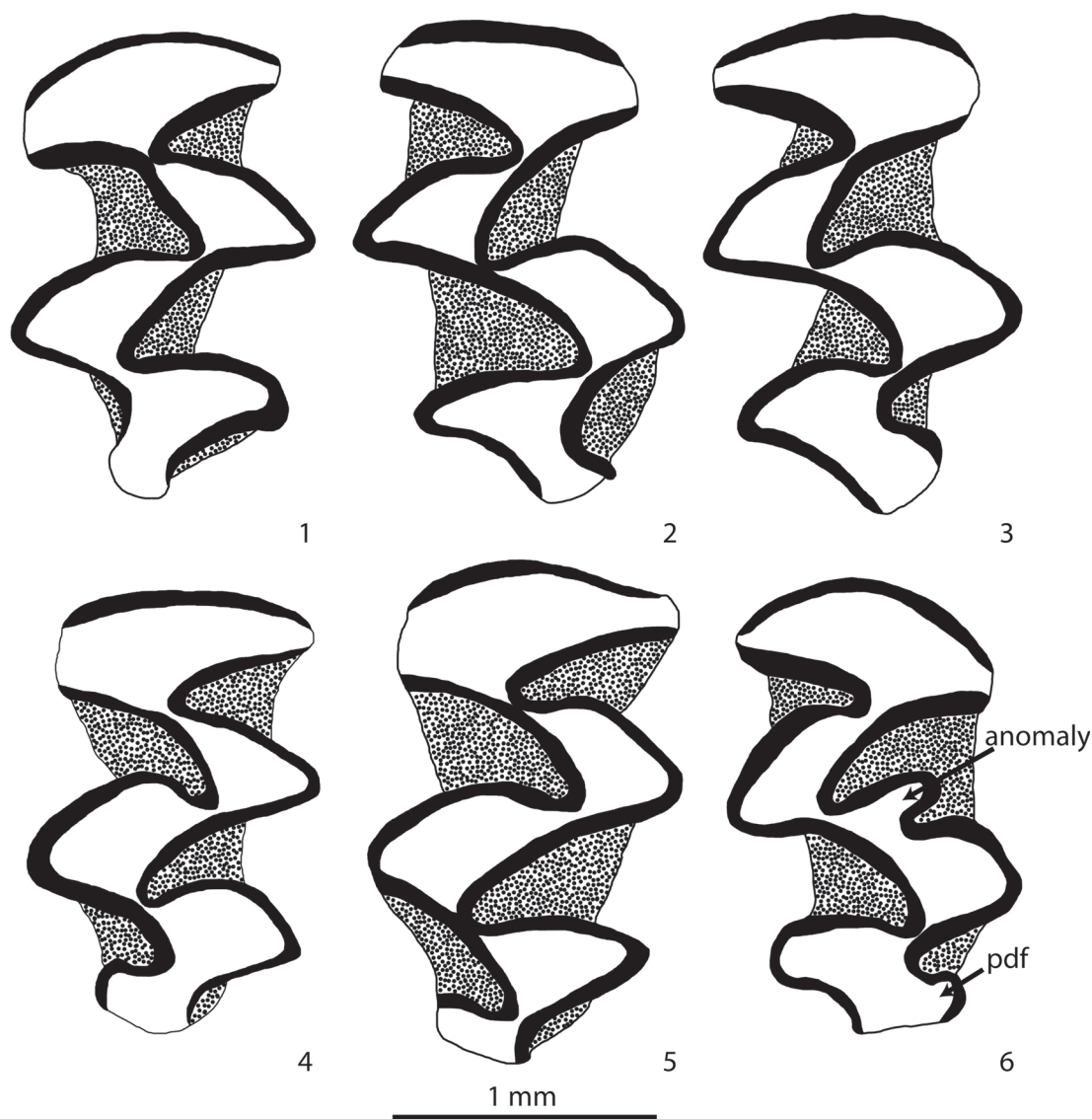


FIGURE 5. Occlusal view of upper second molars (M2) representing the different morphotypes observed in the Fiene Arvicolini sample. Left M2 (VP-13799) exhibiting 'Normal' condition (1). Right M2 (VP-16948) exhibiting incipient posterolingual dentine field (pdf; 2). Right M2 (VP-16953) exhibiting intermediate pdf (3). Left M2 (VP-13794) exhibiting well-developed pdf (4). Left M2 (VP-16911) exhibiting closed pdf (5). Right M2 (VP-16958) exhibiting an intermediate pdf and an anomalous dentine field on T2 (6).

enamel pattern. A disrupted enamel pattern can occur on any triangle (Bell and Repenning, 1999), however, all the disruptions in the Fiene M2s are on the leading edge of T2.

BIOCHRONOLOGY

Based on radiometric dates and paleomagnetic data from other sites, *Allophaiomys* is thought to have existed from slightly less than 2.1 Ma to about 840 Ka; the five closed-triangle *Microtus* from either 1.4? Ma or 840 Ka to the present; *M.*

paroperarius from about 840 Ka to 252 +/- 30 Ka and *M. meadensis* from 820 Ka to 252 +/- 30 Ka (Bell et al., 2004b). *Allophaiomys* is the defining taxon for the Irvingtonian I microtine stage east of the Rocky Mountains. *Microtus meadenesis* defines the Irvingtonian II and *M. ilanensis* helps to characterize the stage (Bell et al., 2004b). The co-occurrence of *Allophaiomys* and *M. meadensis* suggests that the age of the Fiene l.f. is approximately about 840 to 820 Ka. However, a somewhat similar taxonomic assemblage from Cathedral Cave, Nevada, with external age control produced

a significantly younger date (approximately 160 to 113 Ka; Jass, 2005). This information encourages the re-evaluation of the age of Fiene and similar sites as a test of the unique nature and provinciality of the Cathedral Cave assemblage, which may reflect the survival of these morphotypes in high altitude refugia (Jass, 2007).

DISCUSSION

Historically, two schools of thought existed regarding the systematic relationships and taxonomic status of the arvicoline forms closely related to, and currently nested within, *Microtus*. The first school was composed primarily of paleontologists (Van der Meulen, 1978; Repenning, 1983, 1992; Zakrzewski, 1985) who, based on the nature of the fossil record, relied on tooth morphology as their primary data source. The resultant paleontological perspective recognized two primary taxonomic groups. The first group, which was acknowledged explicitly as being paraphyletic with regards to the second, was characterized by three closed triangles on m1 and included the extant *Pitymys* (or *Pedomys*). The second group was recognized based on the presence of four or five closed triangles on m1 and was hypothesized to have evolved out of the three-triangle taxon. All forms in this second group were allocated to *Microtus*.

The second school, composed primarily of mammalogists (Hooper and Hart, 1962; Hooper and Musser, 1964; Anderson, 1985), mined characters from additional anatomical sources (such as the cranium and glans penis) not generally available to the paleontologist. The resultant neontological perspective, although not derived from our current conception of a phylogenetic topology, rejected the recognition of the three-triangle forms as a distinct taxonomic group and considered most, if not all, of these species to be *Microtus*. Some workers shifted between the two perspectives (Martin 1974, 1987).

Since the late 1980s a number of phylogenetic hypotheses based on molecular data have appeared for arvicolines that support the general conclusions of the second school (Chaline and Graf, 1988; Moore and Janeck, 1990; Conroy and Cook, 2000; Galewski et al., 2006). The topologies derived from these studies largely agree that the extant North American species of *Microtus* form a clade and that the extant North American three-triangular forms—*M. pinetorum* and *M. ochrogaster* (i.e., *Pitymys*, *Pedomys*)—evolved independently from taxa with m1s characterized by five closed triangles.

If the topologies of these recent phylogenetic studies continue to be supported and the general systematic community adopts a complex history of dental evolution for this group, what are implications for the ability of the fossil record, based on sites such as Fiene, to provide meaningful data regarding the evolutionary history of *Microtus*? This question is not trivial considering the historical importance of *Microtus* and other arvicolines to our understanding of Neogene biochronology and faunal dynamics. Only considering Fiene, a number of more specific questions are central to understanding the evolutionary history that produced the recovered fauna. Are the three-triangle *M. llanensis* and *M. meadensis* more closely related to five-triangular forms, as suggested for *M. pinetorum* and *M. ochrogaster*? Is *Allophaiomys* monophyletic and how are these forms related to *Microtus*? Is the m1 morphotype of *Allophaiomys* ancestral to the slightly more complex morphotype of *M. llanensis* or are we observing another form of variation as in *Microtus pennsylvanicus* where the number of m1 triangles is correlated to the forms of available vegetation (Davis, 1987)?

All of these questions are dependent on the ability of paleontologists to place isolated teeth within a broad phylogenetic context—a context that includes molecular-based topologies. This ability may well be dependent on expanding our understanding, beginning with extant taxa, of new forms of dental data. These data likely will include the developmental dynamics and evolutionary histories of enamel microstructure, morphometric delineated shape change, and discrete character variability. The beauty of novel hypotheses is not the opportunity they provide to reject previous ideas and the data on which those ideas are based, but rather the stimulus they provide to ask new questions, seek out even more data, and to consider previous observations within a new context. Rather than depressing the importance of the fossil record, the emergence of new phylogenetic hypotheses, whether based on molecular or other forms of data, should serve as a catalyst for exciting new research opportunities in arvicoline paleontology.

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